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The role of habitat quality and climate in the dynamics of occupancy and survival of a population of collared pikas (*Ochotona collaris*) in the Ruby Range, Yukon Territory

by

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ABSTRACT

I examined the role of habitat quality and climate in the dynamics of occupancy and survival of a population of collared pikas in the Yukon Territory, Canada. Annual surveys of marked individuals over an 11 year period (1999 to 2009) within a geographically isolated metapopulation were used to analyze relationships between pika occupancy dynamics and habitat quality and between recruitment and survival and measures of climate based on Pacific Decadal Oscillation (PDO) and downscaled regional climate (Climate WNA).

Occupancy dynamics were correlated with the quality of habitat within pika territories in terms of solar radiation and vegetation quality using Normalized Difference Vegetation Index (NDVI) values derived from a remote sensing image as a proxy for above-ground biomass. Recruitment and survival of pikas were correlated with lagged PDO, with results varying by age, sex and aspect. These results demonstrate that occupancy of territories by collared pikas is non-random and based on habitat conditions and that climate has a strong influence on population dynamics at some life stages. This study also demonstrates applications of GIS and remote sensing data for studies at the scale of a small alpine mammal.

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CHAPTER 1   Introduction

A fundamental area of study in ecology is the relationship between species and their environment. Relationships between populations and their natural environment are complex, with multiple and interacting biotic and abiotic factors influencing observed dynamics (Bjørnstad and Grenfell 2001; Agarawal et al. 2007; Previtali et al. 2009). Research is constantly evolving to apply new technologies and techniques, integrate cross-disciplinary findings and re-visit old assumptions in the context of changing research paradigms.

Ecologists draw from a variety of population metrics such as occupancy, abundance, distribution, survival, and fecundity, depending on the available data, the questions under consideration and the scale(s) of inquiry. Demographic data, such as age and sex, can provide additional resolution as different ages and sexes often respond differently to environmental effects (Benton et al. 2006; Beever et al. 2013).

Studies of occupancy and habitat

Studies of occupancy dynamics often use data from metapopulations, which comprise an assemblage of local populations that are spatially separated but able to interact (Moilenan and Hanski 1998; Baguette and Mennechez 2004). Studies of metapopulation dynamics are foundational in conservation biology in relation to species' responses to natural and anthropogenic fragmentation of landscapes (Hanski 1994; Pellet et al. 2007). The dynamics of many vertebrate and invertebrate species are considered to follow the ‘rules’ of metapopulations, including American pika (*Ochotona princeps*) and collared pika (*Ochotona collaris*) on talus patches (Moilenan et al. 1998; Franken 2002; Franken and Hik 2004b), Kirkland’s warbler (*Dendroica kirlandii*) in early successional forests (Donner et al. 2010), European tree frogs (*Hyla arborea*) in breeding ponds (Pellet et al. 2006), butterflies in riparian areas (*Speyeria nokomis apacheana*) (Fleishman et al. 2002) and flower meadows (*Parnassius smintheus*) (Matter et al. 2009); and bees (*Andrena hattorfiana* (Fabricius) in grasslands (Franzen and Nilsson 2012).

Research on metapopulation dynamics initially focused on mathematical studies relating colonization and extinction to the configuration of patches and connectivity linking them (Hanski 1994; Moilanen et al. 1998). Studies have evolved to include various metrics associated with habitat quality (Fleishman et al., 2002; Franken and Hik 2004b; Schooley and Branch 2009; Franzen and Nillson 2010; Robles and Ciudad 2012) assessed over a broader range of spatial and temporal scales other than individual patches (Weigand et al. 1999; With 2004; Thornton et al. 2011). This evolution represents a marrying of metapopulation biology and landscape ecology and recognizes the need to scale studies of organisms “according to their resource-based concept of habitat” (Baguette and Mennechez 2004, pg 399). For example, the composition of forest bird communities varies in response to biotic and abiotic variables at three spatial scales of plot, patch and landscape (Cushman and McGarigal 2004), while patterns of occupancy and turnover of butterflies differ if one considers a single snapshot in time versus multiple years of data (Fleishman et al. 2002).

Advances in geographic information systems (GIS) and remote sensing technologies have enabled spatially explicit studies of relationships between population dynamics and habitat that can be considered over a range of scales and locations (Pettorelli et al. 2005, 2011). For example, Geographic Information System (GIS) technology has been used to describe metapopulation dynamics in amphibians (e.g., mountain yellow-legged frogs (*Rana muscosa)*; Knapp et al. 2003), Cabrera voles (*Microtus cabrerae*) (Pita et al. 2007), forest rodents (Moore and Swihart 2005) and broad-toothed rats (*Mastacomys fuscus*); O'Brien et al. 2008). Normalized Difference Vegetation Index (NDVI), derived from remote sensing imagery, has been used to examine links between the distribution and productivity of vegetation of wide-ranging animals such as red deer (*Cervus elaphus*) (Mysterud et al. 2008); grizzly bear (*Ursus arctos*) (Wiegand et al. 2008); and reindeer (*Rangifer tarandus*) (Bårdsen and Tveraa 2012) as well as small mammals such as grass and vesper mice (*Akodon azarae; Calomys venustus*) (Andreo et al. 2009), desert rodents (*Octodon degus and Phylootis darwini*) (Previtali et al. 2009) and microtine rodents in the Arctic (Olofsson et al. 2012).

