POPULATION ECOLOGY OF THE AMERICAN PIKA (*OCHOTONA PRINCEPS*) IN AN EXTREME ENVIRONMENT

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ABSTRACT

Alteration of native habitat through human disturbance is generally implicated as the predominant cause of decline in terrestrial biodiversity. Anthropogenic forces destablilize critical processes such as reproductive success and dispersal of individuals; how species will respond depends to a large extent on the plasticity of habitat use. In this vein, habitat specialists may provide valuable opportunities to understand how colonization succeeds (or fails) in novel environments. The American pika (*Ochotona princeps*) is such a habitat specialist, occupying montane regions in western North America. This species is recognized as vulnerable to anthropogenic impacts (e.g. climate change) due to intrinsic characteristics (e.g. low thermal tolerance, low dispersal capability) that make it susceptible to local extirpations. In the southern interior of British Columbia, in a region that features extreme temperature shifts, I compared a population of pikas inhabiting a partially reclaimed mine site, with those found close by in natural habitat. All told, I monitored a total of 174 pikas from 2012-2014 to compare survival, physical characteristics, dispersal and den site attributes. Through mark-recapture and radio-telemetry, I found comparable survival and dispersal rates of pikas and almost no detectable physical differences. Investigation of under-talus temperatures of den sites revealed that microhabitats within the rocks largely were decoupled from the regional macroclimate, providing evidence of microrefugia as a functional buffer against macroscale climate impacts. Rock size of $1m^3$ and cryptogamic cover on talus near den entrances were positively influential to pika survival, whereas winter temperatures < -10°C under the talus negatively impacted survival. This study provides a relatively parsimonious explanation of pika persistence in atypical environments; within an extreme thermal environment such as in my study region, pikas appear capable of utilizing portions of anthropogenic habitat via microrefugia, although future longevity in a changing climate remains unknown.

Keywords: American pika, *Ochotona princeps*, microrefugia, anthropogenic impacts, talus, microhabitat, British Columbia, climate-sensitive species.

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CHAPTER 1

THE ECOLOGICAL NICHE OF A CLIMATE-SENSITIVE SPECIES

INTRODUCTION

Grinnell (1917) first conceptualized the boundary of a species' ecological niche, defining it as the environmental threshold that constrains the ranges of organisms according to physiological and psychological characteristics. Complex interactions at various spatial scales occur between individual organisms and their biotic and abiotic environment (Soberon 2007; Polechova and Storch 2008); the niche encompasses not only where an individual is situated within the ecosystem, but also the range of conditions necessary for survival, reproduction, dispersal and ultimately, the persistence of the species (Hutchinson 1957; Morrison et al. 2006). The idea that these factors delineate locations where a species is viable remains the primary explanation for range boundaries (Angert 2009).

Studies investigating anthropogenic disturbances and range limits have led to an improved understanding of the factors that limit an individual's niche, and therefore, a species' range (Ray et al. 2016). Individuals can utilize habitat in unique ways to counter marginal conditions, producing dispersers able to cope with atypical environments (Rodhouse et al. 2010) that ultimately increase adaptive plasticity in populations (Levins 1968). For example, Ishida et al. (2016) compared Namibia desert elephants (*Loxodonta africana*) to their savanna counterparts and found that migrations of the desert animals appeared to have increased, decreased, or changed in direction in response to climatic factors, hunting and poaching. Although desert elephants are genetically similar to savanna elephants, they exhibit marked learned behaviour and phenotypic plasticity that has contributed to their survival in atypical habitat (Ishida et al. 2016).

Species distributions modelled at the macroscale may accurately forecast occurrences of widespread species. However, predictive species-range models may be incorrect in assuming eventual extinction of all individuals inhabiting seemingly 'inhospitable' areas on the landscape. Microclimatic diversity within a landscape can increase the capacity of locations to function as diversity reservoirs. Models predicting range shifts of species have more recently included the concept of "microrefugia", as applied to populations surviving in unusual microclimates within the broader landscape (Rull 2009). The concept of microrefugia lends a more parsimonious explanation of discrepancies between observed and predicted population occurrences (Mosblech et al. 2011). Through the interaction of geographic, topographic, climatic and biological processes at a microscale, microrefugia in peripheral locations may provide conditions comparable to conditions experienced near the center of the species' geographic range (Varner and Dearing 2014*a*; Ray et al. 2016).

On a microscale, the heterogeneity of habitat characteristics dictates small mammal distributions within macrohabitats (Bellows et al. 2001). Smaller species experience finer spatial processes (Hannah et al. 2014): dispersal capabilities of small mammals may be limited as compared to large, mobile mammals, and habitat disturbances or changing climate may occur much more quickly than the rate at which smaller species can adapt or disperse. Pockets of microrefugia that offer suitable microclimates can influence the development of unique attributes within smaller species, thereby garnering unique responses within smaller species to anthropogenic pressures that increase the capacity for range expansion and thereby decrease the likelihood of extinction (Randin et al. 2009).

Investigating microclimatic environments that are niche-specific to organisms, at finer scales and longer time periods, will be crucial to determine how small mammal species will persist *in situ* throughout stochastic disturbances, anthropogenic impacts and macro-scale changing climate patterns (Varner et al. 2014). Smith et al. (2014) investigated the paleo middens of two closely related species, the desert woodrat (*Neotoma lepida)* and the bushy-tailed woodrat (*Neotoma cinerea)* within a transition zone in Death Valley, California, and uncovered fundamental differences in the adaptive response of these two species in relation to the elevation of the site and local microclimate. As climate and habitat shifted during the late Quaternary, bushy-tailed woodrats were driven to extirpation due to their thermal constraints, along with juniper (*Juniperus sp.)*, which served as both a food source as well as an indicator of the cooler and more mesic microclimate in which this species thrives. Pruitt (1953) studied the northern short-tailed shrew (*Blarina brevicauda*), and found that this species was constrained within its niche space by microclimatic parameters: high humidity was amongst the significant predictors of shrew occupancy. Research conducted by Drickamer and Capone (1977) investigated two sympatric mouse specie: deer mice (*P. maniculatus*) and white-footed mice *(P. leucopus).* Niche separation was indicated between these two *Peromyscus* taxa based on their differential activity levels in relation to microclimatic parameters: the latter was active during warmer temperatures, higher relative humidity, and light precipitation at night. Conversely, deer mice were active under conditions at lower temperatures, lower relative humidity, and in the absence of night- time precipitation.

Microclimatic variation in montane regions results from the influence of interacting geomorphologic characteristics, including cold-air pooling and differential wind exposure (Gentili et al. 2015). Pikas [Order *Lagomorpha* (Brandt 1855), family *Ochotonidae* -Link 1797] are small, montane mammals that may utilize such microclimates within pockets of refugia. There are two distinct ecological niches occupied by different pika species: rocky terrain (talus and lava flows) or burrows in open habitats (meadows and steppe habitat) (Smith 2008). Despite differences in some life history aspects (e.g. reproductive strategies), pika species are considered vulnerable based on shared physiological characteristics: high thermal sensitivity, low vagility, and stochastic metapopulation dynamics (Ge et al. 2013; Smith 2008). For this reason, pikas are believed to be particularly susceptible to anthropogenic impacts and climate change. Currently, the extant ochotonids are represented by only a single genus (*Ochotona*) containing 28 species. Globally, four species are classified as endangered or critically endangered, with climate change implicated as the primary driver of extirpation (Smith and Beever 2016).

The collared pika (*Ochotona collaris*) and the American pika (*Ochotona princeps*) are the sole ochotonids that occupy North America, and both species are rock-dwelling. The collared pika inhabits the tip of northern British Columbia, the Yukon, and western parts of Alaska, whereas the American pika inhabits a range from New Mexico and California up through to central British Columbia (Smith and Weston 1990). The rocky talus matrices in which these pika species dwell likely provide thermal microrefuges that are integral to pika survival. The identification of suitable pika microrefugia is difficult without using biologically relevant finer scales and observations that are specific to the physiological requirements of this organism (Rodhouse et al. 2017). In this vein, a habitat specialist such as the pika affords an excellent opportunity to study the role of microrefugia in determining habitat suitability across a larger-scale landscape.

In this thesis I investigate a population of American pikas occupying atypical, anthropogenic habitat in the hot, dry southern interior British Columbia. My overarching goal was to understand how the ecology of these animals resembled or differed from that of allopatric conspecifics, including the role of microhabitat features. In the remainder of this chapter, I continue to set the backdrop for this work by summarizing what is known about the niche, ecology and physiological constraints of the American pika. I then present details on the study site and climate of the region. In Chapter 2, I focus on the demographics of pikas within my study, principally comparing survival and population viability between the two categories of animals (anthropogenic versus natural habitats). I also provide data collected through radio-telemetry that helps to better understand mortality and dispersal in these animals. In Chapter 3, I look more specifically at habitat features and the pika niche to determine if there were particular aspects of individual den sites that affected the survival of individuals. Chapter 4 briefly summarizes the overall results of my thesis and fits my data into the body of literature focusing on pikas living in atypical habitat. As well, Chapter 4 outlines potential future research priorities and reclamation initiatives on disturbed habitat that can contribute to our understanding and conservation of the American pika.

Study Species

The American pika (Figure 1.1) is a small (150-190 g), diurnal, solitary, territorial herbivore that is thermally sensitive (Smith 1974a) due to a high metabolic rate, low thermal conductance and a low ability to dissipate heat (MacArthur and Wang 1973). Further, pika populations are characterized by low density, low dispersal capability and a low rate of reproduction (Smith et al. 2016). The American pika has twice been nominated for endangered status in the USA, as previous research has suggested that this species is particularly susceptible to a changing climate (e.g., Smith and Beever 2016). In particular. American pikas have elevated body temperatures ($\bar{x}$ = 40.1°C). The combination of these

Figure 1.1. American pika perched in vigilance. Photo by author.

characteristics have contributed to an increase in vulnerability to extirpation of this species as global warming occurs (Smith et al. 2016).

The American pika niche is typically associated with talus slopes in cooler, high-elevation ecosystems, namely alpine to subalpine rocky talus in western North America (Figure 1.2). Open meadows that lie adjacent to rocky talus habitat support a wide variety of vegetation that provides forage (Smith 1974b). Harvested, stored vegetation known as "haypiles" are constructed from mid-July to approximately mid-October (Smith and Ivins 1983); as pikas do not hibernate, these caches of vegetation serve as food sources for pikas during the late fall/winter/early spring months (Tapper 1973 - see Figure 1.3).

American pikas conceive litters before snowmelt, and timing of parturition coincides with the onset of vegetative growth (Smith 1980). Extreme weather conditions (late spring storms, accumulation of snow), lack of nutrition, or poor maternal physiological condition likely affect weaning success (Smith 1980). Juveniles reach adult weight within three months of birth and establish their own territories by fall (inclusive of haying for overwintering). Pikas can initiate two litters per season, but litters can be lost or resorbed, and generally a second litter only is successful should the first fail. Litter size does not vary with age of the female, with most litters commonly 2-3 kits (Smith 1980). Gestation is approximately 30 days and young emerge above ground at approximately 5 weeks of age (Smith 1974a). American pikas are highly territorial and once settled, they rarely disperse (Barash 1973). Juveniles are philopatric, and on average disperse approximately 50 m from the natal den (Smith and Ivins 1983). Generally, death of an adult results in a juvenile of the same sex taking over a territory (Smith 1974b).

The American pika has garnered much attention in terms of anthropogenic disturbance (e.g. Smith and Millar 2018) and have long been regarded as the indicator species for climate change (Beever et al 2003). Pika metapopulations are at least partially constrained by extinction and recolonization rates, as well as the ability of individual pikas to disperse (Smith and Nagy 2015). Recently, historical American pika populations have been labeled as extirpated from several mountain ranges in the Great Basin and Sierra Nevada of the

Figure 1.2. IUCN map of the American pika range in North America. The red dot indicates the location of this study, just outside of the previously documented interior British Columbian range for this species. Map modified from Smith and Beever (2016). (https://www.iucnredlist.org/species/geographic-range)

Figure 1.3. Top photo: American pika carrying vegetation into haypile. Bottom photo: Pika in haypile of *Equisetum* sp. Photos retrieved from Reconyx™ wildlife cameras (used for this study).

western United States, and anthropogenic pressures such as climate change have been implicated in the decline of these populations (Beever et al. 2003; Moritz et al. 2008).

Warming temperatures may perhaps become the most crucial factor affecting the viability of pika populations, when less mobile montane species are expected to shift upslope, subsequently resulting in loss of habitat and ultimately extirpation of the species (Moritz et al. 2008). It is uncertain whether pikas at more northern latitudes have the same niche restrictions as so- called "typical" populations at lower latitudes and higher elevations (Varner et al. 2014), or if these animals may exhibit behavioural plasticity (e.g. adjustment of foraging times or microhabitat use) in response to changing conditions. More recent research has focused on investigating the American pika niche framed in the context of microrefugia. Of interest is "atypical habitat", in which pikas have been discovered at lower elevations or unusual marginal locations such as abandoned industrial sites (e.g. Manning and Hagar 2011). Microrefugia may allow climate-sensitive species such as the American pika to persist in habitat that, at a broader scale, appears unsuitable or atypical for this animal. Recognizing the ecological relevance of niche microrefugia for species survival under climate change will support new strategies of adaptation management in conservation biology (Lenoir et al. 2017).

Study Site

My study was conducted in the southwestern interior of British Columbia, on and adjacent to Highland Valley Copper (hereafter HVC), an open-pit mine (active area approx. 6900 ha- Brick et al. 2018) located approximately 75 km southwest of Kamloops, BC, Canada (50.49° N, 121.04° W). The study region features predominantly within the BC biogeoclimatic zone of Interior Douglas-fir at lower elevations and the Montane Spruce biogeoclimatic zone at higher elevations (FLNRO 2018). The climax tree species in this region is Douglas-fir, alongside lodgepole pine, Engelmann- white spruce and subalpine fir. The study area is situated in a geologic volcanic region known as the Guichon Creek Batholith, within the Nicola Volcanic Belt (Bergey 2007). This region is semi-arid with extreme fluctuations in temperature, atypical to habitat normally associated with the American pika. Climate normals for this region (1981-2010) show average maximum highs of +34˚C in July and average minimum lows of -9.1˚C in December (similar to my study years, 2012/13, Figure 1.4). Extreme 30-year lows of -43.9˚C, coupled with extreme highs of 40˚C characterize this region as seemingly unsuitable for pika persistence (Figure 1.4). Precipitation (rain) is heaviest in June, with an average rainfall of 47.9 mm, and December shows an average snowfall of about 40.8 cm (Environment Canada, Lornex Station 50'28 N, 121'01 W; elevation 1268 msl). Average 30-year snowfall comparison between Kamloops and Highland Valley Lornex weather stations is provided in Table 1.1.

Past reclamation practices at HVC have largely focused on revegetation; more recently, reclamation plans for overburden were modified in an attempt to increase biodiversity of mine waste areas (Teck Sustainability Report 2012), but specific targets for pika habitat have not factored into this work. Of particular interest is the waste rock generated from the mine pits. The gullies and lesser depressions in the industrial landscape were filled with this waste rock and piled along the haul roads across the mine site, and pikas settled in as they would on natural talus (Howie 2008). Pikas were first officially detected here in 2005 by mine workers; following this, Howie (2008) documented pikas via presence/absence surveys.

