The Role of Physiology, Behavior, and Habitat in Seasonal Thermoregulation by Pygmy Rabbits

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Major in Natural Resources
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College of Graduate Studies
University of Idaho
by
Charlotte Rebecca Milling

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Authorization to Submit Dissertation

This dissertation of Charlotte Rebecca Milling, submitted for the degree of Doctorate of Philosophy with a Major in Natural Resources and titled "The Role of Physiology, Behavior, and Habitat in Seasonal Thermoregulation by Pygmy Rabbits," has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

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Abstract

Understanding how organisms respond to the thermal environment is of increasing importance under global climate change. For species that are limited in their ability to disperse because of size, mobility, or habitat connectivity, coping *in situ* via behavioral plasticity or physiological acclimatization may reduce vulnerability. My objective was to evaluate factors contributing to thermoregulation strategies of a sagebrush-obligate, the pygmy rabbit (*Brachylagus idahoensis*), during summer and winter when regulatory costs imposed by the environment would be high. In both seasons, I 1) evaluated the thermal and security properties of rest-sites selected by pygmy rabbits; 2) explored the drivers underlying seasonal activity patterns to identify behavioral plasticity in response to the thermal environment; 3) used indirect-calorimetry to elucidate the relationship between energy expenditure and temperature; 4) evaluated the functional role of the burrow as a thermal refuge; and 5) used field-based measurements to relate habitat structure to the thermal environment, and used emerging unmanned aerial systems (UAS) technology to identify and map thermal microrefugia. Pygmy rabbits in eastern Idaho demonstrated a high capacity for behavioral thermoregulation by selecting shaded rest-sites during summer and reducing activity levels during periods of extreme cold during the winter. Although pygmy rabbits demonstrated seasonal physiological acclimatization, the burrow was an important thermal refuge, especially in winter when predicted thermoregulatory costs were often lower inside the burrow than in above-ground rest sites. Increasing habitat structure resulted in attenuated thermal environments across small spatial scales. Mapping efforts revealed considerable thermal heterogeneity and availability of thermal refugia across sagebrush-steppe habitat that is traditionally considered relatively homogeneous. This work contributes to understanding the capacity of pygmy rabbits to cope with thermal extremes *in situ*, which is associated with greater persistence under changing climates. Global climate change is expected to be the greatest conservation challenge that ecologists now face, and predictions of species responses can be improved by accounting for the processes that contribute to coping locally at spatial and temporal scales that are organism relevant.

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challenging me to think critically (about science and statistics and policy and fun and a million other things), and for believing in my ambition and my talent.

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Dedication

"*There is no faith which has never yet been broken, except that of a truly faithful dog*."
Konrad Lorenz

To Kimber and Sophie,

who do not understand any part of what we did for the last four and a half years but loved it anyway because we did it together.

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General Introduction

Temperature is one of the most important elements of an organism's fundamental niche because it directly affects water and energy balance. As such, a changing global climate will have important ramifications for individual fitness, and consequently populations. The thermal environment that an endotherm experiences is the result of complex interactions between the organism's physiology and behavior, habitat complexity, and climate (Porter and Kearney 2009). Thus, mobile endotherms that inhabit thermally heterogeneous landscapes are likely capable of relying on behavioral or phenotypic plasticity to cope with unfavorable thermal conditions, and might therefore be less vulnerable to climate change (Huey et al. 2012, Buckley et al. 2015).

The pygmy rabbit (*Brachylagus idahoensis*) is a small endotherm that inhabits the sagebrush steppe of the Great Basin and Intermountain West. These animals are active year-round, do not migrate, and are susceptible to cold stress because of their high surface area to volume ratio. Pygmy rabbits are sagebrush dietary specialists, and sage can comprise nearly 100% of their winter diet (Thines et al. 2004). As such, pygmy rabbits might not be confronted with the same energy limitations for thermoregulation that other generalist endotherms would be during periods of extreme cold. They are also obligate burrowers and are one of the few species of *Leporidae* that construct their own burrows (Green and Flinders 1980). Burrows serve as refugia from predators and thermal extremes and are likely important as thermal refugia for co-occurring, non-fossorial sagebrush inhabitants. Pygmy rabbits are a species of conservation concern; the Columbia Basin population is protected under the Endangered Species Act (Federal Register 2003), and in Idaho they are identified as a Species of Greatest Conservation Need (Idaho Department of Fish and Game 2005). These characteristics make the pygmy rabbit a compelling model organism to investigate thermoregulation strategies under hot and cold environmental conditions to contribute to our understanding of species vulnerability under global climate change scenarios.

My objective was to investigate behavioral and physiological responses of pygmy rabbits to summer and winter thermal conditions as well as explore the modifying role of habitat structure on the thermal environment. Pygmy rabbits likely respond to co-occurring thermal risks and risk of predation, and disentangling these behaviors is necessary to fully understand individuals' capacity to behaviorally thermoregulate. Additionally, thermally heterogeneous habitat at organism-relevant spatial scales is necessary for effective behavioral thermoregulation. Sagebrush steppe has traditionally been thought of as a homogeneous landscape, but structural complexity of vegetation can result in microrefugia that are often overlooked by large-scale climate models (Beever et al. 2015). Substantial effort has been devoted to identifying the effects of warming trends on hot-acclimated animals. However, anticipated changes in snow accumulation, distribution, and persistence as a result of climate change may have important ramifications for over-winter survival of cold-sensitive species like pygmy rabbits (Pauli et al. 2013, Williams et al. 2014). Thus, in habitats with strong seasonal variability in the thermal environment, evaluating thermoregulation under hot and cold-acclimatization provides a more complete understanding of thermal sensitivity.

Behavioral or phenotypic plasticity might preclude adaptation to novel environmental conditions associated with climate change in some species (Huey et al. 2003). In temperate habitats, a warming climate may even be associated with increased fitness in some populations up to an unknown threshold (Deutsch et al. 2008). This research is critical for understanding the capacity of pygmy rabbits to rely on behavioral and phenotypic plasticity to confront novel environmental conditions, and it can inform vulnerability assessments of similar endotherms with the capacity to cope with climate change *in situ*.

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Chapter 1: Seasonal variation in behavioral thermoregulation and predator avoidance in a small mammal.

In review for *Behavioral Ecology*

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Abstract

Understanding behavioral responses of animals to the thermal environment is of increasing importance under changing climate regimes. Thermoregulatory behaviors, such as exploitation of thermal refugia or temporal partitioning of activity, can buffer organisms against hot and cold thermal extremes but may conflict with other life history needs. Our objective was to evaluate strategies for behavioral thermoregulation by a small-bodied endotherm to test hypotheses about tradeoffs between thermal and security needs across seasons. We quantified the influence of both thermal and security properties of habitat on selection of rest sites by pygmy rabbits (*Brachylagus idahoensis*), and we identified environmental and endogenous factors affecting levels of activity during summer and winter. Behavioral strategies varied seasonally in response to both thermal challenges and risk of predation. During summer, rabbits selected rest sites with high concealment and low shortwave radiation, but activity levels were independent of ambient temperature. During winter, however, security, but not thermal properties, influenced selection of rest sites, and activity was positively correlated with ambient temperature during the most thermally stressful periods of the day (dawn, dusk, and night). The types of nuanced behavioral plasticity that we documented in response to the thermal environment is likely to be overlooked in evaluations of species tolerance to changing climates. Understanding the potential for behavior to buffer individuals as well as the limits of behavior to shield populations from consequences of climate change is critical for effective conservation of vulnerable species.

Introduction

Anthropogenic climate change is expected to alter the ecology of species in a variety of ways from broad-scale shifts in distributions (Wu 2015) to fine-scale modifications of individual behavior (Kearney et al. 2009). For endotherms, rising temperatures and altered precipitation regimes can directly disrupt behavior (du Plessis et al. 2012, Edwards et al. 2015) and even result in die-offs (Welbergen et al. 2008, McKechnie and Wolf 2009, McKechnie et al. 2012). Recent research has shown, however, that populations of mammals are not responding to climatic changes as predicted in up to 50% of published studies (McCain and King 2014). Behavioral modifications that buffer individuals from thermal extremes could reduce the likelihood of population spatial or demographic changes (Scheffers et al. 2014, McCain and King 2014, Mathewson et al. 2016). However, the same behaviors that allow an organism to adjust to climatic variability may be modulated by a variety of environmental and endogenous factors (Shuai et al. 2014). Disentangling the influence of multiple ecological factors to identify the effect of the thermal environment on behavior can be difficult but is critical under changing climatic regimes.

Behavioral thermoregulation can reduce the physiological consequences of extreme temperatures without resorting to energetically expensive metabolic heating and cooling. Moreover, behavioral options for regulating the temperature that an organism experiences are diverse (Terrien et al. 2011). Exploitation of thermal refugia is one common behavior employed by both endotherms and ectotherms. Vegetative cover can intercept radiation and provide cool microsites during the day (Turlure et al. 2010, Marchand et al. 2015, Pigeon et al. 2016), but cover also can provide warm microsites by insulating and re-radiating heat back to the ground surface at night (Benninghoff 1952, D'Odorico et al. 2013). Similarly, nests and burrows are characterized by relatively moderate and less variable temperatures than the surrounding environment, and these microhabitats can be important resources when thermal conditions exceed physiological tolerances (Long et al. 2005, Scheffers et al. 2014). Temporal partitioning of activity to coincide with periods of reduced thermal stress is another important behavioral mechanism to buffer against extreme temperatures. Flexibility in timing of active bouts can be seasonal (i.e., shifting from diurnal in winter to crepuscular in summer), but it can also occur on much finer temporal scales (i.e., shorter active bouts or fewer bouts on days when temperatures are hot or cold; Cotton and Parker 2001, Murray and Smith 2012). In fact, plasticity in the timing of activity has been identified as a common trait among small mammalian species that have demonstrated resiliency to climate change (McCain and King 2014).

Despite the value of thermoregulatory behaviors in protecting organisms against climatic extremes, such behaviors may be at odds with other life history needs and may force individuals to make tradeoffs between resource requirements. This is especially true for prey species that avoid predators both spatially and temporally (Fenn and McDonald 1995, Carrascal et al. 2001). The distribution and quality of thermal and habitat features that contribute to security (hereafter, security resources) are likely to be positively associated during certain times of the year, but decoupled at other times. For example, overhead canopy might provide refuge from both predators and overheating during summer, whereas open habitats that promote thermoregulation via basking during winter would provide less refuge from predators. Under the decoupled scenario, risk of predation could outweigh costs associated with thermoregulation and force a tradeoff between the use of habitat features for refuge from predators and temperatures (Vaudo and Heithaus 2016). Similarly, the predation risk allocation hypothesis asserts that prey species should engage in activities such as foraging and mate-seeking during periods of low predation risk (Lima and Bednekoff 1999), which may or may not coincide with thermally suitable periods. If prey species were to shift the timing of activity to avoid thermal stress, they may be more vulnerable to predation because of increased exposure to predators or exposure to different predators (Fenn and McDonald 1995). In landscapes where both security resources and diversity of predators are seasonally variable, animal behavior might reflect a tradeoff between co-occurring risks of predation and potentially lethal temperatures at certain times of the day or year. Thus, behavioral thermoregulation strategies might vary between seasons (Diaz and Cabezas-Diaz 2004) reflecting variation in the degree and types of perceived risks.

The objective of this study was to test hypotheses about tradeoffs between thermal and security needs across seasons by evaluating strategies for behavioral thermoregulation by a small endotherm. We investigated selection of thermal resources characterized by microclimate properties such as shortwave radiation, temperature, and wind speed relative to security resources (e.g., concealment and distance to burrow refugia) at rest sites, and we quantified the influence of environmental factors (temperature and moon phase) and endogenous factors (sex and reproductive status) on timing of activity. Our study was conducted on pygmy rabbits (*Brachylagus idahoensis*), which occur in the sagebrush steppe of the western USA where temperatures can exceed 35° C during summer and fall below -20° C during winter. Pygmy rabbits are small mammals (adults weigh approximately 500 g) with a relatively high surface area to volume ratio, and they have higher energy requirements relative to body mass than similar mammals (Shipley et al. 2006). Furthermore, pygmy rabbits must forage under a variety of environmental conditions throughout the year because they do not hibernate or cache food, nor do lagomorphs store large fat reserves in general (Whittaker and Thomas 1983). Predation is likely the most immediate risk for pygmy rabbits and accounts for the majority of documented mortalities for both adults (Crawford et al. 2010) and juveniles (Price et al. 2010). Thus, during climatically challenging periods, the properties of a rest site and variation in activity levels of pygmy rabbits likely represent a balance between risks associated with thermoregulation and predation.

We expected that pygmy rabbits would alter behavior seasonally in response to predation and thermal risks. We hypothesized that pygmy rabbits would use thermal refugia during above-ground resting bouts. We predicted that during summer animals would select rest sites that limited heat gain via radiation and conduction, but animals would select rest sites that facilitated heat gain via radiation and avoided heat loss due to convection during winter. Since predation risk is likely to be high at all times of year, we also hypothesized that individuals would select resting sites that provided relatively high levels of concealment. However, we expected that "basking" behavior during winter (i.e., use of rest sites with increased shortwave radiation) would result in weak selection for concealment from predators during that season. Although pygmy rabbits can be active at all times of day (Katzner 1994, Larrucea and Brussard 2009, Lee et al. 2010), individuals were predicted to alter patterns of activity among days within seasons as a function of the thermal environment. We predicted that nocturnal and crepuscular activity during winter would be positively correlated with ambient temperature because these are often the coldest periods of the day, and animals would avoid engaging in activity when thermal conditions were unfavorable. Additionally, we expected activity during the day in summer would be negatively correlated with ambient temperature because heat generated from activity could exacerbate heat gained from the environment. We had no *a priori* hypotheses regarding the influence of predation risk on the activity patterns of animals in either season because mortality from predation is high year-round (Sanchez 2007, Crawford et al. 2010), but examination of winter activity patterns led us to explore the influence of moon phase on activity in both seasons *post hoc*.

Methods

Study Area

We conducted our study in sagebrush steppe habitat in the Lemhi Valley of east-central Idaho, USA, near the town of Leadore. The valley is considered high-desert shrub-steppe (elevation = 1880–2020 m) and receives on average < 25 cm precipitation annually (Western Regional Climate Center 2016), most of which falls as rain in late spring. Average temperatures range from a daytime low of -15.7° C to a high of -1.2° C in January and a low of 5.4° C to a high of 29° C in July, and weather patterns during our study fell within the 30-year normal for temperature and precipitation in the region (Western Regional Climate Center 2016). The study site is characterized by mounded microtopography known as mima-mounds (Tullis 1995), which tend to have deeper soils than the surrounding matrix that are more suitable for burrowing and also support taller, denser patches of vegetation (Parsons et al. 2016). This microtopography results in heterogeneity in the distribution of shrub cover across the site so that resources related to cover can be either clustered or continuous at fine spatial scales. Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) is the dominant shrub species, with black sagebrush (*A. nova*), three-tip sagebrush (*A. tripartite*), green rabbitbrush (*Chrysothamnus viscidiflorus*), and rubber rabbitbrush (*Ericameria nauseosa*) occurring less frequently. The matrix between clusters of sagebrush supports a highly variable mix of low-growing shrubs, forbs, and bare ground in the lowest elevations, and more continuous grass and forb cover at higher elevations.

Predators in the Lemhi are varied, and can be nocturnal or diurnal, aerial or terrestrial, and resident or migratory. Known predators of pygmy rabbits occurring on our study site include American badgers (*Taxidea taxus*), coyotes (*Canis latrans*), long-tailed weasels (*Mustela frenata*), short-eared owls (*Asio flammeus*), northern harriers (*Circus cyaneus*), rough-legged hawks (*Buteo lagopus*), and Cooper's hawks (*Accipeter cooperii*) (Estes-Zumpf and Rachlow 2009).

We collected site-level climate data using two approaches. During the summer of 2014 and the beginning of winter 2015, we recorded ambient temperature every half hour using Hobo Tidbit Stowaway temperature loggers (model v1, Onset Computer Corporation, Bourne, MA). We identified four random locations roughly evenly distributed across the study site in ArcGIS v. 10.1 (ESRI, Redlands, CA), and we hung the loggers 30 cm off the ground in the canopy of the nearest *A. tridentata*. Adjacent loggers were 450 – 600 m apart with the farthest loggers located 1100 m away from each other. Loggers were housed in polyvinyl chloride pipe caps that were open at the bottom to protect them from direct sunlight and permit air flow around the logger. We averaged the temperatures for the four loggers to generate a single thermal profile for the site. During January of 2015, we erected a Hobo weather station (model S-THB-M008) that recorded temperature at a height of 2 m every 5 minutes, and the same weather station was used during summer 2015. We evaluated the relationship between temperature data collected using the Tidbits and the weather station during a period of overlap in winter 2015. Because the temperatures collected by the two methods were strongly correlated ($R^2 = 0.919$), with divergence occurring only at extreme values, we used temperatures recorded by both devices in our models.

Rest Site Selection

We used radio telemetry to locate pygmy rabbits for assessing rest site selection during summer (June-August) and winter (January-March). Pygmy rabbits were trapped using live traps (Tomahawk, Hazelhurst, WI) covered in burlap placed at burrow entrances. We transferred animals to a mesh handling bag and recorded weight, sex, and reproductive status. Males were determined to be reproductive if their testes had descended, and female reproduction was presumed during the summer season for all adult females. We were able to confirm the reproductive status of females by either weight or hairlessness around the teats for all but one adult female during the summer. Individuals weighing $\geq$ 300 g were fitted with very high frequency (VHF) transmitters (Holohil, Carp, Ontario, CA) using a zip-tie collar (5 g total weight). We captured and radio tracked 11 animals during summer 2014, 24 unique animals and one recaptured summer animal during winter 2015, and 21 unique animals and five recaptured winter animals during summer 2015. All handling and monitoring methods were evaluated and approved by the University of Idaho Institutional Animal Care and Use Committee (Protocols # 2012-23 and #2015-12; Appendix A) and were in accordance with guidelines for the use of wild mammals in research published by the American Society of Mammalogists (Sikes et al. 2016).

We used a hierarchical screening process to differentiate between resting and active behaviors, and we retained only resting locations in our dataset. First, we located individuals during mid-day, which we expected to be the period of least activity (Larrucea and Brussard 2009, Lee et al. 2010). Second, while radio tracking, observers would listen for constancy of the VHF signal strength and direction to evaluate if the animal was stationary or moving. Third, when we observed the radio-collared individual, we included locations if the rabbit was 1) undisturbed, inactive, and observed in a resting posture or 2) observed to flush and we documented a form or fresh excrement at the site and there was no indication of foraging in the immediate vicinity of the rest site. Instances in which animals were located in burrows were not included in the dataset, nor did we include any locations where the animal was observed moving or foraging. We located each individual at rest at least five times on five different days, over an average of 10 days (range 5 – 23 days per animal).

We measured a suite of variables contributing to thermal exchange with the environment and security from predation at each site used by a resting individual and at two randomly-selected available locations situated 10 m from the used site along randomly-generated azimuths. Available locations serve as controls plots in a used-available study design, and selection for habitat covariates was inferred by comparing levels of resources between used and available locations (Manly et al. 2002). We used a 10 m separation between used and available locations to ensure that the available locations were independent microsites from the used rest sites and to represent the relatively fine heterogeneity in distribution of resources on our study site. Microclimate variables included ambient temperature, wind speed, shortwave radiation, ground surface temperature, and relative humidity because these properties directly influence the thermal environment an animal experiences (McNab 2008, Kearney and Porter 2009). We measured wind speed by holding a propeller anemometer (Kestrel, Weather Republic, Downington, PA) perpendicular to wind direction and averaged values over 3 minutes. Ambient temperature and relative humidity were measured simultaneously using a combination probe (ExTech Instruments, Waltham, MA), and probe readings were allowed to stabilize (i.e., remain unchanging over 1 minute) before recording. Relative humidity was converted to absolute humidity for analysis. Ground surface temperature was measured using an infrared temperature sensor (ExTech Instruments, Waltham, MA). Shortwave radiation (360 – 1120 nm) was measured using a silicone-cell pyranometer (Apogee Instruments, Logan, UT) held level and away from the body of the observer. All microclimate measurements were made at a height of 10 cm within 15 minutes of observing the animal at rest sites. Concealment from aerial predators was estimated with a 15 x 15 cm cover board divided into 25 cells. We recorded the number of cells that were ≥ 50% visible when viewed from a height of 1.5 m. Concealment from terrestrial predators was estimated using a 15 x 15 x 15 cm cover cube viewed from a distance of 4 m at an eye-height of 1 m (Camp et al. 2013); values were recorded from the four cardinal directions and averaged to attain an estimate of terrestrial concealment. We measured the distance to the nearest intact burrow opening from all used and available locations, since burrows represent refuge from many predators.

We used a case-control, used – available design to evaluate rest site selection (Johnson 1980, Erickson et al. 2001, Manly et al. 2002) and conditional logistic regression to compare the thermal and security properties at used and available locations. We included the independent thermal variables (wind speed, ambient temperature, absolute humidity, ground surface temperature, and shortwave radiation) and security variables (aerial concealment, terrestrial concealment, and distance to burrow) as fixed effects. We included an interaction between aerial concealment and distance to burrow in the summer models because closer proximity to refuge may reduce pygmy rabbits' perception of predation risk from an aerial predator (Crowell et al. 2016) and therefore its selection patterns for concealment. We also included an interaction between ambient temperature and shortwave radiation in both the summer and winter models because we expected the animals to exhibit shade-seeking behaviors more frequently during hot periods in summer and basking behavior more frequently on cold, clear days during winter. Finally, we included an interaction between shortwave radiation and wind speed in the winter models because heat transfer to the animal via sunlight might offset heat loss due to convection. Observation triplicate (the unique grouping of one used and two available locations specific to each individual) was used as a stratifying variable in the model to account for any random effects that were both observation and animal specific. We developed a set of *a priori*, non-nested candidate models for summer and winter datasets separately that reflected a series of hypotheses describing rest site selection by pygmy rabbits. Because vegetation structure can influence both the thermal and security properties of rest sites, we determined the correlation among all of our predictor variables in both seasons. Highly correlated ($r \geq 0.6$) variables were not included in the same candidate models, and we adjusted *a priori* models as necessary to avoid high levels of collinearity among predictors. We used Akaike's Information Criterion for small sample sizes (AICc) to evaluate support for our candidate models (Burnham and Anderson 2002), and we evaluated parameter significance based on an 85% confidence interval that did not overlap zero (Arnold 2010). We drew inferences regarding selection from odds ratios of significant parameters in the top model for each season. Analyses were completed using the 'AICcmodavg' package in R (R Core Team 2014, Mazerolle 2016).

Activity

To measure activity, individuals were trapped (as described above) and fitted with ActiWatch triaxial accelerometers (CamNTech, Surrey, UK) and a VHF transmitter using the same collar configuration described above. Rabbits were required to weigh > 385 g to bear weight from the collar, which was substantial (approximately 15 g; ≤ 3.9% of body weight). The use of heavier animals also ensured that they were post-dispersal age based on growth curves (Estes-Zumpf and Rachlow 2009, Elias et al. 2013), and activity data would not reflect increased movement of a dispersing individual. A small amount of superglue was used to adhere fur to the underside of the accelerometers to prevent them from rotating around the animals' neck. Because the accelerometers measure and sum motion in all three axes into a single value, the exact orientation of the device was more important for animal comfort than data collection (Shephard et al. 2010). We captured and collared six animals during summer 2014, 11 unique animals and one recaptured animal during winter 2015, and 11 unique animals and one recaptured winter animal during summer 2015. Animals wore the accelerometers for a minimum of two weeks, after which animals were recaptured to retrieve the devices.

We divided the 24-hr day into activity intervals (dawn, day, dusk, and night) based on daily times of sunrise and set. We determined the time of sunrise, sunset, civil twilight, and the date of peak full and new moons using the US Naval Observatory calendar (http://aa.usno.navy.mil/data/index.php). We calculated the time between AM civil twilight and sunrise, and used that time duration before and after sunrise to define "dawn". The same approach was followed to define "dusk" using sunset and PM civil twilight. We used civil twilight as the cutoff for dawn and dusk because it is the limit at which illumination is sufficient, under good weather, for terrestrial objects to be clearly distinguished (US Naval Observatory, http://aa.usno.navy.mil/data/index.php). "Day" was defined as the period between the end of dawn and the beginning of dusk, and "night" was defined as the period between the end of dusk and the beginning of dawn. We set the period of a full moon to be the five days immediately preceding and following a full moon, and the same criterion was used for new moons. All other days were categorized as partial moons for the analyses.