Climate influences on population dynamics

The ability to describe definitive causal relationships linking climate and ecological processes has proven elusive. While correlations necessarily exist between population dynamics and metrics of local climate conditions, such as temperature and precipitation, there are many interactions among climate variables (Krebs and Berteaux 2006; Roland and Matter 2013) and feedbacks occurring at different trophic levels (Agarawal et al. 2007; Walther 2010). Researchers acknowledge the challenges of studies of climate and population dynamics but also emphasize the need to define these relationships, particularly given the imperative of anticipating species' responses to climate change (Hallet et al. 2004; Krebs and Berteaux 2006).

Large-scale climate indices such as the Pacific Decadal Oscillation (PDO; Mantua 2002) have proven useful as integrators of multiple climate factors (Hallett 2004; Stenseth and Mysterud 2005) but they have their own limitations (Knape and de Valpine 2011). The increasing sophistication and accuracy of downscaled climate data increases the feasibility of using local climate variables in population studies (e.g., Hayhoe 2010; Wang et al. 2012).

Arctic and alpine species occur in highly seasonal environments and therefore have specific vulnerabilities to climate. Climate-related effects are expected to become more pronounced under climate change (AMAP 2012; Jentsch et al. 2007) requiring a broadening of climate studies to look beyond average climate statistics and focus on potential vulnerabilities to extreme and stochastic events and to consider non-linear responses (Walther 2010; Roland and Matter 2013).

Integration of research themes moving forward

Studies in ecology have implicitly held a number of simplifying assumptions that need to be re-considered to embrace the complexity of ecological systems (Agarawal et al. 2007; Walther 2010). This includes accounting for interactions and feedbacks, recognizing that these may manifest differently with scale and context (Agarawal et al. 2007). While it would not be possible to model all of the interactions in ecological systems, there are a number of themes that have emerged to more explicitly account for complexity:

- Hypotheses should define simple relationships based on the known biology of the species with *a priori* identification of the most suitable climate or habitat variable(s) (Krebs and Berteaux 2006; Beever et al. 2013; Rolands and Matter 2013).
- There is a need to understand the mechanisms underlying relationships and trends, with a focus on a links between environmental characteristics and conditions and specific life history strategies and traits (Benton et al. 2006; Krebs and Berteaux 2006; Neilsen et al. 2012; Beever et al. 2013; Roland and Matter 2013). Demographic data such as survivorship, fecundity and mortality and physiological condition can provide

additional resolution for identifying specific links to the environment (Benton et al. 2006; Beever et al. 2013).

- Relationships should be considered across the multiple spatial scales at which an organism interacts with its environment (Weigand et al. 1999; Thornton et al. 2011) recognizing that correlations may differ with scale (Agarawal et al. 2006). For example, additional information was revealed by considering local site characteristics in conjunction with geographically extensive analyses of relationships between American pikas and climate (Wilkening et al. 2011; Jeffress et al. 2013).

This sometimes ‘Zenful’ endeavour aims to find simplicity while acknowledging complexity with the goal of continuing stepwise to build and expand on what is known about ecological systems, generally and for each species.

Study species: The ecology of collared pikas

Collared pikas inhabit talus-meadow complexes in alpine areas at higher latitudes in western North America (Figure 1-1). There are two species of rock-dwelling pikas (Order Lagomorpha) in North America: collared pika, *Ochotona collaris* and American pika, *O. princeps.* The distribution of collared pikas extends throughout mountainous regions of Alaska, the Yukon Territory and into the western Northwest Territories and northern British Columbia. The five recognized sub-species of American pika occur in with a discontinuous distribution across southern B.C. and Alberta and the northwestern United States (Figure 1-2). Pikas in North America are monophyletic having evolved from a common ancestor (*O. spanglei*) that migrated from Asia and then diverged between 4.7 and 15.7 million years ago (Lanier and Olson 2012). Collared pikas are separated from American pikas by approximately 800 km of suitable yet unpopulated habitat. This separation is commonly attributed to a disjunction of pika populations by continental and mountain glaciers in the last Ice Age (Guthrie 1973; MacDonald and Jones 1987) although recent molecular analysis suggests the divergence goes back much further in time (Lanier and Olson 2012; Zgurski 2011). While the two species share many characteristics and life history traits, there are differences in reproduction, dispersal behaviour and occupancy that can likely be attributed to differences in their location and environment.

