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

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Abstract

1. Contemporary climate change is altering temperature profiles across the globe. Increasing temperatures can reduce the amount of time during which conditions are suitable for animals to engage in essential activities, such as securing food. Behavioural plasticity, the ability to alter behaviour 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 behaviours, such as food collection, to proximately buffer variation in temperature, however, remains unclear. Even less well understood are the potential performance advantages of flexible strategies among endotherms.

2. We examined the degree to which individuals altered rates of food collection in response to temperature, and two potential benefits, using the American pika (Ochotona princeps), a temperature-sensitive, food-hoarding mammal, as a model.

3. From July–September 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, and the number of events during which pikas were active in temperatures ≥25°C as a measure of potential thermoregulatory stress.

4. 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 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 comparable amount of nitrogen, while simultaneously experiencing fewer occasions in which temperatures eclipsed estimated thermal tolerances.

5. By varying food-collection norms of reaction, individuals were able to plastically respond to temperature-driven reductions in foraging time. Through this increased flexibility, individuals amassed food caches of comparable quality, while minimizing exposure to potentially stressful thermal conditions. Our results suggest that, given sufficient resource quality and availability, plasticity in foraging
activity may help temperature-limited endotherms adjust to climate-related constraints on foraging time.

**KEYWORDS**
adaptive capacity, behavioural flexibility, climate variability, food cache, foraging behaviour, global warming, pika, reaction norm

1 | INTRODUCTION

Endotherms inhabit a wide range of temperature across the globe, from −65°C in the Arctic to 55°C in Death Valley, California (Aguado & Burt, 2004). As such, endothermic animals employ a diverse suite of mechanisms to maintain a relatively constant body temperature ($T_b$). Feldhamer, Drickamer, Verssey, Merritt, & Krajewski, 2007; Boyles, Seebacher, Smit, & McKechnie, 2011). When elevated ambient temperatures ($T_a$) cause $T_b$ to exceed the thermoneutral zone, endotherms can either allow $T_b$ to rise or escalate thermoregulatory effort to maintain $T_b$ within the preferred range (Withers, Cooper, Maloney, Bozinovic, & Ariovaldo, 2016). Both approaches 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 (Withers et al., 2016). Like other heat-sensitive species, cold-adapted endotherms can have reduced capacity to mount a physiological response to increasing $T_a$ (Khalil, Hof, Prinzinger, Böhning-Gaese, & Pfennninger, 2014). Consequently, behavioural thermoregulation, such as avoiding exposure to solar insolation or increasing activity during preferred conditions, may provide an essential mechanism through which thermally sensitive endotherms can persist amidst elevated $T_a$. Yet, the extent of flexibility in behavioural traits that influence thermoregulatory effort, and the corresponding benefits of flexible strategies, remains unclear, especially among wild populations.

Contemporary climate change is altering temperature profiles globally, including increasing mean conditions (IPCC 2013) and changing patterns of temperature variation (Wang & Dillon, 2014). Importantly, these changes are manifesting quickly (Marsicek, Shuman, Bartleina, Shafer, & Brewer, 2018). Predicted rates of temperature change are likely to require rates of climatic-niche evolution that are largely unprecedented (Jezkova & Wiens, 2016; Quintero & Wiens, 2013) for species to keep pace. In addition to ecosystem-level changes, such as shifting community composition (Parmesan, 2006), increasing temperatures can reduce the amount of time during which conditions are suitable for animals to engage in essential activities, including securing food (Whitman et al., 2015). This is especially true in high-latitude and high-elevation ecosystems where climate change has been particularly amplified (Pepin et al., 2015).

Populations that cannot genetically evolve to keep pace with rapidly warming temperatures face increased probability of extinction unless they move to more favourable conditions, or rely on some measure of phenotypic plasticity (Williams, Shoo, Isaac, Hoffmann, & Langham, 2008). Contextual behavioural plasticity describes the ability of an organism to alter behaviour in immediate response to variation in the environment (Snell-Rood, 2013; Stamps, 2016). Like other forms of plasticity, the extent of behavioural plasticity is characterized by reaction norms (Stamps, 2016; Stearns, 1989). Reaction norms are products of the environment, the average level of behaviour exhibited across a range of environmental contexts, and individual responsiveness to environmental variation (Dingemanse, Kazem, Réale, & Wright, 2010; Stearns, 1989). Norms of reaction can vary among individuals and evolve over time (Tuomainen & Candolin, 2011). If an initial response to an environmental change is insufficient, plasticity can be enhanced in the population if there is variation in the magnitude of plasticity (i.e., steeper slope of the reaction norm) upon which selection can act (Murren et al., 2014; Stamps, 2016). If all individuals respond similarly to a change in the environment, however, then the response is fixed and can only be modified through adaptive genetic evolution. This is problematic because the rate of environmental change often can eclipse the rate of genetic evolution among populations (Hoffmann & Sgrò, 2011; Quintero & Wiens, 2013).