We summed motion counts for each animal on each day over the periods of dawn, day, dusk, and night, and log transformed them to achieve approximate normality and homoscedasticity. This value (log activity) became the response variable for each observation. Predictor variables included average temperature during the activity interval, moon phase for that calendar day, Julian day, year (for the summer dataset only), sex, reproductive status, and the interaction between sex and reproductive status. We modeled log activity as a function of the predictor variables in each season and activity interval independently to identify the important underlying drivers of behavior during biologically relevant times of day. We used linear mixed effects models to fit a set of candidate models in each of our eight season × activity interval categories and included individual as a random effect. Candidate models were nested for all winter datasets, but were non-nested for the summer datasets because the global model failed to converge. We used AICc to evaluate support for models during the different activity intervals. The significant parameters from the top models were used to draw inferences about the influence of environmental and endogenous variables on activity (Burnham and Anderson 2002). Residual plots were visually inspected to ensure model assumptions were adequately satisfied. Analyses were completed using the 'lme4' (Bates et al. 2015) and 'AICcmodavg' package in R (R Core Team 2014, Mazerolle 2016).

Results

Rest Site Selection

Both the thermal environment and security influenced rest site selection by pygmy rabbits during summer. We recorded habitat features at 208 groups of used-available locations during summer from 37 individuals (mean = 5.6/individual, range = 5-9). Used sites were characterized by cooler ambient and ground surface temperatures, markedly lower levels of shortwave radiation, and higher aerial and terrestrial concealment than available locations (Table 1.1). Of the 14 *a priori* candidate models for the summer dataset, one model accounted for 95% of the AICc weight and included the parameters for aerial and terrestrial concealment, distance to burrow, and shortwave radiation, all of which were significant (Table 1.2; Appendix C). The odds of a given location being selected over another increased by 38% and 53% for every 10% increase in aerial and terrestrial concealment, respectively. For every additional meter from a burrow entrance, the odds of a rabbit selecting a rest site decreased by approximately 30%. Shade also influenced use of rest sites; every additional 100 W/m^2 increase in shortwave radiation resulted in a 63% reduction in odds of use.

We noted a relationship between warm temperatures and use of depressions in the ground known as "forms" during the summer, which suggested behavioral thermoregulation beyond mere placement of rest sites. During the summer, rabbits used forms at 58% (121) of the rest sites. Air temperature was 8.7° C (SE = 1.04) higher than ground surface temperature in forms, and the ground surface temperature was higher than the air temperature on only 13 occasions (11%, average difference -2.1° C, SE = 0.37). Of the 87 rest sites where animals did not use forms, the average difference between air and ground surface temperature was lower (5.7° C, SE = 0.76). Although not measured, forms varied in their dimensions and were asymmetrical. The deepest part of the form was usually backed up against the trunk of a sagebrush plant, and animals were positioned with their rumps in the deepest part. The positioning of the animal in the form likely facilitated both conductive heat dissipation and visibility of the surrounding terrain for predator detection. Animals were observed to use the same form on multiple occasions.

During winter, security properties of a rest site had a greater influence on selection than the thermal characteristics. Our winter data set included 131 groups of used-available locations on 25 animals (mean = 5.2/individual, range = 5-7). Aerial and terrestrial concealment were both higher at used locations than available, and proximity of rest sites to burrows was especially pronounced, with rabbits located within approximately 1 m, on average, from a burrow entrance (Table 1.1). Contrary to our expectations, the air temperature at used locations in the winter was not noticeably warmer than at available locations, and shortwave radiation was lower at used than available sites (Table 1.1). None of our models had overwhelming support for rest site selection by pygmy rabbits during winter. The model with the greatest overall support ($w_i = 0.53$) included the parameters for distance to burrow and aerial concealment, and these were the only parameters that were consistently significant in all six models in the 95% confidence set of models (Table 1.2; Appendix C). Parameter estimates in the top model suggested that a 1 m increase in distance from burrow was associated with a 40% reduction in odds of a given site being used, and the odds of using a site were 78% higher for each 10% increase in aerial concealment.

Activity

Sampling of activity included two-week periods during winter and summer when some animals of each sex were in reproductive condition. During the summers of 2014 and 2015, we monitored the activity of 19 animals (11 males and 8 females), of which seven were reproductive (1 male and 6 females). During the winter of 2015, we trapped and fitted 12 animals (7 males and 5 females) with accelerometers. Males reached reproductive status earlier than the females, and all four of the reproductive animals were males during this season. One male became reproductive between initial capture and collar retrieval. For analysis, we assumed this animal was non-reproductive for the first half of the monitoring period, and reproductive for the second half.

Pygmy rabbits were active at all times of day during summer and winter despite considerable variation in temperature within and among days (Table 1.3). Averaged over all animals, activity was higher in summer than winter but was generally bimodal in both seasons, with average peak activity occurring during or within minutes of the dawn and dusk activity intervals (Figure 1.1). However, reproductive individuals were generally active throughout the night during both summer and winter. Daytime activity was low in both seasons regardless of sex, reproductive status, or environmental conditions, but activity was higher during the night than the day particularly during the summer and among reproductive males during the winter (Figure 1.2).

During summer, sex and reproductive status influenced activity patterns to varying degrees over the course of a day, but model uncertainty was high and thermal properties had no detectable effect. The model that included only the variable for reproductive status received highest support during the day (w_i = 0.39; Table 1.4; Appendix D) and night (w_i = 0.28). These models predicted that reproductive individuals were 46% more active than their non-reproductive counterparts during the day and 30% more active at night. During the dawn, the model that included an interaction between sex and reproductive status received the highest support (w_i = 0.22), but the sex-only model was indistinguishable (ΔAICc = 0.21; Table 1.4). During the dusk, three models had nearly identical AICc values, including the null model suggesting that the environmental and endogenous variables we measured had little additional influence beyond the effect of individual on the activity patterns of pygmy rabbits during summer.

Activity during winter was influenced by both environmental and endogenous factors, depending on the time of day. The global model was the best supported model during the nighttime with almost all of the model weight (w_i = 0.98; Table 1.5; Appendix D); it included variables for moon phase, temperature, Julian day, and sex and reproductive status. Activity during new moons and partial moons was 51% and 36% higher, respectively, than activity during full moons at constant, mean temperature; assuming the same moon phase, activity increased by 15% with each 5 ° C increase in ambient temperature during the night (Figure 1.3). The sex and reproductive status variable was not significant in the top model, however, the model did predict a 10% increase in activity with each successive week. During the dawn and dusk, the model that included variables for sex and reproductive status, temperature, and Julian day received the highest support (dawn w_i = 0.54, dusk w_i = 0.46; Table 1.5). These models predicted an increase in activity of just under 14% for each 5° C increase in ambient temperature during the dawn and just under 9% for each 5° C increase in temperature during the dusk. During both intervals, Julian day predicted a roughly 10% increase in activity with each successive week. Julian day was not correlated with temperature ($R^2 < 0.001$, p-value = 0.933) or moon phase, but animals became reproductive towards the end of the monitoring season. Thus, the confounding effect of Julian day might have made it difficult to detect the effect of reproductive status on activity. During the daytime in winter, the model that included moon phase received the highest support ($w_i = 0.41$; Table 1.5). This model suggested a 30% reduction in daytime activity on days that corresponded to nights with new moons relative to days when the moon was full. Similarly, daytime activity also was reduced by 25% on days that corresponded to nights with partial moons relative to full moons.

Discussion

Behavioral thermoregulation strategies used by pygmy rabbits varied seasonally in ways that not only buffered animals against hot and cold extremes, but also addressed the risk of predation. During summer, rabbits selected above-ground rest sites with lower levels of shortwave radiation; however, such biophysical parameters had little influence on rest site selection during winter. In addition, animals altered their activity patterns to potentially reduce thermal challenges during the winter but not summer. Rabbits of both sexes were more active with increasing temperatures during the night and crepuscular intervals (i.e., the coldest times of day) in winter. Predation risk seemed to strongly influence both selection of rest sites and activity patterns in both seasons. A *post hoc* exploration of the influence of moonlight on activity revealed that pygmy rabbits avoided activity on full moon nights in winter but not summer, potentially in response to elevated perception of predation risk. These results suggest nuanced behavioral responses to two simultaneous risks that are important for informing predictions about how individuals and populations will respond to a changing climate.

Throughout the year, pygmy rabbits selected strongly for habitat features associated with reduction of predation risk (concealment from aerial and terrestrial predators, and proximity to a burrow system). During summer, the coupling of both thermal and security resources may be advantageous to pygmy rabbits because animals are not forced to make tradeoffs between resource needs. Organisms can cue on light intensity to identify thermally suitable rest sites (Hertz et al. 1994, Lagos et al. 1995), and our animals demonstrated strong avoidance of shortwave radiation in addition to selection for concealment. Although sagebrush structure that provides concealment might concurrently create shade, the relationship between canopy cover and shade is not uniform (Kelley and Krueger 2005). Concealment is a static property of vegetative cover, and unless the structure of the plant itself or the immediate environment changes (e.g., burial of the plant in snow), concealment remains constant throughout the day and across days. Shade, however, is dynamic and is influenced by both the structure of the surrounding vegetation and properties of the larger environment, including sun zenith and angle, cloud cover, and macro- and microtopography (Davies-Colley and Payne 1998, Campbell and Norman 1998). Our results support the hypothesis that pygmy rabbits select rest sites that reduce both predation and thermal risk.

In addition to selecting sites with low levels of shortwave radiation, animals were located resting in forms in nearly two thirds of the summer observations. These depressions constructed by the rabbits and used repeatedly were almost always cooler than the air temperature at the same location and likely facilitated heat dissipation via conduction. Thus, the use of forms might have served a behavioral thermoregulation function even though ground surface temperature was not an important variable in the model of summer rest site selection. Indeed, forms are used by several species of leporids for protection from adverse weather conditions and to decrease heat loads (Althoff et al. 1997, Zollner et al. 2000, Brown and Kaufman 2003).

Contrary to our predictions, animals did not seem to select rest sites with higher shortwave radiation or lower wind speeds relative to available sites during winter. Our quantitative results contrast general observations, suggesting that pygmy rabbits occasionally bask in open microsites during winter when wind speeds are low and skies are clear. Lee et al. (2010) similarly surmised that the increased activity of pygmy rabbits they recorded near burrow entrances during late afternoon in winter was caused by animals taking advantage of warmer temperatures in sunny locations. We expected that thermal and security resources would be inversely related during the winter when structural features that provide concealment also inhibit the thermal benefits of basking, and animals would be forced to make a tradeoff between them. In fact, the structure of the sagebrush canopy that lent itself to providing concealment provided little to no interception of shortwave radiation in the winter. This circumstance negated the necessity for a tradeoff between thermal and security resources in winter, unless exposure to sunny locations increased the animal’s perception of predation risk regardless of the amount of concealment available.

Rabbits selected rest sites near burrows during both seasons, and proximity of a burrow was one of only two key habitat features selected during winter. Higher burrow use during winter relative to other seasons has been documented previously for pygmy rabbits (Larrucea and Brussard 2009, Lee et al. 2010). Predation is the primary cause of mortality (Crawford et al. 2010), and during winter, the amount of cover provided by vegetation is reduced because of the absence of seasonal or ephemeral leaves on sagebrush, absence of herbaceous vegetation, and burial of sagebrush in snow. Thus, rabbits might perceive a higher risk of predation during winter and seek rest sites closer to a burrow refuge. In fact, pygmy rabbits on our study site were rarely found resting more than a meter from a burrow entrance during the winter. A heightened perception of risk might be exacerbated for individuals that bask, and proximity of the burrow might be a strategy for mitigating the threat. Indeed, a similar pattern of selection for basking sites in close proximity to a refuge was observed during winter in the fat-tailed false antechinus (*Pseudantechinus macdonnellensis*; Pavey and Geiser 2008).

An alternative explanation for selection of rest sites near burrow openings is that the burrows also function to provide thermal refuge. The microclimates in burrows on our site were characterized by temperatures that were warmer than above-ground temperatures 54% of the time during winter and cooler than above-ground rest sites during summer (Milling Ch. 2). Many semi-fossorial mammals use burrows during both extreme hot and cold environmental conditions to take advantage of the insulative properties of soil (Chappell and Bartholomew 1981, Reichman and Smith 1990, Bao et al. 2013). Shuttling thermoregulation, in which an animal moves between patches of optimal and sub-optimal thermal conditions to exploit different resources, has been documented for several species of small mammals during hot environmental conditions (Vispo and Bakken 1993, Muchlinski et al. 1998, Long et al. 2005), but less commonly under cold conditions (Sears et al. 2009). Rest sites near a burrow entrance also might reduce the distance over which an animal shuttles to exploit thermal refugia and correspondingly reduce predation risk.

Perceived predation risk and the thermal environment had the greatest influence on activity patterns during winter. Consistent with our predictions, we detected a positive association between increasing temperatures and activity levels of our animals during the night and crepuscular intervals when temperatures were at their lowest. We observed a 9 – 15% increase in activity for every 5° C increase in ambient temperature. Activity patterns of small mammals during winter commonly are influenced by temperature, particularly during extreme cold periods (e.g., northern flying squirrels, *Glaucomys sabrinus*, Cotton and Parker 2000; narrow-headed voles, *Mycrotis gregalus*, Shuai et al. 2014). Increasing locomotion to generate heat is a potentially viable behavioral thermoregulation strategy (Terrien et al. 2011), but given the high surface area to volume ratio of pygmy rabbits, there is undoubtedly a point beyond which environmental temperatures are too cold for that strategy to be effective (Humphries and Careau 2011), and sheltering in a thermally suitable microclimate would be expected. The temperatures we recorded during night and crepuscular intervals spanned a range > 25° C and were uncorrelated with day of the year. Thus, the relationship between temperature and activity that we documented likely reflects behavioral thermoregulation in a cold environment.

Nighttime activity patterns of pygmy rabbits were influenced by perception of predation risk during winter but not summer. Pygmy rabbits were considerably less active under full moons during the winter than under new moons. Moonlight illumination is brighter and the moon remains in the sky longer during winter nights, and this, coupled with a reduction in vegetation cover relative to summer, may increase the perception of predation risk under a full moon. Many species of small mammals have been observed to avoid or reduce activity under full moons as an antipredator strategy (Kaufman and Kaufman 1982, Butynski 1984, Daly 1992, Rogowitz 1997). Although such behavior has been documented in snowshoe hares (*Lepus americanus*; Griffin et al. 2005), this is the first study to identify this behavior in pygmy rabbits. Notably, activity during the daytime in our study revealed a complimentary pattern. Pygmy rabbits were more active at night under new moons and partial moons, but less active during the day relative to full moons. This inversion of levels of activity during the daytime suggests differential partitioning of activity in response to nighttime illumination.

Contrary to our predictions, ambient temperature was not related to activity patterns during the daytime in summer. In general, activity levels of pygmy rabbits tended to be lowest during the day when animals were presumably at rest in microsites that conferred some protection from both thermal and predator risks. Predator avoidance has a strong influence on temporal patterns of activity for many prey species, and an inactive animal may be less likely to encounter diurnal predators (Fenn and Macdonald 1995, Lima and Brednekoff 1999, Liesenjohann and Eccard 2008). Terrestrial predators of pygmy rabbits like coyotes and weasels (*Mustela spp.*) can be active at all times of day, however, coyotes rely primarily on visual detection of prey for hunting (Wells and Lehner 1978, Bender et al. 1996), and their eyes are adapted to diurnal or crepuscular vision (Kavanau and Ramos 1975). Similarly, weasels typically hunt during diurnal or crepuscular hours because they are prey of nocturnal avian predators (Jacob and Brown 2000). Summer activity of reproductive pygmy rabbits was higher than their non-reproductive counterparts during the day. Since our reproductive individuals were almost all females, this pattern was likely because of extended foraging to meet elevated nutritional requirements associated with gestation and lactation (Fortun-Lamothe 2006).

Pygmy rabbits are projected to be extinct by 2080 according to current predictions of global climate change (Leach et al. 2015), however, behavioral plasticity is expected to enhance resilience and persistence (McCain and King 2014, Beever et al. 2015). Our research suggests high levels of plasticity in behavior of pygmy rabbits in response to a variety of factors including predation risk, endogenous traits, and hot and cold thermal risk. We highlight potential behavioral mechanisms that could help small endotherms like pygmy rabbits to persist despite changing climates insofar as physiological tolerances allow.

The capacity for behavioral plasticity rather than physiological adaptation to buffer against environmental change has been termed the Bogert Effect (Huey et al. 2003), and this phenomenon may complicate predictions of a warming climate on populations of wild animals. Species that have a high capacity for behavioral thermoregulation (i.e., live in a thermally heterogeneous landscape and are mobile enough to exploit different microclimates) may be able to persist in warming landscapes without adapting physiologically, and thus selective pressure on heat-tolerant genotypes would be absent (Huey et al. 2012, Buckley et al. 2015). For species that live in temperate climates where environmental conditions are colder than thermal optima, a warming climate may even be associated with increases in fitness (Deustch et al. 2008). This synergy between temporal and spatial thermal heterogeneity and behavioral plasticity can create individual and population level responses that suggest tolerance to warming trends until a threshold is reached beyond which behavior is no longer sufficient for buffering against the physiological consequences of climate change (Huey et al. 2012). Understanding the diversity and limits of such behavioral plasticity is critical to improving predictions about responses to climate change and developing conservation strategies that are effective in enhancing population persistence.

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Table 1.1 Average (± SE) values of thermal and security variables measured at rest sites used by pygmy rabbits (*Brachylagus idahoensis*) and at nearby available sites in east-central Idaho, USA, during the summer 2014 and 2015 and winter 2015.

	Summer		Winter	
Variable	Used	Available	Used	Available
Thermal				
Air temperature (°C)	29.9 ± 0.40	31.8 ± 0.32	3.2 ± 0.53	3.1 ± 0.38
Ground surface temperature (°C)	22.4 ± 0.32	35.3 ± 0.55	4.9 ± 0.55	4.3 ± 0.42
Solar radiation (W/m^2)	107 ± 10.35	607 ± 15.84	238 ± 17.17	319 ± 12.97
Wind speed (m/s)	0.3 ± 0.02	0.5 ± 0.03	0.2 ± 0.03	0.4 ± 0.03
Absolute humidity (%)	9.0 ± 0.17	9.6 ± 0.14	2.6 ± 0.10	2.6 ± 0.07
Security				
Aerial concealment (%)	61.7 ± 2.28	10.2 ± 1.08	31.5 ± 3.14	8.6 ± 1.18
Terrestrial concealment (%)	85.8 ± 1.00	47.6 ± 1.56	75.9 ± 1.57	33.1 ± 1.75
Distance to burrow (m)	12.2 ± 1.06	16.4 ± 0.69	1.2 ± 0.37	9.7 ± 0.19

Table 1.2 The 95% confidence set of models explaining rest site selection by pygmy rabbits (*Brachylagus Idahoensis)* in east-central Idaho, USA, during summer 2014 and 2015 and winter 2015 as a function of thermal (shortwave radiation, ground temperature, and wind speed) and security variables (aerial concealment, terrestrial concealment, distance to burrow). All models included an additional intercept only stratifying variable to account for a random effect that is both individual and observation specific. Concealment (conc.) and distance (dist.) have been abbreviated. * denotes significance based on an 85% CI that does not capture 0.

Season	Model	AICc	ΔAICc	w_i	Σw_i
Summer	*Radiation* + Aerial conc.* + Terrestrial conc.* + Dist. to burrow**	1115.93	0.00	0.95	0.95
Winter	*Aerial conc.* + Dist. to burrow**	683.28	0.00	0.53	0.53
	Aerial conc. + Terrestrial conc. + Dist. to burrow**	686.16	2.88	0.13	0.66
	Ground temp. + Aerial conc.* + Terrestrial conc. + Dist. to burrow**	686.16	2.88	0.13	0.79
	Radiation + Aerial conc.* + Terrestrial conc.* + Dist. to burrow**	686.43	3.15	0.11	0.90
	*Dist. to burrow**	688.15	4.87	0.05	0.94
	Aerial conc. + Terrestrial conc.* + Dist. to burrow* + Wind speed*	689.32	6.04	0.03	0.97

Table 1.3 Average (± SD) of the mean temperature (° C) measured during the dawn, day, dusk, and night activity intervals during the summer 2014 and 2015 and winter 2015 in the Lemhi Valley of east-central Idaho, USA.

Interval	Summer 2014	Winter 2015	Summer 2015
Dawn	11.3 ± 3.0	-2.9 ± 5.9	9.6 ± 3.1
Day	26.5 ± 2.4	-0.4 ± 5.0	20.9 ± 4.2
Dusk	21.5 ± 2.5	-0.6 ± 4.5	18.5 ± 4.2
Night	15.4 ± 1.9	-4.6 ± 5.0	13.1 ± 3.1

Table 1.4 The 95% confidence set of models relating activity by pygmy rabbits (*Brachylagus idahoensis*) in east-central Idaho, USA, during summer 2014 and 2015 to environmental (temperature and moon phase) and endogenous (sex and reproductive status) variables during the day, night, dawn, and dusk intervals. All models included an additional intercept-only random effect for individual, and the null model included only this random effect intercept. * denotes significance based on an 85% CI that does not capture 0.

Interval	Model	AICc	ΔAICc	w_i	Σw_i
Day	*Reproductive status**	439.54	--	0.39	0.39
	Sex× Reproductive status + Year**	441.14	1.60	0.18	0.57
	Sex× Reproductive status + Julian day**	441.53	1.99	0.14	0.71
	*Sex× Reproductive status**	443.33	3.78	0.06	0.77
	Sex× Reproductive status + Temperature + Julian day**	443.52	3.98	0.05	0.82
	Sex× Reproductive status + Temperature*	444.21	4.67	0.04	0.86
	*Year**	444.45	4.91	0.03	0.90
	*Julian day**	444.88	5.34	0.03	0.92
	Null model	445.11	5.56	0.02	0.95
Night	*Reproductive status**	330.41	--	0.28	0.28
	*Sex× Reproductive status**	331.97	1.55	0.13	0.41
	Null model	332.38	1.97	0.10	0.51
	Sex× Reproductive status + Year*	333.72	3.30	0.05	0.57
	*Sex× Reproductive status *+ Julian day*	333.88	3.46	0.05	0.62
	Year	333.91	3.49	0.05	0.66
	Sex× Reproductive status + Moon phase*	333.97	3.56	0.05	0.71

	Sex× Reproductive status + Temperature*	333.98	3.56	0.05	0.76
	Julian day	334.09	3.67	0.04	0.80
	Temperature	334.12	3.70	0.04	0.85
	Sex	334.28	3.86	0.04	0.89
	Moon phase	334.37	3.96	0.04	0.93
	Moon phase + Temperature*	335.66	5.24	0.02	0.95
Dawn	*Sex× Reproductive status**	440.69	--	0.22	0.22
	*Sex**	440.90	0.21	0.20	0.43
	Sex× Reproductive status + Julian day*	442.75	2.07	0.08	0.51
	Sex× Reproductive status + Temperature*	442.77	2.08	0.08	0.59
	Sex× Reproductive status + Year*	442.79	2.10	0.08	0.67
	Null model	442.81	2.12	0.08	0.74
	Sex× Reproductive status + Moon phase*	443.53	2.84	0.05	0.80
	Temperature	444.77	4.08	0.03	0.83
	Sex× Reproductive status + Temperature + Julian day*	444.84	4.15	0.03	0.86
	Year	444.86	4.17	0.03	0.88
	Julian day	444.87	4.18	0.03	0.91
	Reproductive status	444.87	4.18	0.03	0.94
	Moon phase	445.35	4.66	0.02	0.96
Dusk	*Julian day**	245.07	--	0.18	0.18
	*Year**	245.41	0.34	0.15	0.33

Null model	245.60	0.53	0.14	0.47
Sex	246.09	1.02	0.11	0.58
*Moon phase**	246.44	1.36	0.09	0.68
Reproductive status	247.58	2.51	0.05	0.73
Temperature	247.65	2.58	0.05	0.78
Moon phase + Temperature*	247.72	2.65	0.05	0.83
*Sex× Reproductive status + Julian day**	248.05	2.98	0.04	0.87
*Sex× Reproductive status + Year**	248.44	3.37	0.03	0.90
Sex× Reproductive status	249.45	4.38	0.02	0.92
Sex×Reproductive status + Moon phase + Temperature + Julian day*	249.53	4.46	0.02	0.94
Sex× Reproductive status + Temperature + Julian day**	249.91	4.84	0.02	0.96

Table 1.5 The 95% confidence set of models relating activity by pygmy rabbits (*Brachylagus idahoensis*) in east-central Idaho, USA, during winter 2015 to environmental (temperature and moon phase) and endogenous (sex and reproductive status) variables during the day, night, dawn, and dusk intervals. All models included an additional intercept-only random effect for individual, and the null model included only this random effect intercept. * denotes significance based on an 85% CI that does not capture 0.

