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Contemporary climate change affects nearly all biomes, causing shifts in animal distributions, resource availability, and species persistence. In many cases species are challenged to keep up with the rate at which conditions are changing. Behaviors, which are immediately flexible, may provide species with a way to keep pace with warming conditions, but the extent to which species can alter behaviors to deal with climate variability is largely an open question. I examined how well thermally specialized animals can proximately buffer warming temperatures through changes in behavior (hereafter behavioral plasticity), using the American pika (*Ochotona princeps*) as a model species. Pikas are a food-hoarding lagomorph that is sensitive to ambient temperatures, and active year-round in the alpine where conditions are highly variable. I evaluated aspects of three primary pathways through which animals may respond plastically to rapid change. These included association with microclimates, flexibility in resource selection and plasticity in food-collecting behavior. Using information from occurrence surveys (146 surveys), observations of foraging activity (4,370 observations of 72 individuals), assessments of vegetation quality (54 individuals) and *in-situ* temperature measurements collected from 2010-2015 in the central Rocky Mountains, I assessed pika responses to climatic variation. My results indicate that microrefuges were essential to pika occurrence, independent of other critical habitat characteristics, such as forage availability. I also found that individuals exposed to higher daytime temperatures showed stronger selection for high-quality forage, compared to individuals that experienced cooler conditions. Finally, by varying food-collection norms of reaction, individuals were able to plastically respond to

temperature-driven reductions in foraging time and, through this increased flexibility, to simultaneously amass a higher quality overwinter food cache. Taken together my findings suggest that behavioral plasticity, coupled with adequate accesses to suitable microrefuges and quality vegetation, may provide pikas, and perhaps other thermally specialized animals with a tool to proximately modulate increasing temperatures. As climate change continues to manifest, efforts to understand changing animal-habitat relationships will be enhanced by considering resource availability, the capacity of organisms to modify selection dynamics and the degree of plasticity in fitness-linked behaviors.

BEHAVIORAL PLASTICITY AND RESILIENCE OF A MONTANE MAMMAL IN A CHANGING CLIMATE

By

L. Embere Hall

A dissertation submitted to the Program in Ecology
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DEDICATION PAGE

To Roger K. Ferris

Uncle. Artist. Inspiration. Friend.

You are missed.

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CHAPTER ONE

Introduction

Ecology is built on a rich history of understanding and documenting the distribution of living things. In fact, in 1954 Andrewartha and Birch defined ecology as the study of the distribution and abundance of plants and animals[1]. Species' distributions are shaped by long evolutionary histories which have produced finely tuned behaviors[2]. Great tits (*Parus major*), for example, have perfected the timing of egg laying such that nestlings hatch simultaneous with peak food availability[3]. Similarly, terrestrial isopods have developed an optimal balance between sheltering to avoid desiccation and maximizing foraging efficiency so as to survive in dry climates[4].

The environmental conditions under which behaviors have evolved, however, are changing rapidly. Invasive species, habitat fragmentation and climate change are just a few examples of ongoing, global-scale disturbances that expose organisms to circumstances that differ from those that shaped their evolutionary histories. Most of these fast-paced, large-scale perturbations are human-caused, and are examples of human-induced rapid environmental change (HIREC)[5,6]. Unlike other types of environmental change, HIREC is characterized by a fast rate of change, large spatial scale and, often, evolutionary novelty[6]. HIREC produces unique conditions that involve a rate of change beyond what most organisms have experienced in their evolutionary history[7]. Such scale and rapidity means that organisms in all major biomes on Earth are encountering conditions for which there are no modern ecological analogs[8]. In many cases, cues no longer correspond to adaptive fitness outcomes[9], phenotypes are mismatched to current conditions[10] and resources are unavailable during critical developmental periods[11,12]. While many studies have examined patterns of species' responses to HIREC[5,13], much remains to be learned about the mechanisms that influence both the extent and the limits of species' ability to adjust to change. In order to address new and emerging challenges associated with HIREC, we first need to understand the degree to which individuals can cope with the effects of rapid change.

Climate change is perhaps one of the most pervasive forms of HIREC because climate affects nearly all aspects of ecological systems[8,14]. The effects of changing conditions are seen in most biomes and influence all levels of ecological hierarchy - from individual species behavior to whole ecosystem processes[11,12]. With continued warming projected for at least the remainder of the 21st century[14], species across the globe likely will be exposed to novel and, in many cases challenging, conditions.

Of the traits that influence species' responses to climate change, phenotypic plasticity may play a particularly important role[6]. Phenotypic plasticity, the ability of an organism to proximately respond to its environment with a change in form, behavior or movement[15], is an evolutionary response to variable environmental conditions. Plasticity allows organisms to produce a better phenotype-environment match across more environments than is possible by producing a single phenotype in all environments[16]. For example, individual *Daphnia* moderate development of costly armament structures, such as spines, so that defenses are only produced in environments where predators are present[17]. Plastic individuals and populations can often persist in variable conditions that may not otherwise be tolerable, given fixed traits.

Behavioral phenotypic plasticity (hereafter behavioral plasticity) describes the ability of an organism to alter behavior in response to the environment[15]. Behavioral plasticity may allow animals to persist amid rapid environmental change because 1) there is a relatively short lag between a change in the environment and expression of a new behavioral phenotype[18] 2) the costs of flexible behavioral responses may be small, compared to morphological models of plasticity (though much work remains to be done in this area)[19] and 3) behavioral plasticity is reversible, allowing the individual to secure the benefits of a new phenotype without committing to it in the context of an uncertain future[20–22].

Despite increased research on the rate at which species can adjust to climate change, the degree to which behavioral plasticity allows species to proximately buffer climate variability, and the associated limits of plastic responses, are unclear. Behavioral plasticity may be particularly important to the persistence of climate-sensitive species with low reproductive rates, long generation times and limited dispersal capability, as these species are the least likely to adapt quickly or to track preferred habitats across latitude and elevation.

The American pika (*Ochotona princeps*) is well-suited as a case study for evaluating species' responses warming temperatures. Pikas are one of the only vertebrates active year round in alpine ecosystems, where some of the most extreme climate changes are occurring[23,24]. Additionally, with a resting body temperature within 3 C° of their upper lethal temperature[25,26], pikas have a low heat tolerance. To avoid physiologically stressful temperatures, individuals exploit cool microrefuges under rocks (hereafter talus). Pikas also have relatively limited dispersal capability[27], which means that the species cannot easily relocate to more favorable habitats when conditions become unsuitable. Finally, because pikas live in relatively undisturbed talus habitats, they provide a rare opportunity to investigate climate change effects in the absence of physical habitat loss[28].

While some populations of pikas have experienced range contractions[29] and extirpations as a result of climate change[30,31], these trends are not consistent across the species' range or even within biogeographical regions[32,33]. For example, while low-elevation populations in the southern Great Basin recently have shown significant upslope range retractions in response to climate change[31,34], populations in the nearby eastern Sierra Nevada persist despite marginal climatic conditions, atypical habitat and low-quality vegetation[35]. Population-level variation in climate sensitivity (how organisms interact with their climatic environment), exposure (how pronounced climate change is in a given site)[36,37], and local adaptation may explain some of the inconsistencies in range-wide responses. In particular, behavioral plasticity and the availability of microrefuges can influence population persistence. Despite substantial recent interest in pikas and climate change, much remains to be learned about individual and population-level variation in behavioral plasticity, and the role of these responses in population persistence.

Understanding the degree to which individuals can adjust to rapid change requires first evaluating the climatic conditions and habitat characteristics that influence distribution. This is the focus of Chapter 2, *Microrefuges and the occurrence of thermal specialists: Implications for wildlife persistence amidst changing temperatures*. Chapters 3 and 4 build on our findings from Chapter 2 and explore the degree of plasticity in pika foraging behaviors. Flexibility in foraging directly affects energy gain, and can potentially improve an organism's prospects of surviving and reproducing in a changing world. Chapter 3, *What to eat in a warming world: Do increased temperatures necessitate hazardous duty pay?*, addresses the influence of thermoregulatory risk on forage choice. Chapter 4, *Behavioral plasticity modulates temperature-related constraints on foraging time for a montane mammal,* quantifies the extent to which individuals can modulate foraging behaviors to proximately buffer temperature variability.

Contemporary climate change threatens biodiversity across the globe. It is my hope that the body of work contained herein will provide researchers, resource managers, biologists and ecologists with useful tools to continue progress on wildlife conservation in the face of new climate dynamics.

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CHAPTER TWO

Microrefuges and the occurrence of thermal specialists: Implications for wildlife persistence amidst changing temperatures

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Abstract

Background: Contemporary climate change is affecting nearly all biomes, causing shifts in animal distributions, phenology, and persistence. Favorable microclimates may buffer organisms against rapid changes in climate, thereby allowing time for populations to adapt. The degree to which microclimates facilitate the local persistence of climate-sensitive species, however, is largely an open question. We addressed the importance of microrefuges in mammalian thermal specialists, using the American pika (*Ochotona princeps*) as a model organism. Pikas are sensitive to ambient temperatures, and are active year-round in the alpine where conditions are highly variable. We tested four hypotheses about the relationship between microrefuges and pika occurrence: 1) Local-habitat Hypothesis (local-habitat conditions are paramount, regardless of microrefuge); 2) Surface-temperature Hypothesis (surrounding temperatures, unmoderated by microrefuge, best predict occurrence); 3) Interstitial-temperature Hypothesis (temperatures within microrefuges best predict occurrence), and 4) Microrefuge Hypothesis (the degree to which microrefuges moderate the surrounding temperature facilitates occurrence, regardless of other habitat characteristics). We examined pika occurrence at 146 sites across an elevational gradient. We quantified pika presence, physiographic habitat characteristics and forage availability at each site, and deployed paired temperature loggers at a subset of sites to measure surface and subterranean temperatures.

Results: We found strong support for the Microrefuge Hypothesis. Pikas were more likely to occur at sites where the subsurface environment substantially moderated surface temperatures, especially during the warm season. Microrefugium was the strongest predictor of pika occurrence, independent of other critical habitat characteristics, such as forage availability.

Conclusions: By modulating surface temperatures, microrefuges may strongly influence where temperature-limited animals persist in rapidly warming environments. As climate change continues to manifest, efforts to understand the changing dynamics of animal-habitat relationships will be enhanced by considering the quality of microrefuges.

Keywords refuge, global warming, microclimate, microhabitat, mammal, temperature-sensitive

Background

Environments across the globe are changing with unprecedented rapidity. In many cases, habitat cues no longer correspond with adaptive fitness outcomes [1], phenotypes are mismatched to current conditions [2], and resources are unavailable during critical developmental periods [3,4]. Theory suggests that geographically restricted populations with low dispersal capability and long generation times may be particularly ill-equipped to cope with rapid environmental change, especially if the species is also a habitat specialist [5]. For these species, immediate responses, such as the use of microrefuges, may offer an instantaneous mechanism by which individuals can locally persist despite changing conditions. Yet, the role of many plastic responses and the habitat characteristics that facilitate them remain untested.

Climate change is a particularly pervasive form of rapid environmental change. Montane ecosystems, which occupy approximately 20% of the planet's land surface, may be particularly vulnerable to climate change [6]. The higher elevations of the northern Rocky Mountains, USA, for example, have experienced nearly three times the global average temperature increase over the past century, with an unprecedented decrease in snowpack ([7,8], but see [9]). Simultaneously, montane environments often support unique species assemblages and a high degree of endemism which can be disproportionately affected by warming [10–12].

Alpine mammals may provide valuable insights into animal responses to climate change, because they are often highly specialized, geographically restricted species, with relatively long generation times. This combination of characteristics likely limits the role of adaptive evolution in species persistence, emphasizing instead the importance of more immediate responses, such as behavioral plasticity and exploitation of favorable microhabitats [13–15].

Microclimatic refuges

Microrefuges provide enhanced resources compared with the surrounding habitat matrix, and can afford organisms protection from environmental stressors. Unlike refugia which may protect populations during prolonged periods (e.g. centuries) of inhospitable conditions, refuges operate within the life span of an organism [16,17]. The importance of microrefuges for species distribution has been acknowledged for a long time (e.g., [18,19]). Despite this, relatively few species distribution models include microhabitat predictors in efforts to quantify future ranges [20]. As a result, the availability of microrefuges is often excluded from measurements that assess species' vulnerability to rapid environmental change [21]. Organisms can exploit microrefuges immediately to access favorable thermoclimatic profiles, foraging opportunities, nesting sites or shelter from extreme conditions [22–24]. In the case of temperature-sensitive species, individuals can exploit microhabitats that buffer otherwise stressful temperatures [23,25,26]. Microclimate data, coupled with species occurrence information, can therefore help elucidate connections between species persistence and the availability of microrefuges.

American Pikas

The American pika (*Ochotona princeps*), a species of broad conservation concern [27–29], is an ideal species through which to evaluate the importance of microrefuges. Pikas are sensitive to ambient temperatures [30, 31], with hyperthermia and death resulting after brief exposures to ambient temperatures > 28 ° C [32]. Pikas can exploit favorable temperatures in interstitial spaces between rocks (hereafter talus), and are one of the only vertebrates active year-round in montane systems, where some of the most extreme climatic changes are occurring [30,31]. Additionally, pikas are habitat specialists with relatively low fecundity and dispersal capability [30,32]. As a result, immediate responses to changing conditions may be essential to the species' persistence. Pikas also provide a rare opportunity to investigate climate change effects in the absence of physical habitat loss, because they live almost exclusively in relatively undisturbed talus habitats ([33]; but see [34]).

Although some populations of pikas have experienced climate-related range contractions [35] and extirpations as a result of climate change [31,36,37], these patterns are not consistent across the species' range [38–40]. Whereas low-elevation populations in the southern Great Basin recently have shown significant upslope range retractions in response to warming temperatures [36,41], populations in the nearby eastern Sierra Nevada mountains persist despite marginal climatic conditions, atypical habitat and low-quality vegetation [42]. Population-level variation in climate sensitivity (how organisms interact with their climatic environment), exposure (how pronounced climate change is in a given site; [43,44]) and adaptive capacity (ability of a species or associated populations to adjust to change; [45,46]) may explain some of the inconsistencies in range-wide responses. In addition, the availability of microrefuges at a local scale may shed light on fine-grain variation in patterns of persistence.

Hypotheses and predictions

We evaluated four alternative hypotheses about the relative influence of microrefuges on pika occurrence (Table 1). We anticipated that our hypotheses could manifest through two different temperature-based parameters: magnitude (mean value of a temperature parameter) and constancy (standard deviation of a temperature parameter). Consequently, three of our four hypotheses included predictions associated with both magnitude and constancy.

Local-habitat Hypothesis: Local habitat conditions are paramount in predicting pika occurrence. Prediction: Slope, elevation, aspect and/or forage availability should best predict pika occurrence, regardless of microrefuges.

Surface-temperature Hypothesis: Talus-surface temperatures, unmoderated by microrefuge, best predict occurrence. Prediction 1 (magnitude): Pika occurrence should vary quadratically with mean daily surface temperature, such that the probability of occurrence is highest at intermediate temperatures. Prediction 2 (constancy): Pika occurrence should decrease with variation in mean daily surface temperature.

Interstitial-temperature Hypothesis: Subsurface temperatures (temperatures in the talus interstices) best predict occurrence. Prediction 1 (magnitude): Pika occurrence should decrease with increasing mean daily interstitial temperature. Prediction 2 (constancy): Pika occurrence should decrease with increasing variation in mean daily interstitial temperature.

Microrefuge Hypothesis: The degree to which the subterranean environment moderates surface temperatures facilitates occurrence, regardless of other habitat characteristics. Prediction 1 (magnitude): Pika occurrence should be highest at sites where the subsurface temperature substantially buffers surface temperatures. Prediction 2 (constancy): Pika occurrence should be highest at sites where mean daily differences between the surface and subsurface temperatures is consistent.

Methods

Study area

We conducted our research in the central Rocky Mountains in the western United States. The project area was on the Bridger-Teton National Forest in Wyoming (centroid 43.4753° N, 110.7692° W). The Bridger-Teton National Forest encompasses 1.4 million hectares and ranges in elevation from 1713 – 4211 m. The majority (56%) of precipitation falls during the cool season (October – March); average annual precipitation that falls as rain is 0.39 m [47]. January (average temperature = -8° C) and July (average temperature = 17° C) are typically the coldest and warmest months of the year, respectively. Our study sites occurred in coniferous forests, aspen parklands, subalpine and alpine communities. Dominant tree species included Douglas fir (*Pseudotsuga menziesii*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), whitebark pine (*Pinus albicaulis*) and limber pine (*Pinus flexilis*).

Site selection

We used a probabilistic sampling design to create random survey locations. We generated sample points using a Generalized Random Tessellation Stratified (GRTS) sampling method [48–50]. The spatially-balanced GRTS design offered considerable flexibility over simple random and systematic designs, and allowed for sample sites to be added or removed as necessary without affecting selection probabilities and dispersion [48]. We constrained the sample frame to include potential pika habitat, proximity to trails (< 600 m) and mountain slopes that were safe to travel (≤ 35°; [50]). Habitat polygons were buffered by 12 m to exclude habitat edges [49]. Pikas are found almost exclusively in talus habitat [30]. Talus, however, is challenging to delineate from remotely sensed data, and was poorly represented in habitat-cover maps available for our study area [51]. Consequently, we extracted potential habitat from three map units that were closely associated with talus in our system: sparse vegetation, alpine vegetation and barren rock [51]. Prior to surveys, sample points were checked against aerial imagery to confirm that the point intersected talus habitat (*sensu* [50]). Plots were not sampled if they contained < 10% target habitat (talus, rock outcrops, creviced rock; [49,50]). All survey points were stratified by elevation (m): [1715 – 2344], [2345 – 2561], [2562 – 2778] and [2779 – 3702]. We used a stratified approach to ensure complete coverage of the elevational, climatic and habitat variability in our system. We generated 33 sample points and 33 oversample points (additional sample points to use if original points were unsuitable; [52]) per elevation stratum. We also selected 14 U.S. Forest Service pika-monitoring points that had been identified as part of an agency effort to quantify long-term population trends. These points were identified using the same GRTS-based sampling approach, but with only two elevation categories (low and high), rather than four.

Occurrence surveys

We surveyed sites during 24 June – 28 October, 2010 – 2012. A single technician completed a 30-minute occurrence survey at each plot [49,50], except in cases of dual-observer surveys (see below). Surveys began with a 5-minute silent observation period. A single observer subsequently searched the plot for direct or indirect pika sign during the remainder of the survey period. Plots were considered occupied if direct or fresh indirect sign was detected. Indirect sign included visual detections of scat or fresh haypiles, and direct sign included visual or aural detection of pikas. Haypiles are caches of vegetation that pikas harvest during the summer months and primarily consume when green vegetation is no longer available [56]. We did not classify plots as occupied based only on fresh scat because of challenges in confidently ageing scat [40,53] and the length of time that scat can persist in the environment [54].

Two observers conducted surveys at a subset of plots (n = 59) to estimate detection probabilities. The protocols described previously also were used in dual-observer surveys, except that each observer surveyed a site for 15 minutes, rather than 30 minutes. One observer surveyed a plot, followed immediately by the second observer. During each dual-observer survey, observers collected data independently and did not discuss observed sign.

We recorded wind speed (kph) during each survey using a hand-held weather meter (2000 Pocket Wind Meter, KestrelMeters, Birmingham, MI) to determine the suitability of survey conditions. Surveys were not conducted in rain or in high winds (sustained wind speed > 25 kph), as these conditions could have influenced pika detections [55].

Habitat characteristics

Plot characteristics

We recorded plot-level characteristics known to influence pika occurrence, including slope, aspect and elevation at each survey location [40,49,50,56]. Slope and aspect were measured at the center of each plot using a hand-held compass equipped with a clinometer. We calculated the elevation at the center of each plot from a 10-m digital elevation model of the entire study area.

Forage availability also may influence the likelihood that a plot is occupied [56], as pikas have high metabolic requirements, are active overwinter (i.e. do not hibernate), and hoard food resources for consumption during periods when green vegetation is unavailable [50,57,58]. We quantified forage resources at each site using a 100-m line-point-intercept transect [59]. We established four, 25-m transect lines separated by 90°. Each transect started at the plot center. We recorded all vegetation hits $\leq$ 0.50 m in height at each meter mark (1–25 m), for a total of 100 point-measurements per site. Vegetation hits above 0.50 m were considered inaccessible to pikas and were not included in our assessment. Both vascular (grasses, forbs, shrubs and trees) and non-vascular plants were included, as pikas also have been observed foraging on lichens and bryophytes [60–62]. We defined forage availability as the sum of all vegetation hits encountered along the four, 25-m transects.

Surface temperatures and subsurface microrefuges

We deployed 40 pairs of temperature sensors at a subset of survey sites. The sensors allowed us to quantify how much the subsurface environment differed from, and therefore buffered, surface temperatures. We randomly selected 10 sites in each of the four elevation categories as locations for temperature loggers. We placed iButtons (Maxim Integrated Products, model DS1921G, accuracy ±1°C, 0.5 °C increments) in water-tight containers (5 g-jars made of clear plastic). Each jar contained a pinch of dessicant and was sealed with Teflon tape [31,56]. We deployed iButtons < 5 m from pika sign, or if sign was lacking, we placed iButtons near a prominent, overhanging rock closest to the plot center. Each iButton pair included a surface sensor and a subsurface sensor. Surface-temperature measurements were intended to reflect conditions that individuals experienced while on the surface of the talus, rather than ambient temperature. Consequently, the surface iButton was wired to a prominent north-facing rock, completely shaded from direct sun exposure. We suspended the subsurface iButton 0.5 m below the talus surface [31,56,63], except in a few cases where the talus was < 0.5 m deep. In these cases, we suspended the logger a few centimeters above the ground beneath the talus. While this difference in deployment depth may have influenced the temperatures that were logged, it also allowed us to accurately characterize the habitat that was available to individuals at shallow-talus sites. Paired loggers were time-synchronized to record simultaneous temperature readings. Loggers recorded the temperature every 4 hours (0200, 0600, 1000, 1400, 1800, and 2200) for 341 days, or approximately 11 months. We deployed loggers immediately following the occurrence survey at each site. Loggers deployed in one year were retrieved in the next year, when occurrence surveys were repeated. Occurrence data collected on the second visit to sites were used in analyses. These data allowed us to evaluate occurrence patterns that were most likely to result from conditions experienced during the temperature-sampling period.