North American pika species have been used as model species of classic metapopulation dynamics because they occur as local populations in spatially distinct talus patches connected to each other through dispersal across a matrix of alpine meadow (Moilenan et al. 1998; Hanski 1999; Franken 2002; Franken and Hik 2004b) (Figure 1-3). Pikas are useful indicators for population studies for the following reasons:

- Territories are approximately 900m^2 in size (MacDonald and Jones 1987) and can be observed in their entirety on the open alpine landscape. Once established on a territory, individual pikas are highly philopatric. They make frequent trips out into vegetated areas surrounding the talus and back, but rarely forage further than 6 – 10m from talus (Morrison et al. 2004; McIntire and Hik 2005).

- Territories are easy to identify on the landscape and activity can be enumerated with confidence. Pikas are diurnal, have distinct vocalizations (small barks), accumulate dried vegetation in haypiles that are large and very visible, particularly late in the growing season, and leave latrines of distinctive small round pellets (MacDonald and Jones 1987). Previous studies of collared pikas in the Ruby Range have an estimated success rate for trapping and population enumeration at > 99% (Morrison and Hik 2007).
- Pikas do not hibernate, which imbues on them different vulnerabilities across seasons compared to animals that hibernate for the winter months.

Demography

Collared pikas at my study site in southwest Yukon can live up to 5 years (Franken 2002), but the average lifespan during my study period (1999 – 2009) was 2.12 years (unpublished data). Breeding typically occurs early in the spring (April - May) and gestation takes 30 days. Collared pikas are reproductively mature at one year and have one litter of 1 – 4 offspring (MacDonald and Jones 1987) from which an average of two individuals are successfully weaned (Franken and Hik 2004a). Female American pikas may lose some or all of their litter *in utero* following severe weather events and approximately half of litters are lost between birth and weaning (Millar

1974). Because birth and weaning of collared pikas occurs within the talus and beneath snow cover, there is no data available on survival of litters of this species prior to emergence (e.g., maternal condition, birth weight, litter size). Based on the weight of newly emerged juveniles, parturition is estimated to occur from early June to early July and appears to be synchronized to the timing of snowmelt and the first flush of green-up (Franken and Hik 2004a). Juveniles rapidly gain body mass and are able to achieve adult mass by the end of their first growing season (Franken 2002). Over-winter mortality is high at all ages, but is particularly high for young of the year (Franken and Hik 2004a).

Juvenile collared pikas disperse immediately following emergence and, unlike juvenile American pikas that tend to remain within 50m of their natal range (Smith and Ivins 1983), individual collared pikas of both sexes disperse an average of 500m (Zgurski and Hik 2012). Territories are established based on conspecific attraction, with males and females settling next to one another (Smith and Ivins 1983; Zgurski 2011; Zgurski and Hik 2012). American pikas use sexual alternation of territories as a way to maintain the spatial demography of the population (Smith and Ivins 1983) but collared pikas have a less restrictive mating system (Zgurski and Hik 2012).

Life history

Collared pikas are generalist herbivores. They are solitary and territorial, maintaining individual territories that comprise one or more haypiles in the talus and surrounding vegetation (Figure 1-3). Individuals show high levels of philopatry to their territory, particularly as adults. They will vigorously defend that territory against other pikas, particularly during haying (Smith and Ivins 1983).

A number of studies point to the importance of the quality of vegetation (plant species composition, physical size and nutritional quality) to pika fitness. During the growing season, most of the surface time of pikas is spent grazing and gathering vegetation to cure and cache in their haypiles (Figure 1-4). Adult collared pikas begin haying not long after emergence in the spring and continue until meadows are covered by snow in the autumn (K. O'Donovan, unpublished observations). Juveniles begin haying later than adults but amass a haypile by the end of the season (Morrison et al. 2009). Collared pikas gather enough material in their haypiles to last 5 – 6 months, suggesting that hoarding provides a primary food source for the winter months (Morrison et al. 2009), although it is likely that they also graze on cushion plants, evergreen shrubs and lichens that remain available through the winter under the snow (Hudson et al. 2008). Pikas preferentially gather larger (Hudson et al. 2008) and more nutritious (Morrison and Hik 2008) vegetation for their haypiles, which is likely a strategy to optimize the amount and quality of vegetation gathered per trip for these central-place foragers (Huntly et al. 1986; Hudson et al. 2008; Morrison and Hik 2008). Selection of forage species does not change with increasing levels of predation risk, although the amount of vegetation taken is less per trip

(Morrison et al. 2004). Grazing is most intensive up to 6m from the talus and there is evidence of a positive feedback loop between chronic grazing with periodic release and above-ground biomass and species richness (McIntire and Hik 2005).