Sampling locations were selected both north and south of highway 97C based on site occupancy (Figure 1.5). My study animals were situated at an elevational range between 1315-1865 m across the study area, both on site at HVC ("anthropogenic sites"), as well as on adjacent "natural" sites. Natural sites were characterized by talus that was composed of original, undisturbed rock talus matrix (Figure 1.6); and were mainly located north of the mine site. Other mammalian species observed to inhabit talus habitat include yellow-bellied marmots (*Marmota flaviventris*), short-tailed weasels *(Mustela erminea* - a main predator of pikas - Figure 1.7), bushy-tailed woodrats (*Neotoma cinereal)* and yellow-pine chipmunk (*Neotamias amoenus).*

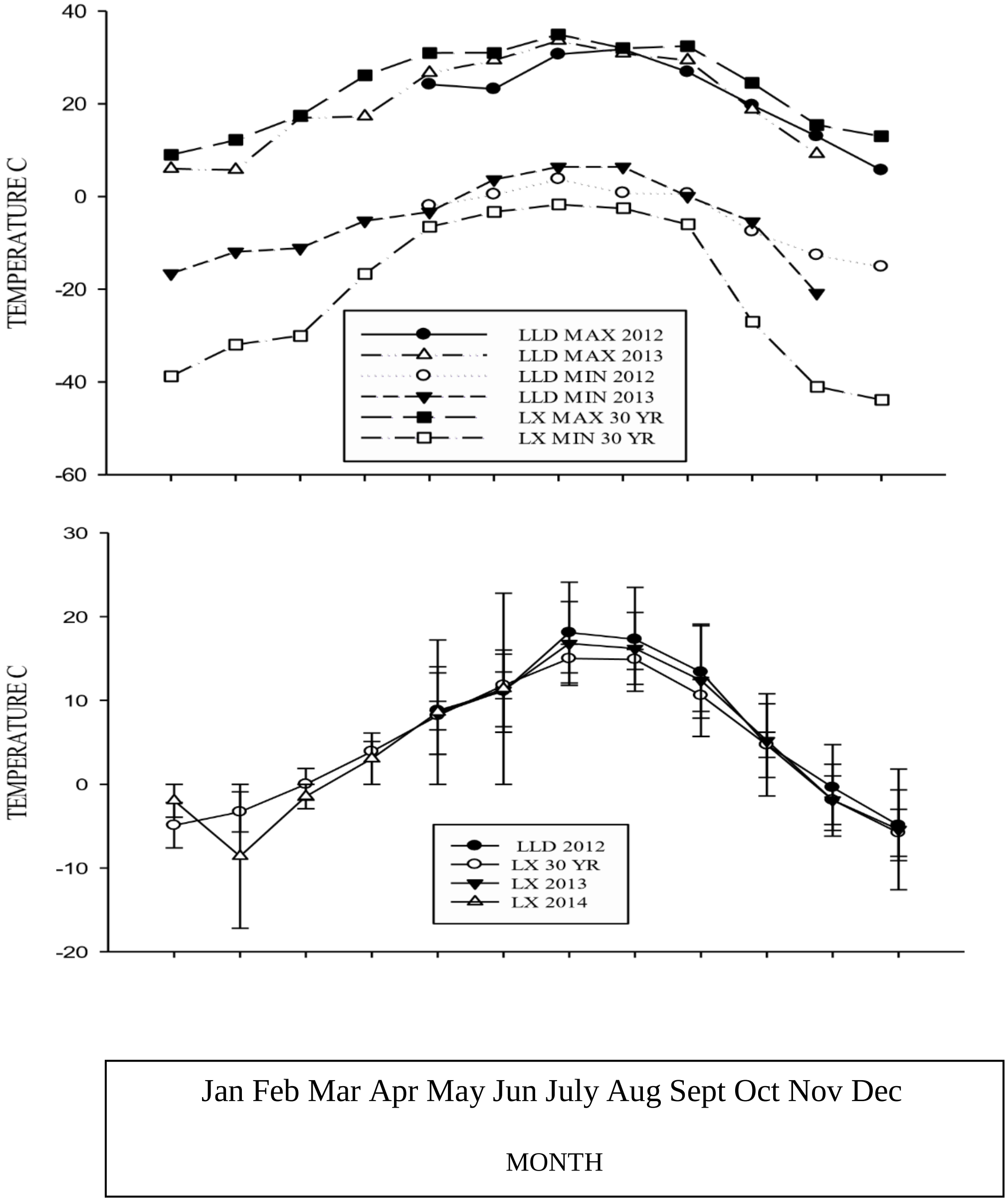

Figure 1.4. Upper graph: Mean monthly temperatures during the years of my study (2012- 2014) garnered from two weather stations operated by HVC, the- Lornex weather station (LX) and LL Dam weather station (LLD). Also shown are mean monthly temperatures for a 30-year period (1981-2010) at LX. Lower graph: Climate min/max for this region from 1981-2010 (LX 30 yr), and during the years of my study (LX 2012, 2013, 2014). Available at Environment Canada: http://climate.weather.gc.ca/climate_normals/results_1981_2010_e.html..

Table 1.1. Average snowfall at Kamloops and LX weather stations, over varying yearly time periods (available at: http//www.climate.weatheroffice.gc.ca/climate_normals/index_e.html).

Station	**Coordinates**	**Elevation**	**1981-2010**	**2012**	**2013**	**2014**
Highland Valley Lornex	50°28’00”N 121°01’00”W	1268 m	149.9 cm	N/A	N/A	N/A
Kamloops	50° 42’08” N, 120°26’31”W	345.3 m	63.5 cm	84.8 cm	N/A	42.4

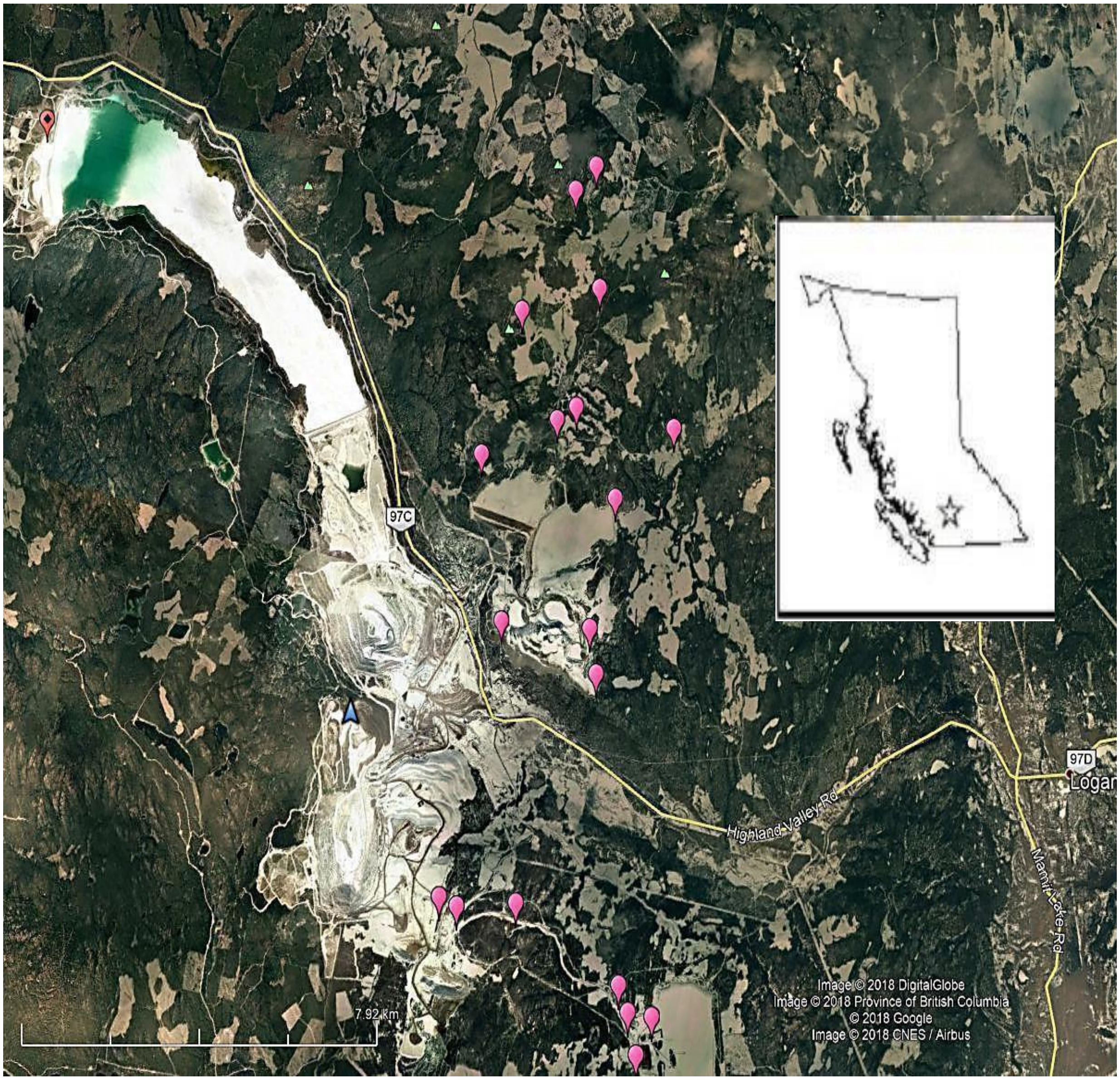

Figure 1.5. Map of study area indicating sampling locations within and around the Highland Valley Copper mine in south central British Columbia (50.49° N, 121.04° W). Pink markers represent pika habitat supporting between 2-14 pikas. Blue marker indicates the approximate location of the HVC Lornex weather station. Red marker indicates approximate location of the LL Dam weather station. Inset illustrates study site location in British Columbia. Aerial photograph obtained from Google™ Earth.

Figure 1.6. Top photo: Waste Rock dump gully on-site at HVC, in which pikas are residing. Bottom photo. Natural pika habitat north of Highland Valley Copper. Photos by author.

Figure 1.7. Top photo: The short-tailed weasel (*Mustela erminea*) is a main predator of pikas. Above photo: weasel moving through natural rock talus occupied by pikas. Bottom photo: Weasel caught during pika trapping session, on-site at HVC. Photos by author.

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CHAPTER 2

A COMPARISON OF AMERICAN PIKA (*OCHOTONA PRINCEPS)* POPULATIONS IN NEIGHBOURING ANTHROPOGENIC AND NATURAL HABITATS

INTRODUCTION

The alteration and fragmentation of native habitat through human activity is commonly implicated as the predominant cause of terrestrial biodiversity loss (Pfeifer et al. 2014). As a result, reclamation of wildlife habitat has become increasingly important as a means to counter these losses. However, the primary short-term goals of reclamation efforts often are to establish vegetative cover, with longer-term objectives for wildlife lacking priority (Eaton et al. 2014). Closure planning of industrial/disturbed areas such as mines tends to focus on geotechnical elements of the landscape, including surface water, soils and vegetation (McKenna 2002), that invoke limited guidelines (Eaton et al. 2014). Further, simply re-vegetating a landscape does not necessarily result in re-colonization and establishment of diverse wildlife populations, nor does it ensure restoration of the original ecosystem condition, structure and function (Cristescu et al. 2013).

Stability of wildlife populations is ensured through reproductive success and dispersal (Kristan 2003), processes likely to be impeded by anthropogenic modification of habitat. Species whose distributions are dependent on recolonization of habitat patches may appear to be demographically viable but may be more susceptible to anthropogenic pressures that would effectively wipe out subpopulations containing unique and rare combination of genes (Donovan et al. 1995). Thus, understanding how wildlife responds to human disturbance and subsequent reclamation practices will require more than broad inventory studies.

Habitat specialists in reclaimed landscapes provide valuable opportunities to understand how the plasticity of wildlife species (or lack thereof) allows colonization of new environments. Populations of species that establish on these types of landscapes may be doing so due to (i) the creation of habitat (macro- and micro-) that intentionally or unintentionally mirrors native conditions, (ii) a plastic behavioural response to conditions outside of their normal habitat envelope, or (iii) some combination of these two processes (Rodhouse et al. 2010).

The American pika (*Ochotona princeps*) is a species considered to be a habitat specialist (Varner and Dearing 2014; Calkins et al. 2012); it is generally associated with alpine to subalpine rocky talus that occurs in western North America from New Mexico and California up through to central British Columbia (Smith and Weston 1990). This animal is a small, territorial herbivore that is considered thermally sensitive (Smith 1974a) and therefore presumed to favor talus slopes associated with cooler, high-elevation ecosystems. In addition to this apparent tie to a narrow range of habitats, the species also is considered vulnerable due to a low reproductive rate and limited dispersal (Beever 2008).

Studies focused on the American pika in non-alpine areas have been limited to relatively few locations, and it is unclear whether patterns of pika occupation observed elsewhere (e.g. Bodie, CA –Smith et al. 2016) are representative of non-alpine habitats in general (Shinderman 2015). Recent evidence has suggested pikas are not necessarily restricted to the narrow bioclimatic envelope that they have been typically associated with (Simpson 2009; Manning et al. 2011; Shinderman 2015; Smith and Millar 2018), rather, the relative influence of habitat features such as microclimate at den sites appears to vary by location (Jeffress et al. 2013). This species has recolonized atypical environments after it has undergone locally extirpation, such as in the post-eruption landscape of Mt. St. Helen’s (where pikas recolonized under debris such as log piles - Bevers 1995) or in anthropogenic environments such as lower elevation rock quarries (Manning and Hagar 2011). Millar et al. (2010) suggest that pika populations in the Sierra Nevada and southwestern Great Basin are sustainable, persist in a wide range of thermal environments, and show little evidence of extirpation or decline; in contrast, central Great Basin pika populations appear subject to the complexity of metapopulation dynamics and climate change, and have shown declines or extirpations in some populations (Beever et al. 2003). Baseline studies of this animal in atypical environments, such as reclaimed landscapes, will continue to provide information into whether the habitat associations of this species are plastic or highly canalized.

To understand better the ability of the American pika to survive in altered landscapes, I conducted comparative research on these animals across a landscape containing both natural and anthropogenic habitat, within an extreme temperature environment characterized by long, cold winters (lows of -40˚C) and short, hot summers (highs of >40˚C). The specific questions I address in this chapter are: Is there a significant difference in demographic and individual characteristics of pikas occupying natural versus anthropogenic habitat, and (ii) are there differences in the life history of the animals that may reflect the two "populations". To this end, I compare between natural and disturbed habitats: the survival of adult and juvenile pikas, weight and zygomatic width of pikas, dispersal of juveniles, and reproductive success of adult females.

METHODS

Study Site

Pikas were studied within the reclaimed landscape of Highland Valley Copper (HVC), an open-pit mine located approximately 75 km southwest of Kamloops, BC, Canada (50.4871° N, 121.0444° W). Pikas first were detected within the re-distributed talus in Highmont in 2005 (the southern portion of the mine landscape – Howie 2008), with conspecifics occupying natural habitat approximately 2-17 km distant. Surface developments from mining operations include open pits, overburden dumps, tailings ponds, infrastructure, water diversions, and roads. The majority of reclamation practices are done directly on tailings and overburden via seeding. Reclamation historically at HVC largely has been structured around revegetation; more recently reclamation plans for overburden are being modified to attempt to increase biodiversity of mine waste areas (Teck Sustainability Report 2012). Average climate normals in this region (1981-2010) show average maximum highs of +34˚C (peaking in July) and average maximum lows of -9.1˚C (December). Extreme 30-year lows of -43.9˚C, coupled with extreme highs of 40˚C characterize this region as seemingly unsuitable for pika persistence (Figure 1.4). Precipitation (rain) tends to occur heaviest in June, with an average rainfall of 47.9 mm, and December shows an average snowfall of approximately 40.8 cm (Environment Canada, Lornex Station 50'28 N, 121'01 W; elevation 1268 msl). The study region is within the Interior Douglas-fir biogeoclimatic zone at lower elevations and the

Montane Spruce biogeoclimatic zone at higher elevations (FLNRO 2018). The study area is situated in a geologic region known as the Guichon Creek Batholith, within the Nicola Volcanic Belt (Bergey 2007). My study animals were situated at an elevational range between 1315-1865 m across the study area. See Chapter 1 for a more detailed comparison of the site and weather conditions during the study years, and the precise location of the study animals.