Statistical analyses

Detection probability

Although pikas have a high probability of detection given presence [31,49], we examined variation in detection probabilities as an initial step in model fitting. We used data from dual-observer surveys to estimate detection probabilities and probability of occupancy. We quantified detection probabilities using a simple single-season model where both detection and occupancy were held constant (program PRESENCE 7.3; [64]).

Local habitat, surface temperature and subsurface microrefuge

We used a two-step modelling approach to test our hypotheses. We suspected that local-habitat characteristics could influence the probability of pika occurrence independent of factors related to microrefuge, so we modeled them first using a suite of logistic-regression models with pika occurrence as the response (local-habitat models; GLM with a binomial link). Local-habitat variables included slope, aspect, elevation and forage availability. Each of the four variables have been shown to affect metrics of pika presence, density or abundance [38,50,56,57,65]. We used the cosine of aspect in our models, which characterized the northness of a site [66]. In addition to these linear effects, we considered a quadratic elevation term, as some studies have suggested an upper as well as a lower elevation limit for pikas [50,56]. We also considered an interaction between elevation and forage availability [56]. Our candidate model suite included nine models: a univariate model for each linear predictor (4 models); an additive model containing the three physiographic terms (slope, elevation, aspect); a quadratic elevation model;

a model with an interaction between elevation and forage availability; an additive model containing all of the linear terms; and a global model.

Next we advanced the best-supported models (summed model probability $\geq$ 90%) from the first model set into a second suite of eight candidate models (surface temperature, subsurface temperature and subsurface-microrefuge models). Due to a smaller sample, models in the second candidate suite included three or fewer predictors to reduce the potential of overfitting [67]. Each candidate model in the second set represented one of our hypotheses about the role of microrefuges as a predictor of pika occurrence (Table 1). We expected a nonlinear relationship between surface temperature and pika occurrence, so we included a quadratic effect of surface temperature in our models.

All temperature metrics reflected the average daily value at each site. We calculated average daily values for surface and subsurface temperatures by first determining the mean value for each sample-day at each site (derived from 6 readings/site/day). Then we averaged these values across the amount of time that the logger was deployed (approximately 11 months), resulting in 1 value per site. We quantified subsurface-microrefuge (the degree to which the talus environment moderated surface temperatures) as the absolute value of the mean daily difference between the surface and subsurface temperatures. We used the absolute difference rather than the actual difference because the absolute value allowed us to evaluate surface-condition moderation independent of season. We subtracted the subsurface temperature from the surface temperature; therefore differences were likely to be positive during the summer when the interstices were cooler than the surface, and negative in winter. These values were calculated by first determining the difference between surface and subsurface temperatures at each 4-hr sampling event. Next, we took the absolute value of these differences. Similar to the process for surface and subsurface temperatures, we next calculated the mean value for each sample-day at each site and averaged these values across the amount of time that the logger pair was deployed. While this approach lacks the temporal specificity to capture fine-scale variation in temperature, it allowed us to match the resolution of our temperature predictors with the annual-resolution of our species-occurrence information.

We expected that subsurface microrefuges could provide a critical buffer for pikas against high temperatures associated with the warm season during which pikas collect vegetation for overwinter caches. Consequently, we also investigated the relative importance of microrefuges during the period in which green vegetation was available. We calculated the dates of maximum rate of green-up and maximum rate of brown-down from a double-logistic curve fitted to Normalized Difference Vegetation Index data (from MOD09Q1 of MODIS terra satellite, 8-day 250 m resolution) [68]. We determined green up and brown down values for 9 representative sites which spanned the gradients of elevation, latitude and aspect in our study area. The values for each site were averaged to determine a single mean date of maximum green up and a single mean date of maximum brown down. The same temperature metrics were developed for our warm-season analysis as for our year-long assessment, except that subsurface microrefuge was represented by the difference between surface and subsurface temperatures, rather than by the absolute value of the difference. Since we did not anticipate an effect of snow cover during the warm season, the absolute value of the temperature difference was unnecessary. Average daily values reflected the period during which green vegetation was available, instead of the full duration of logger deployment.

Finally, to better understand the role of microrefuges in moderating high-temperature extremes, we conducted a *post hoc* analysis that examined temperature metrics at occupied and unoccupied sites during the warmest 7-day period of the study. We calculated mean temperature values for each 4-hour sampling event during the 7 days, grouped by occupancy status. We determined whether temperature metrics were different between occupied and unoccupied sites by examining overlap between bootstrapped, 95% confidence intervals (1000 model iterations).

The relative degree of model support was evaluated using Akaike's Information Criterion corrected for small sample sizes (AIC_c), model probabilities and evidence ratios [69]. We computed AICc-related values using the R package AICcmodavg [70]. Goodness-of-fit of the best-supported model was evaluated using the decile method (χ^2; [71]). We evaluated goodness-of-fit for the best-supported model because we used this model to make inferences about the effects of local-habitat characteristics and microrefuges on pika occurrence. While the decile method indicates whether a model fits, sensitivity and specificity provide a means to quantify model performance. Sensitivity refers to the proportion of points where the species was present that were also predicted by the model to have the species present. Similarly, specificity refers to the proportion of points that were correctly predicted as absences [71]. We used the R package ROCR to generate sensitivity and specificity values [72]. As an additional assessment of model performance, we calculated the area under the Receiver Operating Characteristic curve (hereafter AUC; [71]). We analyzed the AUC and the sensitivity and specificity of our top-ranked model to determine overall model performance. Effect sizes were evaluated using odds ratios and were calculated from the beta coefficients associated with individual variables [71].

To minimize problems with multicollinearity, we did not include strongly correlated variables (Pearson correlation coefficients $\geq$ 0.7; [73]) in our models. All analyses were completed in R (R Core Team 2012).

Results

Detection and proportion of sites occupied

We surveyed 146 sites, and recorded evidence of pika occurrence on 70 of the sites (48%). Our detection probability was 0.82 (95% CI = 0.61 – 0.93), resulting in a 10% increase in estimated site occupancy over the naïve estimate ($\hat{\psi}$ = 58%).

Local-habitat

Sample sites occurred along a wide range of elevation (1750 – 3406 m), slope (0.5 – 45°), aspect (5 – 359°) and forage availability (0 – 108 “hits”). Three models in our candidate set of nine local-habitat models received support, and were included in the 90% confidence set (Table 2; cumulative model probability = 0.94). The top models included linear effects of slope, elevation and aspect. Based on the second-ranked model, which included all three physiographic terms, pikas were most likely to occur on northerly aspects (odds ratio =1.97, CL = 1.24, 3.19, P = 0.005, df = 142). The individual effects of slope (P = 0.163, df = 142) and elevation (P = 0.498, df = 142) on pika occurrence were non-significant.

We advanced the first- and second-ranked models from our local-habitat analyses (cumulative model probability = 0.86). While the third-ranked model was included in the 90% confidence set, it was not advanced because it had a notably lower model probability (W_j = 0.08) and weight of evidence (E_i = 7.9), compared to the other two.

Surface temperature and subsurface microrefuge

Of the 40 deployed logger pairs, two failed to record time-synchronized temperature data. Consequently, the sample size for all temperature-based analyses was 38. We documented evidence of pika occurrence at 25 (66%) of the sites equipped with loggers.

Year-long patterns

The second set of models evaluated support for our hypotheses about the importance of microrefuges. Three models were included in the 90% confidence set (Table 3; (cumulative model probability = 0.90). Two of the three models contained some measure of microrefuge. The magnitude of subsurface microrefuge (absolute value of the daily difference between the surface and subsurface temperatures) was the strongest predictor of pika occurrence ($\beta = 2.89$, $P = 0.038$, df = 36), and the only significant predictor in the 90% confidence set. The top-ranked model included a univariate effect of microrefuge, had considerable support ($W_j = 0.81$), and fit the data adequately ($\chi^2 = 4.93$, $P = 0.553$, df = 6). It had 11.6 times the weight of evidence relative to the next-ranked model. The top model also performed well, with sensitivity and specificity at 75% ($c = 0.60$), and AUC = 0.72. AUC values 0.7 – 0.8 suggest acceptable discrimination between presences and absences [71]. Based on the top model, the odds of pika occurrence increased 17.9 times for each degree increase in the difference between the surface and subsurface temperature (CL = 1.17, 273.30, $P = 0.038$, df = 36; Fig. 1).

Overall, habitat predictors received relatively little support, compared to temperature-based models. A univariate effect of aspect was the top-ranked model in our first candidate set ($W_{j\,=}$ 0.63), but placed near the bottom ($E_{\text{aspect}} = 40.5$) when competing with models that accounted for temperature metrics. Similarly, an additive model containing slope, elevation and aspect had some support in our first model set ($W_j = 0.23$). It ranked last, however, when compared with temperature-based models ($W_j = 0.01$).

Warm-season patterns

The mean date of maximum green up was 29 May (SD = 15.3 d). The mean date of maximum brown down was 5 October (SD = 8.4 d). Given the imprecision associated with our estimates, we simplified the warm season to 1 June – 30 September. This period included the warmest four months in our study area. It also corresponded to peaks in both grazing and haying activity documented in two populations of American pikas elsewhere in the Rocky Mountains [72].

We assessed the same suite of 8 models for the warm season to evaluate the relative importance of microrefuges during the period during which green vegetation was available (Table 4). Similar to the year-long results, the top-ranked model included a significant, univariate effect of subsurface microrefuge ($\beta = 0.702$, $P = 0.02$, df = 36), and received reasonable support ($W_j = 0.75$). Two models were included in the 90% confidence set. The subsurface microrefuge model had 5.4 times the weight of evidence relative to the next-ranked model and 37.5 times the weight of evidence compared to the highest-ranked local-habitat model. A univariate effect of the variation within the talus interstices ranked immediately below the subsurface microrefuge model, but received considerably less support ($W_j= 0.14$).

The warmest 7-day period during the study was 22 July – 29 July, 2011. Interstitial temperatures at occupied sites were cooler than unoccupied sites, both on average (5.06 C° cooler, SD = 1.84 C°) and at nearly every 4-hour sampling event in the 7-day period (Fig. 2). In addition, unoccupied sites tended to maintain heat within the interstices, resulting in warmer nocturnal conditions compared to occupied sites (Figs. 2 and 3). Occupied sites were better buffered from diurnal surface-conditions (1000-1800 hours; occupied sites, mean temperature difference = 9.08 C°, SD = 1.88 C°; unoccupied sites, mean temperature difference = 8.03 C°, SD = 2.17 C°), though this difference was equivocal (Fig.3).

Discussion

Microrefuges may help to buffer climate-sensitive species against temperature changes in warming environments [21,75]. Our research provides evidence that the quality of microrefuges may be essential to the occurrence of mammalian thermal specialists, especially in ecosystems where temperatures are highly variable, such as in the alpine. Importantly, our work connects fine-scale, *in-situ* measurements of both the mean and the variability in microrefuge temperatures with species occurrence. Although other studies have quantified the extent to which microhabitats buffer ambient conditions [21,23,25,76], comparatively few have evaluated the difference between the temperatures that an organism experiences in the surrounding territory (e.g., rock-surface conditions) and the operative conditions within available microrefuges. Even fewer have linked this difference to empirical species-occurrence information (but see [26]). Similar to caves and subterranean burrows, talus habitats provide non-living refuges to animals. Living microhabitats (e.g., ground vegetation) are more impacted by novel climates and, therefore, may provide less stable refuges compared to a non-living resource, such as talus [23].

We found robust support for our Microrefuge Hypothesis. The mean daily difference between surface and subsurface temperatures was the single-best predictor of pika occurrence. This result was particularly evident during the warm season, when green vegetation was available and pikas are most active on the surface of the talus (Fig. 4). Pikas were more likely to occur at sites where the subsurface environment substantially moderated surface temperatures, regardless of local-habitat characteristics or surface temperatures. The Interstitial-temperature Hypothesis received comparatively little support, indicating that the temperature within talus interstices alone was not sufficient to explain variation in pika occurrence. Relatively poor support for the Interstitial-temperature Hypothesis, coupled with strong support for the Microrefuge Hypothesis, especially during the warm season, suggests that microrefuges may shelter pikas from stressful surface conditions while simultaneously allowing access to resource benefits associated with particularly warm surface temperatures. Sites with warm mean daily surface temperatures, for example, are likely to experience earlier spring snowmelt, which provides earlier access to high-quality forage [77,78]. Variation in dates of parturition and initiation of first litters, moreover, has been positively correlated with snowmelt in North American pikas (*O. princeps* and *O. collaris*; [79–81]). Additionally, sites that provide a substantial gradient between surface and subsurface temperatures may allow individuals to shed heat quickly, thereby facilitating rapid cooling during particularly warm periods. Cape ground squirrels (*Xerus inauris*), for example, frequently retreat to subterranean burrows during periods of high solar insulation, thereby moderating body temperature and quickly dissipating heat load [82] .

During the warmest 7-day period of the study, below-talus temperatures were generally cooler than surface temperatures in the hottest parts of the day (1400-1800 hours), and warmer than surface conditions during the coldest (0200-0600 hours; Fig. 3). This is similar to findings by Henry et al. 2012, which showed that subsurface temperatures at pika-occupied sites were lower during the afternoon, and higher in the morning and night, compared to above-talus conditions [83]. The increased degree of temperature moderation at occupied sites likely provided animals with enhanced opportunities for rapid cooling, as well as greater protection from potentially stressful conditions.

The maximum mean daily difference between surface and subsurface temperatures was 2.0 C° over the duration of the sampling period (Fig. 1) and 5.6 C° during the warm season (Fig. 4). While these differences may seem small, a magnitude of even 2 C° reflects consistent modulation of surface-temperature extremes. The instantaneous difference between the surface and subsurface environment routinely exceeded 20 C° at some sites. Pikas maintain a high resting body temperature ($\bar{x}$ = 40.1° C) and a relatively low upper lethal temperature ($\bar{x}$ = 43.1°

C; [30,84]). Endothermic animals compensate for ambient temperatures that exceed their upper critical temperature (UCT) by increasing metabolism [85], or by taking advantage of convective/conductive heat loss. Even a few degrees of surface-temperature moderation may protect pikas from costly shifts in metabolism, as long as refuge temperatures remain below the UCT.

The subsurface temperatures that we observed during the warm season ($\bar{x}$ = 12.69 ° C, SD = 5.39 C°; range -2 ° C – 21.94 ° C) were comparable to other studies across the species' range. Similarly, the average subsurface temperature during the summer in the southern Rocky Mountains was 10.6 ° C (SD = 2.9 C°) [86]; and 12.40 ° C (SD = 1.00 C°) at pika-extant sites and 17.05 ° C (SD = 0.81 C°) at pika-extirpated sites in the hydrographic Great Basin [31]. Lower mean interstitial temperatures were recorded in the Columbia River Gorge [21], though this is likely due to the temperature-buffering effects of moss cover prevalent on the surface of the talus, as well as topographical forcings that moderate temperatures in the gorge [21,87].

Macrohabitat temperatures and biotic habitat characteristics may also influence the importance of microrefuges. For example, microrefuges might be especially important to pika occurrence where surface temperatures exceed physiological tolerances for prolonged periods. Surrounding vegetation can buffer interstitial temperatures through shading or through increased albedo [21]. Similarly, rock-ice features or subsurface water can influence microrefuge temperatures [38,76]. Subsequent studies with sufficient sample sizes to fit a context-dependent model could provide useful insights on the merits of this hypothesis.

We found little support for our Local-habitat hypothesis. Pika occurrence was positively associated with steeper slopes and northerly aspects, however, the effects of these local-habitat characteristics were relatively unimportant compared with effects of subsurface microrefuges. We expected pika occurrence to be positively associated with both forage availability [49,56,57] and elevation [36,50]. However, there was little support for either term in our models. Compared with more arid parts of the species' range, our study sites received relatively high annual precipitation. Consequently, pika populations in our system may be limited less by access to vegetation, compared with dryer areas containing lower plant biomass. The average forage availability at unoccupied sites was only 0.19 vegetation 'hits' less than occupied sites. Although individual pikas have unique diet-selection criteria [88], as a species they are generalist herbivores capable of consuming a variety of graminoids, forbs and bryophytes [61,62]. Our measure of forage availability, however, did not address either vegetation diversity or the ratio of forbs: graminoids, both of which have been closely linked with metrics of pika population density elsewhere in the species' range [86]. Given comparable forage availability across study sites, and relatively flexible diets, forage likely did not constrain pika occurrence in our system.

Elevation has been linked to pika-abundance indices across the range of the species [49,50,56], however, elevation itself likely does not limit pika distribution. Rather, elevation indexes relevant biological parameters that affect persistence. We directly measured the parameters that often are indexed by elevation, such as forage availability and temperature. Temperature metrics were more predictive of pika occurrence than elevation, which only indirectly reflected variation in climate conditions. Efforts both to understand current pika distribution, and to forecast future pika persistence under warming scenarios will be improved by incorporating *in-situ* temperature measurements [21], rather than surrogate variables such as elevation.

Microrefuges have the potential to buffer temperature-sensitive species against warming temperature trends [21,26,43]. They are not, however, a one-size-fits-all solution to facilitate species persistence. Use of microclimates can be costly, for example, if organisms shelter at the expense of other essential activities, such as foraging [22]. In addition, not all species have the behavioral capacity to capitalize on favorable microrefuges (e.g. [89]). If organisms are unable to take advantage of microrefuges, or if exploitation of microclimates inhibits essential processes, then reduced fitness ultimately will lead to extirpation. Species that can modulate behaviors to counter temperature extremes often are better able to exploit beneficial microenvironments. American pikas are capable of proximately adjusting to temperature variation through changes in body shape [33], food cache placement [62] and sheltering [34]. The degree to which behavioral flexibility, in combination with acclimatization and developmental plasticity [85], will facilitate the persistence of pikas and other animals in rapidly warming environments merits additional research.

Warming climate conditions have caused changes in the occurrence, abundance, morphology and phenology of species across the globe [3,4]. The magnitude of these changes, however, is inconsistent among clades, biogeographic regions or even within subpopulations of the same species. Some of this variation may be attributable to fine-scale differences in microclimatic conditions [44]. Broad-scale temperature changes do not inherently produce the same magnitude of change at finer spatial scales [20]. Our understanding of species’ responses to changing climate dynamics will be substantially improved by quantifying the relationships between broad-scale temperature increases and microclimatic variation. One of the simplest steps towards this understanding is to measure climate parameters on scales that are relevant to the organisms under study [20,90], including quantifying climate conditions associated with microrefuges.

Conclusions

Our work provides clear evidence that microrefuges are essential to the occurrence of a mammalian thermal specialist. Models of future climate indicate marked increases not only in average temperature values, but also in variation around the means [90]. In an increasingly unpredictable environment, microrefuges may provide organisms with a critical buffer against otherwise intolerable extremes. Consequently, microrefuges likely will influence where and the degree to which temperature-limited animals can persist in warming environments.

Declarations

Ethics approval

All applicable institutional and national guidelines for the care and use of animals were followed. All research activities were conducted in accordance with U.S. Forest Service permit number 65203.

Consent for publication

Not applicable.

Availability of data and materials

Data are available from LEH upon request. American pika are a Tier II Species of Greatest Conservation Need in Wyoming, and were recently petitioned to be listed as a threatened or endangered species under the Endangered Species Act. Consequently, location-associated information is deemed sensitive.

Competing interests

We have no competing interests to declare.

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Authors' contributions

LEH formulated the idea for the study. LEH and ADC developed the hypotheses. LEH, EAB and AEL designed the research methodologies. AEL and LEH collected field data. LEH completed the statistical analyses and drafted the manuscript. ADC, EAB and AEL provided substantial conceptual and editorial advice.

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Tables

Table 1. Research hypotheses and corresponding model parameters

Hypothesis	**Model parameters**
Local habitat	Best local-habitat model
Surface temperature (magnitude)	SurfTemp.mean + SurfTemp.mean^2
Surface temperature (variation)	SurfTemp.sd
Interstitial temperature (magnitude)	InterstitialTemp.mean
Interstitial temperature (variation)	InterstitialTemp.sd
Microrefuge (magnitude)	|TempDiff.mean|
Microrefuge (variation)	TempDiff.sd

Four alternative hypotheses about the relationship between American pika (*Ochotona princeps*) occurrence and microrefuges, and the corresponding model parameters. Three of our four hypotheses included predictions associated with both magnitude (mean value of a temperature parameter) and constancy (standard deviation of a temperature parameter). These hypotheses, consequently, appear twice.