Little is known about what happens while collared pikas are active beneath the snow during the long winter months, but there must be social interaction because breeding occurs well before snowmelt and parentage analyses show that males travel several hundred metres to mate (Zgurski 2012). The survival of adult females tracks temperature changes associated with the Pacific Decadal Oscillation (PDO), which can be correlated to timing of snow melt (Morrison and Hik 2007). Earlier snowmelt is thought to increase probability of survival because a longer growing season provides individuals with additional time to gain body mass and accumulate their haypiles (Morrison and Hik 2007; Morrison et al. 2009). The interaction of winter temperature and precipitation are also thought to be important to survival, since winter snows provide a critical insulating layer for American and collared pikas, protecting them from events such as freezing rain (Smith 1978; Morrison et al. 2009).

Conservation issues

There is concern that collared and American pikas are vulnerable to rapid warming of high elevation ecosystems under climate change (Bruggeman 2009; Beever et al. 2010; COSEWIC 2011). The Canadian Committee on the Status of Endangered Wildlife in Canada (COSEWIC) assigned collared pikas a status of Special Concern in November 2011 due to the substantial potential for “negative impacts of climate change to the persistence of this species over the long term” (www.cosewic.gc.ca; accessed June 22 2013). The COSEWIC status recognizes the increased vulnerability due to the species’ “demonstrated sensitivity to climate variability… poor dispersal ability and the naturally fragmented nature of its populations” (COSEWIC 2011). NatureServe has ranked collared pikas as Globally Secure (G5; last reviewed in 1996), Nationally Secure in the United States (N5: 1996), Apparently Secure in Canada (N4; down-listed from N5 in 2011) and secure in Alaska (S5) (http://www.natureserve.org/explorer/ranking.htm; accessed June 22 2013). In BC and the Yukon collared pikas have the conservation rank of Vulnerable (now called “Special Concern” in BC) due to “characteristics that make them particularly sensitive to human activities or natural events” (http://www.env.gov.bc.ca/atrisk/, accessed June 22 2013).

Study Area

The Pika Camp study area is located in the Ruby Range, Yukon Territory, at 61°12’N and 138°16’W, to the east of Kluane Lake and Kluane National Park in the St Elias mountain range (Figure 1-5). The elevation of the area ranges from 1500m to 2000m. The overall study area is approximately 2 km x 2 km in size and is naturally divided by topography into four dominant aspects (north, south, east, west). There is one 2m wide stream that flows north-south through the centre of the valley and an ephemeral tributary creek that flows east-west during spring months.

The landscape in this alpine valley consists of talus patches 0.13 ha – 10.0 ha in size separated by meadows of alpine tundra vegetation composed of alpine forbs, graminoid species (sedges, rushes and grasses), shrubs, mosses and lichens. Patches of shrub willow (*Salix* spp.) occur on all aspects. There is evidence of increasing shrub expansion to higher elevations at this site (Myers-Smith 2011). The snow-free growing season is approximately 10 weeks from mid-June to the end of August, but the timing is highly variable. Average monthly temperatures range from -10 to -20°C in winter and 6 to 10°C in the summer, although snow can occur at any time of the year. Precipitation is heaviest and most variable in summer (monthly average 150mm to 300 mm) and lightest in the spring (monthly average 30 - 60 mm) (based on downscaled regional climate data using Climate WNA v4.62 data; Wang et al. 2012).

Collared pikas are sympatric with two other small mammalian herbivores, hoary marmots (*Marmota caligata*) and Arctic ground squirrels (*Urocitellus parryii*) (Patil 2010). Although marmots and pikas both forage close to talus, direct interactions between the two species are infrequent (Patil 2010; Barrio and Hik in review). There is some separation of foraging activity in time as marmots and ground squirrels slow their foraging activities late in the summer in preparation for hibernation while pikas continue harvesting until snowfall (Barash 1973; Morrison et al. 2009).

Marmots make burrows in talus patches, often within close proximity of pikas. Despite their close co-existence, with shared climate and environmental conditions, populations of marmots and pikas fluctuate independently of one another (Patil 2010).

Potential predators of pikas include raptors (rough-legged hawks (*Buteo lagopus* spp.), American kestrels (*Falco sparverius*) and golden eagles (*Aquila chrysaetos*)), red foxes (*Vulpes vulpes*) and short-tailed weasels (*Mustela erminea*). Other animals who pass through the valley include mountain caribou (*Rangifer tarandus*), Dall sheep (*Ovis dalli*), grizzly bear (*Ursus arctos*), wolverine (*Gulo gulo*), and grey wolf (*Canis lupus*).