Mark-recapture/Demographics

Using aerial photography (Google Earth™ 2012), ground surveys, previously recorded pika occupancy (Howie 2008), pika sightings from mine workers, and stratification for rock outcrops north and south of Highway 97C, I randomly selected for live-trapping 20 occupied talus habitat patches that were equally dispersed across the study site. Within these patches the locations of pikas and the elevation of their den sites were recorded using a Garmin 76C hand-held GPS unit with accuracies generally +/-5 metres. I laid out parallel linear transects on talus slopes, approximately 15 meters apart (Beever 2003; Collins and Bauman 2012) and survey points were established approximately 50 meters along the transect lines (Millar and Westfall 2010; Collins and Bauman 2012). Each point survey lasted 20 min and included both active searching and quiet listening; individual pikas were confirmed by direct observation, vocalization, and/or by searches for haypiles (Figure 2.1) or scat (Figure 2.2). A subsample of pikas deemed focal animals (22 collared and 20 non-collared individuals) were observed over daily active periods to determine an average territory size. Individual territory sizes were determined as an approximation, based on measurements of farthest distance observed of where pikas traveled within their territory through activity, foraging bouts, etc. Several observation periods (no less than 3/ focal pika) were conducted throughout summer seasons of the study at each habitat patch, during 2 active periods for pikas – early to mid-morning, and late afternoon to dusk. A tape measure was used to record farthest points out from the main haypile and these points were used to approximate area of the territory.

Sites were classified as ‘natural’ when the surrounding rock matrix was undisturbed by human modifications. Anthropogenic (disturbed) sites involved artificial substrates such as riprap or waste rock dumps generated by mining activities. Other forms of human disturbance such as dirt roads, logging and recreational use were not used as criteria and also were present within/nearby the designated "natural" areas outside the mine perimeter. Such human disturbances as close proximity of roads have been shown to not significantly influence pika habitation (Ray et al. 2016).

Intensive trapping periods that occurred over 3 consecutive years allowed me to assess survival over the intervening time periods. Pikas were captured using Tomahawk (Hazelhurst, WI) model 202 collapsible live traps (Figure 2.3) encased in "weasel baffles" (Fig. 2.3)- an outer covering fitted around the traps, designed during the study to prevent the killing of pikas inside traps by weasels. After initial trap placement, the live traps were locked open for 1-2 weeks and repeatedly pre-baited with dry alfalfa cubes. When I determined that the animals were consistently visiting the traps, live-trapping sessions commenced in the early hours of the morning or evening. Sample sites were exhaustively trapped between May and October 2012 and between May and November 2013, with a final overwinter survival trap in June 2014 [estimated >33,600 trap hours]. Traps were checked once every 2.5-3 hours after setting until ambient temperatures reached 15°C (or in the case of evening trapping, the onset of dusk). Captured animals were admitted into a mesh handling bag (Figure 2.4) and marked with two Monel #1 ear tags (unique number combinations) and one unique color tag for observational purposes (Figure 2.5). A hair sample from each individual was taken for genetic analyses in a related study (Waterhouse et al. 2017). All told, my handling time for individual pikas once ushered into the handling bag was kept under 3 minutes/animal to ensure safety of the animal (Figure 2.6).

Female Reproductive Success

Females were inspected at the time of trapping for swollen nipples (1-2 mm; Smith and Ivins 1983) and/or matted hair around the nipples, as evidence of lactation. Female parentage was determined through trapping records and direct observations; a small number of juveniles had their female parentage affirmed through genetic analysis. (Waterhouse et al. 2017 – Appendix A). Number of offspring (0, 1, >1) was calculated based on the number of offspring detected (visually or through live-trapping) post-emergence (on the surface) (Kreuzer et al. 2003).

Weight, Zygomatic Width and Sex Ratio

Weights of individual pikas were taken to the nearer 0.5 g at each capture session (approximately 3 weights/season taken, late spring-late fall) using a Pesola scale; adult/juvenile classification by weight generally was based on a 150 g threshold (previous studies show 120-176 g for adults, and under 150 g for juveniles (e.g. Tapper, 1973). Colouration and size of the individuals also served to identify juveniles during the summer of its birth (Smith and Millar 2018), along with detections of juveniles emerging from den sites. During capture, zygomatic width measurements were taken with calipers to the nearest 0.5 mm, as a comparison of body size). Zygomatic width measures the widest part of the animal's face, from one arch to the other, and used as a proxy to compare body size Duke (1951). The sex of individuals was determined in the field at time of first capture and subsequent confirmation of a subsample (n= 10) using DNA testing via hair samples (Waterhouse et al. 2017, see Appendix A) verified the accuracy of these field assignments.

Radiotelemetry/Mortality/Dispersal

Subsamples of pikas in my study population were monitored via radio telemetry to provide confirmation that my live-trapping estimates of mortality were accurate. To affix radio-collars, live-trapped animals were ushered into a small handling bag made out of soft mesh and nylon/spandex (Figure 2.5). With the animals inside the mesh of the handling bag, the radio-collars [Holohil Ltd./Model DB-2C (adults) /PD-2C (juveniles) -both ≈ 3% of animal body weight] were secured around the neck (Figure 2.6). Collared individuals were subsequently located via telemetry every 2-3 days in conjunction with detections through direct observation and live-trapping. Telemetered pikas were followed throughout the summer season until settlement or death, at which point a GPS location was taken. Repetitive and stationary signals from collars, consistently located under talus over multiple successive checks, were considered to also reflect mortality. Collars on surviving pikas were removed during last trap in the fall.

Juvenile pikas (young of the year) were observed, targeted, trapped and a subset

Figure 2.1. Top photo: Haypile on HVC site; a mix of raspberry (*Rubus leucodermis)* and Canada thistle (*Cirsium arvense)*. Bottom photo: Haypile of *Equisetum sp*. on natural site. Photos by author.

Figure 2.2. Latrine (scat) pile under a rock outcrop. Photo by author.

Figure 2.3. Top photo: pika taking bait from a locked-open trap. Photo retrieved from Reconyx™ camera. Bottom photo: pika caught during trapping session with trap inside a “weasel baffle”. Photo by author.

Figure 2.4. Top photo: Pika emerging from handling bag. Bottom photo: Two Monel identifying tags, both with numbers. Left ear also has an additional color tag for observational purposes. Photos by author.

Figure 2.5. Pika post-handling: tagged, collared, sexed and weighed, and a hair sample taken. Photo by author.

radio- collared beginning late June to early July, as soon as emergence from the natal den was observed, and continued through into early August. Point of origin of the juvenile was considered to be the home den site of the mother, and dispersal was determined through either direct observation of the juvenile's movement amongst patches or tracked through telemetry. The dispersal (settlement) distances of collared juvenile animals were measured as straight- line distances from the mother's den site. Radio-collars were removed when juveniles had settled: i.e. they were consistently observed in a non-natal territory (usually by early September, and "haying" had begun on territory). A Kolmogorov-Smirnov test was used to compare the dispersal distances (categorized) of the pika offspring originating in natural and anthropogenic habits based on average-size territory increments (Smith 1974b).

RESULTS

Mark-recapture/Demographics

I monitored a total of 20 patches supporting pikas over the course of this study (10 natural, 10 anthropogenic). My observational assessments showed an average of 3,628 m^2 of habitat per patch with a mean estimated individual territory size of approximately 572 m^2, which agrees with previous reports of territory size for this species (e.g. Smith and Weston 1990). A total number of 174 pikas were captured from 2012-2014. Included in this number were 54 adult males, 44 adult females (sex unknown n=11) and 61 juveniles. Sex-ratios for trapped adult animals were not significantly different in early summer and fall between the two habitat types (Table 2.1). Survival of adults between the anthropogenic and natural dens did not differ significantly over the major sample periods. Average juvenile survival over two summers also did not differ significantly over sampling periods, or between anthropogenic or natural habitat (Table 2.1).

Female Reproductive Success

The proportions of adult females that reproduced each summer were similar across the two habitat types and did not differ between years (Table 2.1). Similarly, in both 2012 and 2013, there was no significant difference between habitat types in the proportion of reproducing

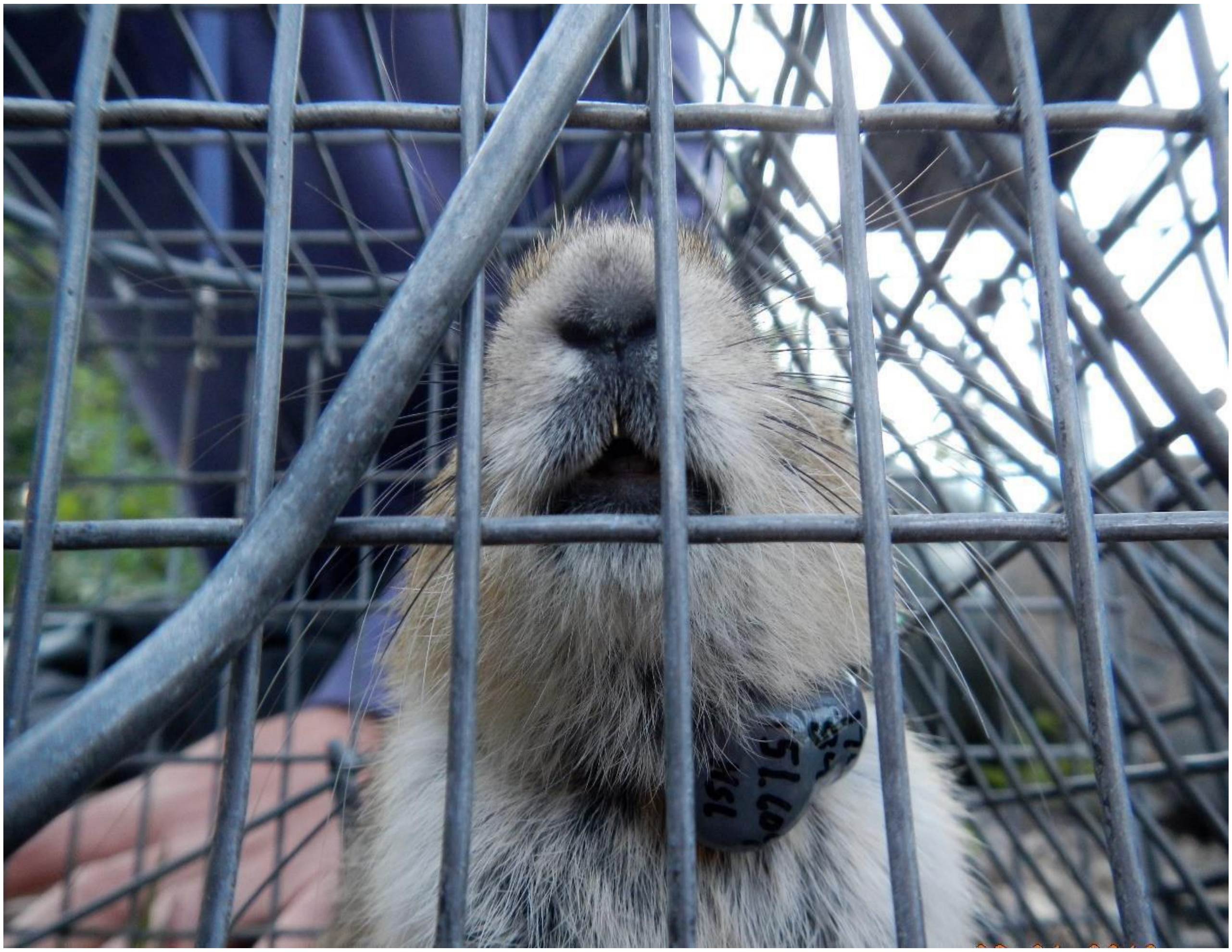

Figure 2.6. Trapped pika illustrating an attached radio-collar. Photo by author.

Table 2.1 Demographic parameters across all field seasons 2012-2014 with comparisons between animals occupying anthropogenic and natural habitats. All statistical comparisons were insignificant at α= 0.05 except for zygomatic width. [a] breeding females/non-breeding females. [b]denotes #females with offspring to surface/# females with more than one offspring to surface. [c]denotes #offspring dispersing <50 m (philopatric)/#offspring dispersing >50m. [d]number of juveniles dispersing varying distances across both habitats. D= K-S test statistic of proportions compared in dispersal distance categories [e] denotes juveniles holding territory the following year after successful settlement.

Parameter	Age	Season	Year	Anthro	Natural	Stat	Prob.
Survival	A	Summer	2012	0.84 (27/32)	0.95 (36/38)	$\chi_1 = 1.97$	0.61
			2013	0.79 (27/34)	0.89 (25/28)	$\chi_1 = 1.11$	0.29
			Pool	0.82 (54/66)	0.92 (61/66)	$\chi_1 = 3.4$	0.07
		Winter	2012	0.41 (11/27)	0.33 (12/36)	$\chi_1 = 0.37$	0.55
			2013	0.30 (8/27)	0.52 (13/25)	$\chi_1 = 2.7$	0.10
			Pool	0.35 (19/54)	0.41 (25/61)	$\chi_1 = 0.41$	0.52
	Juv	Summer	2012	0.89	1	$\chi_1 = 2.0$	0.57
		Winter	2012	0.25	0.29	$\chi_1 = 0.07$	0.79
		Summer	2013	0.79	0.89	$\chi_1 = 1.11$	0.29
♀ **Breeding**[a]	A[a]		2012	12/7	13/3	$\chi_1 = 1.39$	0.24
			2013	12/5	13/5	$\chi_1 = 0.01$	0.91
♀**Repro**[b]	A [b]		2012	8/4	9/4	$\chi_1 = 0.02$	0.89
			2013	8/4	8/5	$\chi_1 = 0.07$	0.79
Weight	A♀		Pool	168.02±14.5g (n=24)	168.8g±12.7 (n=17)	$t_{37.12} = 0.18$	0.86
	A♂		Pool	164.7±16.4g (n=32)	166.2±15.9g (n=30)	$t_{59.9} = 0.37$	0.72
	A♂/♀		Pool	165.0±15.8g (n=56)	168.3±13.6g (n=47)	$t_{94.1} = 1.12$	0.26
Zygomatic	A♀		Pool	24.6±0.8mm (n=24)	24.5±0.7mm (n=23)	$t_{44.9} = 0.57$	0.57
	A♂		Pool	25.0±0.9mm (n=32)	24.5±0.8mm (n=29)	$t_{58.6} = 2.44$	0.02*
	A♂/♀		Pool	24.7±0.9mm (n=56)	24.6±0.8mm (n=52)	$t_{105.2} = 1.17$	0.25
Dispersal	Juv[c]		Pool	19/9	24/6	$\chi_1 = 1.1$	0.29
	Juv[d]		Pool	28	30	D=0.17	0.20
Juv est[e]			2012-13	5/14	5/16	$\chi_1 = 0.07$	0.80
			2013-14	5/14	9/14	$\chi_1 = 2.29$	0.13

females having at least one offspring emerge from the den (Table 2.1).