Table 2. Rankings and relative support for local-habitat models that quantify pika occurrence

Model	***K***	**AIC$_c$**	**Δ AIC$_c$**	***W*$_j$**	***E*$_j$**
Cos(Aspect)	2	197.26	0.00	0.63	n/a
Slope + Elevation + Cos(Aspect)	4	199.29	2.03	0.23	2.74
Slope + Elevation + Cos(Aspect) + Forage	5	201.42	4.16	0.08	7.88
Slope	2	204.06	6.80	0.02	31.50
Global model	7	204.56	7.30	0.02	31.50
Elevation	2	205.98	8.71	0.01	63.00
Forage	2	206.23	8.97	0.01	63.00
Elevation (quadratic)	3	207.52	10.26	0.00	undefined
Elevation x Forage	4	209.12	11.85	0.00	undefined

Model-selection parameters from competing models used to explain the effects of local-habitat parameters on American pika (*Ochotona princeps*) occurrence in western Wyoming, USA, June – October, 2010 – 2012; *K*, number of parameters in the model; AIC$_c$, Akaike Information Criterion corrected for small samples; Δ AIC$_c$, difference for model relative to the smallest AIC$_c$ in the model set; W_j, Akaike weight is the approximate probability in favor of the given model from the set of models considered; E_j represents the weight of evidence in support of a model, compared to the top ranked model (W_{jTop} / W_{ji}).

Table 3. Rankings and relative support for models that quantify the role of microrefuges in pika occurrence

Model	***K***	**AIC_c**	**ΔAIC_c**	**W_j**	**E_j**
Subsurface microrefuge (magnitude)	2	45.65	0.00	0.81	n/a
Interstitial temperature (variation)	2	50.52	4.87	0.07	11.6
Subsurface microrefuge (variation)	2	52.55	6.90	0.03	27.0
Surface temperature (magnitude)	3	52.56	6.91	0.03	27.0
Interstitial temperature (magnitude)	2	52.82	7.18	0.02	40.5
Local habitat - Cos(Aspect)	2	52.89	7.24	0.02	40.5
Surface temperature (variation)	2	53.16	7.51	0.02	40.5
Local habitat - Slope + Elevation + Cos(Aspect)	4	55.81	10.16	0.01	81.0

Model-selection parameters from competing models used to examine the effects of microrefuges and surface temperatures on American pika (*Ochotona princeps*) occurrence in western Wyoming, USA, June – October, 2010 – 2012; *K*, number of parameters in the model; AIC_c, Akaike Information Criterion corrected for small samples; ΔAIC_c, difference for model relative to the smallest AIC_c in the model set; W_j, Akaike weight is the approximate probability in favor of the given model from the set of models considered; E_j represents the weight of evidence in support of a model, compared to the top ranked model (W_{jTop} / W_{ji}).

Table 4. Rankings and relative support for models that quantify the role of microrefuges in pika occurrence during the period in which green vegetation was available (1 June – 30 September)

Model	**K**	**AIC_c**	**Δ AIC_c**	**W_j**	**E_j**
Subsurface microrefuge (magnitude)	2	45.57	0.00	0.75	n/a
Interstitial temperature (variation)	2	48.95	3.38	0.14	5.36
Interstitial temperature (magnitude)	2	51.78	6.22	0.03	25.0
Subsurface microrefuge (variation)	2	52.51	6.94	0.02	37.5
Local habitat - Cos(Aspect)	2	52.89	7.32	0.02	37.5
Surface temperature (variation)	2	52.91	7.34	0.02	37.5
Surface temperature (magnitude)	3	54.23	8.66	0.01	75.0
Local habitat - Slope + Elevation + Cos(Aspect)	4	55.81	10.24	0.00	undefined

Model-selection parameters from competing models used to examine the effects of microrefuges and surface temperatures on American pika (*Ochotona princeps*) occurrence in western Wyoming, USA, 1 June – 30 September; K, number of parameters in the model; AIC_c, Akaike Information Criterion corrected for small samples; Δ AIC_c, difference for model relative to the smallest AIC_c in the model set; W_j, Akaike weight is the approximate probability in favor of the given model from the set of models considered; E_j represents the weight of evidence in support of a model, compared to the top ranked model (W_{jTop} / W_{ji}).

Figure legends

Figure 1. Microrefuge and the predicted probability of pika occurrence

Predicted probability of American pika (*Ochotona princeps*) occurrence as a function of subsurface microrefuge (absolute value of the mean daily difference between surface and subsurface temperatures) in the central Rocky Mountains in the western United States, June – October, 2010 – 2012. Black dots represent observed occurrence data. Solid black line shows predicted values. Shaded band reflects non-parametric, bootstrapped 95% confidence intervals (1000 model iterations) for predicted values.

Figure 2. Observed microrefuge temperatures at occupied and unoccupied sites (year-long)

The observed differences between surface and subsurface temperatures at sites that were occupied and unoccupied by American Pika (*Ochotona princeps*) in the central Rocky Mountains, June – October 2010 – 2012. Data are summarized by Julian date, years averaged, and fit with a 3-day moving average. Two vertical, dashed lines denote the beginning and end of the warm season (1 June, 30 September, respectively), during which green vegetation was available, and pikas were collecting vegetation for overwinter food stores.

Figure 3. Observed interstitial temperatures at occupied and unoccupied sites (warmest 7-day period of the study).

Mean interstitial temperatures at sites that were occupied (dashed, blue line) and unoccupied (brown, solid line) by American Pika (*Ochotona princeps*) in the central Rocky Mountains during the warmest 7-day period of the study (22 July – 29 July). Peaks correspond to the warmest period of the day; troughs to the coolest. The shaded ribbons reflect bootstrapped, 95% confidence intervals (1000 model iterations).

Figure 4. Observed microrefuge temperatures at occupied and unoccupied sites (warmest 7-day period of the study).

Mean differences between surface and subsurface temperatures at sites that were occupied (dashed, blue line) and unoccupied (brown, solid line) by American Pika (*Ochotona princeps*) in the central Rocky Mountains during the warmest 7-day period of the study (22 July – 29 July). Positive values indicate that the subsurface environment was cooler than surface conditions; negative values that the subsurface environment was warmer. Peaks correspond to the warmest period of the day; troughs to the coolest. The shaded ribbons reflect bootstrapped, 95% confidence intervals (1000 model iterations).

Figures

Figure 1.

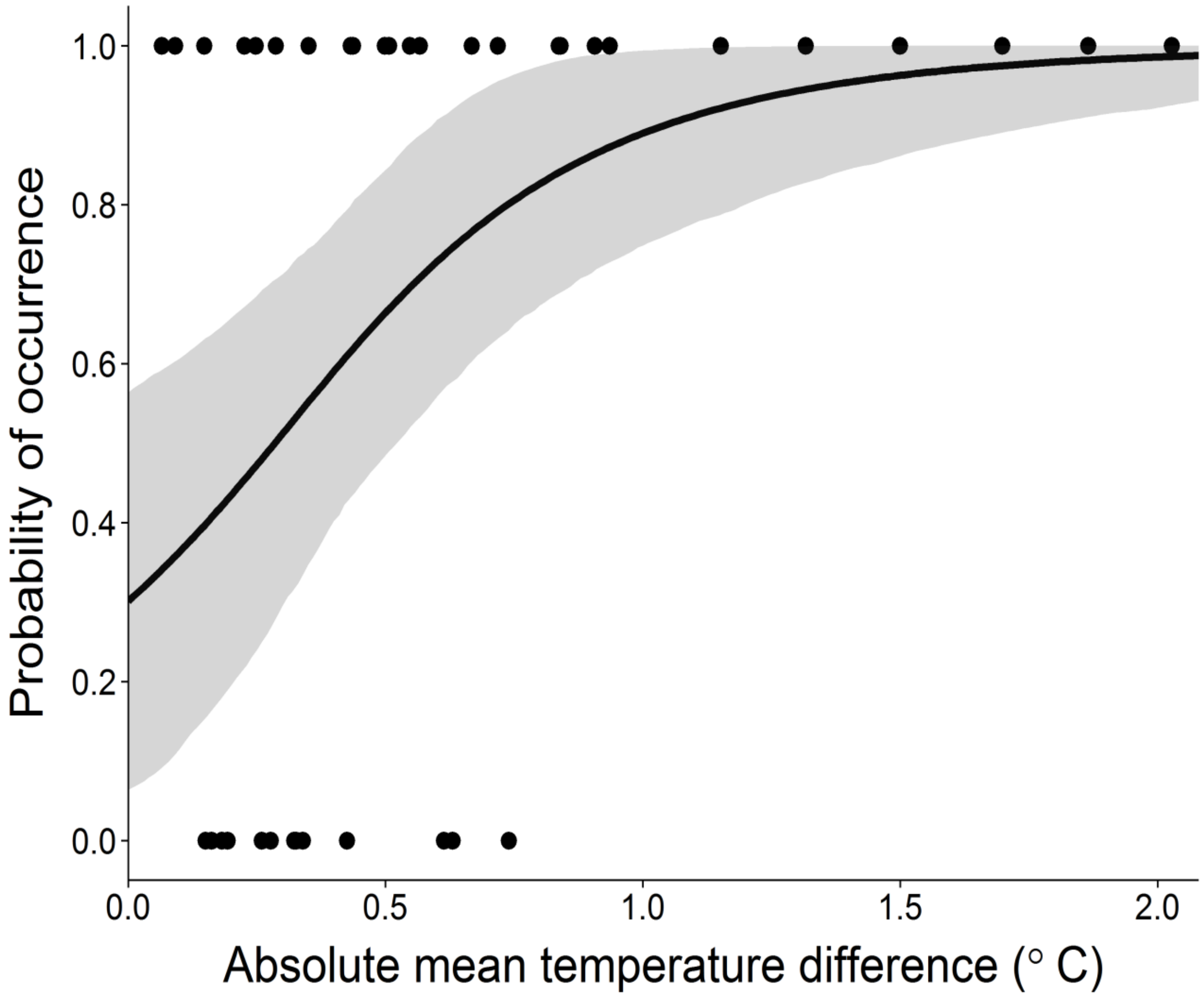


Figure 2.

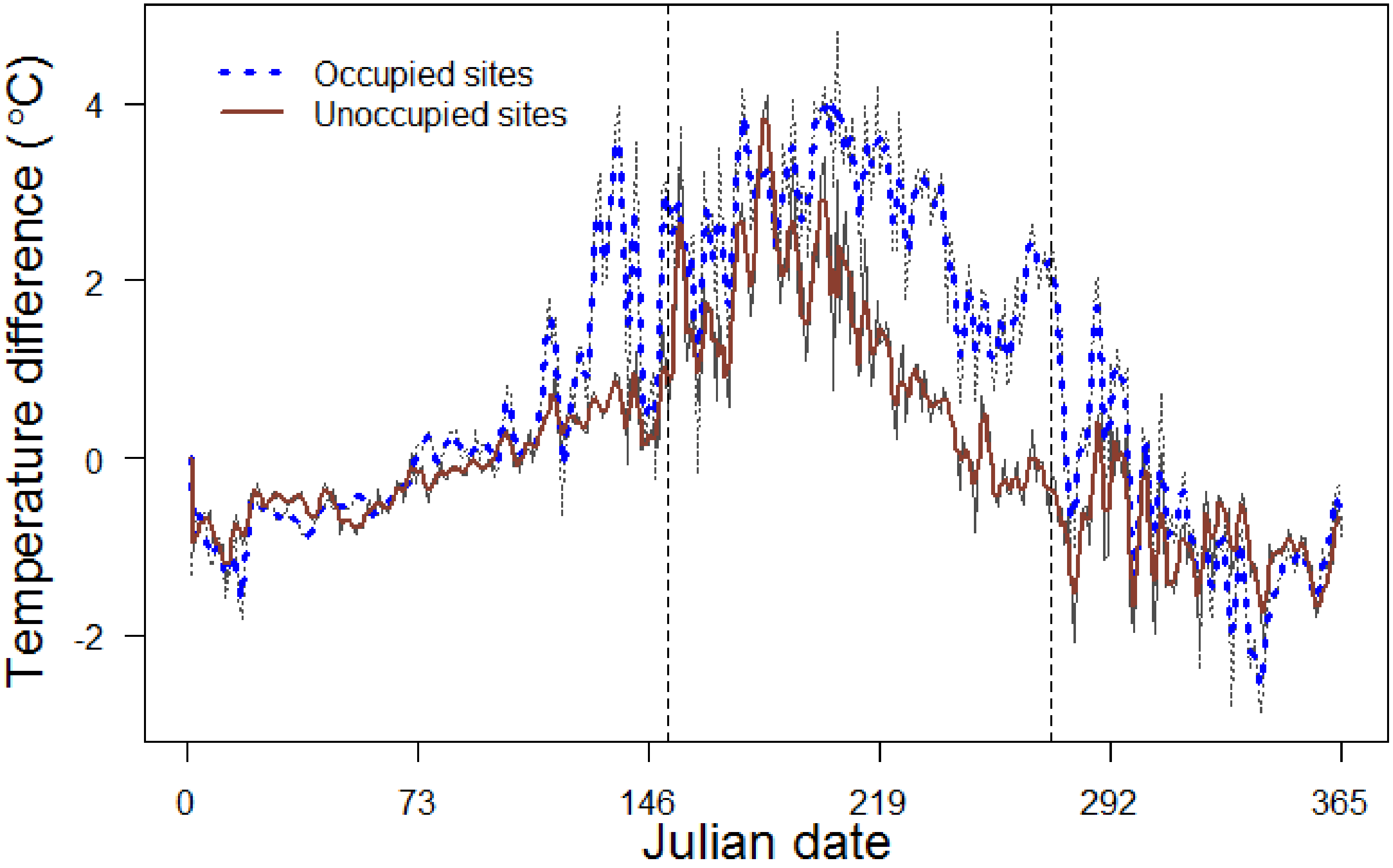
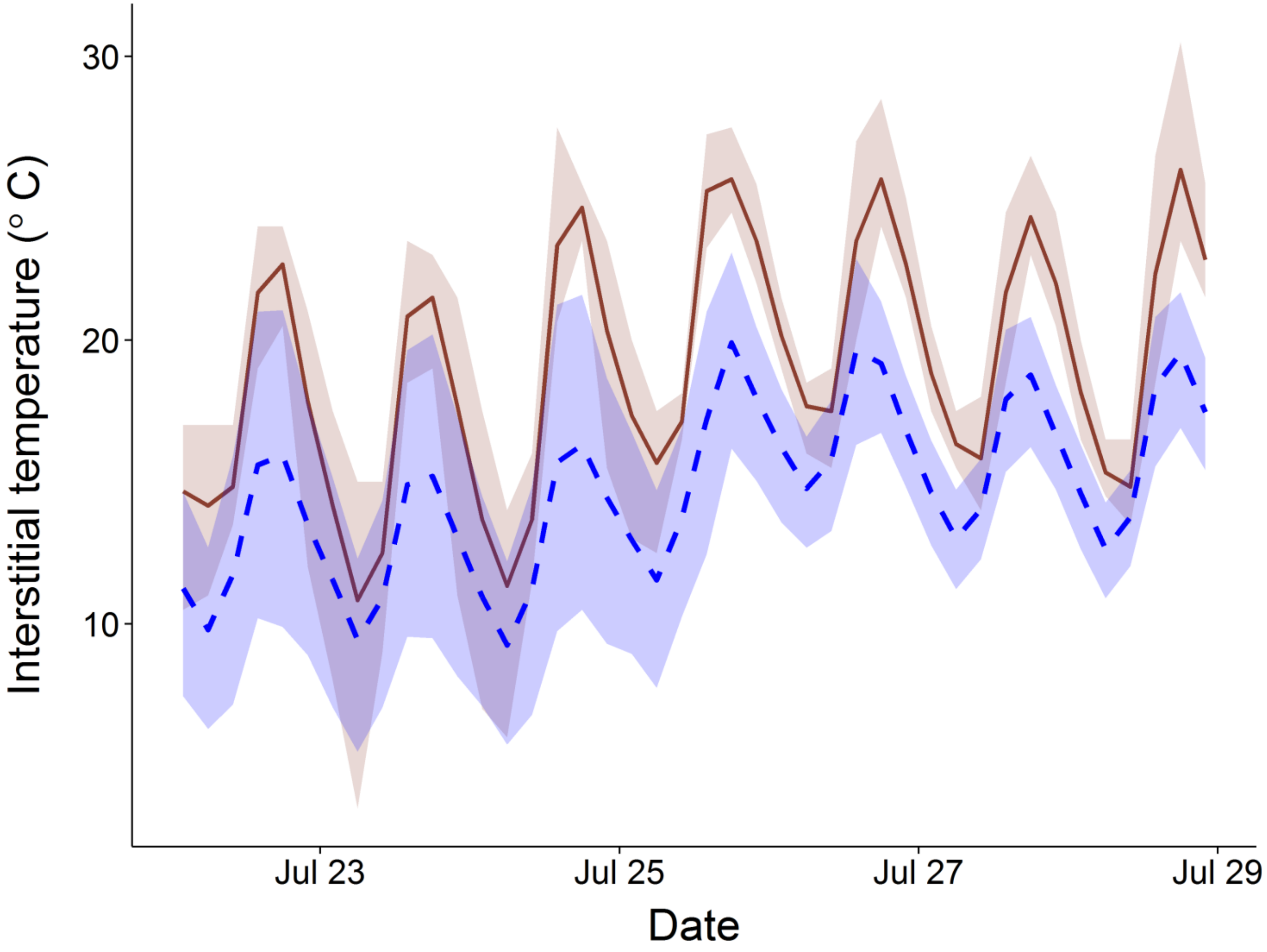
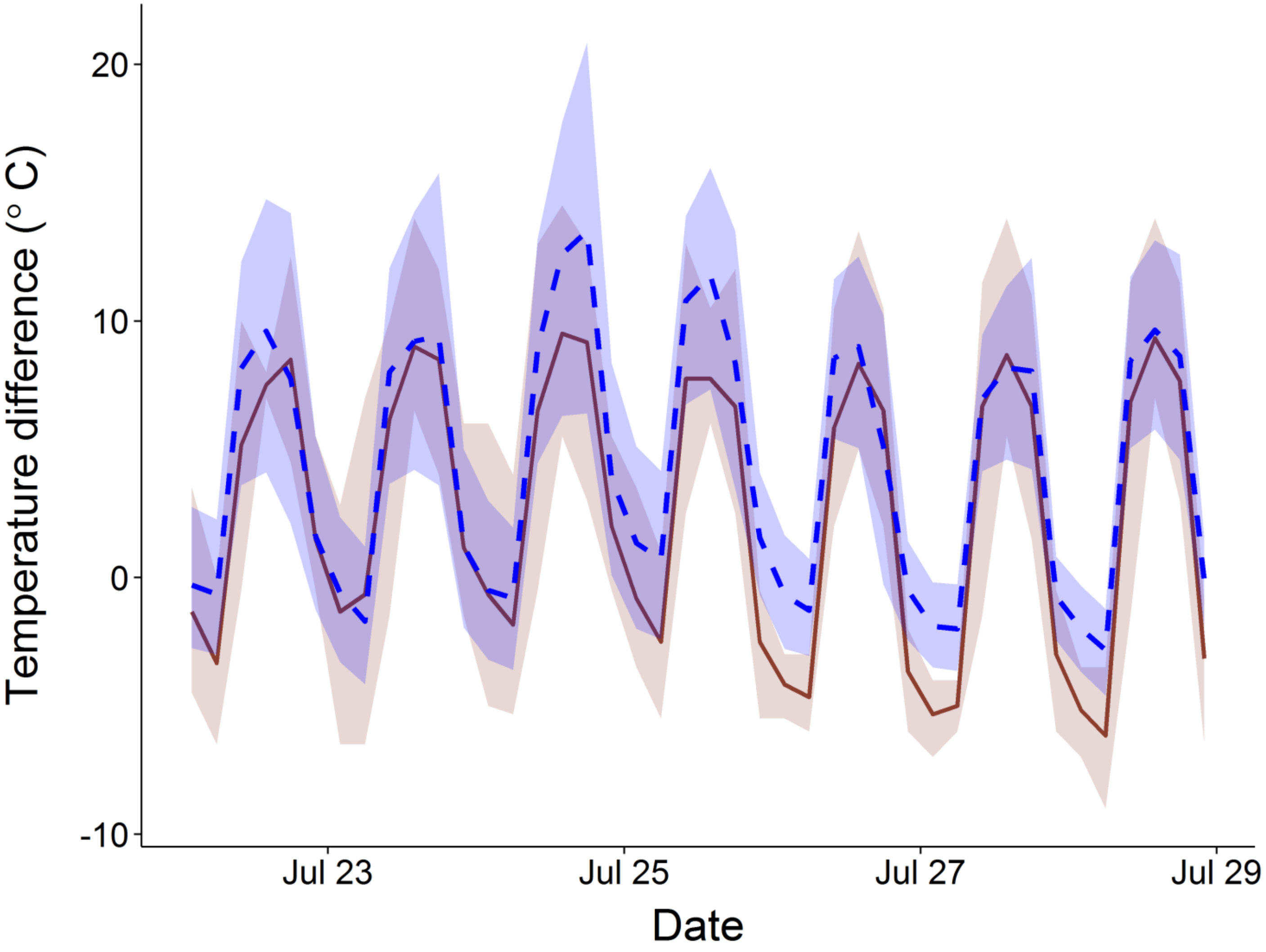

Occupied sites
Unoccupied sites
Temperature difference (°C)
4
2
0
-2
0
73
146
219
292
365
Julian date

Figure 3



30
20
10
Interstitial temperature (° C)
Jul 23
Jul 25
Jul 27
Jul 29
Date

Figure 4


20
10
0
-10
Temperature difference (° C)
Jul 23
Jul 25
Jul 27
Jul 29
Date

CHAPTER THREE

What to eat in a warming world: Do increased temperatures necessitate hazardous duty pay?