Research Objectives

The overall objective of my research was to evaluate relationships between habitat occupancy and survival of collared pikas at three spatial scales: metapopulation, talus patch and territory (Figure 1-6). This research used data from 14 years of population surveys, including 11 years of data on marked individuals, and built on previous studies of occupancy and survival in the study area (Franken 2002; 2004 (a) and (b); Morrison and Hik 2007; Patil 2010). New information included the use of spatial data to assess relationships between occupancy and habitat quality at multiple spatial scales and analysis of population-climate relationships by age and sex.

In Chapter 2, I examined occupancy of patches and territories by collared pikas in relation to indicators of spatial configuration (patch size and distance to the nearest occupied patch), topography (slope and elevation), and the quality of vegetation and talus. I used NDVI values derived from a Quickbird remote sensing image for July 31 2007 as a proxy for vegetation and talus quality and tested this assumption by comparing NDVI values to data on plant community distribution and above-ground biomass (Appendix A).

My hypotheses were that occupancy dynamics at the patch scale are influenced by the quality of habitats experienced by individual pikas at the territory scale and that a multi-scale approach more fully explains the variability in occupancy. Based on these hypotheses, I predicted that response variables at the resolution of territories within a patch would explain variability in occupancy more effectively than presence/absence data for whole patches and that territory selection is non-random and is, at least in part, based on the quality of habitats.

The dynamics of pika occupancy at the territory scale have rarely been explored although one study compared differences in demographic rates of American pikas occupying productive and non-productive habitat types (Kreuzer and Huntly 2003) and recent studies have examined the contribution of local site characteristics and microclimate to the distribution of American pikas (Wilkening et al. 2011; Jeffress et al. 2013). This line of inquiry bridges the fields of metapopulation dynamics and landscape ecology by emphasizing the importance of scale to studies of ecological processes (Wiegand et al. 1999; Prugh et al. 2008; Thornton et al. 2011).

In Chapter 3, I assessed the relationship between different age-sex groupings of pikas and seasonal climate, indicated by PDO Index and local climate variables. My goals were to identify the most appropriate climate measures for assessing relationships to adult survival (PDO or local climate) and to investigate the extent to which those relationships vary by age and sex. This work built on previous studies of this pika population that demonstrated a positive correlation between lagged winter PDO index (Nov – May) and adult female survival (Morrison and Hik 2007; Patil 2010).

I predicted that the strongest relationships would be seen between survival and local climate. My rationale for this prediction was that once collared pikas are established on a territory, they are highly philopatric and remain in their small home range for their entire life (Franken 2002), although they will travel up to 500m to mate in the winter (Zgurski and Hik 2012). Therefore they might be expected to have localized responses to climate conditions.

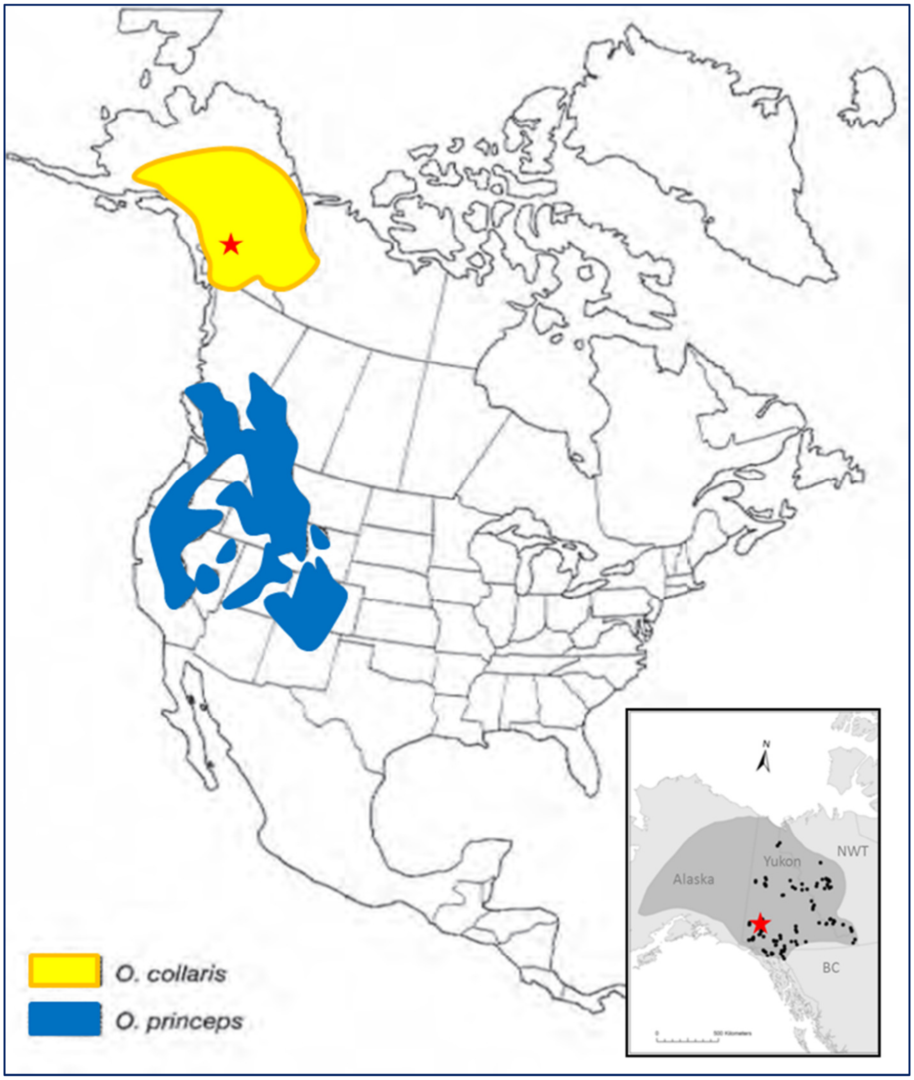
Chapter 4 provides a summary of the key findings of my research chapters and an integration of these findings in the context of current literature. It also provides suggestions for future research.