Weight, Zygomatic Widths and Sex Ratios

No differences were detected in adult weights across the two categories of pikas (Table 2.1). Males ranged from 136-200 g and females ranged from 140-195 g. Females were comparable in weight to males, with no significant difference found between the sexes (Table 2.1). Zygomatic width was 23-26 mm with no significant difference found between the sexes in my study. Females showed no difference in zygomatic width across habitat type (Table 2.1), however, male zygomatic width differed between the habitat types (Table 2.1). Juveniles ranged from 70–149 g in my study, contingent on the time of the season when captured. No significant difference was found either year in sex ratios when comparing natural and anthropogenic sites (Table 2.1).

Radiotelemetry/Mortality/Dispersal

Twenty-two adults were radio-collared during the summer season of 2012-2013. Within the group of telemetered animals, all individuals that did not appear in the trapping program were known to have died (4 pikas), as verified either by remains (2 pikas) or stationary location of the transmitter within talus (2 pikas). I radio-tracked a total of 12 juvenile animals upon emergence from the natal den sites in 2012, subsequently radio-checking each individual for 9-22 non-consecutive days. Two of these animals (17%) died prior to settlement, reflecting the same mortality percentage in the non-collared portion of juveniles over the same life-history period.

Successful settlement was inclusive of both telemetered and non-telemetered juveniles. Settlement distances ranged 24 – 224 m from the natal den ($\bar{x}$ = 46.4 m, SD = 50.9 m). There were no significant differences in settlement distances found between anthropogenic and natural sites for the dispersed juveniles (Table 2.1). Similarly, there were no significant differences in the relative proportions of anthropogenic and natural-site juveniles that settled and held a territory into the following spring (Table 2.1).

DISCUSSION

The American pika has been touted as a specialized, thermally-sensitive, montane alpine mammal (Beever 2003; Calkins et al. 2012), yet pikas in my study appear to be occupying and surviving in a lower-elevation, atypical dry region in the southern interior of British Columbia. Moreover, this species is occupying anthropogenically-modified sites (as well as natural) in a region that experiences exceptionally hot summers and extremely-cold winter temperatures. Despite these seemingly challenging conditions, my comparison of these animals across the two habitats revealed that pikas were remarkably similar in nearly all comparisons. Overall, survival rates of adults and juveniles were comparable between the two habitat types during the years of my study (2012-2014). Pikas exhibited almost no detectable differences in demographic characteristics, with the sole exception of adult male zygomatic width. Subsets of radio-collared animals confirmed the validity of mark- recapture in investigating the demographics of the American pika. Comparable survival rates of both adults and juveniles (verification of efficacy of monitoring individual fates via live-trapping was supported through telemetry data from adults) between anthropogenic and natural habitats suggests these animals attain territories and denning sites of similar quality in both areas.

Elevated body temperatures ($\bar{x}$ = 40.1°C) and relatively low upper-lethal temperatures ($\bar{x}$ =43.1°C- Smith 1974b) reported for pikas suggest that behavioral thermoregulation is required to cope with summer temperatures that would otherwise be lethal to this animal (MacArthur and Wang 1973). The zoogeographic history of *Ochotona* suggests that pikas have been able to shift into varying habitats in response to environmental changes, via behavioural plasticity (Varner et al. 2014) and available microrefugia. Thus, the establishment of these animals in anthropogenic and lower-elevation sites in my study area is not altogether unexpected, as other anthropogenic or “atypical” occupied sites exist elsewhere in western North America (see Bevers 1995; Millar & Westfall 2010; Manning and Hagar 2011; Smith et al. 2016; Millar et al. 2018). Given pikas’ patch fidelity and obligation to talus and talus-like habitats, this research provides further evidence that pikas can utilize a broader array of habitats, albeit suitable microclimates being an important requisite.

Female pikas in my study achieved equal size and demonstrated similar reproductive success, whether occupying anthropogenic or natural habitat, indicating that individual territories used by the two groups of animals afforded similar resources and nesting sites. It was beyond the scope of this study to determine the exact litter size born to individual females, but the number of surviving young post-weaning suggested of comparable resources to both mother and young. A trade-off between energy expended and energy stored for winter thermogenesis and reproduction (Lima et al. 1985) occurs in summer while foraging to "hay" in preparation for winter or nest-building (Stafl and O'Connor 2015; Dearing 1997), and also in foraging during the winter (for example, on evergreen shrubs; Dearing 1997). My results suggest that comparable nutritional availability, caloric intake, and proximity of forage in both habitat types is at least on par. Assumptions of similar resource availability are further substantiated by a related study (Leung 2014), where accessible vegetation and haypile composition was assessed and compared between anthropogenic and natural habitats. Although forage composition differed somewhat between the two habitats, overall nutritional availability did not differ, illustrating dietary plasticity in this generalist herbivore which contributes to comparable survival and reproduction of female pikas in my study region.

Similiar male pika weights in anthropogenic and natural sites also indicated that resources were comparable in both habitat types, yet there was a significant difference in zygomatic width; pikas from natural sites exhibited smaller widths. Cranial measurements are not well reported in the literature, but previous studies have noted that zygomatic measurements for American pikas are smaller elsewhere than in my study population (eg. Hafner and Smith 2010). Research investigating body size in mammals documents selection of larger body size in colder climates and selection for smaller size in warmer climate; a more recent hypothesis has developed that predicts climate warming will cause a reduction in body size (Millien et al. 2006). Although I do not have historic baseline data from this region, of particular interest for future research would be ongoing documentation of physical characteristics of individual pikas in this hot summer region, tracking physical changes as the climate changes. Admittedly, the significance in difference could have been little more than a spurious correlation. Superficially, the difference in zygomatic width did not equate to a difference in survival rate in males between anthropogenic and natural habitats, but selection may favour smaller body size over time as climate warming occurs.

To my knowledge, this is the first study to document dispersal of juvenile pikas using radio-telemetry, and although my sample of radio-collared animals was relatively small, the data generated supported the highly philopatric settlement patterns detected through mark-recapture in this study. Habitat availability and suitability appeared to be comparable in dispersing juveniles in both anthropogenic and natural habitats in this region, based on similarity of settlement distances. In general, juvenile pikas have limited dispersal capabilities (Smith and Ivins 1983a; Tapper, 1973; Peacock 1997) and dispersal may be affected by dynamics on a habitat patch with fully occupied territories, more so if behavioural thermoregulation is not possible via suitable refuge (Smith 1978). A distance of a few hundred meters may pose an impassable barrier to dispersal at lower elevations (Smith et al. 2016). Pikas are known to illustrate high levels of inbreeding (Robson et al. 2016); in a concurrent genetic study, pikas on my study landscape exhibited division into subpopulations despite sometimes very short distances between habitat patches (Waterhouse et al. 2017). Possible explanations included effects of industrial roads or high summer heat on dispersal, but the pattern also demonstrated the high degree of philopatry typical for this animal. Overall, dispersal is on par in this population of pikas in both anthropogenic and natural habitat and comparable to populations studied elsewhere (e.g. Smith and Millar 2018).

The similarities I report for pikas in anthropogenic and natural habitat patches are more striking given that reclamation objectives in this area did not specifically target pika colonization. Waste rock dumps were not strategically placed to create habitat for the pikas; however, the animals inhabiting them appear similar to those in anthropogenic habitat in almost all of the parameters that I investigated. Overall, the present study suggests that even within an extreme thermal environment, pikas are capable of successfully utilizing at least some portions of anthropogenic habitat, and reclamation specifically aimed at supporting this animal (something not present in my study site) may increase even more so the viability of the colonizing populations. Outwardly, it would seem unusual that pikas are occuring in either of the native or anthropogenic habitats in this lower-elevation region due to extreme temperatures that are reached in both summer and winter. However, my results indicate that

(i) no differences are detectable between pikas occupying the two types of habitat, at least in the basic population parameters I measured, and (ii) these parameters in general did not differ substantially from those reported in more southern populations, despite the extreme climate of my study region. Although my comparisons included more than simple measurements of abundance, the length of this study (i.e. 2 years) is insufficient to allow a more confident statement about the long-term persistence of the animals occupying either of the two habitat types. Still, the data presented herein suggest that even species considered ‘specialists’ have the potential to do equally well on reclaimed and atypical landscapes.

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CHAPTER 3

THE AMERICAN PIKA (*OCHOTONA PRINCEPS*): MICROREFUGIA CHARACTERISTICS ACROSS AN ATYPICAL LANDSCAPE

INTRODUCTION

Grinnell (1917) first conceptualized the boundary of a species' ecological niche, defining it as the environmental threshold that constrains the ranges of organisms, according to their physiological characteristics. Since then, the concept of the niche has been more broadly defined, incorporating descriptions of how an organism or population responds to all stimuli, such as the distribution of resources and competitors (Hutchinson 1957). Yet, many studies examining the ecological niche have focused largely on the influence of regional climate in dictating the distribution of species. This may fail to give accurate predictions when interpreted at finer geographical scales, i.e. where individuals within a single population might experience their immediate surroundings differently (Suggitt et al. 2011). Rowe et al. (2014) surveyed small mammals from 2008-2010 (pikas, woodrats, mice, voles, etc.) in California, using data that were collected in the 1920s on the historical ranges of species (ex. Grinnell 1924), and illustrated that populations were impacted differently across regions by shifting climate, and that range shifts were not predictable in relation to changing climate in lower elevation species. Thus, climate modelling of species' distributions has been criticized for failing to integrate necessary components such as dispersal, adaptation and behavioural plasticity of a species (Renn and Schumer 2013; Varner et al. 2014).

Microhabitat (microrefugia) has been an overlooked concept in determining what the response of a species is or will be to changes in its niche space (Lenoir et al. 2017). Growing evidence suggests that microrefugia are relatively stable and buffer species against variability in climate or other environmental conditions (Varner et al. 2014). For example, mountainous regions feature refugia in which cooler microclimates enable local survival of species at relatively low latitudes (Stewart et al. 2010). Those animals that can behaviourally regulate body temperature through habitat selection may be less vulnerable to climate shifts than previously thought (McCain and King 2014). Understanding how and why species are limited by climate and other factors using fine-scale data is important in assessing the ecological and physiological effects of disturbance and anthropogenic impacts, and how microhabitat can offer species a viable option to adapt in situ (Yandow et al. 2015; Horner-Meyer. 2015).

The American pika has long been touted as a sentinel species for the effects of climate change on a montane mammal (Smith and Beever 2016; Erb et al. 2011). Pikas possess many characteristics that have been forecasted to expedite local population extirpations should temperatures continue to increase (Parmesan 2006; Smith et al. 2016). These features (temperature sensitivity, low density, low dispersal capability, and low rate of reproduction) interact to make pikas vulnerable to population extirpation and therefore subsequent regional extinction (Smith et al. 2016), mostly due to a relatively elevated body temperature (mean = 40.1°C) and relatively low upper-lethal body temperatures (mean = 43.1°C; Smith 1974a). Hyperthermia and death are reported to occur at moderate ambient (25.5–29.4°C - MacArthur and Wang 1973; Smith 1974a) or moderately low (>-10°C; Beever et al. 2010) temperatures.

Recent work has documented the loss of historical pika populations from several mountain ranges in the Great Basin of the western United States and has suggested that anthropogenic influences (e.g. climate warming) are likely responsible for the observed decline (Beever et al. 2003). Similarly, anthropogenic climate change has been implicated in the contraction of pika distribution in the Sierra Nevada (Moritz et al. 2008; Manning and Hagar 2011). Yet, there are locations throughout pika distributions (Smith et al. 2018) where these animals appear to be persisting through atypical environmental conditions, outside of their previously described typical niche. Whether pikas can adapt or modify their behaviour to contend with anthropogenic disturbance and changes in climate, across various biogeographic locations, still is unknown.

To better understand how the American pika is surviving in locations seemingly unsuitable for this species, I conducted research on animals across a low-elevation, anthropogenically disturbed landscape at the edge of this species' central northern range, located in atypical habitat within the semi-arid southwestern interior of British Columbia. In Chapter 2, I compared the demographics of two subpopulations of these animals, one occupying a relatively warm anthropogenic landscape, and the other in adjacent, more natural habitat. I found no detectable differences between the two groups of animals, suggesting the pikas in the latter habitat were successful at utilizing the disturbed landscape. In this chapter I combine the data on all individuals and their den sites across the entire landscape and address the following questions: (i) are there substantial differences in individual den characteristics (i.e. rock size, insol, temperature under talus) of pikas across this site and (ii) are these den characteristics a predictor of adult and juvenile survival.

METHODS

Study Area

I conducted my study approximately 75 km southwest of Kamloops, British Columbia, near the Highland Valley Copper Mine site (50.48° N, 121.04° W), across study sites at elevations between 1365m- 1885 m ASL. The study site occurs within British Columbia's Interior Douglas-fir biogeoclimatic zone at lower elevations and the Montane Spruce biogeoclimatic zone at higher elevations (FLNRO 2018). Precipitation here is limited with an average annual amount of 393 mm (Environment Canada) falling heaviest in June. Interestingly, this region is semi-arid with extreme fluctuations in temperature; average climate normals in this region (1981-2010) include average maximum highs of +34°C (with extreme highs of 40°C) in July and average minimum lows of -9.1°C (with extreme lows of -43.9°C) in December, suggesting this region would not readily support pika populations due to the poor thermal tolerance of this species. Pikas were first detected here by mine workers in 2005. Subsequently, Howie (2007) conducted a presence-absence study on the Highmont side of HVC (southern portion of the mine). Additional details on the study site are provided in Chapter 1.

Using aerial photography (Google Earth™ 2012), ground surveys, previously recorded pika occupancy (Howie 2008), pika sightings from mine workers, and stratification for rock outcrops north and south of Highway 97C, I randomly selected 20 talus habitat patches that were dispersed across the study site and likely supported pikas. Locations of pikas and their den sites (and elevation) were confirmed using a Garmin 76C hand held GPS unit with accuracies generally +/-5 metres. I laid out parallel linear transects on talus slopes, approximately 15 meters apart (Beever 2003; Collins and Bauman 2012) and survey points were established approximately 50 meters along the transect lines (Millar and Westfall 2010; Collins and Bauman 2012). Each point survey lasted 20 min and included both active searching and quiet listening within that period; individual pikas were confirmed by direct observation, vocalization, and/or by searches for scat or haypiles. Average territory size of individual pikas at lower elevations have been documented as approximately 400 -600 m^2; this was confirmed through observations in my study, increasing confidence that all occupied sites were detected (e.x. Smith and Weston 1990; Rodhouse et al. 2010). Live traps (Tomahawk model 202, Hazelhurst, WI) enclosed in weasel-baffle cages (Chapter 2) were placed at each den site near the main haypile of the occupant pika. Captured animals were ushered into a mesh handling bag and marked with two Monel #1 ear tags (unique number combinations) and one unique color tag for observational purposes. Sample sites were exhaustively trapped between May and October 2012 and between May and November 2013, with a final overwinter survival trap in June 2014. Additional details on live-trapping are provided in Chapter 2.

Temperature/Climate

I randomly chose and equipped a subsample of 45 den sites from May 2013 to May 2014 with four temperature data loggers (thermochron iButton™ data loggers, model 1921G, Maxim Integrated Products, USA). I used these to record temperature at four-hour intervals at the following locations: subsurface (80cm into rock matrix perpendicular to the slope angle, as per Beever et al. 2010), ambient (approximately 1m above the rock surface), shaded surface (talus rock surface level, placed under shade), and unshaded surface (talus rock at surface level, fully exposed to solar radiation). To compare regional temperatures, I obtained ambient average monthly temperatures from a HVC weather station installed in the Lornex area of the mine site. Of the 180 deployed data loggers, 148 functioned properly (82%) until their retrieval in the spring of 2014. Five den sites had multiple failures and/or disappearances (the latter likely removed by pikas or other mammals) and 3 of the den sites became vacant during summer and winter of 2013. Missing values due to lost or malfunctioned ibuttons were filled in using multivariate imputation for continuous data (JMP® 13.0.0, 2016 SAS Institute Inc; Lee and Carlin 2010; Shane Rollins, pers. comm.). A matrix of Pearson's r tests revealed high autocorrelation between all 4 locations of ibuttons across all den sites (all Ps<0.0001). Therefore, two temperature thresholds were selected as putative predictors of den quality: (i) days above 25.5°C below talus, and (ii) days below -10°C under talus, following previously identified temperature thresholds for American pikas (Jeffress et al. 2013; MacArthur and Wang 1974; Smith 1974a). I averaged the coldest and warmest months to illustrate the buffering effects of the talus against extreme temperatures.

