Food availability, thermal quality, and habitat selection in Yarrow's Spiny Lizards (*Sceloporus jarrovii*)

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Abstract

Elucidating the factors that drive variation in the abundance and distribution of organisms is central to ecology. Variables that explain the spatial variation in the abundance of organisms primarily include environmental (e.g., temperature and precipitation) and biotic factors (e.g., competition, predation, and parasitism). An important mechanism influencing the spatial distribution of organisms, at least at small spatial scales, is habitat selection. Traditionally, habitat selection theory has assumed that animals select habitat based on their ability to acquire depletable resources within that habitat, especially food. Ectotherms, however, may instead select habitat based on their ability to process food within the habitat, given the strong dependence of body temperature (and performance) on environmental temperature in this group.

The major objective of my thesis was to determine whether energy gain, habitat selection, and population density were driven primarily by food availability or by temperature in ectotherms. I used *Sceloporus jarrovii* lizards as a study species because these lizards occur at high densities and in similar habitat across a broad altitudinal range. In Chapter 1, I tested the prediction, central to the thermal coadaptation hypothesis, that juvenile lizards prefer body temperatures that maximize their net energy gain. I also tested whether lizards shifted their preferred body temperatures to correspond to the optimal temperature for different energetic states, as per Huey's (1982) energetics model. In Chapter 2, I determined whether the home range size and density of lizards shifted in response to manipulations of food availability and/or thermal quality within a site. In Chapters 3 and 4, I determined whether mean body condition, individual growth rate, and population density were driven by food availability or thermal quality. In Chapter 3, I visited 32 study sites over a 1,550 m altitudinal range within a year; whereas in Chapter 4, I food-supplemented five out of 10 study sites where I performed mark-recapture over a period of three years.

Overall, my thesis demonstrates that both food availability and thermal quality of the habitat drive energy gain, habitat selection, and population density. Juvenile *S. jarrovii* preferred body temperatures that maximized net energy gain, regardless of energetic state. Although they did not shift their preferred body temperature range depending on energetic state, the difference in the optimal temperature for net energy gain between states (0.4°C), may have been too small to warrant a change in behaviour. Within a site, *S. jarrovii* increased their home range size and occurred at higher densities as natural food availability increased, and decreased their home range size and occurred at lower densities as the thermal quality under the rocks increased. This suggests that *S. jarrovii* respond to food availability and thermal quality at different scales, selecting territories based on thermal quality and home ranges based on food availability. Over 32 sites, the abundance of *S. jarrovii* increased with food availability, whereas the mean body condition increased and the rate at which lizards attained their maximum body size decreased with elevation (at lower thermal quality). In the three-year study, mean body condition and individual growth rate decreased and population density increased with thermal quality, but the strength of the relationship depended on natural food availability. Overall, both food availability and thermal quality of the habitat drive energy gain, habitat selection, and population density; however, thermal quality is often the stronger driver.

Thus, improvements to habitat selection models should incorporate habitat thermal quality to improve predictions on how ectotherms distribute themselves on a landscape.

Résumé

Élucider les variables qui déterminent la variation dans l'abondance et la distribution des organismes est un thème central de l'écologie. Les variables qui expliquent la variation spatiale de l'abondance des organismes sont surtout environnementales (p. ex., la température et les précipitations) et biotiques (p. ex., la compétition, la prédation et le parasitisme). Un mécanisme important qui influence la distribution spatiale des organismes, notamment à de petites échelles spatiales, est la sélection d'habitat. Les théories traditionnelles de la sélection d'habitat supposent que les animaux basent leur sélection sur leur capacité à acquérir des ressources qui peuvent être épuisées, particulièrement la nourriture, dans cet habitat. Les ectothermes, par contre, pourraient sélectionner l'habitat en fonction de leur capacité à assimiler l'énergie dans cet habitat, étant donné la forte dépendance de leur température corporelle (et performance) des températures environnementales.

L'objectif principal de ma thèse était d'évaluer si le gain énergétique, la sélection d'habitat et la densité des populations chez les ectothermes sont déterminés plutôt par la quantité de nourriture disponible ou par la température. J'ai étudié les lézards *Sceloporus jarrovii* car cette espèce est présente à de fortes densités dans des habitats comparables à travers une large zone altitudinale. Au chapitre 1, j'ai testé la prédiction centrale de l'hypothèse de la coadaptation thermique que les lézards préfèrent les températures corporelles qui permettent le gain maximal d'énergie net. J'ai aussi déterminé si les lézards altéraient leur température corporelle préférée pour correspondre à la température optimale pour différents états énergétiques, comme le prédit le modèle de Huey (1982). Au chapitre 2, j'ai déterminé si la taille du domaine vital et la densité des lézards à un site changeaient suivant la manipulation

de la disponibilité de nourriture et/ou de la qualité thermique. Dans mes troisième et quatrième chapitres, j'ai évalué si la condition corporelle moyenne, le taux de croissance individuel moyen et la densité de la population étaient déterminés par la disponibilité de nourriture ou par la qualité thermique. Au chapitre 3, j'ai visité 32 sites d'étude le long d'un gradient de 1550 m d'altitude en un an; alors qu'au chapitre 4, cinq sur dix sites de marquage et recapture visités au cours de 3 ans ont reçu de la nourriture supplémentaire.

En général, ma thèse démontre que la disponibilité de nourriture et la qualité thermique de l'habitat influencent tous les deux le gain énergétique, la sélection d'habitat et la densité de la population. Les *S. jarrovii* juvéniles préféraient les températures corporelles qui maximisaient le gain net d'énergie à différents états énergétiques. Bien qu'ils n'aient pas modifié leur gamme de températures préférées en fonction de leur état énergétique, la différence entre états pour la température optimale du gain énergétique net (0,4°C) était probablement trop faible pour entraîner un changement de comportement. Les lézards ont augmenté la taille du domaine vital et atteignaient des densités plus fortes lorsque la disponibilité de nourriture naturelle augmentait. Ils ont aussi diminué la taille du domaine vital et atteignaient des densités plus faibles lorsque la qualité thermique sous les roches augmentait. Ces résultats suggèrent que les *S. jarrovii* répondent à la disponibilité de nourriture et à la qualité thermique à différentes échelles : ils sélectionnent leur territoire en fonction de la qualité thermique et leur domaine vital en fonction de la disponibilité de nourriture. Parmi les 32 sites, l'abondance apparente des *S. jarrovii* augmentait avec la disponibilité de nourriture, alors que la condition corporelle moyenne augmentait et le taux de croissance jusqu'à la taille maximale diminuait avec l'altitude (qualité thermique plus basse). Dans l'étude de trois ans, la condition corporelle moyenne et le

taux de croissance des individus diminuaient et la densité de la population augmentait avec la qualité thermique, mais la force des liens dépendait de la disponibilité naturelle de nourriture. Dans l'ensemble, la disponibilité de nourriture et la qualité thermique de l'habitat influencent tous les deux le gain énergétique, la sélection d'habitat et la densité de la population; par contre, la qualité thermique est souvent la variable la plus importante. Les modèles de la sélection d'habitat devraient donc être améliorés pour incorporer la qualité thermique de l'habitat pour générer de meilleures prédictions sur la façon dont les ectothermes se répartissent dans un paysage.

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Table of Contents

List of Tables

List of Figures

List of Abbreviations

Chapter 1

AIC_c	Akaike's Information Criterion corrected for small sample sizes
GAM	generalized additive model
GAMM	generalized additive mixed model
LMM	linear mixed model
RMR	resting metabolic rate
SD	standard deviation
SE	standard error
SVL	snout-vent length
T_b	body temperature
T_o	optimal body temperature
T_{set}	preferred body temperature range
$\dot{V}CO_2$	volume of carbon dioxide produced
$\dot{V}O_2$	volume of oxygen consumed

Chapter 2

AIC_c	Akaike's Information Criterion corrected for small sample sizes
DF	degrees of freedom
d_e	thermal quality index, absolute deviations of T_e from T_{set}
GLMM	generalized linear mixed model
LMM	linear mixed model
MCP	minimum convex polygon
SD	standard deviation
SE	standard error
SVL	snout-vent length

T_b	body temperature
T_e	operative environmental temperature
T_{set}	preferred body temperature range

Chapter 3

AIC_c	Akaike's Information Criterion corrected for small sample sizes
DF	degrees of freedom
h_r	hours of restriction of activity
ICC	intra-class correlation coefficient
k	growth rate
L_∞	asymptotic maximum size
LAG	lines of arrested growth
LMM	linear mixed model
SE	standard error
SVL	snout-vent length
T_b	body temperature
T_{set}	preferred body temperature range
VIF	variance inflation factor

Chapter 4

AIC_c	Akaike's Information Criterion corrected for small sample sizes
d_e	thermal quality index, absolute deviations of T_e from T_{set}
LMM	linear mixed model
$\hat{N}$	number of animals in the super-population
p	detection probability at each capture event
pent	probability of unmarked animals from $\hat{N}$ entering the study population
Φ	survival probability between capture events

QAIC_c	quasi-penalized AIC_c
SVL	snout-vent length
T_b	body temperature
T_e	operative environmental temperature
T_{set}	preferred body temperature range
VIF	variance inflation factor

List of Appendices

Appendix 1: Abstracts of other publications completed during my Ph.D.

Appendix 2: Tables of coordinates, elevation, access and other information regarding each study site

General Introduction

The central goal of ecology is to determine the factors that govern the spatial and temporal variation in the abundance and distribution of organisms (Krebs 2001). Species distribution limits are largely constrained by environmental conditions such as temperature and precipitation (Root 1988, Parmesan et al. 1999, Hawkins et al. 2003), although biotic interactions such as predation and competition are also important at smaller spatial scales (Robertson 1996, Jackson et al. 2001, Boulangeat et al. 2012). The abundance of a species within its distribution has been hypothesized to be highest near the centre of its range (the "abundant centre hypothesis", reviewed in Sagarin and Gaines 2002). Proposed mechanisms for this hypothesis include (1) random dispersal of organisms from a high-abundance centre (Grinnell 1922), (2) abundance being determined by environmental gradients (e.g., Andrewartha and Birch 1954) and other ecological conditions such as the presence of predators (Brown 1984), such that abundance is highest in a central area of optimal conditions and declines with distance from the centre as local conditions deviate from the optimum, and (3) overwhelming gene flow from the high-density range centre preventing peripheral populations from adapting to local conditions (Case and Taper 2000). While the abundant centre hypothesis is often not supported (Eckert et al. 2008, Sagarin and Gaines 2002, Sagarin et al. 2006), environmental factors may still influence species abundance patterns, as climatic conditions may be highly heterogeneous and not strongly spatially autocorrelated (e.g., Helmuth et al. 2002).

At small spatial scales, habitat selection may contribute substantially to spatial variation in the abundance of a species (e.g., Boyce and McDonald 1999, Resetarits 2005). Habitat selection is the means by which individuals distribute themselves on a landscape because organisms use preferred habitats disproportionately to maximize their fitness (Jones 2001). Habitat selection affects behavioural and physiological processes (Huey 1991) and thus individual fitness (e.g., Halliday and Blouin-Demers 2016) and population growth rate (given that population growth rate is largely driven by local individual survival and reproduction, Kooijman and Metz 1984, Ozgul et al. 2010). Habitat selection may also influence population dynamics (Holt 1987) and community-level processes (Rosenzweig 1991).

Traditional habitat selection models are based on the premise that individuals preferentially select habitats based on their capacity to acquire depletable resources, especially food, within those habitats. For example, one of the most popular models of habitat selection, the ideal free distribution (Fretwell and Lucas 1969), predicts that individuals preferentially select the habitat of the highest quality until resource depletion in that patch lowers its quality to the point where the fitness returns in that habitat equal those in the habitat of the next highest quality. These models were developed primarily with vertebrate endotherms such as small mammals and birds in mind (e.g., Fretwell and Lucas 1969, Morris 1988, Abramsky et al. 1990). Indeed, much of the support for density-dependent habitat selection comes from mammals (e.g., Ovadia and Abramsky 1995, Lin and Batzli 2002, Tadesse and Kotler 2010) and birds (Shochat et al. 2002, Jensen and Cully 2005, Zimmerman et al. 2009), although evidence for density-dependent habitat selection exists in other taxa (e.g., fish: Rodríguez 1995, Morita et al. 2004, Haugen et al. 2006, Knight et al. 2008; lizards: Paterson and Blouin-Demers 2018; invertebrates: Krasnov et al. 2003, Lerner et al. 2011, Halliday and Blouin-Demers 2014).

Density-dependent habitat selection may not always apply to ectotherms, however, because the physiology and thus the performance of this group are strongly dependent on environmental temperatures (e.g., Bennet 1980, Huey and Kingsolver 1989, Angilletta 2001), which is not a resource that can be appreciably depleted under most conditions. Huey (1991) argued that the primary factor driving habitat selection for many ectotherms was the motivation to maintain their body temperature (T_b) within an optimal range. From an ectotherm's perspective, a habitat in which it can easily maintain its T_b within its preferred T_b range is a habitat of high thermal quality (Huey 1991, Hertz et al. 1993). Body temperature affects most physiological, developmental and behavioural processes, including locomotor performance (Stevenson et al. 1985, Blouin-Demers et al. 2003) and growth rate (Sinervo and Adolph 1989, 1994; Autumn and DeNardo 1995). In particular, given that the rate of food processing (consumption, digestion, and assimilation) depends strongly on T_b (e.g., Troyer 1987, Angilletta 2001), food consumption may be constrained chiefly by processing rather than acquisition rate in vertebrate ectotherms. If food consumption is constrained by processing rate, then habitat selection and population density should be a function of thermal quality rather than food availability. Food availability and thermal quality may also interact: a recent study on beetles (Halliday et al. 2015) found that negative density-dependence (where fitness decreases with population density) was strongest in high thermal quality habitat.

The overall objective of my thesis was to test two hypotheses at different scales. I tested the hypotheses that habitat selection and population density in ectotherms are driven by (1) the food availability and the ability to *acquire* resources in a habitat, and (2) the thermal quality and the ability to *process* resources in a habitat. I used Yarrow's Spiny Lizards (*Sceloporus jarrovii*) as a study species because *S. jarrovii* actively thermoregulate (Middendorf and Simon 1988) and occur at high population densities in similar habitat over a broad altitudinal range (1,400 - 3,200 m, Burns 1970) in the southwestern United States and northern Mexico. As temperature varies drastically with altitude (Körner 2007), *S. jarrovii* populations in close geographic proximity experience significantly different thermal environments. I attempted to answer the following questions:

(1) Do *S. jarrovii* prefer T_bs that maximize net energy gain?

(2) Do *S. jarrovii* select home ranges based on the food availability and/or thermal quality of the habitat?

(3) Do habitats of high food availability and/or thermal quality support populations with higher mean body condition, individual growth rate, and population density?

In my first chapter, I tested the prediction of the thermal coadaptation hypothesis that the optimal T_b for net energy gain falls within the preferred T_b range of juvenile *S. jarrovii*. The thermal coadaptation hypothesis posits that thermal reaction norms have coevolved with thermal preference so that the optimal T_b coincides with temperatures normally experienced in the wild (e.g., Huey and Kingsolver 1989, Dorcas et al. 1997, Angilletta et al. 2002, Halliday and Blouin-Demers 2015). I also tested a prediction from an energetics model proposed by Huey (1982) that net energy gain should be maximized at a higher T_b when more food is available, due to the interaction between gross energy gain (that plateaus at higher T_bs) and energy losses to metabolic rate (that increase exponentially with T_b). To test these predictions, I measured the preferred T_b of 30 juvenile lizards, assigned them to one of five temperature treatments and one of two food availability treatments, and measured their growth rate over nine weeks.

In my second chapter, I tested the hypotheses that habitat selection in *S. jarrovii* is driven by food availability vs. thermoregulatory requirements. I used eight study plots in a before-after-control-impact design, with each plot receiving a food addition, shaded, food addition + shaded, or control treatment. I predicted that the density of lizards would correlate positively and the mean home range size would correlate negatively with the quality (food availability or thermal quality) of the study plot, and (2) that after experimentally increasing plot quality (by food supplementation and/or adding shade cloth), lizard density would increase and the mean home range size would decrease relative to control plots.

In chapters three and four, I tested the hypotheses that mean body condition, individual growth rate and population density are driven by the food availability vs. the thermal quality of the study site. In my third chapter, I employed a correlative approach using 32 study sites along an altitudinal gradient in four mountain chains. I measured body condition directly from snout-vent length and mass measurements, used skeletochronology to age lizards and estimate growth rate for each population, and estimated population density from the number of captures per person-hour. In my fourth chapter, I conducted a food supplementation experiment at 10 paired study sites within one mountain chain. I predicted that mean body condition, individual growth rate and population density would increase with the food availability (or thermal quality) of the habitat, and that body condition, growth rate and population density would increase following food supplementation. I estimated body condition and growth rate directly from repeat snout-vent length and mass measurements, and population density using mark-recapture methods.

Chapter 1

Thermal preference and growth rate in Yarrow's Spiny Lizards (*Sceloporus jarrovii*): testing the thermal coadaptation hypothesis

This chapter formed the basis for the following publication:

Patterson, L.D., Darveau, C.-A., and Blouin-Demers, G. 2017. Support for the thermal coadaptation hypothesis from the growth rates of *Sceloporus jarrovii* lizards. Journal of Thermal Biology 70:86–96.

Abstract

The thermal coadaptation hypothesis posits that ectotherms thermoregulate behaviourally to maintain body temperatures that maximize performance. Huey (1982) suggested that ectotherms thermoregulate to maximize net energy gain, and proposed an energetics model describing how food availability and temperature interact to affect net energy gain. I tested the thermal coadaptation hypothesis and Huey's (1982) energetics model using growth rate in juvenile Yarrow's Spiny Lizards (*Sceloporus jarrovii*). I compared the preferred body temperature range (T_{set}) of lizards in high and low energy states to their optimal temperature (T_o) for growth rate over nine weeks, and determined whether the T_o for growth depended on food availability. I also measured resting metabolic rate at five temperatures to test two assumptions of Huey's (1982) model: that metabolic expenditure would increase exponentially over the temperature range, and that it would not differ between lizards on different diets. The T_{set} of lizards on both diets overlapped with the T_o for growth. The assumptions of Huey's (1982) model concerning metabolic expenditure were verified, but the T_o for net energy gain did not depend on food availability. Therefore, I found support for the thermal coadaptation hypothesis. I did not find support for the energetics model, but this may have been due to low statistical power.

Introduction

Body temperature (T_b) greatly influences the behavioural and physiological capacities of ectotherms (Huey and Stevenson 1979, Stevenson et al. 1985, Hailey and Davies 1986). Because ectotherms, by definition, have limited physiological control over their T_b, they must thermoregulate behaviourally to maintain T_bs that maximize performance and fitness (Huey and Kingsolver 1989, Huey and Berrigan 2001). Reptiles typically strive to maintain their T_b within a narrow range of preferred T_bs (T_{set}, the central 50% of preferred T_bs) that can be achieved when circumstances do not constrain temperature selection (Hertz et al. 1993). The relationship between T_b and performance is described by thermal reaction norms, which are characterized by a gradual increase in performance as T_b increases, followed by a rapid decline (Huey and Kingsolver 1989, Bulté and Blouin-Demers 2006). The T_b that maximizes performance is the optimal temperature (T_o). The coadaptation of thermoregulatory behaviour and thermal physiology should be particularly tight because of the strong effect of selected T_bs on performance and fitness (Huey and Stevenson 1979, Huey 1982, but see Huey and Bennett 1987). According to the thermal coadaptation hypothesis, thermal reaction norms have coevolved with thermal preference so that T_o coincides with temperatures normally experienced in the wild (e.g. Huey and Kingsolver 1989, Hertz et al. 1993, Dorcas et al. 1997, Angilletta et al. 2002, Halliday and Blouin-Demers 2015). One of the central predictions of this hypothesis is that T_o falls within T_{set}.

Until recently, most tests of the thermal coadaptation hypothesis have involved measures of performance that are easily assessed, such as locomotion (e.g. Huey and Bennett 1987, Angilletta et al. 2002, Blouin-Demers et al. 2003) or digestive performance (e.g. Dorcas et al. 1997, Angilletta et al. 2002). However, few studies have used more ultimate measures of fitness such as growth rate or reproductive output (reviewed in Halliday and Blouin-Demers 2015). There is evidence that ectotherms thermoregulate to maximize the rate of energy gain or growth. For example, many species raise their T_b after feeding (reviewed in Angilletta 2009), eastern fence lizards (*Sceloporus undulatus*, Angilletta 2001) optimize their digestive rate at their preferred T_b, leopard geckos (*Eublepharis macularIu*) grow 1.5 times faster when allowed to thermoregulate than when kept at constant low temperatures (Autumn and DeNardo 1995), and *Sceloporus* lizards grow faster when access to radiant energy is increased (Sinervo and Adolph 1989, 1994). Therefore, consistent with the thermal coadaptation hypothesis, the T_o for growth rate can be predicted to coincide with T_{set}.

In addition to temperature, a variable that significantly affects energy gain and growth rate in ectotherms is food availability (e.g., Dunham 1978, Cox et al. 2008). Huey (1982) proposed a model that illustrates the relationship between food availability, temperature, and net energy gain. In this model, the rate at which food is processed (and thus the gross energy gain) increases with temperature until it reaches a plateau (Figure 1-1A). Metabolic expenditure, in contrast, increases exponentially with temperature. The net energy gain (gross energy gain – metabolic expenditure) therefore increases with temperature to a maximum and then rapidly decreases (Figure 1-1B). At a given T_b, the gross energy gain increases with food availability, but the metabolic expenditure remains unchanged. Consequently, the model predicts that net energy gain should be maximized at a higher T_b when food availability is higher. Ectotherms should therefore decrease their T_b when food becomes restricted to maximize net energy gain. Despite the proposal of Huey's (1982) model decades ago, the only studies to my knowledge that test the concurrent effects of food and temperature on net energy gain have been on fish (reviewed in Elliott 1982).

The goals of this study were two-fold. First, I tested the thermal coadaptation hypothesis using growth rate in juvenile Yarrow's Spiny Lizards (*Sceloporus jarrovii*). Growth rate is a more ultimate measure of fitness than the performance measures generally used (reviewed in Halliday and Blouin-Demers 2015), and it has critical fitness consequences for juveniles of this species: larger juveniles are more likely to escape from predators (by occupying better territories, Ferguson et al. 1982; or being faster sprinters, Sinervo and Adolph 1989), to survive both during the active season (Fox 1978) and over the winter (Ferguson and Bohlen 1978), and (in females) to reproduce as yearlings (Ballinger 1979). Larger females also have larger litters (Ballinger 1973, 1979). Thus, I predicted that the growth rate of juvenile *S. jarrovii* would be maximized within their T_{set}.

Second, I tested the central prediction and two assumptions of Huey's (1982) energetics model. I tested the prediction that the T_o for net energy gain at a high food abundance is higher than the T_o for net energy gain a lower food abundance, as well as two assumptions: (1) resting metabolic rate (RMR) increases exponentially over the T_b range experienced by the species, and (2) at a given T_b, RMR does not differ between energetic states (high and low food abundance). I used juvenile growth rate as a metric of net energy gain because juveniles devote a significant proportion of their energy budget to growth. At birth, over 50% of the energy budget is allocated to growth for the overwhelming majority of organisms (West et al. 2001). It is also important to test the assumptions concerning metabolic expenditure because RMR may plateau (Beaupre et al. 1993) or drop at high temperatures (approximately 40°C, Gillooly et al.

2001). Furthermore, as the metabolic rate of many species is depressed during periods of starvation (Wang et al. 2006), and when maintained on a reduced diet in at least one species (*Placopecten magellanicus,* Pilditch and Grant 1999), it is possible that long-term food availability may reduce RMR.

I tested the thermal coadaptation hypothesis and Huey's (1982) model by rearing juvenile *S. jarrovii* in the laboratory under different temperatures and diets, and by measuring their T_{set}. I randomly assigned juvenile *S. jarrovii* to one of two diets (high food and low food) and one of five temperatures (20, 25, 30, 35 and 38°C), and measured their growth rate over a period of nine weeks. From the resulting data, I constructed thermal reaction norms and determined the T_o for growth rate at high and low food availabilities. I was then able to test the prediction that the T_o for growth rate at high food availability is higher than at low food availability. To test the prediction that lizards prefer T_bs that maximize growth rate, I related the T_o for growth rate to T_{set} in each energetic state. To determine the T_{set} of these lizards in different energetic states, I measured preferred T_bs three times per individual in thermal gradients: twice prior to the growth experiment (once after being fed *ad libitum* and once after having been fasted for 48 hours) and once at the end of the growth experiment (after the lizards had been exposed to high or low food diets for several weeks). Finally, to test the assumptions of Huey's (1982) model concerning metabolic expenditures, I used respirometry to measure the volume of oxygen consumed by lizards at the same five temperatures as in the growth experiment.

This study is the first to my knowledge to test Huey's (1982) model with a terrestrial vertebrate ectotherm, and thus provides new insight into the interaction between temperature and food availability in terms of net energy gain. T_{set} is often assumed to match optimal temperatures for physiological processes such that it coincides with T_bs that maximize fitness (Huey 1982), but this assumption has rarely been tested (Martin and Huey 2008). Growth rate is a more ultimate measure of fitness than those normally employed (Halliday and Blouin-Demers 2015) and so provides a relatively stringent test of the thermal coadaptation hypothesis.

Methods

Study Site and Species

Sceloporus jarrovii is a small (average snout-vent length = 97 mm, Cox and John-Alder 2007), heliothermic lizard that is abundant in rocky habitats in southeastern Arizona and northern Mexico. On 30-31 July 2014, I captured 40 hatchling *S. jarrovii* (14 males, 26 females) by noose in the Chiricahua Mountains in Coronado National Forest, Arizona, U.S.A., at elevations between 1,700 and 2,600 m. I sexed the hatchlings using a secondary sexual character (enlarged post-anal scales), weighed them, and measured their snout-vent length (SVL) with callipers. The hatchlings were approximately 3-9 weeks old upon capture (Ballinger 1973, 1979), measuring on average (±SD) 2.8 ± 1.1 g in mass and 43.2 ± 5.9 mm in SVL. This research was conducted with a State of Arizona Scientific Collection Permit (No. SP675429), permission from the U.S. Forest Service, and was approved by the University of Ottawa's Animal Care Committee in accordance with the guidelines of the Canadian Council on Animal Care (No. BL-1788).

Housing and Lizard Care

The lizards were immediately transported to the University of Ottawa, Ottawa, Ontario, Canada and housed in an environmental chamber (CTCL model ER600). The lizards were housed individually in plastic terraria (30 cm x 17 cm x 11 cm) containing newspaper substrate, a water dish, and an opaque plastic tube for shelter. The lizards were provided with water *ad libitum*, and with ultraviolet light from 07:00 to 19:00 via UVB lamps. The environmental chamber operated on a 12 h light: 12 h dark cycle, and cycled between a daytime temperature of 28°C and a night-time temperature of 15°C. Constant temperature regimes are stressful for squamate reptiles (Shine 1983) and cycling thermal regimes are more ecologically realistic (Regal 1967). A heat tape was placed under one side of each terrarium to produce a thermal gradient and allow lizards to thermoregulate. I fed the lizards *ad libitum* with crickets (*Gryllodes sigillatus*) and mealworms (*Tenebrio molitor*) dusted with a 50:50 mixture of calcium and vitamin powder. I recorded the total number of food items consumed by each lizard during each feeding.

In the last week of the temperature and food manipulations, several lizards showed symptoms of a respiratory infection. All lizards were successfully treated with antibiotics (Baytril) prior to their participation in the respirometry trials. After temperature and diet manipulations and thermal gradients, I returned the lizards to their original housing conditions, although I maintained the lizards on their respective diets for the measurements of RMR. All lizards were euthanized after the completion of the respirometry trials.

Estimation of T_o

I estimated the T_o for growth rate to test the predictions that T_o falls within the T_{set} for each energetic state, and that the T_o for growth at high food availability is higher than that at low food availability. I estimated T_o in a three-step process: (1) I manipulated the diet and thermal environment of each lizard, (2) I measured the growth rate of each lizard over the period of the experiment, and (3) I modeled the thermal reaction norms for growth rate for each diet.

Diet and Thermal Manipulations

I manipulated the diet and thermal environment of 30 lizards over a sixteen-week period. I randomly assigned each lizard to one of two diets (high and low food) and one of five temperature treatments (20, 25, 30, 35, and 38°C). Individuals on the high food diet were fed *ad libitum*, whereas those on the low food diet alternated between being fed *ad libitum* for 48 hours and being fasted for 48 hours (Sinervo and Adolph 1994). Temperatures cycled between the assigned daytime treatment temperature (09:00 to 16:00) and a night-time temperature (20:00 to 6:00) of 15°C (Mathies and Andrews 1997). The 20, 25 and 30°C treatments were housed in one chamber and the 35 and 38°C in another. The daytime temperature in each chamber corresponded to the 20 and 35°C treatments, respectively. The 25, 30, and 38°C temperature treatments were maintained by placing the terraria on a heat tape as wide as the length of the terraria. I used a dimmer to adjust the temperature of the heat tape, placed Styrofoam under the heat tape to minimize heat loss, and placed a thin copper sheet (30.5 cm x 18 cm x 0.1 cm) between each terrarium and the heat tape to distribute the heat evenly in the terrarium. To ensure that the appropriate temperatures were maintained, I measured the temperature of each terrarium every 15 minutes with a temperature data logger (Thermochron iButton, model D1S1921G-F5) throughout the experiment. Terraria were shuffled within each chamber periodically and between chambers once to avoid any positional effects (Hurlbert 1984).

To test the assumption that lizards on the high food diet consumed more food, and to determine how food consumption was related to temperature, I ran a generalized additive mixed model (GAMM, Wood 2011) with a negative binomial distribution. The dependent variable was the number of food items consumed weekly, the random effect was lizard ID, and the fixed effects were diet, experimental temperature (smoothed using a thin plate regression spline), mass, and sex. I calculated experimental temperature as the mean daily high temperature (10:00 to 16:00) over the course of each week. I then removed non-significant variables until all remaining variables were significant, and selected the most parsimonious model by comparing AIC_c values (Burnham and Anderson 2002, Table 1-1). In all analyses for food consumption, I only used the data from the first nine weeks, which corresponded to the time period used for the calculation of growth rate (see below).

Growth Rate

To measure the growth rate of each lizard, I recorded its mass (± 0.1 g) and SVL (± 0.01 cm) every week over the sixteen-week period of diet and temperature manipulations. When examining scatterplots of food consumption and mass over time, it became evident that the food consumption and growth rate of the lizards presenting symptoms of respiratory infection in the last week of the sixteen-week period had begun to decrease earlier in the experiment, for some as early as the tenth week. Therefore, I only considered the first nine weeks of the manipulations in the calculation of growth rate. The growth rate over this time period was linear, and so I calculated the growth rate (g/week) for each lizard from the slope of the linear regression between mass and week. To test the linearity of this relationship, I ran a linear mixed model (LMM, nlme package, Pinheiro et al. 2015), fitted by maximizing the log-likelihood, with mass as the dependent variable, week as the fixed effect, and lizard ID as the random effect; examined the residuals for patterns indicating poor fit; and compared the AIC_c of this model to the null model. Repeating my analyses with growth in snout-vent length instead of growth in mass yielded qualitatively similar results.

Thermal Reaction Norms

I constructed thermal reaction norms by fitting several non-linear models to the growth data as a function of temperature (e.g., Bulté and Blouin-Demers, 2006, Table 1-2). I incorporated the critical thermal maximum and minimum for growth (19.0 and 40.2°C) into each model. I estimated 19.0 °C from my data because there was very little (if any) growth at 20°C, and I used 40.2 °C because it is the mean critical thermal maximum value for juvenile *S. jarrovii* (Gilbert and Lattanzio 2016) and no growth should occur above this temperature. I also ran a Generalized Additive Model (GAM, mgcv package, Wood 2011) with growth rate as the dependent variable and temperature (smoothed using a thin plate regression spline) as the independent variable and compared the AIC_c of this GAM to the other non-linear models (Table 1-2). I used the best nonlinear model (GAM) to predict the T_o for growth for each diet. To determine the importance of initial lizard mass, sex, and diet on growth rate, I also ran a GAM with growth rate as the dependent variable and temperature (smoothed using a thin plate regression spline), diet, initial mass, and sex as the independent variables. I used model averaging (conditional average) on models with at least moderate support (AIC_c < 7) to determine the importance of each linear variable (Barton 2016).

Preferred T_b

I measured T_{set} to test the prediction that T_o falls within the T_{set} for each energetic state. I measured the T_{set} of each lizard three times: twice before the growth experiment (once fed *ad libitum*, and once after having fasted for 48 hours, randomizing the order in which each individual was tested (Schuler et al. 2011, N = 33)), and once in the last four weeks of the sixteen-week growth experiment (N = 30, hereafter referred to as the "post-growth experiment" thermal gradients). I used a thermal gradient (Hertz et al. 1993) consisting of a particle board box (122 cm x 39 cm x 39 cm) with three laneways. I placed electric heating pads beneath one end to create a range of temperatures (~20-45°C) within the thermal gradient. Lizards were placed individually into laneways at approximately 17:00 and allowed to habituate overnight prior to the trial. The next day, I measured the dorsal surface temperature of each lizard (Bakken 1992) every 30 minutes from 08:00 to 16:30 using an infrared thermometer (Fluke 566 IR Thermometer). The thermometer was held in line with the lizard's body axis (Hare et al. 2007), approximately 2 cm above the surface immediately behind its pectoral girdle. I used this method instead of inserting a thermocouple into the cloaca (e.g., Brown and Griffin 2005) or pressing an infrared thermometer to the cloaca (e.g., Beal et al. 2014) because of the small size of the lizards, and because repeated handling may increase stress and stress-induced increases in preferred T_bs (Cabanac and Bernieri 2000, Rey et al. 2015). Moreover, skin temperature is a good proxy for T_b in other small lizard species (e.g., Bouazza et al. 2016, Hare et al. 2007, Herczeg et al. 2006). I calculated the T_{set} for each lizard using the 25th and 75th percentiles of T_bs selected (Hertz et al. 1993), and the overall T_{set} by averaging each percentile across lizards.

To determine whether preferred T_b depended on energetic state prior to the growth experiment (fed *ad libitum* vs. fasted for 48 h), I ran two LMMs fitted by maximizing the log-likelihood and with the 25th or 75th percentiles of preferred T_bs as the dependent variable, lizard ID as the random effect, and energetic state, trial order, lane, and sex as fixed effects. For the post-growth experiment comparison (high vs. low food diet), I ran linear models with diet, experimental temperature, lane, and sex as independent variables and the 25th or 75th percentiles of preferred T_bs as the dependent variable. In all cases, I applied a 4th-power transformation to improve normality and homogeneity of variance, sequentially removed non-significant variables, and selected the most parsimonious model using AIC_c (Table 1-3).

To establish whether T_{set} corresponded to the T_o for growth rate, I determined whether the T_o for each diet was found between the 25th and 75th percentiles of T_bs measured during the thermal gradient for lizards on that respective diet.

Metabolic Expenditure

To test the assumptions from Huey's (1982) model that metabolic expenditure increases exponentially over the temperature range, and that metabolic expenditure does not differ between energetic states at a given temperature, I quantified the RMR of the same lizards at five temperatures using flow-through respirometry. I measured the volume of oxygen consumed ($\dot{V}O_2$) and of carbon dioxide produced ($\dot{V}CO_2$) at each temperature in the following randomized order: 20, 30, 35, 25, and 38°C. Every lizard (N = 27) was tested at all temperatures, and was fasted for 48 hours prior to each trial to allow gut evacuation (e.g., Angilletta 2001). There were an average of 7.3 days (range = 4-21) between successive trials.

I placed the lizards in individual airtight respirometry chambers (310 ml) inside a programmable incubator (model 2015, VWR International, Mississauga, Ontario, Canada). The respirometry system was held outside the incubator to draw in outside air. Incurrent air was scrubbed of H_2O using a Drierite column, and was pushed into a multiplexer (MUX-3, Sable Systems International, North Las Vegas, Nevada, U.S.A.) using polyethylene tubing. From the multiplexer, the air moved to a flow meter (Flow-Bar 8, Sable Systems International) and then into one of six respirometry chambers. The excurrent air was dried and the CO_2 measured using an LI-7000 analyzer (LI-COR® Biosciences), and the O_2 measured using an OXZILLA II analyzer (Sable Systems International) after removing CO_2 and H_2O. The flow rate into each container was determined by the lizard's mass and the incubator temperature (Table 1-4). I used a differential mode to calculate O_2 and CO_2 values, sampling an empty reference chamber before and after each lizard. I calibrated the O_2 and CO_2 analysers daily prior to trials.

For the first two hours after the lizards were placed in the respirometry chambers, the incubator temperature ramped from room temperature to the trial temperature, and then was stable for one hour prior to measurements to allow the lizards to habituate to the test temperature. I tested the lizards at two temperatures per night, except for the 38°C trial. The temperature was ramped to the second temperature over an hour and the lizards were given an additional hour to habituate prior to measurements. All measurements were taken during the scotophase, between 19:00 and 7:00. Measurements were taken every second for 40 minutes (20, 25 and 30°C), 60 minutes (35°C) or 80 minutes (38°C) for every lizard. Trials were longer at higher temperatures because the lizards moved more and longer trials increased the likelihood that RMR could be measured. Two temperature data loggers were placed into the incubator to measure the ambient temperature every 15 minutes during respirometry trials.

I calculated the $\dot{V}O_2$ at each temperature for each lizard from the two-minute window with the lowest values over the measurement time period. Measurements were extracted using ExpeData software v.1.1.25 (Sable Systems 2005). The incubator temperature was calculated to be the mean temperature recorded by the two temperature data loggers from the beginning of the acclimation period to the end of the final trial at the given experimental temperature on that date.

To test whether an exponential model was a good fit to the data, I ran a non-linear mixed model (Pinheiro et al. 2015) with $V\dot{O}_2 = a \times (1 + b)^{IT}$ as the formula (IT was the incubator temperature, and a and b were estimated to be 0.02 and 0.13, respectively, by the nlme() function) and lizard ID as the random effect. I compared the AIC_c of this model to that of the comparable LMM, fitted by maximizing the log-likelihood. To test whether diet affected the RMR, I ran another LMM, fitted by maximizing the log-likelihood, with $\dot{V}O_2$ as the dependent variable, mass, temperature during the growth experiment and incubator temperature × diet as fixed effects, and lizard ID as a random effect. To improve the normality and homoscedasticity of the residuals, I $\log_{10}$-transformed $\dot{V}O_2$ and removed four outliers (confirmed by the influence.measures() function, Fox and Weisberg 2011). For both the full dataset and the dataset without outliers, I sequentially removed nonsignificant variables from the original model and selected the most parsimonious model using AIC_c (Burnham and Anderson 2002, Table 1-5). All statistical analyses in this study were performed in JMP 8.0 and R 3.2.2 (R Core

Team 2015). Model R^2 values were calculated using the r.squaredGLMM() function (MuMIn package, Barton 2018).

Results

Food Items Consumed

The assumption that lizards on the high food diet consumed more food items than those on the low food diet was verified. Food consumption was highly influenced by both diet and temperature, and the GAMM model explained much of the variation in the data (adjusted R^2 = 0.42, scale estimate = 0.3, N = 270 within 30 groups). Lizards on the high food diet consumed twice as much food (6 vs. 3 items per week) as those on the low food diet, and ate more as temperature increased, but the quantity of food consumed was independent of mass and sex (Figure 1-2, Table 1-1).

T_o at High vs. Low Food Availability

The prediction from Huey's (1982) model that the T_o for growth rate at a high food availability would be higher than that at a low food availability was not supported. Although lizards grew fastest at 32.0°C on the high food diet and 31.6°C on the low food diet, growth rate was independent of diet in the final GAM model (Table 1-2). Growth rate increased to a maximum and then decreased with temperature, but initial mass and sex did not affect growth rate (Figure 1-3, Table 1-2). The assumption that growth rate over the nine week period was linear was verified because the residual plots of the LMM between mass and week (Table 1-6) showed no patterns indicating nonlinearity, and the AIC_c of this model (529.5) was smaller than the null model (631.2). The mean (± SE) growth rate across all temperature and diets was 0.1 ±

0.009 g per week (Table 1-6), which represents approximately a 2% increase in mass per week for a 4.6 g lizard.

T_o Overlap With T_{set}

The prediction of the thermal coadaptation hypothesis that lizards prefer T_bs that correspond to the T_o for growth rate was supported. The T_o for growth rate (32.0 °C and 31.6 °C for the high and low food diets, respectively: see previous section) fell within T_{set} both prior to (lizards fed *ad libitum*: 30.6–33.2 °C, fasted for 48 h: 30.5–33.1 °C) and after (high food diet: 30.9–34.0 °C, low food diet: 30.9–33.5 °C) experimental manipulations (Figure 1-3). Food availability did not affect the bounds of T_{set} in either comparison (Tables 1-3, 1-6). Preferred T_bs increased with trial order in the short-term comparison, with the lower bound of T_{set} increasing from 30.0 to 31.1 °C and the upper bound increasing from 32.5 to 33.9 °C between trials (Table 1-6). After long-term exposure to different diets and temperatures, only the temperature manipulation significantly affected the lower bound of T_{set}, with lizards who had been exposed to hotter temperatures during the growth experiment preferring cooler temperatures (Table 1-6). Sex and lane did not significantly affect preferred T_b (Tables 1-3, 1-6). Although there were some issues with the normality and homoscedasticity of residuals for all comparisons, I reached the same conclusions for the effect of food availability using non-parametric Kruskall-Wallis tests (lower bound, before manipulations: $\chi^2 = 0.20$, DF = 1, P = 0.76; upper bound, before manipulations: $\chi^2 = 0.16$, DF = 1, P = 0.69; lower bound, after manipulations: $\chi^2 = 0.10$, DF = 1, P = 0.76; upper bound, after manipulations: $\chi^2 = 0.15$, DF = 1, P = 0.70).

Metabolic Expenditure Assumptions

The assumption that the RMR increases exponentially with temperature was supported because the exponential model (30.6) had a lower AIC_c than the LMM (134.7), and the $\log_{10}$-transformed $\dot{V}O_2$ increased linearly with the incubator temperature (Figure 1-4, Tables 1-5, 1-7). The mean ± SD of $\dot{V}O_2$ was 0.65 ± 0.44 ml/h. The assumption that the metabolic expenditure would not differ between food availabilities was also verified, because the $\dot{V}O_2$ was independent of diet (Table 1-5) in the reduced dataset. Larger lizards also had higher RMRs (Table 1-7), but RMR was unaffected by the lizards' treatment temperature during the growth experiment. Diet and an interaction between incubator temperature and diet were both present in equally plausible models, but neither were significant (Table 1-7). Although different conclusions were obtained using the full dataset, because the effect of the incubator temperature on RMR depended on the diet (Tables 1-5, 1-7), this model did not meet the assumptions of normality and homoscedasticity of residuals. This relationship appeared to be driven by four outliers, as it disappeared when those four points were removed. I performed similar analyses on the $\dot{V}CO_2$, and the Q_{10} values of each temperature interval, and obtained the same results qualitatively (data not shown).

Discussion

According to the thermal coadaptation hypothesis, ectotherms should choose T_bs that maximize performance and fitness (reviewed in Angilletta 2009). In this experiment, I tested the thermal coadaptation hypothesis and Huey's (1982) energetics model using growth rate in juvenile *S. jarrovii*. The prediction of the thermal coadaptation hypothesis that the T_o for growth falls within T_{set} was supported, but the prediction that the T_o depends on food availability (Huey's (1982) model) was not. Nevertheless, the assumptions that metabolic expenditure increases exponentially with temperature and is independent of diet (Huey 1982) were verified.

Firstly, the prediction that the growth rate of juvenile *S. jarrovii* is maximized within the T_{set} for its energetic state was supported. Both prior to and after thermal and diet manipulations, the T_{set} of lizards overlapped with the T_o for growth rate in both energetic states. Moreover, lizards always preferred similar T_bs, regardless of their short- or long-term energetic state. Many studies have found that preferred T_bs increase after feeding in reptiles and amphibians (O'Connor and Tracy 1992, Sievert and Andreadis 1999, Blouin-Demers and Weatherhead 2001a, Brown and Griffin 2005), but others found no effect (e.g., Mullens and Hutchison 1992), including a study on adult male *S. jarrovii* (Schuler et al. 2011). These discrepancies in results may be related to the tradeoffs in the benefits and costs of thermoregulation. Thermoregulation also impacts non-energetic traits such as immunity and locomotion (reviewed in Angilletta 2009) and so it is possible that thermoregulation is more closely tied to these traits in some species or circumstances. Although the importance of maximizing net energy gain should be high for juveniles, for whom there are considerable fitness benefits in rapid growth and attaining a larger body size (Fox 1978, Ferguson and Bohlen 1978, Ballinger 1979, Ferguson et al. 1982, Sinervo and Adolph 1989), I found no effect of energetic state on T_{set}. I believe that the lizards failed to alter their T_{set} when in a low energetic state because the energetic benefit was minimal. Lizards often thermoregulate imprecisely (Martin and Huey, 2008), the T_o for net energy gain was only 0.4°C lower on the low food diet, and the T_o for net energy gain for both diets fell within the T_{set} of lizards on the high food diet. Indeed, Brown and Griffin (2005) argued that the decrease in T_b following food deprivation observed in *Anolis carolinensis* would have negligible impacts on energy gain, because it would only lead to a decrease in metabolic rate of approximately 3%.

Although Martin and Huey (2008) predicted that preferred T_bs should be slightly below T_o due to the asymmetrical shape of the thermal reaction norm, my findings corroborated the original prediction of the thermal coadaptation hypothesis (Licht 1967, Angilletta 2009). In juvenile *S. jarrovii*, it may be adaptive for T_o to fall within T_{set} if it allows them to be active when it is too hot for adults. Juveniles of this species have a higher preferred T_b, critical thermal maximum, and T_o for stamina than adults (Gilbert and Lattanzio, 2016) and remain active later into the day (Simon and Middendorf, 1976). As juveniles are born in May and June, immediately prior to the hottest period of the year, they may need to remain active at higher temperatures to meet energetic demands for growth, even if these temperatures are close to their critical thermal maximum temperature. Furthermore, the relationship I found between temperature and growth rate does not appear strongly asymmetrical (Figure 1-3), which Martin and Huey (2008) state as a scenario where organisms may not be expected to prefer T_bs below T_o.

Secondly, the central prediction of Huey's (1982) model, that the T_o for net energy gain when food is highly abundant is higher than when there is little food, was not supported. Although the T_o for growth rate for lizards on the high food diet was 0.4°C higher than for those on the low food diet, lizards did not grow significantly faster when more food was available. This suggests that (1) the difference in food consumption between diets was not large enough to incur a difference in growth rate, (2) the shapes of the curves for gross energy gain or energy loss via metabolic expenditure (Figure 1-1A) are inaccurate for terrestrial ectotherms, or (3) that I had insufficient power to detect a difference. While it is possible that the difference in food consumption between diets was not large enough to incur a difference in growth rate in *S. jarrovii*, lizards on the high food diet consumed significantly more food (0.40 items per day) than those on the low food diet over the course of the experiment. Furthermore, precisely the same high and low food diets incurred a significant difference in growth rate in juveniles of related species (*Sceloporus* o*ccidentalis* and *S. graciosus,* Sinervo and Adolf 1994). It is also possible that a difference in energy loss curves (Figure 1-1A) between diets caused the lack of difference in T_o for growth, because the effect of incubator temperature on RMR depended on diet when I used the full dataset. However, this is unlikely, as the interaction was driven by four outliers (RMR did not differ between diets otherwise), and RMR increased exponentially over the temperature range in both cases. It is more likely that the gross energy curves differ from Huey's (1982) model due to acclimation to thermal or food manipulations, which would enable more efficient performance in response to food shortage or ambient temperature (Angilletta 2009). Finally, I cannot rule out the possibility that the failure to detect a difference in growth rate between diets is due to a lack of statistical power. Although lizards on the high food diet consumed nearly twice as much food on average, the difference was smaller at low temperatures. The passage of food in the gut is slow at low temperatures (Angilletta, 2001) and the resulting convergence of growth rate between diets at low temperatures may have reduced my ability to detect an effect of diet on growth. Furthermore, the variation in growth rate among lizards within treatments was fairly high (Figure 1-3). Inter-individual differences in the thermal sensitivity of performance exist (e.g., Careau et al. 2014), and so the optimal temperature for growth may have varied among lizards. Further studies with larger sample sizes would increase the ability to detect a difference in optimal temperature for growth at different food availabilities if it indeed exists.