Interval	Model	AICc	ΔAICc	w_i	Σw_i
Day	*Moon phase**	300.97	--	0.41	0.41
	Sex×Reproductive status + Moon phase**	301.57	0.59	0.31	0.72
	Moon phase + Temperature*	303.09	2.12	0.14	0.86
	Sex×Reproductive status + Moon phase* + Temperature + Julian day*	305.82	4.85	0.04	0.90
	Null model	306.04	5.06	0.03	0.93
	*Sex×Reproductive status**	306.98	6.01	0.02	0.95
Night	*Sex×Reproductive status + Moon phase* + Temperature* + Julian day**	246.27	--	0.98	0.98
Dawn	*Sex×Reproductive status + Temperature* + Julian day**	478.62	--	0.54	0.54
	Sex×Reproductive status + Temperature**	481.61	2.98	0.12	0.66
	*Julian day**	481.82	3.20	0.11	0.77
	Sex×Reproductive status + Moon phase + Temperature + Julian day**	482.60	3.98	0.07	0.84
	*Temperature**	482.82	4.20	0.07	0.91
	*Sex×Reproductive status + Julian day**	483.64	5.01	0.04	0.95
Dusk	*Sex×Reproductive status* + Temperature* + Julian day**	301.93	--	0.46	0.46
	*Julian day**	302.76	0.84	0.30	0.76
	Sex×Reproductive status + Julian day**	303.72	1.79	0.19	0.94
	Sex×Reproductive status + Moon phase + Temperature* + Julian day**	306.22	4.30	0.05	0.99

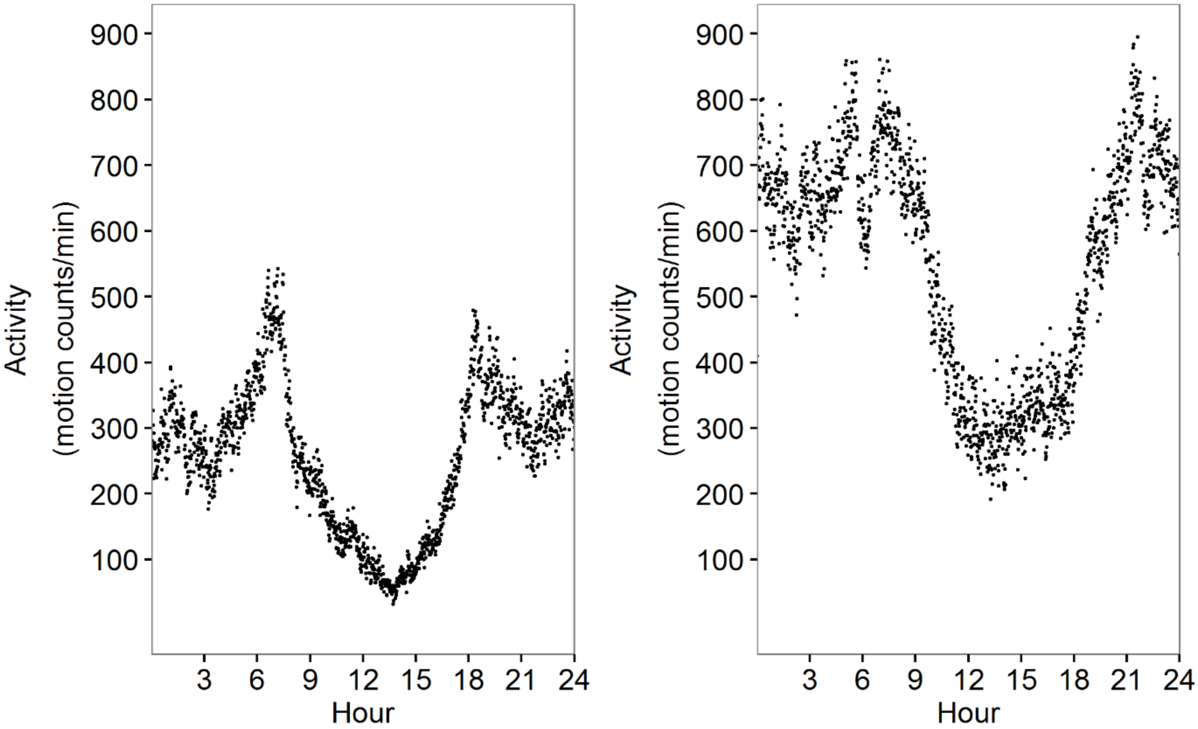

Figure 1.1 Average activity for all pygmy rabbits (*Brachylagus idahoensis*) on all days during winter 2015 (left) and summer 2014 and 2015 (right) in east-central Idaho, USA. Patterns in both seasons were characterized by low activity during the day, with bimodal peaks during dawn and dusk. Nighttime activity during summer was high relative to other intervals, whereas nighttime activity during winter was generally higher than daytime activity, but lower than crepuscular activity.

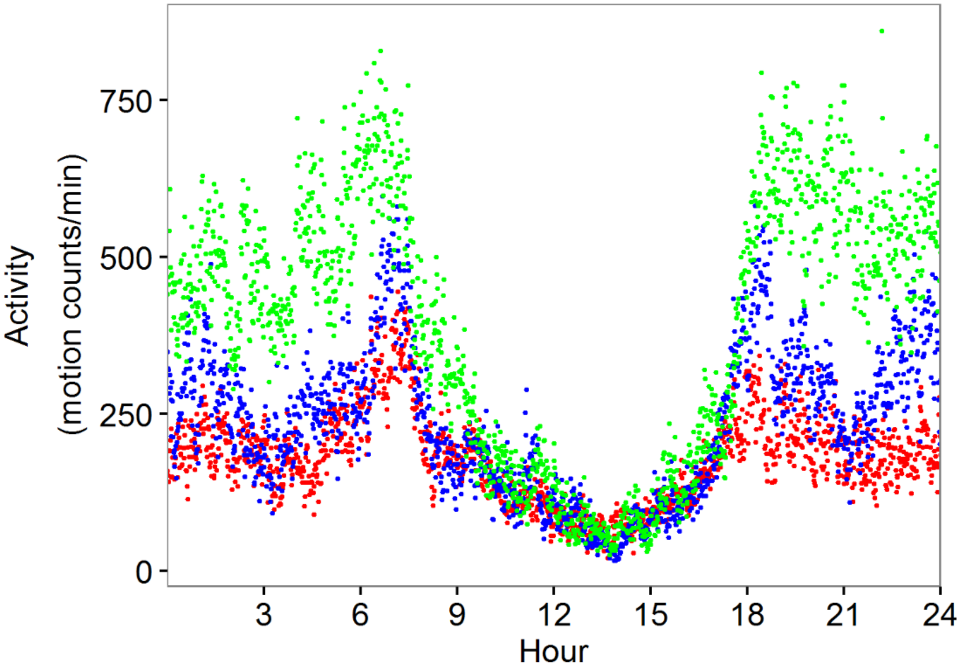

Figure 1.2 Average activity of pygmy rabbits (*Brachylagus idahoensis*) during winter 2015 for reproductive males (green/light grey), non-reproductive males (blue/black), and females (red/dark grey; all non-reproductive) in east-central Idaho, USA. Non-reproductive animals were generally bi-modally active with peaks occurring near dawn and dusk with low overnight activity. Reproductive males, however, had higher levels of activity during most times of day than their non-reproductive counterparts.

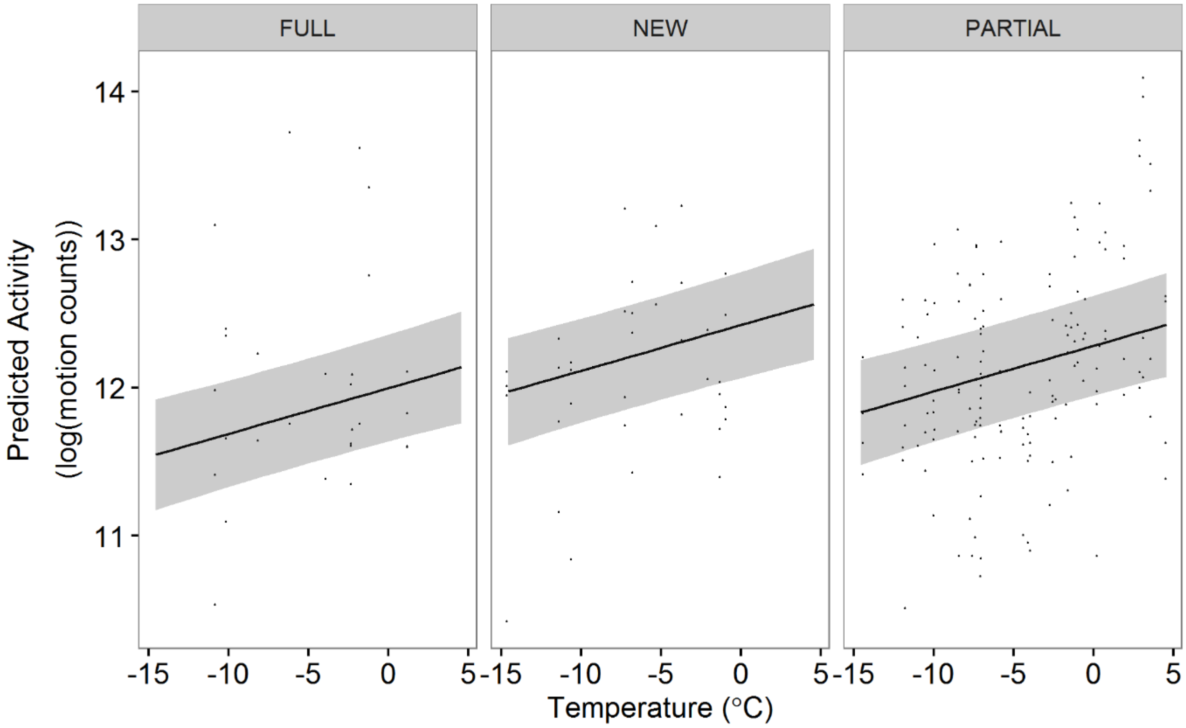

Figure 1.3 Predicted increase in night activity (with 95% confidence bands) for pygmy rabbits (*Brachylagus idahoensis*) in east-central Idaho during winter 2015 as a function of air temperature under full, new, and partial moons.

Chapter 2: Seasonal temperature acclimatization in a semi-fossorial mammal and the role of burrows as thermal refugia.

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Abstract

Small mammals in habitats with strong seasonal variation in the thermal environment often exhibit physiological and behavioral adaptations for coping with thermal extremes and reducing thermoregulatory costs. Burrows are especially important for providing thermal refugia when above-ground temperatures require high regulatory costs (e.g., water or energy) or exceed the physiological tolerances of an organism. Our objective was to explore the role of burrows as thermal refugia for a small endotherm, the pygmy rabbit (*Brachylagus idahoensis*), during the summer and winter by quantifying energetic costs associated with resting above and below ground. We used indirect calorimetry to elucidate the relationship between energy expenditure and ambient temperature over a range of temperatures that pygmy rabbits experience in their natural habitat. We also measured the temperature of above- and below-ground rest sites used by pygmy rabbits in eastern Idaho during summer and winter, and estimated the seasonal thermoregulatory costs of resting in the two microsites. Although pygmy rabbits demonstrated seasonal physiological acclimatization, the burrow was an important thermal refuge, especially in winter. Thermoregulatory costs were lower inside the burrow than in above-ground rest sites for more than 50% of the winter season. In contrast, thermal heterogeneity available in above-ground rest sites during summer reduced the role of burrows as a thermal refuge during all but the hottest periods of the afternoon. Our findings contribute to an understanding of the behavioral ecology of pygmy rabbits and also demonstrate the possible importance of burrows as refuges for other sagebrush-dwelling species.

Introduction

In mid- and high-latitudes, the thermal environment can vary substantially across a variety of spatial and temporal scales, such that ambient conditions can be energetically challenging for animals. For example, black-capped chickadees (*Parus atricapillus)*, least weasels (*Mustela nivalis*), and red squirrels (*Tamiasciurus hudsonicus)* are north temperate endotherms that experience thermal conditions that can impose high thermoregulatory costs during winter (Irving et al. 1955, Casey and Casey 1979, Cooper and Swanson 1994). Adaptations to seasonal climate extremes include hibernation or torpor (Geiser and Ruf 1995), physiological acclimatization (i.e., seasonal changes in insulation or temperature-dependent energy expenditure; Hinds 1977, Heldmaier and Steinlechner 1981, Rogowitz 1990, Sheriff et al. 2009), and behavioral thermoregulation (i.e., temperature-dependent selection of habitats or use of thermal refugia; Sharpe and Van Horne 1999, Walsberg 2000). For small endotherms that do not migrate or hibernate, winter can be especially challenging because scarce food resources might not compensate for the increased energy demands of thermoregulation. Thus, changes in space use in response to the thermal environment may allow animals to persist in habitats with unfavorable thermal conditions while minimizing energy expenditure (Huey 1991, Williams et al. 1999). For many small endotherms, burrows provide thermal refuge critical for maintaining homeothermy and reducing thermoregulatory costs during periods of extreme cold (Chappell 1981, Pauli et al. 2013) and heat (Williams et al. 1999, Walsberg 2000, Long et al. 2005, Zungu et al. 2013).

An understanding of the relationship between temperature and physiology can help to define the thermal roles of habitat features such as burrows. For endotherms, the thermoneutral zone (TNZ) is the range of ambient temperatures over which an animal can maintain body temperature (T_b) through changes in posture, fur or feather orientation, and blood flow at the periphery (McNab 2002, Lighton 2008) without changes in metabolic rate. Energy expenditure within this range is known as thermoneutral or minimal resting metabolic rate (RMR_T) if the animal is inactive. The TNZ is bounded on the cool end by the lower critical temperature (T_{lc}) and on the warm end by the upper critical temperature (T_{uc}). As ambient temperature decreases below the T_{lc}, resting metabolic rate (RMR) increases to maintain T_b, and as temperature increases above the T_{uc}, RMR increases due to evaporative cooling (i.e., sweating or panting). The range of temperatures encompassed by the TNZ, the magnitude of RMR_T, and the relationship between RMR and temperatures below the T_{lc} and above the T_{uc} can allow us to estimate the expected costs of thermoregulation over the range of temperatures animals experience in their environment. The energy costs of thermoregulating in different habitats can affect fitness either incrementally (such as resource acquisition) or directly (such as exposure to predators; Huey 1991, Humphries and Umbanhowar 2007).

Our goal was to understand how a small endotherm, the pygmy rabbit (*Brachylagus idahoensis*), might use the refuge of a burrow to address thermal challenges in a strongly seasonal environment. We conducted our study in the sagebrush steppe of the Intermountain West, USA, which is characterized by extreme diurnal and seasonal fluctuations in temperature (Wise 2012). Winter temperatures can be as low as -40° C, and summer temperatures can reach 45° C (Knapp 1997). Pygmy rabbits are endemic to the arid sagebrush habitats in the Intermountain West (Green and Flinders 1980), and their small size (400-500

g) and high surface area to volume ratio should engender high costs of regulatory heat production in typical winter temperatures. Furthermore, pygmy rabbits do not hibernate, and leporids in general do not have high levels of body fat for insulation or energy reserves (Whittaker and Thomas 1983). Nevertheless, pygmy rabbits can be active at all times of the day throughout the year (Katzner 1994, Larrucea and Brussard 2009, Lee et al. 2010, Milling Ch. 1). Unlike most lagomorphs in North America, pygmy rabbits are obligate burrowers, and the ameliorated temperatures within burrows likely provide refuge from above-ground thermal conditions (Pike et al. 2013). However, burrow use by pygmy rabbits is highly variable among seasons (Larrucea and Brussard 2009, Lee et al. 2010) and individuals (Milling, *unpublished data*), and may be influenced by a number of other factors including reproductive status and perception of predation risk (Rachlow et al. 2005, Camp et al. 2012).

To evaluate the role of burrows for pygmy rabbit thermoregulation, we 1) measured the relationship between temperature and oxygen consumption during summer and winter using indirect calorimetry; 2) measured the thermal environment within burrows and at above-ground rest sites near burrow systems known to be used by pygmy rabbits during summer and winter; and 3) combined these datasets to estimate the approximate thermoregulatory costs of resting in above-ground or burrow microsites during both seasons. We hypothesized that the relationship between energy expenditure and temperature would vary from summer to winter, reflecting seasonal physiological acclimatization to prevailing thermal conditions. Because burrow use by pygmy rabbits is poorly understood and can be influenced by a variety of factors, we sought to quantify the costs associated with thermoregulating inside the burrow relative to above-ground rest sites rather than test specific hypotheses regarding use under different thermal conditions. However, we did expect that the burrow would serve as a thermal refuge for a greater proportion of time during winter than summer because temperatures can remain well below freezing for extended periods during the winter months. We also expected that the thermoregulatory costs associated with resting in the burrow would be lower than above-ground rest sites overnight in winter and during mid-day in summer. In a broader ecological context, the pygmy rabbit is an ecosystem engineer that creates burrow microhabitats used by several other vertebrate species (Parsons et al. 2016). Therefore, elucidating the role of burrows as thermal refugia for pygmy rabbits can also help to quantify the quality of burrow refugia for other sagebrush-dwelling animals.

Methods

Thermal physiology

We evaluated RMR as rates of oxygen consumption by adult pygmy rabbits captured in east-central and south-central Idaho and in southwestern Montana, USA (Idaho Scientific Collection Permits #010813 and #100310, Montana Scientific Collection Permit #2014-062). We maintained the animals in captivity in the Small Mammal Research Facility at Washington State University. Animals were housed individually in 1.8 × 1.2 m mesh pens lined with pine shavings inside of a barn with a roof and partial walls. This arrangement exposed the rabbits to ambient temperatures but protected them from direct solar radiation, wind, and precipitation. Cages had corrugated pipe and nest boxes for enrichment and refuge. Food (Purina Professional Rabbit Chow, Purina Mills, St. Louis, MO, USA) and water were available *ad libitum*. Daytime ambient high temperatures in the facility averaged 7.8° C during winter (sd = 3.4, range = 2.2 – 15° C) and lows averaged 1.1° C (sd = 2.7, range = -4.4 – 6.6° C). During summer, daytime ambient highs averaged 35.5° C (sd = 6.7, range = 23.3 – 45.0° C) and lows average 8.4° C (sd = 2.6, range = 3.3 – 12.2° C).

We measured rates of oxygen consumption ($\dot{V}O_2$, ml O_2/min) for six individuals during winter (1 January – 13 March, 2016) and summer (13 June – 7 July, 2016) across a range of temperatures typical of natural habitats. During winter, we evaluated $\dot{V}O_2$ at seven temperatures ranging from approximately -5 to 25° C and in the summer at six temperatures ranging from approximately 5 to 30° C. Animals were weighed before each trial and placed in an airtight plexiglass metabolic chamber (volume = 4500 cm^3). Because body heat can influence the internal temperature of the metabolic chamber, we measured temperature inside the chamber using two iButtons (T_c; model number DS1921G, Maxim Integrated, San Jose, CA, USA) positioned on diagonally opposed corners. For all temperatures ≥ 0° C, the metabolic chamber was placed inside of a temperature controlled environmental cabinet. For the -5° C winter temperature trials, the chamber was placed inside of a small freezer. We used a wireless infra-red camera (model number NC223W-IR, Shenzhen Anbash Technology, Shenzhen, China) to monitor the activity and welfare of animals.

We used a pushed flow-through respirometry system to measure $\dot{V}O_2$ for two hours, with the first hour allowing acclimation to the trial temperature and the second hour comprising the sampling interval. Water vapor was removed from room air using a Drierite column (W.A. Hammond Drierite Co., Xenia, OH, USA), and the dried air was forced into the metabolic chamber at a controlled flow rate of 4000 mL/min using a mass flow controller (model 32907-71, Cole Parmer, Vernon Hills, IL, USA). Excurrent air was subsampled, scrubbed of moisture and CO_2 using Drierite and indicating soda lime, and pushed into a fuel cell oxygen analyzer (FC-10, Sable Systems, North Las Vegas, NV, USA). Flow rate into the chamber and oxygen concentrations were averaged over 5-second intervals, converted to digital signal by an A-D converter (UI-2, Sable Systems), and recorded to a laptop using Warthog LabHelper software (www.warthog.ucr.edu). We collected baseline concentrations of room air for 3 – 5 minutes at the start of the trial and approximately every 40 minutes thereafter to correct for drift in the oxygen analyzer. We used Warthog LabAnalyst software to fit a regression to baseline oxygen concentrations and corrected oxygen concentrations accordingly. The $\dot{V}O_2$ was calculated by LabAnalyst as:

$$\dot{V}O_2 = (F_iO_2 - F_eO_2)*FR/(1 - F_eO_2)$$

where FR is the incurrent mass flow rate scrubbed of water vapor and CO_2; F_iO_2 is the fractional oxygen concentration in dry, CO_2-free air (0.2095); and F_eO_2 is the fractional oxygen concentration of excurrent air scrubbed of water vapor and CO_2. Data were visually inspected, and mean values of oxygen consumption were obtained when $\dot{V}O_2$ was low and stable, reflecting resting metabolic rate. Precision of the oxygen analyzer was validated via ethanol combustion (Lighton 2008). We estimated thermal conductance (C; mL O_2 hr^{-1} g^{-1} $°C^{-1}$) for each animal at the coldest trial temperature in summer and winter according to the Irving-Scholander model, $C = \dot{V}O_2 / (T_b - T_c)$, using previously reported values of T_b for pygmy rabbits (Katzner et al. 1997). All animal protocols were approved by the Institutional Animal Care and Use Committees at University of Idaho (Protocols #2012-23 and #2015-12; Appendix A) and Washington State University (Protocol #04398-011; Appendix B), and they were in accordance with guidelines for the use of wild mammals in research published by the American Society of Mammalogists (Sikes et al. 2016).

Microsite temperature

We evaluated the thermal environment in above-ground microsites and burrows in sagebrush steppe habitat in the Lemhi Valley of east-central Idaho, USA. The valley is high-desert shrub-steppe (elevation = 1880–2020 m) and receives on average < 25 cm precipitation annually (National Oceanic Atmospheric Administration 2016), most of which falls as rain during late spring. Average temperatures range from a daytime low of -15.7° C to a high of -1.2° C in January and 5.4 to 29° C in July (Western Regional Climate Center 2016). The study site is characterized by mounded microtopography known as mima-mounds (Tullis 1995). These mounds tend to have deeper soils and support taller shrubs than the surrounding matrix, and are where most pygmy rabbit burrow systems are located. Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) is the dominant shrub species, with black sagebrush (*A. nova*), three-tip sagebrush (*A. tripartite*), green rabbitbrush (*Chrysothamnus viscidiflorus*), and rubber rabbitbrush (*Ericameria nauseosa*) occurring less frequently. The matrix between clusters of sagebrush supports a highly variable mix of low-growing shrubs, forbs, and bare ground in the lowest elevations, and more continuous grass and forb cover at higher elevations.