Habitat Parameters + Survival

Habitat measurements were recorded for each pika den site within a 20m circumference around the main haypile/talus entrance. Burnham and Anderson (2001) recommend that biological, rather than statistical, considerations direct the choice of combinations of variables to include in models; therefore, habitat variables measured for this study were selected based on previous pika literature (e.g. Smith et al. 2016; Varner et al 2014; Manning and Hagar 2011; Beever et al. 2003) along with personal observations of these animals.

At each individual densite I measured slope using a Suunto PM-5 Clinometer. Aspect was measured with a Silva Ranger 515 compass, with a bearing taken through center of main haypile/den entrance. Insol is an index of slope and aspect (Varner et al. 2014) that estimates potential solar exposure at a particular site (Jeffress et al. 2013). Following Jeffress et al. (2013), I calculated insol as sine (slope) × cosine (aspect). The resulting values ranged from 1 to -1, with steeper north-facing slopes represented with larger positive values (''northness'') and steeper south-facing slopes represented with larger negative values (''southness''). Visual estimates of rock size on individual pika territories were averaged between 2 observers for precision, with occasional tape measurements used to confirm precision. Rocks were assessed under 4 diameter classes; > $1m^3$, $1m^3$, 40- 60 cm^3 (beachball) and <40 cm^3(baseball) size. Lichen/moss/fungi (cryptogamic) cover and bare ground was recorded as a visual estimate/individual pika territory, also taken between 2 observers at each den site. Several of the habitat parameters showed high correlation (all Ps> 0.001) and thus 3 variables were ultimately selected for subsequent analyses as most likely relevant to pika survival (e.g. Varner et al. 2014): cryptogamic communities, insol, and rock 1m^3.

Analyses

I examined survival of individuals biannually (summer and winter) by modeling binary survival data [alive (1) or dead (0)] in response to habitat variables (predictors). I used a nominal regression model assuming a binomial distribution with a logit link. Candidate models were tested using the habitat variables and their additive or interactive combinations, and were compared following Akaike's Second-Order Information Criterion (AICc) for small sample sizes. The most parsimonious model was determined as outlined in Burnham et al. 2002. Akaike weights (w_i) were used to examine the relative importance of variables. Models with > 10 Δi were omitted from the final candidate set of models (Burnham and Anderson 2000). Models were verified using Receiver Operating Characteristic (ROC) and Area Under the Curve (AUC) between fitted survival probabilities and observed occurrence (Hughes and Bhattacharaya 2013). Model-averaged estimates and unconditional standard error were calculated from the top candidate models. All analyses were conducted in JMP® 13.0.0 (2016 SAS Institute Inc).

RESULTS

I monitored a total of 20 patches supporting pikas over the course of this study), and live-trapped a total of 174 individual pikas from 2012-2014 (estimated +33,600 trap hours). Included in this number were 54 adult males, 44 adult females (sex unknown n=15) and 61 juveniles**.**

Temperature/Climate

Figure 3.1 shows the average daily temperatures over the coldest (December) and hottest (July) months at all four ibutton stations during 2013. The coldest mean ambient temperature measured in winter by ibuttons in 2013/14 was -34.5°C on December 7. On that day, the temperatures under the talus averaged -16°C (+/- 7.6°C) (Figure 3.1).

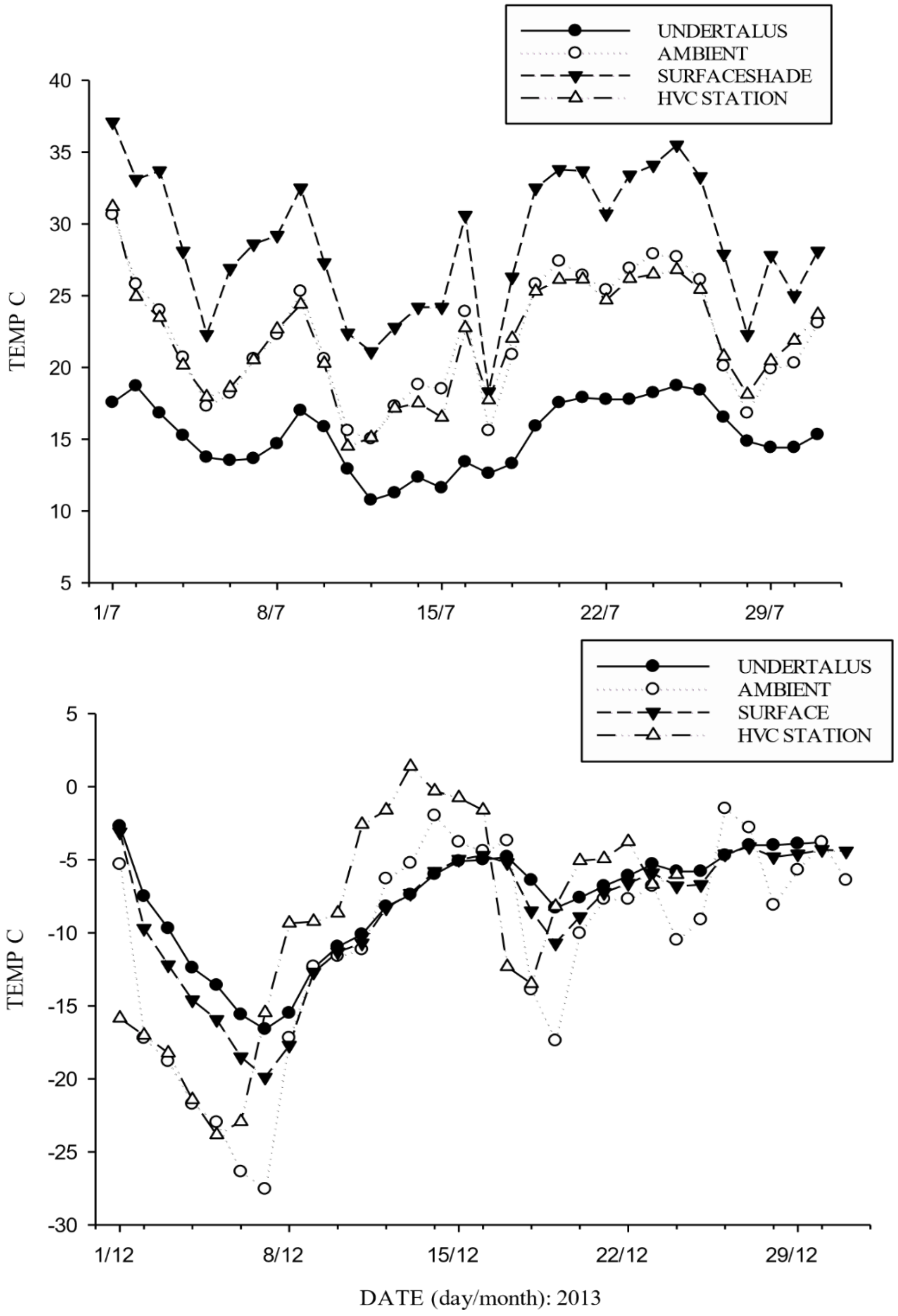

Figure 3.1. Temperatures at pika den sites near Highland Valley Copper, British Columbia, as recorded in 2013 using ibuttons placed at three locations at each den site: under talus (0.8m), ambient (1.5 m above ground), surface (on surface at den site in shade), and additional data from Highland Copper weather station of daily air temperatures. Above: mean maximum in July (hottest month) (n=36); Below: mean minimum temperatures in December (coldest month) (n=32).

Habitat Parameters + Survival

There was no consistency in variables being linked to survival across my four time periods (Table 3.1). A model involving the interaction of the habitat metrics of lichen, rock, and days below talus below -10°C (winter 2013/2014) showed the highest accuracy in predicting pika survival (ROC =0.91, Table 3.1); overall, all candidate models for this season and year were very close in AICc values (Δi <3.03) indicating they were roughly equivalent in predicting pika survivability.

Increased proportion of 1 m^3 -sized rocks in the talus matrix positively influenced pika survival (β= 0.194±0.14SE), increasing percentage of cryptogamic communities (LMF) positively influenced pika survival (β= 0.05±-0.06) and increasing number of days below talus below -10°C negatively influenced pika survival (β= - 0.08±0.15- see Table 3.2).

DISCUSSION

This research investigated the characteristics of pika den sites in an environment subject to substantial climatic fluctuations. My study revealed that cryptogamic communities, combined with larger rock size and the buffering effect of talus matrices against harsher summer and winter climates, were features of pika den sites linked to survival. The occupancy of pikas in microrefugia likely is dictated by several factors, including temperature, precipitation, and elevation (Millar and Westfall 2010; Rodhouse et al. 2010; Wilkening et al. 2011; Varner et al. 2016), and the influence of these parameters appear to vary by location in studies elsewhere (e.g. Jeffress et al. 2013). Some aspects of habitat singled out in this study were similar to those reported for pikas in other regions, such as talus rock size. Alternatively, insol (previously described as a predictor of pika presence - Varner et al. 2014) did not effectively predict survival in this study region over my study periods.

Data in the summer of 2013 indicated that number of days with above talus temperatures above 25.5°C were not a factor linked to pika summer mortality; temperature below the talus stayed much cooler (Figure 3.1) - well below the conventional upper lethal body threshold

Table 3.1. Final candidate set of nominal logistic models for survival at individual pika den sites across study years. Variables include percent cover of rock 1m^3 (R), number of days below talus below -10°C (T), Insol (I) and percent of cryptogamic vegetation cover (LMF). Null corresponds to an intercept only model. AICc=Akaike's information criterion, Δ_i = the difference between the model indicated and the best model, k= number of modeled parameters, W_i = Akaike weights, ROC = Receiver Operating Characteristic.

Season/Year	Model	k	AICc	Δ_i	w_i	ROC
Winter 2013	LMF	1	42.01	0	0.28	0.67
	R + LMF	2	42.96	0.95	0.18	0.70
	R*T	3	43.03	1.02	0.17	0.78
	R	1	44.1	1.97	0.10	0.63
	R+LMF+T	3	44.5	2.49	0.08	0.75
	R*LMF*T	**7**	**44.7**	**2.69**	**0.07**	**0.91**
	T	1	44.85	2.84	0.07	0.61
	R*LMF	3	45.01	3.03	0.06	0.698
Summer 2013	NULL	0	34.5	0	0.19	0.50
	T	1	34.5	0	0.19	0.60
	T+LMF	2	35.5	1	0.12	0.69
	I	1	36.19	1.69	0.084	0.63
	LMF	1	36.25	1.75	0.08	0.55
	R+T	2	36.7	2.2	0.06	0.62
	R	1	36.8	2.3	0.06	0.51
	T+I+LMF	3	37.6	3.1	0.04	0.79
	I+LMF	2	37.8	3.3	0.037	0.71
	I+R	2	38.6	4.1	0.02	0.62
	R+LMF	2	38.6	4.1	0.02	0.51
	T+LMF+I+R	4	40.03	5.53	0.01	0.74
	LMF*T*I	7	49.6	15.1	0	0.79
	LMF*I*R	7	50.3	15.5	0	0.74
Winter 2012/13	L	1	219.1	0	0.58	0.60
	R+LMF	2	220.8	1.7	0.25	0.61
	NULL	0	222.4	3.3	0.11	0.50
	R	1	223.7	4.6	0.06	0.53
Summer 2012/13	NULL	0	132.7	0	0.50	0.50
	R	1	134.7	2	0.19	0.52
	LMF	1	134.7	2	0.19	0.51
	R+LMF	2	136.7	4.1	0.07	0.51
	R*L	3	138.8	4.2	0.06	0.51

Table 3.2. Model-averaged estimates of parameters included in the top candidate models for Winter 2013. Variables include percent cover of rock 1m^3 (R), number of days below talus below -10°C (T) and percent of cryptogamic vegetation cover (LMF).

Parameter	**Model-averaged Estimate** (β)	**Unconditional standard error**
INTERCEPT	-0.63	1.16
LMF	0.05	0.06
R	0.194	0.14
T	-0.076	0.15

temperature associated with this animal. Previous research on this species has mainly focused on ambient regional temperatures in the summer months (Beever et al 2003; Smith et al. 2016) because of the limited thermal tolerance demonstrated by this animal (Smith 1974a). Interstitial temperatures within talus may be dependent processes other than heat-transfer at the surface (Varner et al. 2014), such as cold-air pooling and cold air drainage (Millar and Westfall 2010). The use of periglacial habitats (including volcanic rock talus such as that illustrated throughout my study site) by pikas is exemplified by research in the Sierra Nevada and western Great Basin (Manning et al. 2011). These types of habitat include deeper taluses and subsurface ice/water sources that provide a more stable microclimate (Ray et al. 2012). In the Columbia River Gorge, U.S., Varner et al. (2016) found a 30°C difference between under talus and ambient air temperatures, and the daily variabilities of the matrices were one-half to one-third those of ambient air. This illustrates the buffering capacity of talus matrices, in particular at lower elevations where microclimates are milder and less variable than typical alpine habitat. In turn, this suggests that these atypical locations may actually be more ideal refuge for this species under climate change, as compared to higher elevation sites (Varner et al. 2014). The warmest locality of any long-term investigation of pikas is documented at Bodie, California (Peacock and Smith 1997; Smith et al. 2016), where summer temperatures regularly exceed the upper lethal pika body temperature, yet Bodie has supported a pika metapopulation for over 100 years (Seppanen et al. 2012). These findings are congruent with the results of my study as presented in Chapter 2, which reveal that atypical locations of pikas near their northern latitudinal limits, including “habitat” created anthropogenically, appear to support viability of pika populations. My study contributes to the growing evidence that pikas are able to persist in regions that feature macroclimatic ambient temperaturesmuch higher than the documented upper lethal threshold temperature for these animals, potentially via pockets of microrefugia.

Survival data obtained from my study site (Chapter 2) revealed that most pika mortality occurred during the winter periods. Much lower temperatures were recorded during this period across my study region than studies conducted elsewhere (e.g. Smith and Millar 2018) and are considerably lower than temperatures considered lethal for this animal. However, it was not possible to know precisely where the animals were situated and/or what temperatures they were truly experiencing, implying that either there were warmer pockets of microrefuge within the talus that I could not measure in this study, or that pikas are notably better at thermoregulating in colder temperatures than previously believed. Pikas are somewhat adapted to the cold, but in years of low snowpack (i.e. insulative protection) it has been postulated that they may expend high levels of energy thermoregulating, resulting in higher levels of mortality (Ray et al. 2012). Frequent melt-freeze cycles, coupled with a lack of insulating snow and exposure to windshear, could potentially cause ruined haypiles or cause acute cold stress (Yandow et al. 2015). However, Smith and Millar (2018) found that the winter season (in particular those years with low snowpack) did not result in lower pika densities in Bodie, California the following summer (the winter average daily ambient temperature was -17°C). Further research is needed to determine thermotolerance in this species, as well as assessments of microrefugia and microclimates under talus.

