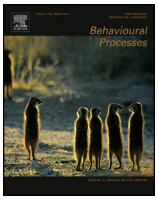
Behavioural Processes 125 (2016) 63–71

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Plastic pikas: Behavioural flexibility in low-elevation pikas (*Ochotona princeps*)

Johanna Varner[a,d,*], Joshua J. Horns[a], Mallory S. Lambert[a], Elizabeth Westberg[a], James S. Ruff[a], Katelyn Wolfenberger[a], Erik A. Beever[b,c], M. Denise Dearing[a]

[a] *University of Utah, Department of Biology, Salt Lake City, UT, USA*
[b] *U.S. Geological Survey, Northern Rocky Mountain Science Center, Bozeman, MT, USA*
[c] *Montana State University, Department of Ecology, Bozeman, MT, USA*
[d] *Colorado Mesa University, Department of Biology, Grand Junction, CO, USA*

ARTICLE INFO

Article history:
Received 11 January 2016
Accepted 25 January 2016
Available online 3 February 2016

Keywords:
Behavioural plasticity
Caching
Foraging
Home range
Ochotona
Pika
Talus
Thermoregulation

ABSTRACT

Behaviour is an important mechanism for accommodating rapid environmental changes. Understanding a species' capacity for behavioural plasticity is therefore a key, but understudied, aspect of developing tractable conservation and management plans under climate-change scenarios. Here, we quantified behavioural differences between American pikas (*Ochotona princeps*) living in an atypical, low-elevation habitat versus those living in a more-typical, alpine habitat. With respect to foraging strategy, low-elevation pikas spent more time consuming vegetation and less time caching food for winter, compared to high-elevation pikas. Low-elevation pikas were also far more likely to be detected in forested microhabitats off the talus than their high-elevation counterparts at midday. Finally, pikas living in the atypical habitat had smaller home range sizes compared to those in typical habitat or any previously published home ranges for this species. Our findings indicate that behavioural plasticity likely allows pikas to accommodate atypical conditions in this low-elevation habitat, and that they may rely on critical habitat factors such as suitable microclimate refugia to behaviourally thermoregulate. Together, these results suggest that behavioural adjustments are one important mechanism by which pikas can persist outside of their previously appreciated dietary and thermal niches.

1. Introduction

Globally, climate change is occurring at an ever-accelerating rate and has already caused changes in population dynamics (Boggs and Inouye, 2012; Kausrud et al., 2008; Townsend et al., in press), distribution and range shifts (Chen et al., 2011; Hannah et al., 2005; Lawler et al., 2009; Moritz et al., 2008), and localized extinctions of many species (Cahill et al., 2013; Prost et al., 2013; Urban et al., 2012; Williams et al., 2007). One rapid mechanism by which individuals of a species can respond to changes in climate is through behavioural plasticity (Muñoz et al., 2015; Sih et al., 2012; Snell-Rood, 2013). Indeed, an organism's capacity for plasticity is a key component of adaptive capacity, or the ability of a species or population to cope with climatic changes (Beever et al., in press; Nicotra et al., 2015). Behavioural changes operate on a much faster time scale than distributional or range shifts, particularly for species with low vagility (Huey et al., 2012). Many behavioural responses have already been documented in response to changing environmental conditions (Tuomainen and Candolin, 2011), including shifts in phenology (Visser and Both, 2005; Walther et al., 2002), reproduction (Blaustein et al., 2012; Lane et al., 2011), and use of food resources (Dawson et al., 2011). In addition, many species can tolerate changes in temperature or precipitation patterns by selecting microhabitats that moderate extreme climates and/or restricting activity to favourable time periods (e.g. Murray and Smith, 2012; Sinervo et al., 2010).

The American pika (*Ochotona princeps*) is a small mammalian herbivore that is largely a habitat specialist in high-elevation talus (rock slides and boulder fields) across western North America. Pikas are an ideal species for investigating behavioural plasticity for several reasons. First, they are diurnal and easily observed when active on the surface (Beever et al., 2008). They also exhibit a range of thermoregulatory and foraging behaviours that vary among habitats (Smith, 1974). Since they do not hibernate, pikas spend the short alpine growing season collecting and storing vegetation in

---

* Corresponding author. Current address: Colorado Mesa University, Department of Biology, 1100 North Ave, Grand Junction, CO 81501, USA. Fax: +1 970 248 1700.
E-mail address: jvarner@coloradomesa.edu (J. Varner).

http://dx.doi.org/10.1016/j.beproc.2016.01.009
0376-6357/

food caches called haypiles, which sustain them over the winter (Dearing, 1997). In this study, we use the term "plasticity" in the sense of "developmental behavioural plasticity", defined by Snell-Rood (2013) as the ability of a population to adopt different behaviours in different environments (as opposed to "activational plasticity," or the ability of an individual to express different behavioural syndromes throughout its lifetime; Snell-Rood, 2013).

Although pika distribution has waxed and waned in concert with glacial-interglacial cycles (Grayson, 2005), more-rapid distributional declines associated with contemporary climate change have occurred in many parts of the species' range (Beever et al., 2013, 2011; Stewart et al., 2015). This species tends to be found in alpine habitats with short, cool summers and long winters with extended snowpack (Hafner, 1993), and it is thought that warmer summer temperatures may preclude foraging, resulting in low-quality food caches for winter (Ray et al., 2009). Furthermore, reduced snowpack observed across western North America (Mote et al., 2005) may expose the animals to more extreme winter temperatures (Beever et al., 2010; Smith, 1978). However, the relationship between climate and pika distributions appears complex. For example, certain aspects of climate (e.g. temperature, precipitation, humidity, etc.) may not constrain the species in the same way across its entire geographic range (Jeffress et al., 2013). Furthermore, the persistence of many low-elevation populations in anthropogenic or seemingly marginal habitats (e.g. Beever et al., 2008; Manning and Hagar, 2011; Millar et al., 2013; Rodhouse et al., 2010; Shinderman, 2015; Simpson, 2009) suggests that pikas may possess more plastic behaviours than is commonly thought. These populations may also be behaviourally capitalizing on favourable microclimates found in otherwise unfavourable thermal landscapes.