We used operative environmental temperature (T_e) to characterize the above-ground thermal environment (Bakken 1980). T_e integrates heat transfer from radiative, conductive, and convective sources into a single index that specifies the equilibrium temperature an animal lacking metabolic heat production or evaporative heat loss would attain in a given combination of air temperature, wind, and sunlight. To measure T_e, we built 10 models of the approximate size and shape of a resting pygmy rabbit (Bakken 1992). Models were hollow copper ovoids (12.7 × 10.2 cm) painted a matte dark gray. We attached two 8 cm segments of pipe to the bottom of the ovoids to prevent the devices from resting directly on the ground and to anchor them to the substrate. An iButton attached to a wooden dowel was inserted into one end of each model sealed in place by a rubber stopper (Fig. 2.1). The iButton recorded temperature every 30 minutes for one month (31 days) in the winter (January 20 – February 19) and summer (July 5 – August 4) of 2015.

Burrow systems were surveyed on foot during October 2014 according to methods described in Price and Rachlow (2011). Ten active burrow systems were randomly selected for temperature monitoring using ArcMAP 10.2 (ESRI, Redlands, CA, USA). Operative temperature models were placed at random locations on the burrow systems by identifying a random direction and distance from the center of the mima mound to capture the range of above-ground microclimates available to pygmy rabbits. We identified 10 additional active burrow systems at which we monitored temperature within burrows; we included only burrows with a minimum of two openings because pygmy rabbits typically construct burrow systems with multiple openings (Green and Flinders 1980). Because the thermal environment inside the burrow is not directly influenced by short wave radiation, and we assumed minimal influence of convection, we measured burrow temperature using Onset Stowaway TBI32 Tidbit temperature loggers (hereafter, tidbit; Onset Computer Corp., Bourne, MA, USA). We deployed one tidbit to a depth of 1 m within a randomly selected opening for each burrow by attaching the tidbit to stiff wire nailed at the burrow entrance. This inhibited removal by animals. Tidbits recorded temperature every 10 minutes for one month in winter and summer of 2015. Of 10 tidbits deployed, data from three sensors over the two seasons were unuseable due to burial and battery failure, resulting in nine burrows monitored during winter and eight burrows monitored during summer. We averaged the temperatures recorded by all tidbits and also by all operative temperature models per hour to estimate below- and above-ground temperatures with the same temporal resolution.

Statistical analysis

Respirometry data were analyzed using non-linear, mixed effects segmented regression to evaluate the relationship between $\dot{V}O_2$ and temperature during summer and winter. We used season and T_c as predictor variables with body mass as a covariate, and included a random effect for individual identity. The model parameterizes the segments of the relationship between $\dot{V}O_2$ and temperature below and within the TNZ, and estimates the influence of season and mass on the height of the function. From this output, we estimated the values of T_{lc} (the breakpoint), quantified the slope of the relationship below T_{lc} in both seasons, and estimated summer RMR_T. Analyses were conducted using the ‘nlme’ package in R (R Core Team 2013, Pinheiro et al. 2016), and results were deemed significant if $p < 0.05$. Values are reported as mean ± SE, unless otherwise specified.

We used results of the regression analyses to estimate approximate seasonal energetic costs of thermoregulation (as $\dot{V}O_2$) for animals at rest in burrows and in above-ground microsites.

We set mass to the average of our study animals and populated our temperature predictor variable (T_c) using field measurements of average T_e and average burrow temperature. We calculated the proportion of time in each season that the burrow could serve as a thermal refuge for a resting pygmy rabbit. In winter, this was defined as the amount of time that average $T_e < T_{lc}$, but the burrow was warmer than average T_e and therefore had lower associated thermoregulatory costs. In summer, it was calculated as the amount of time that $T_e > 35°$ C (the average T_{uc} of pygmy rabbit-size eutherian mammals; see Aurajo et al. 2013), and the burrow was cooler than T_e. Additionally, we calculated the amount of energy (in kJ, where 20.1 J is equal to 1 mL O_2) required to thermoregulate for the entire month in each of the two microhabitats exclusively and by using burrows when they provided thermal refuge. For the winter data, we summed the hourly energy expenditure predicted by the regression for the average burrow temperature and the average T_e for the entire month. We followed the same procedure for estimating the energy expenditure in the burrow for one month during summer, but because pygmy rabbits demonstrated high capacity for behavioral thermoregulation through above-ground rest site selection during summer (Milling 2017), we used the lowest measured hourly T_e in the regression for instances when the average T_e exceeded the estimated T_{uc} of pygmy rabbits. To estimate energy expenditure above 35° C during summer, we assumed that $\dot{V}O_2$ increased at the same rate above the TNZ as it did with increasing cold below the TNZ (Hinds 1973, Hinds 1977).

Results

Thermal physiology

We measured $\dot{V}O_2$ for six females and three males (three animals contributed to both summer and winter datasets). One animal died before completion of the trials, so $\dot{V}O_2$ for that individual was only measured at five temperatures during winter. Additionally, we eliminated 5° C data from two animals (one in summer and one in winter) because they were active during measurements, and we were unable to determine resting $\dot{V}O_2$. The final dataset included 74 trials. Approximately 20% of the variance in the data was attributable to the random effect of individual ($s^2_{animal} = 0.33$, $s^2_{resid} = 1.38$, $s^2_{total} = 1.70$). Animals averaged 462 ± 42.2 g, and mass was positively correlated with RMR ($p = 0.041$).

Season had a significant effect ($p = 0.017$) on the slope of the $\dot{V}O_2$ versus temperature regression below the T_{lc}. During summer, the slope was -0.21 mL O_2 min^{-1} $°C^{-1}$ ($p < 0.001$), but in winter the slope was -0.11 mL O_2 min^{-1} $°C^{-1}$ (Fig. 2.2). This difference equates to 22% higher thermoregulatory costs at 0 ° C in summer than in winter for an average size animal, with the magnitude of the seasonal cost difference decreasing with increasing temperatures (Fig 2.2). Based on visual inspection, the temperatures for our winter trials did not appear to exceed T_{lc}, and therefore, we could not estimate seasonal values for this parameter or RMR_T during winter. T_{lc} was estimated at 25.2 ± 2.9° C during both seasons, and summer RMR_T was 4.78 mL O_2 /min for an animal of average size. We did not detect the T_{uc} in either summer or winter (our test temperatures were not high enough to elicit increased RMR), but we did observe differing postures at high and low trial temperatures. During warmer trials (i.e., 25° C and 30° C), animals extended their bodies and assumed a sprawled posture, presumably to maximize contact with the chamber floor (Fig. 2.3a). This contrasted with the typical spherical posture during cooler trials (Fig. 2.3b). The mean values of *C* for summer- and winter-acclimatized animals was 0.033 ± 0.0035 mL O_2 hr^{-1} g^{-1} $°C^{-1}$ and 0.027 ± 0.0027 mL O_2 hr^{-1} g^{-1} $°C^{-1}$, respectively, but the difference between seasons was not significant ($t = 1.52$, $df = 8$, $p = 0.17$).

Microsite temperature

As expected, the thermal environment (T_e) of above-ground rest sites was more extreme and variable than the burrow thermal environment during both seasons, but burrows provided more stable microclimates during winter than summer. Notably, average temperatures both above ground and in burrows remained below the estimated T_{lc} of pygmy rabbits for nearly the entire duration of winter monitoring. Average hourly T_e ranged from -18.0° C to 23.1 ° C, and burrow temperatures ranged from -4.3 to 1.7° C (Fig. 2.4). Operative temperatures only exceeded the estimated T_{lc} at a monitored, above-ground site on eight out of 31 days and never remained above the T_{lc} for more than five continuous hours (mean = 2.2 h, range = 1 – 5 h). Average hourly T_e in summer ranged from 1.5 to 49.8° C (Fig. 4). However, the minimum hourly T_e reported by a single device ranged from 0 to 39° C. Summer burrow temperatures were cooler than daily high T_e values and less variable, ranging from 13.3 to 21.4° C (Fig. 2.4), which remained below the T_{lc} of our pygmy rabbits.

As expected, the burrow satisfied our definition of thermal refuge for a greater proportion of time during winter than summer. According to our criteria, burrows were thermal refuges on 30 of the 31 days that we monitored temperature during the winter, for an average of 13.4 hours per day (sd = 5.5; 55.8%). Burrows were generally warmer than T_e during the overnight and early morning periods, whereas above-ground microsites were warmer than burrows from approximately 0900 to 1800 hours. During summer, burrows were thermal refuges on 21 of 31 days for an average of 5.0 hours per day (sd = 3.0; 20.6%). Accounting for the lowest average temperature measured by a single T_e sensor in a given hour, the number of days in which T_e exceeded 35° C (the estimated T_{uc}) dropped to 6 days, and T_e remained above 35° C for 2.5 hours per day (sd = 2.0; 10.4%). High temperatures occurred during mid-day (1000 – 1700 hours), likely as a result of solar radiation. During these periods, burrow temperatures averaged 17.7° C (sd = 1.5) and were 22.5° C cooler than T_e, suggesting that burrow use could reduce the energy and water costs of thermoregulation when T_e is considerably greater than T_{uc}.

Although the thermal environment at our study site was variable and was outside of the TNZ of pygmy rabbits during both seasons, the variety of microclimates available suggests opportunities to reduce costs of thermoregulation. The thermoregulatory costs associated with using a burrow as a thermal refuge during winter were lower than using only above-ground or burrow microhabitats exclusively (Table 2.1). During summer, however, predicted thermoregulatory costs associated with resting above ground exclusively were likely to be lower than using a burrow as a thermal refuge during brief periods of high T_e because the burrow temperatures often were below T_{lc} (Table 2.1). Because we were not able to measure RMR above the T_{uc}, the true thermoregulatory costs associated with resting above ground at high T_e will include an unknown increment of metabolic rate from active evaporative cooling (panting, salivation, etc.), and the added water loss also might be ecologically important. However, the thermal heterogeneity present in above-ground rest sites suggested that additional microsites are likely available to reduce the need for regulatory evaporative cooling.

Discussion

Pygmy rabbits at our study site often were exposed to thermal conditions outside of their TNZ, but we documented differences in thermal conductance between summer and winter suggesting that rabbits acclimatized to prevailing thermal conditions. Availability of diverse thermal microsites likely reduced the energy costs of thermoregulation, and burrows provided refuge from extreme, above-ground temperatures during both seasons. This buffering was especially important during winter, when both T_e and burrow temperatures were below the T_{lc}, but estimated cost of thermoregulation in burrows was lower than above ground. Availability of sheltered microsites above ground during summer resulted in relatively short periods when $T_e > 35°$ C across the landscape. During these periods of high temperatures, however, the burrow may be an important resource for ‘shuttling’ thermoregulation (i.e., moving between patches of optimal and sub-optimal thermal conditions to exploit different resources) that behaviorally ameliorates energy and water costs (Chappell and Bartholomew 1981, Vispo and Bakken 1993, Hainsworth 1995). Construction and use of burrows potentially buffers pygmy rabbits from climate variation and also provides thermal shelters for numerous other sagebrush species that use their burrow systems.

The most apparent seasonal acclimation response that we documented was a change in the relationship between temperature and $\dot{V}O_2$ below the T_{lc}. This shift in thermal conductance enhances energy conservation in cold winter conditions while facilitating heat loss at high summer temperatures. At $T_e = 0°$ C, estimated thermoregulatory costs were 22% higher during summer than winter. A similar relationship has been observed in a variety of other cold-acclimatized endotherms and is an important adaptive strategy for inhabiting cold climates (Hinds 1973, Hinds 1977, Swanson 1991, Holloway and Geiser 2001). Additionally, pygmy rabbits have lower minimum thermal conductance (C) during winter than predicted based on their body size (predicted $C = 0.0557$ mL O_2 hr^{-1} g^{-1} $°C^{-1}$ for a 462 g animal, Bradley and Deavers 1980; Katzner et al. 1997), which would enhance energy conservation under cold temperatures, even in the absence of other winter-acclimatization strategies. Notably, we observed identical values of C in winter-acclimatized animals as those reported by Katzner et al. (1997), and slightly higher values of C among summer-acclimatized animals. These results suggest that pygmy rabbits possess important physiological adaptations that allow them to persist in unfavorable winter climates.

The RMR_T that we measured in summer-acclimatized animals, 4.78 mL O_2/min, is similar to the expected BMR for a 462g eutherian mammal (4.94 mL O_2/min, Hayssen and Lacy

1985; 4.65 mL O_2/min, White and Seymour 2004), but lower than predicted for other lagomorphs (7.00 mL O_2/min; Hayssen and Lacy 1985). This value also is lower than previously reported values of RMR_T of winter-acclimatized pygmy rabbits (6.85 mL O_2/min for a 462 g animal; Katzner 1997). Intraspecific variation in RMR_T can be substantial (Bech et al. 1999, Speakman et al. 2004) and can be a function of differences in individual personality (Careau et al. 2008), diet quality (Rosen and Trites 1999), or local adaptation (Mathias et al. 2006). Indeed, different studies have identified dissimilar RMR_T values for American pikas (*Ochotona princeps*; MacArthur and Wang 1973, Otto et al. 2015) and North American porcupines (*Erethizon dorsatum*; DeMatteo and Harlow 1997, Fournier and Thomas 1999). Our values of RMR_T might differ from those documented by Katzner et al. (1997) because of size differences in our respective samples (our animals were slightly larger), differences in husbandry, acclimatization to different environmental conditions (summer versus winter), or population-level differences in RMR_T. Although we were not able to determine the RMR_T of winter-acclimatized animals, our data suggested that a seasonal difference in RMR_T of pygmy rabbits is unlikely.

Although we could not quantify a shift in T_{lc} in winter relative to summer, the data suggest that the difference between summer and winter values were minimal. Small endotherms often are limited in their capacity to add insulation via fat deposits or thicker winter pelage, and T_{lc} fluctuates very little, if at all, as a result (McNab 2002, Marchand 2013). Although a seasonal shift in T_{lc} has been documented for several species of leporids (*Sylvilagus audobonii* – Hinds 1973; *Lepus alleni* and *L. californicus* – Hinds 1977; *L. townsendii* – Rogowitz 1990; *L. timidus* – Pyornila et al. 1992; *L. americanus* – Sheriff et al. 2009), constancy of T_{lc} between seasons has been documented in several small endotherms including red squirrels (Irving et al. 1955), black-capped chickadees (Cooper and Swanson 1994), greenfinches (*Carduelis chloris*; Saarela et al. 1995), and dark-eyed juncos (*Junco hyemalis*; Swanson 1991). Use of thermal refugia has an important influence on thermal physiology (Jackson et al. 2002), and the ability of pygmy rabbits to use burrows may contribute to seasonal constancy of T_{lc} and RMR_T. Exploring relationships between the use of thermal refugia and seasonal morphological and physiological acclimatization in pygmy rabbits remains a fruitful area for future research.

Our data suggest that burrows provide important thermal refuge for pygmy rabbits during winter by reducing the energetic costs of thermoregulation relative to above-ground microsites. Although winter temperatures at our study site rarely warmed to the TNZ of pygmy rabbits, burrows provided buffered microclimates that are predictable both spatially and temporally (Pike et al. 2013). Thermoregulatory costs were lower in burrows than above ground for more than 50% of the time during winter. Although thermoregulatory costs rarely exceed 3 × RMR_T in nature (Campbell and Norman 1998), we suspect that our estimate of thermoregulatory savings from burrow use is conservative because T_e does not incorporate wind-induced reductions in thermal resistance that can greatly increase heat loss (i.e., 'wind chill factors'; Bakken 1980). Our observations of the role of the burrow as thermal refuge are consistent with the behavior of pygmy rabbits during winter. Lee et al. (2010) documented rabbits near burrow openings more frequently during winter than during summer or autumn. Milling (Ch. 1) noted reductions in winter activity levels with cold temperatures during the night and early morning, and proximity of a burrow was the dominant factor in rest site selection by pygmy rabbits during winter, but not summer.

Snow accumulation substantially influences the thermal environment available to organisms through both insulation of below-ground microhabitats (Buck and Barnes 2009, Merritt et al. 2001) and creation of the subniveum – the space between the ground surface and the snow layer (Pauli et al. 2013). These features confer additional thermoregulatory cost savings over above-ground environments in a variety of ways (Pauli et al. 2013). Subnivean burrows provide buffered microclimates for resting animals and are critical for energy conservation, especially for non-fossorial species (Korhonen 1980). Furthermore, an extensive network of subnivean tunnels that connects foraging and rest sites, such as those excavated by pygmy rabbits, can largely or completely reduce exposure to above-ground thermal environments (Green and Flinders 1980, Katzner 1994, McMahon 2017). At our sites, the tall, dense shrub layer on the mima mounds trapped drifting snow, and insulation provided by the snow likely contributed to the buffered microclimate we documented within burrow systems. The influence of snow depth and duration on the burrow microclimate is worth further investigation, because reductions in snow cover are associated with increased thermoregulatory costs for burrow users (Geiser and Turbill 2009) and are predicted under most climate change scenarios (Pauli et al. 2013). Although substantial efforts have focused on effects of climate change-induced shifts in precipitation and temperature on hot-acclimated animals, associated changes in winter ecology may have greater implications for individual fitness and population persistence (Pauli et al. 2013, Williams et al. 2014).

Burrows do not appear to be as critical for thermal refuge for pygmy rabbits during summer. In fact, we predicted lower thermoregulatory costs for an animal that used exclusively above-ground rest sites, rather than both the burrow and above-ground rest sites. Although average T_e at the study site was typically above estimated T_{uc} for several hours daily, T_e at some above-ground microsites was considerably lower and within the TNZ throughout the day. The cost of cooling in those locations was predicted to be lower than the cost of warming inside the burrow at the same time because the difference in temperature between the burrow and T_{lc} was greater than that between the T_{uc} and T_e. Piute ground squirrels (*Spermophilus mollis*) relied on burrows less in sagebrush steppe than in grassland habitats because the structural complexity of sagebrush offered more thermal heterogeneity and suitable microclimates: instead of using burrows for cooling, ground squirrels stretched out on the ground in the shade (Sharpe and Van Horne 1999). We observed similar behavior by free-ranging pygmy rabbits: animals were repeatedly found resting in shallow depressions in the soil (i.e., forms) in the shade, presumably as a behavioral thermoregulation strategy (Milling Ch. 1).

Actual energy expenditure likely differs from our estimates in several way. The lowest summer T_e values on our study site occurred during the night and early morning hours and were colder than the burrow and below the T_{lc}. Pygmy rabbits are active through the night and crepuscular periods during the summer and are likely capable of substituting some heat produced during locomotion (exercise thermogenesis) for regulatory heat production (Humphries and Careau 2011). Our estimates of energy expenditure are for resting animals, but heat generated during activity might explain why extensive overnight use of burrows during summer has not been observed (Lee et al. 2010). Similarly, our estimates of energy expenditure in above-ground rest sites are likely conservative. The relationship between energy expenditure and temperature above the T_{uc} can be steeper than the relationship below T_{lc} because the process of evaporative cooling itself produces heat (Humphries and Umbanhowar 2007). Furthermore, our estimates of energy expenditure do not address evaporative water loss, which is likely also an important factor in the thermal physiology of this species. Nonetheless, because pygmy rabbits demonstrated a high capacity for behavioral thermoregulation (Milling Ch. 1), we believe that our results represent the relative costs of thermoregulation above- and below-ground at this site.

Burrow use also is influenced by other factors besides behavioral thermoregulation including reproduction and predator avoidance (Rachlow et al. 2005, Elias et al. 2006, Camp et al. 2012). Additionally, co-occurring species, such as ground squirrels, other leporids, reptiles and invertebrates use pygmy rabbit burrows (Green and Flinders 1980, Lee et al. 2010), and it is unclear how these interactions might influence burrow use by pygmy rabbits. Our estimation of the thermoregulatory costs associated with resting above and below ground do not allow us to explicitly test hypotheses regarding the specific circumstances under which pygmy rabbits would use burrow systems, but they do provide compelling support for the functional role of a burrow as thermal refuge for the species and how that role might change between seasons.

Microhabitat selection and its influence on physiology can have important ramifications for individual fitness (Huey 1991). Our research suggests that although pygmy rabbits acclimatize seasonally, the burrow is an important thermal refuge, particularly in winter. Our work also quantifies the thermal environment of microsites available to other small, sagebrush steppe inhabitants that might find refuge from climatic extremes in pygmy rabbit burrows. Climate and land-use changes in the future will undoubtedly continue to modify the thermal environment through changes to the sagebrush canopy and shifts in large-scale weather patterns. Understanding the extent to which these changes will influence the value of below-ground refugia, however, begins with understanding the extent to which animals rely on them and the mechanisms that drive burrow use. These questions are particularly important for obligate burrowers like the pygmy rabbit, which is a species of conservation concern with large ecological roles in their communities (Davidson et al. 2012, Parsons et al. 2016).

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Table 2.1 Predicted thermoregulatory costs incurred by pygmy rabbits (*Brachylagus idahoensis*) summed over one month in summer and winter in different microhabitats in east-central Idaho, USA.

Microhabitat	Winter Thermoregulatory Costs	Summer Thermoregulatory Costs
Above ground only	7460.7 kJ	5643.9 kJ [b]
Burrow only	7479.1 kJ	5770.1 kJ
Above ground + burrow refuge [a]	7211.2 kJ	5656.7 kJ

[a] – Burrows were considered to be thermal refugia in summer when above ground T_e > 35° C and in winter when the burrow temperature was warmer than T_e.

[b] – The coolest available above-ground microsites were used to calculate energy expenditure above the T_{uc} during summer.

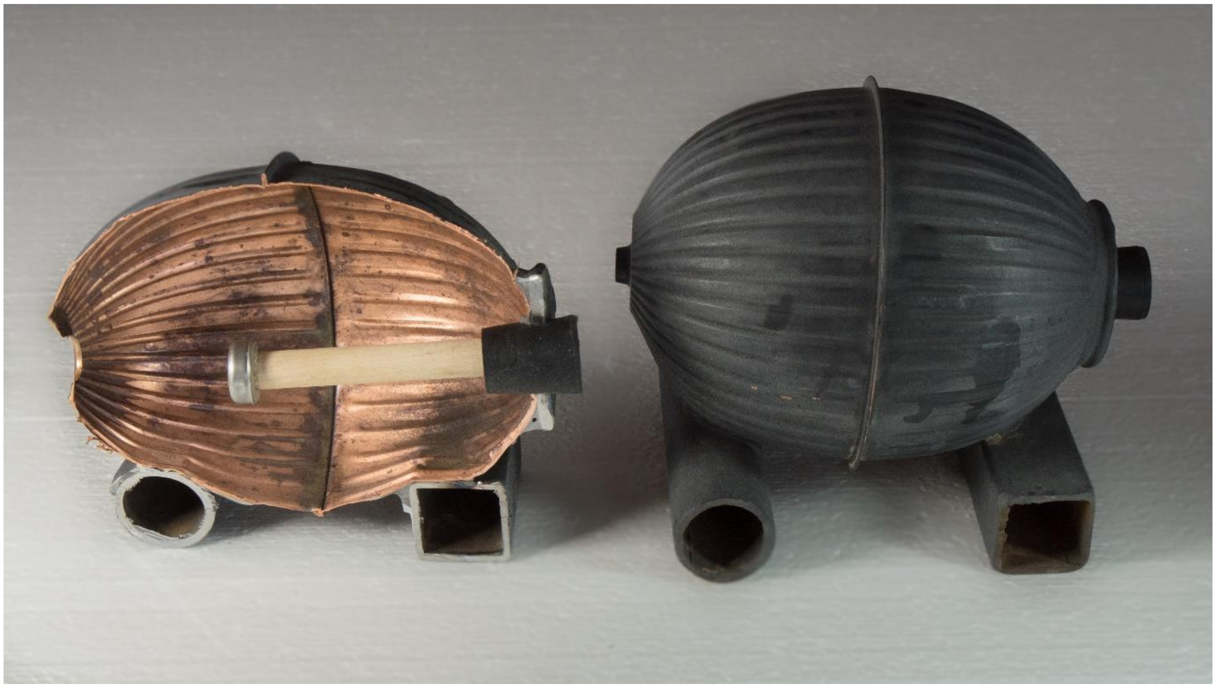

Figure 2.1 Cross-section of an operative temperature (T_e) model (left) and an intact model (right) used to characterize the thermal environment in pygmy rabbit habitat in eastern Idaho, USA. (Photo credit: Charles Peterson)

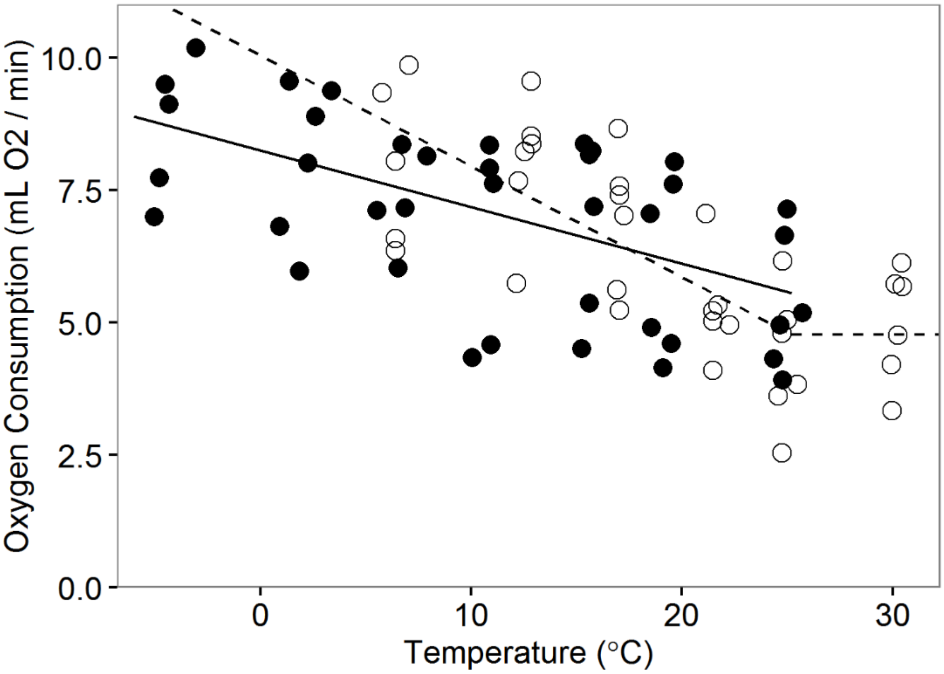

Figure 2.2 Oxygen consumption by pygmy rabbits (*Brachylagus idahoensis*) at different temperatures during summer (open circles, dashed line) and winter (filled circles, solid line). The line segments at temperatures below the breakpoint illustrate the relationship between oxygen consumption and temperature below the lower critical temperature, whereas the line segment above the breakpoint shows minimal resting metabolic rate in the thermoneutral zone of summer-acclimatized animals.