Figure 1-1. Images of collared pikas taken at Pika Valley, gathering vegetation for the haypile (top) and marked with identifying eartags (bottom).

Photo: Hik lab

Photo: Hik lab

Figure 1-2. The relative distributions of collared pikas (*O. collaris*; yellow) and American pika (*O. princeps*; blue) in North America. The inset shows a close-up of the distribution of collared pikas with dots indicating the locations of specimen collections and field observations in Canada.



(Graphic from Franken and Hik 2002;
Inset map from COSEWIC 2011)

Figure 1-3. Landscape view of the study area, showing a talus patch (EK5 Talus) in a matrix of alpine meadow. This particular talus supported active territories of three pikas (two adults and one juvenile) in 2010 when this photo was taken. The research camp is in the background.

Figure 1-4. Images of haypiles in the talus.

(a) Haypile visible beneath large rock overhang in lower centre of the photograph.

(b) Close-up of haypile beneath the rocks, showing fresh and dried vegetation, including leaves of *Petasites frigidus* and *Dryas octopetala*, as well as grasses and forbs.

Figure 1-5. The location of the study site in the Ruby Range, east of Kluane Lake in the southwestern Yukon (map image from Google Maps). The study site is indicated by a red star.

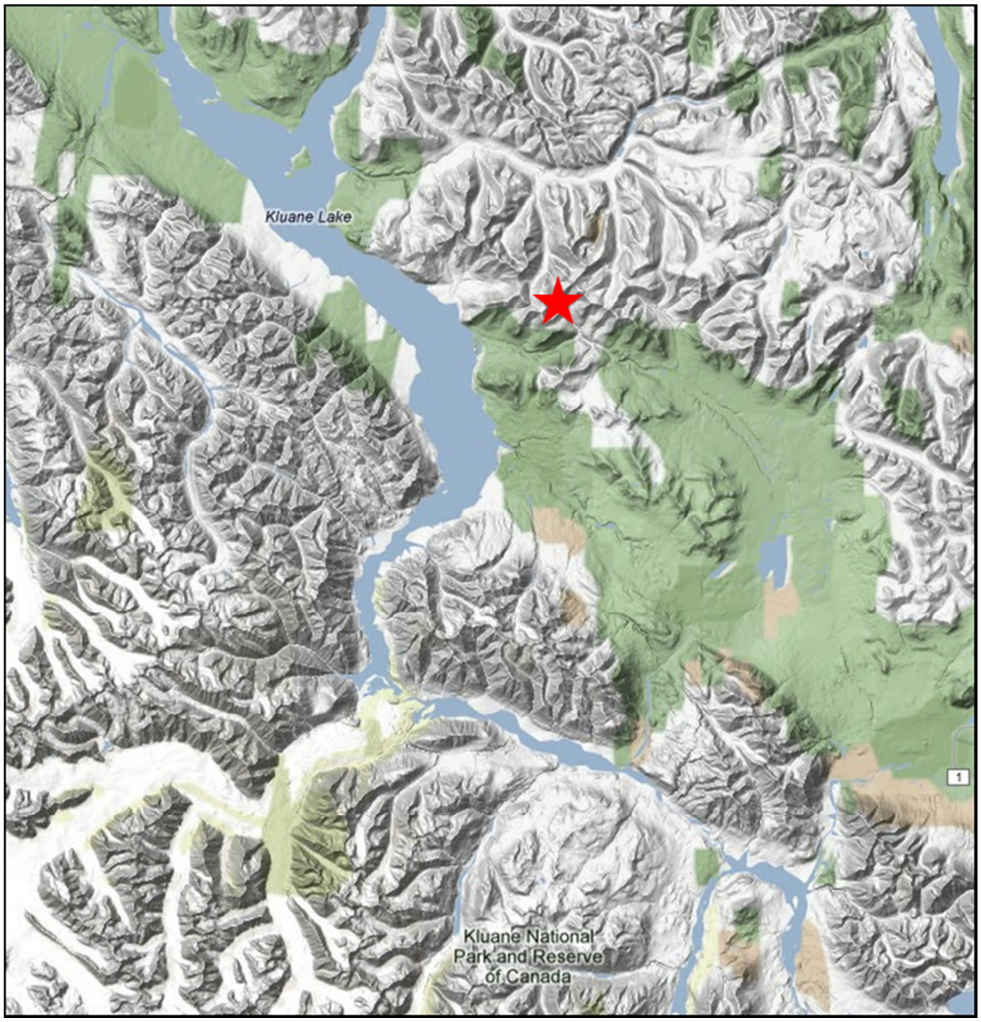
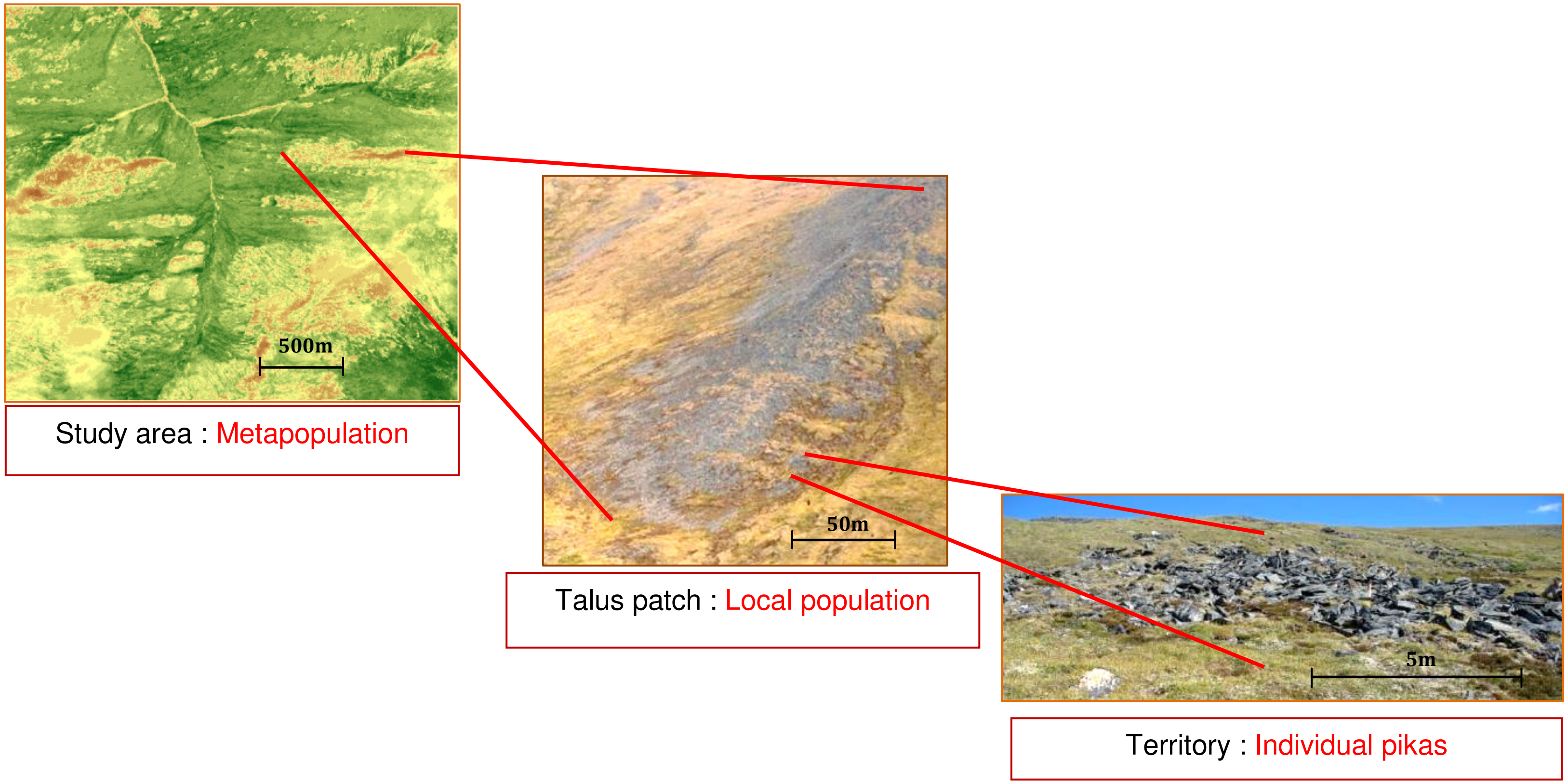


Figure 1-6. Three spatial scales for analysis of collared pika dynamics: metapopulation, talus patch and territory.