Cryptogamic communities were a top interactive predictor of pika survival in my study, likely reflecting a cooler, moister microclimate, and deeper older, talus fields. Lichens also indicate the age of rock structures (McCune et al. 2017) and reflect the spatial stability associated with talus slopes (rock glaciers - Charbonneau, unpublished), which could be an indication of stable, suitable pika habitat. Similar to lichens, mosses tend to grow in moister, shadier conditions, and they also function as a nutrition source for pikas; Varner and Dearing (2014b) illustrated that moss represented more than half of plant consumption in low-elevation pikas in the Columbia River Gorge, U.S.A., providing forage within the safety or thermal refuge of the talus.

Rock clasts that compose the talus matrix also were a top predictor of survival in my study. Larger rocks likely relate to the size and abundance of crevices and retreats that provide access to the subterranean environment, and/or reflect the subsurface structure. Through gravitational sorting, talus slope development can lead to a deep stockpile of rock clasts, up to many meters in depth (Millar and Westfall 2010). American pikas do not excavate burrows (Franken and Hik 2004), nor are they physically able to defend themselves against predators; talus composed of larger rocks provides an abundance of crevices suitable for denning, moving, overwintering, and hiding, as well as perching platforms to survey for predators (Millar and Westfall 2010).

The relationship between habitat disturbance, climate and pika distribution appears complex. The persistence of many low-elevation populations of pikas in “anthropogenic”, “marginal” or “atypical” habitats (Manning and Hagar 2011; Millar et al. 2013; Rodhouse et al. 2010; Shinderman 2015) indicates that pikas may be more versatile than previously considered. Recent research on pika microrefugia in non-alpine environments, either far removed from high elevations or occurring in anthropogenic habitat (rock waste dumps, quarries, etc.), suggests these environments may be less “atypical” for this animal than previously thought. Studies have documented recolonization in these marginal areas long after local extirpations, illustrating that recolonization might require a longer period of time than afforded by short-term research (Millar and Westfall 2010). For example, 12-14 years after the 1988 Mt. St. Helen’s eruption, pikas recolonized in and around the blowdown zone, often in unusual spots such as under log debris (Bevers 1995). In my study area, pikas have colonized an anthropogenically-disturbed landscape generated through the mineral extraction process of a mining operation that began in 1962. My research provides only a snapshot in time of pika persistence on this atypical landscape, however, anecdotal evidence of pikas inhabiting the waste rock was documented circa 2005, 7 years before my study began (Howie 2008). Although it is unknown how long these animals have been colonizing the disturbed sites, other work (Chapter 2) has revealed that these animals appear to be successfully reproducing. In this case, population viability may be attributed to the availability of suitable subterranean habitat throughout summer and winter, rather than a physiological adaptive response to warmer or colder temperatures at macroscales.

In the spirit of Grinnell (1917), the niche is described as a close adjustment of the organism “in various physiological and psychological respects to a narrow range of environmental conditions”. Grinnell proposed the importance of conducting exhaustive research in the general range of species to determine habitat factors that are common (and atypical) to all locations where a species exists. In this vein, the data collected in my study region adds to the growing amount of literature illustrating that the American pika is able to occupy seemingly atypical habitats that superficially do not represent classic alpine/sub-alpine habitat. Given that the region in this study experiences extreme high and low temperatures that far exceed previously-suggested thermal thresholds for this species, my results reaffirm the importance of further research to fully understand the significance of pika microrefugia.

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CHAPTER 4

CONCLUSION

The overarching goal of my research was to investigate if anthropogenically-altered habitat was comparable to natural habitat in supporting viable American pika populations within the dry southern-interior British Columbia. The data I collected has implications on dispersal, climate change, and anthropogenic disturbances that influence the survival of this species in a region where temperatures can reach extreme levels in both summer (+40°C and higher) and winter (as low as -43.9°C). The agenda of the study was narrowed down to the following objectives: (1) investigation of American pika population demographics and viability on an anthropogenically-disturbed mining site as compared to an adjacent “natural” landscape, and survival of the American pika in relation to putative habitat variables, including below- talus temperature. I focused on pika survival and dispersal in both “habitats” via mark- recapture, dispersal of the animals via radio-telemetry, and (3) habitat features of the pika niche in relation to predicting survival in individuals.

The most notable results of my thesis were:

- there were no significant differences in survival of pikas occupying natural vs. anthropogenically-disturbed habitat;
- mortality occurred predominantly over winter season, in contrast to predicted mortality as a result of high summer temperatures;
- talus appeared to buffer external temperature effects within the ground-cover rock matrix, creating a microclimate substantially warmer (winter) or cooler (summer) as compared to ambient temperatures (macroclimate);
- pikas at this latitude comparably disperse as compared to their southern counterparts
- factors that may contribute to the survival of pikas in this region include a buffering capacity of the talus matrix from low/high ambient temperatures, possiblyinfluenced by rock size and cryptogamic vegetative growth on the talus.

My results suggest that anthropogenically-created habitat is mitigating temperature effects at least as well as adjacent natural talus patches in the southern interior of British Columbia.

Microrefuge availability and use by the American pika may mitigate the effects of extreme temperatures previously considered lethal to the animal, pending sufficient resources are in close proximity. Talus properties of rock size and vegetative cover appears to work in tandem to buffer the effects of harsher ambient temperatures and allows for survival and viability in this population of pikas. Reclamation seemingly would have the potential to create suitable habitat so as to mitigate the effects of a future changing climate and deleterious effects that may result. Pikas also may exhibit behavioural plasticity outside of their "normal" condition, as is evidenced by their use of atypical habitat in this study and elsewhere, such as under log debris (Bevers 1995) or rock quarries (Rodhouse et al. 2010). Investigating and quantifying the American pika in "atypical" habitat will further contribute to identifying microrefugia requirements encompassed within the niche of this species, and perhaps expand the definition of habitat requirements and range for the American pika.

MANAGEMENT IMPLICATIONS

In related research (Waterhouse et al. 2017 – Appendix A), genetic discontinuity was revealed in my study population. Pikas occupying artificial habitat exhibited significantly higher relatedness estimates; at a finer scale, pairwise estimates of differentiation and migration rates suggest little gene flow may be occurring among sites across the sampling region. Two possible mechanisms that contributed to this were isolation of habitat pockets on the mine-site surrounded by haul roads, and/or the extreme summer heat limiting dispersal distance. Therefore, reclamation initiatives on industrial landscapes that create continuity via artificial dispersal routes (corridors) between pika habitat patches (artificial or natural) will likely promote gene flow amongst pika patches.

In the summer of 2013, exploratory drill testing for copper within my study site caused alterations in drainage patterns and flooding that eliminated at least three denning sites. Elsewhere, construction of an access road through a small forest stand removed trees that provided shade cover for pika den sites. As the American pika is not considered at-risk in

British Columbia, these and other land-use impacts on the species do not require redress. Still, my study suggests that reclamation of pika habitat may not be overly complicated nor expensive. Reclamation and management plans should include retaining or planting native tree species to provide shade on den sites in summer that may be useful at lower (hot) elevations, and also may contribute to maintaining snowpack (insulation) until temperatures warm in spring. This would also provide shade during summer and therefore, cooler dispersal routes that may contribute to a higher success of territory acquisition by juveniles. As well, understory vegetation adjacent to talus slopes provide nutrition, as pikas do not forage far off of talus. Leaving rock piles and overburden unseeded and allowing native vegetation to grow in patches around and amongst talus can support not only pikas but other species sharing the same habitat, such as marmots and woodrats.

LIMITATIONS AND FUTURE RESEARCH

Studies of wildlife populations on reclaimed habitat are critical to understanding the complex issues involved in returning disturbed land to viable habitat, whether the end target is a particular ecosystem, wildlife community and/or focal species. Where possible, this work should involve a comparison of populations living on the reclaimed land with that of natural habitat. However, maintaining support for long-term wildlife research is difficult, resulting in short-term studies (such as that herein) that may not detect long-term trends or shifts in demographics. These assessments should involve more than simple abundance or density estimates, such as the more detailed comparison presented herein; at the same time, intense, short term data such as mine should not preclude longer term monitoring that will fully reveal population dynamics. I suggest conducting research that is long-term, assessing populations from birth to death of individuals and subsequent documentation of extirpation-recolonization events.

Alongside direct disturbance to pika talus habitat (mining, forestry), there is evidence that other pressures also affect pika viability. The effects of livestock grazing on pika foraging habitat quality has not been well studied, but there is evidence that livestock has a negative effect on pika persistence (Millar 2011). Compaction of soil and overgrazing can lead to changes in plant community structure, thereby potentially reducing pika foraging habitat

(Zhu et al. 2016). In an earlier study conducted at my sites (Leung et al. 2014), plant species located in areas at the base of talus slopes were also found stored in haypiles, suggesting foraging of pikas is not restricted to talus patches. This region of BC provides an excellent study area for future research to determine how pika foraging habitat may be affected by livestock, as ranches and grazing land inundate the region.

Lastly, microclimate appears to play an integral role in the American pika's ability to cope with local temperatures beyond previously described lethal thermal limits for this species. Although data collected in my study illustrated the buffering capacity of the talus, I was constrained in several ways. Monetary and time restrictions allowed only one "group" of ibutton placement at selected den sites. Placement of sensors deeper into the talus (a challenging feat) perhaps would have made for interesting comparisons. Other researchers also have encountered difficulties in achieving consistent and meaningful placement of sensors in crevice depths (Rodhouse et al. 2017; Wilkening et al. 2011). It was beyond the scope of this study to determine exactly when an individual died during the winter, and thus I could not equate specific mortalities to specific temperatures (or other causes of winter death). Physiological tolerances of pikas, when exposed to freezing winter temperatures, are unknown (Smith and Millar 2018); evidence is mounting that winter cold stress may contribute more to American pika extinction risk than summer heat stress (Rodhouse et al. 2017; Smith and Nagy 2015; Schwalm et al. 2016). Investigation of how variation in environmental parameters amongst localities contributes to differences in survival rates of this species based on regions (Jeffress et al. 2013) will fill gaps in understanding this species. Future research should investigate American pika temperature thresholds, as temperature study on this species still invokes Smith et al.'s (1974a) 25.5 °C benchmark as an upper lethal threshold. My research contributes further to knowledge of the range of conditions that the American pika can occupy and remain viable, namely, on a landscape that has undergone severe anthropogenic impacts and that also experiences extreme temperature shifts.

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APPENDIX A

GENETIC VARIATION AND FINE-SCALE POPULATION STRUCTURE IN AMERICAN PIKAS ACROSS A HUMAN-MODIFIED LANDSCAPE[1]

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RESEARCH ARTICLE

Genetic variation and fine-scale population structure in American pikas across a human-modified landscape

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Abstract Natural resource extraction can represent a major human modification to the landscape. Habitat reclamation is becoming an increasingly important strategy for abating the loss of biodiversity associated with these developments; however, the demographic and genetic consequences of colonizing artificial habitat remain unknown in many species. Here, we investigated the genetic consequences of landscape modifications for the American pika (*Ochotona princeps*) relative to two major developments in British Columbia, Canada: a large open-pit copper mine (Highland Valley Copper) under partial reclamation and a bisecting major highway (97C). We assessed microsatellite genotypic data for 109 individuals across 15 sites located either within the mine on artificial habitat or on adjacent natural habitat both north and south of the highway. There were no significant differences in levels of heterozygosity, allelic richness or inbreeding between natural (n = 7) and artificial sites (n = 8). However, pikas residing on artificial habitat exhibited significantly higher relatedness estimates. Bayesian clustering analyses revealed two distinct genetic units corresponding to north and south of the highway, with further substructure detected in the south. Likewise, high genetic friction was detected in the central region of the area, largely corresponding to the highway and modified landscape associated with the mine. At a finer scale, pairwise estimates of differentiation and migration rates suggest little gene flow may be occurring among sites across the sampling area, with some evidence for directional migration from artificial to natural sites. Overall, artificial habitat has been successful in promoting occupancy for American pikas, however, barriers to gene flow likely associated with resource extraction and road construction limit connectivity across the landscape.

Keywords *Ochotona princeps* · Fragmentation · Dispersal · Landscape genetics · Habitat modification · Mining · Reclamation

Introduction

There is a diverse array of research and knowledge on how habitat alterations influence wildlife populations (reviewed in Saunders et al. 1991 and more recently in Keyghobadi 2007). Fragmentation of habitat can cause major impediments to dispersal (Baguette et al. 2003; Buchmann et al. 2013), having disproportionate effects on some taxa, such as small mammals (Sauvajot et al. 1998). Reduced dispersal can hinder metapopulation dynamics (Fischer and Lindenmayer 2007), leading to reduced resilience in the face of ecological stress. Furthermore, barriers to dispersal may limit the potential of a species to shift its range in response to climate change (Parmesan and Yohe 2003). Habitat modifications leading to reductions in population size can also negatively impact genetic diversity (Frankham 1996), which may influence a species' ability to locally adapt to changing environments (Sgrò et al. 2011).

Reclamation activities are increasingly applied to disturbed landscapes in an attempt to improve the suitability of the land to wildlife, with or without a specific target species in mind (Ruiz-Jaen and Aide 2005). For example, many mining operations are now heavily involved in reclamation, often with the end goal of mitigating the initial disturbance and improving habitat recolonization by plants

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and animals (Eaton et al. 2014). Such activities could represent an important mechanism for reducing impacts to biodiversity on multiple scales. However, we have little direct evidence of the potential consequences colonizing artificial habitat may have on the resulting demographic structure of wildlife populations on these landscapes. In particular, the juxtaposition of local, artificial habitat and neighboring natural habitat may influence the extent and direction of gene flow. Moreover, anthropogenic landscape features (e.g., roadways) commonly associated with these areas may lead to further habitat fragmentation. Understanding how ecological processes act within reclaimed landscapes is an important step forward in our efforts to improve the resiliency of wildlife populations.

Species with narrow habitat requirements that are able to colonize human-modified environments may provide good opportunities for investigating the relationship between demography, population genetics, and landscape modifications. The American pika (*Ochotona princeps*) is a small lagomorph which has shown a narrow tolerance range for ambient temperature (Smith 1974; Hafner and Sullivan 1995; Beever et al. 2010; Stewart et al. 2015). This species is patchily distributed in rocky, talus-type habitats across mountainous areas throughout western North America from central British Columbia and Alberta, Canada, south to the Sierra Nevada in California and east to New Mexico, USA. In some instances, American pikas have colonized reclaimed mining landscapes, most notably in Bodie, California, USA (Peacock and Smith 1997a, b). The fragmented nature of their habitat and limited dispersal ability (Henry et al. 2012; Castillo et al. 2014; Robson et al. 2016) has propelled the American pika as a focal mammalian species for studies of metapopulation dynamics, island biogeography, and source-sink dynamics (Peacock and Smith 1997b; Moilanen et al. 1998; Kreuzer and Huntly 2003; Beever et al. 2013).

In this study we investigated the genetic consequences of landscape modifications on the American pika relative to two major developments in British Columbia, Canada, a large open-pit copper mine under partial reclamation and a bisecting major highway. We collected microsatellite genotypic data for individuals sampled at sites within and adjacent to the mine both north and south of the highway, and employed site- and landscape-level analyses to quantify levels of variation and connectivity across this humanmodified landscape.