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Abstract

Contemporary climate change affects nearly all biomes, causing shifts in animal distributions and resource availability. Changes in resource selection may allow individuals to offset climatic stress, thereby providing a mechanism for persistence amidst warming conditions. Whereas the role of predation risk in food choice has been studied broadly, the extent to which individuals respond to thermoregulatory risk by changing resource preferences is an open question. We addressed whether individuals compensated for temperature-related reductions in foraging time by altering forage preferences, using the American pika (*Ochotona princeps*) as a model species. We tested two hypotheses: 1) *Food Quality Hypothesis*: Individuals exposed to temperature extremes should select higher-quality vegetation in return for accepting a physiologically riskier feeding situation; and 2) *Food Availability Hypothesis*: Individuals exposed to temperature extremes should put a premium on foraging quickly, thereby decreasing selection for higher-quality food. We quantified the composition and quality (% moisture, % nitrogen, and fiber content) of available and harvested vegetation, and deployed a network of temperature sensors to measure *in situ* conditions for 30 individuals, July–Sept., 2015. We found unequivocal support for the *Food Quality Hypothesis*. Individuals exposed to more extreme daytime temperatures showed increased selection for high-nitrogen and for low-fiber vegetation. By contrast, pikas that experienced warmer conditions did not reduce selection for any of the three vegetation-quality metrics that we assessed, as predicted by the *Food Availability Hypothesis*. By shifting resource-selection patterns, temperature-limited animals may be able to proximately buffer some of the negative effects associated with rapidly warming environments.

Introduction

The ability of an organism to alter behavior in response to the environment (hereafter behavioral flexibility; West-Eberhard 2003) can provide animals with a mechanism to keep pace with rapidly changing conditions (Van Buskirk 2012; Wong and Candolin 2015). A relatively short lag between a change in the environment and expression of a new behavioral phenotype can facilitate a quick response to new dynamics (Tuomainen and Candolin 2011). Behavioral flexibility is particularly important in the context of human-induced rapid environmental change (Sih et al. 2011) because the pace of environmental change can eclipse the speed at which organisms are able to genetically adapt to new conditions (Quintero and Wiens 2013; Jezkova and Wiens 2016).

Contemporary climate change is affecting nearly all biomes, causing rapid shifts in resource availability, community composition and species persistence (Parmesan 2006). In addition to altering ecosystem structure, temperature increases associated with climate change can also reduce the amount of time that conditions are suitable for fitness-enhancing activities, such as foraging and reproduction (Williams et al. 2008; Rowland et al. 2011; Mathewson et al. 2017). For species with low mobility and high sensitivity to temperature stress, warming temperatures may be particularly challenging (Williams et al. 2008; Rowland et al. 2011). Unlike their more itinerant counterparts (van der Graff et al. 2006; Merkle et al. 2016), organisms with relatively restricted mobility cannot track changes in resources across the landscape, or relocate to areas with more suitable conditions within a single generation. For these species, small-scale behavioral adjustments may offer a critical first response to increasing temperatures, as well as a potential mechanism to persist in warming environments (Nicotra et al. 2015).

Resource selection is a potentially plastic behavior that may provide an important proximate pathway through which to moderate climatic stress. Greater Prairie-chickens (*Tympanuchus cupido*), for example, buffer temperature extremes common to grassland environments by rearing young in locations that are significantly cooler than the surrounding landscape (by as much as 8.0 C°; Hovick et al. 2014). At elevated temperatures planktonic copepods, *Temora longicornis,* increase consumption of high-carbon foods, which may offset the costs of heightened metabolism (Boersma et al. 2016). Shifts in forage selection, such as increasing preference for high-quality foods, may allow species to offset temperature-related constraints on the amount of time during which conditions are suitable for foraging. By selecting higher-quality food, animals may require less biomass and therefore be able to spend less time foraging in physiologically stressful temperatures. However, the degree to which animals alter forage preference to modulate thermal risk, and the associated constraints on foraging time, remain unclear.

Whereas the effects of predation risk on forage selection have been studied broadly (Bednekoff 2007; Brown and Kotler 2007), comparatively little is known about the influence of thermoregulatory risk on forage choice, especially among mammals (Dearing 2013). With global temperatures expected to increase for at least the next century (IPCC 2013), understanding the extent to which heat-sensitive animals can cope with the constraints of stressful conditions is critical.

The relationship between thermoregulatory risk and forage choice may manifest in one of at least two ways. First, individuals that forage during riskier periods (i.e., in temperatures that are more physiologically stressful) should select higher-quality food. This strategy is a logical extension of fear-based foraging models in which animals exposed to increased predation risk require “hazardous duty pay”, or a higher reward (Brown and Kotler 2004). Animals place an energy value on risk. Higher food rewards can coax an animal into accepting a riskier feeding situation. Desert gerbils (*Gerbillus sp*), for example, harvested food in high predation-risk (open) patches only after the open patches were resource-enriched by at least four times, compared to safer patches in the bush (Kotler and Blaustein 1995). Animals exposed to thermoregulatory risk similarly may require a rich food reward. Alternatively, increased thermal risk may place a premium on foraging quickly. In this case animals may be less choosey, opting to collect the most-available food, and thereby minimizing exposure to stressful conditions. This strategy would result in decreased selectivity for high-quality resources (Lucas 1987; Sih 1993). Indeed, optimal diet theory suggests that when energetic profitability conflicts with safety, foragers should switch from a preference for energetically rich prey, to a preference for safer prey, as risk increases (Lima and Dill 1990).

We tested whether individuals compensated for temperature-related reductions in foraging time by altering forage preferences using the American pika (*Ochotona princeps*), a central-place forager (Huntly et al. 1986), as a model organism. American pikas are herbivorous, food-hoarding lagomorphs, native to the western United States and Canada. They are a cold-adapted species (Galbreath et al. 2009) and, as such, are sensitive to heat stress, with hyperthermia and death resulting after brief exposures to temperatures ≥ 25.5 – 29.4°C when behavioral thermoregulation is not allowed (MacArthur and Wang 1973; Smith 1974). To reduce exposure to unfavorable temperatures, pikas shelter beneath the rocks within the talus fields that they inhabit (Millar and Westfall 2010; Hall et al. 2016). Unlike many montane vertebrates, pikas do not migrate or hibernate during the food-scarce winter months. Instead, they remain active in the subnivean environment, feeding on cached piles of vegetation (hereafter haypiles) collected during summer months. Each individual maintains a territory and either a single haypile or a complex of piles that are fiercely defended from conspecifics (Conner 1983). Haypile biomass has been linked to over-winter survival (Dearing 1997a; Morrison et al. 2009, *but see* Varner and Dearing 2014). Several factors influence pika diet-selection, including nitrogen (N; preferred; Morrison and Hik 2008; Smith and Erb 2013), moisture (preferred; Morrison and Hik 2008; Smith and Erb 2013) and fiber (avoided; Hudson et al. 2008; Bhattacharyya et al. 2013). N is limiting for mammalian herbivores, especially small-bodied species that live in low-N environments such as alpine ecosystems (Parsons et al. 2005; Morrison and Hik 2008; Bowman et al. 2012). Moisture is positively correlated to digestibility, and may be particularly important to pikas because they primarily rely on metabolic water to meet nutritional demands. Finally, fiber reflects the structural components of a plant, such as cellulose and lignin, and is inversely related to digestibility in most mammals (Barboza et al. 2009).

We first assessed the extent to which temperature constrained pika foraging activity. We then tested two hypotheses about the relationship between thermoregulatory risk and forage choice: 1) *Food Quality Hypothesis*: Individuals exposed to temperature extremes should select higher-quality vegetation (*sensu* Brown and Kotler 2004); and 2) *Food Availability Hypothesis*: Individuals exposed to temperature extremes should select vegetation that is most available, to limit foraging time and therefore exposure (*sensu* Lucas 1985). Under the *Food Quality Hypothesis* we predicted that pikas exposed to either higher mean temperatures, or to acute-temperature extremes (> 25°C; MacArthur and Wang 1973; Smith 1974), should show stronger selection for plants higher in N and moisture, and/or lower in fiber, compared to individuals that experience more moderate conditions. Under the *Food Availability Hypothesis,* we predicted that pikas exposed to either higher mean temperatures, or to acute-temperature extremes, should show weaker selection for plants that are higher in N and moisture and/or lower in fiber, compared to individuals that experience more moderate conditions.

Methods

Study area

We conducted our research in the central Rocky Mountains in the western United States, during 19 July – 14 Sept., 2015. The project area was within the Bridger-Teton National Forest (BTNF) in Wyoming (centroid 43.4753° N, 110.7692° W). The BTNF encompasses 1.4 million hectares and ranges in elevation from 1713 m – 4211 m. Average annual precipitation ranges from 66-127 cm. January (average temperature = -8°C) and July (average temperature = 17°C) are typically the coldest and warmest months of the year, respectively. Our study sites occurred within subalpine and alpine communities. Common tree species included Douglas fir (*Pseudotsuga menziesii*), and limber pine (*Pinus flexilis*). Herbaceous plants included lupine (*Lupinus* spp), cinquefoil (*Potentilla* spp), yarrow (*Achillea millefolium*), sulfur-flower buckwheat (*Eriogonum umbellatum*) and various sedges and grasses (Knight et al. 2014).

We examined pika foraging behavior at 5 sites that spanned a gradient of temperature. Each site consisted of the talus habitat within a 2-km buffer of the site's center point. Sites were selected from 25 candidate locations where both pikas were present (determined from occurrence surveys) and we had a record of year-round, *in situ* temperature conditions (2010–2012; Hall et al. 2016). We evaluated thermal profiles from temperature loggers deployed 50 cm below the surface of the talus at each candidate location, and selected sites that encompassed a breadth of temperatures during the snow-free period (approximately 1 June – 30 Sept.; range of mean temperatures at selected sites = 8.5 – 16.2°C; Hall et al. 2016).

We searched for focal individuals by locating haypiles within 2 km of the center point of each site. Pikas maintain and defend spatially distinct food caches, such that a single cache or cache complex can be linked clearly to an individual. Search time ranged from 5–8 h, depending on topographic complexity and the distribution of individuals. We selected at least 5 individuals (maximum 14 individuals) at random from all individuals detected at each site.

Pika activity and surface temperature

At each cache we deployed two infrared-enabled trail cameras (Bushnell Trophy Camera, model 119435) to video-record activity patterns over a 24-h period. Cameras were placed within 3 m of the primary haypile and oriented to encompass the most comprehensive view possible of the pile. Typically one camera was located upslope of the pile, and one downslope. In cases of multiple haypiles within a territory, we placed the camera on the largest pile that appeared active. A pile was considered active if there was fresh, green vegetation on the top. Cameras were motion-activated and programmed to record for 60 s following each activation event. We coded each video for foraging-related behaviors using the software program JWatcher™ (Blumstein et al. 2006; Blumstein and Daniel 2007a). To evaluate the influence of observer bias in behavior classification (Blumstein and Daniel 2007b), we double-coded 20% of the videos. We considered three types of behaviors:

> *Haying*: Carrying plant, fecal, or animal material to a haypile (Barash 1973; Conner 1983; Huntly et al. 1986). This included transportation of resources from adjacent meadows, talus interstices or from an unknown origin, as well as movement of material between piles.
>
> *Eating from the haypile*: Consuming material (plants, animal matter, moss, lichen, etc.) directly from the haypile.

Upkeep: Moving or arranging material within a haypile, without consuming it. Digging, churning vegetation (Morrison et al. 2009), sniffing and scent marking within the pile were included.

Simultaneous with camera deployment, we installed a surface-temperature logger (Maxim Integrated Products, model DS1921G, accuracy ±1 C°, 0.5 C° increments) to examine the relationship between temperature and activity at the haypile. Surface-temperature measurements were intended to reflect conditions that individuals experienced while on the surface of the talus, rather than ambient temperature. Temperature loggers were sealed in a water-tight case and wired to the underside of a north-facing rock, protected from direct sun exposure (Beever et al. 2010; Hall et al. 2016). To minimize the influence of rock size on temperature readings, loggers were attached to rocks of similar size and thickness. Loggers recorded the temperature every 10 min for the duration of the camera deployment.

Forage selection

We assessed available vegetation characteristics of plants that were accessible to each individual pika. Pikas rarely forage more than 10 m into meadows, and most foraging activity occurs within 3 m of talus (Huntly 1987; McIntire and Hik 2005). We quantified vegetation composition (plant type) and quality (% moisture, % N, and % fiber content) along two 8-m transects. The first transect was centered on the haypile, positioned perpendicular to the line of steepest slope, and extended 4 m horizontally to each side (*sensu* Wilkening et al. 2011). The second transect started at the talus-meadow margin closest to the haypile and extended into the meadow along a randomly selected bearing. Every 2 m along the transect we placed a 0.2 x 0.5 m Daubenmire frame (Daubenmire 1959) parallel to the transect. The frame was placed on the same side of the transect each time, and was divided into 10 squares (each 0.1 x 0.1 m). At each of the 18 intersections within these squares we measured the plant life form (e.g. graminoid, forb, shrub, nonvascular; Wilkening et al. 2011) at the basal level and at the subsequent two vertical hits on a 50-cm pin flag. Vegetation hits above 50 cm in height were considered inaccessible to pikas and were not included (Huntly 1987; Hall et al. 2016). We clipped vegetation from 5 randomly selected squares at each frame-reading location for use in vegetation-quality analyses. Only the parts of plants that pikas typically consume, such as leaves, flowers and non-woody stems, were included in the sample (Huntly et al. 1986). Collection was standardized by clipping all plants at ground level.

We assessed the composition and quality of cached vegetation along a modified line-point intercept transect (Elzinga et al. 2001) oriented along the widest axis of the haypile. The transect was located on the top of the haypile and reflected the vegetation harvested during the activity sampling-period. Recently collected vegetation was easily distinguished from the rest of the haypile by its vivid green color and pliant (rather than brittle) leaves (Rodhouse et al. 2010). Every 5 cm we recorded the life form and the species of the cached plant that touched the bottom of a pin flag. To assess nutritional quality, we collected live samples of plant species in proportion to their abundance on the transect. Plant samples were harvested from the meadow and talus areas immediately adjacent to the haypile, and were combined into a single, multi-species sample for analysis.

Vegetation samples were placed in a polyvinylchloride (PVC) tube and immediately weighed (American Weigh Scales digital scale, 1000 g x 0.1 g). We subtracted the weight of the PVC tube from the total mass to determine the wet weight of each sample (Smith and Erb 2013). Samples were then transferred to a paper bag and oven-dried at 60°C for 48 h (Livensperger et al. 2016). Moisture content was calculated by subtracting the mass of the dried sample from the initial sample weight. We submitted the samples to the Soil, Water and Plant Testing Laboratory at Colorado State University (http://www.soiltestinglab.colostate.edu/) to assay the % of N and fiber (acid-detergent fiber; ADF, and neutral-detergent fiber; NDF) in each sample (% of dry weight). NDF indexes total fiber content, while ADF reflects the cellulose-lignin content.

Statistical analyses

To understand the effect of thermoregulatory risk on forage choice, we first needed to quantify how temperature affected available foraging time. We examined the proportion of daytime hours in which the mean temperature (average of the 6 temperature values recorded in each h) was within estimated pika thermal tolerances (-5°C (Beever et al. 2010) - 25.5°C (MacArthur and Wang 1973; Smith 1974)) to assess the relationship between surface temperature and the amount of foraging time potentially available to each individual. The daylight period was 0700 – 2000 h, and was established from the timestamps on all infrared videos, rounded to the nearest h. We fit a generalized linear model with a quasibinomial distribution (R package stats; R Core Team 2015) to quantify whether animals that experienced cooler mean daytime surface temperatures also experienced a greater amount of time in which conditions were suitable for foraging activity.

Pika activity was assayed as the total number of events in which pikas were engaged in a foraging-related activity during the 24-h sample period. This included haying, eating from the haypile and haypile upkeep. We used the mean daytime temperature (°C), calculated from the temperature values recorded every 10 min during daylight hours, as our metric of prevailing thermal conditions. We fit a generalized linear mixed-effects model (GLMM) with a negative binomial distribution to evaluate the relationship between pika activity and surface temperature (R package glmmADMB; Fournier et al. 2012; Skaug et al. 2016). We treated site as a random effect because both behavioral patterns and temperature conditions could vary geographically. If the variance estimates for site were $\geq$ 0.1, we considered the effect important. Due to camera-deployment logistics, there was some variation in the sample-period length between individuals. Consequently, we treated sample duration (min) as an offset in our models. Model diagnostics were assessed by visually inspecting plots of fitted values against residuals, and quantile-quantile plots. If model diagnostics suggested poor fit, or if site was unimportant, we fit a generalized linear model with a quasibinomial distribution as an alternative. In this case, the response variable was the number of active events / sample duration, and the offset was correspondingly dropped.

We used a nonparametric bootstrap (1,000 iterations) to calculate population-level mean differences between cached and available vegetation composition and quality. These values allowed us to determine overall forage preferences for our study population. Positive values indicated selection for a given plant type or nutritional parameter, whereas negative values indicated avoidance. Estimated differences with confidence intervals that overlapped zero suggested use in proportion to availability.

We quantified individual forage selection by calculating the difference between the amount (%) of a vegetation parameter (e.g., N) in an individual's cached-vegetation sample (top of the haypile) and the individual's available-vegetation sample (i.e., % cached – available; *sensu* Garshelis 2000). Through this process each individual was assigned a single value (% difference) for each of the four nutrition-quality parameters that we measured (N, ADF, NDF and moisture).

To test predictions of the *Food Quality Hypothesis* and the *Food Availability Hypothesis*, we evaluated the effects of temperature on vegetation selection using GLMMs with a beta distribution (logit link), and site as a random effect (R package glmmADMB). A beta distribution allowed us to account for the bounded nature of our data (-100% – 100%). Selection values were rescaled to 0 – 1 to match the standard unit of the beta distribution. However, we report parameter estimates and confidence limits on the original scale. Given that the diagnostics best-suited for beta regressions (standardized weighted residuals, local displacement, half-normal plots; Ferrari and Cribari-Neto 2004; Espinheira et al. 2008) are not yet available in a mixed-model framework, we assessed significance of predictors using nonparametric, bootstrapped 95% confidence intervals for parameter estimates. This approach allowed us to address the bounded nature of our data, without supposing parametric assumptions that we were unable to verify. All analyses were completed in Program R (R Core Team 2015).

Results

We recorded activity and *in-situ* temperature conditions for 42 individual pikas. Individuals exposed to higher mean daytime temperatures experienced less time during which temperature conditions were within the range of their presumed thermal tolerance (β = -0.34, CL = -0.41 – -0.27; Fig. 1). We documented 1,685 events of pika activity near haypiles (mean activity account per individual = 38.30 events, ± 36.40 SD). Inter-observer reliability, defined as the correlation between behavior classifications completed by different observers, was high (r_{mean} = 0.98, range = 0.90 – 0.99). A quantile-quantile plot of residuals from our initial negative-binomial GLMM signaled problems with normality, so we proceeded with a beta regression. Pika activity decreased with mean surface-temperature (β = -0.04, P = 0.18; Fig. 2), though not significantly.

We collected vegetation composition and quality metrics for 30 of the 42 individuals that were video recorded. Overall, pikas preferred forbs, grasses and shrubs, with no selection for trees (Fig. 3). Pikas generally cached plants that were higher in N and moisture compared to available vegetation, and avoided plants with high ADF composition (Fig.4).

Individuals that experienced higher mean surface temperatures during daylight hours showed increased selection for N (β = 0.04, CL = 0.00 – 0.08; Fig. 5a). Similarly, individuals exposed to a greater number of extreme temperature events also showed stronger selection for N (β = 0.01, CL = 0.00 – 0.01; Fig. 6a), though the effect was weak.

Neither mean-temperature (β = 0.62, CL = -0.45 – 1.95) nor acute-temperature (number of events > 25°C) metrics (β = 0.10, CL = -0.03 – 0.23) significantly affected moisture selection. Selection for moisture, however, was positively associated with increasing mean daytime surface temperature and the number of extreme temperature events.

Temperature strongly influenced ADF selection patterns. Animals exposed to higher mean surface temperatures had significantly higher avoidance of ADF (β = -0.69, CL = -1.20 – -0.25; Fig. 5b). Avoidance of ADF increased 6.80% (CL = 5.60 – 9.30) for each 10 C° increase in mean surface temperature. ADF avoidance also increased with the frequency of extreme temperature events (β = -0.07, CL = -0.14 – -0.02; Fig.6b). Correspondingly, temperature influenced NDF selection. Avoidance of NDF increased with mean surface temperature (β = -0.85, CL = -1.56 – -0.22; Fig. 5c) and with the number of extreme temperature events (β = -0.07, CL = -0.16 – 0.02), though not significantly for the latter.

Discussion

We evaluated the influence of thermoregulatory risk on forage choice, and whether animals can respond to temperature-related reductions in foraging time by shifting food preferences. Given predicted increases in global temperatures over the next century, modifying forage selection may provide heat-sensitive animals with a mechanism to proximately buffer intensifying temperature constraints on the time available to collect food.

Temperature constrained the foraging activity of American pikas, a thermally sensitive montane mammal. Pikas that experienced warmer conditions had less time during which temperatures were within the bounds of their thermal tolerance. Correspondingly, foraging activity tended to decrease with surface temperature. We tested two theoretically distinct manifestations of how temperature might shape forage choice. The *Food Quality Hypothesis* posited that individuals exposed to temperature extremes should show increased selection for high-quality food. Similar to foragers that demand additional energetic benefit to compensate for increased risk of predation (Brown & Kotler 2004), animals that accept the risk of collecting food in climatically stressful conditions should require a higher reward. By contrast, the *Food Availability Hypothesis* predicted that individuals exposed to temperature extremes should select vegetation that is most available, thereby minimizing exposure to thermoregulatory risk (*sensu* Lucas 1987).