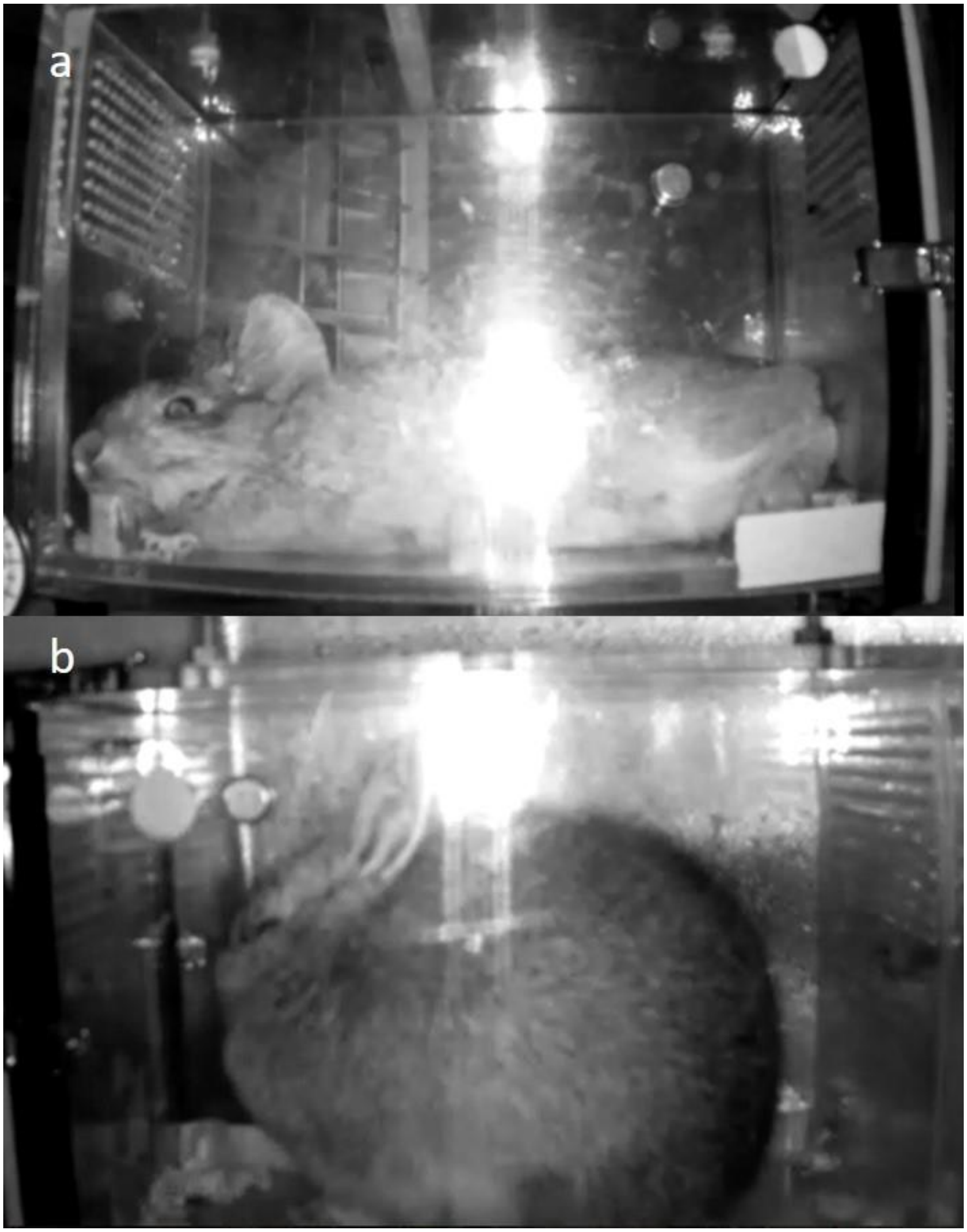

Figure 2.3 Pygmy rabbits (*Brachylagus idahoensis*) assumed different postures when in a metabolic chamber at 30° C (a) and -5° C (b), presumably as a behavioral thermoregulation strategy to dissipate heat at temperatures near body temperature and to conserve heat at cold temperatures.

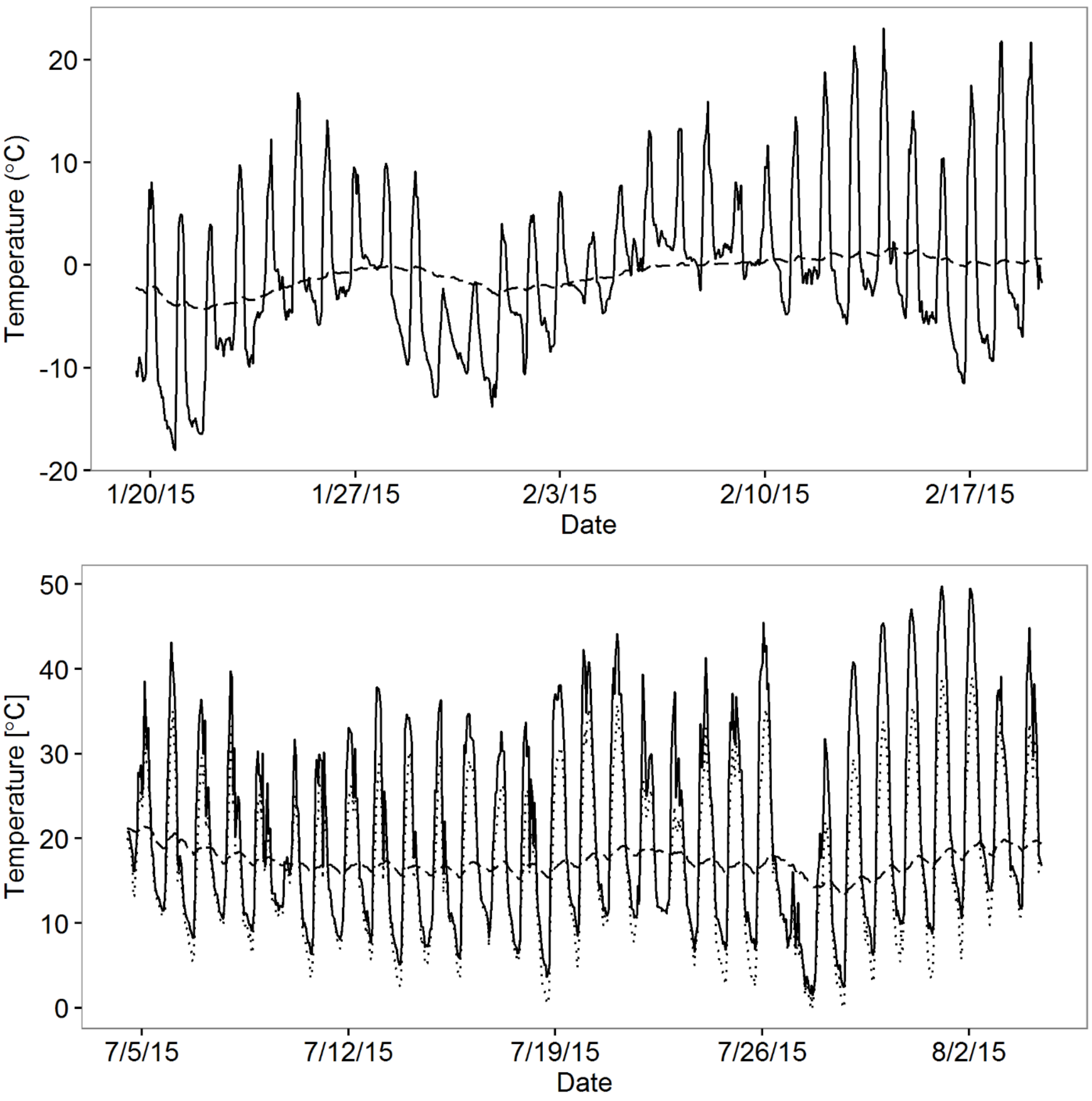

Figure 2.4 Average operative temperature (T_e) at above-ground microsites (solid line) and temperatures within pygmy rabbit (*Brachylagus idahoensis*) burrows (dashed line) during the winter (top) and summer (bottom) 2015 in east-central Idaho, USA. Average above-ground T_e often exceeded the upper critical temperature and body temperature of pygmy rabbits during summer, but there were typically above-ground rest sites available that were cooler than average (lowest hourly T_e measured by a single operative temperature model; dotted line).

Chapter 3: Habitat structure modifies microclimate: an approach for mapping fine-scale thermal heterogeneity.

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Abstract

Habitat structure contributes to thermal heterogeneity at a variety of spatial scales, but quantifying microclimates at organism-relevant resolutions remains a challenge. Landscapes that appear homogeneous at large spatial scales may offer patchily distributed thermal refuge at much finer scales. Our objective was to quantify the relationship between vegetation structure and the thermal environment at a spatial scale relevant to small, terrestrial vertebrates and to illustrate an approach for mapping fine-scale thermal heterogeneity across a landscape. We expected that high levels of vegetation structure would create attenuated microclimates and that the relative influence of vegetation structure would vary seasonally. We measured shrub volume, horizontal cover, and operative temperature (T_e) in a sagebrush shrubsteppe habitat in Idaho, USA, at 534 microsites across two study sites of approximately 1 km^2 each. We modeled the relationship between habitat structure and both mean daily maximum temperature ($\bar{T}_{max}$) and mean diurnal temperature range ($\overline{DTR}$) for each study site during summer and winter. Aerial imagery collected using unmanned aerial systems was used to estimate shrub volume and canopy cover at 1-m resolution across the study sites, and we applied the best fit model to map thermal heterogeneity across broader spatial extents. Our results indicated that increasing shrub volume and cover predicted lower values of $\bar{T}_{max}$ and $\overline{DTR}$, but strength of the relationships differed between study sites. Mapping efforts revealed considerable thermal hetereogeneity and availability of thermal refugia across the sagebrush-steppe rangelands that have traditionally been considered relatively homogeneous habitat. Application of this technique can assist ecologists and land managers in identifying critical thermal refugia that large-scale climate modeling can overlook and thus contribute to an understanding of animal-habitat relationships under changing climates and land uses.

Introduction

Animals and plants exhibit a diversity of responses to climate change (Walther et al. 2002, Parmesan 2006, Rosenzweig et al. 2008), however, species responses are not always in expected ways (e.g., Wolkovich et al. 2012, McCain and King 2014). A growing body of evidence points to the need to consider adaptive capacity of animals in understanding responses to changing climates (Beever et al. 2015). Adaptive capacity encompasses genetic diversity, behavioral plasticity, life history traits, and evolutionary adaptation (Dawson et al. 2011). Behavioral responses of individuals to the thermal environment can include dispersal, changes in timing of activity, and use of thermal refugia. Climate models used in vulnerability assessments often poorly predict species distributions because they do not capture available microclimate refugia that might allow species to persist in otherwise thermally unsuitable macroclimates (Faye et al. 2014, Beever et al. 2015).

Organisms with a variety of life history strategies select microsites based on thermal resources. For example, heliothermic *Anolis* lizards (*Anolis cristatellus*) cue on light intensity to identify thermally optimal rest sites (Hertz et al. 1994); hummingbirds (*Stellula calliope* and *Selasphorus platycercus*) construct nests in locations where heat loss via conduction and convection is minimized during the predawn hours (Calder 1973); and male white-tailed deer (*Odocoileus virginianus*) select cool microsites at midday during the summer (Wiemers et al. 2014). The structural complexity of habitat directly and indirectly influences the thermal environment and can enhance or limit thermal suitability of microsites (Magnuson et al. 1979; Vitt et al. 1998; Singh et al. 2002). Characterizing relationships between microclimates and habitat features would facilitate mapping the thermal environment across larger spatial extents at organism-relevant scales (Vanwalleghem and Meentemeyer 2009), and could aid in identifying thermal refugia and restoring disturbed landscapes (Bakken and Angiletta 2014).

Indices of temperature can simplify the process of mapping the thermal environment at scales that are relevant to individual animals (Bakken and Angiletta 2014). Operative temperature (T_e) composites ambient temperature and heat transfer due to radiation, conduction, and convection into a single measure that is functionally equivalent to the equilibrium temperature an organism would experience when exposed to a combination of temperature, sunlight, and wind in the absence of metabolic heating or cooling (Bakken 1980). Because habitat structure can modify the relative influence of each of these modes of heat transfer, T_e can characterize heterogeneity in the thermal environment of microsites as a function of habitat features.

Our goal was to model thermal microhabitats across the landscape at resolutions that are meaningful for small animals, and we illustrate an approach for doing so in a sagebrush-steppe ecosystem that supports > 80 terrestrial vertebrates of conservation concern (Dobkin and Sauder 2004, Wisdom et al. 2005). Despite early attitudes about sagebrush landscapes in the western United States as a homogenous sagebrush sea (the “Big Empty”; Shallat 2013), the sagebrush steppe is heterogeneous across a variety of spatial scales that influence resource use by animals (Mundt et al. 2006, Parsons et al. 2016). Because our landscape of interest was exposed to the same macroclimate, we expected that variation in the thermal properties of microsites would be a function of the modifying influence of vegetation structure (horizontal cover and shrub volume) that intercepts solar radiation, reduces nocturnal cooling, and blocks wind (Walsberg 1985, D'Odorico et al. 2012, Marchand et al. 2015). We also expected that the ability of vegetation to moderate T_e might differ between seasons because the angle of the sun differs between seasons and might change the capacity of shrubs to provide shade. We used operative temperature models and field-based vegetation measurements to construct models at the microsite scale (1 m^2), and we used imagery gathered by unmanned aerial systems (UAS) to map the thermal environment at high resolution over a broader spatial extent. This approach can provide tools for ecologists to advance understanding of animal-habitat relationships. Integrating thermal and habitat properties can aid in detecting and mitigating the impacts of anthropogenic disturbance and inform evaluations of adaptive capacity under changing climates.

Methods

Study Area

We characterized the thermal environment at two parcels (~1 km^2) of sagebrush rangeland managed by the Bureau of Land Management in Idaho, USA (Fig. 3.1a). One site was in the Lemhi Valley of east-central Idaho (Cedar Gulch; Fig. 3.1b). Elevation at this site ranged from 1890 m to 1920 m. The Lemhi Valley is high-desert sagebrush-steppe and receives on average 23.5 cm precipitation annually, most of which falls in June as rain. Average temperatures range from a daytime low of -15.7° C to a high of -1.2° C in January and a low of 5.4° C to a high of 29° C in July (Western Regional Climate Center 2016). Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) is the dominant shrub species, with black sagebrush (*A. nova*), three-tip sagebrush (*A. tripartite*), green rabbitbrush (*Chrysothamnus viscidiflorus*), and rubber rabbitbrush (*Ericameria nauseosa*) occurring less frequently.

The second study site was on the Camas Prairie in south-central Idaho (Magic Reservoir; Fig. 3.1b). Elevation at this site ranged from 1470 to 1480 m. Average temperatures range from a daytime low of -9.0° C to a high of 0.7° C in January and a low of 13.0° C to a high of 33.0° C in July (Western Regional Climate Center 2016). The site receives approximately 27 cm of precipitation annually on average with the highest precipitation events occurring as snow during winter (Western Regional Climate Center 2016). Wyoming big sagebrush dominates the site, but basin big sagebrush (*A. t. tridentata*) grows on the periphery. The rangeland at both study sites is characterized by mounded microtopography known as mima-mounds (Tullis 1995), which support taller, denser clusters of shrubs than the matrix between mima mounds. A highly heterogeneous mix of shrubs, forbs, grasses and bare ground occur in the matrix between mima mounds.

Field Methods

We stratified each study site by habitat type and distributed monitoring locations across the habitats to sample the diversity of microsites available to small vertebrates (Fig. 3.1c and d). We derived a Normalized Difference Vegetation Index (NDVI) from National Agriculture Imagery Program (NAIP) aerial imagery in ArcGIS v. 10.3 (ESRI, Redlands, CA, USA) to classify three distinct habitat types: on-mound habitat (locations on mima mounds characterized by relatively tall, dense shrub canopy, typically 60 – 120 cm tall), off-mound habitat (locations in the matrix between mima mounds characterized by continuous bands of relatively tall, dense shrub cover, typically 30 – 60 cm tall), and dwarf shrub habitat (locations in the matrix where sagebrush shrubs were sparsely distributed and relatively low growing, typically < 30 cm tall). In each of the three habitat strata, we selected 30 random points for delineation of 3-m radius patches. Within each patch, we identified three focal shrubs by selecting three random distance and direction combinations from the center point. Focal shrubs and the center of the patch were marked with metal tags for repeated monitoring.

To measure T_e, we built 90 physical models by painting hollow copper ovoids a matte, dark gray (Bakken 1992). We secured an iButton temperature logger (model DS1921G, Maxim Integrated, San Jose, CA, USA) to the end of a wooden dowel that was held in place in each model by a rubber stopper (Fig. 3.2). We also attached two 8 cm segments of pipe to the bottom of the ovoid to prevent it from resting directly on the ground and to anchor it to substrate. Models were rotated among focal shrubs in the summer and winter such that T_e was monitored at each location for two weeks in each season. We placed models at a randomly determined direction as close to the base of a focal shrub as was possible without damaging or altering the vegetation. The same orientation was used for each focal shrub during both summer and winter. This design resulted in a total of 1068 T_e data files (Magic Reservoir: 264 stations in winter and summer 2014; and Cedar Gulch: 270 stations winter and summer 2015).

Twenty-seven files were excluded due to sensor damage, data loss, and missing habitat covariates (Appendix E). Because heavy snowfall could encapsulate the T_e models and result in erroneous measures of microclimate, we excised data corresponding to periods of snowfall as recorded by the nearest Idaho Department of Transportation weather station at Magic Reservoir, and at Cedar Gulch we repositioned models on the snow surface following snowfall.

At each monitoring location, we measured two properties of habitat structure (horizontal cover and shrub volume) with the potential to influence microclimates. We selected these parameters, in part, because they could also be estimated from UAS imagery for mapping microclimates across the study sites (Cunliffe et al. 2016). We measured horizontal cover by placing four 15 × 15 cm cover boards with 25 equal-sized cells at each of the four cardinal directions around the base of the focal shrub (Fig. 3.3). A photo was taken of the cover boards from a height of 1.5 m, and the number of cells ≥ 50% concealed on each of the four cover boards was summed to yield a percentage. Shrub volume was estimated by multiplying the maximum height of the focal shrub, excluding inflorescences and dead wood, by the canopy area (maximum width × perpendicular width).

Statistical Analysis

We evaluated two response variables in each season: the average maximum temperature ($\bar{T}_{\max}$) and the average diurnal temperature range ($\overline{DTR}$), which is the difference between the daily maximum and daily minimum temperatures. The $\overline{DTR}$ directly affects endotherm fitness through the cumulative energy costs imposed by large values of $\overline{DTR}$ over extended periods of time, and it is a potentially a superior measure of the thermal quality of habitat (Oberhauser and Peterson 2003, Vasseur et al. 2014, Briga and Verhulst 2015). However, $\bar{T}_{\max}$ also is of interest because sites characterized by high temperatures might be selected for behavioral thermoregulation in winter, but avoided in summer.

We developed a series of nested candidate models to evaluate the seasonal influence of habitat on the thermal environment at the two study sites. We ensured that predictor variables were not highly correlated ($|r| < 0.7$), and used linear mixed models to relate predictors to each temperature response variable. The full model for each study site included fixed effects for horizontal cover, shrub volume, season, and habitat type, as well as random effects for monitoring site, azimuth (direction relative to shrub), and period (monitoring time interval).

We also included interaction terms between season and both horizontal cover and volume to evaluate the seasonal capacity of habitat structure to moderate temperature. This resulted in four candidate model sets: one candidate model set for each response variable ($\bar{T}_{\max}$ and $\overline{DTR}$) at each site (Cedar Gulch and Magic Reservoir). The $\bar{T}_{\max}$ and $\overline{DTR}$ were standardized by season to meet the assumption of normality, and all candidate model sets included an intercept-only null model. We used Akaike's Information Criterion for small sample sizes (AICc) to evaluate support for models in each candidate set (Burnham and Anderson 2002), and for all models ranked above the null with $\Sigma w_i \leq 0.95$, we calculated the marginal and conditional R^2 to evaluate the fit and predictive capacity of the top models (Nakagawa and Schielzeth 2013). The conditional R^2 (R^2_c) is the variance explained by both the random and fixed effects in a mixed effects model, whereas the marginal R^2 (R^2_m) is the variance explained by the fixed factors. We evaluated parameter significance for predictors in the top model from each candidate set based on an 85% confidence interval that did not overlap zero (Arnold 2010). All analyses were performed using the 'lme4', 'MuMIn', and 'AICcmodavg' packages in R (R Core Team 2014, Bates et al. 2015, Barton 2016, Mazerolle 2016).

Predictive Mapping

We developed a map of thermal microsites for a 300 m × 300 m extent at the Cedar Gulch study site by estimating values of the vegetation structure variables at a 1-m resolution from UAS aerial imagery (Fig. 3.4) and applying the predictive model for $\bar{T}_{\max}$ during summer and winter and $\overline{DTR}$ during summer developed from our ground-based measurements. We created a classified map using Focal Statistics (10 ×10 m neighborhood) on the canopy height model in ArcMap 10.3 and verified that habitat types were correctly delineated by deleting erroneous polygons. The top thermal model for each response variable from the Cedar Gulch study site was applied to the classified raster at a 1-m^2 scale, and predicted values were unstandardized to express $\bar{T}_{\max}$ and $\overline{DTR}$ in degrees Celsius.