Behavioural plasticity may facilitate species persistence amid rapidly increasing $T_a$ because there is a relatively short lag between a change in the environment and expression of a new behavioural phenotype (Tuomainen & Candolin, 2011). Because behavioural plasticity is reversible, moreover, individuals can secure the benefits of a new phenotype without committing to it in the context of an uncertain future (Ghalambor, Hojnowski, Carter, & Brashares, 2007; Van Buskirk, 2012). Behavioural 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 (Løe et al., 2016). Whereas the role of behavioural plasticity in species responses to climate change has gained substantial attention in recent years (Beever et al., 2017; Wong & Candolin, 2015), particularly among ectotherms (sensu Dillon, Wang, & Huey, 2010; Sinervo et al., 2010), the extent to which endotherms in the wild can proximately...
modulate foraging behaviours to buffer variation in temperature remains unclear. Even less well understood are the potential performance advantages of flexible strategies among cold-adapted species, which may be particularly sensitive to increasing $T_r$.

We examined plasticity in food-collection rates and timing in response to a natural gradient of temperature, using the American pika (Ochotona princeps) as a model. An iconic species living on the “front lines” of climate change, pikas are cold-adapted, central-place foragers found primarily in montane ecosystems in western North America (Smith & Weston, 1990, but see Shinderman, 2015; Varner et al., 2016). Pikas have several physiological adaptations that allow them to remain active year-round in high-elevation environments, including dense pelage, low thermal conductance and a basal metabolic rate that is 143% of allometric-model predictions (MacArthur & Wang, 1973). Traits that enhance thermoregulatory capabilities during cold months, however, inhibit heat dissipation in warmer conditions, causing pikas to be sensitive to high $T_r$ (Moyer-Horner, Mathewson, Jones, Kearney, & Porter, 2015). Brief exposures to ambient temperatures $>$25.5–28°C can result in hyperthermia and death, if individuals are unable to behaviourally thermoregulate (MacArthur & 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 (Dearing, 1997). The biomass of overwinter caches (hereafter hay-piles) has been linked to metrics of annual survival (Dearing, 1997; Morrison, Pelchat, Donahue, & Hik, 2009, but see Varner & Dearing, 2014). Several factors influence the plants that pikas select for hay-piles, including a preference for vegetation that is high in nitrogen (N; Smith & Erb, 2013; Hall & Chalfoun, 2018b). N is limiting for most herbivorous mammals, especially small-bodied species that live in low N systems such as alpine environments (Bowman, Murgel, Blett, & Porter, 2012; Parsons, Hellgren, Jorgensen, & Leise, 2005). To minimize thermoregulatory stress when green vegetation is available for harvest, pikas shelter in cool interstitial spaces within their rocky habitats (hereafter talus; Moyer-Horner et al., 2015; Mathewson et al., 2017). Given sensitivity to $T_r$, a limited physiological ability to shed heat, and increased activity during the warmest period of the year, behavioural thermoregulation is essential to pika survival (Moyer-Horner et al., 2015; Smith, 1974). Indeed, because of limited dispersal capability (Henry, Sim, & Russello, 2012), and relatively low fecundity (Smith, 1978), behavioural plasticity may play a key role in determining how the species responds to rapidly changing climate.

To better understand how endotherms alter foraging behaviour in response to temperature, and to evaluate the potential benefits of plasticity in terms of nutritional gain and thermal advantage, we tested whether (a) temperature constrained available foraging time for pikas; (b) there was a population-level change in foraging behaviour in response to temperature; (c) individuals exhibited consistent behavioural differences; (d) individuals responded differently to changing temperature, suggesting variation in behavioural flexibility on which selection could act; and (e) individuals that exhibited greater plasticity secured a nutritional or thermal benefit. We predicted that pikas exposed to higher mean temperatures would experience less time during which conditions were suitable for foraging (Hall & Chalfoun, 2018b; Moyer-Horner et al., 2015). We also predicted that individuals exposed to warmer daytime temperatures would forage more often at night when temperatures were cooler (sensu Dussault, Kazem AJ, & Wright, 2004; Maloney, Moss, Cartmell, & Mitchell, 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 and experience fewer potentially stressful thermal events, 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 norms of reaction with in situ temperature and potential fitness benefits.