Thirdly, the assumptions of Huey's (1982) model were verified, as metabolic expenditure increased exponentially over the temperature range used in this study, and did not differ between diets. The exponential increase in RMR observed confirms that the temperature range used in this study was appropriate (Beaupre et al. 1993, Gillooly et al. 2001) and that it did not coincide with a plateau in metabolic rate, as is sometimes observed in reptiles (Waldschmidt et al. 1987). Moreover, the long-term food availability did not affect metabolic expenditure of the lizards in this study. The metabolic rate of a resting ectotherm depends on food intake, as it increases after feeding (e.g. Jobling 1981, Wang et al. 2001), and is depressed during periods of starvation (Wang et al. 2006). The magnitude of the changes in metabolic rate after feeding varies among species and correlates with meal size and hypertrophy of the gastrointestinal tract (Wang et al. 2001). This suggests that the length of the fasting period (48 hours) in each 4-day cycle in this study was not long enough to trigger significant physiological changes in *S. jarrovii*.

In summary, the thermal coadaptation hypothesis was supported, but Huey's (1982) model was not. The support for the prediction that organisms prefer T_bs that coincide with the T_o for growth rate is consistent with other studies in which more ultimate measures of fitness were used (reviewed in Halliday and Blouin-Demers 2015). Given that lizards thermoregulate imprecisely, they may not alter their T_{set} to match a 0.4°C decline in T_o for growth rate. Alternatively, juveniles may not lower their preferred T_bs in response to food deprivation because they need to be active at suboptimal high temperatures to maximize growth prior to the onset of winter. More studies using ultimate measures of fitness to test the thermal coadaptation hypothesis are also required to elucidate how thermal preference directly impacts fitness. I found no support for Huey's (1982) model, which is likely due to lack of power or differences in the gross energy curves which may have occurred because of acclimation of digestive efficiency to thermal and/or dietary conditions (Angilletta 2009). To determine whether Huey's (1982) energetics model holds on a shorter timescale (with little chance for acclimation), further studies should estimate the gross energy gain curves directly, for example by measuring metabolizable energy intake (Angilletta 2001) of ectotherms on different diets and at multiple temperatures. A more complete understanding of the interactions between temperature and food availability, thermoregulation, and growth rate may provide insights into the potential impacts of climate change on the fitness and persistence of ectotherms (e.g. Sinervo et al. 2010, Gilbert and Miles 2016).

Tables and Figures

Table 1-1. Parameter estimates for models for the weekly number of food items consumed and growth rate of *Sceloporus jarrovii* lizards when subjected to different food and temperature treatments over nine weeks. Growth rate models are the most parsimonious (T) and averaged generalized additive models, as determined by AIC_c comparison. The food items model is a generalized additive mixed model with a negative binomial distribution and lizard ID as a random effect. Experimental temperature is smoothed (s(T)) using a thin plate regression spline. Effective degrees of freedom (edf), estimated residual degrees of freedom (ref.df), and F-values are given for smoothed variables; and Estimate, standard error (SE) and t-values are given for parametric variables. Parameter estimates, SE and z-values are given for the averaged growth rate model.

Model	**Variable**	**edf or Estimate**	**ref.df or SE**	**F, t or z**	**P**
Food Items Consumed	s(T)	1	1	53.05	<0.0001
	Diet (Fasted)	-0.64	0.18	-3.52	0.0005
	Mass	0.02	0.05	0.45	0.65
	Sex	0.13	0.17	0.76	0.45
Growth Rate					
T	s(T)	2.96	3.57	9.19	< 0.0001
Averaged	s(T).1	-0.10	0.05	1.72	0.08
	s(T).2	0.06	0.13	0.49	0.62
	s(T).3	-0.05	0.06	0.82	0.41

	s(T).4	-0.03	0.09	0.31	0.76
	s(T).5	-0.02	0.02	0.83	0.40
	s(T).6	0.05	0.05	0.87	0.38
	s(T).7	0.02	0.02	0.88	0.38
	s(T).8	0.23	0.15	1.50	0.13
	s(T).9	-0.09	0.06	1.36	0.17
	Diet (Fasted)	-0.03	0.02	1.37	0.17
	Initial Mass	-0.001	0.02	0.09	0.92
	Sex (Male)	-0.003	0.04	0.07	0.94

Table 1-2. Model selection for non-linear functions describing thermal reaction norms for growth rate in *Sceloporus jarrovii*, showing the Akaike's Information Criterion corrected for small sample size (AIC_c) and the difference between the AIC_c of each model and the model with the lowest AIC_c (ΔAIC_c). The model with the lowest AIC_c is bolded. b_0 to b_4 are the parameters estimated in each model, and T is the experimental temperature.

Model	**AIC_c**	**ΔAIC_c**
Quartic: $b_0 + b_1T + b_2T^2 + b_3T^3 + b_4T^4$	-48.05	14.64
Stevenson et al. (1985)[a]: Logistic × exponential decay: $b_0(\frac{1}{1 + b_1e^{-b_2(T-19.0)}})(1 - e^{b_3(T-40.2)})$	-51.32	11.37
Stevenson et al. (1985)[a]: Exponential decay + exponential: $b_0 + \left(1 - e^{-b_1(T-19.0)}\right) + (1 + e^{b_2(T-40.2)})$	-51.09	11.6
Ratkowsky et al. (1983)[b]: Linear × exponential decay: $(b_0(T - 17.8))(1 - e^{b_1(T-40.2)})$	-55.64	7.05
Generalized Additive Model	**-62.69**	**0**

Table 1-3. Model selection for the upper and lower limits of the preferred body temperature range of *Sceloporus jarrovii*, before and after the growth experiment, in relation to energetic state (Food), sex, the lane of the thermal gradient, trial order, temperature (T) and experimental diet. All models contained lizard ID as a random effect and were fit by maximizing the log-likelihood. AIC_c is the Akaike's Information Criterion corrected for small sample size for that model, and the ΔAIC_c is the difference between the AIC_c of each model and the model with the lowest AIC_c. The bolded models have the lowest AIC_c.

Model Independent Variables	**AIC_c**	**ΔAIC_c**
Prior To, Lower:		
Food + Sex + Lane + Trial	1863.4	5.7
Food + Lane + Trial	1860.8	3.1
Lane + Trial	1858.7	1.0
Trial	**1857.7**	**0**
Prior To, Upper:		
Food + Sex + Lane + Trial	1878.4	4.7
Food + Lane + Trial	1876.0	2.3
Lane + Trial	**1873.7**	**0**
Trial	1873.9	0.2
After, Lower:		
(Diet × T) + Sex + Lane	774.0	19.7
(Diet × T) + Lane	769.3	15.0
Diet + T + Lane	769.8	15.5
T + Lane	765.0	10.7
T	**754.3**	**0**

After, Upper:		
(Diet × T) + Sex + Lane	770.9	16.1
Diet + T + Sex + Lane	765.7	10.9
T + Sex + Lane	760.5	5.7
T + Lane	757.2	2.4
T	**754.8**	**0**
1	755.0	0.2

Table 1-4*.* The air flow rate used for each lizard mass range and incubator temperature range during respirometry trials on *Sceloporus jarrovii*.

Mass (g)	Flow Rate (ml/min)	
	20-35°C	**38°C**
2.9-3.9	40	50
4.0-4.9	50	60
5.0-5.9	55	65
6.0-6.9	60	70
7.0-7.9	70	80
8.0-8.9	75	85
9.0-10.9	80	90

Table 1-5. Model selection for the $\log_{10}$-transformed volume of oxygen consumed ($\dot{V}O_2$) in relation to incubator temperature (IT), growth experiment treatment temperature (T), diet, and mass in *Sceloporus jarrovii*.

Model Independent Variables	**AIC_c**	**ΔAIC_c**
<u>Full Dataset</u>		
IT + Diet + T + Mass + IT × Diet	-135.12	1.07
IT + Diet + Mass + IT × Diet	**-136.27**	**0**
<u>Outliers Removed</u>		
IT + Diet + T + Mass + IT × Diet	-196.26	3.56
IT + Diet + Mass + IT × Diet	-198.11	1.71
IT + Diet + Mass	-198.05	1.77
IT + Mass	**-199.82**	**0**

Table 1-6. Parameter estimates for equally plausible linear and linear mixed models for the determination of factors affecting lizards' mass over time and the preferred body temperature range, as determined through AIC$_c$ model comparison. All analyses (with mass or the bounds of the preferred body temperature range (Preferred T$_b$, with a 4th-power transformation) as dependent variables) had the lizard ID as a random effect and were fitted by maximizing log-likelihood. Week is the number of weeks since the beginning of the growth experiment, T is the growth experimental temperature, and Trial is the trial order. For simplification, I show the ANOVA output for models including Lane.

Model	**Variable**	**Value**	**SE**	**DF**	**T or F**	**P**
Mass ($R^2 = 0.92$)	Week	0.10	0.009	269	11.21	<0.0001
Preferred T$_b$ (Prior, Lower)						
a) Trial + Lane ($R^2 = 0.76$)	Trial			1, 27	13.53	0.001
	Lane			5, 27	2.12	0.09
b) Trial ($R^2 = 0.70$)	Trial	189907	53254.3	32	3.57	0.001
Preferred T$_b$ (Prior, Upper)						
a) Trial + Lane ($R^2 = 0.62$)	Trial			1, 27	11.02	0.003
	Lane			5, 27	2.36	0.07
b) Trial ($R^2 = 0.62$)	Trial	202792	64376	32	3.15	0.004
Preferred T$_b$ (After, Lower) ($R^2 = 0.13$)	T	-31588	14335	1, 24	-2.20	0.04
Preferred T$_b$ (After, Upper) ($R^2 = 0.06$)	T	-23739	14490	1, 24	-1.638	0.11

Table 1-7. Parameter estimates for equally plausible linear mixed models for the determination of the factors affecting resting metabolic rate, as determined through AIC_c model comparison. All analyses had the volume of oxygen consumed ($\dot{V}O_2$) as a dependent variable, lizard ID as a random effect, and were fitted by maximizing log-likelihood. IT is the incubator temperature and T is the growth experimental temperature.

Model	Variable	Value	SE	DF	T or F	P
$\log_{10}\dot{V}O_2$ (Full Dataset)						
a) IT + Diet + Mass + T + (IT × Diet) ($R^2 = 0.85$)	IT	0.05	0.002	101	19.04	<0.0001
	Diet	0.24	0.107	23	2.25	0.03
	Mass	0.04	0.008	101	4.11	0.0001
	T	-0.003	0.003	23	-1.05	0.31
	IT × Diet	-0.008	0.003	101	-2.31	0.02
b) IT + Diet + Mass + (IT × Diet) ($R^2 = 0.85$)	IT	0.05	0.002	101	19.17	<0.0001
	Diet	0.24	0.107	24	2.20	0.04
	Mass	0.03	0.007	101	4.21	0.0001
	IT × Diet	-0.008	0.003	101	-2.33	0.02
$\log_{10}\dot{V}O_2$ (Reduced Dataset)						
a) IT + Diet + Mass + (IT × Diet) ($R^2 = 0.89$)	IT	0.04	0.002	97	21.43	<0.0001
	Diet	0.14	0.084	24	1.63	0.12
	Mass	0.03	0.005	97	5.78	<0.0001
	IT × Diet	-0.004	0.003	97	-1.50	0.14
b) IT + Diet + Mass ($R^2 = 0.89$)	IT	0.04	0.001	98	29.22	<0.0001
	Diet	0.02	0.026	24	0.65	0.52
	Mass	0.03	0.005	98	5.87	<0.0001

c)	IT + Mass ($R^2 = 0.89$)	IT	0.04	0.001	98	29.40	<0.0001
		Mass	0.03	0.005	98	6.27	<0.0001

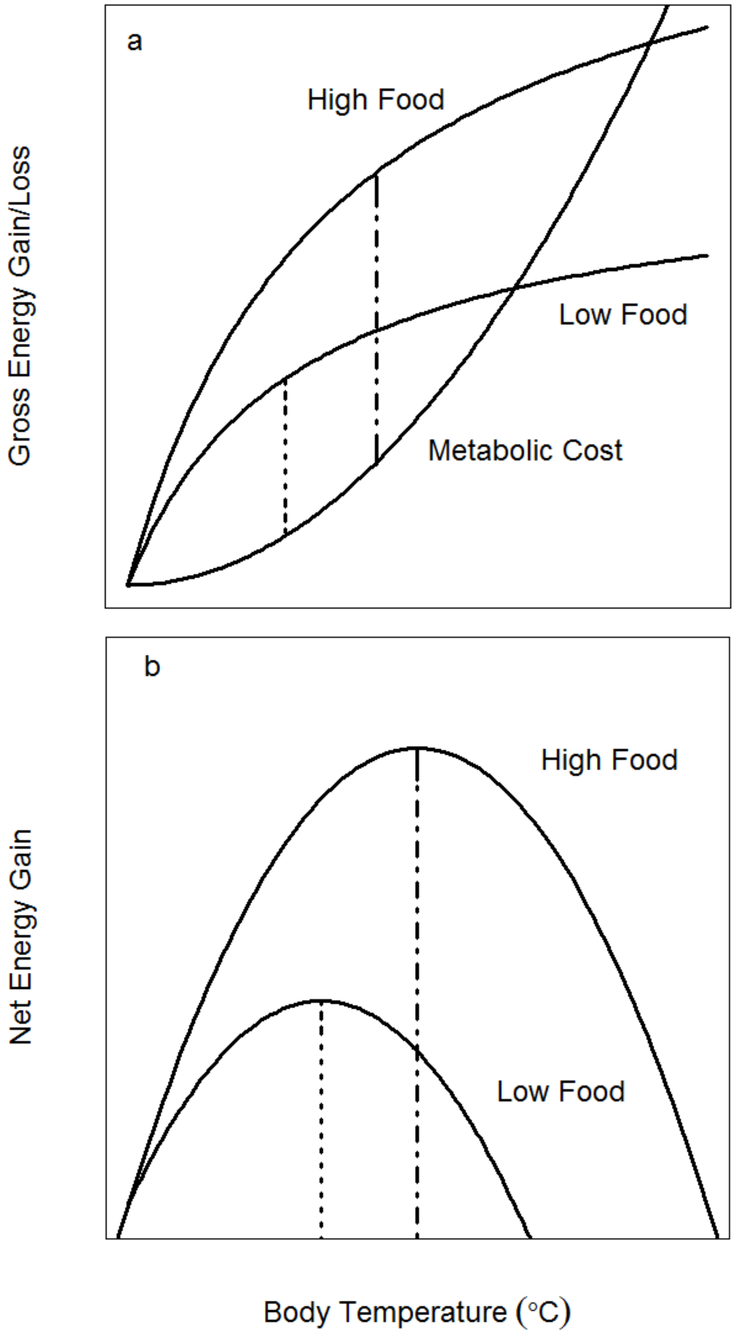


Figure 1-1. (a) Gross energy gain at high and low food availability and metabolic cost functions of body temperature (T_b). (b) Net energy gain (metabolic cost subtracted from gross energy gain) for high and low food availability as a function of T_b. The T_b that maximizes net energy gain for each food availability is indicated with a dotted line. Adapted from Huey (1982).

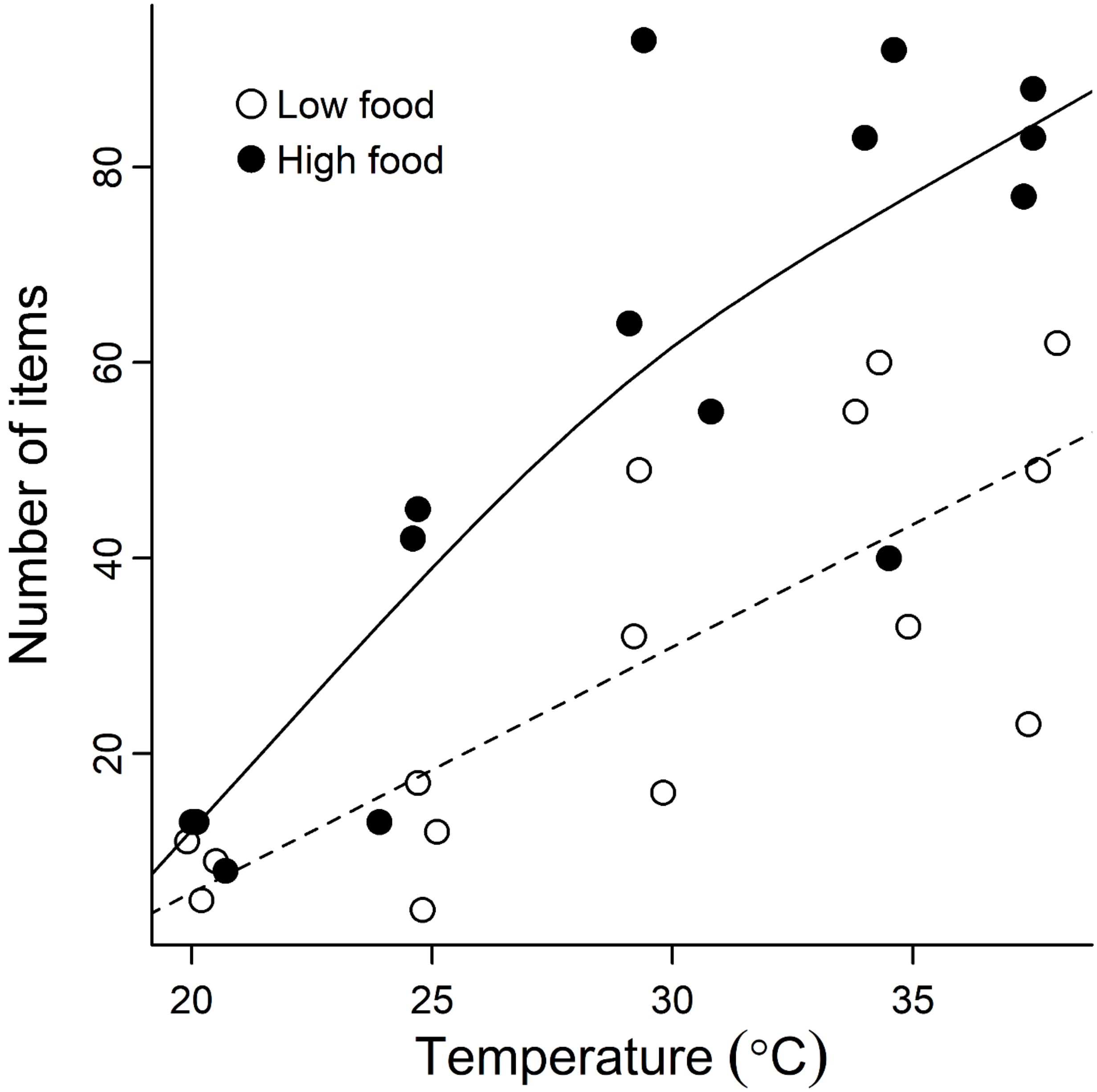


Figure 1-2. The total number of food items consumed by *Sceloporus jarrovii* hatchlings (N = 30) over nine weeks in relation to ambient temperature and diet. The relationship between items consumed and temperature for each diet, predicted from separate generalized additive models, is represented by a dotted (low food) or solid (high food) line.

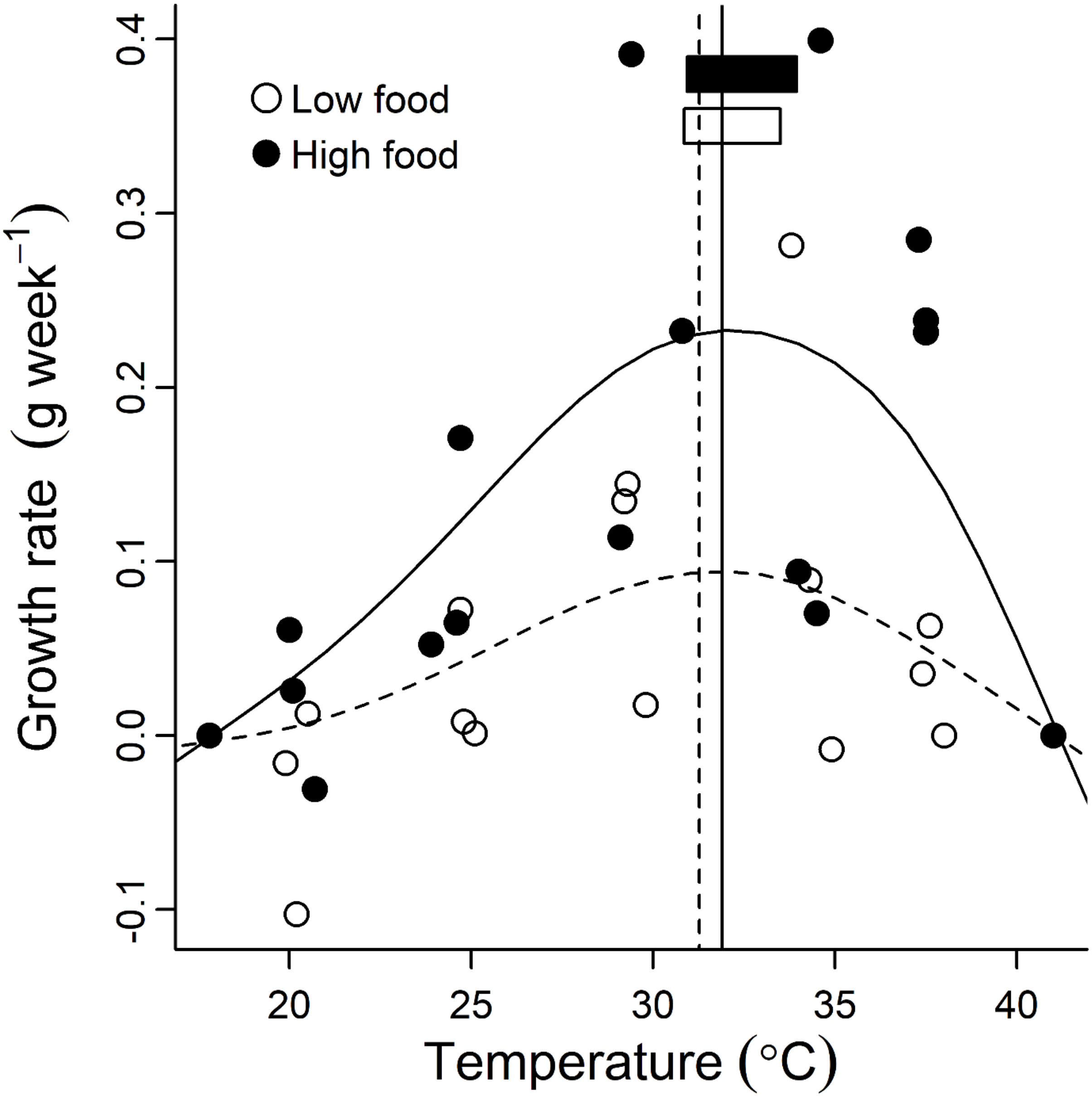


Figure 1-3. The growth rate (g/week) of *Sceloporus jarrovii* hatchlings (N = 30) in relation to ambient temperature and diet (high food: solid lines; low food: dotted lines). The optimal temperature for growth for each diet is indicated with a vertical line. The T_{set} of lizards in each diet is illustrated as a solid (high food) or open (low food) rectangle.

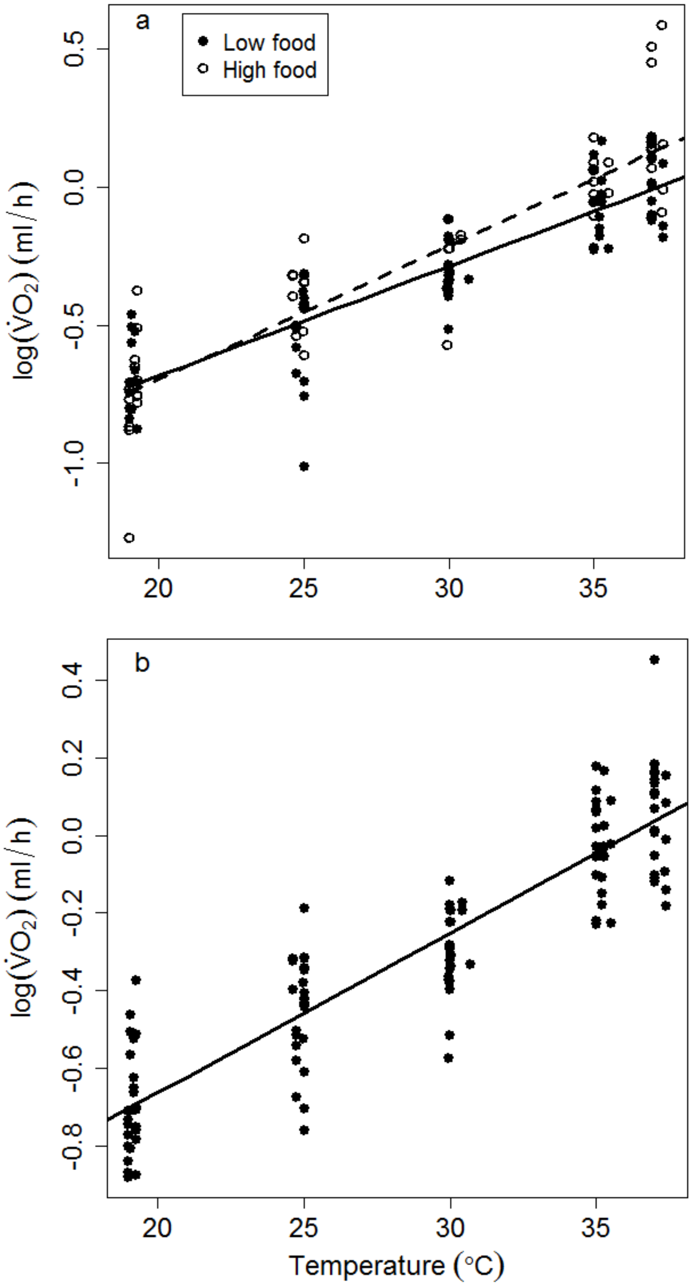


Figure 1-4. The $\log_{10}$-transformed volume of oxygen produced ($\dot{V}O_2$, ml/hour) at rest by juvenile *Sceloporus jarrovii* (N = 27) during respirometry trials at different ambient temperatures, with the full dataset (a) and after removal of four outliers (b). In panel (a), the dotted and solid lines represent the slopes for the high and low food diets, respectively.

Chapter 2

Home range size and density are related to food abundance and to thermal quality in *Sceloporus jarrovii* lizards, but manipulations fail to identify causal relationships

Abstract

According to traditional habitat selection models, animals select habitats based on resource availability, especially food. However, the fitness of ectotherms depends so strongly on temperature that these organisms may select habitats based on their thermal properties rather than food availability. Thus, I tested two hypotheses: that habitat selection in ectotherms is driven by food availability, and that it is driven by thermoregulatory requirements. I predicted that (1) the density of lizards would correlate positively and the average home range size would correlate negatively with the food availability (or thermal quality) of the plot, and (2) after experimentally increasing plot food availability (or thermal quality), lizard density would increase and the average home range area would decrease relative to control plots. I established two plots in each of four treatments (food-supplemented, shaded, food-supplemented and shaded, and control), on a talus slope in Arizona, U.S.A. I measured the density and home range area of Yarrow's Spiny Lizards (*Sceloporus jarrovii*) before and after manipulations, and determined whether lizard density and home range area were related to natural arthropod (food) availability or thermal quality at the surface and in retreat sites. The experimental manipulations had no effect on density or home range area. However, home range area and density both increased with natural arthropod availability, and decreased with higher thermal quality in retreat sites. These results provide partial support for both food availability and thermal quality as drivers of habitat selection in *S. jarrovii*.

Introduction

Determining the factors and interactions that govern the abundance and distribution of organisms is central to ecology (Krebs 2001). Species abundance varies both spatially and temporally (Brown et al. 1995, Ysebaert and Herman 2002), and is driven both by abiotic factors such as temperature and precipitation, and biotic interactions such as competition and predation (Hubbell 2001, Houlahan et al. 2007, Mutshinda et al. 2009). A major behavioural mechanism driving patterns of a species' abundance within its distribution is habitat selection (e.g., Resetarits 2005). Habitat describes the resources and conditions present in an area that influence an organism's ability to survive, reproduce, and persist (Hall et al. 1997). Habitat selection refers to behaviours that result in organisms using certain habitats disproportionately (Rosenzweig 1981, Mayor et al. 2009). Habitat selection influences physiological processes (Huey 1991, Blouin-Demers and Weatherhead 2008), population dynamics (Holt 1987, Kristan 2003) and community-level processes (Rosenzweig 1991, Resetarits et al. 2005), and is the means by which individuals distribute themselves on a landscape.

Why do organisms preferentially use certain habitats over others? Local habitats differ in quality due to variation in abiotic and biotic factors. From an individual organism's perspective, a high quality habitat is one containing the conditions that enable that individual to maximize its fitness (Pulliam 2000, Johnson 2007). According to traditional habitat selection theory, habitat selection and population density depend primarily on individuals' capacity to acquire resources, especially food, in a given area (e.g. Rosenzweig 1991, Mobæk et al. 2009). While food availability is a crucial environmental variable for any organism, affecting growth, reproduction, and higher-level processes such as food web dynamics and spatial structure of communities (Taylor et al. 2005), temperature may be equally if not more important for ectotherms (e.g., Halliday and Blouin-Demers 2014). Ectotherms do not produce enough heat from metabolism to maintain their body temperature (T_b) physiologically, and so their T_b is strongly influenced by environmental temperatures (Bennet 1980). Thus, environmental temperature, through its effects on T_b, affect most physiological, developmental and behavioural processes in ectotherms, including the rate of food processing (Troyer 1987, Angilletta 2009). If an ectotherm cannot maintain appropriate T_bs in a given habitat, its energy gain will be constrained even if food is abundant (Sinervo and Adolph 1989). Thus, the rate of food consumption may be more constrained by temperature, which influences the rate of food processing, than by food availability, which affects the rate of food acquisition.

The obligation to maintain T_b within an optimal range may be the primary factor driving habitat selection in ectotherms (Huey 1991). To maintain T_bs that maximize performance and fitness, many ectotherms must thermoregulate behaviourally (Huey and Kingsolver 1989, Angilletta 2009). Ectotherms typically strive to maintain their T_b within a narrow range (T_{set}, here defined as the central 50% of preferred T_bs) that can be achieved when temperature selection is unconstrained (Hertz et al. 1993). From an ectotherm's perspective, a habitat is of high thermal quality when the difference between environmental temperatures and its T_{set} is minimal (Hertz et al. 1993). Indeed, various reptiles preferentially use habitats of high thermal quality (e.g., snakes, Blouin-Demers and Weatherhead 2001b, Row and Blouin-Demers 2006; turtles, Dubois et al. 2009; lizards, Sabo 2003). Furthermore, areas with desirable thermal properties, such as basking sites, are actively defended against conspecifics in some lizards (e.g., Downes and Shine 1998), turtles (Bury and Wolfheim 1973), and spiders (Hammerstein and Rechert 1988).

The size of an animal's home range is an important indicator of the animal's resource requirements in relation to their availability in the environment (Perry and Garland 2002). A home range is the area traversed during all the animal's activities over a specified time interval, including foraging, mating, and caring for young (Burt 1943, Börger et al. 2006). Home range area may be related to body size, season, weather, age, sex, activity pattern and, importantly, habitat quality (Stickel 1968, Turner et al. 1969, Mysterud et al. 2001). In response to food supplementation in the wild, animals typically reduce their home range area and increase in density (reviewed in Boutin 1990, Mcloughlin and Ferguson 2000), although this pattern is not universal. In particular, of the five studies on reptiles cited by Boutin et al. (1990), two found no effect of food supplementation on home range area (Waldschmidt 1983, Guyer 1988). One possible reason for the inconsistency in results may be that home range area is also influenced by the availability of thermal resources. For example, side-blotched lizards (*Uta stansburiana*) alter their territory size upon the addition or removal of rocks, which affect the range of temperatures available for thermoregulation (Calsbeek and Sinervo 2002). Furthermore, juvenile *U. stansburiana* that occupy home ranges containing more Yucca plants and thus more shelter and shade are more likely to survive (Fox 1978).

Despite evidence that reptiles select habitats based on prey distribution (Madsen and Shine 1996) and temperature (Blouin-Demers and Weatherhead 2001b, Sabo 2003, Row and Blouin-Demers 2006, Dubois et al. 2009), no studies to my knowledge have considered the relative importance of these factors. The purpose of this study was to test two hypotheses concerning habitat selection in ectotherms: that habitat selection is driven by food availability, and that it is driven by thermoregulatory requirements. I used Yarrow's Spiny Lizards (*Sceloporus jarrovii*) as my study species because they are strongly territorial (Ruby 1978) and occur at high densities, actively thermoregulate by basking (Beuchat 1986), and reduce their territory size when given additional food (Simon 1975).

If habitat selection was driven by food availability, I predicted (1) that the density of lizards would correlate positively and the average home range area would correlate negatively with the natural food availability of the plot, and (2) that following food supplementation, lizard density would increase and the average home range area would decrease relative to control plots. Conversely, if habitat selection in *S. jarrovii* was driven by thermoregulatory requirements, I predicted (1) that the density of lizards would correlate positively and the average home range area would correlate negatively with the plot thermal quality, and (2) that after experimentally increasing plot thermal quality, lizard density would increase and the average home range area would decrease relative to control plots. A three-way interaction between food treatment, temperature treatment, and time period would indicate that these factors affect home range area synergistically or antagonistically.

To test these predictions, I established eight plots on a large talus slope, divided among four treatments: food-supplemented, shaded, food-supplemented and shaded, and control. Each lizard was individually marked with paint and its location was recorded each time it was sighted. I measured lizard density, home range area, natural arthropod (food) availability, and thermal quality of each plot before and after experimental manipulations. Thus, I determined both how the lizard density and average home range area were affected by natural food availability and thermal quality, as well as how these variables were affected by experimental manipulations.

Methods

Study Site and Species

Sceloporus jarrovii is a small, heliothermic lizard that feeds on arthropods (Simon 1975) and is abundant in rocky habitats in southern Arizona and New Mexico, U.S.A, and in northern Mexico. Outside of the fall breeding season, lizards aggressively defend territories against conspecifics (Simon 1975), although home ranges overlap (Ruby 1986). *Sceloporus jarrovii* density is strongly related to the extent of rock and number of rock crevices (Ruby 1986) that serve as refuges from predators and unsuitable temperatures (Huey et al. 1989, Sabo 2003). I conducted this experiment on a talus slope at Barfoot Park (elevation 2,500 m) in the Chiricahua Mountains, Arizona, U.S.A. This research was conducted with State of Arizona Scientific Collection Permits (SP675429 and SP713939), permission from the U.S. Forest Service, and approval from the University of Ottawa's Animal Care Committee (BL-1788).

Experimental Design and Manipulations

I conducted the manipulative experiment from 23 May to 21 June 2015, during the dry season, when temperatures are high and natural food availability is low (Ballinger and Ballinger 1979). I established eight circular plots with a 10 m radius (Figure 2-1) that were homogeneously composed of rocks and located at least 10 m from neighbouring plots. Given that the presence of vegetation may influence the availiability and accessibility of both arthropods (Díaz and Carrascal 1991) and environmental temperatures (Sears et al. 2016), plots were located at least 10 m from any vegetation. A plot of 314 m^2 is an adequate size because it could encompass several lizards: mean territory area in *S. jarrovii* has been recorded as 130 m^2 for males and 40 m^2 for females, with considerable overlap between the sexes (Simon 1975).

Plot manipulations were initiated on 3 June 2015. There were two plots in each of four treatments: food-supplemented, shaded, food-supplemented and shaded, and control (Figures 2-1, 2-2). I supplemented each of the four "food-supplemented" plots six times with mealworms (*Tenebrio molitor*) from 3-20 June (approximately every 3 days) and once with house crickets (*Acheta domesticus*) on June 20th. Overall, each plot received 820 mealworms and 100 crickets. Food items were placed in three plastic dishes within 2 m of the plot centre (Simon 1975). I assumed that this food supplementation method was effective because I observed lizards consuming the food items during the experiment. The four "shaded" plots were shaded with three (10 m × 3.7 m) strips of 50% knitted shade cloth attached to metal poles (length: 1.8 m) and radiating from the plot centre. Shading was expected to improve the thermal quality of the plots because it would reduce the temperature of the substrate at mid-day, when substrate temperatures are typically several degrees above T_{set}.

To quantify the effects of the experimental manipulations, I measured several variables both prior to (23 May to 2 June) and after (13-21 June) experimental manipulations. In each time period, I quantified the natural food (arthropod) abundance, thermal quality, lizard density, and the size of lizard home ranges overlapping with each plot.

Natural Food Availability

To confirm that the natural food abundance of each plot did not change following experimental manipulations, I assessed the total number and volume of arthropods caught in sticky traps (e.g., Simon 1975, Niewiarowski and Roosenburg 1993) in each time period. Two lines of evidence suggest that the amount of arthropods caught in sticky traps are a good proxy for the amount of food available to lizards. Firstly, Simon (1975) found the same types of food items on sticky boards as in *S. jarrovii* stomachs, although *S. jarrovii* were more selective. Secondly, there is a positive correlation between sticky trap capture rates and the mass of stomach contents in *Sceloporus undulatus* (Dunham 1978). Sticky traps consisted of rectangles (10 cm × 8 cm) of waterproof paper covered in biodegradable resin (Tree Tanglefoot, Grand Rapids, Michigan, U.S.A.). I set two sticky traps in random locations in each plot for 24 hours. The location of each sticky trap was determined from random numbers (0 to 360° for the direction and 0 to 10 m for the distance from the plot centre).

I counted the number of arthropods on each trap and measured the maximum length and width of each arthropod using callipers. I calculated the total arthropod volume (mm^3) per card by approximating the volume of each arthropod to that of a cylinder ($volume = length \times \pi \times (\frac{width}{2})^2$) and taking the sum (e.g., Werner et al. 1995, Forstner et al. 1998).

I ran separate mixed models (Pinheiro et al. 2015, Bates et al. 2015) for the number and volume of arthropods. In both cases, food treatment (supplemented or not) × time period (before or after) were the fixed effects, plot was the random effect, and the model was fitted by maximizing the log-likelihood. I used a generalized linear mixed model (GLMM) with a Poisson distribution and log-link function for the number of arthropods, and a LMM with a Gaussian distribution for the volume. Volume was $\log_{10}$-transformed to improve normality. In both cases, I sequentially removed non-significant terms until all remaining terms were significant, and compared the AIC_c values to select the most parsimonious model (Burnham and Anderson 2002).

Plot Thermal Quality

To determine whether the experimental manipulations effectively improved the thermal quality relative to control plots, I followed these steps: (1) I validated the use of copper models as physical models that have the same thermal properties as *S. jarrovii* (e.g., Bakken et al. 1985, Huey 1991), (2) I determined the T_{set} of 40 lizards, (3) I assessed the operative temperatures (T_e, the potential equilibrium T_bs that a thermoconforming animal may achieve at every location in its habitat, Huey 1991) of the plots using copper models, (4) I calculated the d_e (a measurement of thermal quality) for each plot, and (5) I compared the d_e prior to and after manipulations. The d_e corresponding to each T_e measurement was calculated as the absolute difference between T_e and the closest bound of T_{set}. Values of T_e falling within T_{set} were assigned a value of 0. Thus, greater deviations from T_{set} indicate a habitat of poorer thermal quality, from the point of view of the lizard (Hertz et al. 1993).

Validation of Copper Models

To select an appropriate physical model, I compared the temperatures measured by the temperature data loggers (Thermochron iButton D1S1921G-F5, Dallas Semiconductor, Sunnyvale, California) in three models to those measured by a temperature data logger inserted into the abdominal cavity of a dead lizard (Blouin-Demers and Weatherhead 2001b). Of the three physical models, there were two copper models (lengths: 6 cm and 10 cm) made from copper pipe (diameter: 2 cm) sealed with rubber stoppers on both ends, and one temperature data logger encased in plastic coating. All three models were painted dark grey to approximate the reflectance of *S. jarrovii* (Peterson et al. 1993). The lizard, an adult male (SVL = 7.20 cm, mass = 13.75 g), had been found dead the previous day during a concurrent study.

The models and lizard were placed on a rock in a wire mesh cage to deter scavengers. Temperatures were recorded every 15 minutes from 08:30 to 19:30. To determine whether lizard T_bs could be predicted from the temperatures recorded by the models, I ran separate linear regressions with the models' T_e measurements as the independent variable and the lizard's T_b measurements as the dependent variable. I also conducted paired t-tests to determine if there were significant differences between the model and lizard temperature measurements. Upon examination of the results (see Results section), the 6 cm model was adopted as the physical model for *S. jarrovii* in this study.

Preferred Body Temperature Range

In May-June 2014, I measured the T_{set} of 40 adult lizards (21 males, 19 females, all at least one year old) in a laboratory thermal gradient (Hertz et al. 1993) at the Southwestern Research Station. The thermal gradients consisted of particle board boxes (122 cm × 39 cm × 39 cm), each with three laneways, placed in an air-conditioned chamber with homogeneous fluorescent lighting. To create a range of operative temperatures (~20-45°C), electric heating pads were placed beneath one end of the thermal gradient. I placed lizards individually into laneways at approximately 21:00 and allowed them to habituate to the thermal gradients overnight. No food or water were provided in the thermal gradients. To approximate natural daylight conditions, the lights were turned on at 05:30 the next morning. I measured the dorsal surface temperature of each lizard (Bakken 1992) every 30 minutes from 08:00 to 17:00 using an infrared thermometer. The thermometer was held in line with the lizard's body axis (Hare et al.

2007), approximately 2 cm above the surface immediately behind its pectoral girdle. I used this method instead of inserting a thermocouple into the cloaca (e.g., Brown and Griffin 2005) or pressing an infrared thermometer to the cloaca (e.g., Beal et al. 2014), because of the small size of the lizards and because repeated handling may increase stress and stress-induced increases in preferred T_bs (Cabanac and Bernieri 2000, Rey et al. 2015). Moreover, skin temperature is a good proxy for T_b in other lizard species (e.g., Herczeg et al. 2006, Hare et al. 2007, Bouazza et al. 2016). I calculated the bounds of the central 50% of T_bs measured for each individual and averaged these values across all lizards to obtain the T_{set} (Hertz et al. 1993).

Operative Temperatures

To measure the T_es, I recorded the temperature every 20 minutes over the course of the experiment by placing two copper models in each plot. Of these, one copper model was placed on a rock in full sun to measure surface T_es, and the other was placed under a large rock to measure retreat-site T_es. The location of each copper model was determined from random numbers (0 to 360° for the direction and 0 to 10 m for the distance from the plot centre). The “retreat” copper models were placed under the largest rock in the vicinity of the random location. In shaded plots, the copper models were completely covered by the shade cloth after experimental manipulations.

Calculation and Analyses of d_e

For each copper model, I calculated the mean daily d_e for all days for which all the T_es had been recorded for daylight hours (05:30 to 19:30), when lizards are typically active (Beuchat 1989). To confirm whether the “shaded” treatment effectively lowered d_e, I ran a linear mixed model (LMM, nlme package, Pinheiro et al. 2015) with mean daily d_e as the dependent variable, the temperature treatment (shaded or not) × time period (before or after) as fixed effects, and plot as a random effect. I ran separate analyses for copper models at the surface and in retreat sites. Because the interaction was significant for copper models on the surface (see Results), I divided the dataset by time period and ran the same models for each time period, except with the temperature treatment as the only fixed effect. Normality and homogeneity of variance were confirmed through visual examination of residual plots. Where applicable, I sequentially removed non-significant terms until all remaining terms were significant, and compared the AIC_c values to select the most parsimonious model (Burnham and Anderson 2002).

Lizard Density and Home Range Area

To measure lizard density and home range areas, I captured all adult (at least one year old) lizards observed on the talus slope by noose. Each lizard was uniquely marked using two methods: permanently with cauterizeration (Vervust and Van Damme 2009) and temporarily with a colour code using non-toxic acrylic paint (Simon and Bissinger 1983). The purpose of the colour codes was to allow observers to identify a lizard without capturing it. Given that many lizards lost their paint after shedding, the permanent mark allowed me to identify previously captured lizards and to re-apply the appropriate colour code. I sexed lizards using secondary sexual characteristics (enlarged postanal scales and femoral pores, and blue patches on the throat and sides of the belly in males, Brennan and Holycross 2006, Figure 2-3) and measured their snout-vent length with manual callipers. I assigned colour codes to 124 lizards (60 males, 64 females, mean ± SD SVL = 5.9 ± 1.2 cm, mass = 7.8 ± 5.3 g). Upon each lizard's initial capture and every time it was seen thereafter, I recorded the location using a handheld GPSmap 78s (Garmin, Olathe, Kansas, U.S.A.). GPS points were averaged over two minutes to improve their accuracy (typically to within 2 m). Subsequent locations of the same lizard were separated by at least 30 minutes to increase the independence of the points. In the field, to focus my efforts on lizards with home ranges in both time periods, new lizards captured on the last two days of the "before" period and throughout the "after" period (N = 116) were marked with an X paint mark (to prevent recapture) and only included in the density analysis.

I calculated lizard densities and home range areas in QGIS 2.4 (QGIS Development Team 2014). As a proxy for density, I used the number of individual lizards observed in each plot (i.e. located within the 10 m buffer around the plot centre) before and after manipulations. To calculate home range areas, I delineated the home ranges of all lizards with at least three sightings in either time period (range 3-17, mean ± SD = 5.3 ± 2.5), using minimum convex polygons (MCP). MCPs, the smallest possible convex polygons that encompass all the recorded locations of an individual (Hayne 1949), are recommended to measure home range area in reptiles (Row and Blouin-Demers 2006). I delineated the boundaries of each plot by creating a 10 m buffer around the plot centre, determined which lizards' home ranges intersected with each plot, and thereby assigned each lizard to a plot. Lizards whose home range intersected with multiple plots were assigned to the plot where it had been seen most often. Lizards that could not be assigned to a plot upon visual examination of their locations were assigned randomly to one of the plots that intersected with their home range.

To determine whether the density or home range area of lizards increased with natural food abundance or d_e (on the surface or in retreat sites under rocks), I fit LMMs by maximizing the log-likelihood, with density (or home range area) as the dependent variable, arthropod volume + d_e (surface) + d_e (retreat) as fixed effects, and plot as the random effect. I $\log_{10}$-

transformed arthropod volume to improve normality, removed non-significant terms until all remaining ones were significant, and selected the most parsimonious model using AIC_c (Burnham and Anderson 2002). The independent variables were tested for correlations using Pearson's method. Given that the d_e (retreat) values from plot 2 were more than two standard deviations from the mean, which may have been an artifact of rock thickness (Huey et al. 1989) and thus may not have been representative of retreat-site thermal quality, I repeated the analyses without this plot. I only used arthropod volume as a measurement of food availability because the number and volume of arthropods were highly correlated ($r = 0.87$).