We found strong support for the *Food Quality Hypothesis*, suggesting that pikas, as mammalian thermal specialists, can respond to temperature-driven decreases in foraging time by altering forage selection. Individuals exposed to warmer daytime temperatures were more choosey, showing stronger selection for N and avoidance of fiber, compared to their cool-temperature counterparts. In all but a few cases, individuals maintained preferences for high-quality food, regardless of the temperature conditions that they experienced. Selection for quality resources, however, became stronger at warmer temperatures. Similar to the hazardous duty pay concept developed to describe foraging patterns in response to predation risk (Brown and Kotler

2004), animals that forage in thermally risky environments may demand a superior food reward to justify the comparatively higher thermoregulatory costs.

Pikas that experienced cooler temperatures, and therefore a greater amount of time during which conditions were suitable for foraging, selected high-N vegetation to a lesser degree than individuals exposed to warmer temperatures. This suggests that, given maximal foraging time, individuals likely select vegetation based on a suite of characteristics in addition to N content, including other nutrients (Morrison et al. 2004), haypile structural-enhancements (Jakopak et al., *in review*) or plant secondary compounds (PSCs; Dearing 1997b). Pikas in our study area were likely N-limited. The mean N composition of available vegetation in our study was 1.63% (SD = 0.50%), well below the 3.19% recommended for phylogenetically related rabbits (family Leporidae; Mathius 1987). Individuals foraging in warmer conditions put a premium on high-N foods, perhaps at the expense of other critical diet components. Animals that increase selection for high-quality food in response to thermoregulatory risk, therefore, may trade other important dietary factors for the maximization of one, likely limiting, nutrient. The shape, limits and context-dependency of this potential tradeoff offers a productive area for additional research.

Our results did not support the *Food Availability Hypothesis*. Of the four vegetation metrics that we assessed, none showed decreasing strength of selection with increasing temperature. Therefore, American pikas do not compensate for reduced foraging time by becoming less choosy at warmer temperatures, or by caching vegetation that is most available.

While pikas overall selected high-moisture plants, individuals did not alter moisture selection in response to either acute or mean measures of temperature stress, as predicted. Since the moisture content of vegetation drops substantially once it cures in the haypile (Huntly et al.

1986; Morrison et al. 2004), high-moisture plants may have provided little added value at higher temperatures. Once the vegetation dries, it likely has comparable moisture content, regardless of surface-temperature conditions.

The overall food preferences that we observed were consistent with other studies of pika diet-choice. Plants high in N also have high crude protein content (Mattson 1980), which is essential for animal growth and reproduction (Barboza et al. 2009). Selection and use of high-N and high-protein foods have been documented across the ranges of both *O. princeps* and *O. collaris* including areas of Canada (Millar and Zwickel 1972; Morrison and Hik 2008), south-central Alaska, USA (Holmes 1991), southern Rocky Mountains (Dearing 1996; Smith and Erb 2013) and the Columbia River Gorge (Varner and Dearing 2014). Pika avoidance of fiber has been similarly documented, though individuals in the Columbia River Gorge incorporate large amounts of high-fiber moss into their diets (> 60% of diet). This seems to be an atypical strategy that is linked to pika persistence in the unusually low-elevation habitat of the Gorge (Varner and Dearing 2014). Given the comparatively high elevations of our sites and the relatively low abundance of moss, we would not expect pikas to employ this strategy in the area that we studied.

We did not examine the influence of PSCs, leaf size (Hudson et al. 2008; Bhattacharyya et al. 2013) or insect herbivory (Barrio et al. 2013) on either overall forage preferences, or on the relationship between temperature and selection. Pikas incorporate plants that are rich in phenolics and PSCs in their winter diets, likely as a way to forestall plant decay (Dearing 1996; Dearing 1997b). Toxic allelochemicals, such as cyanogenic glycosides and some alkaloids, are associated with N-rich plant tissues. However, digestibility-reducing allelochemicals, such as phenolics, tannins and terpenoid compounds, are generally found in N-poor plant tissues

(Mattson 1980). PSC concentrations could have both enhanced (toxic allelochemicals) and attenuated (digestibility reducers) preference for N, likely resulting in high uncertainty around the degree to which pikas selected N. Given the strong selection for N that we observed, we do not think that preference for PSCs played a primary role in our findings.

While our metric of food-collecting activity (number of events during a 24-h period), effectively captured foraging activity, it was insensitive to both the duration of foraging bouts and the size of foods loads delivered to the cache. Individuals exposed to warmer conditions may have adjusted one or both of these factors in order to cope with reduced foraging time. For example, individuals may conduct a greater number of trips, each of relatively short duration, during high-temperature periods. Alternatively, individuals could elect to reduce the number of trips but increase the size of food loads (Tinbergen 1981) under thermally stressful conditions. Compensatory behaviors, such as these, would not have been reflected in our metric of activity and offer a potentially fruitful area for additional work.

We provide a unique evaluation of the degree to which animals shift food choices to cope with temperature-related reductions in foraging time. As such, our work adds to the literature on the impressive capacity that animals have in some contexts to adjust feeding behaviors in response to climatic variation (Beever et al. *in press*). Cape ground squirrels (*Xerus inauris*), for example, modulate temperature stress by positioning their tails above their bodies during midday (Fick et al. 2009). This shading enhances thermal comfort and, in combination with burrow shuttling, allows the squirrels to increase surface foraging time from 3 h to 7 h (Bennett et al. 1984; Fick et al. 2009). Similarly, desert woodrats (*Neotoma lepida*) reduce ingestion of creosote bush (*Larrea tridentata*) in warm conditions because secondary compounds in the plant become prohibitively toxic at high temperatures (Kurnath et al. 2016). In the case of pikas, we show that individuals harvest some plants, and not others, depending on surface-temperature conditions. These choices affect the quality of overwinter food stores and, consequently, may influence the probability of overwinter survival (Vander Wall 1990). Increased selection for high-quality foods in warmer temperatures may provide individuals with a tool to balance thermoregulatory risk with the demand for nutritionally-sufficient stores to survive the winter.

Ecologists have long understood that predation risk affects foraging behavior, including metrics of patch selection (Brown 1999; Fortin et al. 2005; Torres-Dowdal et al. 2012), food-consumption location (Lima et al. 1985; Lima and Valone 1986), diet breadth (Sih 1993) and food intake (Brown et al. 1999; Brown and Kotler 2004; Brown and Kotler 2007). Understanding of how thermoregulatory risk influences forage choice, however, is in its infancy, particularly in endotherms (Dearing 2013). Individual foraging decisions are governed by a careful balance between energy management and danger management (Bednekoff 2007). For many thermally specialized endotherms, increased metabolic costs combined with temperature constraints on foraging time represent a source of “danger”. Ecologists should incorporate these risks into modern foraging models, especially in light of increasing temperatures associated with climate change.

By shifting resource-selection patterns, temperature-limited animals may be able to modulate some of the negative effects associated with rapidly warming environments. The capacity to adjust selection in response to temperature, however, is only useful if adequate resources are available. For example, if pikas increase selection for N in warmer environments, but vegetation communities contain predominantly low-N graminoids (Mattson 1980; Bobbink et al. 2010; Bowman et al. 2012), the ability to shift behavior becomes irrelevant. As climate change continues to manifest, efforts to understand changing animal-habitat relationships therefore will be enhanced by considering both resource availability and the capacity of organisms to modify selection dynamics.

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Figure Legends

Figure 1. Proportion of h during which the mean temperature (average of 6 readings; one every 10-min) was within estimated American pika (*Ochotona princeps*) thermal tolerance (-5°C - 25.5°C), and thus suitable for foraging activity, as a function of the mean daytime temperature on the surface of the talus (°C). Proportions were calculated based on a 14-h period (daylight; 700-2000 h). Data were collected from 42 territories in the central Rocky Mountains, USA, July-Sept., 2015. Solid line shows predicted values. Shaded band reflects non-parametric, bootstrapped 95% confidence intervals.

Figure 2. American pika (*Ochotona princeps*) foraging activity in response to mean temperature on the surface of the talus during daylight hours (700-2000 h). Each individual was sampled for 24 h. Data were collected from 42 territories in the central Rocky Mountains, USA, July-Sept., 2015. Black dots represent observed data. Solid line shows predicted values. Shaded band reflects non-parametric, bootstrapped 95% confidence intervals.

Figure 3. American pika (*Ochotona princeps*) selection for four different plant functional-types in the central Rocky Mountains, USA, July-Sept 2015. Mean differences (black dots) and corresponding 95% confidence intervals were calculated from a non-parametric bootstrap (1000 model iterations).

Figure 4. American pika (*Ochotona princeps*) selection for four different nutrition parameters in the central Rocky Mountains, USA, July-Sept 2015; Acid-detergent fiber (ADF), moisture, NDF (Neutral-detergent fiber) and nitrogen. Mean differences (black dots) and corresponding 95% confidence intervals were calculated from a non-parametric bootstrap (1000 model iterations).

Figure 5. American pika (*Ochotona princeps*) selection for nitrogen (5a) and fiber (acid-detergent (5b) and neutral detergent (5c)) as a function of the mean temperature on the surface of the talus (°C) during 24-h sampling periods in the central Rocky Mountains, USA, July –Sept., 2015. Black dots represent observed data. Solid black lines show predicted values. Shaded bands reflect non-parametric, bootstrapped 95% confidence intervals for predicted values.

Figure 6. American pika (*Ochotona princeps*) selection for nitrogen (6a) and fiber (acid-detergent (6b)) as a function of the number of extreme temperature events (>25°C) on the surface of the talus during 24-h sampling periods in the central Rocky Mountains, USA, July – Sept., 2015. Black dots represent observed data. Solid black lines show predicted values. Shaded bands reflect non-parametric, bootstrapped 95% confidence intervals for predicted values.

Figures

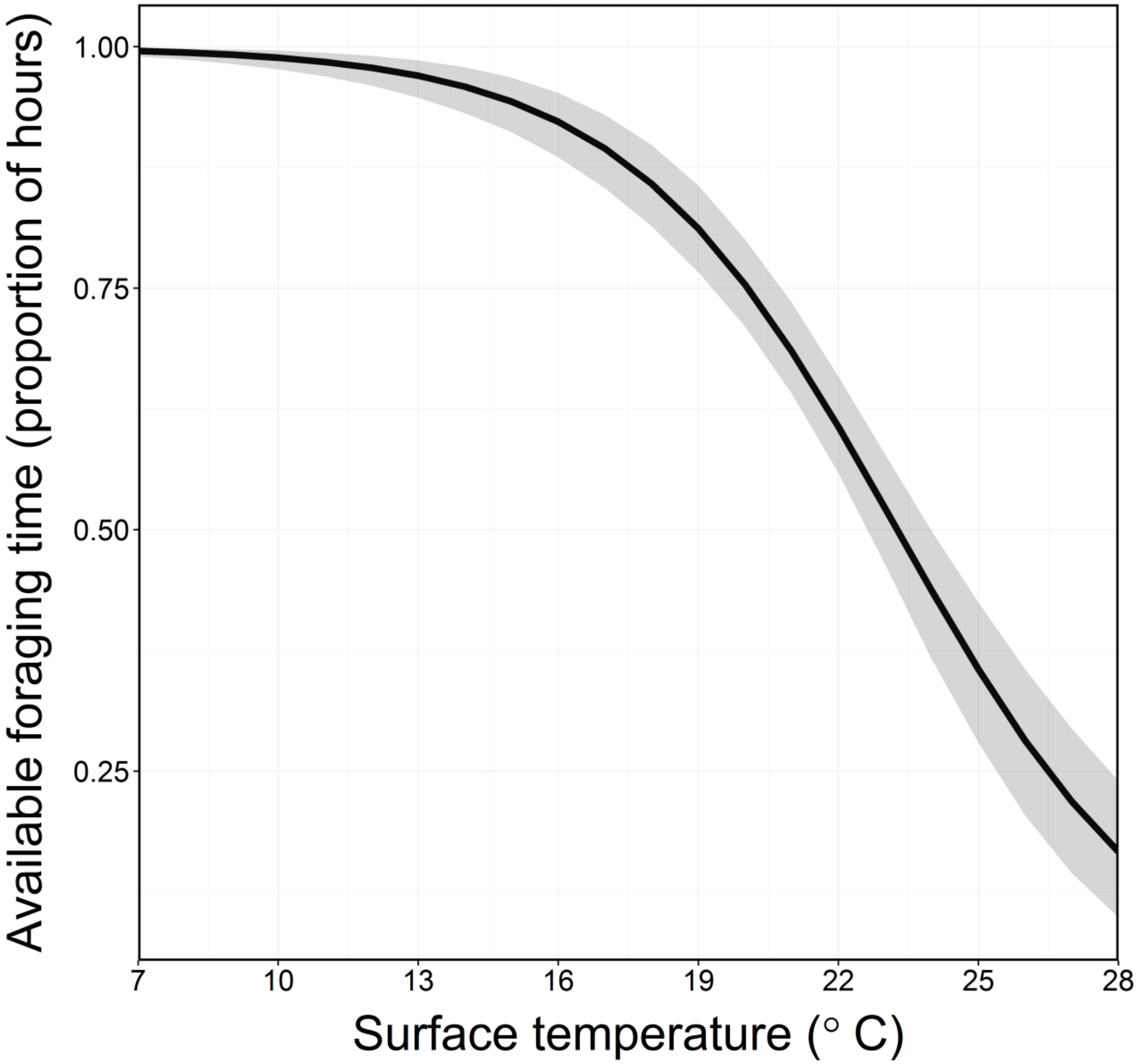

Figure 1.

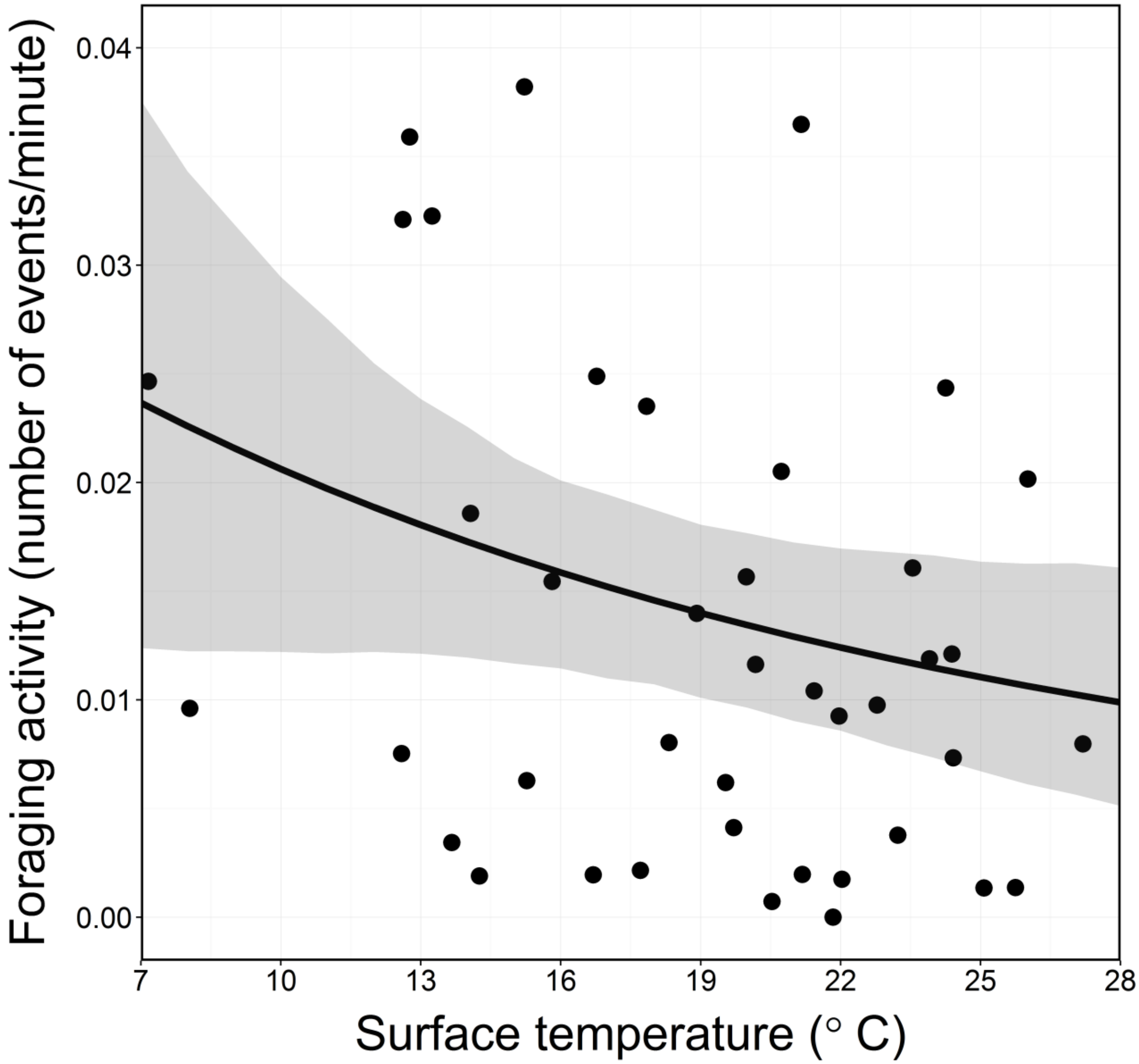
Foraging activity (number of events/minute)
0.04
0.03
0.02
0.01
0.00
7
10
13
16
19
22
25
28
Surface temperature (° C)

Figure 2.

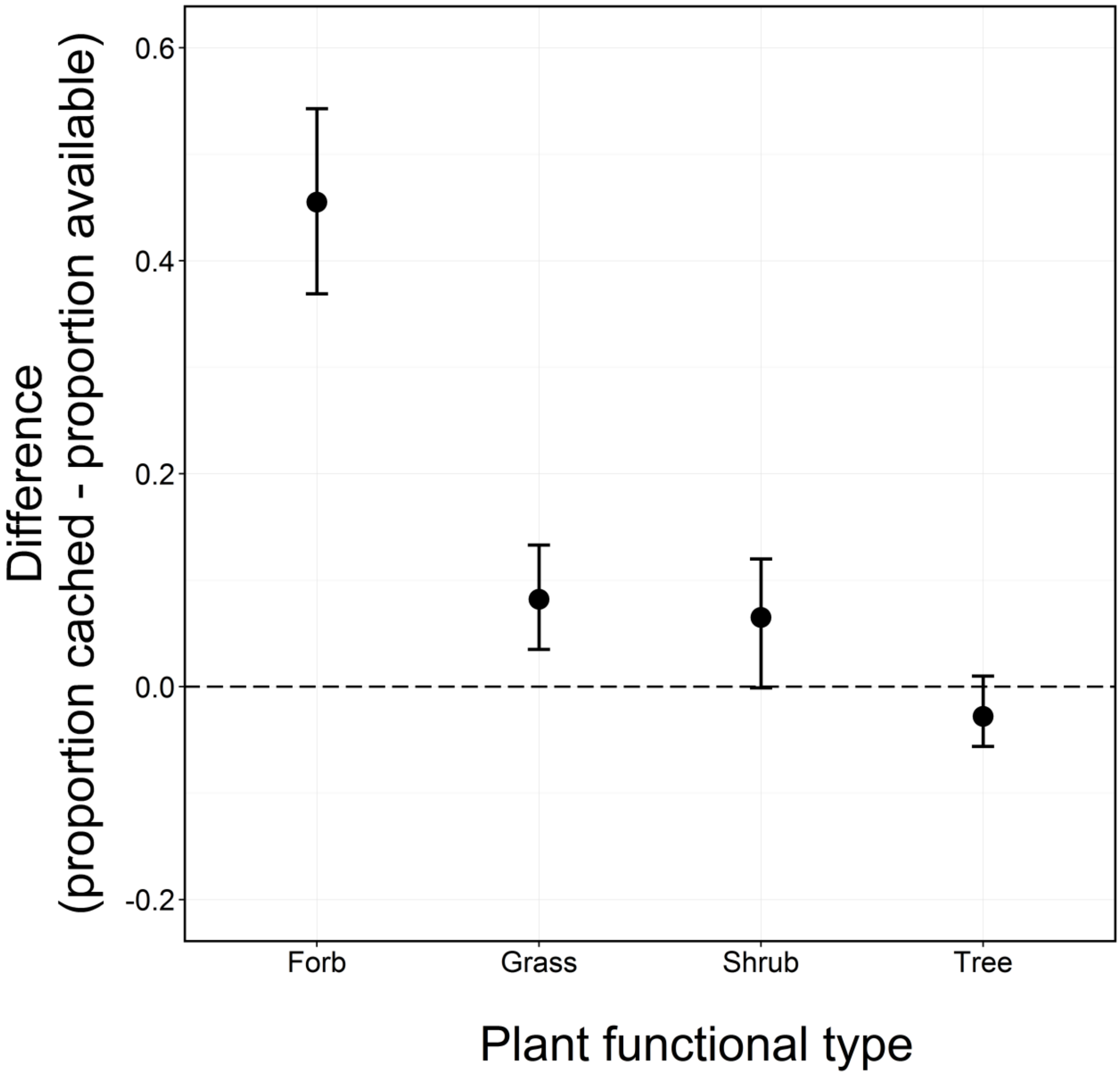
0.6
0.4
0.2
0.0
-0.2
Difference
(proportion cached - proportion available)
Forb
Grass
Shrub
Tree
Plant functional type

Figure 3.