Results

We observed considerable variability in both habitat structure and the thermal environment during summer and winter, suggesting that we captured the diversity of microhabitats available to small animals at these study sites. Horizontal cover and shrub volume varied markedly across study sites, but habitat structure was similar between seasons within each (Table 3.1). This is likely because sagebrush shrubs, which provide almost all the vegetation structure, are slow-growing plants. The presence of ephemeral leaves during summer likely contributed to slightly higher levels of cover at Cedar Gulch during that season, but mean values were nearly identical between seasons at Magic Reservoir. Habitat structure across the three habitat types followed a general gradient from highest horizontal cover and shrub volume in the on-mound habitat to lowest values in the dwarf shrub habitat (Table 3.1). Like structure, T_e values at both study sites varied across our sampling locations suggesting a diversity of thermal microhabitats during summer and winter. $\bar{T}_{\max}$ and $\overline{DTR}$ were similar between study sites and mean values did not differ markedly across habitat types (Table 3.2).

Modeling two measures of T_e by shrub volume and horizontal cover illuminated the influence of habitat structure on the thermal environment at the microsite scale, but results differed between the study sites. $\overline{DTR}$ and $\bar{T}_{\max}$ were highly correlated within study sites and seasons, and so the top models were similar for both response variables. At Cedar Gulch, the model that included shrub volume, horizontal cover, and habitat type was the best supported and accounted for the majority of the model weights (w_i = 0.70 for $\overline{DTR}$ and 0.69 for $\bar{T}_{\max}$; Table 3.3; Appendix F). Both $\overline{DTR}$ and $\bar{T}_{\max}$ decreased with increasing values of horizontal cover and shrub volume (Fig. 3.5), and the effect of habitat structure did not differ between seasons (Table 3.4). Microsites in the off-mound habitat had significantly larger $\overline{DTR}$ than microsites in the dwarf shrub habitat with the same levels of volume and horizontal cover. Habitat type did not have a significant effect on $\bar{T}_{\max}$ based on an 85% confidence interval that captured zero (Table 3.4). The models relating habitat to the thermal environment at Cedar Gulch suggested high predictive capacity. The top model for both response variables accounted for > 70% of the variance in the dataset, of which 12 – 18 % was attributable to the fixed effects (Table 3.3).

In contrast to Cedar Gulch, the thermal environment at Magic Reservoir was less affected by the habitat features we measured. At Magic Reservoir, the global model was the best supported model for both response variables ($\bar{T}_{\max}$: w_i = 0.50; $\overline{DTR}$: w_i = 0.53), but there was considerable model uncertainty, with several models included in the 95% confidence set (Table 3.3; Appendix F). The best model indicated that both $\overline{DTR}$ and $\bar{T}_{\max}$ decreased with increasing levels of shrub volume and horizontal cover (Table 3.4). For both response variables, a significant, positive effect for the season × volume interaction also was supported, indicating that shrub volume had a greater effect on thermal microsites during summer. Although the full models for both response variables had moderately high R^2_c values ($\bar{T}_{\max}$: 0.75; $\overline{DTR}$: 0.62), less than 5% of the variance in temperature was attributable to the fixed effects in both candidate model sets ($\bar{T}_{\max}$ R^2_m: 0.02; $\overline{DTR}$ R^2_m: 0.04), suggesting that habitat had a more limited influence on thermal properties of microsites at the Magic Reservoir study site than at Cedar Gulch.

Because the models of habitat structure on thermal microsites had stronger predictive power at the Cedar Gulch site, we used UAS-derived data to create a spatially explicit model of the thermal environment only at that study site. The results illustrate the heterogeneity of microhabitats across the landscape (Fig. 3.6). The highest values of habitat structure occurred on mima mounds and in the bands of dense shrubs in some of the off-mound habitat, and these locations were predicted to have the lowest values of $\bar{T}_{\max}$ and $\overline{DTR}$. The resulting map indicates that the thermal environment is highly patchy at fine-spatial scales, and that thermal refugia exhibit a clumped distribution associated with underlying patterns of heterogeneity in the habitat structure.

Discussion

Our results revealed a complex relationship between vegetation structure and temperature throughout the year at fine spatial scales in a shrubsteppe habitat often perceived as relatively homogeneous. Habitat structure in the form of shrub volume and cover can modulate the microclimate that animals experience, and increasing habitat structure reduced both $\bar{T}_{\max}$ and $\overline{DTR}$ of microsites during summer and winter. Moderated thermal environments can have physiologic consequences that can manifest in differential fitness (Huey 1991), and organisms often select microhabitats that either reduce thermoregulatory costs or optimize temperature-dependent performance. Evaluation of the thermal environment at organism-relevant scales can help to identify refugia that enhance potential for adaptive capacity under changing climates, and provide a mechanistic understanding of how habitat change might influence habitat quality.

At both study sites during summer and winter, increasing horizontal cover and shrub volume resulted in attenuated thermal microsites (Fig. 3.5). Habitat structure in these systems functions to provide shade to ground-dwelling animals, and the capacity of vegetation structure to do so will vary within and among days (Davies-Colley and Payne 1998, Kelley and Krueger 2005). We expected that the influence of vegetation structure on T_e might differ between seasons, however, we only detected a significant effect of season at Magic Reservoir. At that site, vegetation structure had a stronger effect on T_e during summer than winter (Table 3.4). Pringle et al. (2003) noted that incident radiation intensity was the primary factor influencing microsite temperature, which depended not only on the amount of overhead canopy, but also on the location of canopy gaps relative to the sun's path. The sagebrush shrubs at the Magic Reservoir site tended to be large with more defined trunks and fewer branches near the ground than shrubs at Cedar Gulch; consequently, orientation of the canopy might effectively provide shade during summer when the sun is higher, but might not provide shade for ground-dwelling animals during winter when the sun is at a lower angle.

Our model predicted significantly higher $\overline{DTR}$ at locations in off-mound habitat relative to locations in dwarf shrub habitat with the same levels of horizontal cover and shrub volume at Cedar Gulch (Table 3.4). Plants that grew in the off-mound habitat typically had higher levels of habitat structure than dwarf plants, but this predictor may be masking the effect of some other thermally significant element specific to off-mound and dwarf shrub habitat types that we did not measure. For example, different substrate types in the two habitats (e.g., gravel versus soil) might reflect different amounts of heat (Buxton 1924). When mapped at Cedar Gulch, this relationship suggested that the hottest microsites are found on the periphery of otherwise thermally buffered microsites, rather than exclusively in the less structurally diverse, dwarf shrub habitat (Fig. 3.6).

Evaluating the thermal properties of habitat at organism-relevant scales has received heightened attention with predictions of global climate change (Gillingham et al. 2012, Hannah et al. 2014, George et al. 2015). Fine-scale climatic measurements can help identify thermal refugia overlooked by large-scale modeling approaches, but an organism's size, mobility, and perceptions will influence the scale or scales at which individuals respond to thermal properties (Kotliar and Wiens 1990, Hannah et al. 2014). Landsat imagery has been successfully used to estimate values of habitat structure such as canopy cover in evaluations of thermal quality for moose (*Alces alces*) and grizzly bears (*Ursos arctos;* Olson et al. 2014, Pigeon et al. 2016), but such large-bodied and mobile organisms likely perceive thermal heterogeneity much differently than smaller species. Our results reveal that even modest changes in habitat structure can result in attenuated thermal environments across small spatial scales (Fig. 3.6). Thus, habitat structure might provide opportunities for organisms to cope with climate change by responding behaviorally *in situ*, which would allow them to survive longer to continue to encounter refugia or migrate to more favorable conditions (Liow et al. 2009).

Although our measures of temperature are not a measure of habitat quality per se, identifying the thermal quality of microsites could be accomplished by linking thermal physiology with temperature to quantify, for example, the cost of thermoregulating in different microsites or the quantity of time during which a microsite would be within an animal’s thermoneutral zone or optimum temperature range (Porter and Kearney 2009, Kearney et al. 2011, Milling Ch. 2). At both Cedar Gulch and Magic Reservoir, $\bar{T}_{\max}$ during summer was likely hotter than the thermoneutral zone of a small mammal in all three habitat types, but it was colder than the thermoneutral zone in winter (Table 3.2; Araujo et al. 2013). However, because habitat structure moderates T_e, microhabitats likely provide variable levels of thermal quality during both seasons, allowing animals to behaviorally thermoregulate by moving among microsites. The distribution of thermal resources on the landscape also might influence the quality of a microsite as a thermal refuge. Sears et al. (2016) reported that the spatial distribution of microclimates was directly related to physiological performance of ectotherms, and animals could thermoregulate more efficiently when thermal resources were dispersed rather than clumped. At our study sites, structural complexity was higher on mima mounds and in the bands of taller off-mound sagebrush, and the coolest microsites during the summer were predicted to occur in the center of these clumps (Fig. 3.6). Moving between closely located thermal refugia would require less energy than moving between more distant locations, and for prey species, shorter movements also might reduce predation risk (Huey and Slatkin 1976). Thus, spatial representation of the relationship between habitat structure and temperature can improve our assessments of habitat quality for thermal refuge in changing landscapes.

Temperature regulation is a functional role of habitat structure, and activities and conditions that alter habitat structure can change the availability and distribution of critical thermal refugia. Because of the direct relationship between temperature and physiology, loss of this function can result in changes in the behavior, distribution, or demography of inhabitants (Huey 19991, Sharpe and Van Horne 1999, Hannah et al. 2014). Habitat structure without function, as a result of non-native vegetation invasion for example, might even create ecological traps for organisms whose physiological performance are closely associated with environmental temperatures (Block et al. 2013). Anthropocentric land uses that mimic natural processes may not maintain the functional role of habitat. For example, single-tree removal for lumber production in an Amazonian forest created canopy gaps that were hotter than natural tree falls and were unsuitable habitat for many forest-dwelling species (Vitt et al. 1998). In sagebrush systems in the American West, cattle grazing can affect vegetation composition and shrub cover (Jones 2000, Manier and Hobbs 2007), and consequently, has the potential to alter thermal heterogeneity and habitat quality for sagebrush-reliant species. High resolution maps of the thermal environment could identify thermal refugia and aid restoration efforts on these disturbed landscapes.

We documented substantial heterogeneity in both habitat structure and the thermal environment among sites at approximately a 1-m resolution using direct measurement, but the true utility of this method is in its capacity to quantify fine-scale thermal heterogeneity across large spatial extents (Bakken and Angilletta 2014). Quantification of the influence of habitat on temperature, coupled with emerging remote sensing technology (e.g., UAS), facilitated development of high resolution maps of the thermal environment at a spatial extent that likely exceeds the home range of many small, sagebrush-dwelling species (Hoffmeister 1981, Smith and Johnson 1985, Sanchez and Rachlow 2008). This technique and others like it (e.g., using LiDAR to map habitat structure; George et al. 2015, Olsoy et al. 2015) offer exciting opportunities to rectify scale-mismatches in our evaluation of the effects of climate change and land-use on small organisms.

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Table 3.1 Average (and range) values of habitat structure variables for each of three habitat types during summer (S) and winter (W) at two study sites (Cedar Gulch, CG, and Magic Reservoir, MR) in sagebrush steppe habitats in Idaho, USA.

Study Site	Season	Habitat Type	Volume (m^3)	Horizontal Cover (%)
Cedar Gulch	Summer	Dwarf	0.03 (< 0.01 – 0.31)	9.3 (0 – 42)
		Off-mound	0.15 (< 0.01 – 0.78)	40.2 (0 – 95)
		On-mound	0.33 (< 0.01 – 1.89)	60.3 (2 – 100)
	Winter	Dwarf	0.02 (< 0.01 – 0.26)	8.5 (0 – 37)
		Off-mound	0.13 (< 0.01 – 0.93)	38.1 (0 – 96)
		On-mound	0.26 (< 0.01 – 1.53)	53.6 (0 – 98)
Magic Reservoir	Summer	Dwarf	0.03 (< 0.01 – 0.28)	18.6 (0 – 84)
		Off-mound	0.2 (< 0.01 – 1.58)	47.0 (1 – 98)
		On-mound	0.4 (< 0.01 – 2.99)	52.2 (2 – 98)
	Winter	Dwarf	0.04 (< 0.01 – 0.17)	20.1 (0 – 92)
		Off-mound	0.2 (< 0.01 – 1.41)	47.5 (2 – 96)
		On-mound	0.5 (< 0.01 – 2.57)	51.2 (0 – 100)

Table 3.2 Average (and range) values of two measures of operative temperature (T_e; $\overline{DTR}$ and $\bar{T}_{max}$) for each of three habitat types during summer (S) and winter (W) at two study sites (Cedar Gulch, CG, and Magic Reservoir, MR) in sagebrush steppe habitats in Idaho, USA.

Study Site	Season	Habitat Type	$\overline{DTR}$ (° C)	$\bar{T}_{max}$ (° C)
Cedar Gulch	Summer	Dwarf	35.4 (30.3 – 43.4)	43.3 (38.2 – 55.5)
		Off-mound	35.1 (23.2 – 45.8)	43.1 (30.4 – 55.9)
		On-mound	33.4 (24.5 – 42.4)	42.2 (30.7 – 54.8)
	Winter	Dwarf	27.2 (17.8 – 35.9)	17.7 (11.1 – 24.8)
		Off-mound	25.1 (12.7 – 39.5)	15.8 (2.9 – 27.6)
		On-mound	22.3 (12.0 – 37.7)	13.7 (3.3 – 28.5)
Magic Reservoir	Summer	Dwarf	37.4 (30.3 – 44.1)	47.1 (36.5 – 55.5)
		Off-mound	35.2 (22.7 – 44.1)	45.0 (32.4 – 55.8)
		On-mound	35.9 (25.5 – 44.4)	45.9 (32.7 – 55.9)
	Winter	Dwarf	23.0 (11.7 – 30.3)	16.0 (5.1 – 24.9)
		Off-mound	22.5 (11.4 – 32.9)	15.6 (3.6 – 25.9)
		On-mound	21.5 (10.5 – 30.7)	14.9 (2.4 – 26.9)

Table 3.3 The 95% confidence set of models relating two measures of operative temperature (T_e; $\overline{DTR}$ and $\overline{T}_{\max}$) to structural habitat variables during the summer and winter at two study sites (Cedar Gulch, CG, and Magic Reservoir, MR) in sagebrush steppe habitats in Idaho, USA. All models included random effects for individual plant, period of measurement, and orientation relative to focal shrub.

Study Site	Response Variable	Model[a]	k	AICc	ΔAICc	w_i	Σw_i	R^2_c	R^2_m
CG	$\overline{T}_{\max}$	*Vol + HorCov + HabType*	9	1041.83	--	0.69	0.69	0.75	0.12
		Vol + HorCov + HabType + Season	10	1043.85	2.02	0.25	0.94	0.75	0.12
		Vol + HorCov + HabType + Season + Season×HorCov + Season×Vol	12	1046.94	5.11	0.05	1.00	0.75	0.13
CG	$\overline{DTR}$	*Vol + HorCov + HabType*	9	977.40	--	0.70	0.70	0.70	0.18
		Vol + HorCov + HabType + Season	10	979.42	2.02	0.25	0.95	0.70	0.18
MR	$\overline{T}_{\max}$	*Vol + HorCov + HabType + Season + Season×HorCov + Season×Vol*	12	913.44	--	0.49	0.49	0.75	0.02
		Vol + HorCov + HabType	9	914.96	1.53	0.23	0.72	0.74	0.03
		Vol + HabType + Season + Season×Vol	10	916.17	2.74	0.13	0.85	0.74	0.02
		Vol + HorCov + HabType + Season	10	917.04	3.61	0.08	0.93	0.74	0.02
		Vol + Season + Season×Vol	8	919.27	5.84	0.03	0.95	0.74	0.01
MR	$\overline{DTR}$	*Vol + HorCov + HabType + Season + Season×HorCov + Season×Vol*	12	1164.46	--	0.53	0.53	0.62	0.04
		Vol + HorCov + HabType	9	1165.80	1.34	0.27	0.80	0.61	0.04

Vol + HorCov + HabType + Season	10	1167.88	3.41	0.10	0.90	0.61	0.04
Vol + HabType + Season + Season×Vol	10	1169.11	4.65	0.05	0.95	0.62	0.03

[a] –Main, fixed effects included shrub volume (*Vol*), horizontal cover (*HorCov*), habitat type (*HabType*), and season (*Season*).

Table 3.4 Parameter estimates and 85% confidence intervals for predictors in the top model from each candidate set relating two measures of operative temperature (T_e; $\overline{DTR}$ and $\bar{T}_{max}$) to structural habitat variables during the summer and winter at two study sites (Cedar Gulch, CG, and Magic Reservoir, MR) in sagebrush steppe habitats in Idaho, USA. * indicates predictors that were significant based on a confidence interval that did not capture 0.

Study Site	Response Variable	Predictor Variable	Parameter Estimate	SE	85% LCI	85% UCI
Cedar Gulch	$\bar{T}_{max}$	Intercept	0.3150	0.2767	-0.2823	0.9103
		Volume*	-0.6715	0.1790	-1.0235	-0.3196
		Horizontal Cover*	-0.0086	0.0017	-0.0118	-0.0053
		HabType: Off-mound	0.0842	0.0878	-0.0893	0.2566
		HabType: On-mound	0.0583	0.1016	-0.1424	0.2577
Cedar Gulch	$\overline{DTR}$	Intercept	0.3218	0.2194	-0.0101	0.6517
		Volume*	-0.5849	0.1686	-0.8283	-0.3417
		Horizontal Cover*	-0.0092	0.0016	-0.0114	-0.0069
		HabType: Off-mound*	0.1408	0.0823	0.0217	0.2593
		HabType: On-mound	-0.0141	0.0952	-0.1519	0.1231
Magic Reservoir	$\bar{T}_{max}$	Intercept	0.2502	0.4129	-0.3819	0.8821
		Volume*	-0.3218	0.0967	-0.4615	-0.1823
		Horizontal Cover*	-0.0036	0.0014	-0.0057	-0.0016
		HabType: Off-mound	-0.0824	0.0721	-0.1863	0.0217
		HabType: On-mound	-0.0896	0.0796	-0.2045	0.0254
		Season	-0.1594	0.5751	-1.0425	0.7241
		Season × Horizontal Cover	0.0020	0.0017	-0.0004	0.0045
		Season × Volume*	0.2689	0.1252	0.0882	0.4498
Magic Reservoir	$\overline{DTR}$	Intercept	0.3539	0.3573	-0.1907	0.8979
		Volume*	-0.3949	0.1237	-0.5735	-0.2164
		Horizontal Cover*	-0.0053	0.0018	-0.0079	-0.0027
		HabType: Off-mound*	-0.1431	0.0946	-0.2797	-0.0064
		HabType: On-mound	-0.1396	0.1043	-0.2895	0.0118
		Season	-0.1668	0.4889	-0.9160	0.5833
		Season × Horizontal Cover	0.0027	0.0021	-0.0004	0.0058
		Season × Volume*	0.3235	0.1580	0.0959	0.5522

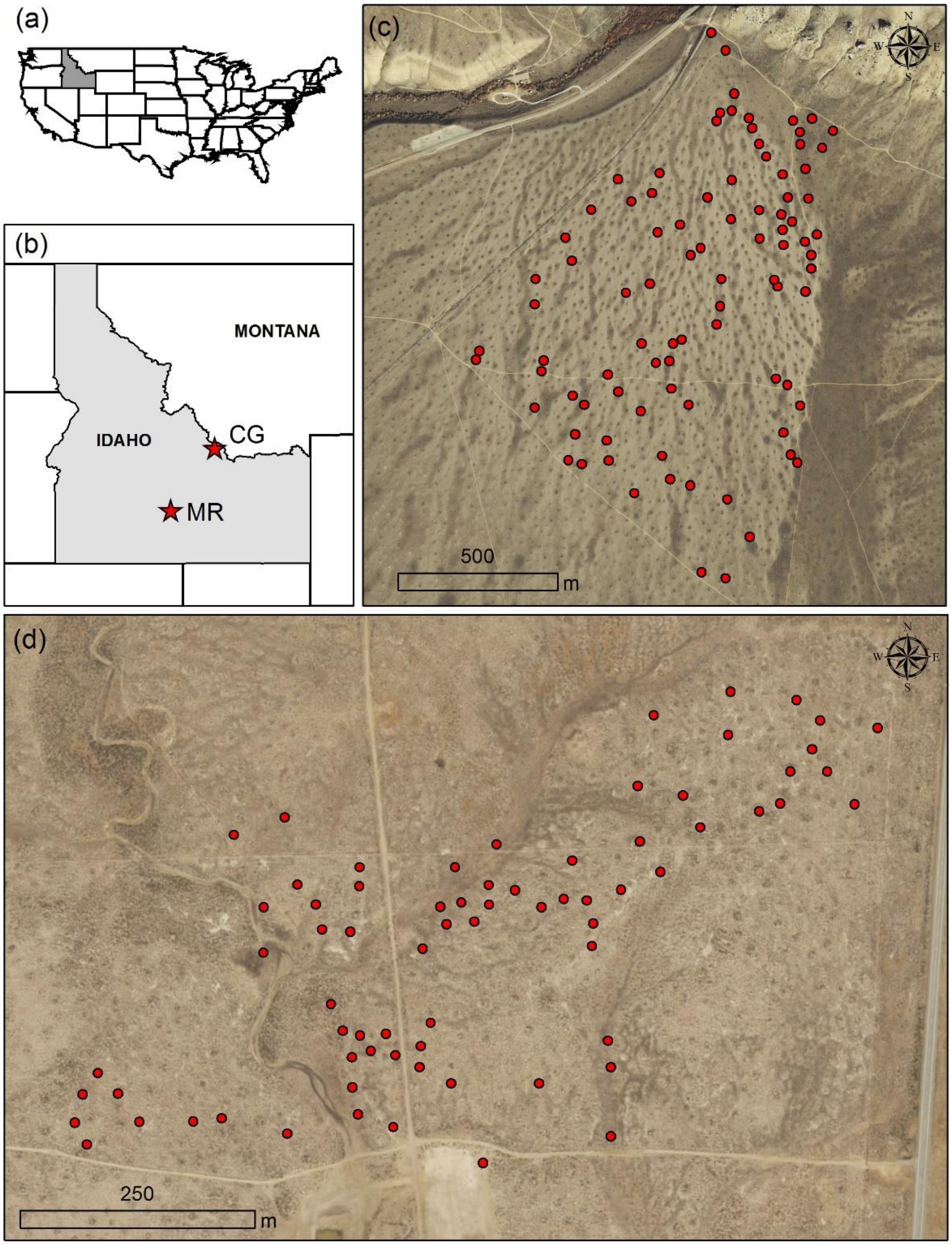


Figure 3.1 Study sites were located in sagebrush steppe rangelands in Idaho, USA (a) in the Lemhi Valley (Cedar Gulch, CG) and the Camas Prairie (Magic Reservoir, MG; b). Monitoring locations at Cedar Gulch (c) and Magic Reservoir (d) were distributed among three habitat types over an area of approximately 1 km^2 in east-central Idaho, USA. In National Agriculture Imagery Program (NAIP) imagery, round, discreet clusters of dark vegetation are on-mound habitat, continuous bands of vegetation are off-mound habitat, and the matrix between mounds is the dwarf shrub habitat.