To determine whether the density of lizards in manipulated plots increased following food supplementation and/or shading, I ran a GLMM with a Poisson distribution and log-link function. I used the number of lizards observed as the dependent variable, food treatment × temperature treatment × time period as fixed effects, and plot as the random effect. I subsequently removed non-significant terms until all the remaining ones were significant, and selected the most parsimonious model using AIC_c (Burnham and Anderson 2002).

To determine whether the home range area of lizards in manipulated plots changed following food supplementation and/or shading, I ran a LMM with the home range area as the dependent variable, food treatment × temperature treatment × time period, SVL, and sex as fixed effects; and lizard ID nested within plot as the random effects. I applied a log(x) transformation to home range area to improve the normality and homoscedasticity of residuals. I included SVL and sex as fixed effects because home range area increases with body size, and males have larger home ranges than females in *S. jarrovii* (Simon 1975, Ruby 1978). I fit the model by maximizing the log-likelihood. I then removed non-significant terms until all remaining terms were significant, and chose the most parsimonious model using AIC_c (Burnham and Anderson 2002).

All statistical analyses were done in R (R Core Team 2015). Model R^2 values were calculated using the r.squaredGLMM() function (MuMIn package, Barton 2018) and the percent deviance explained was calculated using the Dsquared() function (modEvA package, Barbosa et al. 2016).

Results

Natural Food Availability

The assumptions that natural food availability was similar between food-supplemented and control plots, and that this did not change after food supplementation, were verified. No terms were significant in the best model for arthropod volume (Table 2-1). Time period was present in an equally plausible model, but it was not significant (model $R^2 = 0.21$, Value = 0.15, SE = 0.13, $t_{1,23} = -1.22$, P = 0.23). There were 0.41 fewer arthropods per trap in the later time period (model $R^2 = 0.35$, Estimate: -0.41, SE = 0.21, z = -1.95, P = 0.051), but this change occurred across all plots, regardless of supplementation treatment (Table 2-1).

Plot Thermal Quality

Copper Model Validation

Lizard T_bs could be accurately predicted from all three physical models (6 cm: $R^2 = 0.98$, estimate: 0.98, SE = 0.02, $t_{1,43} = 50.8$, P < 0.001; 10 cm: $R^2 = 0.99$, estimate: 1.08, SE = 0.02, $t_{1,43} = 60.1$, P < 0.001; temperature data logger: $R^2 = 0.98$, estimate = 0.98, SE = 0.02, $t_{1,43} = 44.2$, P < 0.001). There were no significant differences between the lizard's T_b and either the temperature data logger (t_{44} = -0.35, P = 0.73) or the 10 cm copper model (t_{44} = -0.29, P = 0.78), but the 6 cm model overestimated the lizard's T_b by 0.5°C (mean ± SD = 0.48 ± 1.29, t_{44} = -2.48, P = 0.02). These differences in temperature measurements were not biologically significant because they were small, there was a three-minute time lag between lizard and model temperature measurements, and the temperature data loggers are only accurate to 0.5°C. I selected the 6 cm model as the physical model for *S. jarrovii* because it was intermediate in size between the other two models.

Calculation of T_{set} and d_e

The assumption that shading plots would improve thermal quality was verified for copper models on the rock surface, but not for those in retreat sites under rocks. The bounds of T_{set} were 30.4-33.2°C (median: 32.1°C). The rock surface during the hottest parts of the day was cooler under shade cloth, and so the differences between T_es and T_{set} were reduced (Figure 2-4), but the T_es in retreat sites were unchanged when the surface was shaded (Figure 2-5). The mean daily d_e (± SE) at the surface decreased from 8.4 ± 0.2°C to 6.7 ± 0.3°C between time periods in shaded plots, but did not change in control plots (before: 9.4 ± 0.2°C, after: 9.6 ± 0.3°C). At the surface, there was a temperature treatment × time period interaction (model R^2 = 0.48, value = 1.95, SE = 0.47, DF = 142, t = -4.15, P = 0.0001), whereby d_e did not differ between plots prior to experimental manipulations (model R^2 = 0.51, value = 1.00, SE = 0.52, DF = 6, t = -1.92, P = 0.10), but the addition of shade cloth increased thermal quality relative to control plots (model R^2 = 0.46, value = -2.96, SE = 0.55, $t_{1,6}$ = -5.34, P = 0.002).

In retreat sites, the thermal quality improved between time periods (model $R^2 = 0.82$, value = -2.59, SE = 0.38, DF = 135, t = -6.74, $P < 0.0001$), but there was no effect of shading because the temperature treatment × time period interaction was not present in the most parsimonious model (Table 2-2). Temperature treatment was included in an equally plausible model (model $R^2 = 0.82$), but was not significant (Value (Shaded) = 3.2, SE = 3.1, DF = 6, t = -1.0, P = 0.34). The mean daily d_e (± SE) decreased from 10.8 ± 0.3°C to 8.4 ± 0.4°C between time periods in shaded plots, and from 14.2 ± 1.1°C to 11.5 ± 1.1°C in control plots.

Lizard Density and Home Range Area

The prediction that the density of lizards would increase with natural food availability was supported because there were more lizards in plots with more arthropods available. Density increased by 0.3 lizards for every 10% increase in arthropod volume (model $R^2 = 0.44$, value = 6.91, SE = 2.14, DF = 7, t = 3.24, P = 0.01, Table 2-3, Figure 2-6). However, lizards in plots with more food also had larger home ranges, with home range area increasing by 62 m^2 for every 10% increase in arthropod volume (model $R^2 = 0.42$, value = 1507.2, SE = 515.6, DF = 6, t = 2.92, P = 0.03, Table 2-3, Figure 2-6).

The predictions that the density of lizards would increase and the home range area would decrease with plot thermal quality were refuted for the surface because there were no relationships between surface d_e and either lizard density or home range area. The surface d_e was not present in any final or equally plausible model (Table 2-3). The prediction for lizard density was also refuted for thermal quality in retreat sites, because retreat site d_e was not present in the final model when all plots were included, and there were fewer lizards in plots of higher thermal quality when plot 2 was excluded (Figure 2-7). When plot 2 was excluded, the density increased by 1.0 lizards when d_e increased by 1°C (model $R^2 = 0.75$, value = 1.05, SE = 0.39, DF = 5, t = 2.69, P = 0.04). The prediction that home range area would increase with thermal quality, however, received mixed support for retreat sites, because retreat site d_e was not present in the final model when all plots were considered, but lizards had smaller home ranges in plots of better thermal quality when plot 2 was excluded. In the latter scenario, home range area decreased by 343 m^2 for each 1°C decrease in d_e (model $R^2 = 0.77$, value = 342.7, SE = 85.3, DF = 4, t = 4.02, P = 0.02, Figure 2-8).

The predictions that the density of lizards would increase in food-supplemented and shaded plots were refuted because there were no interactions between the time period and either treatment variable in the most parsimonious model (Table 2-4). Lizard density declined after manipulations (Estimate = -0.56, SE = 0.20, z = -2.82, P = 0.005, Figure 2-9), and there was an interaction between the food and temperature treatment (Estimate = 1.18, SE = 0.40, z = -2.94, P = 0.003), but there were no interactions between time period and either food or temperature treatment (model explains 50% of deviance). This indicates that the number of lizards present varied between plots, but that these numbers did not change due to shading or food addition.

The predictions that the home range area of lizards would decrease in shaded and food-supplemented plots were refuted because home ranges remained of similar size throughout the experiment (Figure 2-10). There were no significant terms in the most parsimonious model (Table 2-4). Three other models, including a model with a three-way interaction between the food treatment, temperature treatment and time period, were equally plausible but contained no significant terms (Table 2-5).

Discussion

I found mixed support for both the hypothesis that habitat selection is driven by food availability, and that it is driven by thermal quality in *S. jarrovii*. I had predicted that density would increase and home range area would decrease with higher resource (food and thermal) availability. However, the density and home range area of lizards both increased with natural food availability and were unaffected by the thermal quality at the surface. There was weak evidence that home range area and density decreased with the thermal quality in retreat sites under rocks, as the effect was only present when plot 2 was excluded. Neither lizard density nor home range area were affected by food addition or shading, although there was no difference in natural arthropod (food) availability between supplemented and control plots in either time period, and adding shade cloth improved surface thermal quality.

A possible explanation for the conflicting results (that density and home range area both increased with natural food availability and decreased with thermal quality in retreat sites) is that lizards respond to resources differently at various spatial scales (Mayor et al. 2009). At different spatial scales, there are often different (Orians and Wittenberger 1991, Luck 2002) or conflicting (Compton et al. 2002) habitat selection patterns within a species. For example, food availability dictates the density of female yellowheaded blackbirds in different marshes, but not between territories within a marsh (Orians and Wittenberger 1991), because female blackbirds feed outside of the territories where they reside. *Sceloporus jarrovii* clearly select rocky habitats at a large spatial scale: Ruby (1986) found higher densities of female *S. jarrovii* in areas with many rocks and crevices, and the *S. jarrovii* at the current study site occur at high densities on talus slopes, but are virtually absent in the surrounding forest (pers. obs.). Similarly to yellowheaded blackbirds (Orians and Wittenberger 1991), *S. jarrovii* may have feeding areas outside of their defended territory, but still within their home range. Thus, plots with more food may attract lizards from further away, and thus contain more lizards with larger home ranges. If territory size is more closely related to thermal quality than to food availability, and territories of high thermal quality are more vigorously defended (Arnott and Elwood 2008), then plots with warmer refuges may have fewer non-resident lizards and thus lower density. Ruby (1978, 1986) found no correlation between natural arthropod availability and *S. jarrovii* female density, and no significant changes in home range area throughout the active season, despite changes in food availability. Given that these findings reflect female behaviour, the pattern in the current study may be driven by males, who have larger home ranges than females throughout the year (Ruby 1978).

The conflicting patterns for habitat selection may also have occurred if there are trade-offs between food availability, thermal quality and another variable, such as mate availability or predation risk. For example, male *S. jarrovii* select home ranges during the fall breeding season (September-October) based on female availability: they increase the size of their home range and shift the centre to maximize overlap with neighbouring females (Ruby 1978). However, these home range shifts occur in late summer, 2-3 months later than when our study was conducted (Ruby 1978). On the other hand, trade-offs between foraging quality and predation risk in terms of habitat or patch selection have been found in a diversity of taxa (reviewed in Lima and Dill 1990), including fish (Magnhagen 1988), birds (Caldwell 1986), amphibians (Holomuzki 1986), insects (Heads 1986) and other invertebrates (Raess and Maly 1986). Trade-offs between thermal quality and predation risk in terms of habitat use and selection also exist.

Bluegill sunfish (*Lepomis macrochirus*) tolerate higher T_bs in the presence of predatory largemouth bass (Fischer et al. 1987), juvenile broad-headed snakes (*Hoplocephalus bungaroides*) limit basking behaviour due to a trade-off between thermal benefits and predation risk (Webb and Whiting 2005), and velvet geckos (*Oedura lesueurii*) place more importance on predator avoidance than temperature in retreat site selection (Downes and Shine 1998). The effects of food supplementation or thermal quality on lizard density may also be dampened if predators are attracted to these high-density areas (Boutin et al. 1986). Thus, the density and home range selection of *S. jarrovii* at this site may be a function of the distribution of predators such as twin-spotted rattlesnakes (*Crotalus pricei*), as well as food availability and thermal quality.

The results also suggest that lizards select habitats based on the thermal properties of retreat sites rather than surface locations, because both lizard density and home range area were affected by the thermal quality under rocks but not at the surface. Furthermore, the addition of shade cloth did not change the thermal quality under rocks in shaded plots relative to control plots. If lizards select habitats based on the thermal properties of retreat sites, the lack of response of lizard density or home range area to shading is unsurprising. Many temperate-zone reptiles spend most of the day under rocks or in other retreats (Huey 1982). Depending on the thermal properties of their retreat site, sequestered ectotherms may experience T_es very different from those associated with above-ground activity (e.g. Bustard 1967, Christian et al. 1984, Peterson 1987). Examples of species that select retreat sites based on thermal properties include western fence lizards (*Sceloporus occidentalis*, Sabo 2003), velvet geckos (*Oedura lesueurii*, Downes and Shine 1998) and gartersnakes (*Thamnophis elegans*, Huey et al. 1989). *Sceloporus jarrovii* spend a significant amount of time (active or inactive) in the rocky maze under the rocks, as most lizards are inactive during the hottest part of the day (Beuchat 1989) and are only active above-ground 2.5 to 6 days per week (Simon and Middendorf 1976, Beuchat 1989). Thus, *S. jarrovii* may select microhabitats primarily based on the T_es available beneath rocks, particularly in the hottest period of the year. The thermal quality under the rocks improved in the later time period, with warmer T_es that were closer to or even within T_{set} (Figure 2-5). Indeed, fewer lizards were active at once after experimental manipulations: the average number of lizard locations recorded per person hour declined from 6.1 to 5.5 between time periods. The reduction of 0.6 lizards per hour is a conservative estimate because over twice more lizards were caught in the earlier time period, and pursuing a lizard is more time-consuming than simply recording its location. Thus, *S. jarrovii* may select microhabitats based on the thermal quality of retreat sites rather than the thermal quality at the surface.

Finally, the lack of observed changes in response to manipulations may have been due to methodological issues. In particular, the lack of response to food supplementation may have occurred if the plots were not supplied with enough food, or if they were not supplied consistently enough throughout the manipulation period, because site fidelity is higher when food availability is more predictable (e.g., Lurz et al. 1997). Simon (1975) found that *S. jarrovii* decreased their territory size in response to mealworm addition, but these territories were supplemented continuously during daylight hours. Other sources of error may have included, firstly, low sample size (two replicate plots per treatment) and power, which may have caused a Type II error (Zar 1974). Secondly, the plots were not independent, because 23% of lizards for whom home range area was estimated had home ranges that overlapped with more than one plot. These lizards would have been influenced by more than one treatment. Thirdly, the MCP method may have underestimated the home range areas because the number of sightings per lizard was lower (mean = 5.3 sightings per home range) than the recommended minimum of 18 sightings (Rose 1982). Inaccurate home range estimates in either time period may have obscured changes in home range area following experimental manipulations. Finally, although the substrate was homogeneous in all plots (100% rocks), a larger number of copper models per plot may have improved the accuracy of the distribution of T_es measured and thus the accuracy of the d_e measurements.

In conclusion, I found mixed support for the hypotheses that habitat selection is driven by food and thermoregulatory requirements in *S. jarrovii*. Both natural food availability and thermal quality of refuges were important to habitat selection, but the thermal quality at the surface did not predict lizard density or home range area. The conflicting results may have occurred because *S. jarrovii* may respond to different resources at different scales, or because there may be trade-offs with other variables such as predation risk. Interestingly, *S. jarrovii* appear to select habitat based on the properties of retreat sites rather than of the surface. Future studies should replicate the manipulative experiment using semi-natural enclosures, which would allow greater control over the distribution and availability of food and microclimates, and easier access to the lizards so that their density and home range area could more easily be measured. In such an experiment, half of the lizards in each shade treatment could be fed individually to determine whether home range area shifts with changing energetic state, and whether the magnitude of the response depends on the habitat's thermal quality.

Another intriguing line of research would be to determine the relative importance of the thermal properties of the surface and retreat sites in terms of habitat selection in terrestrial vertebrate ectotherms.

Tables and Figures

Table 2-1. Comparison of models for natural arthropod abundance and volume present in study plots, in relation to the food-supplementation treatment (Food) and time period (Period). All models contain the study plot as a random effect. AIC_c refers to Aikaike's Information Criterion for small sample sizes (Burnham and Anderson 2002). Models within 2 AIC_c of the most parsimonious model (in bold) are equally plausible.

Model Structure	AIC_c	ΔAIC_c
Volume		
Food × Period	42.9	5.6
Food + Period	41.2	3.9
Period	38.4	1.1
1	**37.3**	**0**
Abundance		
Food × Period	135.2	4.4
Food + Period	133.4	2.6
Period	**130.8**	**0**

Table 2-2. Comparison of models for the thermal quality index (d_e) derived from operative temperatures (T_e) measured under rocks, in relation to the temperature treatment (Temp) and the time period (Period). All models contained the study plot as a random effect and were fit by maximizing the log-likelihood. AIC_c refers to Aikaike's Information Criterion for small sample sizes (Burnham and Anderson 2002). Models within 2 AIC_c of the most parsimonious model are equally plausible.

Model Structure	AIC_c	ΔAIC_c
Temp × Period	690.9	3.1
Temp + Period	688.9	1.1
Period	**687.8**	**0**

Table 2-3. Comparison of models for density and home range area (HR) of *Sceloporus jarrovii*, in relation to the $\log_{10}$-transformed natural volume of arthropods available (logVol), thermal quality at the surface (d_e surface), and thermal quality in retreat sites under rocks (d_e retreat). Thermal quality and d_e are inversely related. All models contain the study plot as a random effect and were fit by maximizing log-likelihood. AIC_c refers to Aikaike's Information Criterion for small sample sizes (Burnham and Anderson 2002).

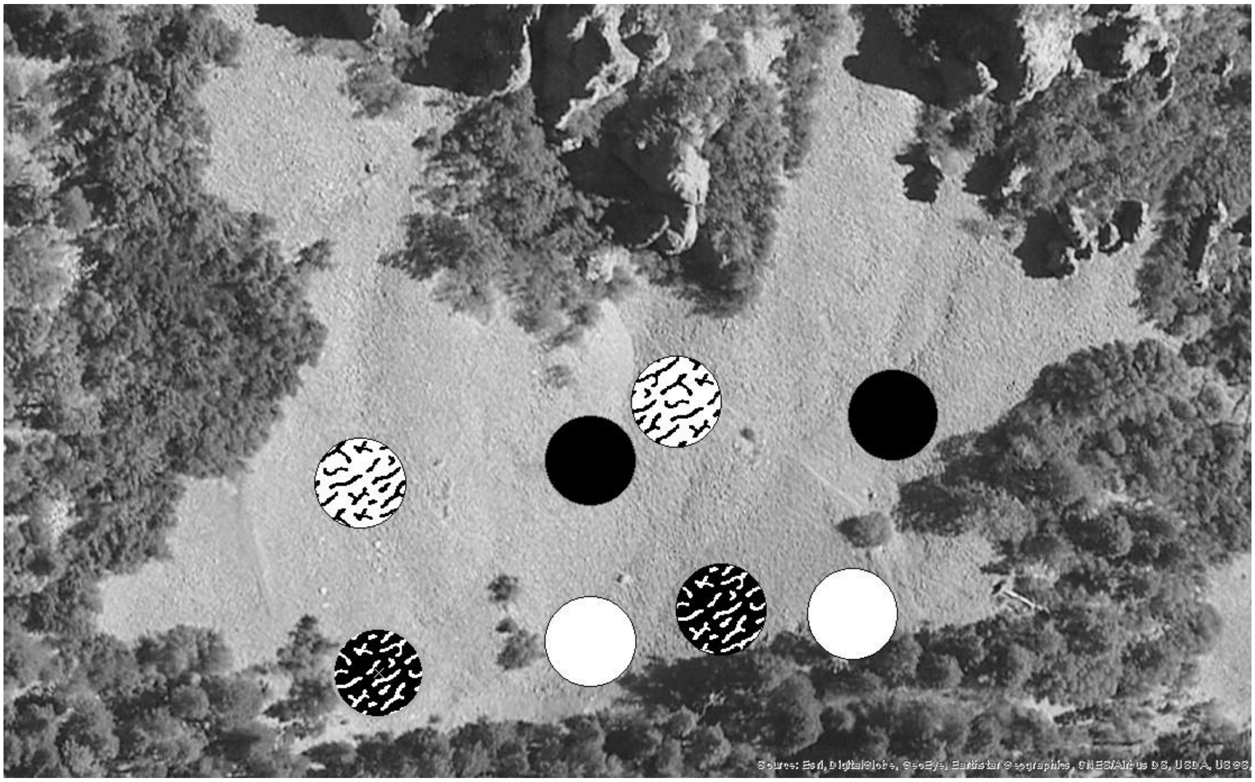
Model Structure	AIC_c	ΔAIC_c
Density (all plots)		
logVol + d_e surface + d_e retreat	94.6	8.7
logVol + d_e retreat	89.3	3.4
logVol	**85.9**	**0**
HR (all plots)		
logVol + d_e surface + d_e retreat	253.2	8.9
logVol + d_e retreat	247.5	3.2
logVol	**244.3**	**0**
Density (excluding plot 2)		
logVol + d_e surface + d_e retreat	82.3	6.5
logVol + d_e retreat	**75.8**	**0**
HR (excluding plot 2)		
logVol + d_e surface + d_e retreat	216.1	7.0
logVol + d_e retreat	**209.1**	**0**

Table 2-4. Comparison of models for density and home range area of *Sceloporus jarrovii*, in relation to the food-supplementation treatment (Food), temperature treatment (Temp), time period (Period), and lizard's snout-vent length (SVL). All density models contain the study plot as a random effect, whereas all home range models contain lizard ID nested within study plot. AIC_c refers to Aikaike's Information Criterion for small sample sizes (Burnham and Anderson 2002). Models within 2 AIC_c of the model with the lowest AIC_c (in bold) are equally plausible.

Model Structure	AIC_c	ΔAIC_c
Density		
Food × Temp × Period	113.3	23.9
Food + Temp + Period + Food:Temp + Food:Period + Temp:Period	103.6	14.2
Food + Temp + Period + Food:Temp + Food:Period	95.1	5.7
Food + Temp + Period + Food:Temp	**89.4**	**0**
Home Range		
Food × Temp × Period + Sex + SVL	252.4	16.7
Food + Temp + Period + Food:Temp + Food:Period + Temp:Period	239.3	3.6
Food + Temp + Period + Food:Period	238.6	2.9
Food + Temp + Period + Food:Temp + Food:Period	238.5	2.8
Food × Temp × Period + Sex	238.1	2.4
Food + Period	237.7	2.0
Food + Period + Food:Period	237.3	1.6
Period	236.5	0.8
1	236.0	0.3
Food × Temp × Period	**235.7**	**0**

Table 2-5. Statistical results for the equally plausible linear mixed models for the influence of the food supplementation treatment (Food), temperature treatment (Temp), and time period (Period) on home range area of *Sceloporus jarrovii* lizards. All models contain lizard ID nested within study plot as random effects. SE is the standard error and DF is the degrees of freedom.

Variable	**Value**	**SE**	**DF**	**t-value**	**P-value**
Model a (R^2=0.31)					
Temp (Shaded)	0.45	1.11	4	0.40	0.71
Food (Yes)	-0.02	1.14	4	-0.02	0.98
Period (After)	0.56	0.86	9	0.65	0.53
Temp:Food	-0.27	1.58	4	-0.17	0.87
Temp:Period	-2.66	2.03	9	-1.31	0.22
Food:Period	-2.73	1.40	9	-1.95	0.08
Temp:Food:Period	4.30	2.43	9	1.77	0.11
Model b (R^2=0.12)					
Food (Yes)	-0.15	0.72	6	-0.21	0.84
Period (After)	0.07	0.77	11	0.09	0.93
Food:Period	-1.08	0.99	11	-1.09	0.30
Model c (R^2=0.35)					
Period (After)	-0.59	0.46	12	-1.30	0.22



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS,

Figure 2-1. The experimental set-up for the manipulative experiment determining the effect of food availability and thermal quality on the home range area and density of *Sceloporus jarrovii* lizards (aerial view). Plots are represented by circles with a black (shaded treatment) or white (unshaded treatment) background. Food-supplemented plots are indicated by wiggly lines.

Figure 2-2. The experimental set-up for the manipulative experiment determining the effect of food availability and thermal quality on the home range size and density of *Sceloporus jarrovii* lizards (view from the ground).

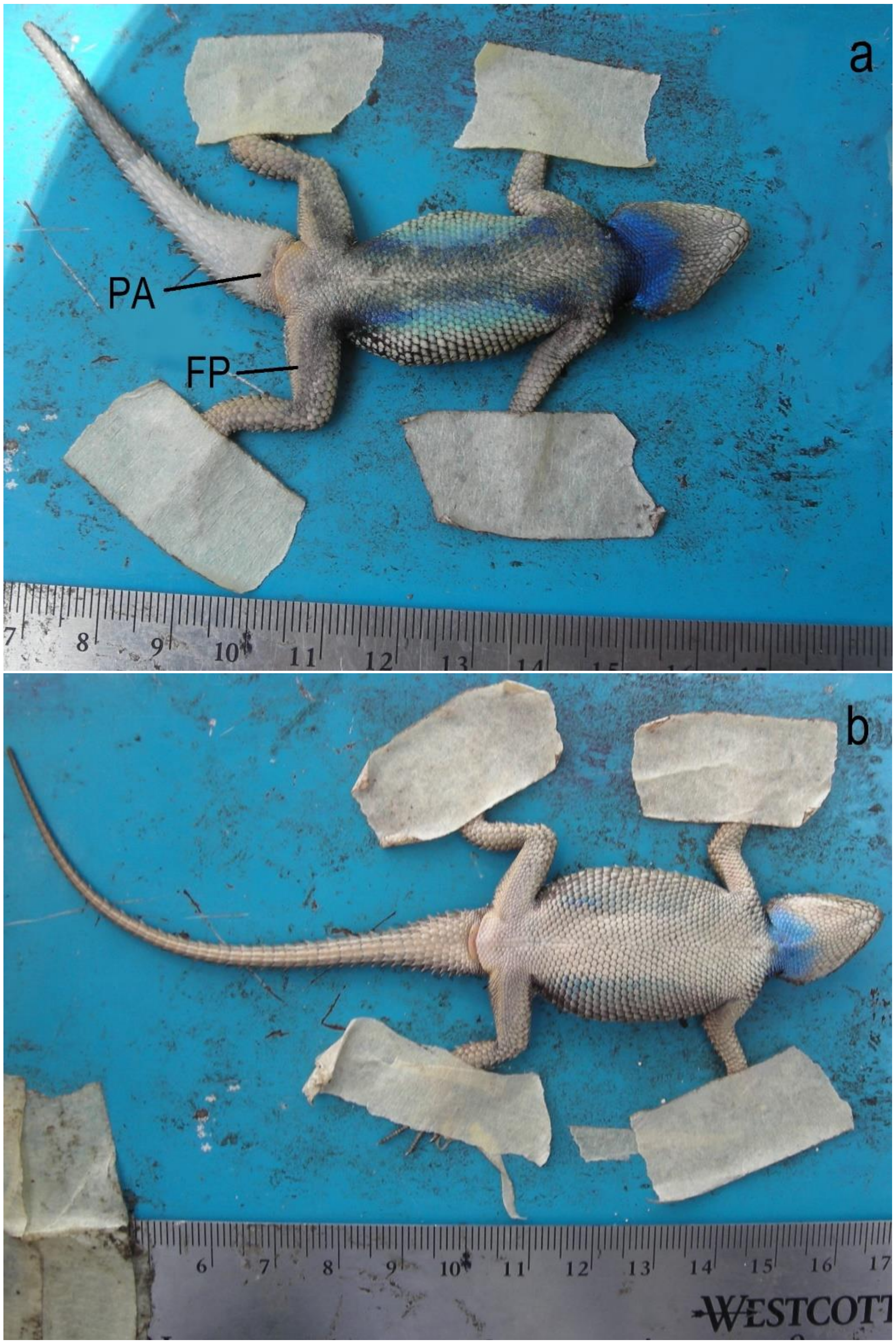


Figure 2-3. A visual comparison of the ventral side of adult (a) male and (b) female *Sceloporus jarrovii* lizards from Coronado National Forest in Arizona, U.S.A. Males are identified by their more extensive blue colouration, enlarged post-anal scales (PA), and enlarged femoral pores (FP).

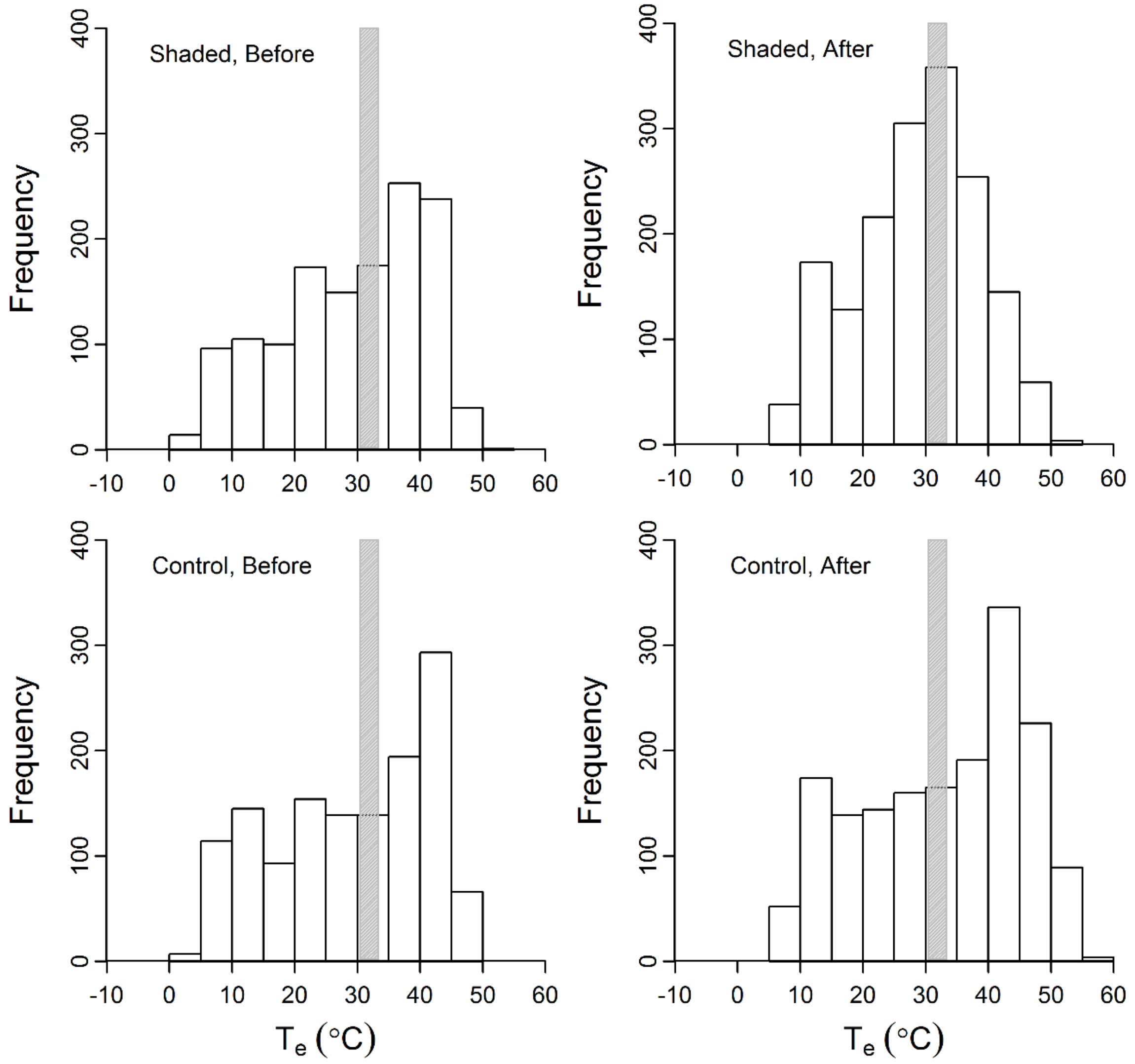


Figure 2-4. Distribution of available daytime (5:30-19:30) operative temperatures (T_e) of copper models placed on rock surfaces in control and shaded plots, before and after the addition of shade cloth. Measurements were taken every 20 minutes over 8 days (before) and 10 days (after) in each of four plots per treatment. The grey rectangle represents the range of preferred body temperatures (T_{set}) of Yarrow's Spiny Lizards (*Sceloporus jarrovii*).

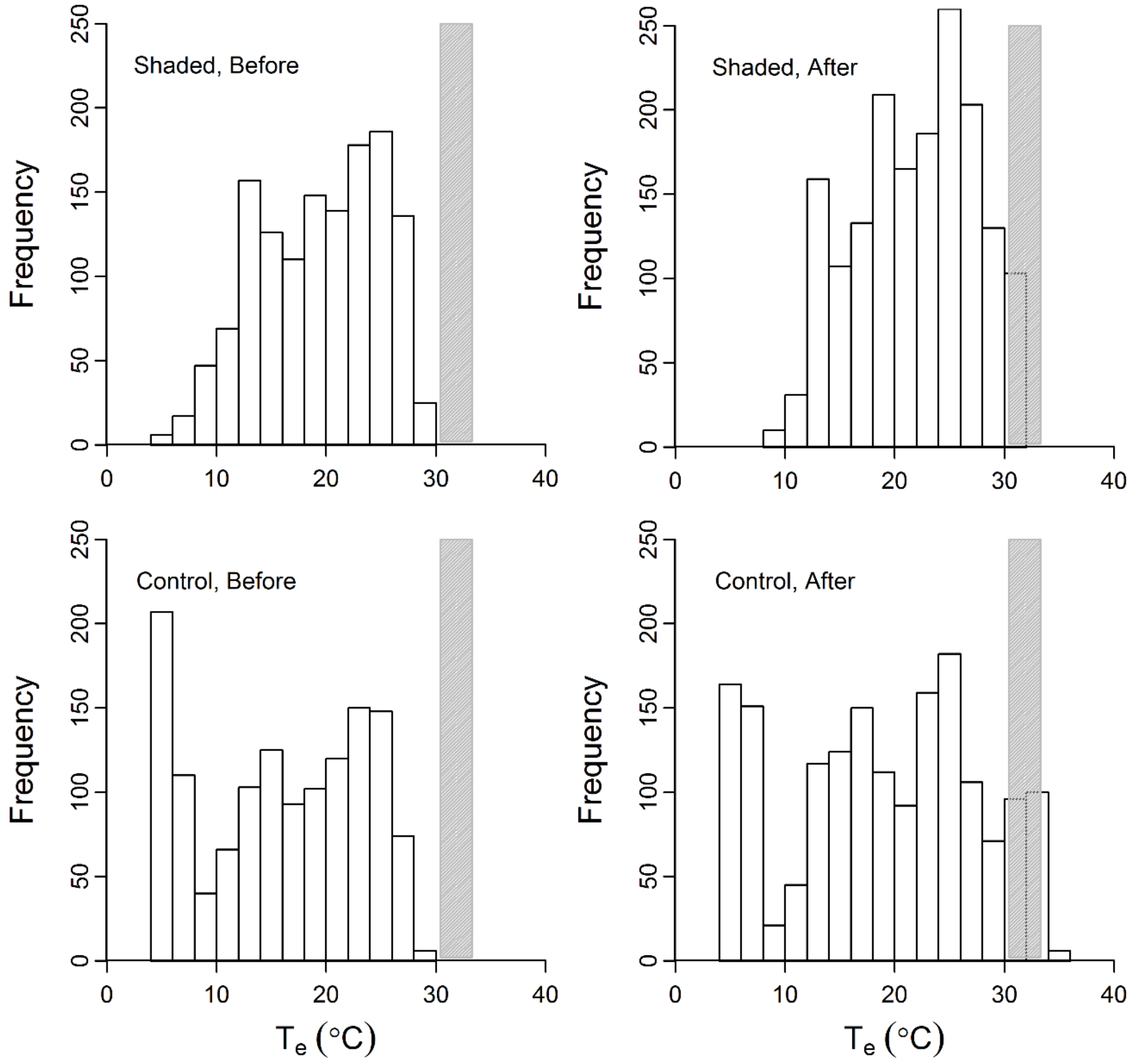


Figure 2-5. Distribution of available daytime (5:30-19:30) operative temperatures (T_e) of copper models placed in retreat sites under rocks in control and shaded plots, before and after the addition of shade cloth. Measurements were taken every 20 minutes over 8 (before) and 10 (after) days in each of four plots per treatment. The grey rectangle represents the range of preferred body temperatures (T_{set}) of Yarrow's Spiny Lizards (*Sceloporus jarrovii*).

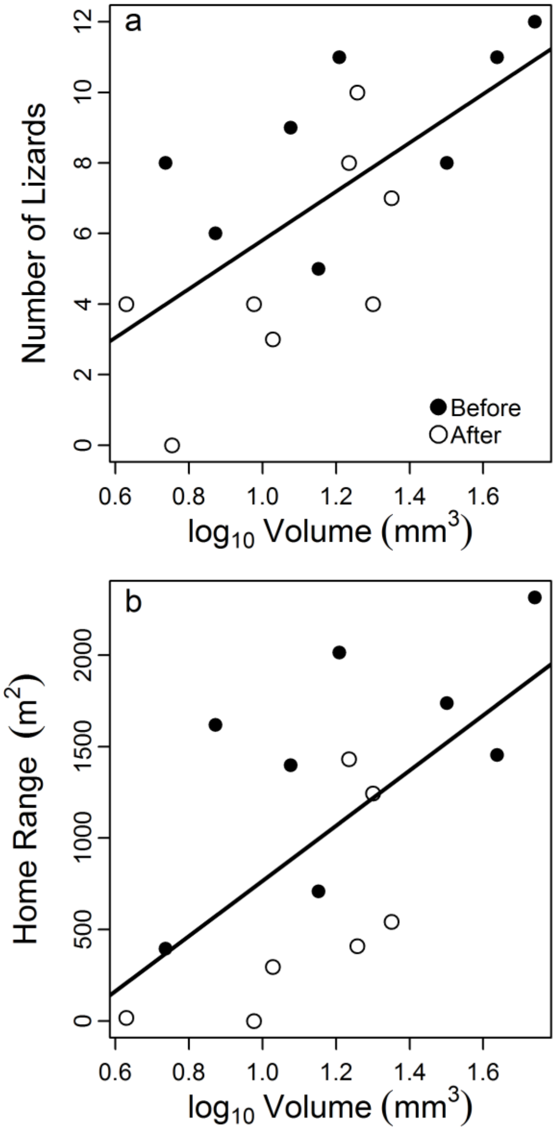


Figure 2-6. The density (a) and average home range size (m^2) (b) of Yarrow's Spiny Lizards (*Sceloporus jarrovii*) in eight study plots in relation to the log$_{10}$-transformed volume of arthropods caught per plot, before and after experimental manipulations.

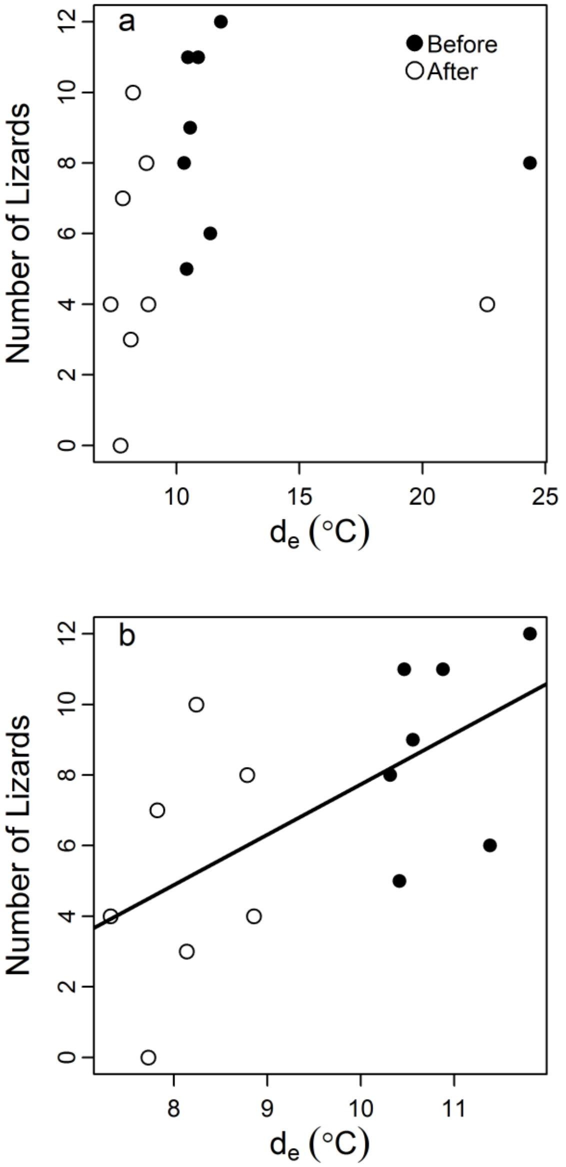


Figure 2-7. Density of Yarrow's Spiny Lizards (*Sceloporus jarrovii*) in eight study plots before and after experimental manipulations, in relation to an index of the thermal quality under rocks (d_e), with (a) and without (b) plot 2.

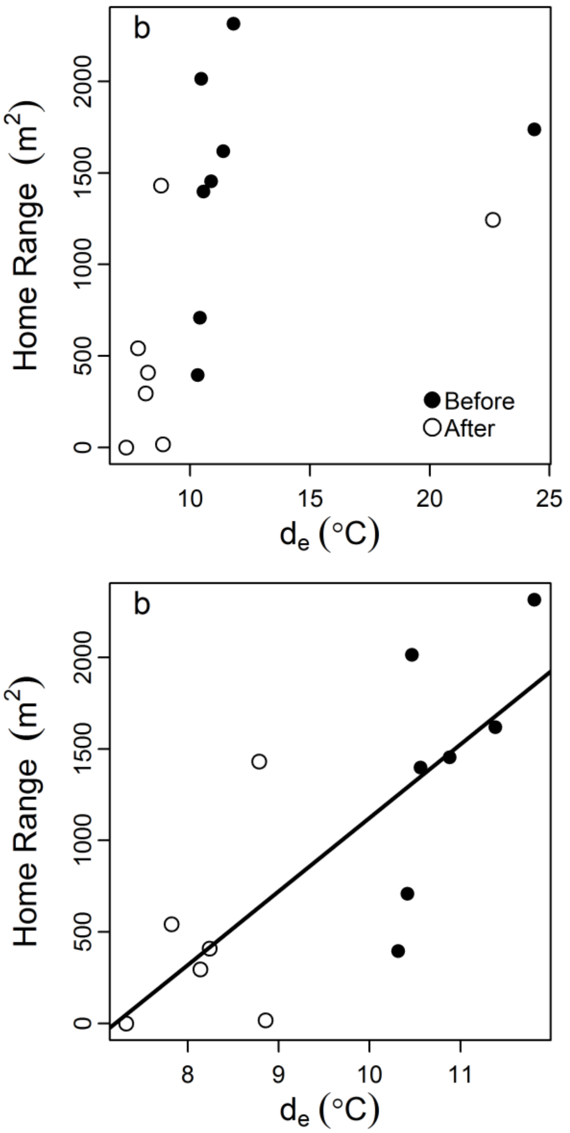


Figure 2-8. Average home range size (m^2) of Yarrow's Spiny Lizards (*Sceloporus jarrovii*) in eight study plots before and after experimental manipulations, in relation to an index of the thermal quality in retreat sites under rocks (d$_e$), with (a) and without (b) plot 2.

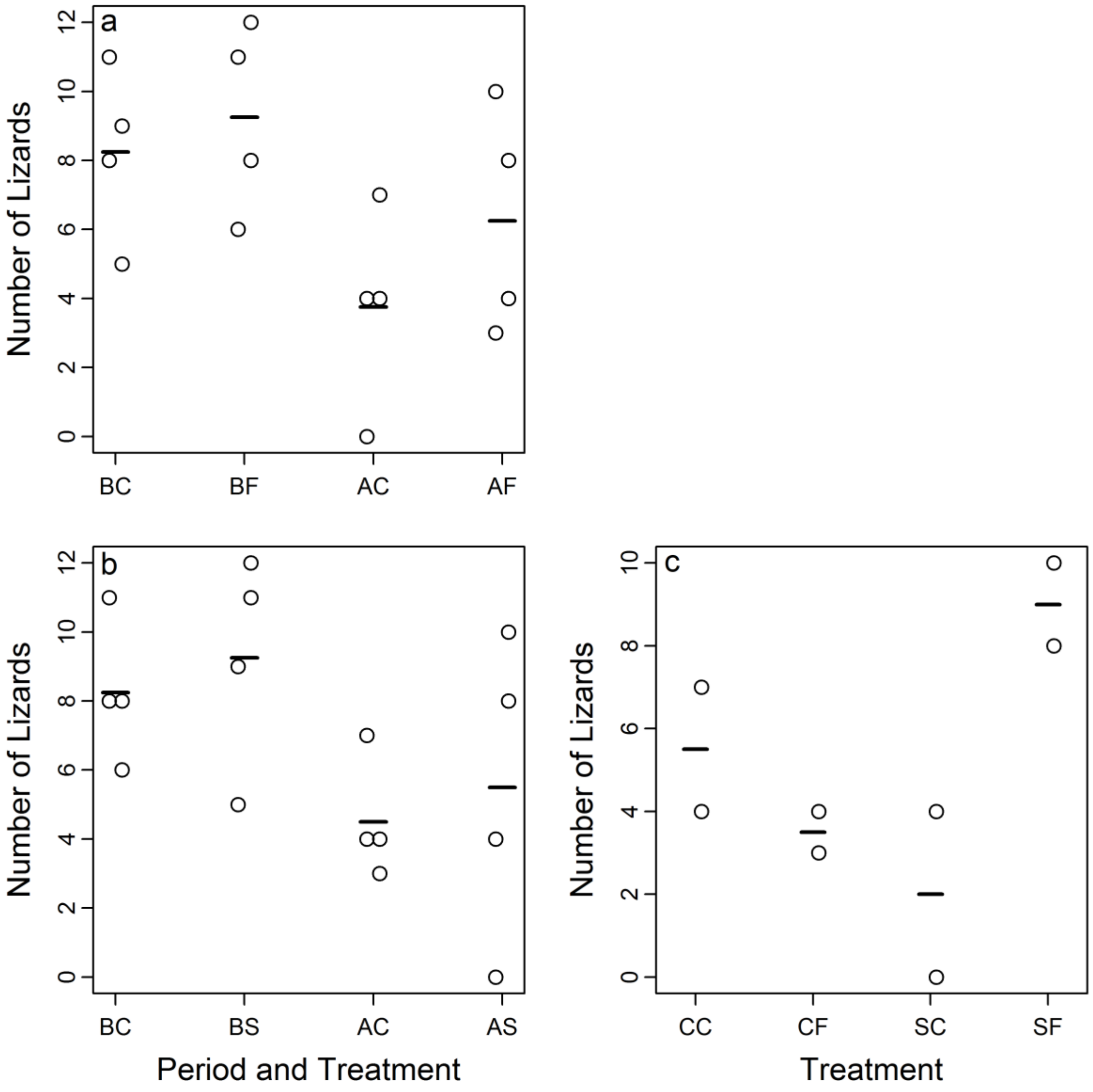


Figure 2-9. Density of Yarrow's Spiny Lizards (*Sceloporus jarrovii*) in study plots by time period (B, before experimental manipulations; A, after experimental manipulations) and experimental treatment (C, control; F, food-supplemented; and S, shaded). Values from all eight plots are shown for both the food-supplementation treatment comparison (a) and the temperature treatment comparison (b). Only the values from the period after manipulations are shown in

panel (c). Horizontal lines represent mean values in each time period by treatment. Points are slightly offset for visibility.