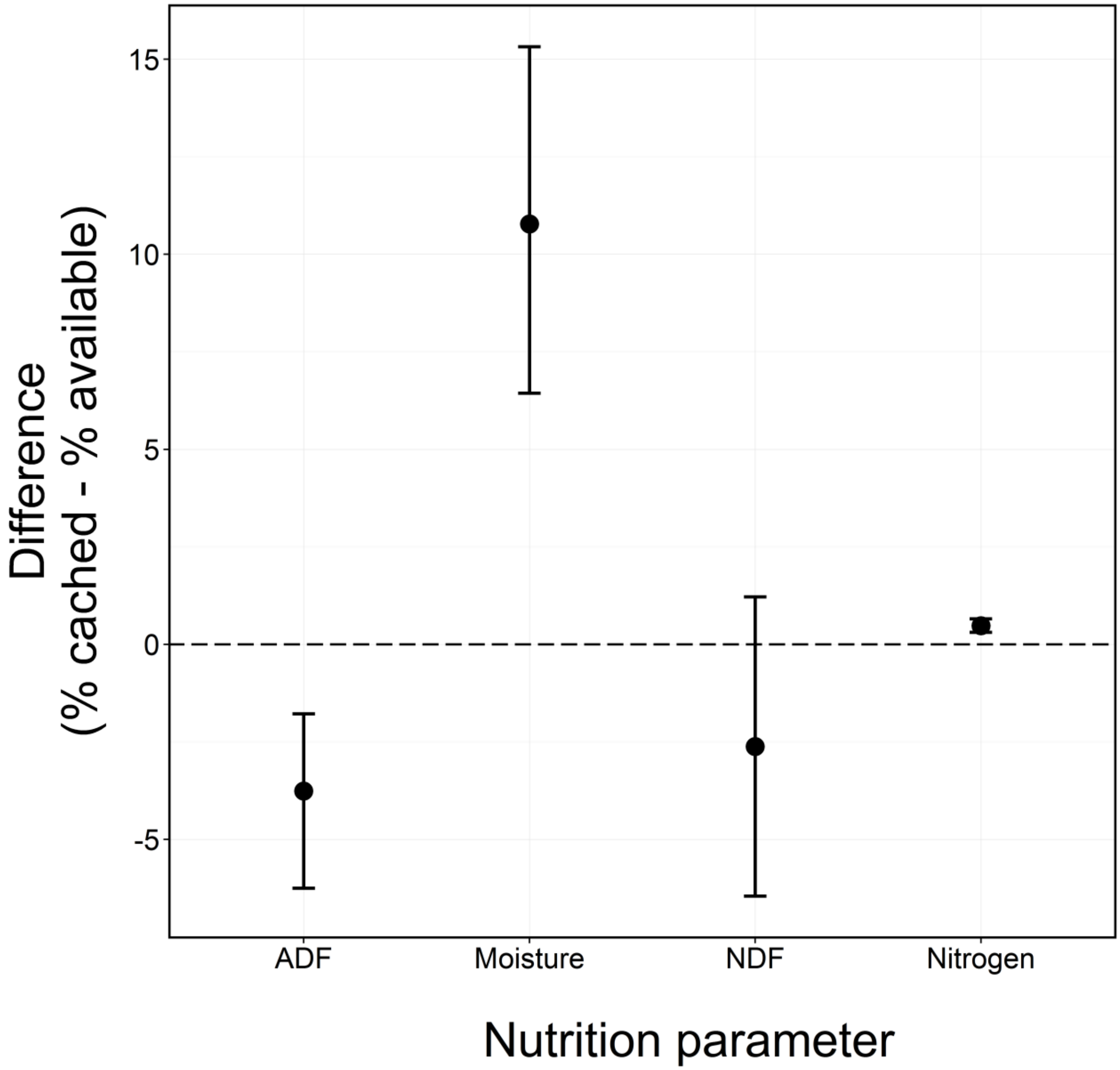
Difference
(% cached - % available)
15
10
5
0
-5
ADF
Moisture
NDF
Nitrogen
Nutrition parameter

Figure 4.

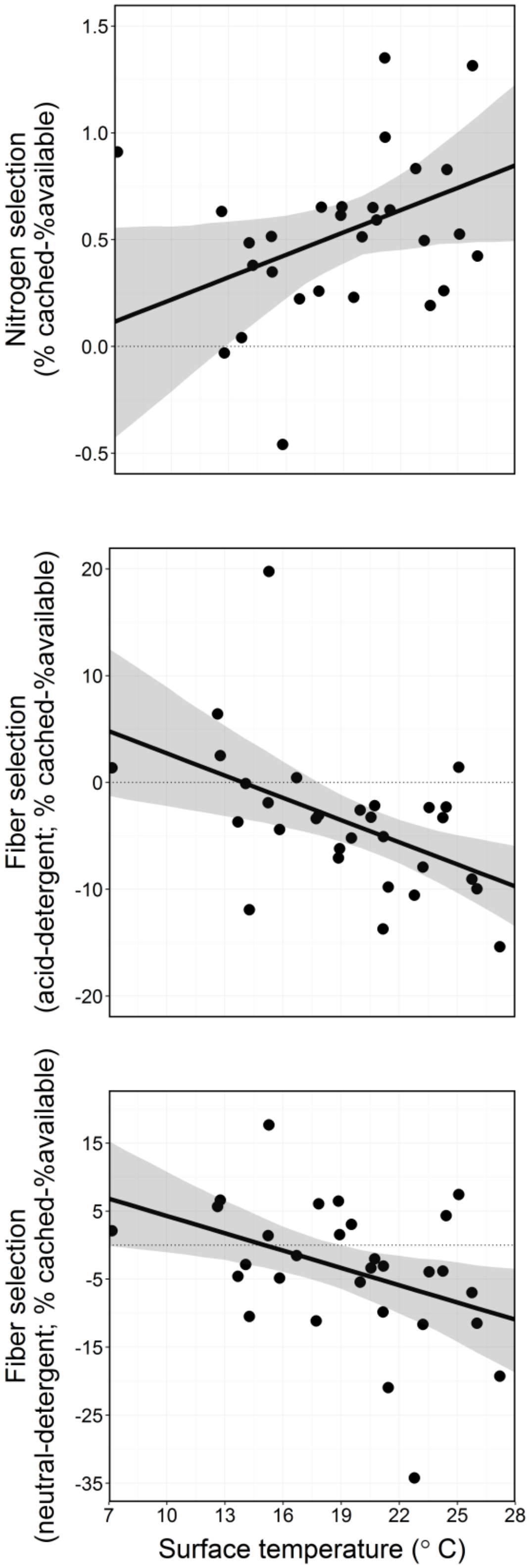
Nitrogen selection
(% cached-%available)
1.5
1.0
0.5
0.0
-0.5
Fiber selection
(acid-detergent; % cached-%available)
20
10
0
-10
-20
Fiber selection
(neutral-detergent; % cached-%available)
15
5
-5
-15
-25
-35
7
10
13
16
19
22
25
28
Surface temperature (° C)

Figure 5.

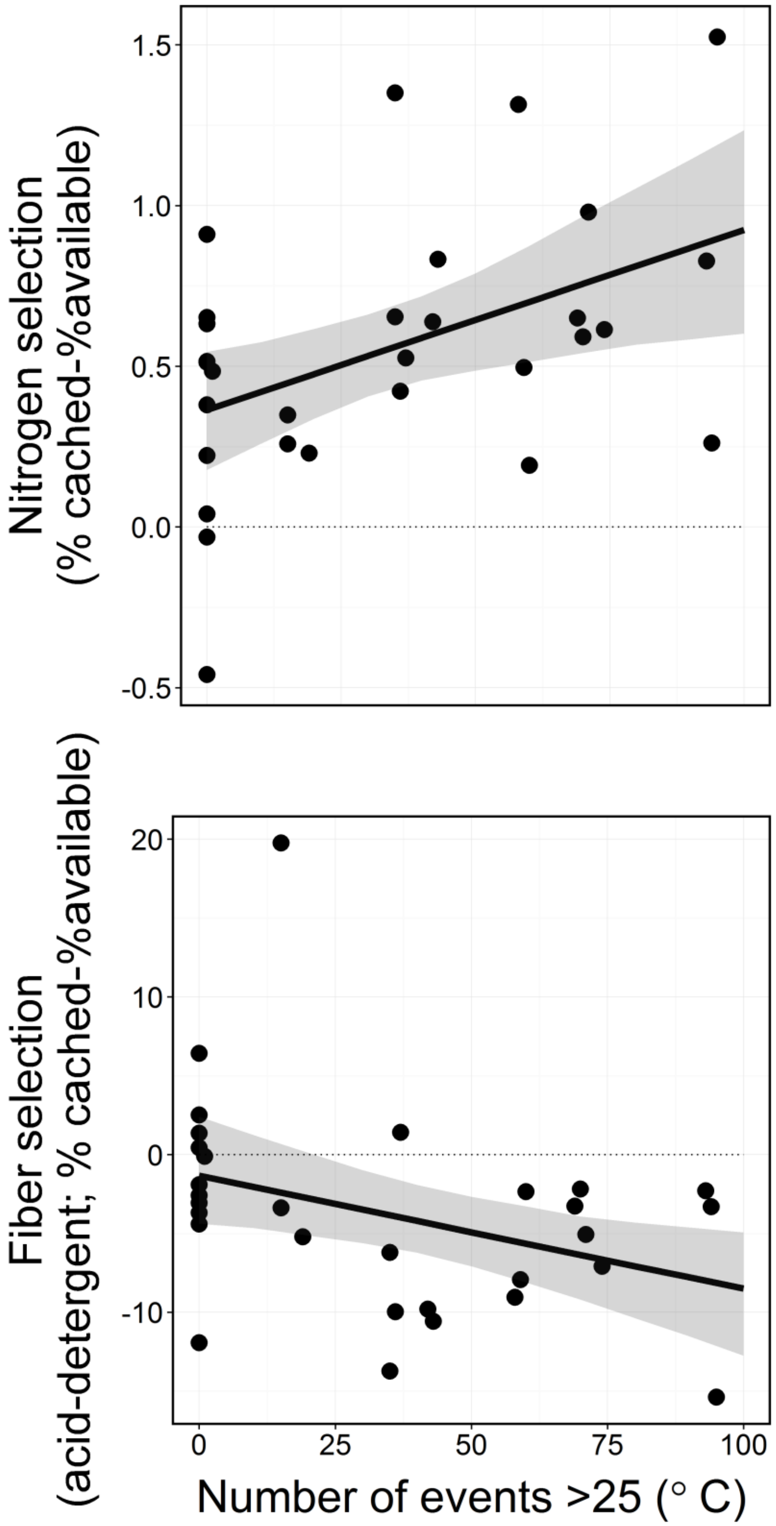
Nitrogen selection
(% cached-%available)
1.5
1.0
0.5
0.0
-0.5
Fiber selection
(acid-detergent; % cached-%available)
20
10
0
-10
0
25
50
75
100
Number of events >25 (° C)

Figure 6.

CHAPTER FOUR

Behavioral plasticity modulates temperature-related constraints on foraging time for a montane mammal

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Abstract

Contemporary climate change is altering temperature profiles across the globe. Among numerous ecological effects, increasing temperatures can reduce the amount of time during which conditions are suitable for animals to engage in essential activities, such as securing food. Behavioral plasticity, the ability to alter behavior in response to the environment, may provide animals with a tool to adjust to changes in the availability of suitable thermal conditions. The extent to which individuals can alter fitness-enhancing behaviors, such as food collection, to proximately buffer temperature variation, however, remains unclear. Even less well understood are the potential performance advantages of flexible strategies among endotherms. We examined the degree to which individuals altered rates of food collection in response to temperature, and the corresponding nutritional benefits, using the American pika (*Ochotona princeps*), a temperature-sensitive, food-hoarding mammal, as model species. From July – Sept, 2013-2015, we used motion-activated cameras and *in situ* temperature loggers to examine pika food-caching activity for 72 individuals across 10 sites in the central Rocky Mountains, USA. We quantified % nitrogen by cache volume as a metric of cache quality. We found a strong negative effect of temperature on the rate at which pikas cached food. Individual responses to temperature varied substantially in both the mean level of food-collecting activity and in the degree to which individuals shifted activity with warming temperature. After accounting for available foraging time, individuals that exhibited greater plasticity collected a significantly higher amount of nitrogen by cache volume. By varying food-collection norms of reaction, individuals were able to plastically respond to temperature-driven reductions in foraging time and, through this increased flexibility, to simultaneously amass a higher-quality overwinter food resource. Our results suggest that, given sufficient resource availability, plasticity in foraging activity may help temperature-limited endotherms to adjust to climate-related constraints on foraging time.

Introduction

Across the globe, endotherms inhabit a wide range of temperature. From -65°C in the Arctic to 55°C in parts of Death Valley, California (Aguado & Burt 2004), endothermic animals employ a diverse suite of physiological and behavioral mechanisms to maintain a relatively constant body temperature ($T_{b;}$ Feldhammer et al. 2007, Boyles et al. 2011). When elevated ambient temperatures (T_a) cause T_b to deviate from neutral conditions, endothermic animals can engage in two primary strategies: allow T_b to rise, or escalate thermoregulatory effort to maintain T_b within the preferred range (Scholander et al. 1950). Both approaches, however, can be energetically costly (Boyles et al. 2011), and may divert energy from other fitness-enhancing activities such as collecting food or finding mates. Cold-adapted species may be particularly challenged by high T_a, as selection for traits that facilitate survival in sub-zero conditions, such as thick layers of insulative fat, fur or feathers, can inhibit essential heat loss (McNabb 2002). Like other thermal specialists, cold-adapted endotherms may have reduced capacity to mount a physiological response in response to increasing T_a (Khaliq et al. 2014). Consequently, behavioral thermoregulation, such as avoiding exposure to solar insolation or increasing activity during preferred conditions, may provide an essential mechanism through which thermally specialized endotherms can persist amidst elevated T_a. Yet, the extent of flexibility in behavioral traits that influence thermoregulatory effort, and the corresponding benefits of flexible strategies, remain unclear, especially among wild populations.

Contemporary climate change is altering temperature profiles globally including increasing mean conditions (IPCC 2013) and shifting trends in temporal temperature variation (Wang and Dillon 2014). Importantly, these changes are manifesting quickly. Predicted rates of temperature change are likely to require rates of climatic-niche evolution that are largely unprecedented (Quintero and Wiens 2013, Jezkova and Wiens 2016), in order for species to keep pace. Warming temperatures have been linked to changing species distributions, phenological mismatches between resources and consumers, and increased risk of extinction (Walther et al. 2002, Parmesan 2006). In addition to these ecosystem-level changes, increasing temperatures can reduce the amount of time during which conditions are suitable for animals to engage in essential activities, including raising young (Peacock 2011) and securing food (Whiteman et al. 2015). This is especially true in high-latitude and high-elevation ecosystems where climate change has had a particularly strong effect (Pauli et al. 1996, Gottfried et al. 2012). The higher elevations of the northern Rocky Mountains, USA, for example, have experienced nearly three times the global average temperature increase over the past century, with an unprecedented decrease in snowpack (Pederson et al. 2011, Shuman 2012, *but see* Oyler et al. 2015).

Contextual behavioral plasticity, also known as activational plasticity, describes the ability of an organism to alter behavior in immediate response to variation in the environment (Snell-Rood 2013, Stamps 2016). Both population-level and individual-level responses to environmental variation are characterized by reaction norms (Stearns 1989, Stamps 2016). Reaction norms are product of the environment [E], the average level of behavior exhibited across a range of environmental contexts [I], and individual responsiveness to environmental variation [I*E] (Stearns 1989, Dingemanse et al. 2010). Population-level responses to a change in the environment depend on the reaction norms of individuals. Reaction norms can vary among individuals, and evolve over time depending on inter-individual variation and on environmental selection pressures (Tuomainen and Candolin 2011). If, for example, an initial response to a change in the environment is insufficient, plasticity can only be enhanced if there is variation in the trait upon which selection can act (Murren et al. 2014, Stamps 2016).

Behavioral plasticity may facilitate species persistence amid rapidly increasing T_a because 1) there is a relatively short lag between a change in the environment and expression of a new behavioral phenotype (Tuomainen and Candolin 2011), 2) the costs of flexible behavioral responses may be small compared to morphological models of plasticity (Van Buskirk and Steiner 2009) and 3) behavioral plasticity is reversible, allowing the individual to secure the benefits of a new phenotype without committing to it in the context of an uncertain future (Ghalambor et al. 2007, Chevin et al. 2010, Van Buskirk 2012). Furthermore, behavioral modification can improve an organism's survival and reproduction if behavioral shifts are linked to measures of performance, such as nutrition or energy gain. Individual Great tits (*Parus major*), for example, tracked rapidly advancing peak biomass of larval winter moths (*Operophtera brumata*) across nearly 5 decades by concomitantly advancing egg-laying dates (Charmantier et al. 2008). Similarly, female Svalbard reindeer (*Rangifer tarandus platyrhynchus*) immigrated to less icy areas with better feeding conditions in response to intermittent rain-on-snow events that restricted food access on traditional winter ranges (Loe et al. 2016).

While the role of behavioral plasticity in species responses to climate change has gained substantial attention in recent years (Beever et al. *in press*, Van Buskirk 2012, Wong and Candolin 2015), particularly among ectotherms (*sensu* Dillon et al. 2010, Sinervo et al. 2010), the extent to which endotherms can modulate foraging behaviors to proximately buffer temperature variability remains unclear. Even less well understood are the potential performance advantages of flexible strategies among cold-adapted species, which may be particularly affected by increasing T_a.

We examined the degree to which individuals shifted forage-collection rates in response to variability in temperature, using the American pika (*Ochotona princeps*), an herbivorous central-place forager, as model species. Pikas are cold-adapted (Galbreath et al. 2009) and are found primarily in montane ecosystems in western North America (Smith and Weston 1990, *but see* Shinderman 2015, Varner et al. 2016). Pikas possess several physiological adaptations that allow them to remain active year-round in cold, high-elevation environments. These include dense pelage, low thermal conductance, and a basal metabolic rate that is 143% of allometric-model predictions (MacArthur and Wang 1973). Traits that enhance thermoregulatory capabilities during cold months, however, inhibit heat dissipation in warmer conditions, causing pikas to be sensitive to high T_a (Moyer-Horner et al. 2015). Brief exposures to ambient temperatures > 25.5 - 28°C can result in hyperthermia and death, if individuals are unable to behaviorally thermoregulate (MacArthur and Wang 1973, Smith 1974).

Despite their heat-sensitivity, pikas engage in substantial foraging activity during the summer (Conner 1983), simultaneously consuming food to satisfy daily caloric demands, and caching plants for sustenance through the winter (Huntly et al. 1986, Dearing 1997). The biomass of overwinter caches (hereafter haypiles) has been linked to metrics of annual survival (Dearing 1997, Morrison et al. 2009, *but see* Varner and Dearing 2014). Several factors influence the plants that pikas select for haypiles, including a preference for vegetation that is high in nitrogen (N; Hall and Chalfoun *in prep*., Smith and Erb 2013). N is limiting for most herbivorous mammals, especially small-bodied species that live in low-N systems such as alpine environments (Parsons et al. 2005, Morrison and Hik 2008, Bowman et al. 2012). To minimize thermoregulatory stress when green vegetation is available for harvest, pikas shelter in cool interstitial spaces in the rocks where they live (hereafter talus; Moyer-Horner et al. 2015, Mathewson et al. 2017). Given sensitivity to T_a, a limited physiological ability to shed heat, and increased activity during the warmest period of the year, behavioral thermoregulation is essential to pika survival (Smith 1974, Moyer-Horner et al. 2015). Indeed, given limited dispersal capability (Henry et al. 2012), and relatively low fecundity (Smith 1978), behavioral plasticity may play a key role in determining how the species responds to rapidly changing climate.

To better understand how endotherms alter foraging behavior in response to temperature, and to evaluate the potential benefits of plasticity in terms of nutritional gain, we tested whether 1) temperature constrained available foraging time for pikas; 2) there was a population-level change in foraging behavior in response to temperature [E]; 3) individuals exhibited consistent behavioral differences [I]; 4) individuals responded differently to changing temperature [I * E]; and 5) individuals that exhibited greater plasticity secured a nutritional benefit. We predicted that pikas exposed to higher mean temperatures would experience less time during which conditions were suitable for foraging (Aublet et al. 2009, Moyer-Horner et al. 2015). We expected that individuals exposed to daytime temperature extremes would forage more often at night when temperatures were cooler (*sensu* Dussault et al. 2004, Maloney et al. 2005), and that exposure to high mean daytime temperatures would reduce the rate at which individuals cached food. Finally, we predicted that, given limited foraging time, individuals that exhibited greater plasticity would secure a higher food reward, compared to less-plastic individuals. By conducting our work on wild populations, we were able to assess the potential benefits of foraging plasticity under ecologically relevant conditions (Brommer 2013). Although several studies have examined population-level shifts in activity in response to temperature, few have simultaneously linked individual variation in foraging behavior norms of reaction with *in situ* temperature and a measure of performance.