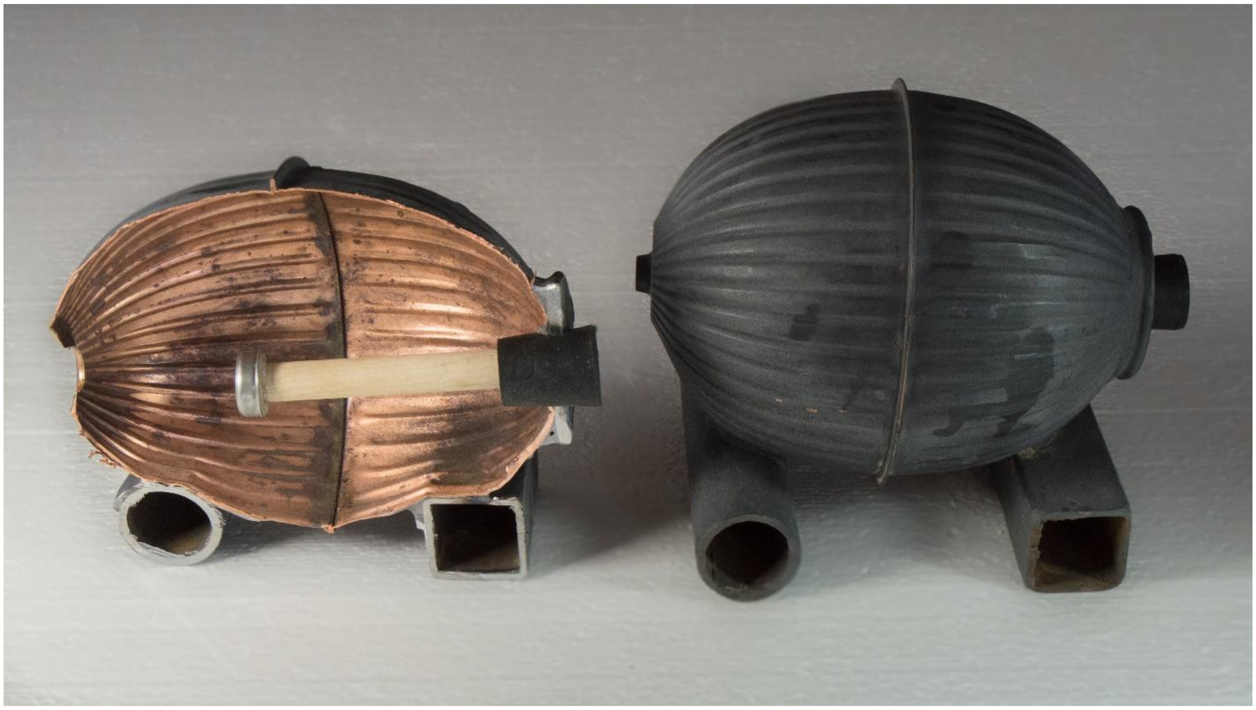


Figure 3.2 Cross-section of an operative temperature (T_e) model (left) and intact model (right) used to characterize the thermal environment in sagebrush steppe in Idaho, USA. (Photo credit: Charles Peterson)

Figure 3.3 Horizontal cover of a focal shrub was estimated by using four 15 × 15 cm cover boards placed around the base of a shrub and counting the number of cells ≥ 50% concealed when viewed from a height of 1.5 m.

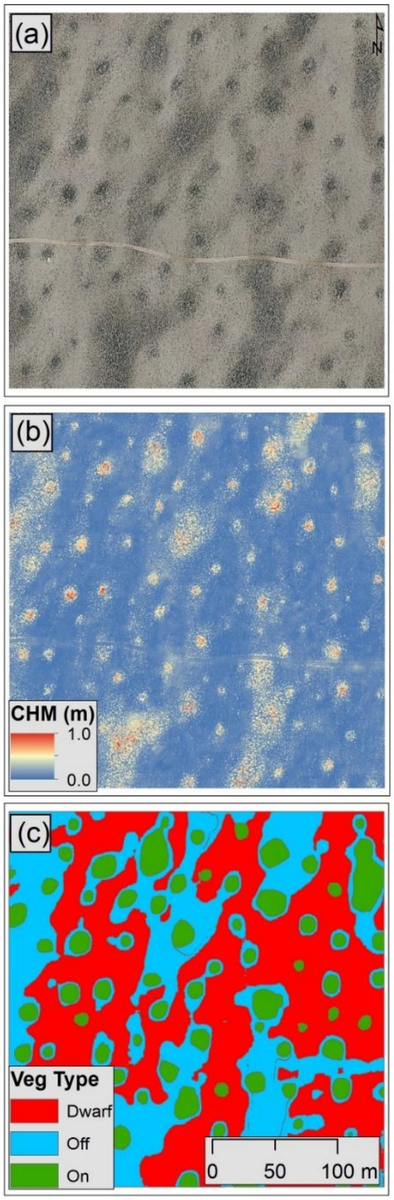


Figure 3.4 A 300 m × 300 m extent of the spatial data used to map the predicted thermal landscape at the Cedar Gulch study site in east-central Idaho, USA. (a) High resolution (3-cm) unmanned aerial systems (UAS) imagery (the distribution of shrubs is visible as darker areas associated with mima mounds and broad bands of shrub cover between mounds). (b) The canopy height model (CHM) was created from UAS imagery to quantify shrub volume and canopy cover across the study site. (c) Three habitat types (on-mound, off-mound and dwarf shrub) were classified using Focal Statistics (10 × 10 m neighborhood) on the CHM.

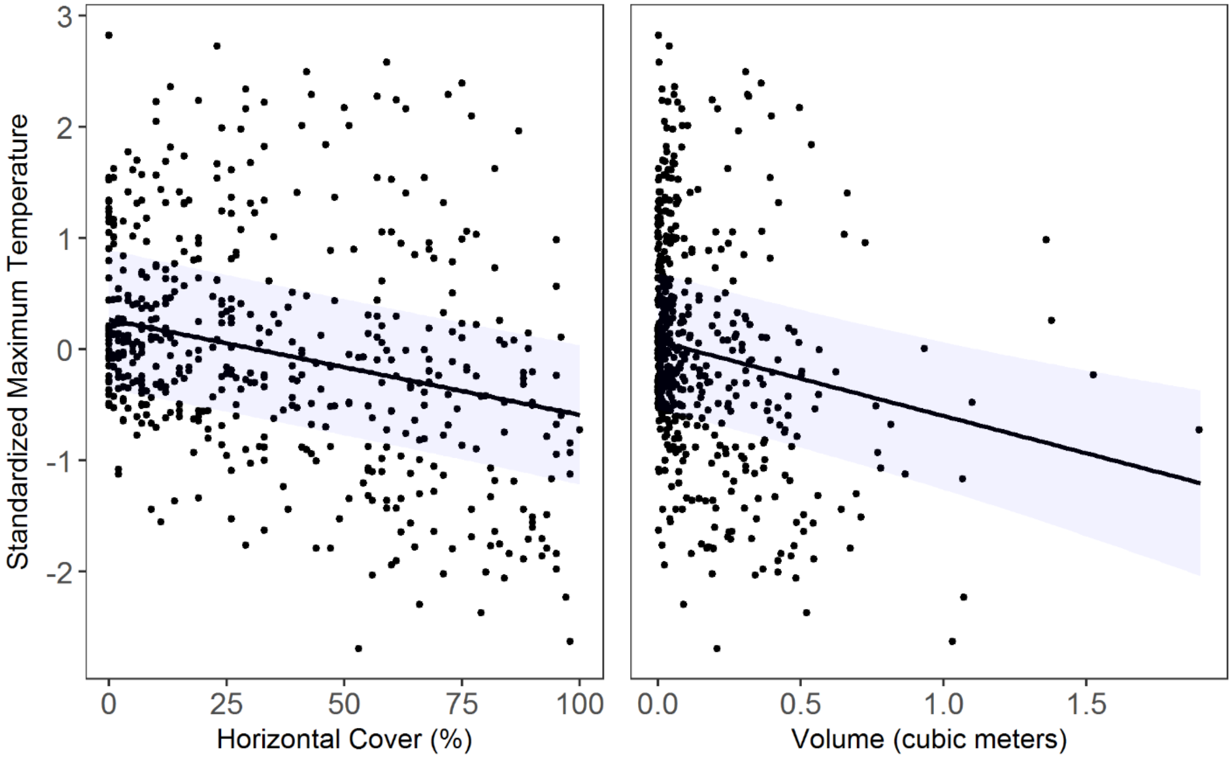


Figure 3.5 Predicted mean daily maximum temperature ($\bar{T}_{\text{max}}$; with 95% confidence bands) at microsites decreased with increasing horizontal cover (left) and shrub volume (right) at the Cedar Gulch study site in east-central Idaho, USA.

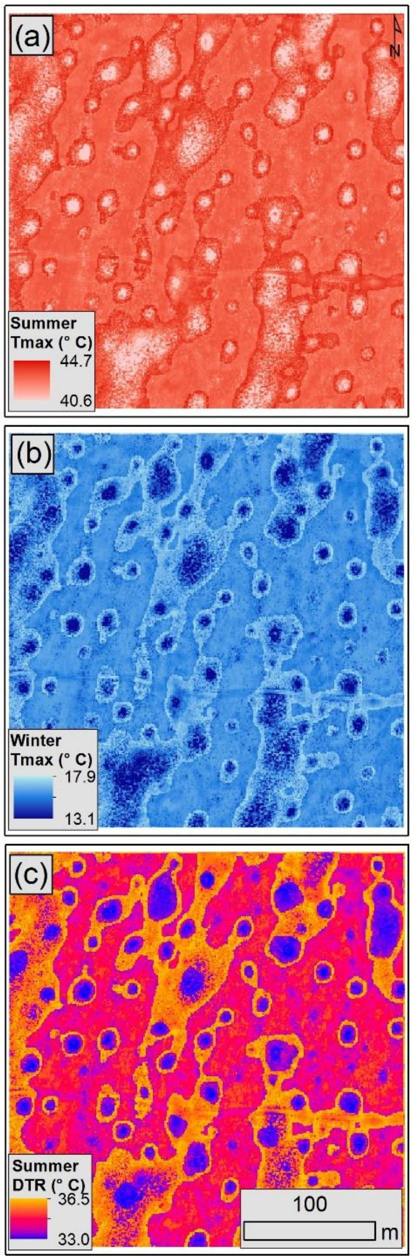


Figure 3.6 The predicted thermal map across a 300 m × 300 m at the Cedar Gulch study site in east-central Idaho, USA illustrates fine-scale heterogeneity at high resolution (1-m). (a) The coolest microsites during summer occur in a clumped distribution associated with mima mounds. (b) The warmest microsites during winter occur along the periphery between habitat types where vegetation structure is varied. (c) $\overline{DTR}$ during summer is lowest on mima mounds where vegetation tends to be tall and dense.

General Conclusion

The objective of this research was to investigate the role of behavioral plasticity, physiological acclimatization, and habitat structure in summer and winter thermoregulation by pygmy rabbits (*Brachylagus idahoensis*) in Idaho. I found that pygmy rabbits demonstrated a high capacity for behavioral thermoregulation by selecting shaded rest sites with cool microclimates during the summer and partitioning activity to avoid the coldest periods of the 24-hour day during the winter. In addition, pygmy rabbit behavior was modulated by perception of predation risk. Animals selected rest sites that were concealed from predators and close to burrows during summer and winter. Pygmy rabbits also avoided night time activity under full moons and seemingly shifted active bouts to less risky day time intervals. Pygmy rabbits acclimatized physiologically to seasonal thermal conditions; winter-acclimatized animals had lower thermal conductance and expended less energy to thermoregulate with increasing cold relative to summer-acclimatized animals. Despite these changes in thermal physiology, the burrow represented an important thermal refuge during the winter, when thermoregulatory costs imposed by using a burrow during the coldest times of day were lower than those imposed by using only above-ground microsites. During summer, however, the burrow had a limited role as a thermal refuge because of the considerable thermal heterogeneity available in above-ground rest sites. Habitat structure, such as shrub volume and canopy cover, created microrefugia at fine spatial scales, which were illuminated using a combination of direct measurement and unmanned aerial systems imagery. This heterogeneity in the thermal landscapes at spatial scales relevant to pygmy rabbits contributed to opportunities for behavioral thermoregulation above ground.

Pygmy rabbits are predicted to be extinct by 2080 based on bioclimatic envelope modelling (Leach et al. 2015), but predictions of mammalian response to climate change are infrequently accurate (McCain and King 2014). Bioclimatic modeling approaches often account for exposure to climate change only, and fail to account for sensitivity or adaptive capacity (such as behavioral thermoregulation or physiological acclimatization; Dawson et al. 2011). Furthermore, large-scale approaches to prediction often underestimate the availability and distribution of important microrefugia for small animals (Beever et al. 2015). It is also becoming increasingly apparent that anticipated changes in intensity and frequency of extreme events may be as consequential as gradual changes in climate (Jentsch et al. 2008, Thorton 2014). This research highlights intrinsic properties at the individual level that contribute to resiliency, as well as habitat heterogeneity that provides opportunity for coping *in situ* for a species of conservation concern. Acknowledging the importance of these factors and incorporating them into predictive modeling efforts has the potential to improve the accuracy of predictions. This will allow management resource to be more precisely allocated and improve the likelihood of success success of proactive management strategies.

References

Beever, E. A., J. O'Leary, C. Mengelt, J. M. West, S. Julius, N. Green, D. Magness, L. Petes, B. Stein, A. B. Nicotra, J. J. Hellmann, A. L. Robertson, M. D. Staudinger, A. A. Rosenberg, E. Babij, J. Brennan, G. W. Schuurman, and G. E. Hofmann. 2015. Improving conservation outcomes with a new paradigm for understanding species' fundamental and realized adaptive capacity. *Conservation Letters* 9:131-137.

Dawson, T. P., S. T. Jackson, J. L. House, I. C. Prentice, and G. M. Mace. 2011. Beyond predictions: biodiversity conservation in a changing climate. *Science* 332:53-58.

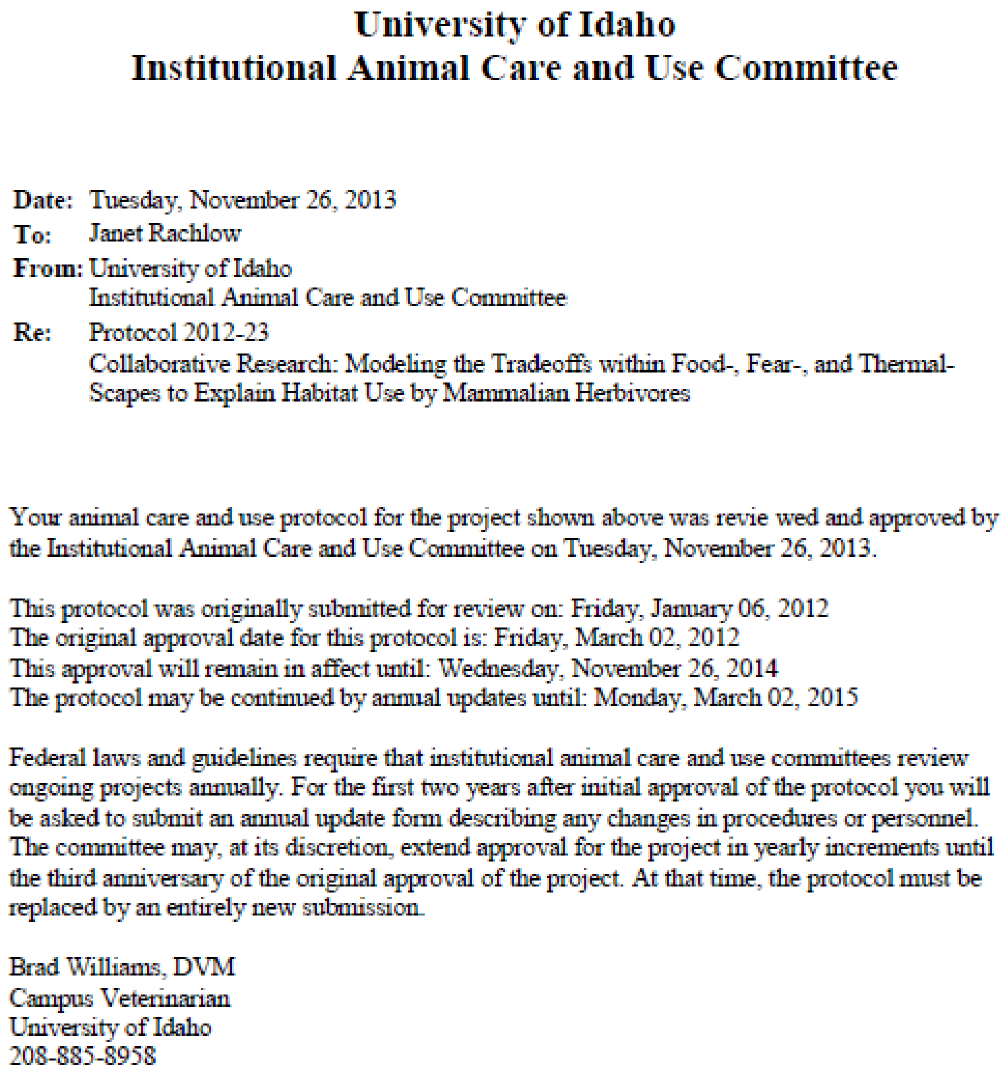
Jentsch, A., J. Kreyling, J. Boettcher-Treschkow, and C. Beierkuhnlein. 2009. Beyond gradual warming: extreme weather events alter flower phenology of European grassland and heath species. *Global Change Biology* 15:837-849.

Leach K., R. Kelly, A. Cameron, W. I. Montgomery, and N. Reid. 2015. Expertly validated models and phylogenetically-controlled analysis suggests responses to climate change are related to species traits in the order *Lagomorpha*. *PLoS ONE* 10:e0122267.

McCain, C. M. and S. R. B. King. 2014. Body size and activity times mediate mammalian responses to climate change. *Global Change Biology* 20:1760-1769.

Thornton, P. K., P. J. Ericksen, M. Herrero, and A. J. Challinor. 2014. Climate variability and vulnerability to climate change: a review. *Global Change Biology* 20:3313-3328.

Appendix A:
University of Idaho Institutional Animal Care and Use Committee
Protocol Approval



University of Idaho
Institutional Animal Care and Use Committee

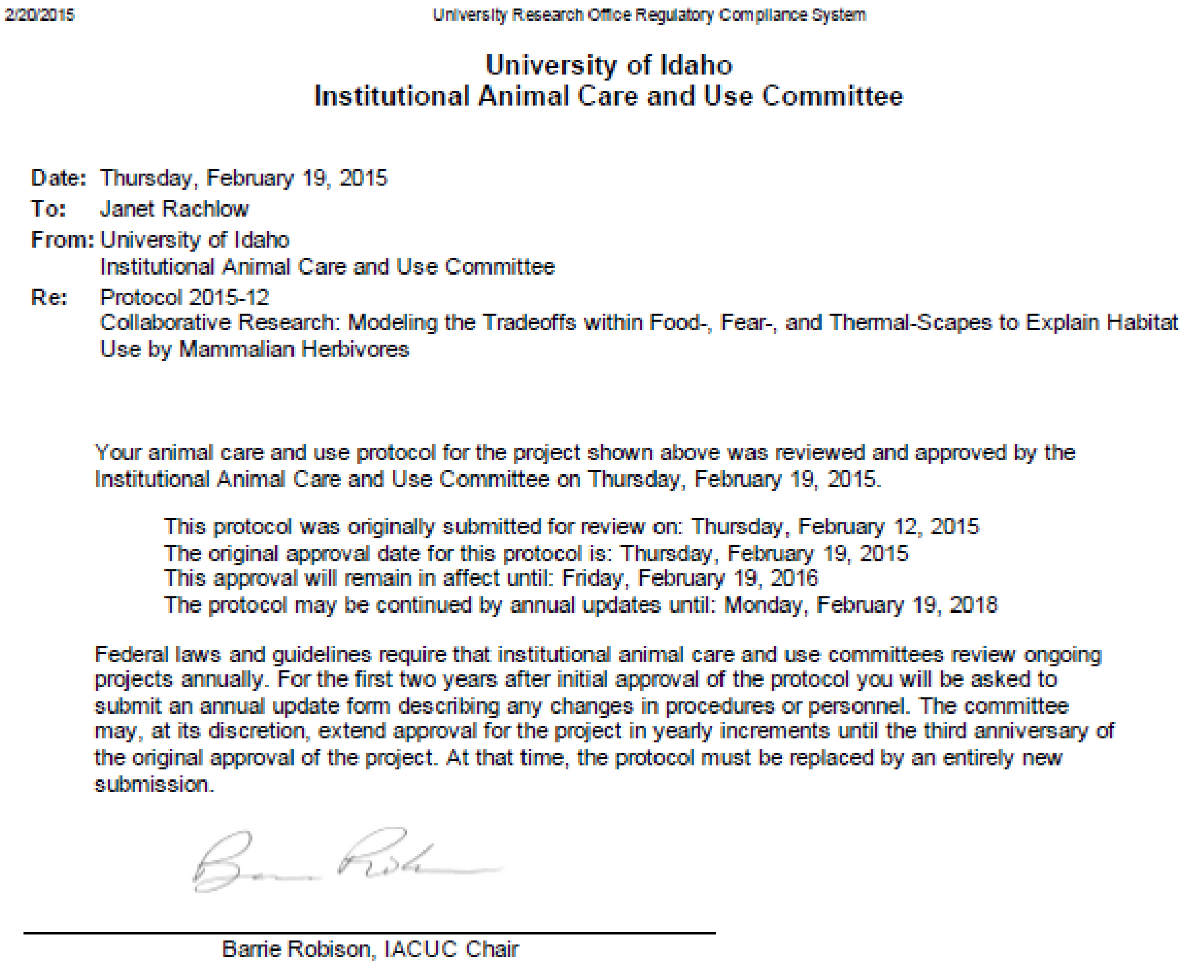
Date: Tuesday, November 26, 2013
To: Janet Rachlow
From: University of Idaho
Institutional Animal Care and Use Committee
Re: Protocol 2012-23
Collaborative Research: Modeling the Tradeoffs within Food-, Fear-, and Thermal-Scapes to Explain Habitat Use by Mammalian Herbivores

Your animal care and use protocol for the project shown above was revie wed and approved by the Institutional Animal Care and Use Committee on Tuesday, November 26, 2013.

This protocol was originally submitted for review on: Friday, January 06, 2012
The original approval date for this protocol is: Friday, March 02, 2012
This approval will remain in affect until: Wednesday, November 26, 2014
The protocol may be continued by annual updates until: Monday, March 02, 2015

Federal laws and guidelines require that institutional animal care and use committees review ongoing projects annually. For the first two years after initial approval of the protocol you will be asked to submit an annual update form describing any changes in procedures or personnel. The committee may, at its discretion, extend approval for the project in yearly increments until the third anniversary of the original approval of the project. At that time, the protocol must be replaced by an entirely new submission.

Brad Williams, DVM
Campus Veterinarian
University of Idaho
208-885-8958



2/20/2015 University Research Office Regulatory Compliance System

University of Idaho
Institutional Animal Care and Use Committee

Date: Thursday, February 19, 2015
To: Janet Rachlow
From: University of Idaho
Institutional Animal Care and Use Committee
Re: Protocol 2015-12
Collaborative Research: Modeling the Tradeoffs within Food-, Fear-, and Thermal-Scapes to Explain Habitat Use by Mammalian Herbivores

Your animal care and use protocol for the project shown above was reviewed and approved by the Institutional Animal Care and Use Committee on Thursday, February 19, 2015.