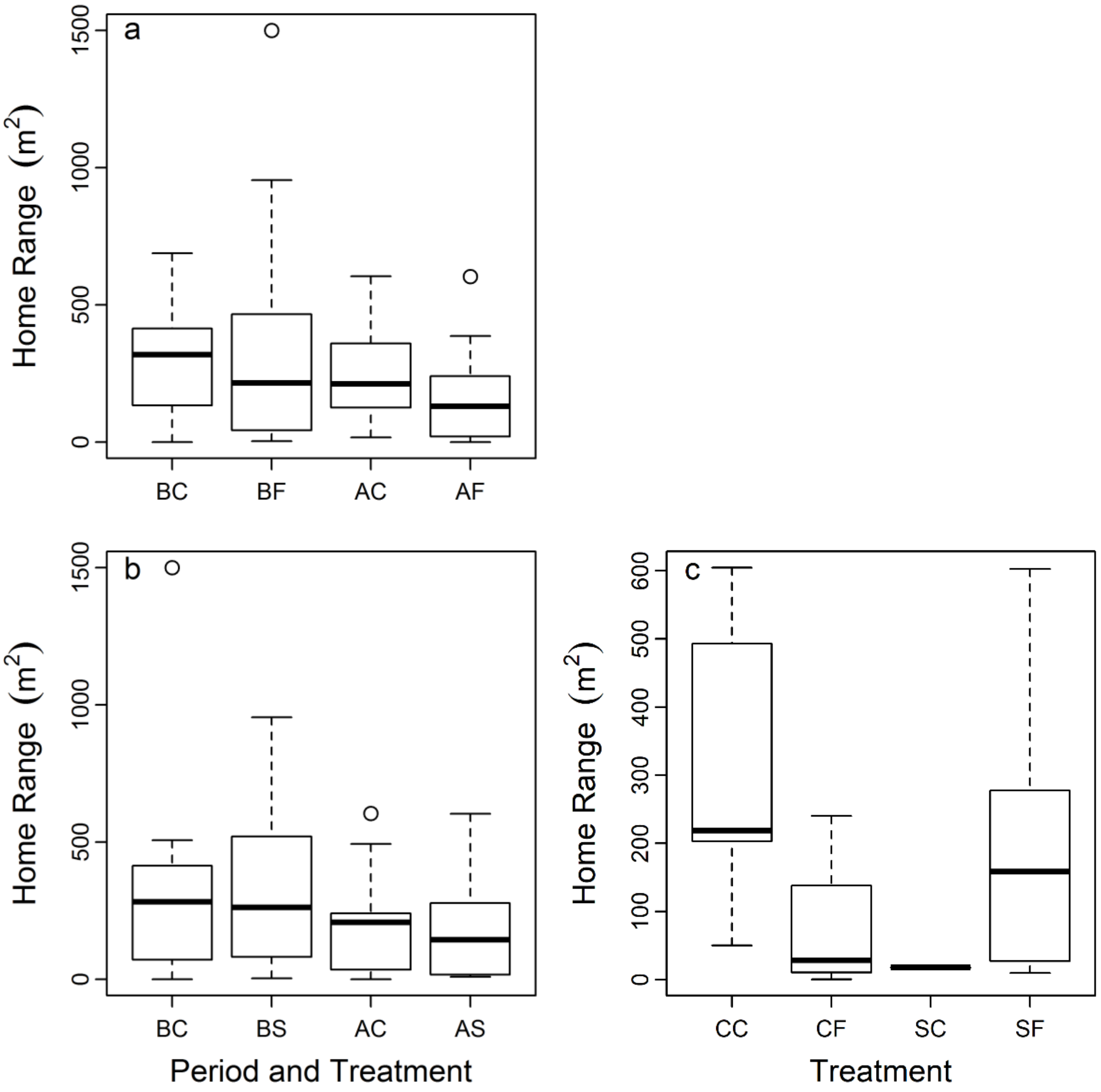


Figure 2-10. Area (m^2) of 57 home ranges of 44 Yarrow's Spiny Lizards (*Sceloporus jarrovii*) overlapping with eight study plots, shown by time period (B, before experimental manipulations; A, after experimental manipulations) and treatment (C, control; F, food-supplemented; and S, shaded). The same data are shown for both the (a) food-supplementation and (b) temperature treatment comparisons. The (c) panel shows only the data from the period after manipulations.

Chapter 3

Elevation and food availability affect abundance, body condition, and individual growth rate in *Sceloporus jarrovii* lizards

Abstract

Although there is some debate over the factors that determine the abundance of a species within its range, one possibility is that environmental variables that affect the mean individual fitness in a population drive population abundance. The two most likely drivers of mean individual fitness in ectotherms are the food availability and thermal quality of the habitat, due to their role in limiting energy gain. Traditional habitat selection models predict that habitats containing more resources can support a larger number of animals. However, many aspects of physiology, behaviour and performance are affected by body temperature, and the extent to which ectotherms maintain optimal body temperatures depends on how closely environmental temperatures match their optimal body temperature. I tested two hypotheses: that the mean individual energy gain in a population and the population abundance in ectotherms is driven by (1) the availability of food or (2) the thermal quality of the habitat. I tested these hypotheses by assessing the mean body condition, mean individual growth rate, and population abundance of *Sceloporus jarrovii* lizards at 32 sites along an altitudinal gradient in southeastern Arizona and relating them to the arthropod (food) availability and elevation of the site. Elevation is inversely related to habitat thermal quality in this species. Body condition, individual growth rate and population abundance should increase with the habitat quality (food availability or thermal quality). Body condition increased and growth rate decreased with elevation. Population abundance increased with food availability. Therefore, both food availability and thermal quality of the habitat influence the mean individual energy gain and abundance of ectotherm populations.

Introduction

The abundance of organisms varies over both space and time (Brown et al. 1995, Ysebaert and Herman 2002), and determining the factors that govern this variation is central to ecology (Krebs 2001). What factors drive population abundance within a species' range? According to the abundant centre hypothesis, a species is most abundant near the centre of its range and declines toward the edges (reviewed in Sagarin and Gaines 2002). Several mechanisms have been proposed for this hypothesis. For example, animals may randomly disperse from a high-abundance centre like molecules of gas (Grinnell 1922). Abundance may instead be determined by environmental gradients, with abundance being highest in a central area of optimal environmental conditions, and declining with distance from the centre as conditions become increasingly unfavourable (e.g., Andrewartha and Birch 1954). Similarly, Brown (1984) argued that abundance was determined by the extent to which the area met the needs of the species along several niche axes, and so abundance distributions should be influenced both by environmental (e.g., temperature, precipitation) and ecological (e.g., presence of predators) conditions. Assuming that the niche axes are spatially autocorrelated, the capacity of the habitat to meet the multidimensional niche needs of the species should decline with distance from the areas with optimal conditions. Population genetics may also contribute to the abundant center, if overwhelming gene flow from the high-density range centre under optimal conditions prevents local adaptation to more marginal conditions in peripheral populations (Case and Taper 2000). While the abundant centre hypothesis is often not supported (Eckert et al. 2008, Sagarin and Gaines 2002, Sagarin et al. 2006), species abundance may nonetheless be strongly influenced by environmental factors, as these may be highly heterogeneous and not strongly spatially autocorrelated (e.g., Helmuth et al. 2002).

Spatial variation in abundance is ultimately a function of the spatial variation in the mean individual fitness in populations (Levins 1962, MacArthur and Levins 1964, MacArthur and Pianka 1966), because the rate of population growth is largely driven by local individual survival and reproduction (e.g., Kooijman and Metz 1984, Ozgul et al. 2010). Therefore, spatial variation in abundance should vary with habitat characteristics that increase the mean individual fitness. According to traditional habitat selection models, habitat patches with more resources (particularly food) are preferentially selected and thus support a higher abundance of individuals (Fretwell and Lucas 1969) than resource-poor habitats. The fitness of ectotherms, however, may be more strongly influenced by a habitat's temperature than its food availability (e.g., Halliday and Blouin-Demers 2014, 2016). Environmental temperatures strongly influence the body temperature (T_b) of ectotherms because these organisms do not produce enough heat from metabolism to maintain their T_b physiologically (Hill et al. 2004). T_b affects physiological, developmental, and behavioural processes (Angilletta 2009) including locomotor performance (Stevenson et al. 1985, Blouin-Demers et al. 2003), digestion (Troyer 1987, Angilletta 2001), and growth rate (Sinervo and Adolph 1989, 1994; Autumn and DeNardo 1995). As a result, many ectotherms thermoregulate behaviourally to maintain their T_b within the range that coincides with the optimal temperatures for performance (e.g., Huey and Kingsolver 1989, Dorcas et al. 1997, Blouin-Demers et al. 2003, Angilletta 2009, Patterson et al. 2017).

Although ectotherms may compensate for unsuitable environmental temperatures through behavioural thermoregulation (e.g., Hertz and Huey 1981), their success depends on the availability of suitable thermal microclimates (Huey 1991). A habitat in which an ectotherm can easily maintain its T_b within its preferred T_b range is a habitat of high thermal quality for that organism (Huey 1991, Hertz et al. 1993). The thermal quality of a habitat determines the amount of time that environmental temperatures are suitable for activity, which in turn limits the rates of prey encounter and food ingestion (Grant and Dunham 1988, Van Damme et al. 1991). The rate of energy assimilation (and thus potential growth) is also a function of the activity window, because the T_bs that maximize energy assimilation approximate T_bs exhibited during activity (Angilletta 2001, Niewiarowski 2001). If the activity window is too short, energy gains may be reduced below the levels needed for reproduction, which raises the probability of local extinction (Sinervo et al. 2010). Studies have shown that locomotor performance (Blouin-Demers and Weatherhead 2008), growth rate (Halliday and Blouin-Demers 2016) and reproductive success (Halliday and Blouin-Demers 2016) are lower in poor thermal quality habitats, and that ectotherms prefer habitats of higher thermal quality (e.g., Row and Blouin-Demers 2006, Picard et al. 2011, Halliday and Blouin-Demers 2016).

Demographic parameters and population abundance of ectotherms may vary across latitudes and altitudes due to the variation in habitat thermal quality along these gradients. Through its effect on T_b, habitat thermal quality may affect the short-term performance of ectotherms (e.g., Huey and Stevenson 1979, Waldschmidt and Tracy 1983, Stevenson et al. 1985, Gilbert and Miles 2016), and constrain allocation to longer-term processes such as individual growth rate (e.g., Kingsolver 1989, Sinervo and Adolph 1989, Grant and Dunham 1990), energy storage (e.g., Herczeg et al. 2006, Reading 2007), and fecundity (e.g., Adolph and Porter 1993, Halliday and Blouin-Demers 2014). If these allocations are summed over the individuals of a population, then population-level rates (i.e., birth, death, immigration and emigration rates) and ultimately population abundance should be a function of habitat thermal quality (Dunham et al. 1989, Huey 1991). Across latitudinal and altitudinal gradients, both environmental temperatures and T_bs can vary drastically (e.g., Grant and Dunham 1990, Hertz 1992, reviewed in Clusella-Trullas and Chown 2014). On average, air temperature drops by 6°C per 1,000 m increase in elevation (Barry 2008). Thus, demographic parameters and population abundance of ectotherms may also vary across these gradients. Indeed, comparisons between reptile populations at different elevations and latitudes have shown differences in body size (Ashton and Feldman 2003, Angilletta et al. 2004), hatching date (Iraeta et al. 2006), growth rate (Olsson and Shine 2002, Sears 2005, Iraeta et al. 2006), age at maturation (Ballinger 1979), survival (Ballinger 1979, Sears 2005), and population abundance (Díaz 1997, Monasterio et al. 2010). However, these studies typically only compared two or three populations, making it difficult to determine whether significant results are due to elevation or to other unmeasured differences between sites (Hurlbert 1984).

The purpose of this study was to test two hypotheses: that the mean individual energy gain in ectotherm populations and their abundance are driven by (1) the availability of food, or (2) the thermal quality of the habitat. As habitat quality (food availability or thermal quality) increases, body condition, individual growth rate, and population abundance should also increase. These variables should increase with food availability because of the greater amount of energy available to fuel tissue development, energy storage and reproductive output. Indeed, food supplementation increases relative body mass (Licht 1974, Rose 1982) and juvenile growth rate (Andrews 1976, Stamps and Tanaka 1981, Madsen and Shine 2000) in lizards and snakes, and is related to an increase in population density across taxa (reviewed in Boutin 1990). However, ectotherms are strongly dependent on temperature for prey capture and digestive performance (Huey 1991, Grant and Dunham 1988, Van Damme et al. 1991, Angilletta 2001), and so body condition, individual growth rate, and population abundance should increase with habitat thermal quality. Temperature is strongly related to elevation (Körner 2007), and so, assuming that cooler temperatures at high elevations result in habitats of relatively low thermal quality for lizards (e.g., Díaz 1997, Gvoždík 2002, Gutiérrez et al. 2010), body condition, individual growth rate, and population abundance should decrease with elevation.

I measured body condition and growth rate because these traits are related to energy gain and may significantly impact fitness. Body condition is a measure of the energetic reserves available to an individual through feeding, including fat and protein (Peig and Green 2009). Animals in better condition may increase their investment in immunity (e.g., via a larger spleen, Møller et al. 1998), or have a higher overwinter survival (e.g., Fullerton et al. 2000) or an increased ability to reproduce (e.g., Weimerskirch 1992, Naulleau and Bonnet 1996). Growth represents a significant energy investment. At birth, for example, most organisms allocate over 50% of their energy budget to growth (West et al. 2001). Growth rate may significantly impact fitness because larger juveniles are more likely to escape from predators (by being faster sprinters, Christian and Tracy 1981, Sinervo and Adolph 1989, Sinervo and Huey 1990) and to survive both during the active season (Fox 1978) and over the winter (Ferguson and Bohlen 1978). Faster-growing individuals also reproduce earlier (Ballinger 1979, Bauwens and Verheyen 1987), and larger females have larger litters (Ballinger 1973, 1979).

To test these predictions, I measured arthropod (food) availability, body condition, individual growth rate, and population abundance of *Sceloporus jarrovii* lizards at 32 rock talus slopes across an elevation gradient in Arizona, U.S.A. Although a number of studies have compared demographic variables or abundance of populations of a species at different elevations or latitudes, most studies have compared two to three populations (e.g., Ballinger 1979, Grant and Dunham 1990, Díaz 1997, Olsson and Shine 2002, Sears 2005, Iraeta et al. 2006, but see Angilletta et al. 2004, Monasterio et al. 2010). Furthermore, Dunham et al. (1989) stressed the importance of studying the interaction of biophysical factors (especially temperature) and resource availability in driving population dynamics. This is the first study to my knowledge to assess the concurrent effects of food availability and elevation on body condition, individual growth rate and population abundance in a terrestrial vertebrate ectotherm, using a sufficiently large number of study sites to achieve reasonable statistical power.

Methods

Species and Study Sites

Yarrow's Spiny Lizards (*Sceloporus jarrovii*) are small lizards (mean ± SD of adult snout-vent length (SVL) = 7.6 ± 0.6 cm) that occur in mountainous regions of northern Mexico, and southern Arizona and New Mexico, U.S.A., over a large elevation range (1,400 - 3,200 m, Burns 1970). This species is strongly associated with rocky habitat (Ruby 1986) and consumes a variety of arthropods (Simon 1975).

From May to August 2016, I visited 32 study sites (Table 3-1, Figure 3-1) within four mountain chains in Coronado National Forest, Arizona: the Chiricahua, Santa Rita, Huachuca, and Pinaleño (Graham) Mountains. The elevation of the sites ranged from 1,650 to 3,200 m. Each site was a talus slope: a large area of loose rocks largely devoid of vegetation (Figure 3-2). The vegetation in the area surrounding the study sites ranged from Madrean evergreen woodland at low elevation, dominated by Arizona sycamore (*Platanus wrightii)*, Arizona madrone (*Arbutus arizonica)*, silverleaf oak (*Quercus hypoleucoides)*, alligator juniper (*Juniperus deppeana*) and Mexican pinyon pine (*Pinus cembroides)*; to petran subalpine conifer forest at high elevation, dominated by Engelmann spruce (*Picea engelmannii)*, douglas fir (*Pseudotsuga menziesii*) and trembling aspen (*Populus tremuloides*) (Brennan and Holycross 2006). The first capture event occurred in May or early June for all sites; however, some sites were revisited in an effort to increase the sample size per site to at least ten lizards. This research was conducted with a State of Arizona Scientific Collection Permit (SP735332) and approval from the University of Ottawa's Animal Care Committee (BL-1788).

Food Availability

To estimate the relative food availability at each study site, I calculated the volume of arthropods caught in nine sticky traps over a 24 hour period (e.g., Simon 1975, Niewiarowski and Roosenburg 1993). Two lines of evidence suggest that the amount of arthropods caught in sticky traps is a good proxy for food availability for *S. jarrovii*: the same types of food items are found on sticky traps and in *S. jarrovii* stomachs (Simon 1975), and sticky trap capture rates correlate positively with the mass of stomach contents in *S. undulatus* (Dunham 1978).

I measured the relative arthropod availability at all sites during the dry season (May-June) because arthropod abundance is correlated with precipitation (Dunham 1978), and rainfall increases substantially during the monsoon season in July and August. Sticky traps consisted of 10 cm × 8 cm rectangles of waterproof paper covered in biodegradable resin (Tree Tanglefoot, Grand Rapids, Michigan, U.S.A.). Within a site, I placed three sticky traps in each of the following microhabitats: (1) the bottom, within the talus slope and less than 10 m of the treeline at the bottom, (2) the edge, in complete shade and under the vegetation within 5 m of the outer edge of the talus slope, and (3) the inside, within the talus slope and more than 10 m from any vegetation. I used random numbers to assign coordinates (number of meters up and across the slope) for each sticky trap. I calculated the volume of each arthropod caught using the formula for the volume of a cylinder: $V = \pi(\frac{width}{2})^2 * length$, and summed the volume of all arthropods caught at each site (e.g., Werner et al. 1995).

Thermal Quality

I used elevation as a proxy for thermal quality because there was a strong positive correlation between the d_e index (Hertz et al. 1993) and elevation in a subsample of 10 study sites from the Chiricahua Mountains (Pearson's r = 0.90, Figure 3-3a). I calculated the average d_e (the absolute difference between the operative environmental temperatures and nearest limit of the preferred body temperature range (T_{set})) for summers 2015-2016 as an index of thermal quality. To calculate d_e, I measured the T_{set} of 40 adult lizards in a thermal gradient (see chapter 2), and the operative environmental temperatures of each site using copper models (see chapter 4). The positive correlation between the d_e index and elevation indicates that thermal quality is poorer at high elevation sites.

To determine the elevation of each site, I traced the outline of the talus slope using the polygon tool in ArcGIS (version 10.4.1, Environmental Systems Research Institute, Redlands, CA) and calculated the coordinates of the centroid of the polygon. I determined the elevation of each centroid in Google Earth (version 7.1.8, Google Inc.). I visited sites of different elevations throughout the study period to avoid the confounding effects of elevation and seasonality, but elevation and Julian date of the initial visit were still moderately positively correlated (Pearson's $r = 0.35$).

Field Measurements of Lizards

I captured lizards by noose and placed them individually into cloth bags until processing. Lizards were sexed using the presence of secondary sexual characteristics (enlarged post-anal scales and femoral pores, and more extensive blue patches on the throat and belly in males, Figure 2-3, Brennan and Holycross 2006). I also weighed the lizards (± 0.01 g) with a digital scale, measured SVL (± 0.001 cm) with digital callipers, and assessed them for tail autotomy (a missing or regenerated tail). I released all lizards within five hours of capture. Population abundance was estimated as the number of lizards captured per person-hour of search effort during the first visit to the site.

Body Condition

I assessed the body condition of each lizard using the scaled mass index (Peig and Green 2009), which uses a scaling relationship to calculate the predicted mass of each individual at a fixed body size (L_o). The scaled mass index accounts for the scaling between body length and mass measurements better than the raw residuals of a log-log regression (Peig and Green 2009). I used the scaled mass index because the residuals from the log-log regression for several hatchlings were disproportionately large or small relative to other size classes, and the scaled mass index corrected this problem. The scaled mass index equation is $\widehat{M}_i = M_i \times (\frac{L_o}{L_i})^b$, where M_i and L_i are the mass and SVL of the individual, L_o is the mean SVL of the population (5.87 cm), b is the slope of the log-log regression of mass and SVL (3.17), and $\widehat{M}_i$ is the predicted body mass for individual i when SVL is standardized to L_o. I used the slope of the ordinary least squares regression as b because the correlation coefficient between log(mass) and log(SVL) was very high ($r = 0.99$). I excluded lizards with tail autotomy from the body condition analysis because they are necessarily lighter for their SVL than other lizards.

Growth Rate

To calculate the mean individual growth rate of each population, I toe-clipped a subsample of lizards, aged them using skeletochronology, calculated a growth curve for each population, and obtained the growth coefficient of each curve. Although the best method to estimate age is to follow animals from birth using mark-recapture methods (Castanet et al. 1993), this was not feasible given the short-term nature of the study. Skeletochronology consists of estimating the age of lizards by counting the number of growth rings in the periosteal of phalange bone (Figure 3-4). Growth rings appear as broad layers interspaced by narrow and dense bands of lamellar bone (LAGs, lines of arrested growth) that indicate periods of decreased growth (Castanet et al. 1993). Growth rings can be used to age an organism if they correspond to an environmental rhythm of known periodicity (e.g., annual changes in climate, Castanet 1985). In *S. jarrovii*, annual LAGs should be deposited in the winter.

I clipped the third digit of the back right foot of up to 11 lizards per site (range: 1-11, mean 8.9) and stored it in 95% ethanol. In the laboratory, the samples were decalcified for 15 hours in CalEx solution, rinsed in distilled water for eight hours, and cross-sectioned at a thickness of 20 µm with a cryostat at -20°C. The slides, mounted with at least 20 diaphyseal cross-sections, were fixed in 99% methanol, stained with Harris' haematoxylin stain, and rinsed in distilled water. I photographed several rehydrated cross-sections per lizard with a compound microscope (Olympus CX21) at a 100 × magnification. Four observers (L.D. Patterson, J. Paterson, L. Eaton, and N. Libreros) counted the number of LAGs in the photographs to estimate the age (in years) of each lizard. I verified the repeatability of LAG counts within lizards using the intraclass correlation coefficient (Fletcher 2010). I averaged the lizards' estimated ages across observers, and rounded each to the nearest whole number (0.5 values were randomly rounded up or down). I converted the lizards' ages to months based on the date of capture and the assumption that lizards were born on June 1st at low elevation and June 15th at high elevation (Ballinger 1979, Cox 2006). Given that *S. jarrovii* have minimal growth during the inactive period (mid-November to early April at low elevation and mid-October to late April at high elevation (Ballinger 1979)), I estimated the lizards' age as the number of months where growth was possible. I subtracted 6 months per year for lizards at high elevation (> 2,450 m) sites and 4 months per year for lizards at low elevation (< 2,450 m) sites (Cox 2006). I estimated age as the number of growth months because the von Bertalanffy model (see below) assumes that growth is constant over time (Dunham 1978). I divided the sites according to elevation because of the large differences in birth date and number of months with temperatures suitable for growth (Ballinger 1979). I used 2,450 m as the division between “high” and “low” elevation sites because of the distinct vegetation shift observed around this elevation: all talus slopes above 2,450 m were found in petran montane conifer forest or petran subalpine conifer forest. Given that “binning” a continuous variable like elevation into “high” and “low” categories is arbitrary, I tested the robustness of my results by also analysing data where lizards from all populations were aged similarly (see statistical analyses).

I calculated growth curves using the von Bertalanffy (1938) equation, which typically best fits the relation between body size and age in lizards (e.g., James 1991, Sears 2005, Roitberg and Smirina 2006). The von Bertalanffy growth equation is: $L_t = L_\infty(1 - e^{-k(t-t_0)})$, where L_t is length at age t , L_∞ is the asymptotic maximum length, e is the base of the natural logarithm, k is a growth coefficient indicating how quickly the curve reaches its asymptote, and t_0 is the age at hatching (i.e., $t_0 = 0$), which is the starting point of the growth interval under the present study. I used SVL as opposed to mass to calculate growth rate because mass is subject to variation due to nutritional or reproductive state (Dunham 1978, Olsson et al. 2000). To obtain estimates for the k and L_∞ parameters, I first fitted an overall growth curve as a non-linear mixed model in R (nlme package, Pinheiro et al. 2015), with the study site as a random effect, for all known-age lizards (N = 503). Known-age lizards included toe-sampled individuals; hatchlings, who are visibly smaller than adults; lizards with an SVL < 5 cm in May, who were considered to be one year old; and lizards who were caught as hatchlings in previous years in a mark-recapture study (see chapter 4). The histogram of all the SVL measurements I took in July from 2014-2016 (N = 1,087, Figure 3-5) suggests that (1) there is virtually no overlap in SVL between hatchling and adult lizards, and (2) the minimum SVL for adults in July is 5 cm, so any lizard with an SVL < 5 cm the following May must have been born the previous year. Ruby and Baird (1994) also used an SVL of 5 cm to distinguish hatchling from adult *S. jarrovii* in August-September. For lizards captured more than once, I randomly selected one SVL and age measurement. To ensure that all age classes were represented in the growth models (Dunham 1978), I also added one data point per site for a (fictional) newborn lizard with an SVL of 2.8 cm (Cox 2006), because size at birth is consistent across elevations (Ballinger 1979). To obtain a growth rate estimate (k) for each population in which there were at least eight aged individuals (N = 29), I ran separate non-linear models (R Core Team 2015), using the k and L_∞ values obtained from the non-linear mixed model as starting parameters. To determine whether L_∞ changed with elevation, I ran a linear model with L_∞ as the dependent variable and site elevation as the independent variable. Given that k partially depends on L_∞, and lizards attained a larger maximum body size at high elevation (Figure 3-6), I ran a second series of analyses to estimate the k value for each site, identical to the first except that I fixed L_∞at the overall average asymptotic maximum SVL.

Confounding Variables

I quantified three variables that may affect the body condition, growth rate, or (apparent) abundance of lizards: ectoparasite load, predation rate, and air temperature on the day of capture. Parasites divert resources from the host (Candolin and Voigt 2001) and may therefore reduce the host's body condition (Khokhlova et al. 2002), reproductive success (Schall 1983, Fitze et al. 2004), and population density (Lafferty 1993). In lizards, chigger infection causes inflammation and lesions (Goldberg and Holshuh 1992). *Sceloporus jarrovii* are predominantly infected by two mite species: *Eutrobicula lipovskyana* and *Geckobiella texana* (Goldberg and Holshuh 1992). The prevalence of infection of *S. jarrovii* lizards by chiggers (*E. lipovskyana)* is close to 100%, but the intensity of infection is highly variable (e.g., Goldberg and Bursey 1993, Bulté et al. 2009, Halliday et al. 2014). To quantify ectoparasite load, I counted the number of chiggers infecting each lizard using a hand lens. I used the raw values for the body condition analysis, but I averaged the number of chiggers over the total number of lizards captured at that site for the abundance and growth rate analyses, where there was one data point per study site.

Predation may decrease the apparent population abundance by reducing the population density (e.g., Buckley and Jetz 2007), or by reducing the amount of time that lizards are active (e.g., Downes and Shine 1998, Thiemann and Wassersug 2000) and therefore the probability of capture. Body condition and growth rate may also decrease with predation risk due to the time and energetic costs associated with increased wariness and fleeing activities (Ydenberg and Dill 1986, Lima and Dill 1990, Diego-Rasilla 2003), or to reduced opportunities to feed and thermoregulate (Downes and Shine 1998, reviewed in Brown and Kotler 2004). I used the proportion of lizards in the population with broken or regenerated tails (percent autotomy) as an indicator of predation rate (Pianka 1970, Ballinger 1979). I considered a lizard to have suffered tail autotomy if it was missing or had regenerated any part of its tail.

Air temperature may strongly influence the activity level of lizards on a given day, and thus the capture rate and apparent population abundance. *Sceloporus jarrovii* remain hidden in rock crevices when the temperature is too low, for example early in the morning and on overcast or rainy days (Burns 1970, Beuchat 1986). The same is true of high temperatures, as lizards avoid rock surfaces at mid-day, or may not emerge at all on hot days (Burns 1970, Beuchat 1986). I measured the air temperature in full shade during the hottest part of the day (11:00 to 14:00) with a standard alcohol thermometer as an index of the relative air temperature of each capture event.

Statistical Analyses

To determine how food availability and elevation of the study site affected the lizards' body condition, growth rate and population abundance, I used a separate linear mixed model (LMM, nlme package, Pinheiro et al. 2015) for each dependent variable. All models were fitted by maximizing the log-likelihood. In all analyses, I removed non-significant variables sequentially until all remaining variables in the model were significant. I used Akaike's Information Criterion corrected for small sample sizes (AIC_c) to select the most parsimonious model (Burnham and Anderson 2002). I also tested the model assumptions of (1) no multicollinearity among independent variables, and (2) no spatial autocorrelation in the data. All conditional R^2 values for mixed models were calculated using the r.squaredGLMM() function in the MuMIn package (Barton 2018). All statistical analyses were conducted in R (R Core Team 2015).

To determine if there was multicollinearity between the independent variables, I calculated the variance inflation factor (VIF, usdm package, Naimi 2015) score of each variable. I did this separately for lizard body condition (independent variables: elevation, arthropod volume, Julian date of capture, and ectoparasite load), growth rate (independent variables: elevation, arthropod volume, percent autotomy, and log-transformed average ectoparasite load), and abundance (independent variables: elevation, air temperature, arthropod volume, proportion of autotomized lizards, average ectoparasite load, and Julian date). A rule of thumb is that significant multicollinearity is considered to be present when the VIF scores are greater than 4 (O'Brien 2007).

To determine if there was spatial autocorrelation for all three analyses (body condition, growth rate, and population abundance), I visually examined the correlograms and variograms (Pebesma 2004, Gräler et al. 2016, Pebesma and Bivand 2005, Bjørnstad 2016), and compared the fit of three LMM's (with the mountain chain as a random effect, and fit by maximizing the log-likelihood) using AIC_c: (1) modelling spatial autocorrelation with a Gaussian correlation structure, (2) modelling spatial autocorrelation with an exponential correlation structure, and (3) no modelling of spatial autocorrelation. In the LMM's, I used as independent variables those that were significant in the most parsimonious or equally plausible models ($\Delta AIC_c < 2$): elevation, percent autotomy and the log-transformed average chigger load for growth rate; arthropod volume, percent tail autotomy, air temperature, and Julian date for population abundance; and elevation for body condition. Sex was not included in the spatial autocorrelation LMM for body condition because I used the average body condition of each site.

Once the assumptions had been tested, I determined how food availability and elevation of the study site affected the mean body condition, growth rate, and abundance of the population. For the analysis of body condition, I used elevation, arthropod volume, ectoparasite load, Julian date of capture, sex, and the interaction between elevation and arthropod volume as fixed effects; and site nested within mountain chain as random effects.

I then determined how food availability and elevation affected the lizards' individual growth rate. I used the growth coefficient (k) of the site as the dependent variable, the elevation, volume of arthropods, percent autotomy, mean ectoparasite load, and the interaction between elevation and volume of arthropods as fixed effects, and mountain chain as the random effect. Ectoparasite load was log-transformed to linearize the relationship with k. I tested the robustness of the results from the analyses of growth rate by re-running the analyses twice. Firstly, I tested whether the results were similar using the growth rates (k) obtained when the asymptotic maximum SVL (L_∞) was fixed to 6.88 cm for all populations. This analysis was important because populations with larger adults may take longer to attain their maximum body size, and L_∞ for the lizard populations in this study increases by 0.9 cm for every 1000 m increase in elevation (estimate = 0.0009, SE = 0.0002, t = 4.89, $P < 0.0001$, Figure 3-6). Secondly, I ran the analyses using k values obtained when lizards from all populations were aged using June 7th as a median birthdate and seven months of growth per year. This analysis was important because "binning" a continuous variable like elevation into "high" and "low" categories is somewhat arbitrary. In this analysis, I also log-transformed the k values and the percent autotomy to improve the homoscedasticity of the residuals. Given the long time period over which growth rate was measured and the fact that arthropod abundance varies over time, I used the arthropod availability data from the ten mark-recapture sites (see chapter 4) to test the assumption that the rank order in food availability among sites remained consistent over time. I calculated Pearson's r for four comparisons of the volume of arthropods: dry season 2015 to wet season 2015, dry season 2016 to wet season 2016, dry season 2015 to dry seaon 2016, and wet season 2015 to wet season 2016. The volume of arthropods in each site was weighted by microhabitat availability.

Finally, I determined how food availability and elevation affected population abundance. I used the population abundance as the dependent variable; the site elevation, air temperature on the day of sampling, arthropod volume, mean ectoparasite load, percent autotomy, Julian date, and the interaction between elevation and arthropod volume as fixed effects; and mountain chain as a random effect. To test the robustness of my results, I also ran the population abundance analyses using, as the "ectoparasite load" and "percent autotomy" variables, the residuals of the linear regression between the number of lizards captured and the number of chiggers (or number of lizards with tail autotomy) counted at each site. This procedure reduces the error associated with the same variable (the number of lizards captured) being present on both the x and y axes of a regression.

Results

Multicollinearity and Spatial Autocorrelation

I did not find strong evidence of either multicollinearity or spatial autocorrelation in my analyses. The independent variables were not strongly multicollinear, as the VIF scores were all lower than 4. For population abundance, the VIF scores were: 2.5 (elevation), 2.4 percent autotomy), 1.9 (average chigger load), 1.5 (arthropod volume), 1.4 (air temperature), and 1.4 (Julian date). Elevation, the variable with the highest VIF score, was moderately correlated with the other independent variables ($|r| = 0.42\text{-}0.60$). For body condition, the VIF scores were: 1.1 (Julian date and ectoparasite load), and 1.3 (elevation and volume). Elevation was weakly correlated with Julian date (r = -0.08), and moderately correlated with chigger load (r = 0.30) and arthropod volume (r = 0.42). For growth rate, the VIF scores were 2.1 (population abundance), 2.4 (elevation), 1.5 (arthropod volume), 2.0 (percent autotomy), and 1.7 (log-transformed average ectoparasite load). Elevation was moderately correlated with the other independent variables (r = 0.51-0.61).

Only one result suggested possible spatial autocorrelation: the bubble plot for population abundance showed more positive residuals for the Chiricahua and Pinaleño mountains. However, I found no evidence of spatial autocorrelation in any other correlogram or variogram, or from model comparisons, and I used mixed models with mountain chain as a random effect in the analyses. The models incorporating spatial autocorrelation did not significantly improve the model fit for population abundance (AIC_c = 99.5 (no correlation structure), 103.1 (exponential) and 103.1 (Gaussian)), body condition (AIC_c = 50.5 (no correlation structure), 51.0 (exponential), 50.6 (Gaussian)), or growth rate (AIC_c = 4.1 (no correlation structure), 7.6 (exponential) and 7.6 (Gaussian)).

Body Condition

Body condition increased with elevation and was higher in males (Figure 3-7, Tables 3-2, 3-3). A lizard of average length (SVL = 5.87 cm) was 0.04 g heavier for every 100 m increase in elevation. A male of average length was 0.14 g heavier than a female of the same length. Julian date, chigger load, and air temperature were included in equally plausible models, but did not significantly affect body condition.

Growth Rate

Lizards grew fastest at lower elevations and at sites with lower rates of tail autotomy (Table 3-4, Figure 3-8). The most parsimonious model (Table 3-5) contained only percent autotomy, with the growth coefficient declining by 0.01 for every percent increase in autotomy (model $R^2 = 0.44$, estimate = -0.01, SE = 0.003, DF = 24, t = -4.51, P = 0.0001). However, elevation was significant in an equally plausible model ($R^2 = 0.57$), with the growth coefficient declining by 0.3 for every 1000 m increase in elevation (estimate = -0.0003, SE = 0.0001, DF = 22, t = -2.48, P = 0.02). Ectoparasite load was also included in this model but was not significant (estimate = 0.10, SE = 0.05, DF = 22, t = 1.85, P = 0.08). LAG counts were moderately repeatable (ICC = 0.59). In the overall von Bertalanffy model (Figure 3-9), the growth coefficient was 0.79 (value = 0.79, SE = 0.04, DF = 502, t = 19.25, P < 0.0001) and the asymptotic maximum SVL was 6.9 cm (value = 6.88, SE = 0.07, DF = 502, t = 102.67, P < 0.0001).

The results were qualitatively similar when re-analysed two different ways. In the series of analyses where L_∞ was fixed to obtain k values, the results were similar except that the lizards from populations with higher chigger loads grew faster (model $R^2 = 0.47$, value = 0.12, SE = 0.05, DF = 20, t = 2.20, P = 0.04) and the significance of elevation decreased to marginal (value = -0.0002, SE = 0.0001, DF = 20, t = -1.99, P = 0.06). The results for the analyses where lizards for all populations were assumed to have the same birth date and number of growth months per year were based on 28 sites because the von Bertalanffy model failed to converge for one site. The most parsimonious model included elevation, percent autotomy and the log-transformed chigger load (model $R^2 = 0.65$). Lizards grew fastest at low elevations (value = -0.0003, SE = 0.0001 DF = 21, t = -2.43, P = 0.02), when the rate of tail autotomy was low (value = -0.01, SE =

0.003, DF = 21, t = -3.81, P = 0.001), and when parasitism by chiggers was high (value = 0.12, SE = 0.05, DF = 21, t = 2.22, P = 0.04).

The rank order in the food availability between sites was not consistent because the volume of arthropods among sites was poorly correlated between seasons (r = 0.46 in 2015 and r = -0.02 in 2016) and years (r = 0.58 for the wet season and r = -0.48 for the dry season).

Population Abundance

I analysed the population abundance data twice: once using the mean number of chiggers per lizard and the percent autotomy as independent variables, and once using the residuals from the regressions of the number of autotomized lizards and the number of chiggers versus the number of lizards captured. In both analyses, the number of lizards captured per person-hour increased with the volume of arthropods and the rate of tail autotomy, and declined with air temperature and Julian date of the capture event (Tables 3-6, 3-7).

Using the raw numbers per lizards captured, as the proportion of autotomized lizards increased by 1%, the number of lizards captured per person-hour increased by 0.04 lizards (Figure 3-10b). As air temperature increased by 1°C, the capture rate declined by 0.16 lizards per hour (Figure 3-10a). As the relative volume of arthropods increased by 1 mm^3, the capture rate increased by 0.003 lizards per hour (Figure 3-10d). The effect of arthropod volume was driven by a single site (BF2) because the effect disappeared when this site was removed (Table 3-6). As the capture date advanced by one day, the capture rate declined by 0.04 lizards per hour (Figure 3-10c). The analyses with the residuals of the number of chiggers and number of lizards with tail autotomy with respect to the number of lizards caught yielded qualitatively similar results (Tables 3-6, 3-7).

Discussion

The goal of this study was to test the hypotheses that the mean energy gain and abundance of ectotherm populations are driven by (1) the food availability or (2) the thermal quality of the habitat, using *S. jarrovii* as a study species. If the mean energy gain and population abundance are driven by food availability (e.g., Licht 1974, Stamps and Tanaka 1981, Boutin 1990), I predicted that body condition, individual growth rate, and population abundance would increase with arthropod availability. Alternatively, if energy gain and population abundance are driven by habitat thermal quality, and if thermal quality decreases with elevation (e.g., Díaz 1997, Gvoždík 2002), I predicted that at higher elevations, mean body condition, individual growth rate, and population abundance would decrease. There was partial support for both hypotheses. Body condition and growth rate were unrelated to food availability. More lizards were captured at sites with more food, although the evidence was weak (it only occurred in the statistical model using percentages, and the effect disappeared when one site was removed). Similarly, growth rate decreased with elevation, but body condition increased and the lizard capture rate was unrelated to elevation.

The finding that neither body condition nor growth rate were related to food availability is surprising, given that food limitation affects individual growth, fat storage, and reproductive capacity in other lizard species (Licht 1974, Ballinger 1977, Paterson and Blouin-Demers 2018). One explanation is that the lizards may not have been food-limited in the year of the study. Arthropod abundance depends on precipitation, and precipitation fluctuates greatly between years in southeastern Arizona (Ballinger 1977). The year 2016 was wetter than the 10-year average, and close to the historical average, for all four mountain chains when considering annual precipitation data from the nearest town (Figure 3-11). Therefore, an effect of food availability on body condition and growth rate may only be detectable in a drought year. Another possible reason that I did not detect any effect of food availability on growth rate is that the sampled food availability may not have been representative of its availability over the lifespan of the lizards, given that arthropods were only measured once. The rank order of a subset of ten sites in terms of arthropod availability was not consistent between seasons or years. To address this shortcoming, I measured food availability and growth rate over the same time scale in chapter 4.

Conversely, the finding that population abundance increased with food availability is consistent with traditional habitat selection theory such as the ideal free distribution (Fretwell and Lucas 1969), where more individuals settle in resource-rich habitats. This is also consistent with other studies: population density of the *Norops humilis* anole doubles following food supplementation (Guyer 1988), and lizard population density across species declines as a power law of energy use, suggesting energetic constraints (Buckley and Jetz 2007). However, Buckley and Jetz (2010) found that lizard abundance was unrelated to net primary productivity.

The finding that *S. jarrovii* grew more slowly at high elevation was consistent with the prediction that growth rate would increase in warmer habitats, because the lizards would experience T_bs closer to their T_{set} at which feeding and energy assimilation are maximized (Angilletta 2001). However, low-elevation lizards were also in poorer condition, which suggests a trade-off in energy allocation between growth and energy reserves (e.g., Forsman and Lindell 1990). This may be explained by different reproductive strategies at different elevations. Ballinger (1979) found that female *S. jarrovii* reproduce in their first year at low elevation if they attain a minimum size by the fall breeding season. However, yearling females at high elevation delay reproduction until the following year, presumably because of their later birth date and shorter active season. As yearling females produce 40% of hatchlings at low elevation (Ballinger 1979), and fecundity increases with body size (Ballinger 1979), rapid growth may increase reproductive success for *S. jarrovii* at low elevation, whereas higher body condition may enhance overwinter survival (e.g., Shine et al. 2001) and allow future reproduction at a larger body size at high elevation (Ballinger 1979).

The apparent population abundance was unrelated to elevation, but declined sharply as the maximum air temperature on the capture day increased. The number of animals captured during a single capture event is influenced both by the population abundance and the detectability of individuals (Williams et al. 2002). It is unlikely that the air temperature on a single day, within the temperature range observed, would drastically affect the underlying population abundance. Thus, the decline in captures with increasing air temperature implies that the detectability of *S. jarrovii* decreases on hot days. Burns (1970) and Beuchat (1986) noted that *S. jarrovii* are less active on rock surfaces and increase their use of thermal refuges at high temperatures. Assuming that the number of captures remains a good proxy for population abundance, the lack of relationship between elevation and population abundance could be the result of different reproductive strategies at different elevations being equally successful on average. According to Mangel and Stamps (2001), similar fitness can be achieved at a wide range of growth rates when there are strong trade-offs between growth and mortality. A second possibility is that the cost of thermoregulation at different sites along the elevation gradient is similar (Huey and Slatkin 1976). Under clear skies, solar radiation increases with elevation and, on rocky talus slopes in full sun, may enable lizards to thermoregulate effectively despite the cooler air temperatures at higher elevations (Körner 2007). Furthermore, refuges from excessive heat are easily accessible on talus slopes, as temperature plunges rapidly under the rocks. The *Psammodromus algirus* lizard maintains similar T_bs along a 2,200 m altitudinal gradient by using different thermoregulatory strategies (Zamora-Camacho et al. 2013). If *S. jarrovii* are able to maintain similar T_bs across the elevation gradient at a similar cost, differences in elevation may not translate into differences in population abundance.

The effect of elevation on population abundance and demographic parameters in lizards is mixed in the literature. Growth rate and population abundance have been found to be highest at high (Sears 2005, Iraeta et al. 2006, Ballinger 1979, Díaz 1997), medium (Grant and Dunham 1990) or low (Olsson and Shine 2002) elevation, or to be unrelated to elevation (Buckley and Jetz 2010). Several authors have argued that temperature and food availability at different elevations interact to cause differences in individual growth rate or population abundance in lizards (e.g., Grant and Dunham 1990, Iraeta et al. 2006). Angilletta et al. (2004) warn that environmental temperatures may covary with other factors that potentially affect demographic parameters, such as resource availability (Atkinson et al. 2003) or predation risk (e.g., Lampert 1989). Körner (2007) also warns against drawing general inferences about elevation, because many variables (e.g., moisture) may also vary with elevation. Although I did not find evidence of strong multicollinearity in my analyses, there were moderate correlations between independent variables. These correlations may have influenced model selection and thus which variables were significant in the final models in this study. It is also possible that elevation affected population and demographic parameters indirectly, through its effect on other independent variables in the model (Shipley 2000).

The conclusions of this study are based on the assumption that sites at high elevation are of poorer thermal quality than those at lower elevation. Indeed, the d_e index (Hertz et al. 1993) increases with elevation (Pearson's r = 0.90, Figure 3-3a), and d_e is inversely related to thermal quality. However, the negative correlation (Pearson's r = -0.80, Figure 3-3b) between elevation and the h_r index (Sinervo et al. 2010) suggests instead that high elevation sites are of high thermal quality. Sinervo et al. (2010) showed that *Sceloporus* lizard populations have a higher risk of extinction as the cumulative number of hours per day exceeding the preferred body temperature (h_r) increases. Sinervo et al. (2010) argued that extinction rate increases with the number of hours where lizards retreat to thermal refuges to avoid overheating because foraging time is restricted during this time. Reduced foraging in turn constrains growth, maintenance, and reproductive, and thereby limits population growth rate (Sinervo et al. 2010). Since the number of hours exceeding the upper limit of T_{set} decreases with elevation in this study, it is possible that the directionality of the conclusions about the effects of thermal quality are reversed (i.e., lizards grow faster but are in poorer condition when thermal quality is poor). The difference in directionality between the indices may occur because d_e incorporates operative environmental temperatures both above and below T_{set} and is largely driven by colder temperatures in this system. The h_r index may be more appropriate if *S. jarrovii* are more negatively affected by temperatures above than below T_{set}. Given the asymmetrical shape of the thermal performance curve, body temperatures above T_{set} are more detrimental to performance than temperatures at an equivalent distance below T_{set} (Martin and Huey 2008), and this asymmetry is not taken into account in the d_e index.

Interestingly, there were also significant relationships between predation risk and both the individual growth rate and the population abundance. Growth rate decreased as the proportion of lizards with tail autotomy increased. There appeared to be a threshold effect (Figure 3-8a), with the mean individual growth rate at a site being highly variable when the percent tail autotomy was below 40%, but being consistently low above 40%. Lizards with tail autotomy may grow more slowly because energy must be allocated to tail regeneration (Ballinger and Tinkle 1979). Indeed, tail loss reduces hatchling growth rate in several lizard species (Ballinger and Tinkle 1979, Niewarowski et al. 1997). In contrast, the lizard capture rate increased with the rate of tail autotomy. It is possible that population abundance increases with predation risk if the behaviour of lizards at high-risk sites increases their survival (Niewarowski et al. 1997). Higher survival rates for lizards with broken tails have been reported both for juvenile (Niewarowski et al. 1997) and adult (in one population examined, Althoff and Thompson 1994) *Uta stansburiana* lizards. The relationship between the number of lizards captured and the rate of tail autotomy could also be due to differences in activity level between populations. If certain lizard populations are more active (for example, if they spend more time thermoregulating or foraging), then both the number of lizard captures and predator encounters may increase (e.g., Skelly 1994, Anholt and Werner 1998).

In short, there was partial support for both hypotheses, that energy gain and population abundance are driven by the food availability and thermal quality of the habitat. The results imply that thermal quality drives energy gain, but population abundance is driven by food availability. The lack of relationship between thermal quality and population abundance may occur if the positive effect on growth rate and negative effect on body condition reflect different reproductive strategies (Ballinger 1979) that are equally successful. However, to verify the conclusions obtained in this study, future studies should measure thermal quality indices (e.g., d_e, Hertz et al. 1993) and population abundance directly; and to span several years of varying food availability. In chapter 4, I attempted to remedy these shortcomings by calculating thermal quality indices directly from operative environmental temperatures and population abundance from mark-recapture methods at ten study sites over a period of three years.