Materials and methods

Study site

Highland Valley Copper (HVC) is located approximately 54 km southwest of Kamloops, BC (Fig. 1a). The original mine was commissioned in 1962, although mineral explorations in the area date back to 1954. Originally, three mines operated in the Highland Valley. In 1986, they were amalgamated into one mine, which is now one of the world's largest open-pit copper mines. Currently, mining operations occupy approximately 6200 ha (Freberg and Gizikoff 1999). Surface developments from the operation of the mine include open pits, waste rock dumps, tailings, infrastructure, water diversions, and roads. Several natural and anthropogenic features punctuate the landscape. The Highland Valley runs east to west through the study site representing an approximate 300 m change in elevation with a seasonal stream (Witches Brook) at the bottom. Additionally, Highway 97C was completed in 1990 running along the bottom of this valley and bisects the HVC mine. Approximately 1320 vehicles use this highway daily, with peak hours between 5 and 8 am and 4–8 pm (British Columbia Ministry of Transportation and Highways 2009).

Major mining operations in the section of HVC north of the highway ceased in 1982 while the southern section remains active. Extensive reclamation activities at HVC were initiated in the late 1980s (Freberg and Gizikoff 1999) and have largely been structured around revegetation and lake remediation. Revegetation goals include: the establishment of forage for cattle, native shrubs and trees for wildlife browse, and conifers for wildlife corridors (Bloodgood et al. 1998). More recently, reclamation plans have been modified to increase biodiversity of the mine (Teck Resources Limited 2012). These plans have never specifically identified American pikas as a target species, but the presence of a population across the reclaimed landscape was first observed by mine workers around 2005, and then formally documented by Howie (2007). The closest natural population of American pikas is adjacent to the mine property within 0.5 km. The elevation of pika-occupied sites in the mine (1350–1550 MSL) is comparable to occupied surrounding sites (1350–1850 MSL).

Sampling

This study is part of a larger project investigating the population ecology of pikas both within and near the HVC operating area (Blair and Larsen unpubl.). Sampling locations were selected on both natural (n = 7) and artificial (n = 8) habitat north and south of Highway 97C based on site occupancy. Pika-occupied sites were initially located by using aerial mapping and local knowledge to identify rocky

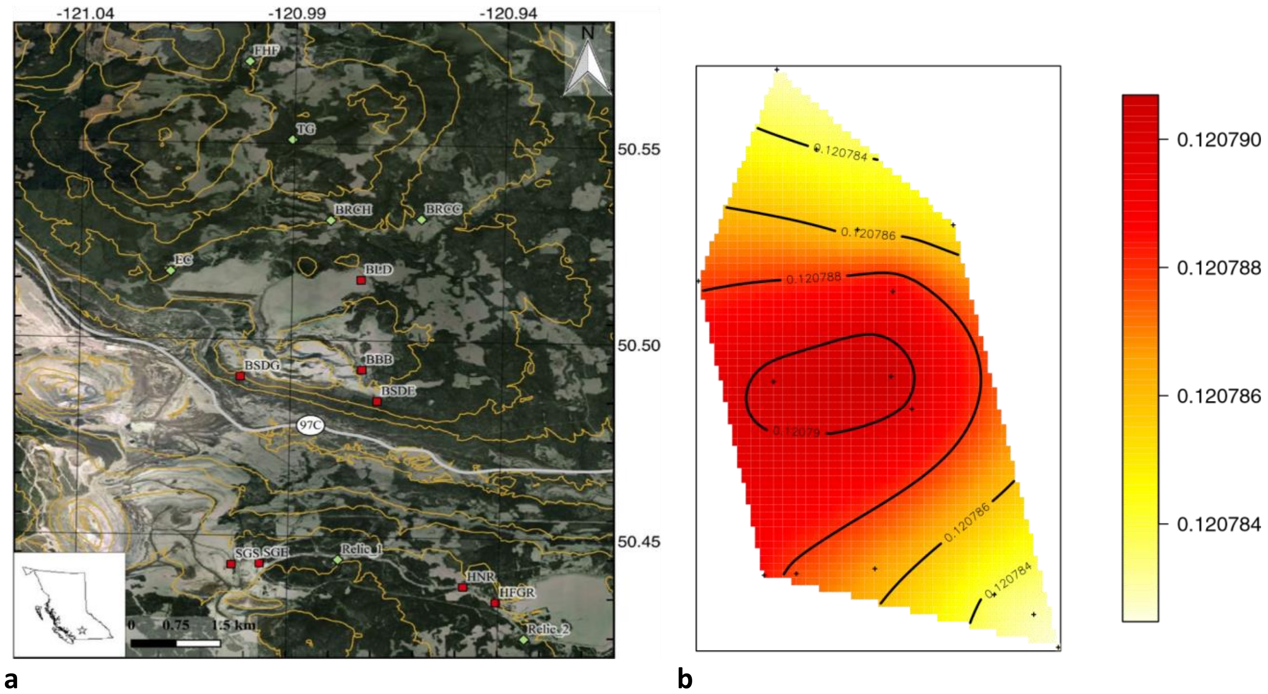

Fig. 1 **a** Map of study area indicating sampling locations within and around the Highland Valley Copper mine in south central British Columbia. See Table 1 for site descriptions. *Green diamonds* represent sites with natural habitat while *red squares* represent sites with artificial habitat. Topographic lines show 100 m changes in elevation and highway 97C is shown. Gridlines show 0.05° changes in latitude and longitude. Two large open pit mines are visible at (−121.04, 50.59) and (−121.04, 50.45). *Darker* areas represent wooded areas whereas lighter areas represent cleared areas from mining or other human activities; talus is not visible at this scale. Aerial photograph obtained from Google™ Earth. **b** Genetic friction map computed across American pika sampling locations. The degree of genetic friction is indicated by the *inset* contour *lines* and *color* (*red* indicates a relative increase in genetic differentiation per unit of geographic distance). *Points* indicate relative locations of sampling sites as shown on the site map. (Color figure online)

areas of both natural and artificial habitat. Intense searching on the ground was then conducted to identify individual pika territories through direct observation of the animals and/or their hay piles. Pika territories were considered to be in artificial habitat when in waste rock dumps and/or riprap from road construction (Fig. 2a). All other sites were considered ‘natural’ and represented talus patches in a relatively undisturbed state (Fig. 2b). Sites were exhaustively trapped between April and October 2012 and between April and November 2013, allowing for the identification of individual pika territories. Pikas were captured using Tomahawk (Hazelhurst, WI) model 202 collapsible live traps in accordance with BC Ministry of Forests, Lands and Natural Resource Operations wildlife permits KA12-78714 and KA13-86652, and Animal Ethics Protocol #100,102 (Thompson Rivers University, BC). All habitat patches within a 500 m radius were considered part of the sample site and were measured using a range finder and tape measure to approximate the total area of habitat for each site. A GPS coordinate was taken at each individual territory and all GPS points within the 500 m radius were averaged to obtain site coordinates.

To determine the age class of captured animals, we combined observational data with estimates of mass using a spring scale and cranial diameter using calipers. Individuals with a mass under 150 g and cranial diameter under 2.5 cm were categorized as juveniles (informed by Smith and Weston 1990); all such individuals were generally trapped emerging from their natal nest and were considered young of the year. To eliminate resampling individuals, each pika was marked with two Monel #1 ear tags (unique number combinations) and one unique color tag. A small tuft of hair was plucked and stored in a coin envelope for subsequent genetic analysis.

Genetic data collection

DNA was extracted using the Macherey–Nagel NucleoSpin Tissue kit (Macherey–Nagel GmbH & Co. KG, Duren, Germany) and manufacturer’s protocols. Eleven polymorphic microsatellite loci were used to genotype each sample (Supplemental Table 1; Peacock et al. 2002; Peacock and Kirchoff, unpublished report). Conditions for PCR amplification followed Henry et al. (2012) including one additional locus (Ocp 10) that was not previously used, but was amplified under the same touchdown PCR protocol. PCR products were co-loaded and run on an ABI 3130XL DNA automated sequencer (Applied Biosystems, Foster City, CA) with GeneScan™ 500 LIZ® size standard. Genotype calls were made using GeneMapper 4.0 (Applied

Biosystems, Foster City, CA). To assess allele-scoring error, 40% of the samples were re-amplified and re-genotyped independently and compared to the original scores.

Sex was determined for each sample by the selective coamplification of an allosomal-linked locus (SRY) and an autosomal control locus (Ocp 10) as described by Lamb et al. (2013). Scoring was conducted by running the PCR product on a 1.5% agarose gel containing 2.5% SYBR Safe (Invitrogen, Carlsbad, California).

The genotypic data were examined for evidence of large allele dropout and null alleles using Microchecker (Van Oosterhout et al. 2004). All loci were tested for deviations from Hardy–Weinberg expectations (HWE) in each sample site using an exact test implemented in Genepop 4.0 (Raymond and Rousset 1995; Rousset 2008). Linkage disequilibrium was tested between all pairs of loci in each site using the exact test of Guo and Thompson (1992) as implemented in Genepop 4.0. Type I error rates for tests of linkage disequilibrium and departure from HWE were corrected for multiple comparisons using the sequential Bonferroni method (Rice 1989).

Site-level analysis

Sex ratios (M:F) were calculated for each site based on the molecular sexing data. We tested for even sex ratios using a chi-squared (χ^2) goodness-of-fit test and the *chisq. test* function in R version 3.3.1 (R Core Team 2015) between the number of males and females for all artificial and natural sites, respectively. Unbiased expected heterozygosity (H_e) was calculated using arlequin 3.5 (Excoffier and Lischer 2010) for each population. Allelic richness (A_R) was estimated using a rarefaction method described by Leberg (2002) to account for biases caused by unequal sample sizes as implemented in hp-rare v1.0 (Kalinowski 2005).

The inbreeding coefficient (F_{is}) was calculated for each site and tested for statistical deviations from zero using 10,000 permutations in Genetix (Belkhir et al. 2004). Pairwise relatedness was calculated between all samples at each site using the estimator developed by Queller and Goodnight (1989) and tested for significance using a permutation test with 1000 replicates in Genalex (Peakall and Smouse 2006). Heterozygosity, rarefied allelic richness, site-level relatedness, and F_{is} were compared between natural and artificial sites using a two-tailed *t* test assuming unequal variances using the *t test* function in R.

Landscape-level analysis

The presence of discrete genetic units was assessed using a Bayesian clustering method implemented in Structure 2.3.4 (Pritchard et al. 2000). An admixture model with correlated allele frequencies was used with a run length of 1,000,000 MCMC replicates after a burn-in period of 500,000. The most likely number of clusters (*K*) was determined by varying *K* from 1 to 17 with 25 iterations per value of *K* and implementing the Δ*K* method (Evanno et al. 2005) using Structure harveSter (Earl and VonHoldt 2011). additional population structure was assessed by rerunning the Structure analysis for each resolved genetic unit separately using the same parameters but varying *K* from 1 to the number of sampling sites in the resolved genetic unit plus 2. An Analysis of Molecular Variance (AMOVA) was performed in Genalex using the resolved genetic groups from the Structure analysis in addition to the natural/artificial classification to determine the degree of genetic differentiation explained by these groupings and tested for significance using a permutation test with 1000 replicates.

The level of genetic differentiation between pairwise comparisons of sites was estimated using θ (Weir and Cockerham 1984) and tested for significance using 10,000 permutations as calculated in Genetix (Belkhir et al. 2004) and corrected for multiple comparisons using the false discovery rate correction (Benjamini and Hochberg 1995). To test for a pattern of isolation-by-distance (IBD), a matrix of genetic distances (θ) was compared to a matrix of Euclidean distances using a Mantel test implemented in the isolation by DiStance Web Service (Jensen et al. 2005) with default parameters and tested for significance using 1000 permutations. This analysis was repeated using the same parameters, but using only sites north or south of highway 97C, respectively. Additionally, to examine the possibility of spatially variable IBD patterns, we first constructed a genetic similarity matrix of ($1-\theta$) between all pairwise comparisons of sites. We then used this genetic similarity matrix to construct a non-stationary genetic friction map displaying the relative genetic divergence per unit of geographic distance as implemented in localDiff (DuforetFrebourg and Blum 2014) using 4 simulated neighbors at a distance of 0.1 and 100 posterior replicates.

The direction and magnitude of contemporary gene flow was assessed using a non-equilibrium Bayesian method implemented in bayesass v. 3 (Wilson and Rannala 2003). A run length of 10,000,000 MCMC replicates with a burnin period of 1,000,000 replicates was used, sampling the chain every 100 iterations. To evaluate consistency, the program was run five times with a different random seed. Given the recovered structure in the dataset (see Results below), we grouped sites for this analysis as follows: north natural, north artificial, south natural, and south artificial. Significance was assumed when the 95% credibility set [mean ± 1.96 × standard deviation (sd)] did not encompass zero, as recommended by the developers (Wilson and Rannala 2003).

Results

Data quality

A total of 109 pikas were sampled from 15 sites, 8 artificial and 7 natural, with an average sample size of 7.3 animals per site (Table 1). Our habitat assessment showed an average of 4117 m^2 of habitat per site with a mean territory of approximately 590 m^2. These parameters agree with previous reports (Smith and Weston 1990) indicating our sampling was likely representative of the total population at these sites. Of these samples, 37 were unambiguously assigned as juveniles, 66 were assigned as adults, and the remaining 6 were indeterminate. The overall dataset contained 1.0% missing genotypic data, with no sample having missing data at more than 3 loci. Independently genotyping 47 random samples showed a 1.4% allelic scoring error rate, which is within reasonable expectations for the use of hair as a genetic source material and is not expected to skew population genetic analyses (Smith and Wang 2014). There was no evidence for large allele dropout or null alleles at any sampling sites with the exception of Ocp 15, which showed evidence of null alleles at four sites (HFGR, Relic_1, SGS, and FHF). Following sequential Bonferroni

Table 1 Sample locations, approximate patch size (m^2), sample sizes (*n*), and genetic diversity metrics for the 15 sampling sites

Site	Area	*n*	*M:F*	Type	H_e	A_R	F_{is}	r_{xy}
BBB	2120	6	1.0	Artificial	0.582	2.21	−0.007	0.363*
BLD	9800	6	5.0	Artificial	0.603	2.32	−0.179	0.394*
BRCC	1200	4	3.0	Natural	0.675	2.48	0.254*	0.072
BRCH	2200	6	0.5	Natural	0.707	2.58	0.018	0.028
BSDE	195	3	2.0	Artificial	0.618	2.35	0.200	0.111
BSDG	7000	5	1.5	Artificial	0.604	2.27	0.008	0.283*
EC	1800	3	2.0	Natural	0.530	2.20	0.270*	0.210
FHF	10,960	13	1.2	Natural	0.654	2.45	0.083	0.143*
HFGR	1740	14	1.3	Artificial	0.590	2.24	−0.038	0.248*
HNR	1285	6	0.5	Artificial	0.601	2.30	0.021	0.206*
Relic_1	8000	16	1.7	Natural	0.596	2.31	0.073	0.209*
Relic_2	1800	4	0.3	Natural	0.601	2.34	0.018	0.180*
SGE	5800	7	0.8	Artificial	0.638	2.40	−0.025	0.143*
SGS	4720	12	3.0	Artificial	0.557	2.14	0.024	0.262*
TG	3135	4	0.3	Natural	0.594	2.31	0.022	0.180*

Sex ratios are expressed in the number of males per female (*M:F*), type indicates either natural talus or artificial habitat. Unbiased expected heterozygosity (H_e), rarified allelic richness (A_R), inbreeding coefficient (F_{is}), and relatedness (r_{xy}) are shown for each site. Significance (<0.05) is shown by an asterisk for F_{is} and r_{xy}

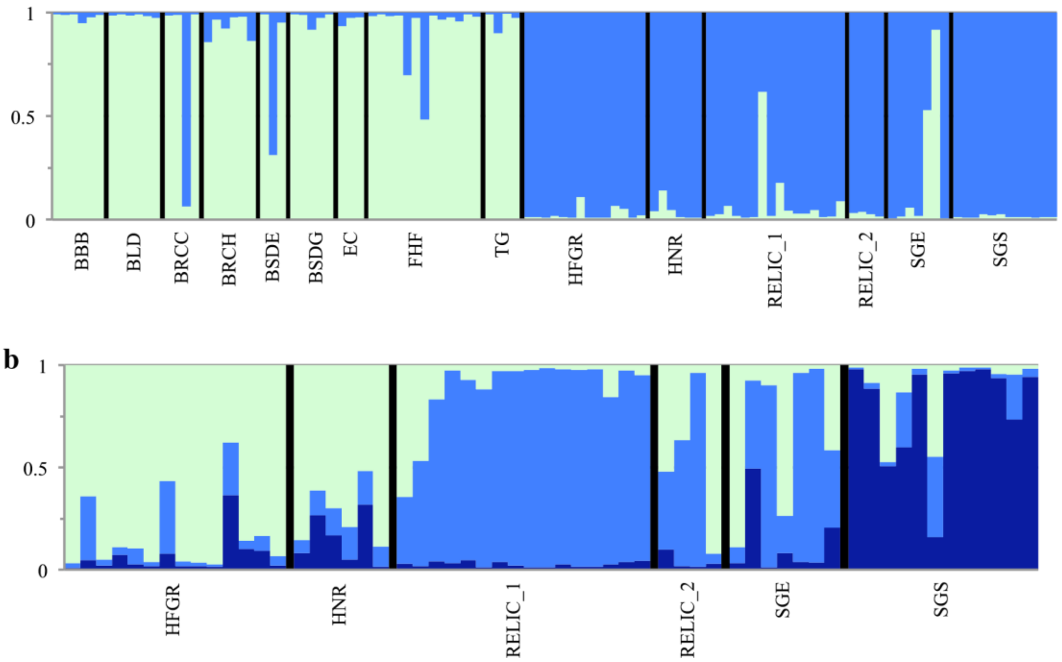

Fig. 2 Photograph depicting typical artificial habitat (**a**) contrasted with natural habitat (**b**) in the Highland Valley Copper mine. Artificial habitat consisted of rock dumps generated from mining activities or road construction. Relatively undisturbed talus patches were considered natural habitat

corrections, no locus deviated from HWE or showed evidence of linkage disequilibrium. Given the lack of a consistent trend in the evidence for null alleles across sites, all loci were retained for further analysis.