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted our work within alpine and subalpine habitats on the Bridger-Teton National Forest in the central Rocky Mountains of western Wyoming, USA. Elevations ranged from 1,713 to 4,211 m. Common tree and shrub species included Douglas fir (Pseudotsuga menziesii), limber pine (Pinus flexilis) and shrubby cinquefoil (Dasiphora fruticosa). Herbaceous vegetation included lupine (Lupinus spp.), yarrow (Achillea millefolium), sulfur-flower buckwheat (Eriogonum umbellatum) and various sedges and grasses (Knight, Jones, Reiners, & Romme, 2014).

2.2 | 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, Chalfoun, Beever, & Loosen, 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 September; 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 centre point of each site. Pikas defend spatially distinct caches, such that a single haypile or cache complex can be matched unambiguously to an individual (Millar & Zwicker, 1972). Search time ranged from 5 to 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. Individuals were sampled once during the study.
2.3 | Behaviour and temperature

We deployed infrared-enabled trail cameras (Bushnell Trophy Camera, model 119435) from late July–early September 2013–2015, to video-record individual pika behaviour at the haypile over a 24-hr 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. One min of video footage (focal observation; Altmann, 1974) was recorded following each motion-activation event (Hall & Chalfoun, 2018b). We coded the pika activity in each video using the software program JWather™ (Blumstein & Evans, 2006). All behaviours were classified as events and were considered mutually exclusive (e.g., haying could not occur simultaneously with haypile maintenance; see definitions below). We doubled-coded 20% of the videos in which pikas were active to evaluate the influence of observer bias (Blumstein & Daniel, 2007). Five behaviours were included in our ethogram of pika haypile activity:

- **Eating from the haypile**: Consuming material (plants, animal matter, moss, etc.) directly from the haypile.
- **Haying**: Carrying plant, faecal or animal material to a haypile (Conner, 1983; 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-hr sample period. The sensors were intended to capture the temperatures that pikas were experiencing on the talus surface, rather than ambient conditions. We wired each logger to the underside of a rock, such that it was not exposed to direct sunlight, and sealed it in a water-tight 5-g jar made of clear plastic (Beever, Ray, Mote, & Wilkening, 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.

2.4 | Cache quality

We assessed the quantity and quality of the haypile by measuring the volume of the pile (m³) and quantifying the N content (%). Cache attributes were assessed immediately following each individual’s behaviour observations. Using a jointed, engineer’s scale ruler (Lufkin, Apex Tool Group), we measured the width, length (orthogonal to width) and height of the pile (m) on the longest axis of each dimension. We included inner-crevice vegetation in our measurements (Dearing, 1997) by extending the 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, Salzer, & Willoughby, 2001) oriented across the widest span of the cache. 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 sample the overall composition of the cache. Every 5 cm along each transect, we recorded the species of the vegetation that touched the bottom of a pin flag. We then collected live samples of all cached plant species in proportion to their abundance (number of times encountered) along the transects (Hall & Chalfoun, 2018b; Jakopak, Hall, & Chalfoun, 2017). Plant samples were harvested from the meadow and talus areas immediately adjacent to the haypile (Huntly, 1987; McIntire & 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, Smith, & Ivins, 1986), were included in the sample.

Each sample was placed in a paper bag and oven-dried at 60°C for 48 hr (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.

2.5 | Statistical analyses

Initial data-exploration steps for all hypotheses included examination of the response-variable distribution (histogram), evaluation of the number and type of zeros (Zuur, Ieno, Walker, & Saveliev, 2009; frequency plot) and assessment of collinearity between predictors (Zuur, Ieno, & Elphick, 2010). Following model fitting, model assumptions were assessed by visually inspecting plots of fitted values against residuals, examining overdispersion and testing for autocorrelation 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 & 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, and by evaluating Akaike’s information criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2002). The model with the lowest AICc value was considered the strongest...
of the candidate suite. Variance values >0.1 further suggested that a random effect was important (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Non-overlapping 95% confidence limits and p-values were used to assess the importance of fixed effects.