Tables and Figures

Table 3-1. The elevation (m) and geographical coordinates in latitude (x) and longitude (y) of the centroids of the study sites in Coronado National Forest, Arizona, U.S.A.

Mountain chain	General location	Site code	Elevation (m)	x	y
Chiricahuas	Barfoot	BF2	2535	-109.279	31.91881
		BF4	2589	-109.275	31.91687
		BF5	2611	-109.278	31.91191
	Price Canyon	PC1	1850	-109.259	31.76232
		PCX	1884	-109.258	31.76157
	Rucker Canyon	RC2	2162	-109.292	31.79971
		RC5	2134	-109.275	31.79632
	Rustler's Campground	RS1	2709	-109.287	31.88896
		RSF	2605	-109.289	31.88994
	Sulphur Canyon	SC1	1723	-109.157	31.83346
		SC4	1647	-109.154	31.83256
	South Fork	SF1	1741	-109.192	31.85138
		SF3	1757	-109.187	31.85768
		SF4	1666	-109.189	31.86175
	Saulsbury Trail	ST1	2509	-109.298	31.87206
Huachucas	Carr Canyon	CC1	1981	-110.299	31.43273
		CC2	2025	-110.301	31.43365
	Miller Canyon	MC2	2017	-110.280	31.42247
		MC3	2070	-110.280	31.42640
	Ramsey Canyon	RA1	1868	-110.303	31.44548

		RA3	1840	-110.307	31.44357
		RA4	1947	-110.316	31.43830
Santa Ritas	Mount Wrightson	MD6	2359	-110.854	31.69101
		MD7	2427	-110.847	31.68811
		MDF	2349	-110.848	31.68664
Pinaleños	Chelsey Flat	CH1	2906	-109.945	32.71653
	Mount Graham	GH1	3194	-109.869	32.70264
		GH2	2978	-109.866	32.70481
	Swift Trail Road	SW2	2663	-109.843	32.63357
		SW3	2751	-109.845	32.65738
		SW4	2789	-109.847	32.66032
		SW6	2779	-109.842	32.63610

Table 3-2. Statistical results for the most parsimonious (a) and equally plausible (b-d) linear mixed models for factors influencing the body condition of *Sceloporus jarrovii* lizards. Elevation refers to the site elevation (m), volume to the volume of arthropods caught in sticky traps, autotomy to the rate of tail breaks in the population, date to the Julian date of capture, SE to standard error, and DF to denominator degrees of freedom.

Variable	**Value**	**SE**	**DF**	**t-value**	**P-value**
Model a (R^2 = 0.32)					
Elevation	0.0004	0.0002	27	2.08	0.047
Sex (male)	0.14	0.05	660	2.68	0.01
Model b (R^2 = 0.33)					
Elevation	0.0004	0.0002	27	2.10	0.045
Date	0.002	0.001	659	1.71	0.09
Sex (male)	0.13	0.05	659	2.57	0.01
Model c (R^2 = 0.32)					
Elevation	0.0004	0.0002	27	1.94	0.06
Chiggers	0.0006	0.0004	658	1.43	0.15
Date	0.0015	0.0010	658	1.55	0.12
Sex (male)	0.13	0.05	658	2.59	0.01
Model d (R^2 = 0.33)					
Elevation	0.0004	0.0002	27	2.05	0.050
Chiggers	0.0006	0.0004	657	1.37	0.17
Volume	-0.0003	0.0003	657	-0.89	0.37

Date	0.001	0.001	657	1.15	0.25
Sex (male)	0.13	0.05	657	2.61	0.01

Table 3-3. Comparison of the linear mixed models with the factors influencing the body condition of *Sceloporus jarrovii* lizards using Akaike's Information Criterion corrected for small sample sizes (AIC_c) and model weight (w_i). Volume refers to the volume of arthropods caught in sticky traps, chiggers to the relative ectoparasite (chigger) load, and date to the Julian date that the lizard was captured. Site nested within mountain chain are the random effects in all models. The most parsimonious model is bolded.

Model structure	**AIC_c**	**ΔAIC_c**	**w_i**
Elevation × Volume + Chiggers + Date + Sex	1434.0	3.30	0.06
Elevation + Volume + Chiggers + Date + Sex	1432.0	1.31	0.16
Elevation + Chiggers + Date + Sex	1430.8	0.05	0.29
Elevation + Date + Sex	1430.7	0	0.30
Elevation + Sex	**1431.6**	**0.86**	**0.19**

Table 3-4. Statistical results for the most parsimonious (a) and equally plausible (b-c) linear models for factors influencing the individual growth rate of *Sceloporus jarrovii* lizards. Elevation refers to the site elevation (m), chiggers refers to the log-transformed average ectoparasite (chigger) load, autotomy to the percentage of lizards with tail autotomy in the population, SE to standard error, and DF to denominator degrees of freedom.

Variable	**Value**	**SE**	**DF**	**t-value**	**P-value**
Model a (R^2 = 0.44)					
Autotomy	-0.01	0.003	24	-4.51	0.0001
Model b (R^2 = 0.51)					
Elevation	-0.0002	0.0001	23	-1.86	0.07
Autotomy	-0.01	0.003	23	-2.58	0.02
Model c (R^2 = 0.57)					
Elevation	-0.0003	0.0001	22	-2.48	0.02
Autotomy	-0.01	0.003	22	-3.11	0.005
Chiggers	0.10	0.05	22	1.85	0.08

Table 3-5. Comparison of the linear models with the factors influencing the individual growth rate (K coefficient in the von Bertalanffy equation) of *Sceloporus jarrovii* lizards using Akaike's Information Criterion corrected for small sample sizes (AIC_c). Volume refers to the volume of arthropods caught in sticky traps, Chiggers to the log-transformed average ectoparasite (chigger) load, Autotomy to the percentage of lizards with tail autotomy in the population, abundance to the number of lizards captured per person-hour, and w_i to the model weights. The most parsimonious model is bolded.

Model structure	**AIC_c**	**ΔAIC_c**	**w_i**
Elevation × Volume + Autotomy + Chiggers	11.4	7.3	0.01
Elevation + Volume + Autotomy + Chiggers	7.6	3.5	0.07
Elevation + Autotomy + Chiggers	4.1	0	0.39
Elevation + Autotomy	4.6	0.5	0.31
Autotomy	**5.2**	**1.2**	**0.22**

Table 3-6. Statistical results for the most parsimonious models for factors influencing the (log-transformed) number of *Sceloporus jarrovii* lizards captured per person-hour. Volume refers to the volume of arthropods, autotomy to the rate of tail loss in the population, temperature to the daily high air temperature on the capture date, Date to the Julian date of the day of capture, SE to standard error, and DF to the denominator degrees of freedom. The reduced model does not include the BF2 site, which appeared to be an outlier.

Variable	**Value**	**SE**	**DF**	**t-value**	**P-value**
Model: residuals[a] ($R^2 = 0.69$)					
Volume	0.004	0.001	24	6.07	0.006
Autotomy	0.909	0.384	24	2.37	0.026
Temperature	-0.126	0.050	24	-2.53	0.018
Date	-0.047	0.013	24	-3.60	0.001
Model: percentages[b] ($R^2 = 0.71$)					
Volume	0.003	0.001	24	2.34	0.028
Autotomy	0.038	0.011	24	3.52	0.002
Temperature	-0.163	0.042	24	-3.87	<0.001
Date	-0.042	0.012	24	-3.53	0.002
Model: percentages[b] **(reduced)** ($R^2 = 0.71$)					
Volume	0.001	0.002	23	0.46	0.65
Autotomy	0.039	0.010	23	3.71	0.001
Temperature	-0.171	0.041	23	-4.18	0.0004
Date	-0.033	0.013	23	-2.60	0.02

[a] the autotomy variable in this model is composed of the residuals of the linear regression of the number of autotomized individuals vs. the number of lizards captured

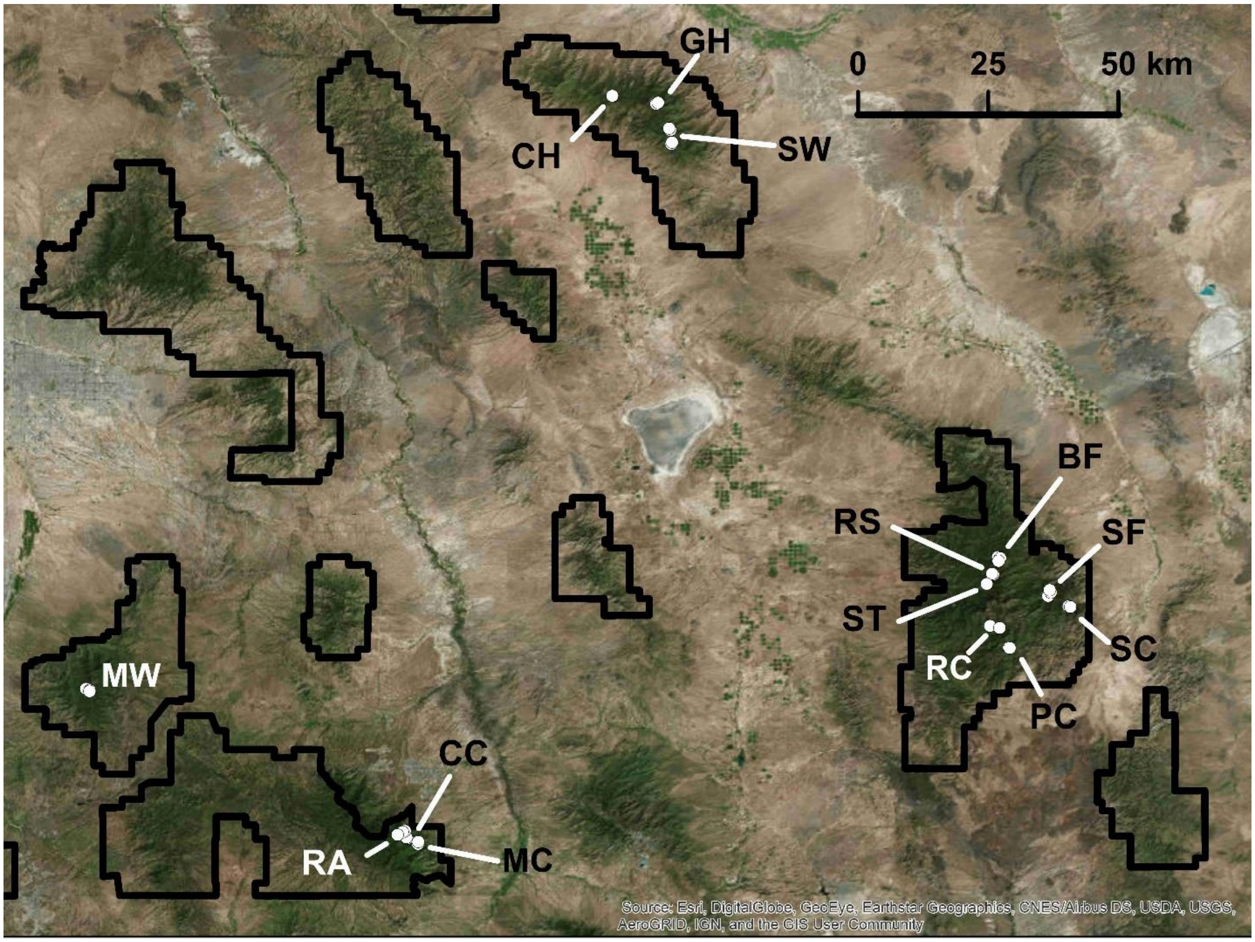
[b] the autotomy variable in this model is composed of the number of autotomized lizards divided by the number of lizards captured

Table 3-7. Comparison of linear mixed models for the factors influencing the number of *Sceloporus jarrovii* lizards captured per person-hour using Akaike's Information Criterion for small sample sizes (AIC_c). Volume refers to the volume of arthropods caught in sticky traps, Chiggers to the relative ectoparasite (chigger) load, Autotomy to the rate of tail loss in the population, Temp to the air temperature during the capture event, and Date to the Julian date of the capture event. Mountain chain is the random effect in all models. The most parsimonious models are bolded.

Model structure	**AIC_c**	**ΔAIC_c**	**w_i**
Model: residuals[a]			
Elevation × Volume + Chiggers + Autotomy + Temp + Date	115.1	11.5	0.00
Elevation + Volume + Chiggers + Autotomy + Temp + Date	111.2	7.5	0.02
Elevation + Volume + Autotomy + Temp + Date	107.2	3.6	0.14
Volume + Autotomy + Temp + Date	**103.7**	**0**	**0.84**
Model: percentages[b]			
Elevation × Volume + Chiggers + Autotomy + Temp + Date	108.3	8.7	0.01
Elevation + Volume + Chiggers + Autotomy +Temp + Date	104.9	5.3	0.05
Volume + Chiggers + Autotomy + Temp + Date	101.1	1.6	0.29
Volume + Autotomy + Temp + Date	**99.5**	**0**	**0.65**

[a] the chigger load and autotomy variables in these models are the residuals of the linear regressions of number of chiggers and number of autotomized individuals vs. the number of lizards captured

[b] the chigger load and autotomy variables in these models are the number of chiggers and the number of autotomized lizards divided by the number of lizards captured



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure 3-1. A map of the study sites (N = 32) within Coronado National Forest, Arizona, U.S.A., in the following locations: Barfoot Park (BF), Carr Canyon (CC), Chelsea Flat (CH), Mount Graham (GH), Miller Canyon (MC), Mount Wrightson (MW), Price Canyon (PC), Ramsey Canyon (RA), Rucker Canyon (RC), Rustler Campground (RS), Sulphur Canyon (SC), South Fork (SF), Saulsbury Trail (ST), and Swift Trail Road (SW).

Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, US

Figure 3-2. A visual representation of a talus slope in Arizona, U.S.A., both (a) from an aerial viewpoint, and (b) a viewpoint on the ground.

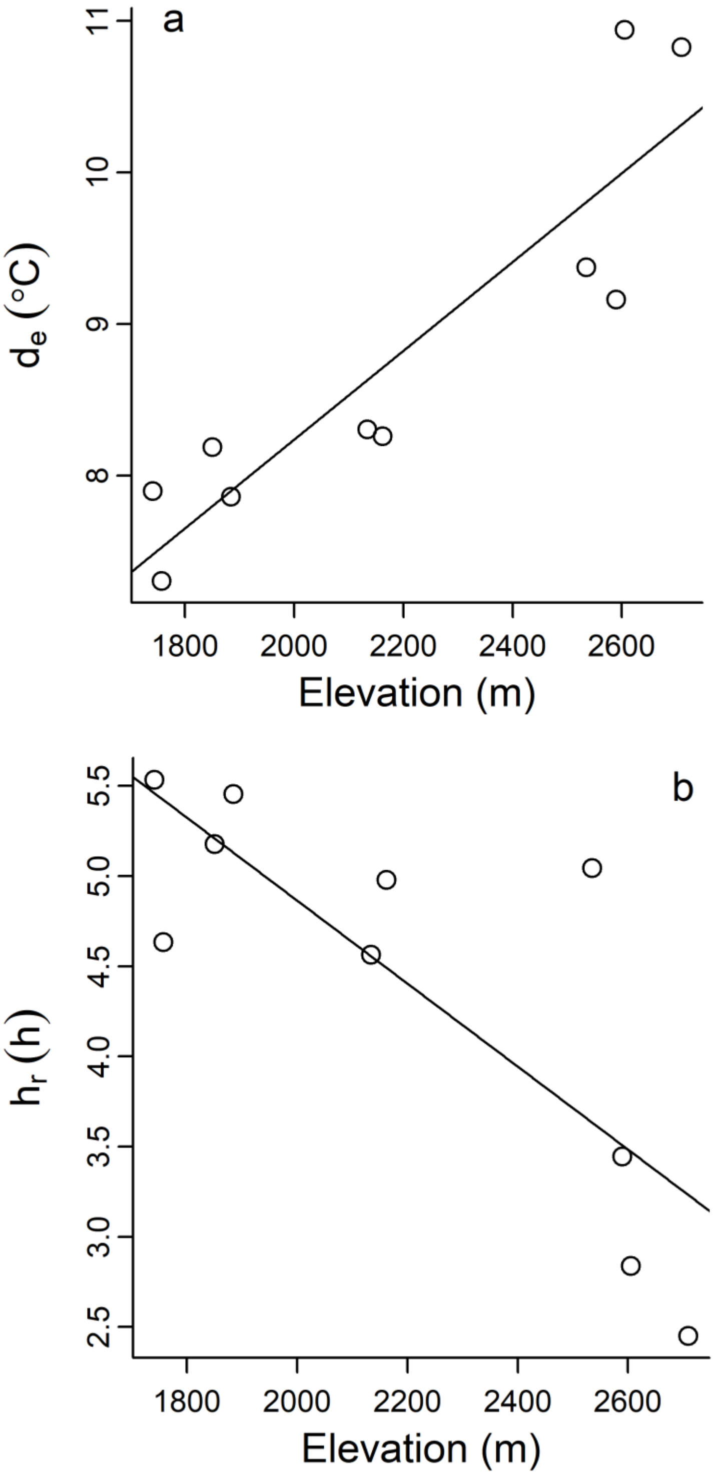


Figure 3-3. The relationship between elevation (m) and two indices of thermal quality for *Sceloporus jarrovii* lizards at 10 talus slopes in the Chiricahua Mountains, Arizona, U.S.A: d_e (°C, Hertz et al. 1993) and the hours of restricted activity (h_r, Sinervo et al. 2010).

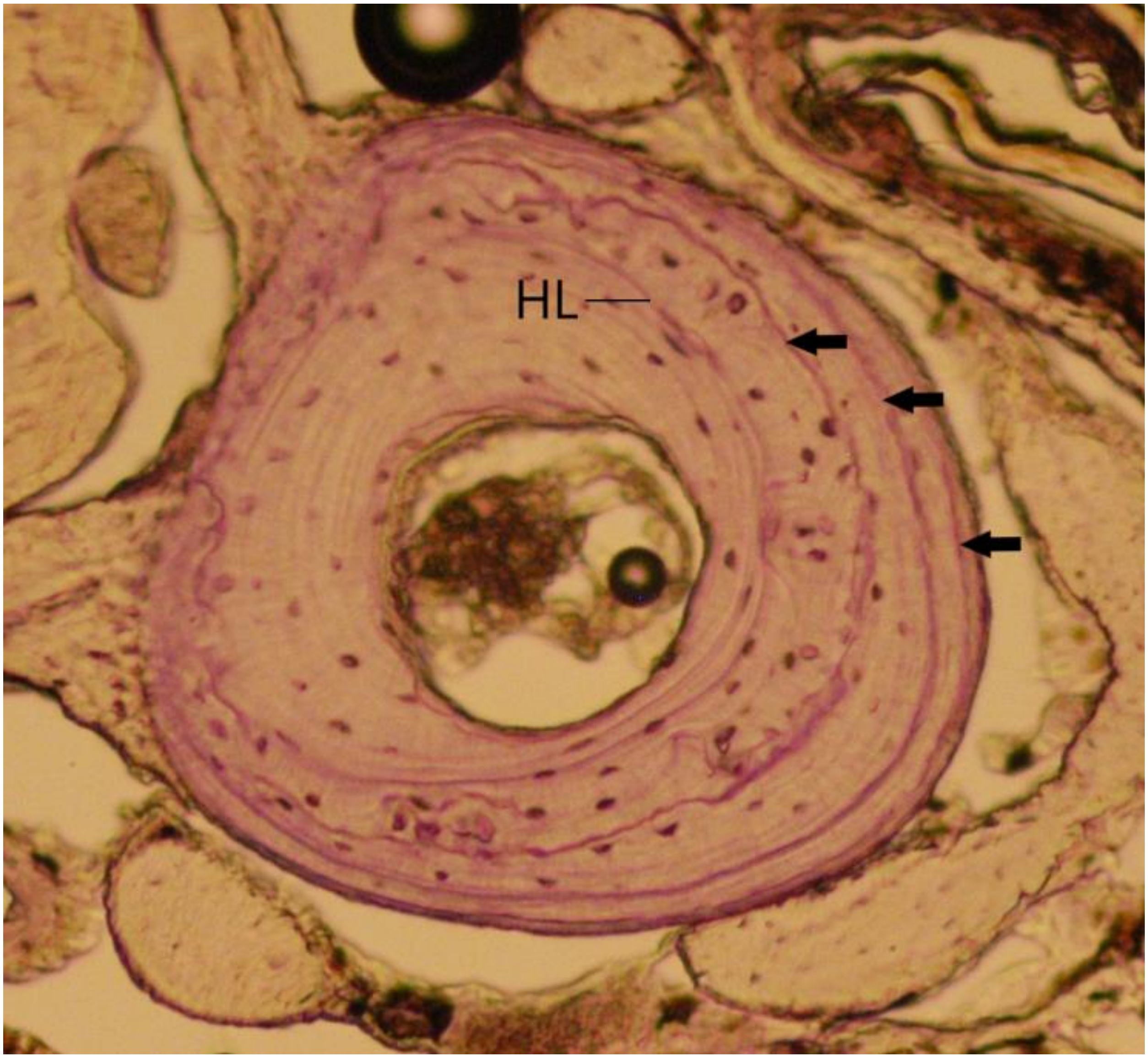


Figure 3-4. A cross-section of the phalange bone of a *Sceloporus jarrovii* lizard from the Pinaleño Mountains, showing three lines of arrested growth (black arrows) and a fainter “hatching line” (HL). Photo taken at 100 × magnification.

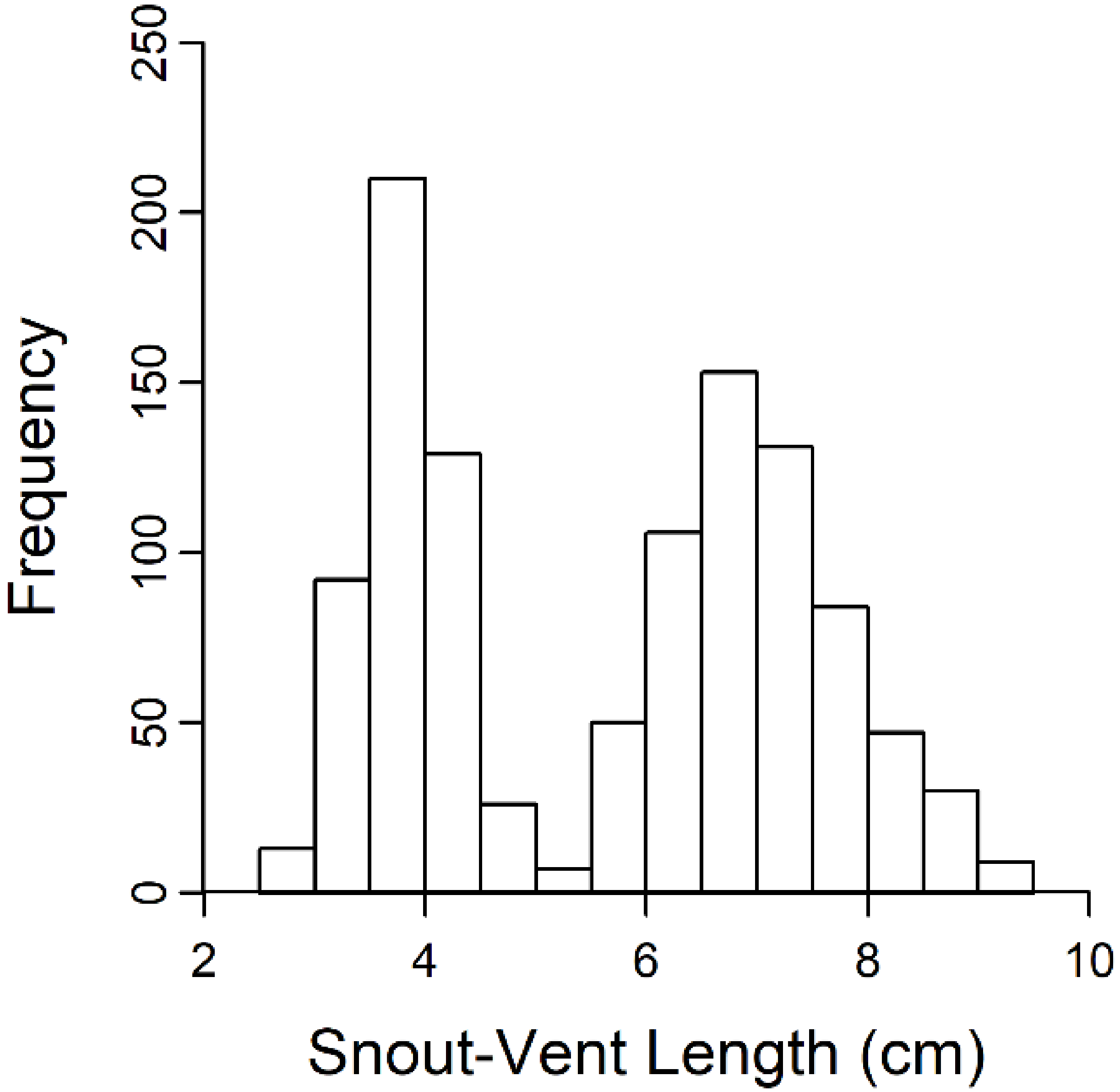


Figure 3-5. The distribution of snout-vent length (cm) measurements (N = 1087) of *Sceloporus jarrovii* lizards captured in the month of July (2014-2016) in southeastern Arizona, U.S.A.

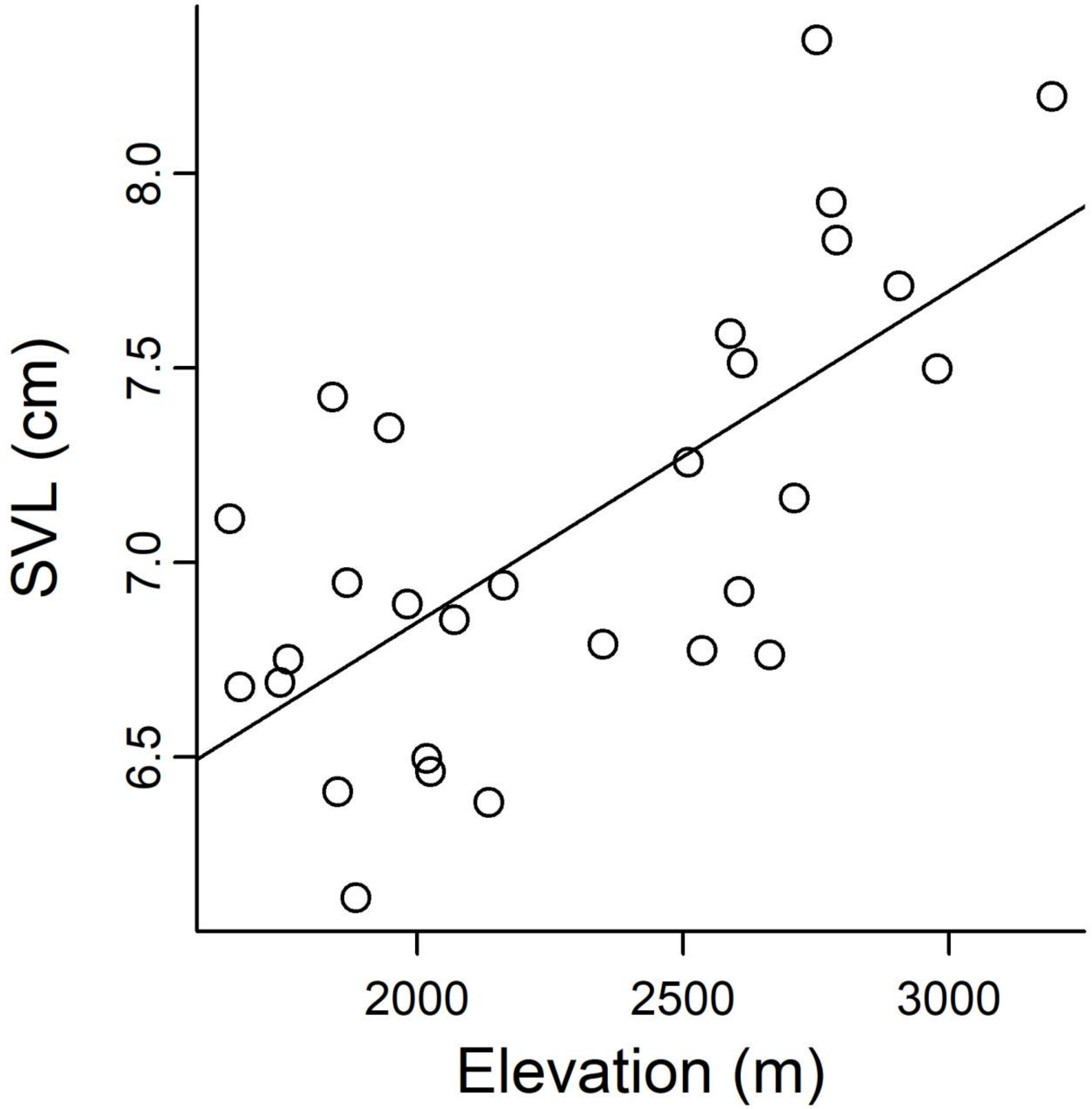


Figure 3-6. The relationship between the maximum asymptotic snout-vent length (SVL, cm, calculated as L_∞ in the von Bertalanffy equation), and elevation (m) in *Sceloporus jarrovii* lizards at 29 sites in southeastern Arizona, U.S.A.

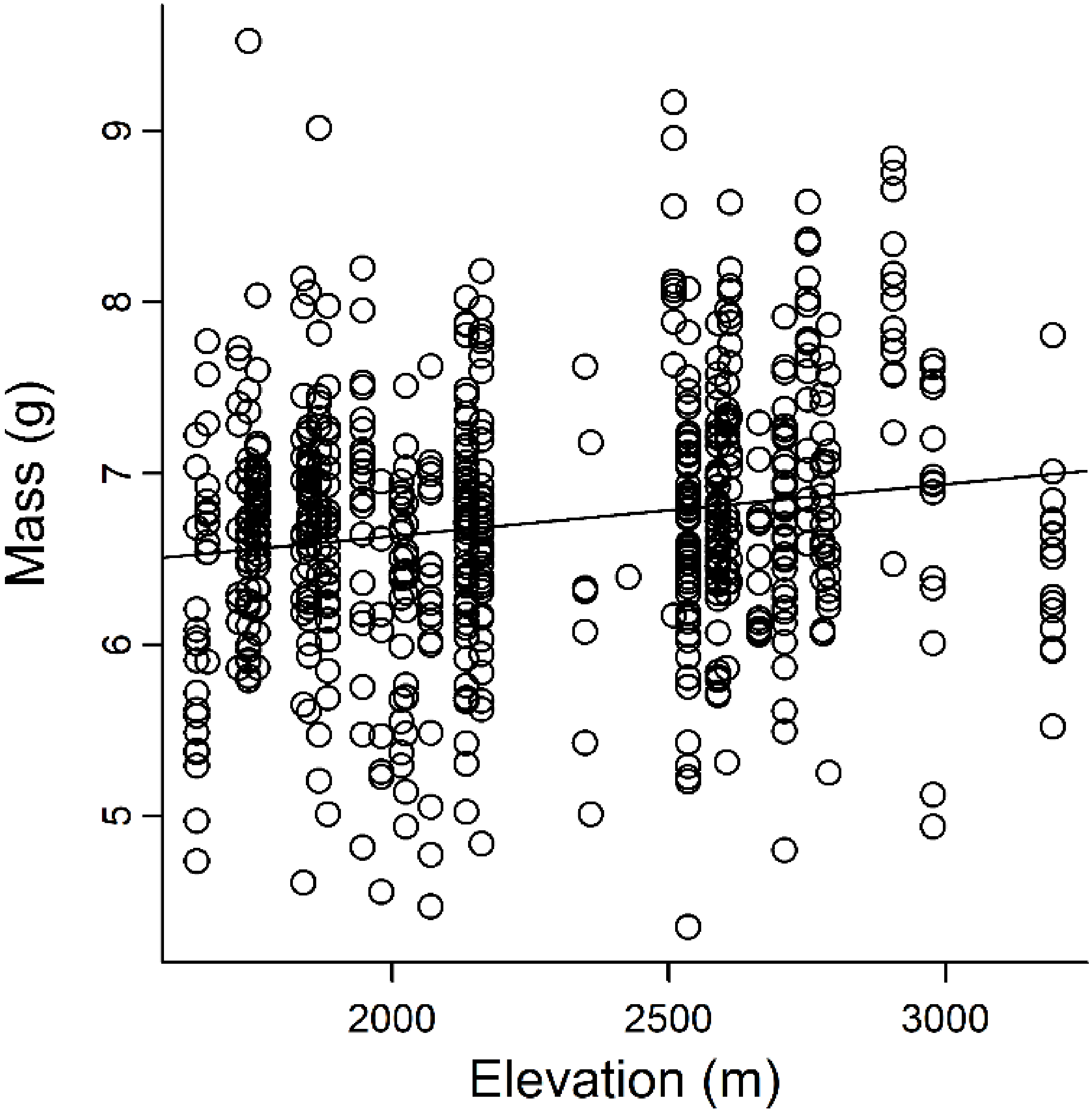


Figure 3-7. The scaled mass index (g) of *Sceloporus jarrovii* lizards (N = 693) from 32 locations in southeastern Arizona, U.S.A., by elevation (m). The scaled mass index is a measure of body condition, where the mass of each lizard is scaled to represent the mass of that lizard at a snout-vent length of 5.87 cm.

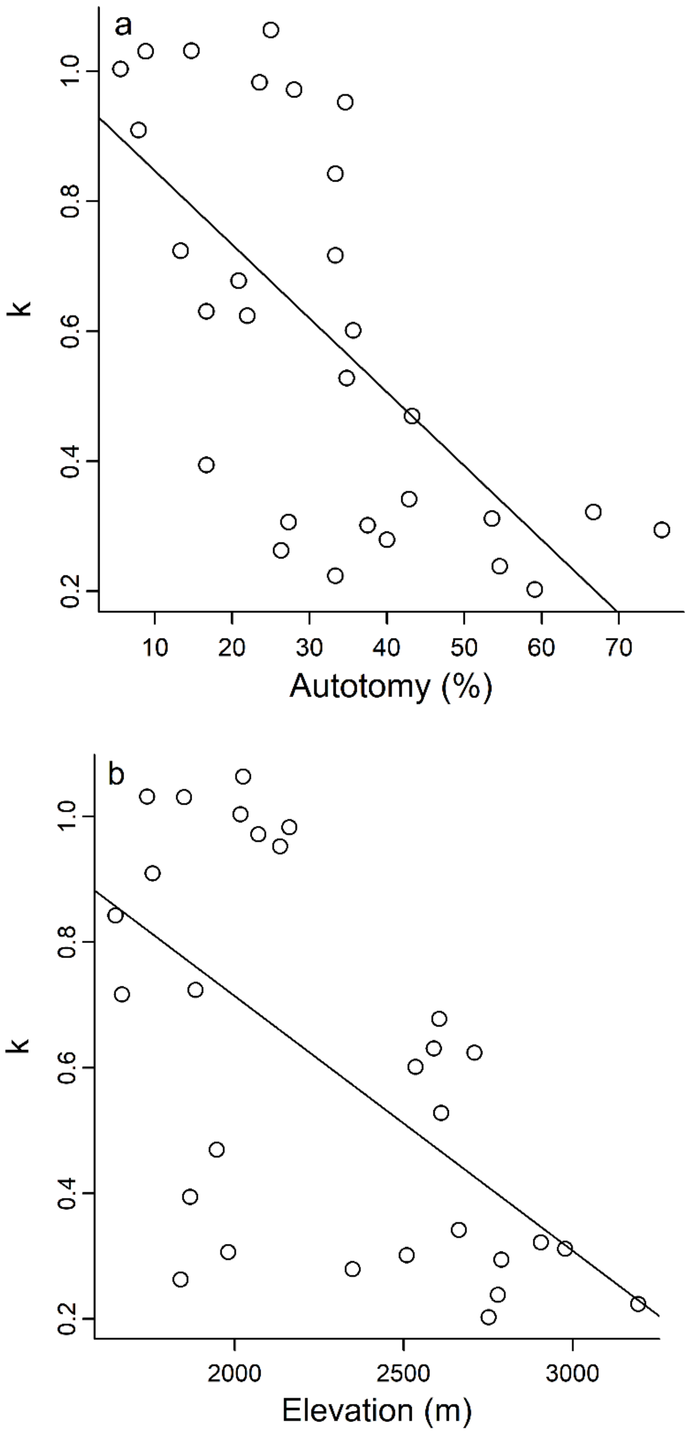


Figure 3-8. The relationship between the population growth rate coefficient (k) of *Sceloporus jarrovii* lizards and the proportion of lizards with autotomized tails in the population (a) and site elevation (b) at 29 sites in southeastern Arizona, U.S.A.

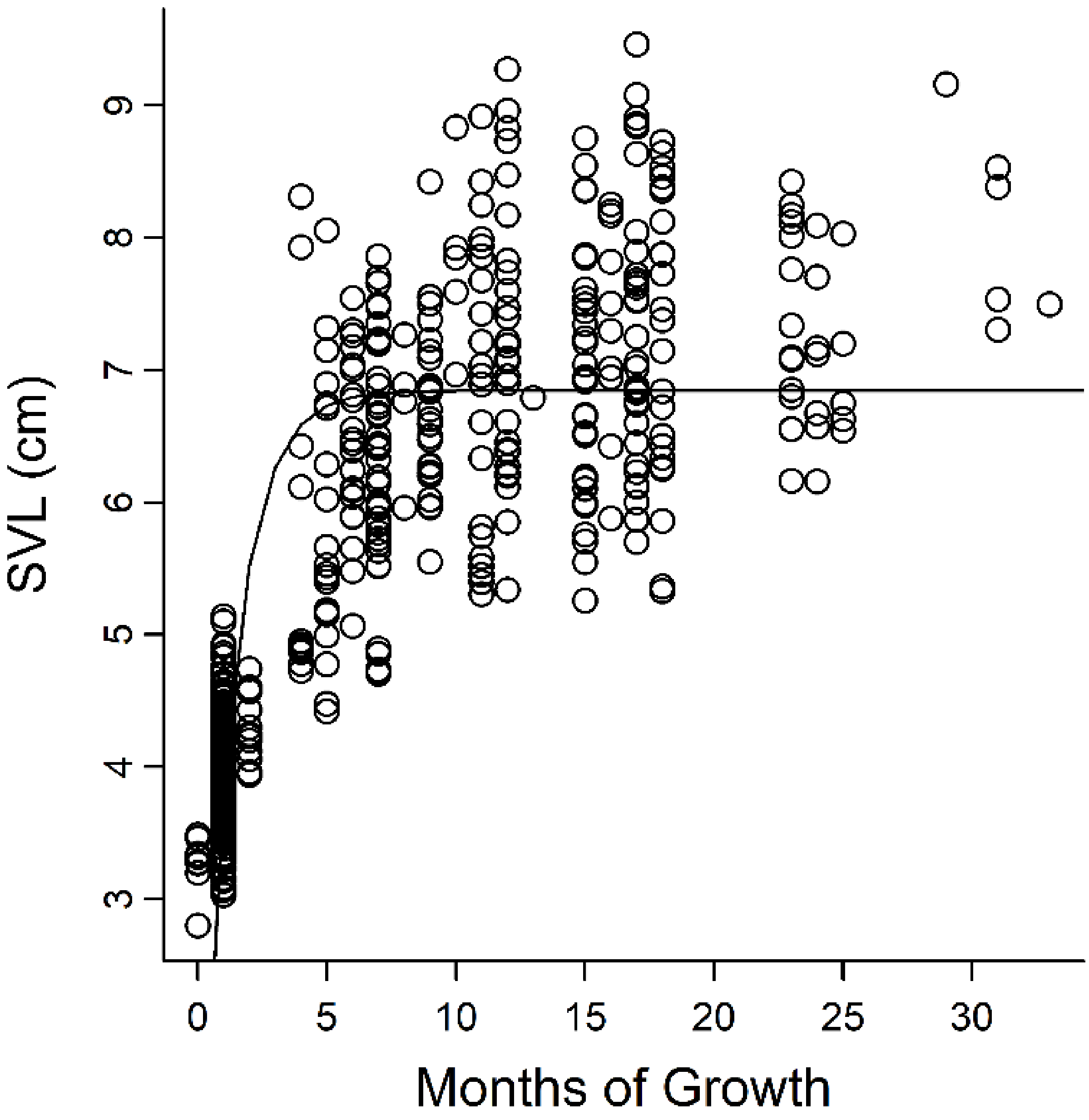


Figure 3-9. The relationship between the number of months of growth and snout-vent length (cm) for *Sceloporus jarrovii* lizards (N = 503) at 32 talus slopes in southeastern Arizona, U.S.A. The line represents the von Bertalanffy (1938) growth model.

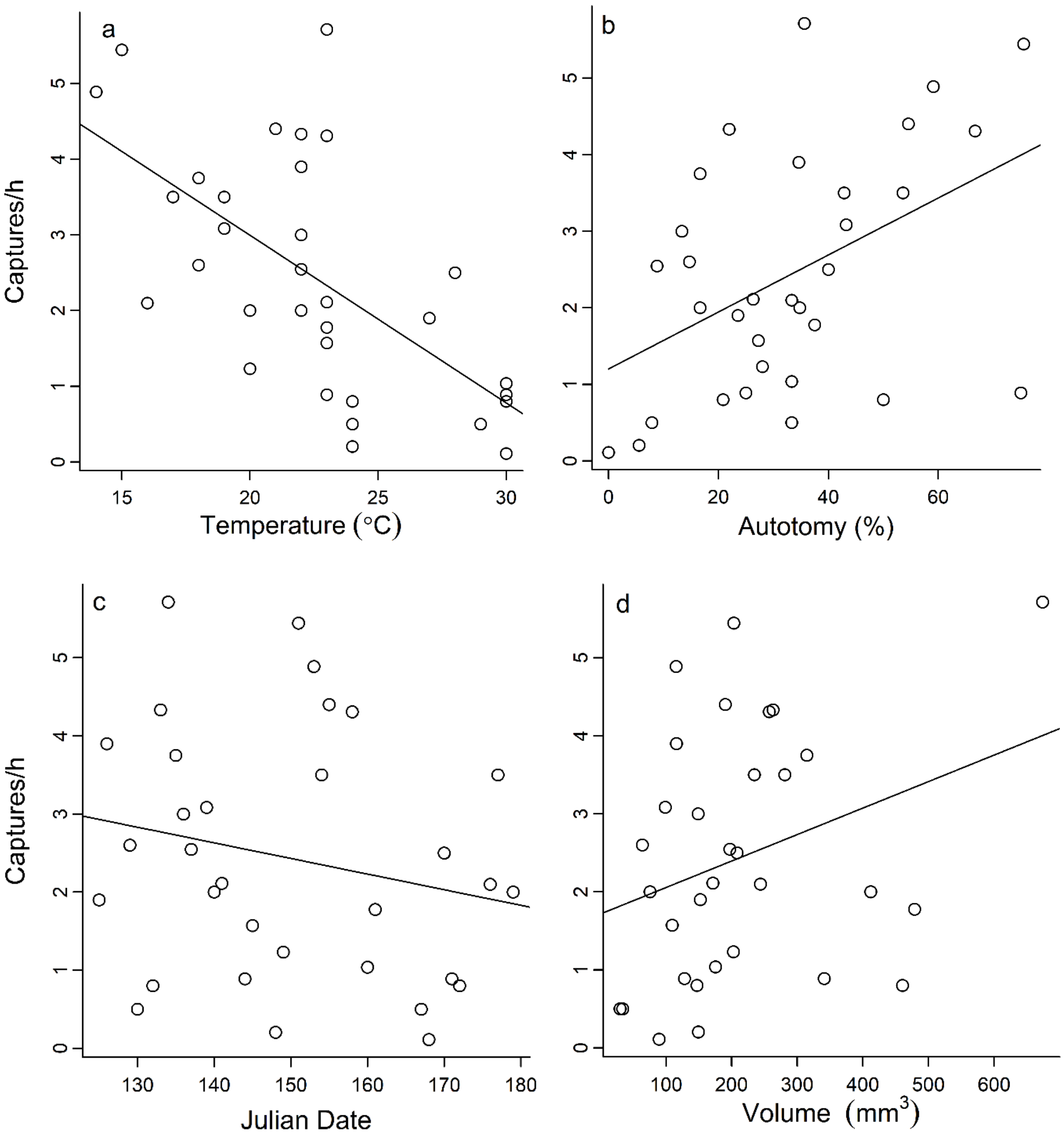


Figure 3-10. The number of *Sceloporus jarrovii* lizards captured per person hour in relation to (a) the daily maximum air temperature (°C), (b) rate of tail autotomy in the population (%), (c) Julian date and (d) the volume of arthropods caught in sticky traps over 24 hours (mm^3) of the study site at 32 locations in southeastern Arizona, U.S.A.

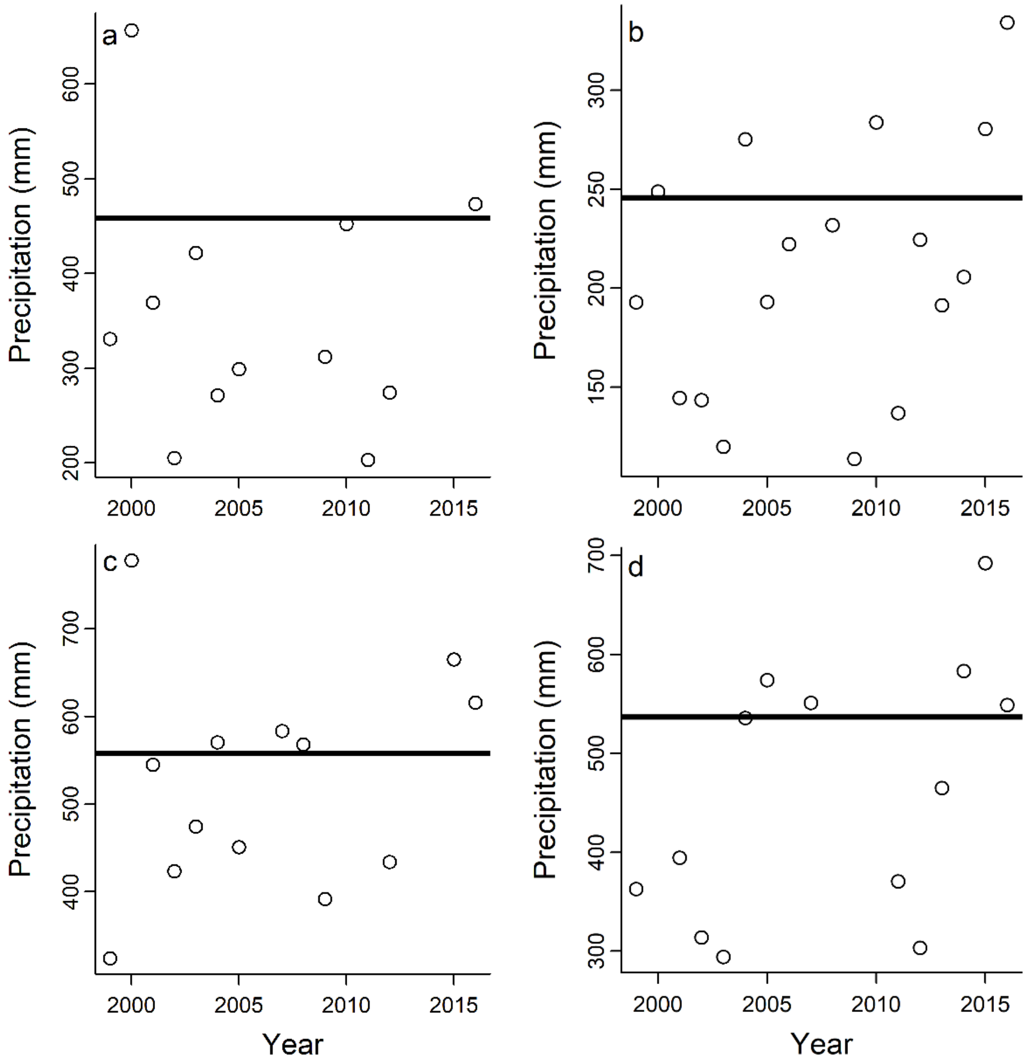


Figure 3-11. Average annual precipitation (mm) recorded at the weather station with available data closest to each mountain chain (a) Nogales (Santa Ritas), (b) Safford Agricultural Center (Pinaleños), (c) Coronado National Memorial Headquarters (Huachucas), and (d) Portal (Chiricahuas), Arizona. The line represents the historical average annual precipitation (1981-2010). Annual precipitation data from: https://www.ncdc.noaa.gov/cdo-web/datatools/findstation. Historical average precipitation data from: www.wrh.noaa.gov/twc/climate/seaz_rainfall_normals.php. Websites accessed 2017-11-17.