Although pikas are known to exhibit a range of behaviours that vary across habitat types (e.g. Smith, 1974), their capacity for behavioural plasticity in the context of warmer climates is still not well understood. For example, pikas may be able to mitigate the effects of warmer summer temperatures by restricting their surface activity to times of day when ambient temperatures are tolerable and by spending the hottest parts of the day in the cooler talus microclimates (Bhattacharyya et al., 2014; MacArthur and Wang, 1973, 1974; Smith, 1974). However, this restriction could also constrain essential activities, such as reproduction (Sinervo et al., 2010) or foraging (Ray et al., 2009), and therefore be of limited advantage. Furthermore, some aspects of climate change could simply become so extreme that they cannot be accommodated by behavioural shifts alone, particularly if the thermal buffering capacity of the talus refuge is reduced (Nicotra et al., 2015).

In many cases, studying behavioural plasticity in a marginal habitat can provide information about habitat features that are crucial for persistence under unfavourable conditions (Ashcroft, 2010; Keppel and Wardell-Johnson, 2012). Similarly, marginal habitats may also elucidate a species' capacity for plasticity in response to environmental stressors (Channell and Lomolino, 2000), which may become more frequent in the future under continued climate change. The Columbia River Gorge (CRG) in Oregon, USA, provides an excellent opportunity for investigating the behavioural plasticity of this species in response to both atypical resource availability and climate. The ca. 50-km stretch of the CRG in which pikas are distributed is generally characterized by dense Douglas fir (*Pseudotsuga menziesii*) forest, and talus patches in this region are often covered in a thick carpet of moss. Furthermore, the CRG exhibits steep gradients in ambient temperature, relative humidity, precipitation and insolation; thus, a range of environmental conditions can be sampled within a relatively small area, especially compared with the species' geographic range.

The CRG also represents the lowest elevations at which American pikas have been detected (Horsfall, 1925; E. Beever, unpubl. data.), and the species persists here in a climate that appears to be unsuitable, based on the species' previously described thermal niche (Simpson, 2009). However, the microclimates in this habitat are highly spatially heterogeneous, in part because the moss cover insulates the talus interstices from temperature fluctuations at the surface (Varner and Dearing, 2014b). Specifically, temperatures measured within a few meters of each other in talus interstices may differ by 3–5 °C, providing pikas with a unique opportunity to adjust their thermoregulation. This region also contains vegetation resources that are unusual for this species, and pikas in this habitat demonstrate plasticity in their diet by facultatively specializing on the abundantly available mosses (Varner and Dearing, 2014a).

In this study, we observed the foraging, thermoregulatory and territorial behaviours of pikas living in the atypical, low-elevation habitats of the CRG. We then compared these behaviours to those of pikas living in high-elevation habitat on nearby Mt. Hood. Because food resources (e.g. mosses, evergreen shrubs, and ferns) are available year-round at low elevations, we hypothesized that pikas at low elevations would be under less pressure to cache food for winter and would instead spend more time in summer grazing (i.e. actively consuming vegetation).

We also sought to document microhabitat selection at high versus low elevations. First, we systematically investigated the use of off-talus forest microhabitats as a potential midday thermal refuge. We hypothesized that, due to higher ambient temperatures at low elevations, pikas in the CRG would use these refuges at a higher rate, particularly at sites of low moss cover. We also measured the sizes of home ranges in the CRG and Mt. Hood as indicators of space use. We hypothesized that, due to increased resource availability at low elevations, CRG pikas would have smaller home ranges and reduced territorial behaviour, compared to high-elevation pikas. Understanding whether behavioural modifications are present in a highly atypical habitat may provide critical information about a species' capacity for behavioural plasticity in tolerating new environmental conditions and, by extension, its capacity to tolerate future changes (Beever et al., in press; Nicotra et al., 2015).

2. Methods

2.1. Study area and sites

Behavioural observations were conducted at six, north- to northwest-facing talus patches (i.e. "sites"). Each site was nested within a "region": either the low-elevation CRG ($N=4$ sites, 194–437 m elevation) or high-elevation Mt. Hood ($N=2$ sites, 905 and 1682 m elevation).

Sites in the CRG were ca. 15 000 m^2 each, 32–35° in slope angle, and surrounded by a dense forest dominated by Douglas fir, western redcedar (*Thuja plicata*), and bigleaf maple (*Acer macrophyllum*). One of the notable features of talus in this region is a thick layer of mosses that covers the surface of each rockslide (Varner and Dearing, 2014a,b). Low-elevation sites varied in moss cover from over 65% ("high moss cover": sites 1 & 2) to less than 30% ("low moss cover": sites 3 & 4); however, forb and grass communities were similar among sites. The average pairwise distance between sites in the CRG was mean ± SD = 17.7 ± 16.6 km (range: 0.64–35.9 km), as measured by the Path Ruler tool in Google Earth. This tool takes into account the contours of the landscape, thereby providing a more biologically meaningful assessment of distance between sites. Importantly, each of these sites is approximately 1000 m lower in elevation than pikas are predicted to occur at this latitude and longitude (Hafner, 1993), based on their previously described bioclimatic envelope (Simpson, 2009).

For comparison with more typical, high-elevation habitat, we also conducted behavioural surveys at two sites (sites 5 and 6) on