2.6 Surface temperature and available foraging time

To confirm that temperature constrained available foraging time for pikas in our system, 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 to 25.5°C; MacArthur & Wang, 1973; Beever et al., 2010). This allowed us to assess the relationship between surface temperature and the amount of foraging time potentially available to each individual. The daytime 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 (GLM) 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.

2.7 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 of 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.

### 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 behavioural plasticity, and the associated benefits. Data were collected from in the central Rocky Mountains, Wyoming, USA, July–September 2014-2015

<table>
<thead>
<tr>
<th>Analysis</th>
<th>Model</th>
<th>Distribution</th>
<th>Response</th>
<th>Fixed effects</th>
<th>Random effects</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature and available foraging time</td>
<td>GLM</td>
<td>Quasibinomial</td>
<td>Proportion of daytime hours within estimated pika thermal tolerance</td>
<td>Mean daytime surface temperature</td>
<td>None</td>
</tr>
<tr>
<td>Nocturnal food-collecting activity in response to temperature</td>
<td>GLM</td>
<td>Negative binomial</td>
<td>Nocturnal food-collecting activity</td>
<td>Mean daytime surface temperature</td>
<td>None</td>
</tr>
<tr>
<td>Population-level activity in response to temperature</td>
<td>Zero-inflated GLMM</td>
<td>Negative binomial</td>
<td>Total activity; Food-collecting activity</td>
<td>Hourly daytime surface temperature (mean centred)</td>
<td>Hourly daytime surface temperature (mean centred; slope); Individual (intercept); Sample h (intercept)</td>
</tr>
<tr>
<td>Individual-level activity in response to temperature (reaction norms)</td>
<td>Zero-inflated GLMM</td>
<td>Negative binomial</td>
<td>Food-collecting activity</td>
<td>Hourly daytime surface temperature (mean centred)</td>
<td>Hourly daytime surface temperature (mean centred; slope); Individual (intercept); Sample h (intercept)</td>
</tr>
<tr>
<td>Benefit of plasticity (% Nitrogen)</td>
<td>GLM</td>
<td>Gamma</td>
<td>% Nitrogen/haypile volume</td>
<td>Plasticity score; Proportion of daytime hours within estimated pika thermal tolerance; Plasticity score * proportion of hours</td>
<td>None</td>
</tr>
<tr>
<td>Benefit of plasticity (thermal stress avoidance)</td>
<td>GLM</td>
<td>Negative binomial</td>
<td>Number of events ≥25°C during which individuals were active</td>
<td>Plasticity score</td>
<td>None</td>
</tr>
</tbody>
</table>

Note. GLM: generalized linear model; GLMM: generalized linear mixed-effects model.
To evaluate the influence of daytime temperature on nocturnal food-collecting activity, we fit a GLM 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, Fournier, Nielsen, Magnusson, & Bolker, 2013). 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 (zero-inflated GLMM; Zuur, Ieno, Walker, & Saveliev, 2009). The negative binomial distribution allowed us to account for overdispersion in our data (Bolker, 2008), while zero-inflation addressed the high proportion of zeros (more zeros than expected, based on our data's dispersion 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, Ieno, Walker, & Saveliev, 2009). We treated mean hourly surface temperature (continuous) as a fixed effect. We centred temperature values on the population mean (i.e., $x_{ij} - \bar{x}_{population}$, where $x_{ij}$ represented the temperature at measurement i for individual j). Since behavioural observations were grouped by individual, and individuals might alter behaviour in response to temperature at different rates, we treated individual (categorical) as a random intercept and surface temperature as a random slope. We expected that behaviour patterns and temperature conditions could vary geographically (e.g., by elevation or drainage), and by sample date. Since individuals at a site were located at a similar elevation and sampled over the same 8-day period, we tested the importance of site (categorical) as a random intercept. Finally, we tested the influence of sample hour (categorical, random intercept) because we anticipated that pika activity might be affected by time-of-day (Table 1). Including sample hour as a random effect also allowed us to examine potential confounding between time-of-day and temperature.