Chapter 4

Temperature, then food: thermal quality and arthropod availability interact to drive *Sceloporus jarrovii* density

Abstract

One of the major aims of ecology is to understand the factors that regulate the spatial and temporal variation in population density. Although food availability is a major driver of population density, thermal quality of the habitat may be of similar or greater importance for ectothermic animals, whose body temperatures and thus physiological rates are strongly influenced by environmental temperatures. I tested the hypotheses that population density is driven by the food availability vs. thermal quality of the habitat in terrestrial vertebrate ectotherms. If population density is driven by food availability, then body condition, individual growth rate and population density should increase both with natural food availability and following food supplementation. If population density is driven by habitat thermal quality, then body condition, individual growth rate and population density should increase with habitat thermal quality. I captured *Sceloporus jarrovii* lizards at 10 study sites over an altitudinal gradient of 1,000 m, supplemented half the sites with mealworm larvae (*Tenebrio molitor*), and related body condition, individual growth rate and population density to site thermal quality and relative arthropod availability. Lizards were in worse condition and grew more slowly, but were found at higher densities in habitats of high thermal quality. Food availability did not affect body condition, growth rate or population density directly, but modulated the strength of the effect of thermal quality on these variables. Interestingly, this suggests that while food availability and habitat thermal quality interacted in driving population density, thermal quality was the stronger driver.

Introduction

The abundance of organisms varies spatially and temporally (Brown et al. 1995, Ysebaert and Herman 2002), and understanding the factors that regulate this variation is central to ecology (Krebs 2001). Species distributions may be limited by environmental conditions such as temperature and precipitation (Root 1988, Parmesan et al. 1999, Hawkins et al. 2003) or, at finer scales, by biotic interactions such as predation and competition (Robertson 1996, Jackson et al. 2001, Boulangeat et al. 2012). Environmental and biotic factors may also drive the spatial variation in the population density of a species within its distribution. Brown (1984) argued that local population abundance was determined by the extent to which an area met the species' needs along several niche axes, including both environmental and ecological (biotic) conditions.

Ultimately, spatial variation in population density is a function of the spatial variation in population mean fitness (Levins 1962, MacArthur and Levins 1964, MacArthur and Pianka 1966). Indeed, population growth rate is largely driven by local individual survival and reproduction (e.g., Kooijman and Metz 1984, Ozgul et al. 2010). Furthermore, habitat selection theory predicts that habitats of higher quality should support more individuals. According to the ideal free distribution (Fretwell and Lucas 1969), individuals select habitat based on the potential fitness achievable within that habitat. Thus, resource-rich (high quality) habitats should be preferentially selected and support a higher density of individuals than resource-poor habitats.

One factor likely to be a major driver of population mean fitness and density is food availability, because it provides energy for tissue development, energy storage and reproductive output. Several lines of evidence suggest that population densities are limited by energetic constraints. Firstly, across taxa, larger species occur at lower densities following an inverse-scaling relationship (reviewed in White et al. 2007) because metabolic energy needs increase with body size (Nagy 2005). Furthermore, typical consumer-resource population models portray population growth rate as a function of resource availability (e.g., Bayliss and Choquenot 2002). Several studies have shown that individual growth and reproductive output decline in years of low food availability (Parker and Pianka 1975, Ballinger 1977, Dunham 1978, Ballinger and Congdon 1980, Madsen and Shine 2000). Finally, supplemental food increases relative body mass (Licht 1974, Rose 1982), growth rate (Stamps and Tanaka 1981, Wright et al. 2013, but see Niewiarowski 1995), reproductive output (Taylor et al. 2005, Wright et al. 2013), and population density (reviewed in Boutin 1990).

In ectotherms, however, the thermal quality of the habitat may be equally if not more important than food availability in driving population mean fitness and density. Animal physiology is regulated by body temperature (T_b, Hill et al. 2004), and so the rates of energy acquisition and assimilation also depend on T_b (Congdon 1989, Angilletta 2001, Niewiarowski 2001). In ectotherms, T_b is heavily influenced by environmental temperatures (T_e, Hertz et al. 1993). To maintain physiologically optimal T_bs, ectotherms may thermoregulate behaviourally (e.g., Huey and Kingsolver 1989, Huey 1991, Hertz et al. 1993), but thermoregulation incurs costs such as increased predation risk and lost time and energy (Huey and Slatkin 1976, Gvoždík 2002, Webb and Whiting 2005, Brewster et al. 2013). Success of thermoregulation also depends on availability of suitable T_es in the habitat (Huey 1991). A habitat characterized by T_es that strongly overlap with an ectotherm's preferred T_b range is of high thermal quality because the ectotherm may achieve optimal T_bs with minimal effort (Huey 1991, Hertz et al. 1993). Preference for habitats of high thermal quality has been observed in several ectothermic taxa (Ahnesjö and Forsman 2006, Row and Blouin-Demers 2006, Picard et al. 2011, Halliday and Blouin-Demers 2014, 2016; Freitas et al. 2016). Furthermore, locomotor performance (Blouin-Demers and Weatherhead 2008), growth rate (Calsbeek and Sinervo 2002, Halliday and Blouin-Demers 2016) and fecundity (Halliday and Blouin-Demers 2014, 2016) are higher within or through selection of high thermal quality habitats. Population abundance is also higher in habitats of higher thermal quality (Halliday and Blouin-Demers 2016, Paterson and Blouin-Demers 2018), but not sites at different altitudes (Díaz 1997).

I therefore tested two hypotheses concerning the forces driving local population density in terrestrial vertebrate ectotherms. Firstly, I hypothesized that population density was driven by the food availability in the habitat, because habitats with more food can support more individuals (reviewed in Bayliss and Choquenot 2002). Secondly, I hypothesized that population density was driven by the thermal quality of the habitat, because ectotherms can maximize net energy gain and reproductive output when T_es more closely coincide with physiologically optimal T_bs (Huey 1991). If population density was driven by food availability, I predicted that body condition, individual growth rate and population density would (1) increase following food supplementation, and (2) increase with natural food availability. If, however, population density was driven by thermal quality, I predicted that body condition, individual growth rate and population density would increase with thermal quality. I also expected an interaction with food availability, such that body condition, individual growth rate and population density would be unaffected by food availability at sites of low thermal quality (because net energy gain should be constrained by low temperatures and thus low assimilation rates (Huey 1982)), but increase with food availability when thermal quality is high (when food availability becomes the constraining factor).

I used body condition and individual growth rate as indicators of energy gain, which is related to fitness. Individuals in good body condition have higher energy reserves (Schulte-Hostedde et al. 2001) that can be allocated to growth or reproduction (e.g., Doughty and Shine 1998). Males in good condition outperform their rivals in mating and aggressive behaviours in many taxa (Given 1988, reviewed in Lailvaux and Irschick 2006) and females in good condition have higher fecundity (e.g., Bonnet et al. 2001). High body condition may also enhance overwinter survival (e.g., Shine et al. 2001, Pangle et al. 2004). Growth rate affects fitness in lizards because larger individuals are more likely be more dominant (Carpenter 1995), hold higher quality territories (Ferguson et al. 1982), survive, particularly at high population density (Fox 1978, Calsbeek and Smith 2007); and produce more offspring (Ballinger 1973, 1979; Olsson et al. 2002).

To test these hypotheses, I captured Yarrow's Spiny Lizards (*Sceloporus jarrovii*) at 10 paired study sites along an altitudinal gradient in the Chiricahua Mountains, Arizona, U.S.A., from 2014 - 2016. I used *S. jarrovii* as a study species because this lizard occurs in similar habitat over a broad altitudinal range, and so populations in close proximity experience very different thermal conditions. Furthermore, the availability of arthropods, which form the basis of the diet of *S. jarrovii* (Simon 1975), fluctuates considerably with precipitation (e.g., Ballinger 1977, Dunham 1978, Ballinger and Congdon 1980). At each site, I measured the thermal quality and relative availability of arthropods, and supplemented half the sites with mealworms using a

BACI (before-after-control-impact) study design. I then related thermal quality and food availability to body condition, individual growth rate and population density.

Methods

Study Site, Species and Approach

Sceloporus jarrovii is a small (mean ± SD of adult snout-vent length (SVL) = 7.6 ± 0.6 cm), heliothermic lizard that feeds on arthropods (Simon 1975) and occurs in mountainous regions of southern Arizona and New Mexico, U.S.A., and in northern Mexico. This lizard occurs from 1,400 - 3,200 m in altitude (Burns 1970) and is strongly associated with rocky habitat containing numerous crevices (Ruby 1986) that serve as refuges from predators and unsuitable temperatures (Huey et al. 1989, Sabo 2003). The mating season occurs in the fall, with parturition occurring the following spring from May to June (Ballinger 1973).

I conducted this experiment over three summers (May to August 2014-2016) in the Chiricahua Mountains in Coronado National Forest, Arizona, U.S.A. I had 10 paired study sites (elevation range: 1,700 to 2,700 m, Table 4-1, Figure 4-1) consisting of talus slopes (Figure 3-2): relatively homogeneous rock piles with a mean (± SE) area of 4,186 ± 1,324 m^2. I used mark-recapture methods to estimate the mean body condition, individual growth rate, and population density of lizards at each site and time period. Halfway through the study, in June 2015 and May 2016, I manipulated food availability by adding mealworm larvae (*Tenebrio molitor*) to half of the sites. I food-supplemented during the dry season (May and June) because arthropods are less abundant when there is less precipitation (Dunham 1978) and so food limitation is more likely to occur during these months. Two to four people were involved in the food supplementation of each slope. Observers began from the same location on the edge of the site and walked in different directions. Each observer tossed a handful of mealworms onto the slope approximately every 20 m. In this manner, I added a total of 2,500 mealworm larvae per site.This research was conducted with State of Arizona Scientific Collection Permits (SP675429, SP713939 and SP735332) and approval from the University of Ottawa's Animal Care Committee (BL-1788).

Field Measurements of Lizards

To estimate the mean body condition, individual growth rate, and population density of each site, I used mark-recapture methods. I captured lizards three times per year, giving a total of nine captures per site, except for three sites established in 2015 (SF1, SF3 and RSF) that had only six capture events. Lizards were captured by noose and individually marked on their ventral side with a medical cauterizer (Vervust and Van Damme 2009, Ekner et al. 2011). I recorded the identity and sex of each lizard, measured its snout-vent length (SVL, ± 0.01 cm) with callipers and mass (± 0.01 g) with a digital scale, and recorded its reproductive status (gravid or not). Lizards were sexed using the presence of secondary sexual characteristics (enlarged post-anal scales and femoral pores, and more extensive blue patches on the throat and belly in males, Figure 2-3, Brennan and Holycross 2006). I also noted if a lizard was missing or had regrown any part of its tail (tail autotomy), and counted the number of chiggers infecting it with a hand lens. *Sceloporus jarrovii* are predominantly infected by two mite species: *Eutrobicula lipovskyana* and *Geckobiella texana* (Goldberg and Holshuh 1992). I released all lizards within five hours of capture.

Body Condition

I estimated body condition for all lizards except those with tail autotomy because those lizards are necessarily lighter for their SVL than other lizards. I calculated the scaled mass index (Peig and Green 2009) as an index of body condition. The scaled mass index uses a scaling relationship to predict the mass of each individual at a fixed body size (L_o). It is calculated using the following equation: $\widehat{M}_i = M_i \times (\frac{L_o}{L_i})^b$, where M_i and L_i are the mass and SVL of the lizard, L_o is the mean SVL of the population (5.73 cm), b is the slope of the log-log regression of mass and SVL (3.15), and $\widehat{M}_i$ is the predicted body mass for lizard *i* when SVL is standardized to L_o. The scaled mass index accounts for the scaling between body length and mass measurements better than the raw residuals of a log-log regression (Peig and Green 2009). I used the slope of the ordinary least squares regression as b because the correlation coefficient between log(mass) and log(SVL) was very high (r = 0.99).

Growth Rate

I calculated individual growth rate of recaptured lizards by dividing the difference between the final and initial SVL by the number of growth days. I used SVL rather than mass because mass is more subject to variation with changes in reproductive or nutritional state (Dunham 1978, Olsson et al. 2000). I excluded growth measurements from lizards who switched study sites or who were recaptured within 10 days of the initial SVL measurement (n = 5). Growth days are limited to the active period, because *S. jarrovii* grow little over the winter (mid-November to early April at low elevation and mid-October to late April at high elevation, Ballinger 1979). Therefore, for lizards caught in multiple years, I subtracted 6 months per year for lizards at high elevation (> 2,450 m) sites and 4 months per year for lizards at low elevation

(< 2,450 m) sites (Cox 2006). I chose 2,450 m as the dividing altitude due to the shift in vegetation to petran montane conifer forest at sites above this altitude (Brennan and Holycross 2006). Supplemental analyses with the same number of inactive days for all sites did not change my conclusions (see Statistical Analyses section).

Population Density

I estimated the population abundance at each capture event using the POPAN formulation (Schwarz and Arnason 1996) of the Jolly-Seber open population model (Jolly 1965, Seber 1965). The POPAN formulation estimates four population parameters by maximizing the log-likelihood: the survival probability between subsequent capture events (Φ), detection probability at each capture event (p), the total number of animals present in the "super-population" ($\hat{N}$), and the probability of unmarked individuals from $\hat{N}$ entering the study site at each capture event (pent). I estimated population abundance for each site separately using the package 'RMark' (Laake 2013) to access the program MARK (White and Burnham 1999) in R (R Core Team 2015). For each site, I started with a general model that allowed Φ to vary with sex and year; p to vary with sex, sampling effort, and maximum daily temperature; and pent to vary with time. I constrained $\hat{N}$ to be constant. To quantify sampling effort, I calculated the number of person-hours per capture event. I obtained the maximum daily temperature for each capture day from the nearest National Oceanic and Atmospheric Administration weather station (https://www.ncdc.noaa.gov/cdo-web/datatools/findstation): USR0000ARUC for the Rucker Canyon and Price Canyon sites, and USC00026716 for all other sites. For capture events spanning more than one day, I averaged the maximum daily temperatures over those days.

I assessed the goodness-of-fit of the equivalent general Cormack-Jolly-Seber model (Cormack 1964, Joly 1965, Seber 1965) for each site (Supplementary Information 1, Table 4-S1). The p(Sex) parameter was removed from the general model for the RSF site because data scarcity caused singularity in this parameter. I constructed all possible subsets of the general model and ranked them based on Akaike's Information Criterion corrected for small sample sizes (AIC_c) or the analogous quasi-penalized criterion ($QAIC_c$) correcting for overdispersion (Appendix 1, Burnham and Anderson 2002). The models with the most support (within 4 AIC_c or $QAIC_c$ of the model with the lowest AIC_c or $QAIC_c$ value) are summarized in Supplementary Information 1 (Tables 4-S2 to 4-S11). I obtained population abundance estimates for each occasion from the average of these models, based on model weights (Burnham and Anderson 2002, Cade 2015). Finally, I obtained the population density (lizards per 1,000 m^2) of each site and capture occasion by dividing the estimated abundance by the area of the study site. The area of the study site was calculated in ArcGIS (v.10.4.1, Environmental Systems Research Institute, Redlands, CA).

Natural Food Availability

I measured natural food availability as the volume of arthropods collected in sticky traps over 24 hours (e.g., Simon 1975, Niewiarowski and Roosenburg 1993). The volume of arthropods caught in sticky traps is a good estimator of the relative natural food availability because (1) the same types of food items are found on sticky boards and in *S. jarrovii* stomachs (Simon 1975), and (2) sticky trap capture rates and the mass of stomach contents correlate positively in *S. undulatus* (Dunham 1978). Sticky traps consisted of waterproof paper (10 cm × 8 cm) covered in biodegradable resin (Tree Tanglefoot, Grand Rapids, Michigan, U.S.A.). I placed three sticky traps in each of three microhabitats: bottom, edge, and inside of the talus slope. The location of each sticky trap was determined from random numbers: beginning from one of the bottom corners of each talus slope, “bottom” traps were located 0 to 10 steps up and 0 to 150 steps across the slope, “edge” traps were located 11 to 150 steps up, and “inside” traps were located 11 to 150 steps up and 5 to 150 steps across. When required, the upper limits to the number of steps was adjusted according to the dimensions of the slope. Food availability was determined twice per year: once in the dry season (May-June) and once in the rainy season (July).

I counted the number of arthropods on each trap and measured the maximum length and width of each arthropod using callipers. I calculated the total arthropod volume (mm^3) per card by approximating the volume of each arthropod to that of a cylinder ($volume = length \times \pi \times (\frac{width}{2})^2$) and taking the sum (e.g., Werner et al. 1995). To calculate the food availability for the site in each time period, I averaged the number and volume of arthropods in each microhabitat, and then weighted them according to the percentage of the site composed of that microhabitat type.

Habitat Thermal Quality

To assess the thermal quality of each site, I (1) measured the preferred body temperature range (T_{set}, the 25th and 75th percentiles of body temperatures selected in an unconstrained environment, Hertz et al. 1993) of 40 adult *S. jarrovii* (T_{set} = 30.4-33.2°C, see chapter 2), (2) measured the operative environmental temperatures of the site (T_e, the potential equilibrium T_b’s that a thermoconforming animal may achieve at every location in its habitat, Huey 1991), and (3) calculated an index of thermal quality (d_e, Hertz et al. 1993). To measure the T_es of each site, I placed a copper model in each of three microhabitats within the site (on rocks in the inside, edge, and bottom of the talus slope). Edge habitat was defined as being in full shade, under vegetation within the talus slope or within a 5 m buffer around the outer limit of the slope. Bottom habitat was defined as being within 5 m of either side of the bottom edge of the slope where rocks met vegetation. Inside habitat encompassed the remainder of the slope, characterized by open rocks. Copper models consisted of a copper pipe (6 cm × 2 cm) sealed with rubber stoppers and painted dark gray to approximate the thermal properties of lizards (e.g., Herczeg et al. 2006). Each copper model contained a temperature data logger (Thermochron iButton D1S1921G-F5, Dallas Semiconductor, Sunnyvale, California) that took temperature measurements every 15 (2014) or 20 (2015-2016) minutes from early May to early August every year. In chapter 2, I validated the use of copper models with the carcass of an adult.

To calculate the d_e index of thermal quality, I used the mean deviation of T_e above and below the limits of T_{set}, where a T_e within T_{set} is assigned a d_e value of 0 (Hertz et al. 1993). I calculated a mean daily value of d_e for each microhabitat (inside, edge and bottom) for daylight hours (05:30 to 19:30) when lizards are typically active (Beuchat 1989), for each month (May, June and July). I then calculated the proportion of each site that consisted of inside, edge and bottom habitat in ArcGIS (v.10.4.1, Environmental Systems Research Institute, Redlands, CA) and used these proportions to obtain an overall monthly d_e per site, weighted by the availability of each microhabitat. On the rare occasions where there were no T_e values for a certain copper model in a certain month (e.g., when a temperature datalogger died), I predicted the missing T_e

values for that copper model from the regression with the T_e values from another copper model at the site (the one with the highest R^2 value).

I also calculated alternative indices of thermal quality for comparison (Appendix B). All indices were moderately to strongly correlated (Pearson's r = 0.36 to r = 0.95, Supplementary Information 2, Table 4-S12), but the directionality depended on the indices compared. I opted to use d_e as it is the most commonly used thermal quality index (Hertz et al. 1993).

Confounding Factors

Factors that may affect body condition, growth rate or population density include tail autotomy and parasite load. Lizards that have lost their tail are necessarily lighter for their length than other lizards, and may grow more slowly (Niewiarowski et al. 1997) or have a reduced survival probability (Fox and McCoy 2000). The rate of tail loss may also be an indicator of predation rate for the population (Turner et al. 1982). Parasitism may result in poorer body condition or slower growth in the host (Khokhlova et al. 2002) because parasites pilfer their host's resources (Candolin and Voigt 2001). Parasitism may also reduce the hosts' reproductive success (Schall 1983, Fitze et al. 2004) and therefore population density (Lafferty 1993). The prevalence of infection of *S. jarrovii* lizards by chiggers (*E. lipovskyana)* is close to 100%, but the intensity of infection is highly variable among lizards (e.g., Goldberg and Bursey 1993, Bulté et al. 2009, Halliday et al. 2014).

I accounted for these confounding factors statistically in the following manner. To account for tail autotomy, I excluded autotomized lizards altogether from the body condition analyses, included a tail status variable for the growth analyses (whether or not lizards had lost any part of their tail), and included a rate of tail autotomy variable (number of lizards with tail autotomy/total number of captures * 100) in the population density analyses. For parasite load, I quantified the number of chiggers per lizard, included this variable in the body condition analyses, and calculated the mean chigger load of both captures for the growth rate analyses. For the population density analyses, I calculated the mean chigger load for the population for each capture event.

Statistical Analyses

I ran two sets of analyses for each demographic parameter (mean body condition, individual growth rate and population density). The purpose of the first set of analyses ("before and after") was to determine whether body condition, growth rate and population density of *S. jarrovii* increased following food supplementation, and whether the response depended on the thermal quality of the site. The purpose of the second set of analyses ("correlation") was to determine whether body condition, individual growth rate and population density increased with the natural food availability and thermal quality of the study site.

Data from 2014 were excluded from analyses because of inconsistencies in the methods used to measure d_e and arthropod availability between 2014 and subsequent years. The only data from 2014 that were retained were initial SVL measurements used to calculate the growth rate of lizards recaptured in 2015. In all analyses, homogeneity of variance and normality of the residuals were checked through visual examination of the residual plots. All models were linear mixed models (nlme library, Pinheiro et al., 2015) fitted by maximizing the log-likelihood. In all cases, I removed non-significant terms from the general model until all remaining terms were significant, then ranked the models using Akaike's Information Criterion corrected for small sample sizes (AIC_c; Tables 4-2, 4-3, 4-4, 4-5) and averaged them using model weights (Burnham and Anderson 2002). All conditional R^2 values for mixed models were calculated using the r.squaredGLMM() function in the MuMIn package (Barton 2018). All statistical analyses were conducted in R (R Core Team 2015).

Multicollinearity

To determine if there was multicollinearity between the independent variables, I calculated the variance inflation factor (VIF, usdm package, Naimi 2015) score of each variable. I did this separately for lizard body condition (independent variables: d_e, arthropod volume, chigger load, Julian date of capture), individual growth rate (independent variables: d_e, arthropod volume, average chigger load, initial SVL), and population density (independent variables: d_e, arthropod volume, average chigger load, Julian date, proportion of lizards with tail autotomy). Multicollinearity is generally considered to be significant when the VIF scores are greater than 4 (O'Brien 2007).

"Before and After" Analyses

To determine the effect of food supplementation on body condition, I compared values from May 2015 (before) to May 2016 (after), using the site d_e averaged over the month of May, as well as the arthropod volume measured in the dry season of each year. The general model contained the body condition (scaled mass index) as the dependent variable, d_e × time period (before and after) × site type (supplemented or control), volume of arthropods naturally available, Julian date of capture, chigger load, gravidity status (yes or no) and sex as fixed effects, and study site as a random effect. Given that most lizards were caught only once, the general model including lizard ID as a random effect was overparametrized. Thus, to avoid pseudoreplication, I randomly selected a single measurement of body condition for each lizard.

To determine the effect of food supplementation on growth rate, I compared the growth rates (mm/month) of lizards prior to food supplementation (final SVL measured before or on the second capture event in 2015) and after food supplementation (initial SVL measured on or after the second capture event in 2015). I used growth rate as the dependent variable, time period × site type × d_e, arthropod volume, mean chigger load, autotomy status, sex and initial SVL as fixed effects; and lizard ID nested within study site as random effects. I assigned the mean d_e of May and June 2015 as the thermal quality before manipulations and the mean d_e of May and June 2016 as the thermal quality after manipulations. I assigned the arthropod volume value measured during the dry season (May-June) in 2015 and 2016 as the arthropod volume before and after manipulations, respectively.

Finally, to determine the effect of food supplementation on population density, I compared log-transformed population densities from May 2015 (before) to May 2016 (after). I used the mean site d_e in May, as well as the arthropod volume in the dry season, for each time period. The fixed effects were time period × site type × d_e, arthropod volume, mean chigger load, and percentage of lizards with tail autotomy; whereas the random effect was the study site. Given the significant interaction between time period and site type (Table 4-6), I divided the data by time period and ran LMMs on each subset.

Correlation Analyses

Firstly, I determined how thermal quality and natural food availability affect lizard body condition. I included the body condition (scaled mass index) as the dependent variable, d_e × arthropod volume, Julian date, chigger load, sex, and gravidity status as fixed effects; and year nested within study site as the random effects. The d_e was averaged for the month of sampling.

All body condition measurements from July were assigned the arthropod volume measured during the wet season of that year. However, for the dry season (May-June) of every year, I only included body condition measurements from lizards captured during the capture event closest to the date of arthropod sampling during the dry season, because arthropods were only sampled once during the dry season every year. As in the "before and after" analyses of body condition, I retained a single randomly selected measurement for each lizard. Due to a significant interaction between d_e and volume (Table 4-7a), I subset the data into "high" and "low" d_e and volume, based on their median values. I determined the effect of d_e on body condition at high and low arthropod availabilities, as well as the effect of arthropod availability at high and low d_e, by running LMMs on each subset. In these models, I also included as fixed effects the terms that significantly affected growth rate in the averaged general model. For each subset, I removed non-significant terms until all remaining ones were significant, ranked the models based on their AIC_c values, and averaged them based on the model weights (Table 4-7b-e).

Secondly, I determined how thermal quality and natural food availability affected individual growth rate. I included growth rate (mm/month) as the dependent variable, site d_e × volume of arthropods, mean ectoparasite load (the mean of the final and initial chigger loads over the growth period), tail autotomy status at the final capture (tail loss or not), sex, and initial SVL as fixed effects; and lizard ID nested within study site as random effects. Due to the sparse thermal quality and food availability data for 2014, I did not consider growth rates that only spanned 2014. The d_e and arthropod volume values for every lizard were either a mean from 2015 (when the initial and final captures both occurred in 2015), 2016 (when both captures occurred in 2016), or an overall mean from 2015 and 2016 (when lizards were captured in multiple years). Due to a significant interaction between d_e and arthropod volume (Table 4-8), I subset the data into "high" and "low" d_e and arthropod volume, based on the median values of each. I then determined the effect of d_e on growth rate at high and low arthropod availabilities, as well as the effect of arthropod volume at high and low d_e, by running LMMs on each subset. In these LMMs, I also included as fixed effects the terms that significantly affected growth rate in the averaged general model.

To calculate the number of growth days for each lizard, I had divided the study sites based on an arbitrary altitude, such that I considered lizards at sites above 2,450 m to have six growth months per year and those at sites below 2,450 m to have eight. Given that dividing sites along an altitudinal gradient into "high" and "low" elevation is arbitrary, I tested the robustness of the results by analysing the data using seven growth months per year for lizards at all elevations.

Finally, I determined how thermal quality and natural food availability affect population density. I retained one population density measurement each from the dry season (May-June) and wet season (July) per year. I retained the density measurement from the capture event closest to the date upon which arthropod availability was measured. The d_e value assigned to each population density consisted of the mean d_e for the month of the capture event. I determined how thermal quality (d_e), arthropod volume and their interaction, mean chigger load in the population, percentage of lizards with tail autotomy in the population, and Julian date of the capture event affected the population density (lizards per 1,000 m^2) of lizards. I specified the study site as a random effect. Arthropod volume was log-transformed to linearize the relationship with population density and improve the fit of the model. Given the significant interaction between d_e and arthropod volume (Table 4-9a), I determined the median d_e and arthropod volume, and then subset the data into high and low d_e, and then by high and low arthropod volume. I then ran LMMs on each of the subsets.

Results

From 2014 to 2016 at the ten study sites, I captured 1,241 individual lizards (1,667 captures total). From 2015 to 2016, the mean monthly d_e index varied from 6.6 to 12.4°C, increasing at a rate of 2.4°C per 1,000 m increase in elevation. Similarly, from 2015 to 2016, I caught 2,950 arthropods in sticky traps, with the volume per trap night (weighted by microhabitat availability) varying between 9.9 and 530 mm^3.

Multicollinearity

I found no evidence of multicollinearity among any of the “correlation” analyses because the independent variables were all weakly or moderately correlated, and the variance inflation factors (VIF) were all below 4 (O’Brien 2007). Pearson’s correlation coefficients between independent variables ranged between r = -0.01 to r = 0.38 for growth, r = 0.09 to r = -0.21 for body condition, and r = 0.09 to r = 0.46 for population density. VIF scores ranged from 1.05 to 1.31 for growth rate, 1.04 to 1.13 for body condition, and 1.14 and 1.87 for population density.

“Before and After” Analyses

Food supplementation had no effect on body condition, individual growth rate, or population density. There were no interactions between time period (before and after) and type of site (supplemented or control) for growth rate or body condition (Tables 4-10, 4-11). While the interaction between time period and site type was significant in the population density analyses, population density did not differ between supplemented and control plots either before (Table 4-6b) or after (Table 4-6c) food supplementation. Furthermore, there were no three-way interactions for any of the demographic parameters (Tables 4-6, 4-10, 4-11), suggesting that there was no interaction between food supplementation and d_e following manipulations (Figure 4-2).

Correlation Analyses

Body Condition

Body condition depended on thermal quality, food availability, Julian date, ectoparasite load, sex and reproductive status. There was a significant interaction between site d_e and relative volume of arthropods, such that body condition was unaffected by d_e when arthropod volume was high (Table 4-7b, Figure 4-3a), but mass increased by 0.16 g for a lizard of average length (SVL = 5.73 cm) for each 1°C increase in d_e (decrease in thermal quality, Table 4-7c, Figure 4-3b) when arthropod volume was low. However, there was no effect of arthropod volume on body condition at either high d_e (low thermal quality, Table 4-7c, Figure 4-3c) or low d_e (high thermal quality, Table 4-7d, Figure 4-3d). A lizard of average length became 0.005 g heavier every day over the active season and was 0.001 g lighter for every additional chigger infecting it (Table 4-7a). An average-length lizard was 0.17 g heavier if it was male rather than female, and 0.70 g heavier if it was gravid rather than non-gravid.

Growth Rate

Individual growth rate depended on thermal quality, food availability, initial size, sex, and ectoparasite load, but not tail autotomy. There was a significant interaction between d_e and arthropod volume, whereby lizards always grew faster as d_e increased (and thermal quality decreased), but the rate of increase in growth rate with d_e was higher when there were few arthropods available (1.3 mm/month for every increase of 1°C in d_e, Table 4-8c, Figure 4-4b) than when the relative volume of arthropods was high (0.6 mm/month for every increase of 1°C in d_e, Table 4-8b, Figure 4-4a). When d_e was high (low thermal quality), growth rate decreased by 0.005 mm/month as the volume of arthropods caught in sticky traps increased by 1 cm^3 (Table 4-8d, Figure 4-4c), but the effect was only marginally significant. At low d_e (high thermal quality), there was no effect of arthropod volume on growth rate (Table 4-8e, Figure 4-4d). Larger lizards grew more slowly, as growth rate decreased by 1.9 mm/month for every increase of 1 cm in SVL (Table 4-8a). Males grew 2.4 mm/month faster than females, and lizards grew 0.01 mm/month faster for every additional chigger infecting them. I obtained qualitatively similar results when I re-analysed the data using seven months of growth per year for all study sites.

Population Density

Population density at each capture event varied from one to 42 lizards per 1,000 m^2. Population density depended on thermal quality, food availability, and mean chigger load. There was a significant interaction between d_e and arthropod volume (Table 4-9a). Sites with lower d_e (higher thermal quality) were more densely populated, although high thermal quality more strongly benefitted populations when food availability was high (6.8 more lizards per

1,000 m^2 for every 1°C decrease in d_e, Table 4-9d, Figure 4-5a) than at low food availability (2.7 more lizards per 1,000 m^2 for every 1°C decrease in d_e, Table 4-9e, Figure 4-5b). At high d_e (low thermal quality), arthropod availability did not affect population density (Table 4-9b, Figure 4-5c). At low d_e (high thermal quality), population density increased by 4.3 lizards per 1,000 m^2 for every 1% increase in arthropod volume, but the effect was only of marginal significance (Table 4-9c, Figure 4-5d). Population density increased by 0.1 lizards per 1,000 m^2 for every additional chigger infecting lizards on average (Table 4-9a).

Discussion

The hypothesis that population density in *S. jarrovii* is driven by food availability was only weakly supported. Contrary to predictions, there was no effect of food supplementation on body condition, individual growth rate or population density. Furthermore, the relative volume of arthropods available only affected these variables by modulating the strength of their relationship with thermal quality.

The lack of effect of food supplementation on body condition, growth rate and population density in these *S. jarrovii* populations indicated either that population density was not constrained by food availability, or that food limitation existed but was not detected. I may have failed to detect food limitation if (i) I added too few mealworms to significantly increase body condition, individual growth rate or population density, (ii) supplemental food only reached a subset of the population due to resource monopolization by dominant individuals (Monaghan and Metcalfe 1985), (iii) a large fraction of lizards who benefitted from supplemental food were non-residents or emigrated from the study site, or (iv) local benefits of food supplementation were dampened by immigration (reviewed in Wirsing and Murray 2007). Although all of these scenarios are possible, explanations (ii), (iii) and (iv) are unlikely. *Sceloporus jarrovii* successfully defend localized food sources (e.g., Simon 1975), but mealworms were scattered throughout the study site. Therefore, it is improbable that a small number of dominant lizards could have monopolized the supplemental food. It is also unlikely that the benefits of food supplementation were diminished by migration of lizards to and from the study site because rates of migration were low. The study sites were largely surrounded by poor quality forest habitat, and only six out of the 1,241 lizards captured were observed to migrate between study sites. However, I cannot rule out the possibility that too little food was added to detect a change. Furthermore, the lack of effect of natural arthropod availability on demographic parameters, except through an interaction with thermal quality, suggested only weak support for the hypothesis that population density is driven by food availability in this system. Other studies have also found little correlation between demographic parameters in *Sceloporus* lizards and arthropod abundance. Natural food availability has no effect on litter size (Ballinger 1979) or female density between study plots (Ruby 1986) in *S. jarrovii*, or on growth rates in *S. graciosus* (Sears 2005). Grant and Dunham (1990) found that *S. merriami* exhibited the slowest growth rates at the site with the highest food availability.

The hypothesis that population density is driven by thermal quality, on the other hand, was more strongly supported. Body condition, individual growth rate and population density were all significantly affected by d_e. Surprisingly, although the population density of *S. jarrovii* increased with thermal quality as predicted, the opposite trend was observed for body condition and individual growth rate. Given the inverse correlation between mean daily d_e and

T_e in the habitat (Figure 4-6), it can be interpreted that *S. jarrovii* had fewer energy reserves and grew more slowly, but were found at higher densities, in warmer habitats. There are two possible explanations for this result: firstly, that there is a life-history trade-off between self-maintenance (investment in energetic reserves and individual growth to improve survival and future reproduction) and early reproduction (Stearns 1992); and secondly, that energy gain (body condition and individual growth rate) and population density are driven by different mechanisms.

Previous observations of different life-history strategies at different elevations in *S. jarrovii* suggest that there may be a trade-off between self-maintenance (investment in energetic reserves and individual growth to improve survival and future reproduction) and early reproduction. Ballinger (1973, 1979) found that female *S. jarrovii* reproduced earlier on average at low elevation. At low elevation, 60% of females reproduced in their first year, whereas all females delayed reproduction until their second year at high elevation. Delayed maturation in colder environments allows females to grow larger and increase fecundity at first reproduction, and is favoured when increased fecundity outweighs the cost of reduced survival to maturity (Stearns 1992, Roff 2002). If females allocate more energy to reproduction than to body condition and growth in habitats of high thermal quality, and their mean lifetime reproductive success is higher than for females in habitats of low thermal quality, then it is possible that mean body condition and individual growth rate decrease with thermal quality, while population density increases.

Alternatively, different mechanisms could be driving body condition and individual growth rate as opposed to population density. Possible mechanisms for a decline in body condition and individual growth rate in warmer habitats include more competition for resources due to higher population density (Jenkins et al. 1999, Choquenot 1991, Lorenzon and Enberg 2002), or a reduction in net energy gain at temperatures above the optimum (Brett 1971, Huey 1982). Population density, conversely, may be constrained by overwinter conditions, if colder overwinter temperatures in cooler habitats reduce survival and/or reproductive success (Hurst and Conover 1998, Qualls and Andrews 1999, Frederiksen and Bregnballe 2001).

The first possible explanation for declining body condition and growth rate at sites of higher thermal quality is that the high population densities at these sites increases competition for resources. Lizards can occur at very high densities where competition and resource depletion are likely (Buckley and Jetz 2007), and high levels of competition may reduce individual fitness and population growth rate (Hassell 1975, Ohman and Hirche 2001, Rotger et al. 2016). Growth rate frequently decreases with density in lizards (Massot et al. 1992, Tinkle et al. 1993, Mugabo et al. 2013, Rotger et al. 2016, but see Paterson and Blouin-Demers 2018). In *S. jarrovii*, females have smaller home ranges and are more aggressive and territorial at low elevation (Ruby and Baird 1994), which is consistent with the idea that there is stronger competition for resources in habitats of high thermal quality. If body condition and growth rate were constrained at high thermal quality sites by competition for resources, we would expect an increase in these variables as food abundance increased. Halliday and Blouin-Demers (2014), for example, observed strong density-dependence in red flour beetles (*Tribolium castaneum*): fecundity increased sharply with food abundance in high thermal quality habitat. However, I did not detect an increase in body condition or growth rate following food supplementation, or as relative arthropod availability increased at sites with low d_e (Figures 4-3d and 4-4d).

Another explanation for declining body condition and growth rate at sites of higher thermal quality is that lizards at these sites may experience a higher frequency of hot temperatures that reduce net energy gain. Net energy gain decreases at high T_b because standard metabolic rate (energy loss) increases exponentially with T_b, whereas the rate of food assimilation (gross energy gain) plateaus and eventually can no longer compensate for metabolic losses (Huey 1982). Furthermore, thermal performance curves are asymmetrical and T_bs above the optimal T_b reduce the net energy gained to a greater extent than T_bs an equal distance below the optimum (Martin and Huey 2008). Net energy gain may also decline in warmer habitats if lizards lower their activity levels (and thus their rate of food consumption) to avoid lethal T_bs or reduce their risk of desiccation (Jones et al. 1987, Grant and Dunham 1988). Because T_bs that maximize energy assimilation often approximate those exhibited during activity, the rate of energy assimilation typically increases with the activity window (Angilletta 2001, Niewiarowski 2001). In fact, *S. jarrovii* lizards have been observed to reduce their activity level at mid-day to avoid hot temperatures (Burns 1970, Beuchat 1989). If net energy gain is constrained at high T_bs by metabolic losses, and these losses are exacerbated when food is limited (Huey 1982), then body condition and growth rate should decline more rapidly with rising temperatures at lower food availability. Indeed, the finding that body condition and growth rate decrease more quickly with decreasing d_e when food availability is low (Figures 4-3, 4-4) supports the idea that these variables are driven by energetics at high temperatures.

In contrast, population density may be regulated primarily by overwintering conditions. Higher elevations tend to experience colder winters with greater snowfall in the southwestern United States (Ruby 1977, Körner 2007), and increased severity and length of winters reduces survival (Hurst and Conover 1998, Frederiksen and Bregnballe 2001, McCaffrey and Maxell 2010). Furthermore, cold incubation temperatures may have detrimental effects on embryos, such as smaller size and lower locomotor performance, growth rate, and survival (e.g., Qualls and Andrews 1999, Patterson and Blouin-Demers 2008). In *S. jarrovii*, Ruby (1977) found that gravid females maintained at constant cold temperatures in the lab over the winter had low survival and high weight loss, and that parturition in the field occurred later following colder winters. The larger adult body size of *S. jarrovii* at higher elevations (Ballinger 1973, 1979; see chapter 3) also suggests the importance of overwinter survival in habitats of poor thermal quality, because larger individuals tend to have higher overwinter survival (Civantos et al. 1999, Zani 2008). *S. jarrovii* hatchlings are born later at higher elevations (Ballinger 1979) and so are smaller upon hibernation. Increased growth rate sometimes evolves to compensate for a short growing season (e.g., Conover and Present 1990). If a larger body size and larger energetic reserves increase overwinter survival, there may be selective pressure for *S. jarrovii* at high elevations to grow more quickly and allocate more energy to fat reserves.

Population density was also influenced by an interaction between thermal quality and food availability, such that density increased faster with thermal quality when more food was available (Figure 4-5a-b). This suggests that thermal quality is the main constraint on population density, but when thermal quality is high, food availability becomes constraining. Thermal quality has also been found to be a stronger driver of abundance than food availability in snakes. Halliday and Blouin-Demers (2016) found that three snake species were more abundant in high thermal quality field habitat than forest habitat, despite a similar availability of food items in both habitats. Similarly, in a two-habitat experiment, Halliday and Blouin-Demers (2014) found that the abundance of red flour beetles was higher in the warm habitat than the cold habitat in all cases, except when food availability was higher in the cold habitat and overall food competition was high.

One potential source of error in this study is that I did not quantify the spatial arrangement of surface T_es in each slope. Talus slopes are different sizes and shapes, and so the average accessibility of surface shade under vegetation may differ by site. Sears et al. (2016) demonstrated that *S. jarrovii* thermoregulated more accurately in an arena with a sandy substrate and a dispersed distribution of sun and shade than in one with a clumped distribution of sun and shade, suggesting that the spatial arrangement of T_es is important for thermal quality. On a talus slope, however, sub-surface T_es are several degrees cooler than the surface (L. Patterson, unpublished data) and are easily accessible at every point in the habitat within a meter below the loose rocks. The spatial arrangement of surface shade temperatures is less likely to influence the accuracy of thermoregulation in rocky talus slope habitat than in an arena with a flat substrate devoid of thermal refuges.

It is also possible that body condition, growth rate and/or population density are driven by variables that were not measured in this study. Although I attempted to measure potentially confounding factors such as predation risk and parasite load, I did not measure moisture or precipitation. Precipitation may affect energy gain or population density indirectly, through its effect on arthropod abundance (Dunham 1978) or microhabitat selection (Ryan et al. 2016); or may affect energy gain directly. Lack of moisture, for example, hampers growth in *Lacerta vivipara* (Lorenzon et al. 1999). A future direction of research would be to investigate the interaction of precipitation, thermal quality and food availability on energy gain and population density.

Overall, my results suggest that, in terrestrial vertebrate ectotherms, thermal quality is a stronger driver of population density than food availability, but that the strength of the relationship depends on food availability. Furthermore, the mechanism appears to be different for energy gain and population density. Body condition and growth rate declined with thermal quality, probably due to the detrimental effect of more frequent T_bs above the optimal temperature for net energy gain at warmer sites (Huey 1982, Martin and Huey 2008), and this effect was exacerbated when less food was available (Huey 1982). Population density, on the other hand, increased with thermal quality, likely because of the effect of cold temperatures overwinter at sites of poor thermal quality on survival and/or reproductive success (Hurst and Conover 1998, Qualls and Andrews 1999, Frederiksen and Bregnballe 2001, McCaffrey and Maxell 2010). Population density also increased faster with thermal quality when more food was available (Figure 4-5a-b). Linking patterns of energy gain and population density to aspects of habitat quality is important because it allows us to more accurately predict the density and distribution of species. The links between habitat thermal quality, energy gain and population density is particularly important in predicting the response of ectothermic animals to climate change (e.g., Kearney et al. 2009, Sinervo et al. 2010).

Tables and Figures

Table 4-1. The elevation (m) and geographical coordinates in latitude (x) and longitude (y) of the centroids of the study sites in the Chiricahua Mountains of Coronado National Forest, Arizona, U.S.A. The area (m^2) of the study site is also indicated.

General location	Site code	Elevation (m)	x	y	Area (m^2)
Barfoot	BF2	2,535	-109.279	31.91881	6,281.7
	BF4	2,589	-109.275	31.91687	16,050.2
Price Canyon	PC1	1,850	-109.259	31.76232	4,607.4
	PCX	1,884	-109.258	31.76157	2,846.1
Rucker Canyon	RC2	2,162	-109.292	31.79971	4,476.3
	RC5	2,134	-109.275	31.79632	9,756. 6
Rustler's Campground	RS1	2,709	-109.287	31.88896	5,098.9
	RSF	2,605	-109.289	31.88994	4,019.9
South Fork	SF1	1,741	-109.192	31.85138	3,554.3
	SF3	1,757	-109.187	31.85768	1,783.4

Table 4-2. Comparison of linear mixed models related to the (a) body condition, (b) individual growth rate and (c) population density of *Sceloporus jarrovii* lizards at ten study sites in the Chiricahua Mountains, Arizona, U.S.A. (correlation analyses). The fixed effects included an index of site thermal quality (d_e), site arthropod availability (Vol), chigger load (Chig for individual and avChig for average), sex, Julian date of capture (Julian), gravidity status (gravid or not), tail autotomy (Auto for individual and avAuto for average) and initial snout-vent length (SVL_i). The random effects for body condition models were year nested within study site, for growth models were lizard ID nested within study site, and for population density models were study site. Models were fitted by maximizing the log-likelihood. Models are ranked by Akaike's Information Criterion corrected for small sample sizes (AIC_c). Also shown are the model degrees of freedom (DF) and weights (w_i).

Model	Fixed effects	DF	AIC_c	ΔAIC_c	w_i
(a)	$d_e \times$ Vol + Chig + Sex + Julian + Gravid	11	1498.1	0.0	0.68
	$d_e \times$ Vol + Sex + Julian + Gravid	10	1499.6	1.5	0.32
(b)	$d_e \times$ Vol + Auto + avChig + Sex + SVL_i	11	1494.9	0.5	0.43
	d_e + Vol + Auto + avChig + Sex + SVL_i	10	1494.4	0.0	0.57
(c)	$d_e \times$ Vol + avChig + avAuto + Julian	9	277.6	4.9	0.06
	$d_e \times$ Vol + avChig + Julian	8	274.2	1.5	0.31
	$d_e \times$ Vol + avChig	7	272.7	0.0	0.64

Table 4-3. Comparison of linear mixed models related to the body condition of *Sceloporus jarrovii* lizards at ten study sites in the Chiricahua Mountains, Arizona, U.S.A. (before and after comparison). The fixed effects included an index of site thermal quality (d_e), site arthropod availability (Volume), chigger load (Chig), sex, Julian date of capture, gravidity status (Gravid), time period (BA) and site type (Sup, supplemented or not). All models included study site as a random effect and were fitted by maximizing the log-likelihood. Models are ranked by Akaike's Information Criterion corrected for small sample sizes (AIC_c). Also shown are the model degrees of freedom (DF) and weights (w_i).