Methods

Study area

We conducted our work in montane communities on the Bridger-Teton National Forest in the central Rocky Mountains of western Wyoming, USA. Elevations ranged 1713 m – 4211 m (Jakopak et al. *in review*). July is typically the warmest month of the year. Average annual precipitation ranges from 66 – 127 cm. Our sites were located in alpine and subalpine habitats. Common tree and shrub species included Douglas fir (*Pseudotsuga menziesii*), limber pine (*Pinus flexilis*), shrubby cinquefoil (*Dasiphora fruticose*) and raspberry (*Rubus* spp.). Herbaceous vegetation included lupine (*Lupinus* spp.), yarrow (*Achillea millefolium*), sulfur-flower buckwheat (*Eriogonum umbellatum*) and various sedges and grasses (Knight et al. 2014)

Site selection

We selected 10 sites from a candidate set of 25 where both pikas were present (determined from occurrence surveys) and we had year-round, *in situ* thermal profiles (2010 – 2012; Hall et al. 2016). We evaluated temperature data from loggers deployed 50 cm below the surface of the talus at each candidate location, and selected sites that encompassed a range of temperatures during the snow-free period (1 June – 30 Sept; range of mean temperatures at selected sites = 8.5 – 16.2°C; Hall et al. 2016). We searched for focal individuals by locating food caches within 2 km of the center point of each site. Pikas defend spatially distinct caches, such that a single haypile or cache complex can be matched unambiguously to an individual. Search time ranged from 5 – 8 h per site, depending on topographic complexity and the distribution of individuals. We selected 5 – 14 individuals randomly from each site, using a random-number table.

Behavior and temperature

We deployed infrared-enabled trail cameras (Bushnell Trophy Camera, model 119435) from late July – early Sept, 2013-2015, to video-record individual pika behavior at the haypile over a 24-h period. Two cameras were placed within 3 m of each individual's haypile. In cases of multiple haypiles, we focused on the largest pile in the cache complex that contained fresh, green vegetation on the top. We sited the cameras to provide the best possible view of the pile. Typically, one camera was positioned upslope of the pile and one downslope. Cameras were motion-activated. One min of video footage was recorded following each activation event. We coded the pika activity in each video using the software program JWatcher^{TM} (Blumstein et al. 2006, Blumstein and Daniel 2007a). All behaviors were classified as events and were considered mutually exclusive. We doubled-coded 20% of the videos in which pikas were active to evaluate the influence of observer bias (Blumstein and Daniel 2007b). Five behaviors were included in our ethogram of pika haypile-activity.

> *Eating from the haypile*: Consuming material (plants, animal matter, moss, lichen, etc.) directly from the haypile.
>
> *Haying*: Carrying plant, fecal, or animal material to a haypile (Conner 1983, Huntly et al. 1986, Varner et al. 2016). This included transportation of resources from adjacent meadows, talus interstices or from an unknown origin, as well as movement of material between spatially distinct piles. Piles were considered distinct if the vegetation did not touch another pile.
>
> *Haypile maintenance*: Moving or arranging material within a haypile, without consuming it. Digging, churning vegetation (Morrison et al. 2009), sniffing and scent marking within the pile were included.
>
> *Sitting on the haypile*: Sitting or otherwise inactive on the haypile.

Departing the haypile: Departure (at least 1 pika-body length) from the haypile with no immediate (< 5 s) return (Conner 1983).

Concurrent with camera deployment, we installed a temperature logger (Maxim Integrated Products, model DS1921G, accuracy ±1 C°, 0.5 C° increments) within 5 m of the haypile to examine the relationship between temperature and pika activity. Loggers were time-synchronized with the cameras, and recorded a temperature reading every 10 min for the duration of the 24-h sample period. We sealed each logger in a water-tight 5-g jar made of clear plastic and wired it to the underside of a rock, such that it was not exposed to direct sunlight (Beever et al. 2010, Hall et al. 2016). Loggers were attached to rocks with similar exposed surface area and thickness to minimize the influence of rock size on the temperatures that we recorded.

Cache quality

We assessed the quantity and quality of the haypile by quantifying the N content (%), and calculating the volume of the pile (m^3). Using a jointed, 2-m, engineer's-scale ruler (Lufkin, Apex Tool Group) we measured the width, length (measured orthogonal to width) and height of the pile on the longest axis of each dimension. We included inner-crevice vegetation in our measurements (Dearing 1997) by extending the wood ruler into the rock crevice until we reached the extent of the vegetation. We evaluated N content along three modified line-point intercept transects (Elzinga et al. 2001) oriented across the widest span of the haypile. One transect was located on the top of the haypile, and reflected the vegetation cached during the activity sampling-period. The two remaining transects were read in the middle and the bottom portions of the haypile to assess the composition of the entire cache. Every 5 cm along each transect we recorded the species of the vegetation that touched the bottom of a pin flag held at the mark. We collected live samples of all cached plants species in proportion to their abundance along the transects. Plant samples were harvested from the meadow and talus areas immediately adjacent to the haypile (Huntly 1987, McIntire and Hik 2005) and were combined into a single, multi-species sample for analysis. Only the parts of plants that pikas typically consume, such as stems, leaves and flowers (Huntly et al. 1986), were included in the sample.

Each sample was placed in a paper bag and oven-dried at 60°C for 48 h (Livensperger et al. 2016). We submitted the samples to the Soil, Water and Plant Testing Laboratory at Colorado State University (http://www.soiltestinglab.colostate.edu/) to assay the %N by dry sample weight.

Statistical analyses

Initial data-exploration steps for all hypotheses included graphical assessments of potential outliers (boxplot), examination of the response-variable distribution (histogram), evaluation of the number and type of zeros (Zuur et al. 2009a; frequency plot) and assessment of collinearity between predictors (if appropriate; scatterplot and Variance Inflation Factor; Zuur et al. 2010). Outliers were removed only if they were in error. Otherwise, analyses were conducted with and without the data point to contextualize the influence on model results. Following model fitting, model assumptions were assessed by visually inspecting plots of fitted values against residuals, examining overdispersion and testing for autocovariance in model residuals (R package stats; R Core Team 2015). If necessary, we addressed nested structures and potential violations of independence by fitting a suite of random effects, selected *a priori* based on the study design and on likely biological relationships (Zuur and Ieno 2016). For models that included mixed effects, we determined the optimal structure of the random component (random intercept or random intercept and slope) prior to evaluating fixed effects. We assessed the importance of random effects by examining the estimated variance attributed to the effect in our models. Values < 0.1 indicated that the effect was unimportant (Zuur et al. 2009b). We used Akaike's Information Criterion (AIC; Burnham and Anderson 2002) to choose between random-effects parameterizations. Non-overlapping 95% confidence limits and, when appropriate, *P* values were used to assess the importance of fixed effects.

Surface temperature and available foraging time

We examined the proportion of daytime hours in which the mean temperature (average of the 6 temperature values recorded in each h) was within estimated pika thermal tolerances (-5°C (Beever et al. 2010) – 25.5°C (MacArthur and Wang 1973, Smith 1974)) to assess the relationship between surface temperature and the amount of foraging time potentially available to each individual. The daylight period was 0700 – 2000 h, and was established from the timestamps on all infrared videos, rounded to the nearest h. We fit a generalized linear model with a quasibinomial distribution (R package stats) to quantify whether animals that experienced cooler mean daytime surface temperatures also experienced a greater amount of time in which conditions were suitable for foraging activity (Table 1). The quasibinomial distribution allowed us to account for both the proportional nature of our response variable (proportion of hours during which the mean temperature was within estimated thermal tolerances), and potential overdispersion.

Pika activity and temperature

We considered two metrics of pika activity: total activity and food-collection activity. Total activity was measured as the number of events in which pikas engaged in activity at the haypile. This included haying, sitting, eating from the haypile, departing from the haypile and haypile maintenance. Food-collection activity was measured as the number events in which pikas engaged in food collection or manipulation. This included haying and haypile maintenance, as both activities involved the transportation, manipulation and management of food items.

To evaluate the influence of daytime temperature on nocturnal food-collecting activity, we fit a generalized linear model with the number of nocturnal events as the response (count), and either the mean daytime surface temperature (continuous) or the number of hours during which the mean temperature exceeded 25°C (count) as the predictor (R package glmmADMB; Fournier et al. 2012, Skaug et al. 2016). We used a negative binomial distribution to account for overdispersion (Table 1; Bolker 2008).

For all other analyses, activity counts were summed by hour. Since individuals were sampled for 24-h, this resulted in 24 activity values for each individual. We calculated mean hourly surface temperatures by averaging the 6 surface-temperature readings recorded during each hour in an individual's territory. This produced 24 *in situ* temperature values for each individual, which temporally matched the 24 activity values.

We evaluated the relationship between temperature and both metrics of activity (total activity and food-collection activity) using a zero-inflated mixed-effects model with a negative binomial distribution (Zuur et al. 2009a). The negative binomial distribution allowed us to account for overdisperison in our data (Bolker 2008), while zero-inflation addressed the high proportion of zeros (more zeros than expected, based on the negative binomial distribution; Zuur et al. 2009a). We treated mean hourly surface-temperature (continuous) as a fixed effect. We expected a nonlinear relationship between surface temperature and pika activity (count; Smith 1974, Morrison et al. 2009), so we included a quadratic effect of surface temperature in our models. Since behavior observations were grouped by individual, we treated individual (categorical) as a random intercept. We expected that behavior patterns and temperature conditions could vary geographically, so we also tested the importance of site (categorical) as a random intercept. Finally, we tested the influence of sample h (categorical, random intercept) because we anticipated that pika activity might be affected by time-of-day (Table 1).

Individual responses to temperature

We used a two-step approach to determine the extent to which individuals differed in their responses to temperature. First, we examined the variance associated with the random intercept term for individual in our model of food-collecting activity. The random effect of individual allowed for the fitted line obtained from the fixed effects in our model to be shifted up or down on the y-axis for each individual. If the variance was ≥ 0.1, we assumed that the term for individual explained a meaningful amount of variation, and that intercepts were substantially different (Zuur et al. 2009b). Assuming that individual intercepts differed, we next fit a zero-inflated mixed effects model with food-collecting activity as the response, individual, mean daytime surface temperature and an interaction between individual and temperature as fixed effects (hereafter individual-plasticity model; IPM; Table 1). Sample h was treated as a random intercept. The model was fit with a negative binomial distribution to account for overdispersion. To facilitate model convergence, individuals with < 5 food-collecting events were removed. This part of our analysis allowed us to both visualize individual reaction norms (i.e. how individuals shifted food-collecting activity in response to temperature), and to calculate an estimate of plasticity for each pika. We quantified individual-level plasticity by iteratively re-fitting the IPM with each individual as the reference level, and extracting the corresponding coefficient (and standard error) for the linear effect of temperature. This process yielded one slope coefficient and standard error value for each pika. We treated these coefficients as our measure of individual plasticity (hereafter plasticity score).

Plasticity and available foraging time

To understand the influence of available foraging time on individual plasticity, we examined the relationship between the number of hours in which the average daytime temperature was $\geq$ 25°C and individual plasticity scores. Each individual was therefore represented by a single point (x = number of hours during which conditions were unsuitable; y = plasticity score). We fit a mixed-effects linear regression (R package nlme; Pinheiro et al. 2016) with a Gaussian distribution and site as a random effect to quantify the relationship. If site was unimportant, we refit a simple linear regression (R package stats; R Core Team 2015; Table 1). To account for the error associated with individual plasticity-score estimates, we ran a weighted version of the model (R package stats), which weighted plasticity scores by the inverse of their standard errors.

Benefit of plasticity

We evaluated whether increased plasticity in food-collecting behavior resulted in a higher quality cache by assessing the % N in each haypile, relative to the volume of the pile (N / haypile volume). The amount of suitable foraging time likely influenced the degree of food-collecting flexibility that each individual displayed. Consequently, we used the residuals from our regression of individual plasticity and available foraging time in our assessment of plasticity and cache quality. These residuals represented the plasticity that individuals expressed, after accounting for available foraging time (hereafter residual plasticity). We fit a mixed-effects regression with a gamma distribution (R package glmmADMB) to quantify the influence of individual plasticity on cache quality. We treated N by volume (continuous) as the response and residual plasticity (continuous) as the predictor, with site as a random effect (Table 1). The gamma distribution allowed us to account for the positive, continuous nature of our response variable. We ran two versions of this model; one that used residuals from our unweighted regression of individual plasticity and available foraging time, and one that used residuals from the weighted regression.

Results

We sampled 72 individual pikas across 10 sites, and collected 4,370 videos in which pikas were active at haypiles. We documented 7,840 active events. Pikas were most frequently recorded sitting on haypiles (32.4% of events), followed closely by departing from the haypile (28.5%), haypile maintenance (21.9%) and haying (13.2%). Eating directly from the haypile comprised 4.1% of active events. Pikas were surface-active during every hour of the 24-h sample period, with a peak at 0600-1000 h (Fig. 1). Individuals were least active in the late evening through the early morning (2200-0500 h).

Surface temperature and available foraging time

We deployed temperature sensors that were time-synchronized with cameras for 61 of the 72 individuals. The proportion of hours with a mean temperature that was within the range of estimated pika thermal tolerance decreased with surface temperature ($\beta = -0.370$, CL = -0.433, -0.312, $P = < 0.001$; Fig. 2). The proportion of hours with suitable foraging conditions decreased markedly once mean daytime temperatures exceeded 16°C.

Behavior in response to temperature

The number of nocturnal food-collecting events was unrelated to mean daytime temperature ($\beta = -0.02$, CL = -0.11, 0.07, $P = 0.65$) and to the number of hours during which the mean temperature exceeded 25°C ($\beta = -0.03$, CL = -0.17, 0.11, $P = 0.64$).

Pikas decreased total activity ($\beta = -0.072$, CL = -0.108, -0.037, $P = < 0.001$), as well as the amount of food-collection activity ($\beta = -0.10$, CL = -0.15, -0.05, $P = < 0.001$, Fig. 3) with increasing temperature. The best supported random-effect parameterization for food-collecting activity included individual and sample hour as random intercepts, and temperature as a random slope. Individuals varied substantially in mean level of food-collection activity ($\sigma^2_{\text{individual}} = 1.25$) and in degree of plasticity in response to temperature.

Foraging plasticity tended to increase with the number of hours during which the mean temperature was $\geq$ 25°C (β = -0.013, CL = -0.043, 0.016, P = 0.35; weighted β = 0.001, CL = -0.014, 0.016, P = 0.883). This trend suggested that individuals exhibited greater plasticity as estimated time to collect food decreased. After accounting for available foraging time, individuals with higher residual plasticity collected a significantly greater amount of nitrogen by haypile volume (β = 1.513, CL = 0.250, 2.77, P = 0.014; weighted β = 1.469, CL = 0.279, 2.659, P = 0.016; Fig 5).

Discussion

We tested the degree to which cold-adapted endotherms can respond plastically to temperature-related constraints on foraging time, using the American pika as a model. Behavioral shifts, such as increasing activity during preferred conditions, may provide thermally specialized endotherms with a mechanism to persist amidst increased temperatures associated with climate change. The extent of flexibility in behaviors that modulate thermoregulatory risk, and the potential benefits of flexible strategies, however, remain unclear. While the relationship between temperature, thermal stress and foraging activity has been well studied in ectotherms (Kearney et al. 2009), our work is among the first to explicitly show flexibility in individual foraging norms of reaction in response to *in situ* temperature conditions, and to simultaneously quantify a performance benefit among wild mammals.

We found a strong negative effect of temperature [E] on the rate at which pikas cached food. Individual responses to temperature varied substantially in both the mean level of food-collecting activity [I] and in the degree to which individuals shifted activity with warming temperature [I * E]. Plasticity in food-collection behavior provided a significant nutritional benefit. By varying food-collection norms of reaction, individuals were able to plastically respond to temperature-driven reductions in foraging time and, through this increased flexibility, to simultaneously amass a higher-quality overwinter food resource.

Pikas exhibited variation in both mean levels of food-collection behavior, and responsiveness to the environment. If the initial level of plasticity exhibited by a population is insufficient to match the environment, as might be expected under rapid climate change, continued evolution of reaction norms is possible only if there is individual variation upon which selection can act (Barrett and Hendry 2012). Our results suggest that pikas maintain at least some of the underlying variation necessary to accommodate increased selection for plasticity. Individuals with the steepest reaction norms (i.e., greatest plasticity) engaged in more food-collecting activity when temperatures were suitable, compared to less-plastic individuals. This strategy allowed individuals to capitalize on cooler conditions that likely were less physiologically stressful, thereby minimizing costly autonomic temperature regulation (Seebacher 2009).

The degree to which behavioral plasticity can facilitate persistence in rapidly changing environments depends on both the benefit of flexibility compared to canalization, and the cost of preserving the capacity to be plastic (Van Buskirk 2012, Wong and Candolin 2015). Previous research in our study area has shown that pikas in our system were likely N-limited (Hall and Chalfoun *in prep*). Individuals that expressed greater plasticity collected overwinter food caches that were proportionally higher in %N, relative to more canalized phenotypes. Haypiles provide an important, and sometimes exclusive, food source during winter when resources are scarce (Millar and Zwickel 1972, Dearing 1997, Morrison et al. 2009). Consequently, behaviors that enhance the quality of these stores likely provide a substantial benefit (Vander Wall 1990). The relative benefit of plasticity, however, is also shaped by the cost of maintaining the mechanisms that underlie plastic traits (DeWitt et al. 1998). Such mechanisms include sensory machinery, regulatory pathways and information acquisition processes (Schlichting and Pigliucci 1998), and were beyond the scope of this study. Behavioral plasticity is costly when 1) plastic individuals cannot produce a mean trait value as near to the phenotypic optimum as canalized individuals and/or; 2) plastic individuals incur lower fitness when producing the same mean trait value as non-plastic individuals (DeWitt et al. 1998, Van Buskirk 2012). Empirically, however, costs of plasticity are difficult to show (DeWitt et al. 1998, Hendry 2016) and are likely dependent on ecological context (Van Buskirk and Steiner 2009). In the case of pikas, if the costs of maintaining plastic foraging behaviors exceeds the benefit, or if the benefit does not translate to enhanced fitness, food-collecting activity in response to temperature may become canalized over time.

Similar to several species of grassland and shrubland herbivores (Belovsky and Slade 1986, Maloney et al. 2005), alpine mammals (Aublet et al. 2009) and Otididae birds (e.g. great bustard, *Otis tarda*; Alonso et al. 2016), pikas reduced foraging activity in response to temperature. Pikas were most active during the morning hours, which were cooler, followed by a smaller peak in activity during the early evening (1700-2100 h). These findings are consistent with other studies that documented increased pika activity in cool ambient temperatures (Smith 1974, Moyer-Horner et al. 2015). Pikas were also active at night, albeit at lower levels than during the day. Due to the infra-red capabilities of the cameras that we used, our study is the first to unambiguously document patterns of American pika activity in the absence of sunlight (*but see* Smith 1974) for anecdotal observations). Nocturnal activity has also been recorded in collared pikas (*O. collaris*), however much of this activity was in association with extended day length at the high-latitude study site (Morrison et al. 2009). Contrary to our predictions, pikas exposed to higher daytime temperatures did not increase food-collecting activity at night. While much remains to be learned about the role of nocturnal food-collection in pikas, night-time activity may be constrained by increased predation risk. Nocturnally active pikas may also be exposed to increased thermoregulatory costs. At night, interstitial spaces in the talus are warmer than ambient temperatures (Hall et al. 2016, Millar et al. 2016). Individuals that collect food at night, and are therefore active in ambient conditions, may be more likely to experience temperatures that are below their estimated lower-critical temperature (28.1°C; Otto et al. 2015). Exposure to these conditions would necessitate increased energy expenditure on T_b regulation. Additional research on the limits of nocturnal activity in diurnal, temperature-sensitive animals offers a potentially fruitful area for additional work.

Plasticity in foraging activity may allow temperature-limited endotherms to adjust to climate-related constraints on foraging time. The efficacy of performance benefits, such as nutritional gain, combined with the relative costs of maintaining flexible norms of reaction will determine the extent to which plasticity can facilitate persistence amidst warming temperatures. Increased foraging activity during favorable thermal conditions, however, is only effective if the animal continues to have the ability to shed heat (Boyles et al. 2011), and if flexible strategies do not inhibit other critical activities, such as finding mates (Sinervo et al. 2010). Once ambient temperatures exceed the level at which animals can dissipate heat loads, no amount of behavioral flexibility will facilitate persistence, at least not without a concomitant microevolution in thermal tolerance (Huey et al. 2012, Buckley et al. 2015).

As climate change continues to affect ecosystems across the globe, cold-adapted endotherms may be faced with increasingly unfavorable conditions that will likely impact the balance between thermoregulation and other fitness-related activities. Efforts to understand the effects of new temperature dynamics will be enhanced by considering both the degree of plasticity in fitness-linked behaviors, as well as the extent to which flexible strategies influence survival and reproduction.

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Tables

Table 1. Summary of modelling approaches used to address the extent to which American pikas (*Ochotona princeps*) moderated temperature-related reductions in foraging time through behavioral plasticity, and the associated benefits. Data were collected from 61 territories in the central Rocky Mountains, Wyoming, USA, July – Sept., 2014 – 2015.

Analysis	Model	Distribution	Response	Fixed effects	Random effects
Surface temperature and available foraging time	Generalized linear model	Quasibinomial	Proportion of daytime hours within estimated pika thermal tolerance	Mean daytime surface temperature	None
Nocturnal food-collecting activity in response to daytime temperature	Generalized linear model	Negative binomial	Nocturnal food-collecting activity	Mean daytime surface temperature; Number of hours during which mean daytime temperature ≥ 25°C	None
Population-level activity in response to surface temperature	Zero-inflated generalized linear mixed-effects model	Negative binomial	Total activity; Food-collecting activity	Hourly daytime surface temperature (linear and quadratic)	Hourly daytime surface temperature (slope); Individual (intercept); Sample h (intercept)
Individual-level activity in response to surface	Zero-inflated generalized linear mixed-effects	Negative binomial	Food-collecting activity	Hourly daytime surface temperature;	Sample h (intercept)

temperature (reaction norms)	model			Individual; Individual * Hourly daytime surface temperature	
Plasticity in response to available foraging time	Linear mixed-effects model	Gaussian	Plasticity score	Number of hours with unsuitable mean temperature	None
Benefit of plasticity	Generalized linear mixed-effects model	Gamma	%N / haypile volume	Residual plasticity	Site (intercept)

Figure Legends

Figure 1. Number of events in which American pikas (*Ochotona princeps*) were active at haypiles, by hour. Data were collected from the central Rocky Mountains in western Wyoming, USA, July – Sept, 2013 – 2015. Each boxplot displays the median value (horizontal line), 25th and 75th percentiles (top and bottom of box) and the 10th and 90th percentiles (whiskers).