### 2.8 Individual responses to temperature

We used two lines of evidence 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 $>0.1$, and the model with individual fitted as a random effect had a lower AIC$_C$ value than the models without, we assumed that the term for individual explained a meaningful amount of variation, and that intercepts were substantially different (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Assuming that individuals differed, we extracted slope and intercept coefficients associated with the random effect of individual to visualize within-individual variation in plasticity. These estimates, calculated in a random regression framework, accounted for intercept–slope covariance. We also estimated intercept–slope covariance directly to quantify the relationship between activity at the overall mean temperature, and the degree to which activity changed across the temperature gradient (Dingemanse et al., 2010). 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 (random slope coefficient for the effect of temperature). We treated these coefficients as our measure of individual plasticity (hereafter plasticity score).

### 2.9 Benefit of plasticity

We evaluated whether increased plasticity in food-collecting behaviour resulted in a higher quality cache by assessing the % N in each haypile, relative to the volume of the pile (N content per m$^2$). This metric allowed us to account for variation in the amount of vegetation that each individual collected. We fit a generalized linear 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 plasticity score (continuous) as a predictor. The amount of suitable foraging time likely influenced the degree of food-collecting flexibility that each individual displayed. Consequently, we fit an interaction between plasticity score and the proportion of daytime hours in which the mean temperature was within estimated pika thermal tolerances. The gamma distribution allowed us to account for the positive, continuous nature of our response variable (Table 1). Analyses based on best unbiased linear predictors, such as the coefficients associated with random effects, can produce anti-conservative results because the individual plasticity scores were estimated with error that, if not carried forward, can lead to spurious $p$-values (Hadfield, Wilson, Garant, Sheldon, & Kruuk, 2010; Houslay & Wilson, 2017). To address this, we used a two-stage bootstrap (Buckland et al., 2009). First, we generated a random resample (with replacement) of individual activity values and associated temperatures. Using the resample, we then refit our initial model of food-collecting activity and temperature, extracted the associated plasticity scores for each individual and refit the model of plasticity and cache quality. We repeated this process 500 times. We calculated the mean coefficient value for the effect of plasticity, and a corresponding 95% confidence interval based on the bootstrap replicates. This allowed us to incorporate the uncertainty associated with our estimated plasticity scores, thereby minimizing the risk of potential increases in Type I (false positive) error.

Individuals that altered food-collection activity in response to temperature might also have benefited from reduced exposure to extreme temperatures. We tested whether animals that expressed greater plasticity also experienced fewer events in which temperatures reached or exceeded 25°C using a GLM with a negative binomial distribution (R (Zuur, Ieno, Walker, Saveliev, & Smith, 2009).
package glmmADMB). We treated the total number of events ≥25°C in which an individual was active (count) as the response, and plasticity score as the predictor. Similar to our assessment of plasticity and cache quality, we used a two-stage bootstrap with 500 replicates to account for error associated with the estimates of individual plasticity. We report the mean coefficient value for the effect of plasticity, and a corresponding 95% confidence interval based on the bootstrap replicates.

3 | 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 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-hr sample period, with a peak at 0600–1000 hr (Figure 1). Individuals were least active in the late evening through the early morning (2200–0500 hr).

We deployed temperature sensors that were time-synchronized with cameras for 57 of the 72 individuals. Individuals that experienced warmer mean daytime temperatures also had less time during which temperatures were appropriate for food collection (quasibinomial GLM: \( \beta = -0.373, \text{CL} = -0.440, \text{CL} = -0.313, p < 0.001, n = 57 \)).

Pikas decreased total activity (zero-inflated GLMM: \( \beta = -0.072, \text{CL} = -0.108, \text{CL} = -0.037, p < 0.001, n = 1,368 \) (57 individuals × 24 repeated activity measures; Dingemanse & Dochtermann, 2013)), and food-collection activity (zero-inflated GLMM: \( \beta = -0.094, \text{CL} = -0.143, -0.45, p < 0.001, n = 1,368 \); Figure 2; Supporting Information Table S1) with increasing temperature. However, individuals varied substantially in their level of food-collection activity (zero-inflated GLMM: \( \sigma^2_{\text{individual}} = 1.47 \)) and in degree of plasticity in response to temperature (reaction norms; Figure 3). The correlation between individual intercepts

![FIGURE 1](https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.12925)

**FIGURE 1** Number of events in which 72 American pikas (*Ochotona princeps*) were active at haypiles, by hour. Data were collected from the central Rocky Mountains in western Wyoming, USA, July–September 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). Open circles reflect outliers (points >1.5 times the interquartile range above the third quartile).