Fixed effects	DF	AIC_c	ΔAIC_c	w_i
d_e × BA × Sup + Vol + Julian + Chig + Gravid + Sex	15	485.7	14.3	0
d_e + BA + Sup + Vol + Julian + Chig + Gravid + Sex + d_e:BA + d_e:Sup + BA:Sup	14	483.7	12.3	0
d_e + BA + Sup + Vol + Julian + Chig + Gravid + Sex + d_e:BA + BA:Sup	13	481.5	10.1	0
d_e + BA + Sup + Vol + Julian + Chig + Gravid + d_e:BA + BA:Sup	12	479.4	8.0	0.01
d_e + BA + Sup + Vol + Julian + Chig + Gravid + d_e:BA	11	477.5	6.1	0.02
d_e + BA + Vol + Julian + Chig + Gravid + d_e:BA	10	475.3	3.9	0.07
d_e + BA + Vol + Chig + Gravid + d_e:BA	9	473.7	2.3	0.15
d_e + BA + Vol + Gravid + d_e:BA	8	472.3	0.9	0.3
d_e + BA + Vol + Gravid	7	471.4	0	0.46

Table 4-4. Comparison of linear mixed models related to individual growth rate of *Sceloporus jarrovii* lizards at ten study sites in the Chiricahua Mountains, Arizona, U.S.A. (before and after analysis). The fixed effects included an index of site thermal quality (d_e), site arthropod availability (Vol), average chigger load (avChig), tail autotomy status (Auto), time period (BA) and site type (Sup), sex, and initial snout-vent length (SVLi). All models included lizard ID nested within study site as a random effect and were fitted by maximizing the log-likelihood. Models are ranked by Akaike's Information Criterion corrected for small sample sizes (AIC_c). Also shown are the model degrees of freedom (DF) and weights (w_i).

Fixed effects	DF	AIC_c	ΔAIC_c	w_i
BA × d_e × Sup + avChig + Auto + Volume + Sex + SVLi	16	1343.1	10.7	0
BA × d_e × Sup + avChig + Volume + Sex + SVLi	15	1341.4	9.0	0.01
BA + d_e + Sup + avChig + Volume + Sex + SVLi + BA:d_e + Sup:d_e + BA:Sup	14	1339.9	7.6	0.01
BA + d_e + Sup + avChig + Volume + Sex + SVLi + BA:d_e + BA:Sup	13	1337.9	5.5	0.03
BA + d_e + Sup + avChig + Sex + SVLi + BA:d_e + BA:Sup	12	1336.8	4.4	0.06
BA + d_e + Sup + avChig + Sex + SVLi + BA:d_e	11	1335.3	2.9	0.11
BA + d_e + avChig + Sex + SVLi + BA:d_e	10	1333.4	1.1	0.29
BA + d_e + Sex + SVLi + BA:d_e	9	1332.4	0.0	0.49

Table 4-5. Comparison of linear mixed models related to population density of *Sceloporus jarrovii* lizards at ten study sites in the Chiricahua Mountains, Arizona, U.S.A. (before and after analysis). The fixed effects included an index of site thermal quality (d_e), site arthropod availability (Vol), average chigger load (avChig), percentage of lizards with tail autotomy (Auto), time period (BA) and site type (Sup). All models included study site as a random effect and were fitted by maximizing the log-likelihood. Models are ranked by Akaike's Information Criterion corrected for small sample sizes (AIC_c). Also shown are the model degrees of freedom (DF) and weights (w_i).

Fixed effects	DF	AIC_c	ΔAIC_c	w_i
BA × d_e × Sup + avChig + Auto + Volume	13	51.4	45.7	0
BA + d_e + Sup + avChig + Auto + Volume + BA:d_e + Sup:d_e + BA:Sup	12	34.0	28.3	0
BA + d_e + Sup + avChig + Auto + Volume + BA:d_e + BA:Sup	11	22.1	16.4	0
BA + d_e + Sup + avChig + Auto + Volume + BA:Sup	10	21.9	16.2	0
BA + d_e + Sup + avChig + Volume + BA:Sup	9	19.5	13.8	0
BA + d_e + Sup + avChig + Volume	8	17.8	12.1	0
BA + d_e + avChig + Volume	7	12.4	6.8	0.01
BA + avChig + Volume	6	8.4	2.8	0.11
BA + avChig	5	8.0	2.3	0.14
avChig	4	6.3	0.6	0.32
1	3	5.7	0	0.43

Table 4-6. Parameter estimates of the averaged linear mixed models relating to population density in *Sceloporus jarrovii* lizards at ten sites in the Chiricahua Mountains, Arizona, U.S.A. (before and after analysis). The fixed effects include indices of site thermal quality (d_e) and log-transformed arthropod availability (Vol), Julian date of capture, average ectoparasite load (avChig), and proportion of lizards with tail autotomy (Auto), whereas the random effect was study site for all models. All models were fitted by maximizing the log-likelihood. Presented are the results for the (a) general model, (b) "before" subset, (c) "after" subset. SE refers to standard error and DF to degrees of freedom. Model subsets were not averaged and so the model R^2, values, DFs and t-values are reported.

Model	Fixed effects	Estimate (or value)	SE	Adjusted SE (or DF)	z-value (or t-value)	P
(a)	BA	0.10	0.07	0.08	1.36	0.17
	Sup	0.16	0.23	0.27	0.60	0.55
	d_e	0.05	0.05	0.06	0.74	0.46
	Vol	-0.001	0.001	0.001	1.58	0.12
	avChig	0.006	0.004	0.004	1.45	0.15
	Auto	0.005	0.002	0.003	1.90	0.06
	BA:Sup	-0.19	0.07	0.09	2.00	0.046
	BA:d_e	-0.07	0.02	0.04	1.94	0.05
	d_e:Sup	-0.03	0.03	0.07	0.44	0.66
	BA:d_e:Sup	0.05	0.09	0.61	0.09	0.93

(b) ($R^2 < 0.01$)	Sup	-0.007	0.20	8	-0.03	0.97
(c) ($R^2 = 0.06$)	Sup	0.15	0.20	8	0.72	0.49

Table 4-7. Parameter estimates of the averaged linear mixed models relating to body condition in *Sceloporus jarrovii* lizards at ten sites in the Chiricahua Mountains, Arizona, U.S.A. (correlation). The fixed effects include indices of site thermal quality (d_e) and arthropod availability (Volume), Julian date of capture, ectoparasite load (Chig), sex, and gravidity status (Gravid), whereas the random effects were year nested within study site for all models. All models were fitted by maximizing the log-likelihood. Presented are the results for the (a) general model, and for the (b) high food, (c) low food, (d) high d_e, and (e) low d_e subsets.

Model	Fixed effects	Estimate	SE	Adjusted SE	z-value	P
(a)	d_e	0.14	0.04	0.04	3.94	<0.0001
	Volume	0.004	0.002	0.002	2.58	0.01
	Julian	0.005	0.001	0.001	4.72	<0.0001
	Chig	-0.001	0.001	0.001	1.89	0.06
	Sex	0.17	0.05	0.05	3.34	0.0008
	Gravid	0.70	0.10	0.10	6.76	<0.0001
	d_e:Volume	-0.0005	0.0002	0.0002	2.72	0.006
(b)	d_e	0.001	0.03	0.03	0.04	0.97
	Julian	0.01	0.002	0.002	6.28	<0.0001
	Chig	-0.002	0.001	0.001	2.35	0.02
	Sex	0.24	0.08	0.08	3.12	0.002
	Gravid	1.01	0.14	0.14	7.12	<0.0001

(c)	d_e	0.16	0.05	0.05	3.19	0.001
	Julian	0.003	0.002	0.002	2.02	0.04
	Chig	-0.0004	0.0007	0.0007	0.65	0.52
	Sex	0.12	0.06	0.06	2.01	0.04
	Gravid	0.43	0.15	0.15	2.89	0.004
(d)	Volume	-0.001	0.0004	0.0004	1.41	0.16
	Julian	0.003	0.001	0.001	2.16	0.03
	Chig	-0.001	0.001	0.001	0.82	0.41
	Sex	0.17	0.07	0.07	2.36	0.02
	Gravid	0.67	0.13	0.13	5.38	<0.0001
(e)	Volume	0.001	0.001	0.001	1.55	0.12
	Julian	0.01	0.002	0.002	4.56	<0.0001
	Chig	-0.004	0.002	0.002	2.18	0.03
	Sex	0.18	0.07	0.07	2.59	0.01
	Gravid	0.94	0.20	0.20	4.79	<0.0001

Table 4-8. Averaged parameter estimates for the effects of thermal quality (d_e), arthropod volume, average chigger load (avChig), sex, initial snout-vent length (SVL_i), and tail autotomy (Auto) on the individual growth rate of *Sceloporus jarrovii* lizards in the Chiricahua Mountains, Arizona, U.S.A. (correlation analysis). SE is the standard error. Parameter estimates are shown for (a) the general model, (b) the "high food" subset, (c) the "low food" subset, (d) the "high d_e" subset, and (e) the "low d_e" subset. The (c) model was not averaged and so I present the model R^2, degrees of freedom (DF) and the t-value.

Model	Parameters	Estimate	SE	Adjusted SE (or DF)	z-value (or t-value)	P
(a)	d_e	1.15	0.20	0.21	5.54	<0.0001
	Volume	0.03	0.01	0.01	2.27	0.02
	avChig	0.01	0.004	0.004	2.48	0.01
	Sex	2.41	0.24	0.24	9.89	<0.0001
	SVL_i	-1.86	0.10	0.11	17.83	<0.0001
	Auto	-0.32	0.26	0.26	1.23	0.22
	d_e:Volume	-0.003	0.001	0.001	2.60	0.01
(b)	d_e	0.55	0.26	0.26	2.09	0.04
	avChig	0.01	0.01	0.01	1.18	0.24
	Sex	2.52	0.28	0.28	9.06	<0.0001
	SVL_i	-1.88	0.12	0.13	14.61	<0.0001

(c) ($R^2 = 0.58$)	d_e	1.32	0.21	18	6.35	<0.0001
	avChig	0.02	0.01	18	3.16	0.005
	Sex	2.08	0.42	108	5.00	<0.0001
	SVL_i	-1.96	0.16	18	-12.62	<0.0001
(d)	Volume	-0.01	0.003	0.003	1.91	0.06
	avChig	0.01	0.005	0.01	2.27	0.02
	Sex	2.09	0.30	0.30	6.90	<0.0001
	SVL_i	-1.86	0.14	0.14	13.22	<0.0001
(e)	Volume	-0.002	0.003	0.003	0.55	0.58
	avChig	0.01	0.01	0.01	0.59	0.56
	Sex	3.04	0.40	0.40	7.52	<0.0001
	SVL_i	-1.80	0.14	0.15	12.27	<0.0001

Table 4-9. Parameter estimates of the averaged linear mixed models relating to population density in *Sceloporus jarrovii* lizards at ten sites in the Chiricahua Mountains, Arizona, U.S.A. (correlation analysis). The fixed effects include indices of site thermal quality (d_e) and log-transformed arthropod availability (Vol), Julian date of capture, average chigger load (avChig), and proportion of lizards with tail autotomy (Auto), whereas the random effect was study site for all models. All models were fitted by maximizing the log-likelihood. Presented are the results for the (a) general model, and for the (b) high food, (c) low food, (d) high d_e, and (e) low d_e subsets. SE refers to standard error and DF to degrees of freedom. Model subsets were not averaged and so the model R^2, values, DFs and t-values are reported.

Model	Fixed effects	Estimate (or value)	SE	Adjusted SE (or DF)	z-value (or t-value)	P
(a)	d_e	5.64	3.69	3.88	1.46	0.15
	Vol	19.97	7.05	7.42	2.69	0.01
	avChig	0.14	0.07	0.07	1.99	0.046
	Julian	0.05	0.04	0.04	1.18	0.24
	Auto	0.004	0.10	0.11	0.04	0.97
	d_e : Vol	-2.05	0.82	0.86	2.39	0.02
(b) R^2 = 0.81	d_e	-6.80	1.80	8	-3.78	0.01
	avChig	0.23	0.09	8	2.52	0.04

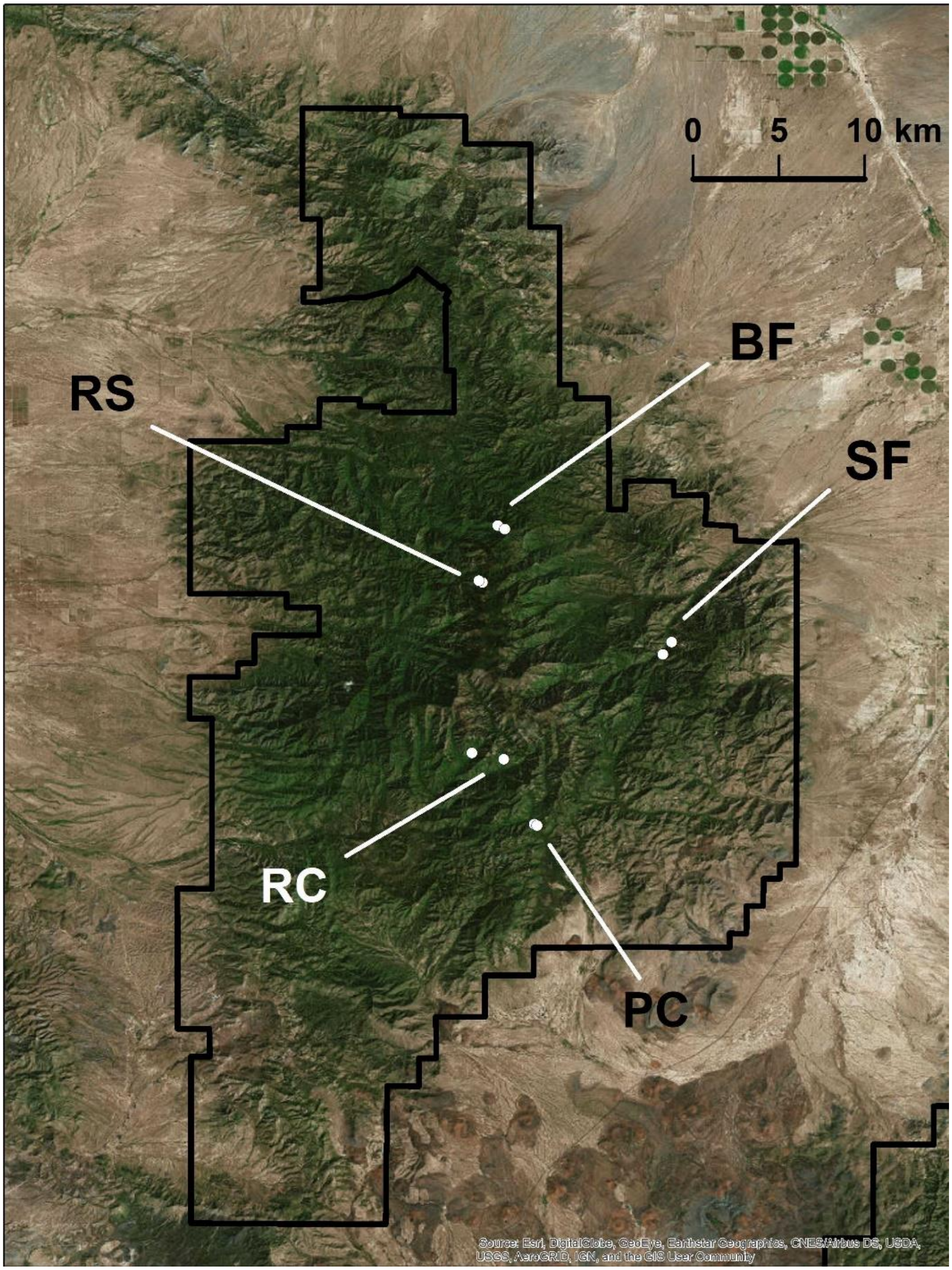
(c) R^2=0.57	d_e	-2.67	1.07	7	-2.50	0.04
	avChig	0.16	0.07	7	2.23	0.06
(d) R^2=0.87	Vol	-0.62	0.74	11	-0.84	0.42
	avChig	0.07	0.02	11	3.02	0.01
(e) R^2 = 0.75	Vol	4.26	1.95	11	2.18	0.052
	avChig	0.36	0.17	11	2.13	0.06

Table 4-10. Parameter estimates of the averaged linear mixed models relating to body condition in *Sceloporus jarrovii* lizards at ten sites in the Chiricahua Mountains, Arizona, U.S.A. (before and after analysis). The fixed effects include indices of site thermal quality (d_e) and arthropod availability (Vol), time period (BA), site type (Sup), Julian date of capture, chigger load (Chig), sex, and gravidity status (Gravid), whereas the random effects were year nested within study site for all models. All models were fitted by maximizing the log-likelihood.

Fixed effects	Estimate	SE	Adjusted SE	z-value	P
d_e	0.24	0.05	0.05	5.09	<0.0001
BA	0.02	0.90	0.91	0.02	0.99
Sup	0.02	0.26	0.30	0.08	0.94
Vol	-0.002	0.001	0.001	2.33	0.02
Gravid	0.50	0.08	0.08	6.14	<0.0001
Sex	0.04	0.10	0.10	0.38	0.71
Chig	-0.001	0.001	0.001	0.82	0.41
Julian	-0.01	0.01	0.01	0.71	0.48
BA:Sup	-0.11	0.38	0.38	0.28	0.78
BA:d_e	-0.11	0.11	0.11	1.02	0.31
d_e:Sup	-0.02	0.12	0.12	0.17	0.87
BA:d_e:Sup	0.09	0.20	0.20	0.43	0.67

Table 4-11. Parameter estimates of the averaged linear mixed models relating to individual growth rate in *Sceloporus jarrovii* lizards at ten sites in the Chiricahua Mountains, Arizona, U.S.A. (before and after analysis). The fixed effects included an index of site thermal quality (d_e), site arthropod availability (Vol), average chigger load (avChig), tail autotomy status (Auto), time period (BA) and site type (Sup), sex, and initial snout-vent length (SVL_i), whereas the random effect was lizard ID nested within study site for all models. All models were fitted by maximizing the log-likelihood. Presented are the results for the general model. SE refers to standard error and DF to degrees of freedom.

Fixed effects	Estimate	SE	Adjusted SE	z-value	P
BA	6.98	3.55	3.63	1.92	0.055
Sup	0.21	2.11	2.42	0.09	0.93
d_e	1.05	0.38	0.39	2.66	0.01
Volume	-0.004	0.004	0.004	1.01	0.31
avChig	0.01	0.01	0.01	1.02	0.31
Auto	-0.22	0.30	0.30	0.72	0.47
Sex	2.79	0.28	0.28	9.91	<0.0001
SVL_i	-1.89	0.12	0.12	15.69	<0.0001
d_e:Sup	0.04	0.77	0.77	0.06	0.95
BA:Sup	1.24	3.07	3.07	0.40	0.69
BA:d_e	-0.78	0.40	0.40	1.93	0.054
BA:d_e:Sup	-0.86	0.90	0.91	0.95	0.34



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure 4-1. Map of the 10 study sites in the Chiricahua Mountains, Arizona, U.S.A., in each of five areas: Barfoot Park (BF), Price Canyon (PC), Rucker Canyon (RC), Rustler Park (RS), and South Fork (SF).

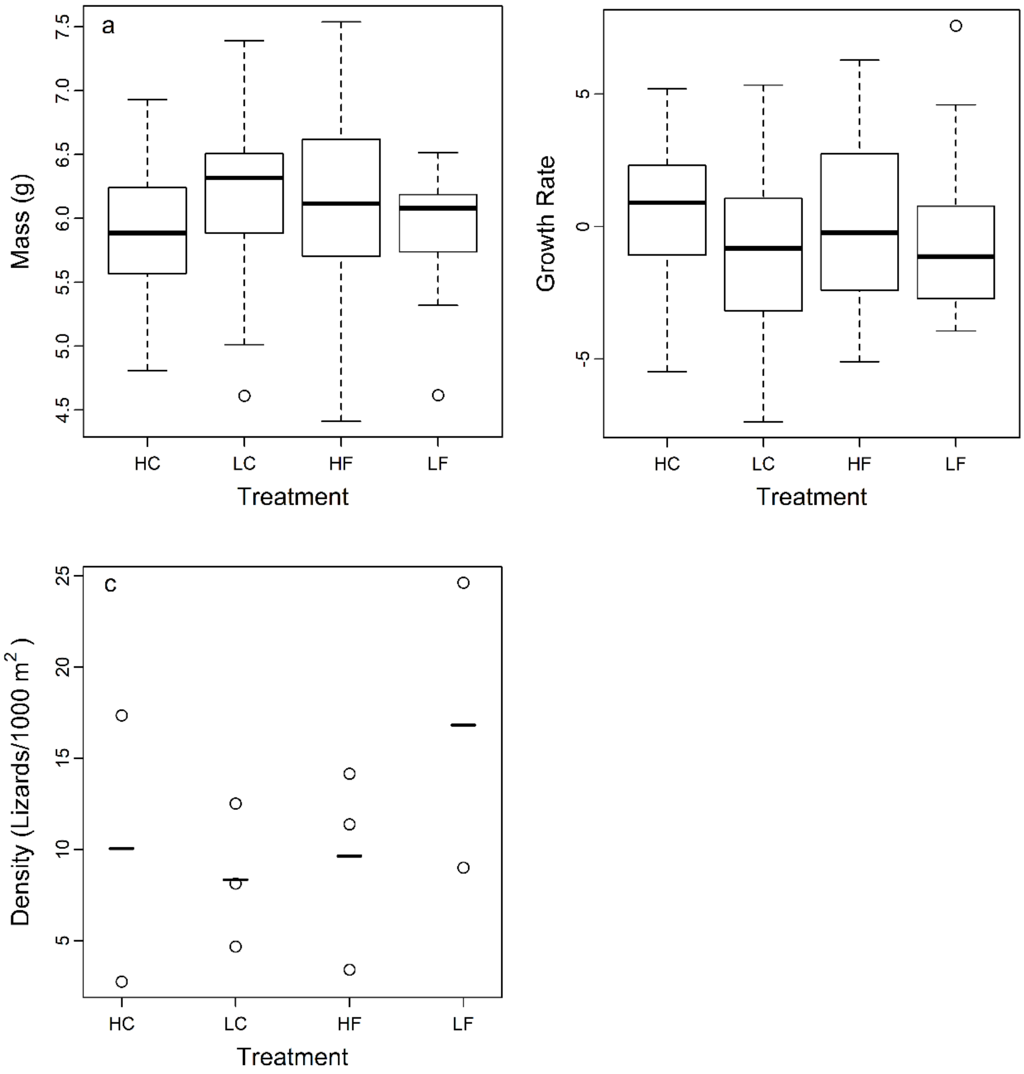


Figure 4-2. The effect of food-supplementation and thermal quality (d_e, °C) on the (a) body condition, (b) growth rate, and (c) density (lizards/1,000 m^2) of *Sceloporus jarrovii* lizards at 10 study sites after manipulations. Treatments include high d_e (H), low d_e (L), control (C) and food-supplemented (F). Sites are binned into high and low d_e based on the median d_e value to illustrate food × thermal quality interactions (if present). Body condition is represented as the scaled mass index: the predicted mass (g) of a lizard with a snout-vent length of 5.73 cm. The residuals of the linear regression of growth rate on initial snout-vent length are presented as growth rate.

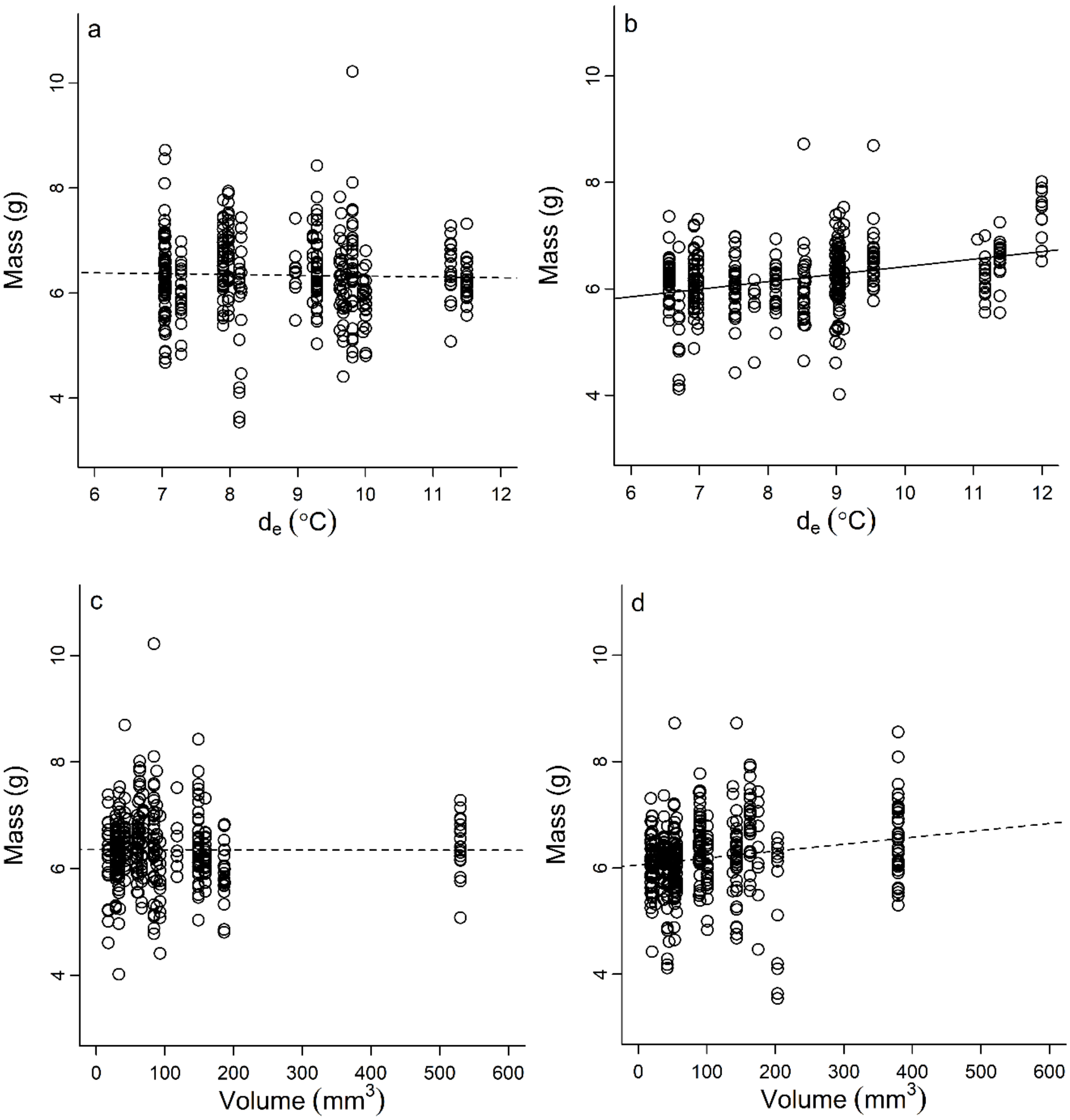


Figure 4-3. The effect of site thermal quality (d_e, °C) and food availability (arthropod volume, mm^3) on body condition of *Sceloporus jarrovii* lizards at 10 study sites in the Chiricahua Mountains, Arizona, U.S.A. Body condition is represented as the scaled mass index: the predicted mass of a lizard with a snout-vent length of 5.73 cm. Relationships are shown for (a) high food, (b) low food, (c) high d_e, and (d) low d_e conditions. Solid lines represent trends significant at $\alpha = 0.05$, whereas dotted lines represent non-significant trends.

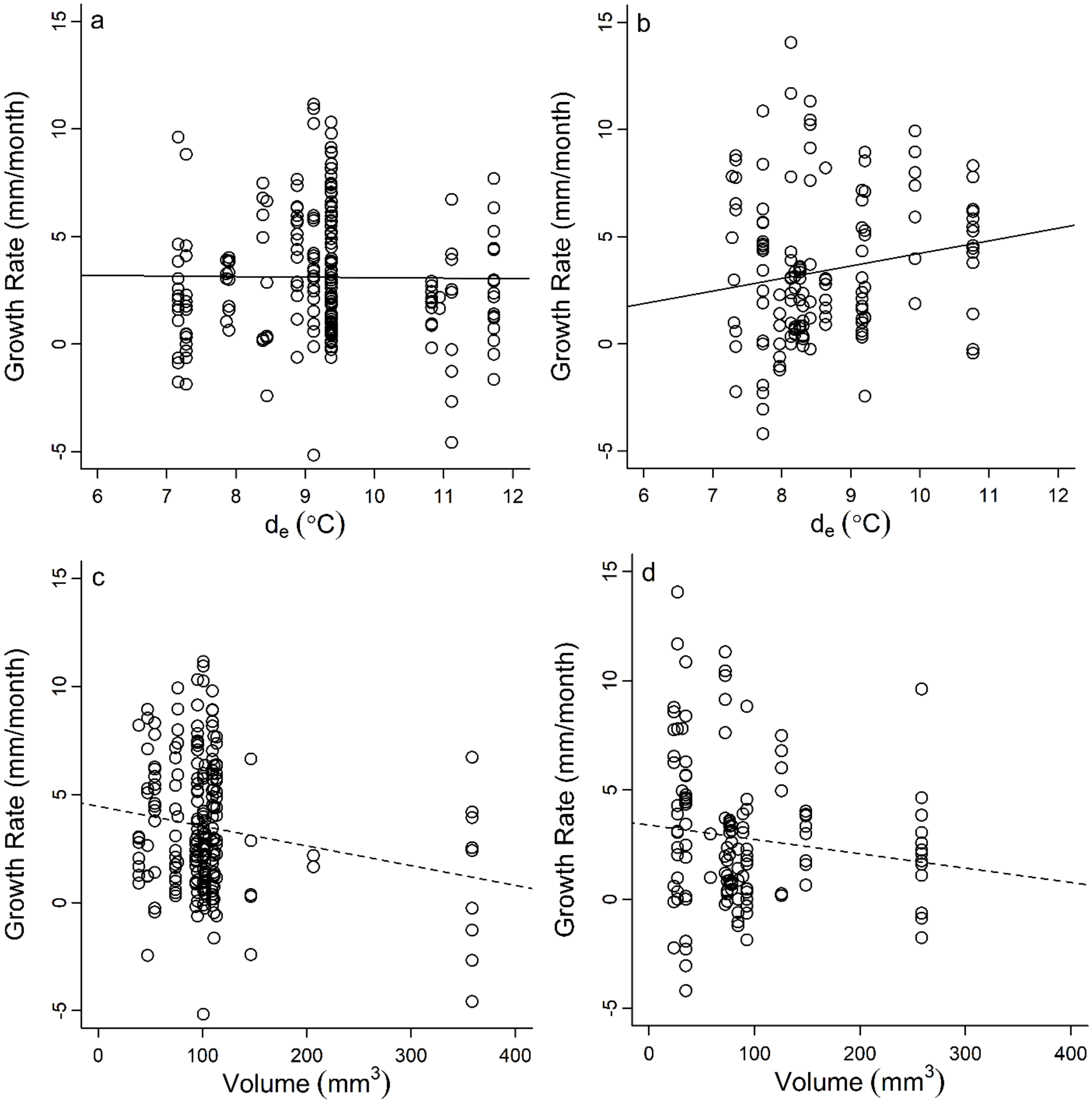


Figure 4-4. The effect of the indices of site thermal quality (d_e, °C) and food availability (arthropod volume, mm^3) on growth rate (mm/month) of *Sceloporus jarrovii* lizards at 10 study sites in the Chiricahua Mountains, Arizona, U.S.A. Relationships are shown for (a) high food, (b) low food, (c) high d_e, and (d) low d_e conditions. Solid lines represent trends significant at $\alpha = 0.05$, whereas dotted lines represent non-significant trends.

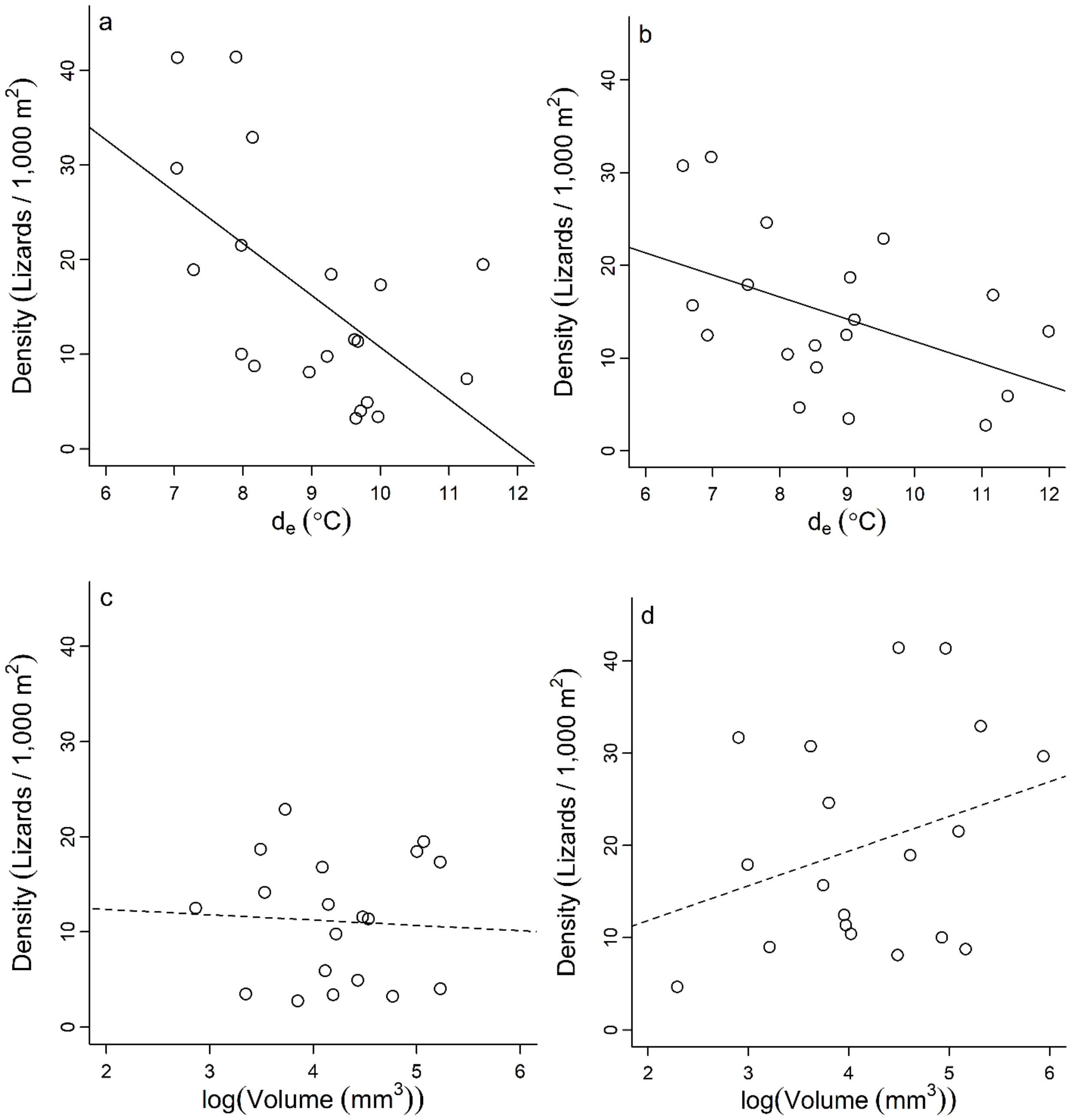


Figure 4-5. The effect of the indices of site thermal quality (d_e, °C) and food availability (arthropod volume, mm^3) on population density (number/1,000 m^2) of *Sceloporus jarrovii* lizards at 10 study sites in the Chiricahua Mountains, Arizona, U.S.A. Relationships are shown for (a) high food, (b) low food, (c) high d_e, and (d) low d_e conditions. Solid lines represent trends significant at α = 0.05, whereas dotted lines represent non-significant trends.

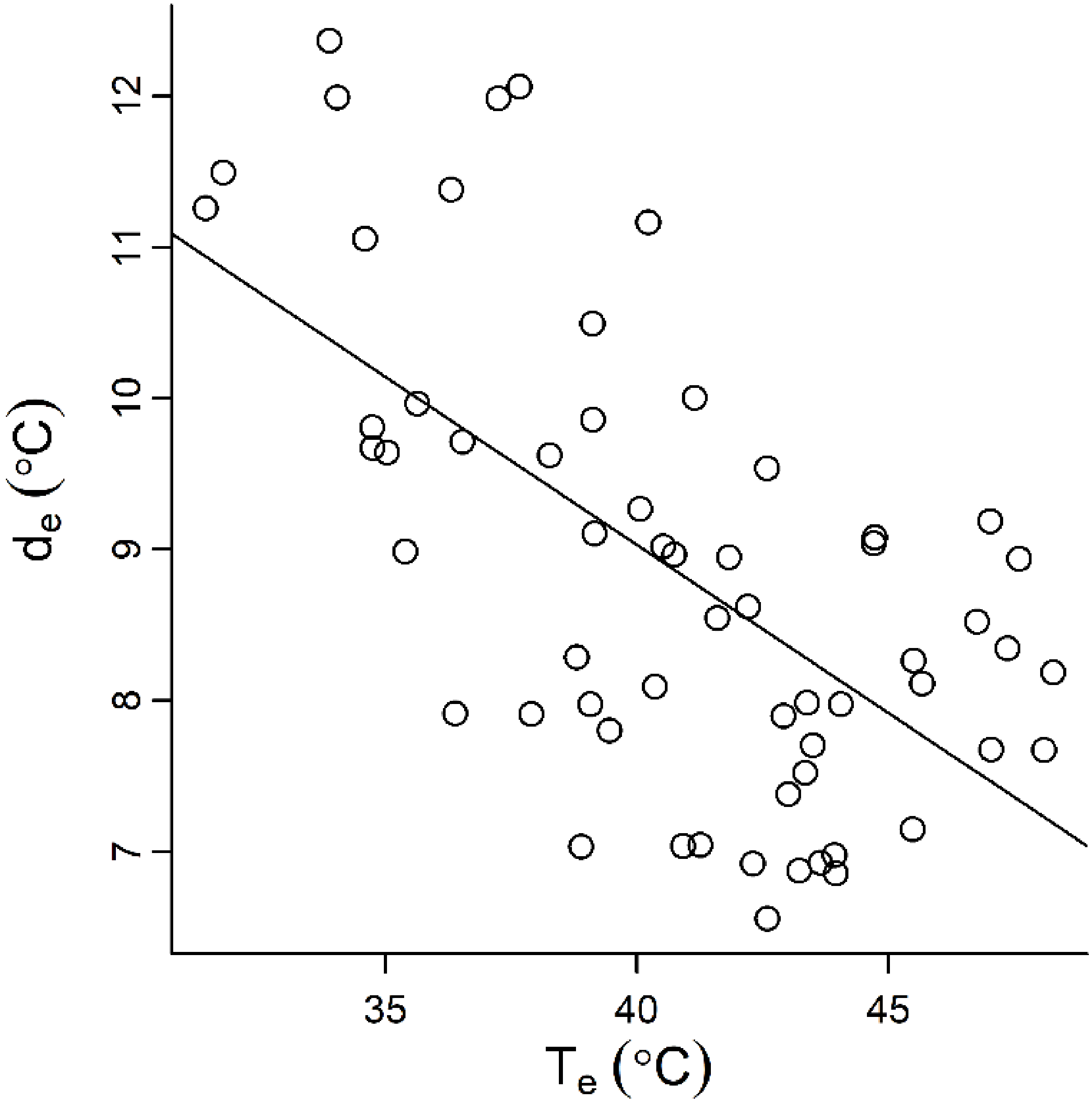


Figure 4-6. Thermal quality (d_e, °C) as a function of the daily high operative environmental temperature (T_e, °C), both averaged by month, at 10 study sites in the Chiricahua Mountains, Arizona, U.S.A.

Supplementary Information 1

Goodness of fit testing and model results for mark-recapture analyses

Here, I show how I tested whether my models met the assumptions of Jolly-Seber (JS) mark-recapture models, and summarize the models I used to estimate the abundance of every site and capture event. The assumptions of JS mark-recapture models (Jolly 1965, Seber 1965) include:

1. The marks identifying animals are not lost, missed, or misread
2. Sampling is instantaneous relative to the time differences between samples
3. The study area is constant
4. All animals (marked and unmarked) have the same probability of capture
5. All animals (marked and unmarked) have the same probability of survival between sampling occasions

It is unlikely that assumptions 1 to 3 were violated. While it is possible that some marks were missed or misread, the chances of this occurring should have been minimal as I carefully checked every lizard for marks upon capture and later double-checked identifications with photos that were also taken at each capture. Capture events were much shorter than intervals between events: capture events lasted a mean (±SE) of 1.1 ± 0.05 days, and were 96 ± 13 days apart. Furthermore, the area of each study site remained constant over time.

To assess assumptions 4 and 5, I tested the goodness-of-fit of the analogous Cormack-Jolly-Seber models (CJS, Cormack 1989) to the general models at each site. I estimated the variance inflation factor (ĉ) using bootstrapping (Lebreton et al. 1992), the median ĉ method (Cooch and White 2012), and the Fletcher method (Fletcher 2012). CJS and JS models estimate survival and detection probability using the same likelihood components (Cooch and White 2012). If the general models fit the data reasonably well and all assumptions are met, then ĉ =1. Extra-binomial variation caused by either sparse data or incorrect model structure because of assumption violations causes increases in ĉ. In general, when ĉ is between 1 and 3, the model results can be adjusted by changing ĉ and using penalized quasi-likelihood estimates ($QAIC_c$) to rank different models (Burnham and Anderson 2002). When ĉ > 3, however, the structure of the general model does not adequately fit the data (Lebreton et al. 1992). To be conservative, I adjusted the ĉ of each site to the highest estimate of the three methods used. The estimated ĉ for each method and site is presented in Table A1. In Tables A2-A11, I summarize the models with moderate support (within 4 AIC_c or $QAIC_c$ of the most parsimonious model) that were used to estimate the abundance at each site.

Table 4-S1. The Fletcher, median and bootstrap (1000 iterations) variance inflation factor ($\hat{c}$) estimates for the general Cormack-Jolly-Seber models analogous to the Jolly-Seber models used to estimate the abundance of *Sceloporus jarrovii* at 10 study sites in the Chiricahua Mountains, Arizona.

Site	Fletcher	Median	Bootstrap
BF2	1.019	1.306	0.542
BF4	0.941	1.138	0.576
PC1	0.915	1.152	0.404
PCX	0.641	2.352	0.482
RC2	1.030	1.813	0.599
RC5	1.021	1.333	0.556
RS1	0.920	0.985	0.507
RSF	0.485	Not estimable	0.008
SF1	0.974	1.490	0.690
SF3	0.621	0.905	0.344

Table 4-S2. Jolly-Seber models averaged to obtain abundance estimates of *Sceloporus jarrovii* lizards at site BF2 in the Chiricahua Mountains, Arizona. The number of parameters (NP), Akaike's Information Criterion corrected for small sample sizes and penalized using quasi-likelihood ($QAIC_c$), difference in $QAIC_c$ between each model and the model with the lowest $QAIC_c$ ($\Delta QAICc$), model weight (w_i), and deviance of all models with moderate support ($\Delta QAICc < 4$). The overdispersion parameter ($\hat{c}$) was 1.306. The parameters estimated in each model included the probability of survival between capture events (Phi), the probability of capture (p), the probability of entrance into the study population (pent), and the total number of individuals available to enter into the study population (N). These parameters varied with sex, year, temperature (Temp), sampling effort (Effort), and/or sampling occasion (time).

Model	NP	$QAIC_c$	$\Delta QAIC_c$	w_i	Deviance
Phi(~1)p(~1)pent(~time)N(~1)	11	510.16	0.00	0.31	-606.12
Phi(~Sex)p(~1)pent(~time)N(~1)	12	511.90	1.74	0.13	-606.53
Phi(~1)p(~Sex)pent(~time)N(~1)	12	512.18	2.02	0.11	-606.25
Phi(~1)p(~Temp)pent(~time)N(~1)	12	512.24	2.08	0.11	-606.19
Phi(~1)p(~Effort)pent(~time)N(~1)	12	512.30	2.14	0.11	-606.13
Phi(~Year)p(~1)pent(~time)N(~1)	13	512.55	2.39	0.09	-608.04
Phi(~Sex)p(~Temp)pent(~time)N(~1)	13	514.00	3.83	0.05	-606.59
Phi(~Sex)p(~Effort)pent(~time)N(~1)	13	514.06	3.90	0.04	-606.53
Phi(~Sex)p(~Sex)pent(~time)N(~1)	13	514.06	3.90	0.04	-606.53

Table 4-S3. Jolly-Seber models averaged to obtain abundance estimates of *Sceloporus jarrovii* lizards at site BF4 in the Chiricahua Mountains, Arizona. The number of parameters (NP), Akaike's Information Criterion corrected for small sample sizes and penalized using quasi-likelihood ($QAIC_c$), difference in $QAIC_c$ between each model and the model with the lowest $QAIC_c$ (ΔQAICc), model weight (w_i), and quasi-penalized deviance of all models with moderate support (ΔQAICc < 4). The overdispersion parameter ($\hat{c}$) was 1.138. The parameters estimated in each model included the probability of survival between capture events (Phi), the probability of capture (p), the probability of entrance into the study population (pent), and the total number of individuals available to enter into the study population (N). These parameters varied with sex, year, temperature (Temp), sampling effort (Effort), and/or sampling occasion (time).

Model	NP	$QAIC_c$	$\Delta QAIC_c$	w_i	Deviance
Phi(~1)p(~Effort)pent(~1)N(~1)	5	309.94	0.00	0.16	-276.60
Phi(~Year)p(~Effort)pent(~1)N(~1)	7	310.19	0.25	0.14	-280.67
Phi(~Year)p(~Temp+Effort)pent(~time)N(~1)	16	311.34	1.40	0.08	-300.35
Phi(~Year)p(~Temp+Effort)pent(~1)N(~1)	8	311.37	1.44	0.08	-281.69
Phi(~Year)p(~Temp)pent(~time)N(~1)	15	311.40	1.46	0.08	-297.86
Phi(~Sex)p(~Effort)pent(~1)N(~1)	6	311.97	2.03	0.06	-276.72
Phi(~1)p(~Sex+Effort)pent(~1)N(~1)	6	312.03	2.09	0.06	-276.66
Phi(~1)p(~Temp+Effort)pent(~1)N(~1)	6	312.08	2.14	0.05	-276.61
Phi(~Year)p(~Sex+Effort)pent(~1)N(~1)	8	312.34	2.41	0.05	-280.72
Phi(~Sex+Year)p(~Effort)pent(~1)N(~1)	8	312.36	2.42	0.05	-280.70
Phi(~Year)p(~Effort)pent(~time)N(~1)	15	312.92	2.98	0.04	-296.34
Phi(~Year)p(~Sex+Temp+Effort)pent(~1)N(~1)	9	313.53	3.60	0.03	-281.76
Phi(~Year)p(~Sex+Temp)pent(~time)N(~1)	16	313.57	3.63	0.03	-298.12
Phi(~Sex+Year)p(~Temp+Effort)pent(~1)N(~1)	9	313.58	3.65	0.03	-281.71
Phi(~Year)p(~Sex+Temp+Effort)pent(~time)N(~1)	17	313.68	3.74	0.02	-300.48
Phi(~Sex+Year)p(~Temp+Effort)pent(~time)N(~1)	17	313.79	3.85	0.02	-300.36
Phi(~Year)p(~1)pent(~Time)N(~1)	14	313.83	3.89	0.02	-293.03
Phi(~Sex+Year)p(~Temp)pent(~time)N(~1)	16	313.83	3.90	0.02	-297.86

Table 4-S4. Jolly-Seber models averaged to obtain abundance estimates of *Sceloporus jarrovii* lizards at site PC1 in the Chiricahua Mountains, Arizona. The number of parameters (NP), Akaike's Information Criterion corrected for small sample sizes and penalized using quasi-likelihood ($QAIC_c$), difference in $QAIC_c$ between each model and the model with the lowest $QAIC_c$ (ΔQAICc), model weight (w_i), and quasi-penalized deviance of all models with moderate support (ΔQAICc < 4). The overdispersion parameter ($\hat{c}$) was 1.152. The parameters estimated in each model included the probability of survival between capture events (Phi), the probability of capture (p), the probability of entrance into the study population (pent), and the total number of individuals available to enter into the study population (N). These parameters varied with sex, year, temperature (Temp), sampling effort (Effort), and/or sampling occasion (time).