Site-level genetic analysis

The average sex ratio (M:F) was 1.9 (SD 1.5) for artificial sites and 1.3 (SD 1.0) for natural sites (Table 1). There was no significant difference between the number of males and females on either natural sites ($\chi^2 = 5.43$, df = 7, $p = 0.61$) or on artificial sites ($\chi^2 = 5.00$, df = 6, $p = 0.54$). Site-level heterozygosity ranged from 0.530 (EC) to 0.707 (BRCH), while A_R ranged from 2.14 (SGS) to 2.58 (BRCH). Sitelevel relatedness ranged from 0.028 to 0.394 and was significantly greater than expected under random mating for 11 of 15 sites (Table 1). Inbreeding estimates ranged from −0.179 to 0.270; 2 of the 15 sites exhibited inbreeding estimates significantly greater than 0. There was no difference in mean genetic diversity estimates between natural and artificial sites for H_e ($t = 0.965$, df = 7.694, $p = 0.82$), A_R ($t = 1.816$, df = 9.996, $p = 0.95$), or F_{is} ($t = 1.034$, df = 11.628, $p = 0.84$). Relatedness was significantly higher at artificial sites (mean = 0.251, SD 0.098) than natural sites (mean = 0.146, SD 0.071; $t = -2.396$, df = 12.580, $p = 0.016$).

a

Landscape-level genetic analysis

The Structure analysis revealed evidence for $K = 2$, corresponding to clusters of sites north and south of highway 97C ($\Delta K = 507.9$; Fig. 3a). Further analysis did not reveal additional genetic units in the north, but resolved three southern genetic units ($\Delta K = 73.7$; Fig. 3b). The two natural sites (Relic_1 and Relic_2) grouped together with an artificial, admixed site (SGE). Two additional artificial sites (HNR and HFGR) grouped together, while one artificial site (SGS) formed a largely distinct cluster from the other southern sites. The AMOVA results showed the north/south divide of highway 97C consistently explained the greatest amount of genetic variation, and the natural/ artificial demarcation explained the least (Table 2). While all grouping scenarios were significant, the four genetic clusters resolved by the Structure analysis were the most explanatory followed by the natural/artificial grouping when the north/south divide was added to the hierarchical structure ($K = 4$).

Significant genetic differentiation was found for 35 of 105 of the pairwise site comparisons of θ (Table 3). A weak but significant pattern of IBD was also detected ($r^2 = 0.080$, $p = 0.009$) where genetic distance increased with geographic distance when considering all sites. This pattern did not hold when only considering sites north ($r^2 = 0.003$,

Fig. 3 Structure bar plots averaged over 25 iterations showing the ($\Delta K = 73.7$). No further genetic subdivisions were resolved within the genetic division (**a**) between sites north and south of highway 97C northern genetic unit ($\Delta K = 507.9$) and (**b**) in the south only when analyzed independently

Table 2 AMOVA results showing the distribution of genetic variation explained by different hierarchical classification schemes

	Among groups (%)	Among sites within groups (%)	Within sites (%)	Significance
Structure clusters ($K = 2$)	5.7	10.5	83.8	<0.001
Structure clusters ($K = 4$)	6.7	8.7	84.6	<0.001
Natural/artificial ($K = 2$)	0.9	13.4	85.7	<0.005
Natural/artificial ($K = 4$)	6.0	9.0	85.0	<0.001

The Structure clusters ($K = 2$) represent the north/south divide of highway 97C, while the Structure clusters ($K = 4$) takes into account the observed substructure in the south. Natural/artificial ($K = 2$) groups sites by habitat type, while natural/artificial ($K = 4$) includes groupings by habitat type divided into north and south of highway 97C.

Table 3 Pairwise site comparisons of genetic differentiation (θ) for American pikas within and around Highland Valley Copper and highway 97C

	BLD	BRCC	BRCH	BSDE	BSDG	EC	FHF	TG	HFGR	HNR	Relic_1	Relic_2	SGE	SGS
BBB	0.234	0.160	0.115	0.117	0.169	0.178	0.163*	0.152	0.253*	0.224	0.210*	0.177	0.165*	0.191*
BLD		0.131	0.168	0.116	0.080	0.253	0.134*	0.194	0.200*	0.209	0.228*	0.255	0.215*	0.268*
BRCC			0.048	0.132	0.064	−0.005	0.070	0.059	0.118	0.131	0.097	0.107	0.107	0.216*
BRCH				0.092	0.109	0.080	0.037	0.080	0.096*	0.053	0.097*	0.110	0.043	0.102*
BSDE					0.084	0.174	0.131	0.103	0.147	0.110	0.124	0.099	0.103	0.210
BSDG						0.175	0.121*	0.137	0.161*	0.174	0.195*	0.188	0.163	0.211*
EC							0.121	0.127	0.188	0.194	0.149	0.167	0.114	0.217
FHF								0.046	0.142*	0.105*	0.141*	0.156*	0.092*	0.202*
TG									0.186*	0.152	0.181*	0.143	0.152	0.261*
HFGR										0.024	0.108*	0.055	0.092*	0.151*
HNR											0.088*	0.023	0.063	0.094*
Relic_1												0.042	0.017	0.178*
Relic_2													0.039	0.157*
SGE														0.115*

*Values that are statistically significant after correction for false discovery rate, $P_{critical} < 0.015$

$p = 0.402$) or south ($r^2 = 0.087$, $p = 0.122$) of highway 97C. The genetic friction map resolved a localized area of disproportionately high genetic differentiation in the central region of the study area largely corresponding with landscape modification associated with HVC and highway 97C (indicated in red; Fig. 1b).

There was no genetic evidence of migration between the northern and southern genetic units. Within these genetic units, 7.6% (SD 3.8%) and 24.8% (SD 6.7) of pikas residing on natural sites in the north and south, respectively, were estimated to be recent migrants from adjacent artificial sites. No significant migration from natural to artificial sites was detected in either region.

Discussion

In this study, we investigated genetic variation and connectivity within and among sites occupied by American pikas across a human-modified landscape. We detected evidence that American pikas are influenced by habitat modification at both site- and landscape-level spatial scales, the nature of which may have implications for

(Smith 1980; Moilanen et al. 1998), which may have potential genetic consequences. For example, American pika-occupied sites in ore dumps in Bodie, California averaged 2.49 alleles per locus (Klinger and Peacock, in prep), similar to the levels reported for artificial sites here (A_R = 2.33). These values are substantially lower than those reported by studies that used partially overlapping loci within natural habitat in the range core in Nevada (A_R = 4.4; Meredith 2002), and Oregon (A_R = 5.7; Castillo et al. 2014). It is important to note, however, that our study occurred towards the northern range margin of the American pika; theory predicts that levels of within-population genetic diversity declines towards range peripheries (Lesica and Allendorf 1995; Durka 1999; Eckert et al. 2008). As a case in point, levels of allelic richness and heterozygosity detected in the current study were similar to those reported at natural sites at the northern range margin in Tweedsmuir South Provincial Park in British Columbia (A_R = 2.8, H_e = 0.62; Henry et al. 2012). Consequently, we cannot disentangle the relative impacts of fine-scale landscape modification from broader-scale range-wide patterns in interpreting the low levels of within-site genetic variation in and around HVC.

Additionally, we saw no difference in either heterozygosity or allelic richness between artificial and natural sites possibly owing to the limited sample sizes associated with such a fine-scale assessment or a lack of significant demographic perturbation associated with development. There was, however, a significant increase in relatedness on artificial sites. Artificial sites were originally formed by mining activities (1962 or newer). Given their relatively contemporary origin, these sites were likely colonized much more recently than surrounding natural sites, and are therefore potentially subject to founder effects (Mayr 1963; Nei et al. 1975). Moreover, the artificial sites show some evidence of isolation, exhibiting both detectable levels of genetic divergence from and unidirectional migration towards natural sites, which may have contributed to the elevated levels of relatedness.

The evidence of directional migration from artificial to natural sites also has implications for metapopulation dynamics in this system. Peacock and Smith (1997b) found that dispersal in American pikas is resource dependent, where the primary resource is available habitat, and dispersing individuals generally settle on the first available territory. Moreover, immigration patterns in American pikas are largely a function of local demographic processes of birth rates and habitat saturation (Kreuzer and Huntly 2003). Habitat saturation can be highly variable, but can occur even in artificial habitat in a mine setting (Smith 1980). In this context, the artificial sites studied here may have a lower carrying capacity, spurring directional movement towards more natural settings. As a case in point, preliminary analyses indicate significant differences of both thermal and vegetative characteristics between our artificial and natural sites. Both surface and subsurface temperatures at American pika territories on artificial habitat were significantly more variable than their natural counterparts, and ambient temperatures tended to be higher on artificial habitat (Spilker, unpublished data). Additionally, there were marked differences in the plant (forage) communities between the artificial and natural territories, due in part to the types of species used in the reclamation process. However, nutritional (i.e., nitrogen) composition did not notably differ in the plants appearing in haypiles at the two territory types (Leung, unpublished data). These thermal and vegetative differences could alter habitat quality for American pikas on artificial sites and, in turn, influence local metapopulation dynamics and patterns of gene flow as has been found in other well-studied pika populations (Moilanen et al. 1998). Ongoing ecological assessment of American pikas at our study site could further elucidate metapopulation dynamics in the region and help determine the degree to which variable habitat quality may play a role.

On a broader scale, we resolved extensive genetic structure associated with landscape features. We found evidence for a significant genetic break in this system, corresponding to north and south of the highway, respectively (Fig. 3). Moreover, the central region of the study system bisected by the highway also constitutes an area of high genetic friction (Fig. 1). An increase in genetic structure from reduced connectivity is a central prediction of the genetic effects of roads on wildlife (Balkenhol and Waits 2009), and can occur over relatively short timespans (Martínez-Cruz et al. 2007). However, the degree of genetic impact is species- and context-specific as exemplified by the lack of genetic structure detected in the pygmy rabbit (*Brachylagus idahoensis*), another small bodied lagomorph with a presumed limited dispersal ability (Estes-Zumpf et al. 2010). While this study was conducted over a similar geographic scale and across comparable landscape impediments such as highways, creeks, and reservoirs, the study area contained no mining activity or associated reclaimed habitat.

At a finer level, three genetic units were detected south of the highway, one of which was comprised of a single site, SGS, that formed a unique genetic unit despite close proximity to site SGE (550 m). This distance is well within the American pika dispersal capacity reported elsewhere across the range (maximum distances between 2 and 10 km; Hafner and Sullivan 1995; Peacock 1997). Interestingly, SGS is the only site completely surrounded by intense mining activity (Cheryl Blair, personal observation). Although direct mining activities may have contributed to the isolation of SGS, the additional structure detected south of the highway may be the result of differing sources or timing of colonization of newly created habitat with landscape modifications subsequently limiting gene flow. This hypothesis could be tested in the future with broader sampling of potential source populations to the south.

There are several natural geographic barriers to gene flow that may account, in part, for the genetic structure observed around the mining site. The highway lies at the bottom of a valley representing an approximate 300 m change in elevation, with a small seasonal creek at the bottom. Previous research indicates that both topographic relief (Henry et al. 2012) and water bodies (Castillo et al. 2014) can significantly inhibit pika movement, making natural geographic boundaries a possible alternative explanation for the north/south genetic division. However, this would only account for the north–south genetic division and not the degree of genetic structure observed in the south nor the pattern of genetic friction across the landscape since no other natural barriers to gene flow were observed. Additionally, the degree of topographic relief previously shown to inhibit American pika dispersal was far more extreme than anything found around HVC (Henry et al. 2012; Robson et al. 2016). Future research could potentially disentangle the influence of natural and anthropogenic barriers to gene flow by using a larger sampling of the American pika genome and coalescence-based genetic analyses to determine if the development of observed genetic structure was concurrent with human modifications of the landscape.

In summary, we found evidence that landscape modifications have likely influenced the distribution of genetic variation within this study system, documenting several of the expected patterns of fragmentation on small mammals (Gaines et al. 1997). Specifically, we detected site-level changes in genetic characteristics, a slight but significant degree of genetic differentiation of American pikas inhabiting artificial sites, and significant impacts on genetic structuring and migration that were likely associated with landscape modifications. These alterations could influence metapopulation dynamics, including responses to future environmental stressors. In general, it appears that inhabiting artificial habitat might predispose some species to develop fine-scale genetic structure due, in part, to the colonization patterns of the newly available area. Additionally, by its nature, artificial habitat is generally in close proximity to other landscape modifications; in this study, the artificial habitat sites were bisected by a major highway. These additional landscape modifications could act to further reinforce the development of fine-scale genetic structure.

Overall, this area of reclamation appears successful in promoting occupancy for American pikas within HVC, even though the species was not specifically targeted; however, barriers to gene flow likely associated with resource extraction and road construction may limit connectivity across the landscape. Mitigation strategies for promoting connectivity may be limited for American pikas given their thermal sensitivity and habitat requirements. However, American pikas have been documented inhabiting riprap around a small bridge (Henry et al. 2012), indicating habitat corridors and highway bypasses may be effective in this species, but additional study is required. Furthermore, awareness of the potential demographic and genetic consequences of similar landscape alterations may help encourage the integration of mitigation promoting connectivity directly into management planning in order to benefit other wildlife species in the affected areas. Additionally, this study may serve as a reference point for fine-scale genetic analysis across a human-modified landscape enabling contrast between natural and anthropogenically-induced genetic structure in the American pika.

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