![FIGURE 2](https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.12925)

**FIGURE 2** American pika (*Ochotona princeps*) foraging activity in response to relative temperature (°C) 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. Temperature is scaled relative to the population mean (15.2°C; \( x_j - \bar{x}_{\text{population}} \)). Data were collected on 57 individuals in the central Rocky Mountains, Wyoming, USA, July–September 2014–2015.

![FIGURE 3](https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.12925)

**FIGURE 3** Individual American pika (*Ochotona princeps*) foraging activity in response to relative mean temperature on the surface of the talus (°C) in the central Rocky Mountains, Wyoming, USA, July–September 2014–2015. Temperature is scaled to the population mean (15.2°C; \( x_j - \bar{x}_{\text{population}} \)). Lines represent predicted values for each of 57 individuals.
The degree to which a cold-adapted mammal can respond plastically to temperature-related constraints on foraging time: (a) whereas nearly all American pikas decreased food-collecting activity with temperature, individual reaction norms varied substantially in both the level of food-collecting activity and in the degree to which individuals shifted activity with warming temperature; and (b) more plastic individuals collected caches of comparable volume and quality to those of less-plastic individuals, suggesting that increased plasticity may provide individuals with a strategy to gather sufficient food resources, while also avoiding thermoregulatory stress associated with high temperatures. 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, simultaneously amass a quality overwinter food resource. Whereas the relationship between temperature, thermal stress and foraging activity has been well studied in ectotherms (Kearney, Shine, & Porter, 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 performance benefits among wild mammals.

Pikas exhibited substantial variation in 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 & Hendry, 2012). Our results suggest that pikas at our sites have maintained 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. Cooler conditions on the surface of the rocks may have been a result of ambient temperature, as well as location-specific habitat characteristics, including shade from adjacent vegetation, aspect (Jeffress, Rodhouse, Ray, Wolff, & Epps, 2013) and proximity to cold-air pools (Millar, Westfall, & Delany, 2014). Regardless of the cooling mechanism, 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 behavioural 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 & Candolin, 2015). Individuals that expressed greater plasticity collected overwinter food caches that had comparable % N, relative to more canalized phenotypes. This is important because N plays an essential role in animal diets (Parsons et al., 2005), and pikas in our system were very likely N-limited (Hall & Chalfoun, 2018b). Haypiles provide a critical, and sometimes exclusive, food source during winter when resources are scarce (Dearing, 1997; Morrison et al., 2009). Consequently, behaviours that facilitate the quality of these stores likely provide a substantial benefit (Vander Wall, 1990). More plastic individuals might have been more selective for plants with high N content or may have traded other dietary components for the maximization of N. Another plausible alternative was that pikas in territories with more nutritious forage were able to be more selective and therefore better able to restrict haying activity during high temperatures. In a post hoc analysis, however, we tested whether the patterns in individual flexibility that we observed were driven by the quality of forage (% N) available to each individual. The nutritional composition of available vegetation was determined from samples collected along two 8-m transects in each focal animal’s territory, immediately following behaviour observations (Hall & Chalfoun, 2018b). Vegetation quality was unrelated to foraging plasticity (GLM: \( \beta = 0.033, CL = -0.150, 0.215 \); weighted \( \beta = 0.069, CL = -0.054, 0.193 \)), suggesting that the extent of individual flexibility that we observed was not simply due to variation in available vegetation. Additionally, equivalent cache quality between more and less-plastic individuals was not an artefact of the amount of vegetation that each individual collected. Our metric of haypile quality (% N per m\(^2\) of vegetation) standardized % N by the volume of the cache.

Individuals that expressed greater plasticity in food-collecting activity also experienced fewer occasions in which temperatures exceeded thermal tolerances. Avoidance of high-temperature events may be important to minimizing individual physiological stress (MacArthur & Wang, 1973; Wilkening, Ray, & Varner, 2015), which can have substantial impacts on fitness (Sheriff, Krebs, & Boonstra, 2009). Given that relatively brief exposure to temperatures >25.5°C can be lethal among some populations of pikas (MacArthur & Wang, 1973; Smith, 1974), modulating exposure to extreme events may be critical to individual survival. Taken together, our findings point towards increased plasticity as an alternative behavioural strategy that produces comparable overwinter stores, while simultaneously reducing exposure to potentially stressful environmental conditions.