Model	NP	$QAIC_c$	$\Delta QAIC_c$	w_i	Deviance
Phi(~Year)p(~Sex)pent(~time)N(~1)	14	237.12	0.00	0.11	-254.94
Phi(~Sex+Year)p(~1)pent(~time)N(~1)	14	237.61	0.49	0.08	-254.45
Phi(~Sex+Year)p(~Sex)pent(~time)N(~1)	15	238.23	1.11	0.06	-256.37
Phi(~Sex+Year)p(~Temp+effort)pent(~time)N(~1)	16	238.37	1.25	0.06	-258.83
Phi(~Sex+Year)p(~Temp)pent(~time)N(~1)	15	238.80	1.68	0.05	-255.81
Phi(~Year)p(~Sex+Temp)pent(~time)N(~1)	15	238.85	1.73	0.05	-255.75
Phi(~Year)p(~Sex+effort)pent(~time)N(~1)	15	239.22	2.11	0.04	-255.38
Phi(~Year)p(~Sex+Temp+effort)pent(~time)N(~1)	16	239.38	2.26	0.03	-257.82
Phi(~Sex+Year)p(~Temp)pent(~1)N(~1)	8	239.38	2.27	0.03	-238.25
Phi(~Sex)p(~Temp)pent(~1)N(~1)	6	239.42	2.30	0.03	-233.72
Phi(~Sex+Year)p(~effort)pent(~time)N(~1)	15	239.44	2.32	0.03	-255.16
Phi(~Sex+Year)p(~Sex+Temp+effort)pent(~time)N(~1)	17	239.52	2.41	0.03	-260.31
Phi(~1)p(~Sex)pent(~time)N(~1)	12	239.56	2.44	0.03	-247.53
Phi(~1)p(~Sex+Temp)pent(~1)N(~1)	6	239.61	2.50	0.03	-233.52
Phi(~Year)p(~Sex+Temp)pent(~1)N(~1)	8	239.65	2.53	0.03	-237.98
Phi(~Sex)p(~1)pent(~time)N(~1)	12	239.65	2.54	0.03	-247.43
Phi(~Sex+Year)p(~Sex+Temp)pent(~time)N(~1)	16	239.83	2.71	0.03	-257.36
Phi(~Sex)p(~Temp+effort)pent(~1)N(~1)	7	239.88	2.77	0.03	-235.48
Phi(~1)p(~Sex+Temp+effort)pent(~1)N(~1)	7	240.11	3.00	0.02	-235.25
Phi(~Sex+Year)p(~Sex+effort)pent(~time)N(~1)	16	240.20	3.09	0.02	-256.99
Phi(~Sex)p(~Sex+Temp)pent(~1)N(~1)	7	240.24	3.12	0.02	-235.13
Phi(~Sex+Year)p(~Sex+Temp)pent(~1)N(~1)	9	240.26	3.15	0.02	-239.68

Phi(~Sex)p(~Sex)pent(~time)N(~1)	13	240.53	3.41	0.02	-249.02
Phi(~Sex+Year)p(~Temp+effort)pent(~1)N(~1)	9	240.58	3.47	0.02	-239.35
Phi(~Sex)p(~Sex+Temp+effort)pent(~1)N(~1)	8	240.76	3.65	0.02	-236.87
Phi(~Year)p(~Sex+Temp+effort)pent(~1)N(~1)	9	240.87	3.75	0.02	-239.07
Phi(~Sex)p(~Temp)pent(~time)N(~1)	13	240.96	3.84	0.02	-248.59
Phi(~Year)p(~1)pent(~time)N(~1)	13	241.08	3.96	0.01	-248.47
Phi(~1)p(~Sex+Temp)pent(~time)N(~1)	13	241.11	3.99	0.01	-248.44

Table 4-S5. Jolly-Seber models averaged to obtain abundance estimates of *Sceloporus jarrovii* lizards at site PCX in the Chiricahua Mountains, Arizona. The number of parameters (NP), Akaike's Information Criterion corrected for small sample sizes and penalized using quasi-likelihood ($QAIC_c$), difference in $QAIC_c$ between each model and the model with the lowest $QAIC_c$ (ΔQAICc), model weight (w_i), and quasi-penalized deviance of all models with moderate support (ΔQAICc < 4). The overdispersion parameter ($\hat{c}$) was 2.352. The parameters estimated in each model included the probability of survival between capture events (Phi), the probability of capture (p), the probability of entrance into the study population (pent), and the total number of individuals available to enter into the study population (N). These parameters varied with sex, year, temperature (Temp), sampling effort (Effort), and/or sampling occasion (time).

Model	NP	$QAIC_c$	$\Delta QAIC_c$	w_i	Deviance
Phi(~1)p(~Effort)pent(~1)N(~1)	5	95.66	0.00	0.21	-87.55
Phi(~1)p(~Temp+Effort)pent(~1)N(~1)	6	96.06	0.41	0.17	-89.38
Phi(~1)p(~Sex+Effort)pent(~1)N(~1)	6	96.60	0.94	0.13	-88.85
Phi(~Sex)p(~Effort)pent(~1)N(~1)	6	96.77	1.11	0.12	-88.68
Phi(~1)p(~Sex+Temp+Effort)pent(~1)N(~1)	7	97.22	1.56	0.10	-90.51
Phi(~Sex)p(~Temp+Effort)pent(~1)N(~1)	7	97.35	1.69	0.09	-90.38
Phi(~Sex)p(~Sex+Effort)pent(~1)N(~1)	7	98.79	3.14	0.04	-88.94
Phi(~Year)p(~Effort)pent(~1)N(~1)	7	98.88	3.22	0.04	-88.85
Phi(~1)p(~Temp)pent(~1)N(~1)	5	98.97	3.31	0.04	-84.23
Phi(~1)p(~1)pent(~1)N(~1)	4	99.39	3.73	0.03	-81.62
Phi(~Sex)p(~Sex+Temp+Effort)pent(~1)N(~1)	8	99.43	3.78	0.03	-90.63

Table 4-S6. Jolly-Seber models averaged to obtain abundance estimates of *Sceloporus jarrovii* lizards at site RC2 in the Chiricahua Mountains, Arizona. The number of parameters (NP), Akaike's Information Criterion corrected for small sample sizes and penalized using quasi-likelihood ($QAIC_c$), difference in $QAIC_c$ between each model and the model with the lowest $QAIC_c$ (ΔQAICc), model weight (w_i), and quasi-penalized deviance of all models with moderate support (ΔQAICc < 4). The overdispersion parameter ($\hat{c}$) was 1.813. The parameters estimated in each model included the probability of survival between capture events (Phi), the probability of capture (p), the probability of entrance into the study population (pent), and the total number of individuals available to enter into the study population (N). These parameters varied with sex, year, temperature (Temp), sampling effort (Effort), and/or sampling occasion (time).

Model	NP	$QAIC_c$	$\Delta QAIC_c$	w_i	Deviance
Phi(~1)p(~Effort)pent(~1)N(~1)	5	160.39	0.00	0.28	-159.36
Phi(~1)p(~Temp+Effort)pent(~1)N(~1)	6	161.77	1.38	0.14	-160.15
Phi(~Sex)p(~Effort)pent(~1)N(~1)	6	162.49	2.11	0.10	-159.43
Phi(~1)p(~Sex+Effort)pent(~1)N(~1)	6	162.53	2.14	0.10	-159.39
Phi(~1)p(~Temp)pent(~1)N(~1)	5	162.91	2.52	0.08	-156.84
Phi(~Year)p(~Effort)pent(~1)N(~1)	7	162.91	2.52	0.08	-161.22
Phi(~Year)p(~Temp+Effort)pent(~1)N(~1)	8	163.14	2.75	0.07	-163.23
Phi(~Year)p(~Temp)pent(~1)N(~1)	7	163.59	3.20	0.06	-160.54
Phi(~Sex)p(~Temp+Effort)pent(~1)N(~1)	7	163.91	3.53	0.05	-160.22
Phi(~1)p(~Sex+Temp+Effort)pent(~1)N(~1)	7	163.94	3.55	0.05	-160.19

Table 4-S7. Jolly-Seber models averaged to obtain abundance estimates of *Sceloporus jarrovii* lizards at site RC5 in the Chiricahua Mountains, Arizona. The number of parameters (NP), Akaike's Information Criterion corrected for small sample sizes and penalized using quasi-likelihood ($QAIC_c$), difference in $QAIC_c$ between each model and the model with the lowest $QAIC_c$ (ΔQAICc), model weight (w_i), and quasi-penalized deviance of all models with moderate support (ΔQAICc < 4). The overdispersion parameter ($\hat{c}$) was 1.333. The parameters estimated in each model included the probability of survival between capture events (Phi), the probability of capture (p), the probability of entrance into the study population (pent), and the total number of individuals available to enter into the study population (N). These parameters varied with sex, year, temperature (Temp), sampling effort (Effort), and/or sampling occasion (time).

Model	NP	$QAIC_c$	$\Delta QAIC_c$	w_i	Deviance
Phi(~1)p(~Sex+Effort)pent(~time)N(~1)	13	310.86	0.00	0.15	-423.32
Phi(~1)p(~Effort)pent(~time)N(~1)	12	310.89	0.02	0.15	-421.05
Phi(~Sex)p(~Effort)pent(~time)N(~1)	13	311.12	0.25	0.13	-423.07
Phi(~1)p(~Sex+Temp+Effort)pent(~time)N(~1)	14	311.84	0.98	0.09	-424.61
Phi(~1)p(~Temp+Effort)pent(~time)N(~1)	13	312.02	1.15	0.09	-422.17
Phi(~Sex)p(~Temp+Effort)pent(~time)N(~1)	14	312.49	1.63	0.07	-423.96
Phi(~1)p(~Sex+Temp)pent(~time)N(~1)	13	312.60	1.74	0.06	-421.58
Phi(~1)p(~Temp)pent(~time)N(~1)	12	312.64	1.77	0.06	-419.30
Phi(~Sex)p(~Sex+Effort)pent(~time)N(~1)	14	312.78	1.91	0.06	-423.68
Phi(~Sex)p(~Temp)pent(~time)N(~1)	13	313.02	2.16	0.05	-421.16
Phi(~Sex)p(~Sex+Temp+Effort)pent(~time)N(~1)	15	313.91	3.04	0.03	-424.84
Phi(~Sex)p(~Sex+Temp)pent(~time)N(~1)	14	314.57	3.71	0.02	-421.88
Phi(~Year)p(~Sex+Effort)pent(~time)N(~1)	15	314.86	4.00	0.02	-423.88

Table 4-S8. Jolly-Seber models averaged to obtain abundance estimates of *Sceloporus jarrovii* lizards at site RS1 in the Chiricahua Mountains, Arizona. The number of parameters (NP), Akaike's Information Criterion corrected for small sample sizes (AIC_c), difference in AIC_c between each model and the model with the lowest AIC_c (ΔAICc), model weight (w_i), and quasi-penalized deviance of all models with moderate support (ΔAICc < 4). The parameters estimated in each model included the probability of survival between capture events (Phi), the probability of capture (p), the probability of entrance into the study population (pent), and the total number of individuals available to enter into the study population (N). These parameters varied with sex, year, temperature (Temp), sampling effort (Effort), and/or sampling occasion (time).

Model	NP	AIC_c	ΔAIC_c	w_i	Deviance
Phi(~Sex+Year)p(~1)pent(~1)N(~1)	7	387.65	0.00	0.17	-401.28
Phi(~Sex)p(~Effort)pent(~1)N(~1)	6	387.80	0.15	0.16	-398.97
Phi(~Sex+Year)p(~Effort)pent(~1)N(~1)	8	388.49	0.84	0.11	-402.63
Phi(~Sex)p(~1)pent(~1)N(~1)	5	389.28	1.62	0.08	-395.36
Phi(~Sex+Year)p(~Temp)pent(~1)N(~1)	8	389.39	1.74	0.07	-401.72
Phi(~Sex)p(~Temp+Effort)pent(~1)N(~1)	7	389.58	1.93	0.07	-399.35
Phi(~Sex+Year)p(~Sex)pent(~1)N(~1)	8	389.77	2.12	0.06	-401.35
Phi(~Sex)p(~Sex+Effort)pent(~1)N(~1)	7	389.96	2.31	0.05	-398.97
Phi(~Sex+Year)p(~Temp+Effort)pent(~1)N(~1)	9	390.63	2.97	0.04	-402.70
Phi(~Sex+Year)p(~Sex+Effort)pent(~1)N(~1)	9	390.66	3.00	0.04	-402.67
Phi(~1)p(~Sex+Effort)pent(~1)N(~1)	6	390.70	3.05	0.04	-396.07
Phi(~1)p(~Effort)pent(~1)N(~1)	5	390.90	3.25	0.03	-393.74
Phi(~Sex)p(~Temp)pent(~1)N(~1)	6	391.34	3.68	0.03	-395.44
Phi(~Sex)p(~Sex)pent(~1)N(~1)	6	391.40	3.75	0.03	-395.37
Phi(~Sex+Year)p(~Sex+Temp)pent(~1)N(~1)	9	391.54	3.88	0.02	-401.79

Table 4-S9. Jolly-Seber models averaged to obtain abundance estimates of *Sceloporus jarrovii* lizards at site RSF in the Chiricahua Mountains, Arizona. The number of parameters (NP), Akaike's Information Criterion corrected for small sample sizes (AIC_c), difference in AIC_c between each model and the model with the lowest AIC_c (ΔAICc), model weight (w_i), and quasi-penalized deviance of all models with moderate support (ΔAICc < 4). The parameters estimated in each model included the probability of survival between capture events (Phi), the probability of capture (p), the probability of entrance into the study population (pent), and the total number of individuals available to enter into the study population (N). These parameters varied with sex, year, temperature (Temp), sampling effort (Effort), and/or sampling occasion (time).

Model	NP	AIC_c	ΔAIC_c	w_i	Deviance
Phi(~1)p(~Temp)pent(~time)N(~1)	9	109.35	0.00	0.18	-110.36
Phi(~Sex)p(~Temp)pent(~time)N(~1)	10	110.15	0.80	0.12	-112.18
Phi(~1)p(~Effort+Temp)pent(~1)N(~1)	6	110.60	1.26	0.10	-101.69
Phi(~1)p(~Temp)pent(~1)N(~1)	5	110.64	1.29	0.09	-99.32
Phi(~Sex)p(~Effort+Temp)pent(~1)N(~1)	7	110.88	1.53	0.08	-103.82
Phi(~Sex)p(~Temp)pent(~1)N(~1)	6	110.96	1.61	0.08	-101.33
Phi(~Year)p(~Temp)pent(~time)N(~1)	10	111.49	2.15	0.06	-110.84
Phi(~1)p(~Effort+Temp)pent(~time)N(~1)	10	111.88	2.53	0.05	-110.45
Phi(~Sex+Year)p(~Temp)pent(~time)N(~1)	11	111.95	2.60	0.05	-113.07
Phi(~Sex+Year)p(~Effort+Temp)pent(~1)N(~1)	8	112.23	2.88	0.04	-104.94
Phi(~Year)p(~Effort+Temp)pent(~1)N(~1)	7	112.45	3.11	0.04	-102.24
Phi(~Year)p(~Temp)pent(~1)N(~1)	6	112.51	3.16	0.04	-99.78
Phi(~Sex+Year)p(~Temp)pent(~1)N(~1)	7	112.52	3.18	0.04	-102.17
Phi(~Sex)p(~Effort+Temp)pent(~time)N(~1)	11	112.69	3.34	0.03	-112.33

Table 4-S10. Jolly-Seber models averaged to obtain abundance estimates of *Sceloporus jarrovii* lizards at site SF1 in the Chiricahua Mountains, Arizona. The number of parameters (NP), Akaike's Information Criterion corrected for small sample sizes and penalized using quasi-likelihood ($QAIC_c$), difference in $QAIC_c$ between each model and the model with the lowest $QAIC_c$ (ΔQAICc), model weight (w_i), and quasi-penalized deviance of all models with moderate support (ΔQAICc < 4). The overdispersion parameter (ĉ) was 1.490. The parameters estimated in each model included the probability of survival between capture events (Phi), the probability of capture (p), the probability of entrance into the study population (pent), and the total number of individuals available to enter into the study population (N). These parameters varied with sex, year, temperature (Temp), sampling effort (Effort), and/or sampling occasion (time).

Model	NP	$QAIC_c$	$\Delta QAIC_c$	w_i	Deviance
Phi(~Sex)p(~1)pent(~time)N(~1)	9	145.27	0.00	0.23	-113.95
Phi(~Sex+Year)p(~1)pent(~time)N(~1)	10	146.17	0.89	0.15	-115.46
Phi(~Sex)p(~Temp)pent(~time)N(~1)	10	146.94	1.67	0.10	-114.69
Phi(~Sex)p(~Temp+Effort)pent(~1)N(~1)	7	147.40	2.13	0.08	-107.14
Phi(~Sex)p(~Effort)pent(~time)N(~1)	10	147.59	2.32	0.07	-114.04
Phi(~Sex)p(~Sex)pent(~time)N(~1)	10	147.68	2.41	0.07	-113.95
Phi(~1)p(~Sex+Temp+Effort)pent(~1)N(~1)	7	148.04	2.77	0.06	-106.50
Phi(~Sex+Year)p(~Temp)pent(~time)N(~1)	11	148.60	3.33	0.04	-115.49
Phi(~Sex+Year)p(~Sex)pent(~time)N(~1)	11	148.62	3.35	0.04	-115.47
Phi(~Sex)p(~Sex+Temp+Effort)pent(~1)N(~1)	8	148.62	3.35	0.04	-108.24
Phi(~Sex+Year)p(~Effort)pent(~time)N(~1)	11	148.62	3.35	0.04	-115.46
Phi(~Sex)p(~Temp+Effort)pent(~time)N(~1)	11	148.69	3.42	0.04	-115.39
Phi(~Sex+Year)p(~Temp+Effort)pent(~1)N(~1)	8	148.74	3.47	0.04	-108.12

Table 4-S11. Jolly-Seber models averaged to obtain abundance estimates of *Sceloporus jarrovii* lizards at site SF3 in the Chiricahua Mountains, Arizona. The number of parameters (NP), Akaike's Information Criterion corrected for small sample sizes (AIC_c), difference in AIC_c between each model and the model with the lowest AIC_c (ΔAICc), model weight (w_i), and quasi-penalized deviance of all models with moderate support (ΔAICc < 4). The parameters estimated in each model included the probability of survival between capture events (Phi), the probability of capture (p), the probability of entrance into the study population (pent), and the total number of individuals available to enter into the study population (N). These parameters varied with sex, year, temperature (Temp), sampling effort (Effort), and/or sampling occasion (time).

Model	NP	AIC_c	ΔAIC_c	w_i	Deviance
Phi(~Sex)p(~Effort)pent(~time)N(~1)	10	167.23	0.00	0.13	-220.87
Phi(~Sex)p(~1)pent(~time)N(~1)	9	167.41	0.18	0.12	-218.30
Phi(~1)p(~Effort)pent(~time)N(~1)	9	167.44	0.21	0.12	-218.27
Phi(~1)p(~1)pent(~time)N(~1)	8	168.22	1.00	0.08	-215.14
Phi(~Sex+Year)p(~Effort)pent(~time)N(~1)	11	168.33	1.10	0.07	-222.21
Phi(~Year)p(~Effort)pent(~time)N(~1)	10	169.18	1.96	0.05	-218.92
Phi(~Sex)p(~Temp+Effort)pent(~time)N(~1)	11	169.20	1.97	0.05	-221.34
Phi(~1)p(~Temp+Effort)pent(~time)N(~1)	10	169.35	2.12	0.04	-218.75
Phi(~Sex)p(~Temp)pent(~time)N(~1)	10	169.35	2.13	0.04	-218.75
Phi(~Sex)p(~Sex+Effort)pent(~time)N(~1)	11	169.53	2.30	0.04	-221.01
Phi(~1)p(~Sex+Effort)pent(~time)N(~1)	10	169.68	2.45	0.04	-218.42
Phi(~Sex)p(~Sex)pent(~time)N(~1)	10	169.72	2.50	0.04	-218.38
Phi(~Sex+Year)p(~1)pent(~time)N(~1)	10	169.79	2.56	0.04	-218.31
Phi(~1)p(~Temp)pent(~time)N(~1)	9	169.83	2.60	0.04	-215.88
Phi(~1)p(~Sex)pent(~time)N(~1)	9	170.28	3.05	0.03	-215.43
Phi(~Year)p(~1)pent(~time)N(~1)	9	170.57	3.34	0.02	-215.14
Phi(~Sex+Year)p(~Sex+Effort)pent(~time)N(~1)	12	170.72	3.49	0.02	-222.30
Phi(~Sex+Year)p(~Temp+Effort)pent(~time)N(~1)	12	170.78	3.56	0.02	-222.23
Phi(~Sex+Year)p(~Temp)pent(~time)N(~1)	11	171.14	3.91	0.02	-219.40

Supplementary Information 2

Thermal Quality Indices

I calculated several thermal quality indices from the operative environmental temperatures (T_e), to compare to the standard d_e index of thermal quality (Hertz et al. 1993). In all cases, indices were weighted by the proportion of the study site in each microhabitat (inside, bottom and edge) and averaged by month. I calculated the following indices:

(1) d_e: This was the standard index using T_e values from the copper models placed at the surface of the rocks. This index was calculated as the deviation between the T_e and the closest limit of the preferred body temperature range (T_{set}), where T_e values within T_{set} were assigned a value of 0.

(2) d_eU: This index was calculated in the same way as the standard d_e, except using the T_e values from copper models placed under rocks as opposed to those at the surface. I calculated this index due to the large amount of time that *S. jarrovii* spend under the rocks (Burns 1970, pers. obs.).

(3) d_eC: Blouin-Demers and Weatherhead (2001b) argued that the d_e index for black ratsnakes (*Elaphe obsoleta*) living along forest edges should only include T_e values below T_{set}, because T_es in the forest were virtually always below T_{set}. Therefore, the snakes were always able to cool off at little cost even if the T_e in the field was over T_{set}. The same could be argued for *S. jarrovii* living on talus slopes, because cool temperatures are easily accessible under the rocks regardless of the temperature at the surface. Therefore, I calculated d_eC, where I assigned a value of 0 to any T_e measurements above

the lower threshold of T_{set}. For T_e values below T_{set}, I calculated the deviation between T_e and the lower threshold of T_{set}.

(4) h_r: Sinervo et al. (2010) calculated h_r as the number of hours where activity was restricted because T_es were above the preferred body temperature of lizards. Therefore, I calculated h_r as the mean number of hours per day where T_e was above the higher threshold of T_{set}.

(5) d_eH: If the fitness of lizards is most constrained by temperatures above T_{set} as proposed by Sinervo et al. (2010), then the deviations above T_{set} may be a stronger predictor of fitness-related traits than the hours of restricted activity (h_r). Therefore, I calculated d_eH, where I assigned a value of 0 to any T_e measurements below the higher threshold of T_{set}, and I calculated the deviation between T_e values above T_{set} and the higher threshold of T_{set}.

(6) WiT_{set}: This index is calculated as the proportion of T_e measurements within T_{set}, because the optimal temperature for physiological measures should overlap with the preferred body temperature range according to the thermal coadaptation hypothesis (Angilletta 2009).

All indices were moderately to strongly correlated, with the Pearson's correlation coefficients ranging from r = 0.36 and r = 0.95 (Table B1). The d_e index was positively correlated with d_eU and d_eC, and negatively correlated with h_r, d_eH, and WiT_{set}, which suggests that the d_e index is driven primarily by colder temperatures in this system.

Table 4-S12. The Pearson correlation coefficients between six different thermal quality indices, using the average monthly value for May, June and July in 2015 and 2016 for 10 study sites in the Chiricahua Mountains, Arizona.

	d_eU	d_eH	d_eC	h_r	WiT_{set}
d_e	0.77	-0.49	0.88	-0.60	-0.64
d_eU		-0.74	0.87	-0.75	-0.46
d_eH			-0.85	0.95	0.36
d_eC				-0.88	-0.59
h_r					0.43

General Conclusion

The general objective of my thesis was to test the hypotheses that habitat selection and population density in ectotherms are driven by (1) the ability to acquire resources in a habitat (food availability), and (2) the ability to process resources in a habitat (thermal quality). Specifically, I attempted to determine whether *S. jarrovii* lizards prefer T_bs that maximize net energy gain, whether they select habitat within a study site based on its food availability or thermal quality, and whether study sites with high food availability and/or thermal quality support *S. jarrovii* populations with higher mean body condition, individual growth rate, and population density.

Overall, my thesis demonstrates that both the food availability and the thermal quality of the habitat drive habitat selection and population density. Juvenile *S. jarrovii* prefer T_bs that maximize their net energy gain, regardless of the quantity of food available (Chapter 1). Although the lizards did not shift their T_{set} in response to a low energetic state, the difference in the T_o for growth rate between high and low food diets was negligible (0.4°C) and so may not have warranted a change in behaviour given that thermoregulation is often imprecise (Martin and Huey 2008). Among plots within a study site, the density and home range size of *S. jarrovii* both increased with natural food availability, and (when an outlier plot was removed) decreased with the thermal quality in retreat sites under the rocks (Chapter 2). This suggests that lizards respond to different resources at different scales (e.g., Mayor et al. 2009): lizards may defend territories with retreat sites of high thermal quality, but travel within a larger home range to acquire sufficient food. Along an altitudinal gradient (1,650 to 3,200 m) representing nearly the entire altitudinal range of the species (Burns 1970), the number of *S. jarrovii* caught per person-hour increased with food availability and decreased as the daily high temperature increased (Chapter 3). Furthermore, mean body condition increased and the rate at which lizards attained their maximum body size decreased at higher elevations (lower thermal quality). Lastly, mean body condition, individual growth rate, and population density depended both on food availability and on thermal quality across an altitudinal gradient in the Chiricahua Mountains, although thermal quality was the stronger driver (Chapter 4). Discrepancies between my third and fourth chapters may have been due to differences in methodology (specifically, using a timed capture rather than mark-recapture methods to estimate abundance, and using the von Bertalanffy (1938) equation for lizards aged by skeletochronology rather than the difference in SVL between captures to estimate growth rates). Together, the results of these two chapters suggest that there are life-history trade-offs among different elevations (Ballinger 1979); or that body condition, growth rate, and population density are driven by different mechanisms. Body condition and growth rate may be limited by very hot temperatures that decrease energy gain directly due to metabolic losses (Huey 1982) or indirectly due to a reduction in the activity window (e.g., Angilletta 2001), whereas population density may be limited primarily by poor survival during cold overwintering temperatures (Ruby 1977) at high elevations, and by food competition (Lack 1954) at lower elevations where thermal quality is higher.

My findings suggest that traditional habitat selection models may not apply to ectotherms because both natural food availability and thermal quality affected home range size, traits related to energy gain (body condition and individual growth rate), and population density. Importantly, thermal quality was often a stronger driver of energy gain and population density than food availability. A common habitat selection model, the ideal free distribution (Fretwell and Lucas 1969), assumes that competition for limited resources reduces habitat quality and mean fitness. As such, this model may be inappropriate if habitat selection is based primarily on a resource that cannot be depleted, such as temperature (although depletion may be possible if individuals exclude competitors from locations with good thermal properties; e.g., Lovich 1988, Calsbeek and Sinervo 2002). Recent studies have also found evidence that traditional habitat selection models do not always apply to ectotherms. Habitat selection is density-independent for gartersnakes (*Thamnophis sirtalis*) and their fitness is unrelated to food abundance, although this species may occur at densities too low to detect density-dependence (Halliday and Blouin-Demers 2016). Similarly, the strength of density-dependence in flour beetles (*Tribolium castaneum*) is modulated by temperature (Halliday et al. 2015). Halliday and Blouin-Demers (2018) modified the predictions of isodar theory for ectotherms to accommodate temperature, such that the strength of density-dependence weakens as environmental temperatures deviate from the organism's physiologically optimal temperature.

Yet Halliday and Blouin-Demers (2018) only tested the prediction that the strength of density-dependence weakens as the habitat thermal quality decreases using constant temperatures below T_{set}. Does density-dependence also weaken at temperatures above T_{set}, or in habitats where temperatures fluctuate daily above and below T_{set}? In the *S. jarrovii* system, where T_es fluctuated several degrees above and below T_{set} on most days throughout the summer at all 10 sites where T_es were measured, there was only weak evidence of density-dependence. Body condition and individual growth rate decreased as thermal quality (and population density) increased (Chapter 4), but did not increase with food availability at high thermal quality sites, suggesting that they were not limited by food competition. Body temperatures above and below T_{set} have physiologically different effects. Net energy gain, for example, is reduced at cold temperatures by slower movement (e.g., Crowley 1985) and thus ability to catch prey, and lower rates of digestion and energy assimilation (e.g., Angilletta 2001, Pafilis et al. 2006). At high temperatures, however, net energy gain is limited chiefly by energetic losses to metabolism (Huey 1982). Because energy losses typically increase exponentially with T_b in ectotherms (Huey 1982, Chapter 1), more food may be required to avoid starvation at high temperatures. Indeed, under conditions of food deprivation, many species lower their T_b to avoid starvation (reviewed in Wang et al. 2006). Therefore, food competition and density-dependence may actually be *stronger* above T_{set}. Furthermore, temperature fluctuations can have different effects on physiology and performance than constant temperatures even if the mean temperature is the same (e.g., in developing embryos, Patterson and Blouin-Demers 2008). Future work could test the applicability of the prediction that the strength of density-dependence weakens as temperatures deviate from T_{set} using T_es above T_{set}, as well with the magnitude of temperature fluctuations.

Finally, my findings have implications for theories concerning spatial variation in population abundance within a species' range. Sites of higher thermal quality in an altitudinal gradient supported more dense populations of *S. jarrovii*, suggesting that the abundance of ectotherms can vary substantially within a small geographical area as a function of environmental temperatures. The abundant centre hypothesis predicts that population abundance is highest at the centre of a species' range and declines toward the edges (reviewed in Sagarin and Gaines 2002), and one of the suggested mechanisms is that environmental conditions are most suitable at the centre of the range and decline with distance from this centre (Andrewartha and Birch 1954). The dependence of population density on thermal quality, and its variation along an altitudinal gradient within a small geographical area, may partially explain why the abundant centre hypothesis is often not supported (Eckert et al. 2008, Sagarin and Gaines 2002, Sagarin et al. 2006), at least in ectotherms.

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Appendix 1

Abstracts of other publications completed during my Ph.D.

Halliday, W.D.*, Paterson, J.E.*, **Patterson, L.D.***, Cooke, S.J., and Blouin-Demers, G. 2014. Testosterone, body size, and sexual signals predict parasite load in Yarrow's spiny lizards (*Sceloporus jarrovii*). Canadian Journal of Zoology 92:1075-1082. *contributed equally to the manuscript and considered joint first authors

Parasite load significantly impacts host health and fitness, and may vary substantially among individuals within a population. The immunocompetence handicap hypothesis posits that sexual signals are honest indicators of male quality because they are maintained by testosterone, an immunosuppressant that yields higher parasite loads. Additionally, testosterone may influence parasite load by increasing activity levels. We examined these two hypotheses in a wild population of Yarrow's spiny lizards (Sceloporus jarrovii Cope, 1875) in Arizona. We 1) compared fecal testosterone levels to ectoparasite and haemoparasite loads, 2) tested if sexual signals (total coloured area, aggression, and head size), locomotor activity, and body size correlated with testosterone levels, and 3) compared sexual signals, locomotor activity, and body size to parasite load. Ectoparasite loads increased with total coloured area, and tended to increase with testosterone, but this latter relationship was only nearly significant. Parasite loads increased with body size. Thus, we found some support for the immunocompetence handicap hypothesis, and none for the activity hypothesis. Our results are consistent with an alternative hypothesis that larger individuals have more parasites because they have more surface area and/or have had longer to accumulate parasites. Future studies should examine the relative contributions of testosterone and glucocorticoids in driving variation in parasite loads.

Sopinka, N.M., **Patterson, L.D.**, Redfern, J.C., Pleizier, N.K., Belanger, C.B., Midwood, J.D., Crossin, G.T., and Cooke, S.J. 2015. Manipulating glucocorticoids in wild animals: basic and applied perspectives. Conservation Physiology 3: doi:10.1093/conphys/cov031.

One of the most comprehensively studied responses to stressors in vertebrates is the endogenous production and regulation of glucocorticoids (GCs). Extensive laboratory research using experimental elevation of GCs in model species is instrumental in learning about stressor-induced physiological and behavioural mechanisms; however, such studies fail to inform our understanding of ecological and evolutionary processes in the wild. We reviewed emerging research that has used GC manipulations in wild vertebrates to assess GC-mediated effects on survival, physiology, behaviour, reproduction and offspring quality. Within and across taxa, exogenous manipulation of GCs increased, decreased or had no effect on traits examined in the reviewed studies. The notable diversity in responses to GC manipulation could be associated with variation in experimental methods, inherent differences among species, morphs, sexes and age classes, and the ecological conditions in which responses were measured. In their current form, results from experimental studies may be applied to animal conservation on a case-by-case basis in contexts such as threshold-based management. We discuss ways to integrate mechanistic explanations for changes in animal abundance in altered environments with functional applications that inform conservation practitioners of which species and traits may be most responsive to environmental change or human disturbance. Experimental GC manipulation holds promise for determining mechanisms underlying fitness impairment and population declines. Future work in this area should examine multiple life-history traits, with consideration of individual variation and, most importantly, validation of GC manipulations within naturally occurring and physiologically relevant ranges.

Patterson, L.D., Darveau, C.-A., and Blouin-Demers, G. 2017. Support for the thermal coadaptation hypothesis from the growth rates of *Sceloporus jarrovii* lizards. Journal of Thermal Biology 70:86–96.

The thermal coadaptation hypothesis posits that ectotherms thermoregulate behaviorally to maintain body temperatures (T_b) that maximize performance, such as net energy gain. Huey's (1982) energetics model describes how food availability and T_b interact to affect net energy gain. We tested the thermal coadaptation hypothesis and Huey's energetics model with growth rates of juvenile Yarrow's spiny lizards (*Sceloporus jarrovii*). We compared the preferred (selected) T_b range (T_{sel}) of lizards in high and low energy states to their optimal temperature (T_o) for growth over nine weeks, and determined whether the T_o for growth depended on food availability. We also measured the same lizards' resting metabolic rate at five T_bs to test the energetics model assumptions that metabolic cost increases exponentially with Tb and does not differ between energy states. The T_{sel} of lizards on both diets overlapped with the T_o for growth. The assumptions of the energetics model were verified, but the T_o for net energy gain did not depend on food availability. Therefore, we found support for the thermal coadaptation hypothesis. We did not find support for the energetics model, but this may have been due to low statistical power.

Appendix 2

Tables of coordinates, elevation, access and other information regarding each study site

Table A2-1. The easting and northing (in UTMs) and elevation (m) of the study site centre, as well as the area (m^2), direction that the slope is facing (bearing, °), and vegetation and accessibility information for study sites in the Chiricahua Mountains, Arizona, U.S.A.

Study Site	**X**	**Y**	**Elevation (m)**	**Area (m^2)**	**Bearing (°)**	**Comments**
Barfoot 1	662562	3532763	2,535	21,385		Drive to Barfoot Park. Park at Barfoot 2, then take the abandoned road on the left down to Barfoot 1. Englemann spruce, Ponderosa pine, Gambel oak.
Barfoot 2	662752	3532718	2,535	6,282	160	Drive to Barfoot Park and park at the foot of Barfoot 2. Rocks are small to large, but there is a large, flat, stable bottom. Englemann spruce, Ponderosa pine, Gambel oak.
Barfoot 4	663111	3532543	2,589	16,050	298	Drive to Barfoot Park. Park at the camping spot at the foot of Barfoot 4. Rocks mostly small to medium, with shifty sections. Englemann spruce, Ponderosa pine, Gambel oak.
Barfoot 5	662859	3531970	2,611	6,605	274	Drive to Barfoot Park. Park at Barfoot 2, then take the Crest Trail (the trailhead is past the meadow). Veer right off the trail to cut across the burned area. The hike is 15 minutes. Rocks are small to medium and unstable. Trembling aspen and unknown prickly shrubs are growing up amongst the burned snags.
Price 1	664829	3515395	1,850	4,607	230	Drive to the end of Price Canyon Road (right at the unmarked fork) and park at the cattle tank. Follow the wash for 10 minutes and access the slope on the right. Watch out for poison ivy at

						the access point. Rocks are mostly medium to large and stable, though some large rocks are unstable. Arizona madrone, Arizona oak, silverleaf oak.
Price X	664977	3515315	1,884	2,846	193	Drive to the end of Price Canyon Road (right at the unmarked fork) and park at the cattle tank. Bushwhack straight up on the slope on the right for 20 minutes. This slope is visible from the road. Rocks small to large, with many small shifty rocks. Arizona madrone, Arizona oak, silverleaf oak.
Rucker 2	661683	3519492	2,162	4,476	150	Park at the campground at the end of Rucker Canyon Road. The trailhead is at the far end of the campground. Take the trail on the left and hike for 45 minutes. The slope is on the left after a 45 minute hike. Rocks small to large. The bottom and the track in the middle are stable, but other sections are shifty. Cherry species.
Rucker 5	663274	3519157	2,134	9,757	260	Park at the campground at the end of Rucker Canyon Road. The trailhead is at the far end of the campground. Take the trail on the right until you reach a large clearing, then bushwhack up the canyon on the left. The hike is ~1.25 h when the wash is not running. Rocks mostly large and stable. Arizona madrone.
Rustler 1	662040	3529401	2,709	5,099	235	Park at the trailhead before the Rustler Park campground. Walk along the road and then take the trailhead on the right to the Crest Trail. The slope is on the right but not visible from the trail (from this direction). Bushwhack down to the second giant boulder from the left to access the

						slope. Rocks are small to medium at the top and large boulders at the bottom. Trembling aspen.
Rustler F	661850	3529510	2,605	4,019	260	Park at the trailhead before the campground. Walk along the road and then take the trailhead on the right to the Crest Trail. Climb to the bottom of Rustler 1 and then cut across 200 m to Rustler F, angling slightly downwards. Rocks small to medium and shifty. Trembling aspen.
Saulsbury 1	661010	3527499	2,509	6,716	145	Park at Long Park (warning: poorly maintained road), take the crest trail, then Saulsbury trail, then bushwhack down 185 m at the point closest to the slope. The hike is 1.5 hours. Most of the rocks are small and shifty, though there is a band of small to medium rocks down the center. Chihuahua pine, Douglas fir, Ponderosa pine, Arizona oak.
SouthFork 1	671060	3525387	1,741	3,554	250	Take the trail at the end of the South Fork road, past the fence, then take the first wash to the left. Bushwhack straight up to access the slope. The rocks are small to large and mostly stable.
SouthFork 3	671484	3526096	1,757	1,783	270	Take the trail at the end of the South Fork road, and then the wash closest to the slope (to the left of the trail). Take the left fork when the wash splits in two. Rocks are small to large and fairly stable.
SouthFork 4	671286	3526537	1,666	2,532	257	Take the trail at the end of the South Fork road and hike 700 m. The slope is visible on the left side of the trail.

						Small to medium rocks. Arizona sycamore, silverleaf oak, Douglas fir, Arizona oak. The slope does not get sun until 9:00 AM due to the large overhanging cliff.
Sulphur 1	674440	3523455	1,723	3,432	65	Take Sulphur Canyon Road until the road disappears, then hike along the wash and trail for 2 km. The slope is between the forks in the wash, but access it from the left fork. Small to large rocks, mostly medium and stable. Vegetation is sparse: some shrubby silverleaf oaks and sumac species.
Sulphur 4	674746	3523403	1,647	23,236	306	Take Sulphur Canyon Road until the road disappears, then hike along the wash and trail for 2 km. Take the left fork of the wash when it splits in two. The slope is visible from the wash. Small to large rocks and relatively stable. Vegetation is sparse: some Mexican pinyon pine and silverleaf oak, but mostly shrubs.

Table A2-2. The easting and northing (in UTMs) and elevation of the centre (m), area (m^2), direction that the slope is facing (bearing, °), and vegetation and accessibility information for study sites in Huachuca Mountains, Arizona, U.S.A.

Study Site	**X**	**Y**	**Elevation (m)**	**Area (m^2)**	**Bearing (°)**	**Comments**
Carr 1	566635	3477781	1,981	4,025	326	Accessible via Comfort Springs Trail from the Ramsey Vista campground, then along the wash (there is an abandoned trail). Approximately 20 min further along wash than Carr 2. Access is from the slope bottom. It is a slanted slope with an area of large boulders and areas of smaller rocks. Douglas fir, Mexican pinyon pine, Gambel oak, velvet ash.
Carr 2	566485	3477860	2,025	2,333	142	Accessible via Comfort Springs trail from the Ramsey Vista campground, then along the wash (there is an abandoned trail). The hike is 1.5 hours long. Silverleaf oak, southwestern white pine, Arizona oak, Arizona madrone, Mexican pinyon pine. Rocks are largely small, but with areas of larger rocks.
Miller 2	568415	3476623	2,017	6,617	118	Park at the trailhead parking at the end of Miller Canyon Road. Take Clark Spring Trail, then bushwhack up. The ascent take 30 minutes. Vegetation sparse: some silverleaf oak. Rocks large and stable, some small ones near top.
Miller 3	568479	3477057	2,070	4,954	87	Park at the trailhead parking at the end of Miller Canyon Road. Accessible from Clark Spring Trail, further along than Miller 2. Rocks are mostly large and stable, with some giant boulders. Vegetation sparse: some silverleaf oak and Arizona madrone.
Ramsey 1	566216	3479193	1,868	2,555	288	Park at the Ramsey Canyon visitor's centre. Bushwhack up near the visitor's centre (careful

						not to go on private land). There are both sections of small, slippery rocks and of large rocks. Arizona madrone, silverleaf oak.
Ramsey 3	565850	3478970	1,840	1,262		Park at the Ramsey Canyon visitor's centre. Accessible via an abandoned trail between the visitors' centre and the research cabin. The slope is trapezoid-shaped, with its bottom much longer than the edges. Roughly 50% small rocks, but with a band of large rocks at the bottom. Arizona madrone, silverleaf oak, Arizona oak.
Ramsey 4	565016	3478388	1,947	3,228	268	Park at the Ramsey Canyon visitor's centre. Accessible via the Hamburg trail. Silverleaf oak, Arizona oak, Arizona sycamores, alligator junipers. Rocks mostly large and stable.

Table A2-3. The easting and northing (in UTMs) and elevation of the centre (m), area (m^2), direction that the slope is facing (bearing, °), and vegetation and accessibility information for study sites in the Pinaleño (Graham) Mountains, Arizona, U.S.A.

Study Site	**X**	**Y**	**Elevation (m)**	**Area (m^2)**	**Bearing (°)**	**Comments**
Chelsea 1	598863	3620345	2,906	2,730	273	Accessible from the first unmarked road (#4522) on the right after the Chelsey Flat monument in the field on Swift Trail Road. Park at the camping spot or at the meadow, and keep walking up the road to the closest access point, 100 m from the slope. Giant boulders. Douglas fir, trembling aspen, Englemann spruce.
Graham 1	606016	3618896	3,194	4,896	144	Access to the Red Squirrel Refugium requires a special permit from the USFS, and permission from the University of Arizona. The gate key can be obtained from the USFS office in Safford, and the radio from the University of Arizona office across from the jail. Take the access road to the Mount Graham Observatory (entrance near Columbine) and park at the top. Bushwhack 1.8 km across the burned area (45 minutes). Vegetation sparse, mostly trembling aspen. Rocks are small to large and mostly stable.
Graham 2	606306	3619126	2,978	4,497	81	Access to the Red Squirrel Refugium requires a special permit from the USFS, and permission from the University of Arizona. The gate key can be obtained from the USFS office in Safford, and the radio from the University of Arizona office across from the jail. Take the access road to the Mount Graham Observatory (entrance near Columbine) and park at the top. Bushwhack to Graham 1 and go to the bottom of that slope. Cut left for another 45 minutes of bushwhacking. Access is also possible along the

						top but it is not recommended. Rocks small to large, many of which are unstable. Trembling aspen, cherry species.
SwiftTrail 2	608569	3611264	2,663	1,912	280	Accessible from the Swift Trail road. Visible from the road and is 10 m down from it Park at the pull-off at the turn 30 m past the slope if driving from Shannon Campground. Medium-sized rocks. Gambel oak, Douglas fir, ponderosa pine.
SwiftTrail 3	608348	3613899	2,751	3,572		Accessible from the Arcadia trail (trailhead in Shannon campground). Hike past the junction for Heliograph Lookout (take the trail going down). The slope is visible from the trail. The hike from the trail is 1 hour. Giant boulders. Trembling aspen.
SwiftTrail 4	608145	3614219	2,789	1,969	338	Accessible from the Arcadia trail (trailhead in Shannon campground). Hike 20 minutes. The slope is visible from the trail. Fairly small and flat slope. Rocks are completely covered in lichen and are stable. Trembling aspen, Colorado fir, Englemann spruce.
SwiftTrail 6	608654	3611537	2,779	795	160	Accessible from Swift Trail Road. Climb up at the culvert. The talus slope is a 10-15 minute bushwhack up from the road. Small slope (long and narrow), medium to large rocks. Gambel oak and other shrubs.

Table A2-4. The easting and northing (in UTMs) and elevation of the centre (m), area (m^2), direction that the slope is facing (bearing, °), and vegetation and accessibility information for study sites in the Santa Rita Mountains, Arizona, U.S.A.

Study Site	X	Y	Elevation (m)	Area (m^2)	Bearing (°)	Comments
Madera F	514442	3505736	2,349	2,884	256	Park at the Mount Wrightson trailhead and take Old Baldy Trail and then the Supertrail at the saddle. Access is via a wash that goes down from the trail. Bushwhack 20 m through the thick bushes to the slope. The hike is 2.5 hours. The slope has small to large rocks and is fairly stable. Arizona madrones, very dense shrubs of an oak species.
Madera 6	513867	3506196	2,359	1,141	210	Park at the Mount Wrightson trailhead and take Old Baldy Trail and then the Supertrail at the saddle. The hike is 2 hours. The slope crosses the trail. Rocks are small to medium and shifty. Dense shrubs of an oak species.
Madera 7	514495	3505883	2,427	378	210	Park at the Mount Wrightson trailhead and take Old Baldy Trail and then the Supertrail at the saddle. The slope is 2 minutes past the wash for Madera F, and crosses the trail. Small to medium rocks and fairly shifty. Silverleaf oak, dense shrubs of an oak species.