Figure 2. Proportion of hours during which the mean temperature (average of 6 readings; one every 10 min) was within American pika (*Ochotona princeps*) thermal tolerance (-5° C - 25.5° C), and thus suitable for foraging activity, as a function of the mean daytime temperature on the surface of the talus (° C). Proportions were calculated based on a 14-h period (daylight; 700-2000 h). Data were collected from 61 territories in the central Rocky Mountains, Wyoming, USA, July – Sept., 2014 – 2015. Solid line shows predicted values. Shaded band reflects non-parametric, bootstrapped 95% confidence intervals.

Figure 3. American pika (*Ochotona princeps*) foraging activity in response to mean temperature on the surface of the talus. Activity values are plotted on the log scale to facilitate visualization of 95% confidence limits (dashed lines). The solid line represents predicted values. Data were collected on 57 individuals in the central Rocky Mountains, Wyoming, USA, July – Sept 2014 – 2015.

Figure 4. Individual American pika (*Ochotona princeps*) foraging activity in response to mean temperature on the surface of the talus in the central Rocky Mountains, Wyoming, USA, July – Sept 2014 – 2015. Solid lines represent predicted values for each pika.

Figure 5. Amount of nitrogen cached relative to haypile volume, as a function of foraging plasticity in American pikas (*Ochotona princeps*), in the central Rocky Mountains, Wyoming, USA, July – Sept 2015. The solid line represents predicted values. The dashed lines indicate 95% confidence limits.

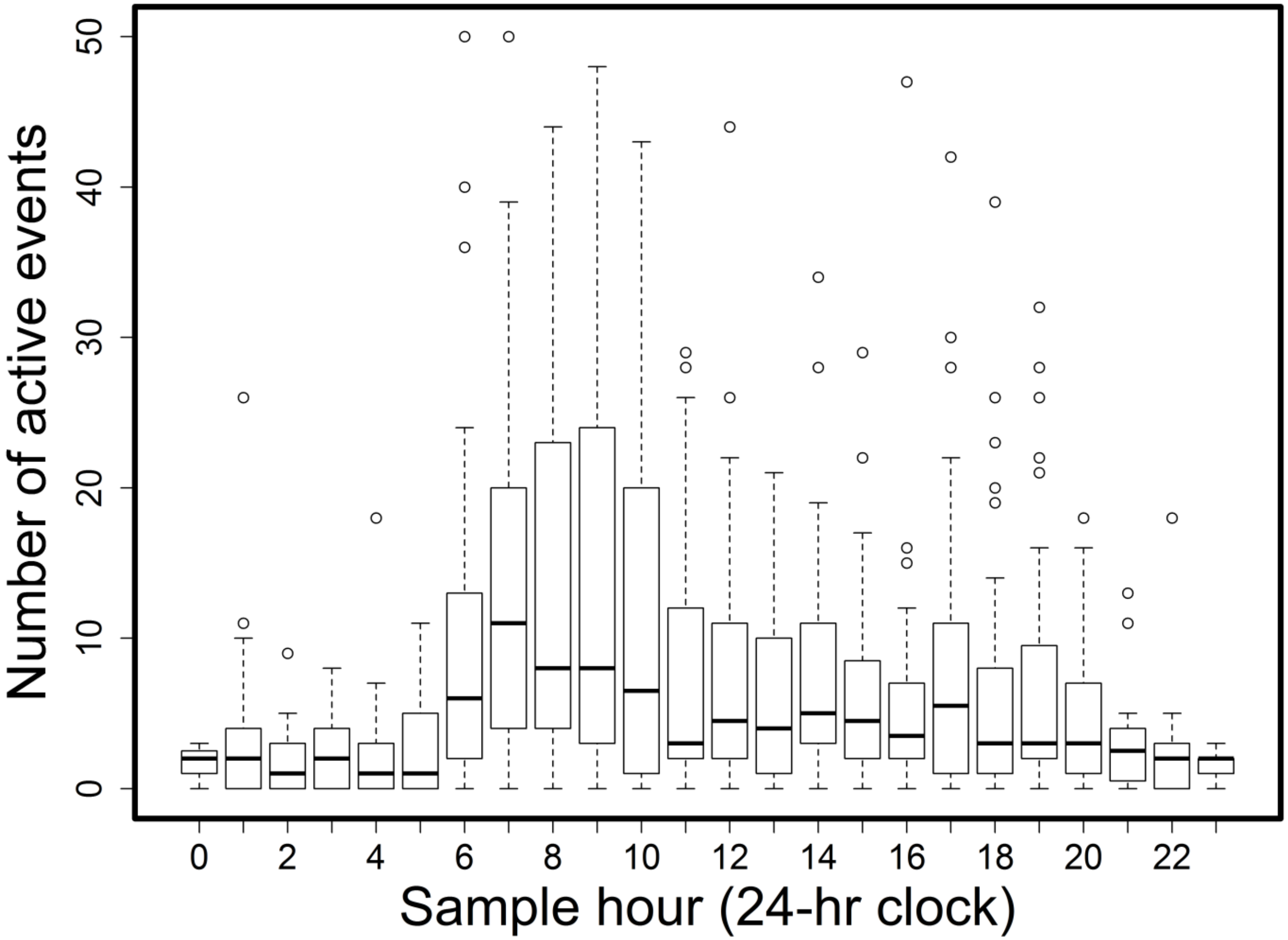
Number of active events
0
10
20
30
40
50
0
2
4
6
8
10
12
14
16
18
20
22
Sample hour (24-hr clock)

Figure 1.

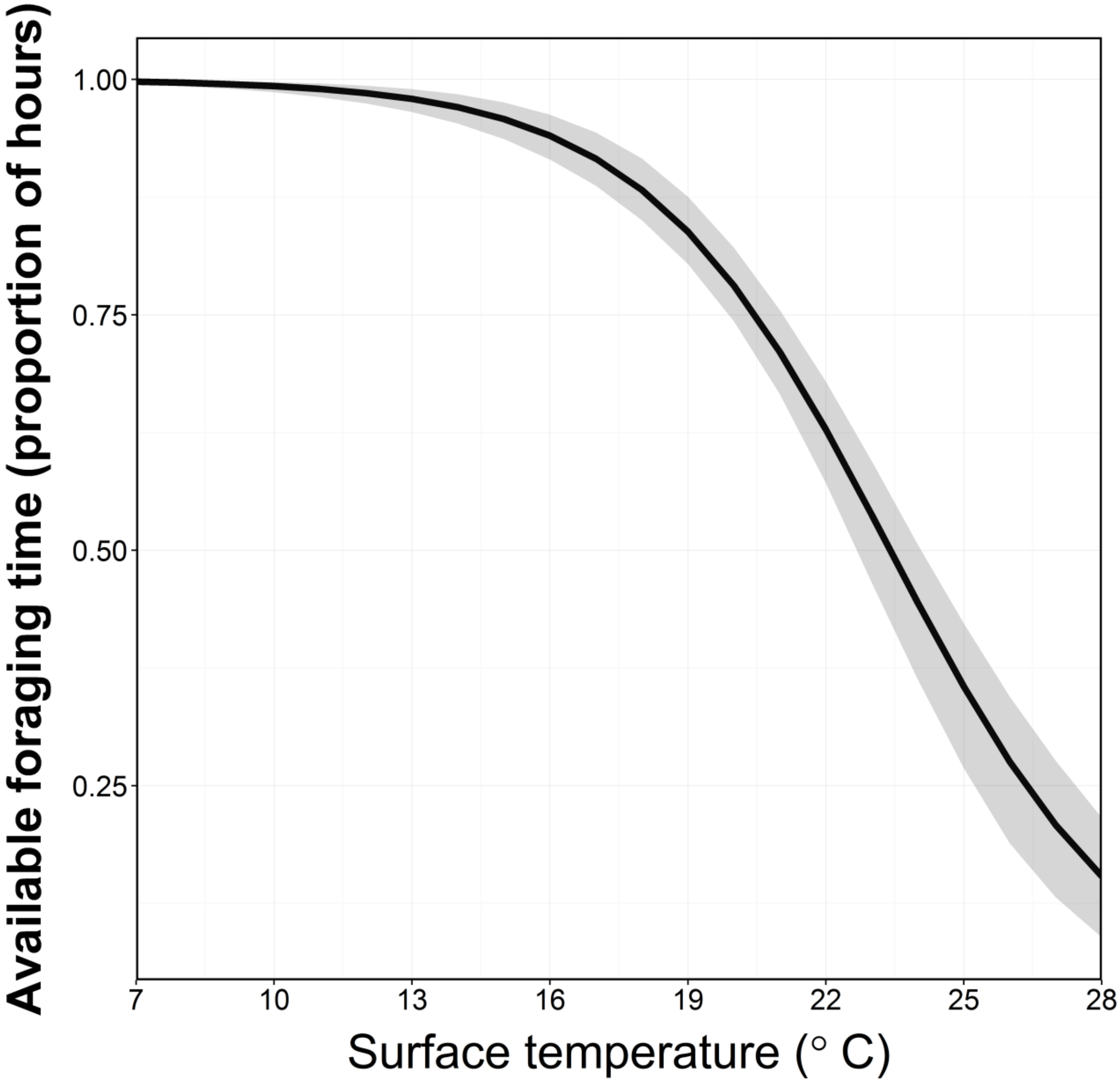
Available foraging time (proportion of hours)
1.00
0.75
0.50
0.25
7
10
13
16
19
22
25
28
Surface temperature (° C)

Figure 2.

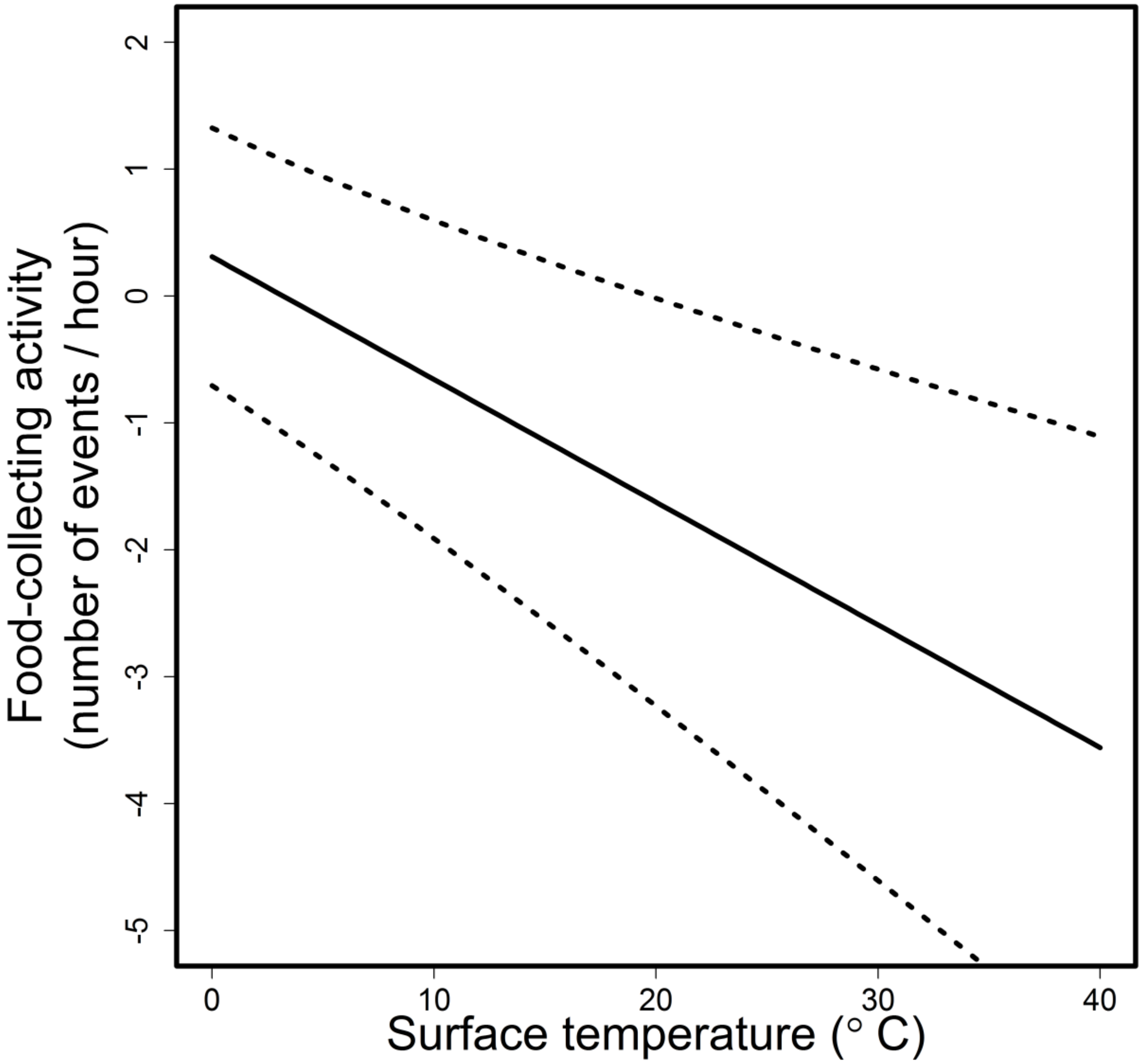
Food-collecting activity
(number of events / hour)
2
1
0
-1
-2
-3
-4
-5
0
10
20
30
40
Surface temperature (° C)

Figure 3.

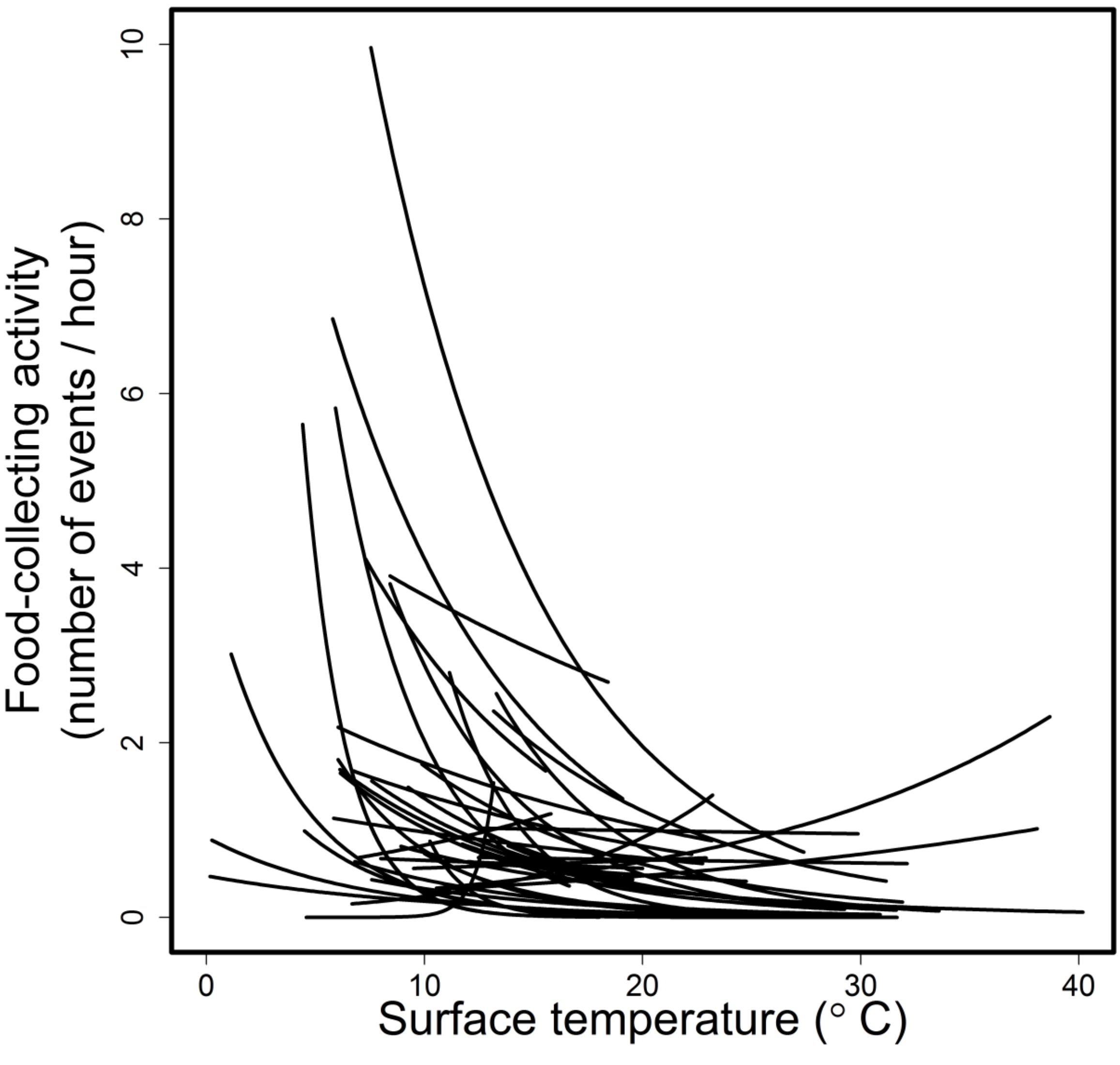
Food-collecting activity
(number of events / hour)
0
2
4
6
8
10
0
10
20
30
40
Surface temperature (° C)

Figure 4.

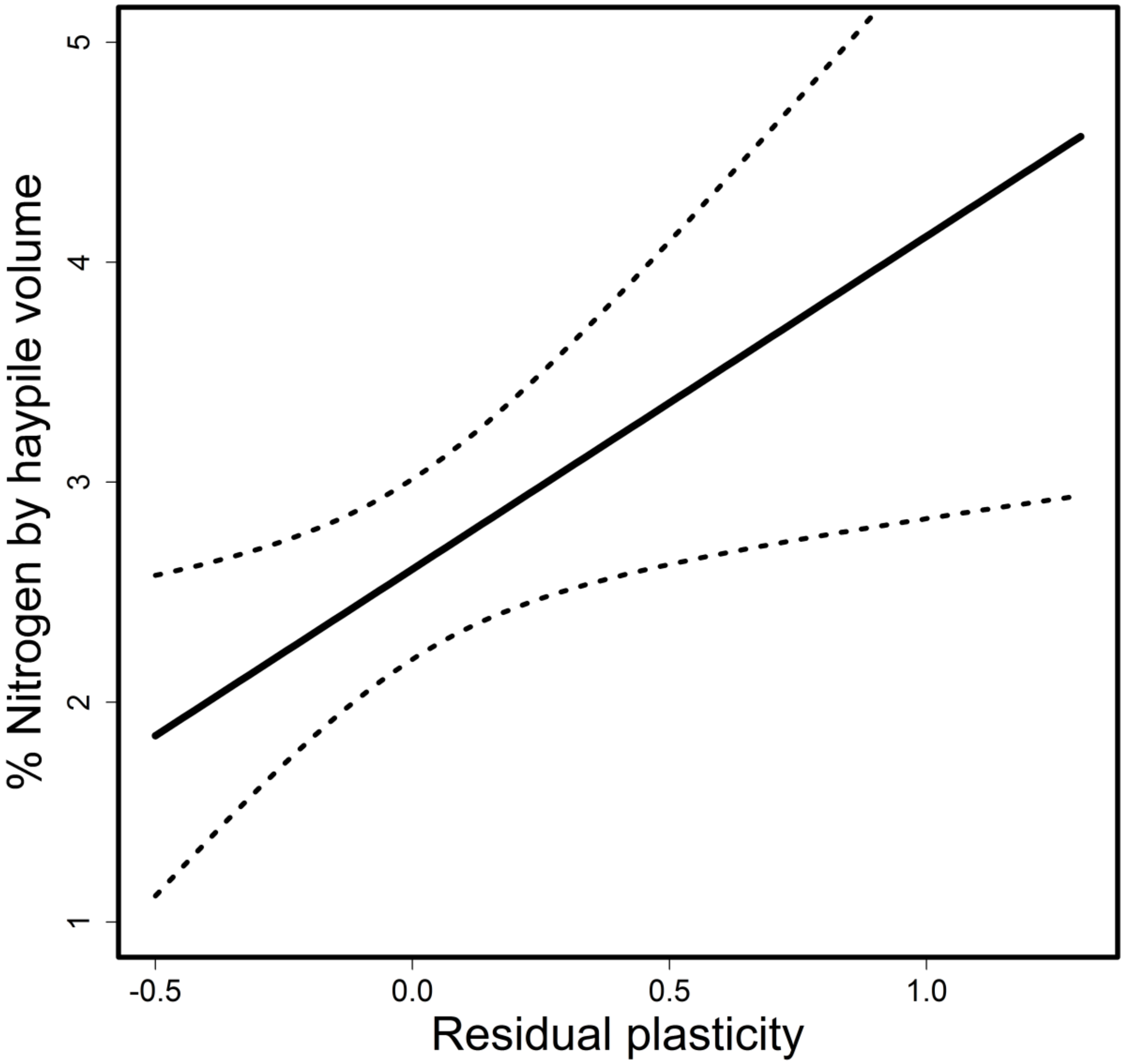
% Nitrogen by haypile volume
1
2
3
4
5
-0.5
0.0
0.5
1.0
Residual plasticity

Figure 5.

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