Our measure of % N stockpiled by each individual could have been influenced by cache layering if the transects for a given haypile happened to correspond with layers of particular plant functional groups (Jakopak et al., 2017). We doubt, however, that this would have introduced a consistent bias in our results, as we would have had an equal chance of sampling layers of high N foods (e.g., forbs) or low N foods (e.g., grasses), regardless of the plasticity that an individual expressed.

The relative benefit of plasticity is shaped by the cost of maintaining the mechanisms that underlie plastic traits (DeWitt, Sih, & Wilson, 1998), such as sensory machinery, regulatory pathways and information acquisition processes (Schlichting & Pigliucci, 1998), and was beyond the scope of this study. Behavioural plasticity is costly when (a) plastic individuals cannot produce a mean trait value as near to the phenotypic optimum as canalized individuals and/or; (b) plastic individuals incur lower fitness when producing the same mean trait value as non-plastic individuals (DeWitt et al., 1998; Van Buskirk, 2012). In the case of pikas, if the costs of maintaining plastic foraging behaviours exceed the benefit, or if the benefit does not translate to enhanced fitness, food-collecting reaction norms may become canalized over time.

Similar to several species of grassland and shrubland herbivores (Belovsky & Slade, 1986; Maloney et al., 2005), alpine ibex (Capra ibex; Aublet, Festa-Bianchet, Bergero, & Bassano, 2009) and Otididae birds (e.g., great bustard, Otis tarda; Alonso, Salgado, & Palacin, 2016), American 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 hr). These findings are consistent with other studies that documented increased pika activity in cool ambient temperatures (Moyer-Horner et al., 2015; Smith, 1974). Much of an endotherm’s ability to deal with high heat loads depends on capacity for evaporative heat loss (Rezende & Bacigalupo, 2015). If individuals consume food with high water content, this could facilitate enhanced cooling, thereby allowing them to be more active in warm temperatures. Consequently, variation in water availability might either facilitate or limit behavioural flexibility in endotherms that experience sustained periods of otherwise intolerable conditions.

Pikas were also active at night, albeit at lower levels than during the day. Due to the infrared 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, nighttime activity may be constrained by increased predation risk (Maor, Dayan, Ferguson-Gow, & Jones, 2017) and/or other factors (Gaynor, Hojnowski, Carter, & Brashares, 2018). 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, Westfall, & Delany, 2016). Individuals that collect food at night, therefore, may be more likely to experience temperatures that are below thermoneutrality (Otto, Wilson, & Beever, 2015), which would necessitate increased energy expenditure on $T_b$ regulation. The extent to which populations can temporarily expand their activity periods will likely be influenced by both predation and thermoregulatory risk. Research on the limits of nocturnal activity in diurnal, heat-sensitive animals offers a potentially fruitful area for additional work.

Plasticity in foraging activity may allow temperature-limited endotherms to adjust to climate-related limitations on foraging time, thereby enhancing capacity to adapt to climate change (Beever et al., 2016; Staudinger et al., 2013). The efficacy of performance benefits, such as nutritional gain, combined with the relative costs of maintaining flexible norms of reaction (Van Buskirk & Steiner, 2009) will determine the extent to which plasticity can facilitate persistence amidst warming temperatures. While variation in the magnitude of plasticity, and the corresponding benefits that we document, may suggest a hopeful future for pika and other cold-adapted vertebrates, behavioural plasticity likely offers an incomplete solution to the challenges of climate change. Increased foraging activity during favourable thermal conditions 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) and avoiding predators. Once ambient temperatures exceed the level at which endotherms can dissipate excess heat loads physiological stress from increased temperatures would likely override the benefits of plasticity. In this case, no amount of behavioural flexibility will facilitate persistence, at least not without concomitant microevolution in thermal tolerance (Buckley, Ehrenberger, & Angilletta, 2015; Huey et al., 2012).

As climate change continues to affect ecosystems across the globe, cold-adapted endotherms may be faced with increasingly unfavourable 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 behaviours, and the extent to which flexible strategies influence survival and reproduction.

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**AUTHORS’ CONTRIBUTIONS**

L.E.H. and A.D.C. formulated the idea, developed the hypotheses and designed the study. L.E.H. collected the data, completed the analyses and drafted the manuscript. A.D.C. provided critical feedback on manuscript drafts, and essential intellectual input throughout the entirety of the study.

**DATA ACCESSIBILITY**

Data supporting the results are archived in the University of Wyoming Research Data Repository: https://doi.org/10.15786/txtc-0835 (Hall & Chalfoun, 2018a).

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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