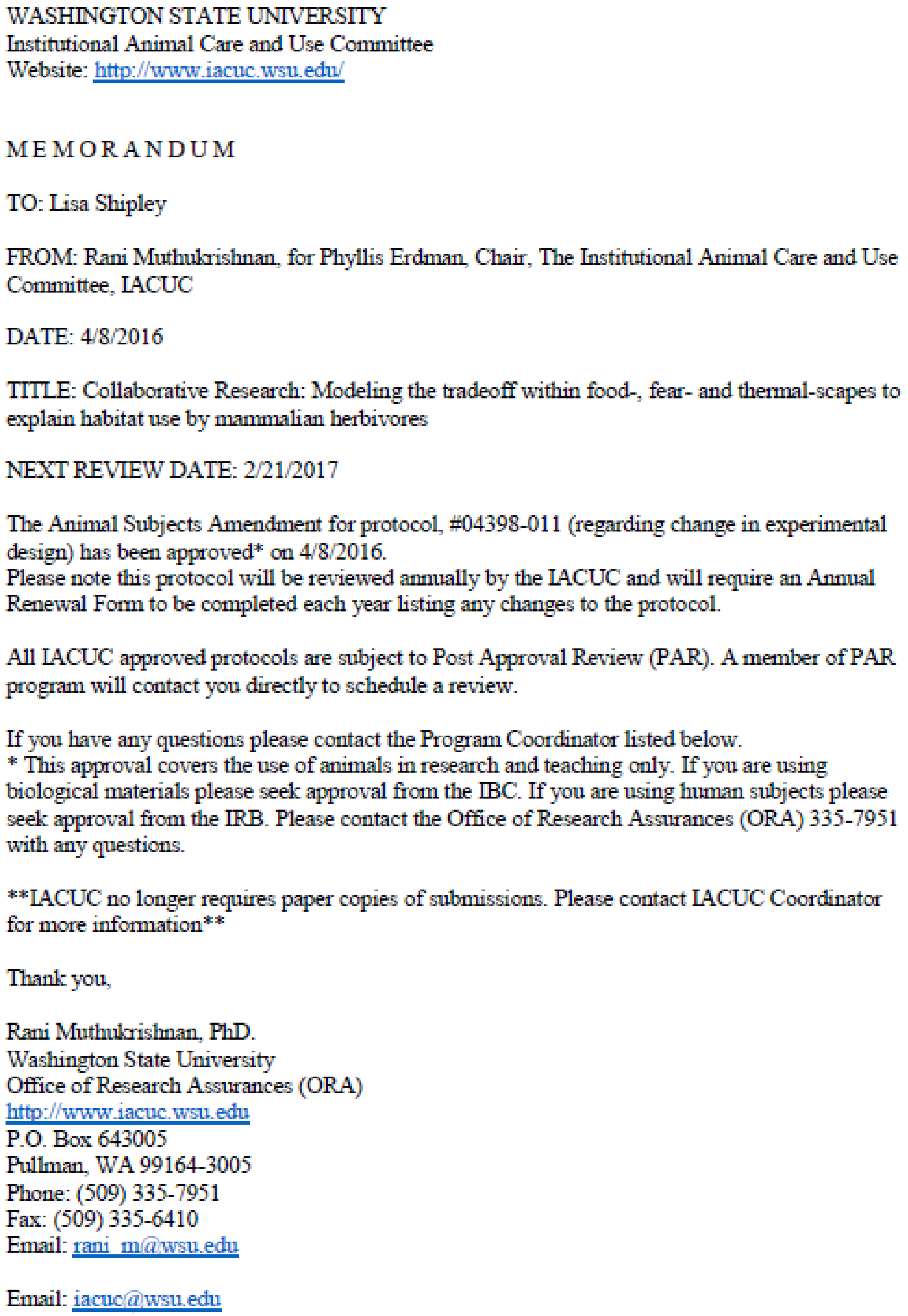
This protocol was originally submitted for review on: Thursday, February 12, 2015
The original approval date for this protocol is: Thursday, February 19, 2015
This approval will remain in affect until: Friday, February 19, 2016
The protocol may be continued by annual updates until: Monday, February 19, 2018

Federal laws and guidelines require that institutional animal care and use committees review ongoing projects annually. For the first two years after initial approval of the protocol you will be asked to submit an annual update form describing any changes in procedures or personnel. The committee may, at its discretion, extend approval for the project in yearly increments until the third anniversary of the original approval of the project. At that time, the protocol must be replaced by an entirely new submission.

Barrie Robison, IACUC Chair

Appendix B:

Washington State University Institutional Animal Care and Use Committee Protocol Approval



WASHINGTON STATE UNIVERSITY
Institutional Animal Care and Use Committee
Website: http://www.iacuc.wsu.edu/

MEMORANDUM

TO: Lisa Shipley

FROM: Rani Muthukrishnan, for Phyllis Erdman, Chair, The Institutional Animal Care and Use Committee, IACUC

DATE: 4/8/2016

TITLE: Collaborative Research: Modeling the tradeoff within food-, fear- and thermal-scapes to explain habitat use by mammalian herbivores

NEXT REVIEW DATE: 2/21/2017

The Animal Subjects Amendment for protocol, #04398-011 (regarding change in experimental design) has been approved* on 4/8/2016.
Please note this protocol will be reviewed annually by the IACUC and will require an Annual Renewal Form to be completed each year listing any changes to the protocol.

All IACUC approved protocols are subject to Post Approval Review (PAR). A member of PAR program will contact you directly to schedule a review.

If you have any questions please contact the Program Coordinator listed below.
* This approval covers the use of animals in research and teaching only. If you are using biological materials please seek approval from the IBC. If you are using human subjects please seek approval from the IRB. Please contact the Office of Research Assurances (ORA) 335-7951 with any questions.

IACUC no longer requires paper copies of submissions. Please contact IACUC Coordinator for more information

Thank you,

Rani Muthukrishnan, PhD.
Washington State University
Office of Research Assurances (ORA)
http://www.iacuc.wsu.edu
P.O. Box 643005
Pullman, WA 99164-3005
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Fax: (509) 335-6410
Email: rani_m@wsu.edu

Email: iacuc@wsu.edu

Appendix C:

Candidate Model Sets and AICc Values for Summer and Winter Rest Site Resource Selection Functions

Candidate models to evaluate rest site selection by pygmy rabbits in relation to thermal and security resources during the winter and summer.

Candidate Models	AICc	ΔAICc	w_i	Σw_i
Winter RSF				
Use ~ AC + DB	683.28	--	0.53	0.53
Use ~ AC + TC + DB	686.16	2.88	0.13	0.66
Use ~ GT + AC + TC + DB	686.16	2.88	0.13	0.79
Use ~ R + AC + TC + DB	686.43	3.15	0.11	0.90
Use ~ DB	688.15	4.87	0.05	0.94
Use ~ AC + TC + DB + W	689.32	6.04	0.03	0.97
Use ~ GT + R + AC + TC + DB	689.70	6.41	0.02	0.99
Use ~ R + DB + AT + R×AT	692.96	9.68	0.00	0.99
Use ~ AT + R + AC + TC + DB + R×AT	693.78	10.49	0.00	1.00
Use ~ R + GT + W + AC + TC + DB	694.24	10.96	0.00	1.00
Use ~ W + GT + R + AC + TC + DB + R×W	698.93	15.65	0.00	1.00
Use ~ GT + AH + R + W + R×W	895.58	212.30	0.00	1.00
Use ~ AT + AH + R + W + R×AT + R×W	910.95	227.67	0.00	1.00
Use ~ R	920.52	237.23	0.00	1.00
Null	944.34	261.06	0.00	1.00
Use ~ AT	948.38	265.10	0.00	1.00
Summer RSF Candidate Models				
Use ~ R + AC + TC + DB	1115.93	--	0.95	0.95
Use ~ GT + W + AC + TC + DB	1123.05	7.12	0.03	0.97
Use ~ GT + AC + TC + DB + AC×DB	1123.15	7.22	0.03	1.00
Use ~ R + AT + W + AT×R + AC + TC + DB	1129.02	13.09	0.00	1.00
Use ~ R + W + AC + TC	1134.72	18.79	0.00	1.00
Use ~ G + W + AC + TC	1136.49	20.56	0.00	1.00
Use ~ R + AT + W + AT×R + AC + TC	1142.09	26.16	0.00	1.00
Use ~ R	1151.96	36.03	0.00	1.00
Use ~ AC + TC + DB + AC×DB	1159.03	43.10	0.00	1.00
Use ~ R + AH + AT×R + W	1161.56	45.63	0.00	1.00
Use ~ AC + TC + DB + W + AC×DB	1163.46	47.52	0.00	1.00
Use ~ AC + TC	1177.26	61.33	0.00	1.00

Use ~ GT	1198.94	83.01	0.00	1.00
Null model	1498.53	382.59	0..00	1.00

Predictor variable abbreviations:
R – Shortwave radiation
AT – Ambient air temperature
GT – Ground surface temperature
W – Wind speed
AH – Absolute humidity
AC – Aerial concealment
TC – Terrestrial concealment
DB – Distance to burrow

Appendix D:

Candidate Model Sets and AICc Values for Summer and Winter Activity Intervals

Candidate models used to evaluate the relationship between pygmy rabbits activity levels and a suite of environmental and endogenous variables during biologically relevant times of day during summer and winter.

Model	AICc	ΔAICc	w_i	Σw_i
Summer – Day				
Activity ~ Repro	439.54	--	0.39	0.39
Activity ~ Sex×Repro + Year	441.14	1.60	0.18	0.57
Activity ~ Sex×Repro + JD	441.53	1.99	0.14	0.71
Activity ~ Sex×Repro	443.33	3.78	0.06	0.77
Activity ~ Sex×Repro + Temp + JD	443.52	3.98	0.05	0.82
Activity ~ Sex×Repro + Temp	444.21	4.67	0.04	0.86
Activity ~ Year	444.45	4.91	0.03	0.90
Activity ~ JD	444.88	5.34	0.03	0.92
Null model	445.11	5.56	0.02	0.95
Activity ~ Sex	445.19	5.64	0.02	0.97
Activity ~ Temp	446.78	7.23	0.01	0.98
Activity ~ Sex×Repro + MoonPhase	447.09	7.55	0.01	0.99
Activity ~ Sex×Repro + MoonPhase + Temp	448.37	8.82	0.00	1.00
Activity ~ MoonPhase	449.05	9.51	0.00	1.00
Activity ~ MoonPhase + Temp	450.90	11.35	0.00	1.00
Summer – Night				
Activity ~ Repro	330.41	--	0.28	0.28
Activity ~ Sex×Repro	331.97	1.55	0.13	0.41
Null model	332.38	1.97	0.10	0.51
Activity ~ Sex×Repro + Year	333.72	3.30	0.05	0.57
Activity ~ Sex×Repro + JD	333.88	3.46	0.05	0.62
Activity ~ Year	333.91	3.49	0.05	0.66
Activity ~ Sex×Repro + MoonPhase	333.97	3.56	0.05	0.71
Activity ~ Sex×Repro + Temp	333.98	3.56	0.05	0.76
Activity ~ JD	334.09	3.67	0.04	0.80
Activity ~ Temp	334.12	3.70	0.04	0.85
Activity ~ Sex	334.28	3.86	0.04	0.89
Activity ~ MoonPhase	334.37	3.96	0.04	0.93
Activity ~ MoonPhase + Temp	335.66	5.24	0.02	0.95
Activity ~ Sex×Repro + MoonPhase + Temp	335.67	5.25	0.02	0.97

Activity ~ Sex×Repro + Temp + JD	335.95	5.54	0.02	0.98
Activity ~ Sex×Repro + MoonPhase + Temp + Year	337.56	7.15	0.01	0.99
Activity ~ Sex×Repro + MoonPhase + Temp + JD	337.70	7.29	0.01	1.00
Summer – Dawn				
Activity ~ Sex×Repro	440.69	--	0.22	0.22
Activity ~ Sex	440.90	0.21	0.20	0.43
Activity ~ Sex×Repro + JD	442.75	2.07	0.08	0.51
Activity ~ Sex×Repro + Temp	442.77	2.08	0.08	0.59
Activity ~ Sex×Repro + Year	442.79	2.10	0.08	0.67
Null model	442.81	2.12	0.08	0.74
Activity ~ Sex×Repro + MoonPhase	443.53	2.84	0.05	0.80
Activity ~ Temp	444.77	4.08	0.03	0.83
Activity ~ Sex×Repro + Temp + JD	444.84	4.15	0.03	0.86
Activity ~ Year	444.86	4.17	0.03	0.88
Activity ~ JD	444.87	4.18	0.03	0.91
Activity ~ Repro	444.87	4.18	0.03	0.94
Activity ~ MoonPhase	445.35	4.66	0.02	0.96
Activity ~ Sex×Repro + MoonPhase + Temp	445.67	4.98	0.02	0.98
Activity ~ MoonPhase + Temp	447.39	6.70	0.01	0.99
Activity ~ Sex×Repro + MoonPhase + Temp + JD	447.78	7.09	0.01	0.99
Activity ~ Sex×Repro + MoonPhase + Temp + Year	447.81	7.12	0.01	1.00
Summer—Dusk				
Activity ~ JD	245.07	--	0.18	0.18
Activity ~ Year	245.41	0.34	0.15	0.33
Null model	245.60	0.53	0.14	0.47
Activity ~ Sex	246.09	1.02	0.11	0.58
Activity ~ MoonPhase	246.44	1.36	0.09	0.68
Activity ~ Repro	247.58	2.51	0.05	0.73
Activity ~ Temp	247.65	2.58	0.05	0.78
Activity ~ MoonPhase + Temp	247.72	2.65	0.05	0.83
Activity ~ Sex×Repro + JD	248.05	2.98	0.04	0.87
Activity ~ Sex×Repro + Year	248.44	3.37	0.03	0.90
Activity ~ Sex×Repro	249.45	4.38	0.02	0.92
Activity ~ Sex×Repro + MoonPhase + Temp + JD	249.53	4.46	0.02	0.94
Activity ~ Sex×Repro + Temp + JD	249.91	4.84	0.02	0.96
Activity ~ Sex×Repro + MoonPhase + Temp + Year	249.97	4.90	0.02	0.97
Activity ~ Sex×Repro + MoonPhase	250.21	5.14	0.01	0.99

Activity ~ Sex×Repro + MoonPhase + Temp	251.49	6.42	0.01	0.99
Activity ~ Sex×Repro + Temp	251.55	6.48	0.01	1.00
Winter – Day				
Activity ~ MoonPhase	*300.97*	*--*	*0.41*	*0.41*
Activity ~ Sex×Repro + MoonPhase	*301.57*	*0.59*	*0.31*	*0.72*
Activity ~ MoonPhase + Temp	*303.09*	*2.12*	*0.14*	*0.86*
Activity ~ Sex×Repro + MoonPhase + Temp + JD	*305.82*	*4.85*	*0.04*	*0.90*
Null model	*306.04*	*5.06*	*0.03*	*0.93*
Activity ~ Sex×Repro	*306.98*	*6.01*	*0.02*	*0.95*
Activity ~ JD	*307.17*	*6.20*	*0.02*	*0.97*
Activity ~ Temp	*308.11*	*7.14*	*0.01*	*0.98*
Activity ~ Sex×Repro + JD	*308.88*	*7.91*	*0.01*	*0.99*
Activity ~ Sex×Repro + Temp	*309.05*	*8.08*	*0.01*	*1.00*
Activity ~ Sex×Repro + Temp + JD	*310.93*	*9.96*	*0.00*	*1.00*
Winter – Night				
Activity ~ Sex×Repro + MoonPhase + Temp + JD	*246.27*	*--*	*0.98*	*0.98*
Activity ~ Sex×Repro + MoonPhase + Temp	*255.38*	*9.11*	*0.01*	*0.99*
Activity ~ MoonPhase + Temp	*255.55*	*9.29*	*0.01*	*1.00*
Activity ~ Sex×Repro + Temp + JD	*258.28*	*12.01*	*0.00*	*1.00*
Activity ~ Sex×Repro + Temp	*265.65*	*19.38*	*0.00*	*1.00*
Activity ~ Temp	*266.86*	*20.60*	*0.00*	*1.00*
Activity ~ JD	*269.07*	*22.80*	*0.00*	*1.00*
Activity ~ Sex×Repro + JD	*272.19*	*25.92*	*0.00*	*1.00*
Activity ~ Sex×Repro + MoonPhase	*272.62*	*26.35*	*0.00*	*1.00*
Activity ~ MoonPhase	*272.84*	*26.58*	*0.00*	*1.00*
Activity ~ Sex×Repro	*281.34*	*35.07*	*0.00*	*1.00*
Null model	*282.17*	*35.91*	*0.00*	*1.00*
Winter – Dawn				
Activity ~ Sex×Repro + Temp + JD	*478.62*	*--*	*0.54*	*0.54*
Activity ~ Sex×Repro + Temp	*481.61*	*2.98*	*0.12*	*0.66*
Activity ~ JD	*481.82*	*3.20*	*0.11*	*0.77*
Activity ~ Sex×Repro + MoonPhase + Temp + JD	*482.60*	*3.98*	*0.07*	*0.84*
Activity ~ Temp	*482.82*	*4.20*	*0.07*	*0.91*
Activity ~ Sex×Repro + JD	*483.64*	*5.01*	*0.04*	*0.95*
Activity ~ Sex×Repro + MoonPhase + Temp	*485.42*	*6.80*	*0.02*	*0.97*
Activity ~ Sex×Repro	*486.48*	*7.85*	*0.01*	*0.98*
Activity ~ MoonPhase + Temp	*486.70*	*8.08*	*0.01*	*0.99*

Null model	*487.68*	*9.05*	*0.01*	*1.00*
Activity ~ Sex×Repro + MoonPhase	*489.94*	*11.32*	*0.00*	*1.00*
Activity ~ MoonPhase	*491.46*	*12.84*	*0.00*	*1.00*
Winter -Dusk				
Activity ~ Sex×Repro + Temp + JD	*301.93*	*--*	*0.46*	*0.46*
Activity ~ JD	*302.76*	*0.84*	*0.30*	*0.76*
Activity ~ Sex×Repro + JD	*303.72*	*1.79*	*0.19*	*0.94*
Activity ~ Sex×Repro + MoonPhase + Temp + JD	*306.22*	*4.30*	*0.05*	*0.99*
Activity ~ Sex×Repro + Temp	*311.58*	*9.66*	*0.00*	*1.00*
Activity ~ Sex×Repro	*314.42*	*12.50*	*0.00*	*1.00*
Activity ~ Sex×Repro + MoonPhase + Temp	*315.70*	*13.77*	*0.00*	*1.00*
Activity ~ Temp	*316.61*	*14.68*	*0.00*	*1.00*
Activity ~ Sex×Repro + MoonPhase	*318.35*	*16.42*	*0.00*	*1.00*
Null model	*318.89*	*16.96*	*0.00*	*1.00*
Activity ~ MoonPhase + Temp	*320.64*	*18.71*	*0.00*	*1.00*
Activity ~ MoonPhase	*322.91*	*20.99*	*0.00*	*1.00*

Predictor variable abbreviations:
Sex – Sex (Male or Female)
Repro – Reproductive status (0 – nonreproductive, 1 – reproductive)
MoonPhase – Moon phase (Full, new, partial)
Temp – Temperature
JD – Julian day
Year – Year

Appendix E:

Excluded Operative Temperature Records

List of all of the datapoints that were not included in the temperature analysis by site, season, and station identifier.

Site[1]	Season[2]	Station	Reason for omission
CG	W	11	No temperature data – file lost
CG	W	102	Habitat covariates not measured
CG	W	196	No temperature data – file lost
CG	W	233	No temperature data – sensor failed to launch
CG	W	234	No temperature data – sensor failed to launch
CG	W	250	Aerial concealment value missing
CG	S	141	Aerial concealment value missing
CG	S	142	Aerial concealment value missing
CG	S	143	Aerial concealment value missing
CG	S	144	Aerial concealment value missing
CG	S	145	Aerial concealment value missing
CG	S	146	Aerial concealment value missing
CG	S	173	Temperature file lost during offload process
CG	S	174	Temperature file lost during offload process
CG	S	282	No temperature file or record of monitoring
CG	S	81	No temperature data – sensor failed
MR	W	7A	Temperature not measured – incorrect plant measured 2x
MR	W	11B	Temperature not measured – incorrect plant measured 2x
MR	W	25A	Habitat covariates not measured
MR	W	49A	Habitat covariates not measured
MR	S	18A	No temperature data – sensor failed
MR	S	18B	No temperature data – sensor failed
MR	S	31A	Aerial concealment value missing
MR	S	42A	Habitat covariates not measured
MR	S	42B	Sensor destroyed by cow
MR	S	42C	Habitat covariates not measured
MR	S	77B	Temperature not measured – incorrect plant measured 2x

[1] Cedar Gulch (CG) and Magic Reservoir (MR). [2] Summer (S) and winter (W).

Appendix F:
Candidate Model Sets and AICc Values Relating Habitat Variables to Operative Temperature

Candidate models used to evaluate the relationship between two measures of operative temperature (T_e; $\overline{DTR}$ and $\bar{T}_{max}$) and habitat variables at two study sites in Idaho, USA.

Model	AICc	ΔAICc	w_i	Σw_i
Cedar Gulch				0.69
$\bar{T}_{max}$ ~ *Vol + HorCov + HabType*	1041.83	--	0.69	0.94
$\bar{T}_{max}$ ~ *Vol + HorCov + HabType + Season*	1043.85	2.02	0.25	1.00
$\bar{T}_{max}$ ~ *Vol + HorCov + HabType + Season + Season × HorCov + Season × Vol*	1046.94	5.11	0.05	1.00
$\bar{T}_{max}$ ~ *HorCov + Season + Season × HorCov*	1055.29	13.45	0.00	1.00
$\bar{T}_{max}$ ~ *HorCov + HabType + Season + Season × HorCov*	1057.65	15.82	0.00	1.00
$\bar{T}_{max}$ ~ *Vol + HabType + Season*	1066.90	25.6	0.00	1.00
$\bar{T}_{max}$ ~ *Vol + Season + HabType + Season × Vol*	1068.98	27.14	0.00	1.00
$\bar{T}_{max}$ ~ *Vol + Season + Season × Vol*	1070.44	28.61	0.00	1.00
Null model	1145.55	103.72	0.00	1.00
$\bar{T}_{max}$ ~ *Season*	1147.58	105.74	0.00	1.00
$\bar{T}_{max}$ ~ *HabType + Season*	1457.76	415.93	0.00	1.00
$\overline{DTR}$ ~ *Vol + HorCov + HabType*	977.40	--	0.70	0.70
$\overline{DTR}$ ~ *Vol + HorCov + HabType + Season*	979.42	2.02	0.25	0.95
$\overline{DTR}$ ~ *Vol + HorCov + HabType + Season + Season × HorCov + Season × Vol*	982.64	5.24	0.05	1.00
$\overline{DTR}$ ~ *HorCov + HabType + Season + Season × HorCov*	991.11	13.71	0.00	1.00
$\overline{DTR}$ ~ *HorCov + Season + Season × HorCov*	994.72	17.32	0.00	1.00
$\overline{DTR}$ ~ *Vol + HabType + Season*	1009.41	32.01	0.00	1.00
$\overline{DTR}$ ~ *Vol + Season + HabType + Season × Vol*	1011.42	34.01	0.00	1.00
$\overline{DTR}$ ~ *Vol + Season + Season × Vol*	1020.94	43.54	0.00	1.00
Null model	1103.92	126.52	0.00	1.00
$\overline{DTR}$ ~ *Season*	1105.96	128.55	0.00	1.00
$\overline{DTR}$ ~ *HabType + Season*	1320.61	343.21	0.00	1.00

Magic Reservoir				
$\bar{T}_{max} \sim Vol + HorCov + HabType + Season + Season \times HorCov + Season \times Vol$	913.44	--	0.49	0.49
$\bar{T}_{max} \sim Vol + HorCov + HabType$	914.96	1.53	0.23	0.72
$\bar{T}_{max} \sim Vol + Season + HabType + Season \times Vol$	916.17	2.74	0.13	0.85
$\bar{T}_{max} \sim Vol + HorCov + HabType + Season$	917.04	3.61	0.08	0.93
$\bar{T}_{max} \sim Vol + Season + Season \times Vol$	919.27	5.84	0.03	0.95
$\bar{T}_{max} \sim HorCov + HabType + Season + Season \times HorCov$	920.19	6.75	0.02	0.97
$\bar{T}_{max} \sim Vol + HabType + Season$	920.31	6.87	0.02	0.99
$\bar{T}_{max} \sim HorCov + Season + Season \times HorCov$	920.79	7.35	0.01	1.00
Null model	934.18	20.74	0.00	1.00
$\bar{T}_{max} \sim Season$	936.22	22.79	0.00	1.00
$\bar{T}_{max} \sim HabType + Season$	1476.15	562.72	0.00	1.00
$\overline{DTR} \sim Vol + HorCov + HabType + Season + Season \times HorCov + Season \times Vol$	1164.46	--	0.53	0.53
$\overline{DTR} \sim Vol + HorCov + HabType$	1165.80	1.34	0.27	0.80
$\overline{DTR} \sim Vol + HorCov + HabType + Season$	1167.88	3.41	0.10	0.90
$\overline{DTR} \sim Vol + Season + HabType + Season \times Vol$	1169.11	4.65	0.05	0.95
$\overline{DTR} \sim HorCov + HabType + Season + Season \times HorCov$	1170.35	5.89	0.03	0.98
$\overline{DTR} \sim HorCov + Season + Season \times HorCov$	1171.88	7.42	0.01	0.99
$\overline{DTR} \sim Vol + HabType + Season$	1172.87	8.41	0.01	1.00
$\overline{DTR} \sim Vol + Season + Season \times Vol$	1175.37	10.91	0.00	1.00
Null model	1189.90	25.44	0.00	1.00
$\overline{DTR} \sim Season$	1191.95	27.49	0.00	1.00
$\overline{DTR} \sim HabType + Season$	1470.36	305.90	0.00	1.00

Predictor variable abbreviations:
Vol – Volume
HorCov – Horizontal cover
Season – Season (S – Summer, W – Winter)
HabType – Habitat type