LITERATURE CITED

Agarawal, A.A., D.D. Ackerly, F. Adler, A.E. Arnold, C. Cáceres, D.F. Doak, E. Post, P.J. Hudson, J. Maron, K.A. Mooney, M. Power, D. Schemske, J. Stachowicz, S. Strauss, M.G. Turner, and E. Werner. 2007. Filling key gaps in population and community ecology. Frontiers in Ecology and Environment 5(3): 145 – 152.

Aitchison, C.W. 2001. The effect of snow cover on small animals. In Snow Ecology: An Interdisciplinary Examination of Snow-Covered Ecosystems. (H.G. Jones, J.W. Pomeroy, D.A. Walker and R.W. Hoham eds). Cambridge University Press, Cambridge, U.K. pp 229 – 265.

AMAP (Arctic Monitoring and Assessment Programme). 2012. Arctic Climate Issues 2011: Changes in Arctic Snow, Water, Ice and Permafrost. SWIPA 2011 Overview Report.

Andreo, V., M. Lima, C. Provensal, J. Priotto, and J. Polop. 2009. Population dynamics of two rodent species in agro-ecosystems of central Argentina: intra-specific competition, land-use and climate effects. Population Ecology 51: 297 – 306.

Baguette, M. and G. Mennechez. 2004. Resource and habitat patches, landscape ecology and metapopulation biology: a consensual viewpoint. Oikos 106(2): 399 – 403.

Barash, D.P. 1973. Habitat utilization in three species of subalpine mammals. Journal of Mammalogy 54(1): 247 – 250.

Bårdsen, B-J., and T. Tveraa. 2012. Density-dependence vs. density-independence – linking reproductive allocation to population abundance and vegetation greenness. Journal of Animal Ecology 81: 264 – 376.

Beever, E.A., C. Ray, P.W. Mote, and J.L. Wilkening. 2010. Testing alternative models of climate-mediated extirpations. Ecological Applications 20(1): 164 – 178.

Beever, E. A., S. Z. Dobrowski, J. Long, A. R. Mynsberge, and N. B. Piekielek. In press. Understanding relationships among abundance, extirpation, and climate at ecoregional scales. Ecology.

Benton, T.G., S.J. Plaistow, and T.N. Coulson. 2006. Complex population dynamics and complex causation: devils, details and demography. Proceedings of the Royal Society B 273: 1173 – 1181.

Bjørnstad, O.N., and B.T. Grenfell. 2001. Noisy clockwork: time series analysis of population fluctuations in animals. Science 293: 638 – 643.

Bruggerman, J.E. 2010. Pilot Study on Factors Affecting Pika Populations in the North Cascades Ecosystem: Final Report. Beartooth Wildlife Research, Farmington, Minnesota.

COSEWIC. 2011. COSEWIC assessment and status report on the Collared Pika, *Ochotona collaris,* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. (http://www.sararegistry.gc.ca/virtual_sara/files/cosewic/sr%5Fcollared%5Fpika%5Fcollier%5F0912%5Fe%2Epdf)

Cushman, S.A. and K. McGarigal. 2004. Hierarchical analysis of forest bird species-environment relationships in the Oregon Coast Range. Ecological Applications 14(4): 1090 – 1105.

Donner, D.M., C.A. Ribic, and J.R. Probst. 2010. Patch dynamics and the timing of colonization – abandonment events by male Kirtlands's Warblers in an early succession habitat. Biological Conservation 143: 1159 – 1167.

Fleishman, E., C. Ray, P. Sjögren-Gulve, C.L. Boggs and D.D. Murphy. 2002. Assessing the roles of patch quality, area and isolation in predicting metapopulation dynamics. Conservation Biology 16(3): 706 – 716.

Franken, R.J. 2002. Demography and metapopulation dynamics of collared pikas (*Ochotona collaris*) in the southwest Yukon. M.Sc. Thesis. University of Alberta, Edmonton.

Franken, R.J. and D.S. Hik. 2004a. Interannual variation in timing of parturition and growth of collared pikas (*Ochotona collaris*) in the southwest Yukon. Integrative and Comparative Biology 44: 186 – 193.

Franken, R.J. and D.S. Hik. 2004b. Influence of habitat quality, patch size and connectivity on colonization and extinction dynamics of collared pikas, *Ochotona collaris*. Journal of Animal Ecology 73: 889 – 896.

Franzen, M. and S.G. Nilsson. 2010. Both population size and patch quality affect local extinctions and colonizations. Proceedings of the Royal Society B 277: 79 - 85.

Hallet, T.B., T Coulson, J.G. Pilkington, T.H. Clutton-Brock, J.M. Pemberton, and B.T. Grenfell. 2004. Why large-scale climate indices seem to predict ecological processes better than local climate. Nature 430: 71 – 75.

Hanski, I. 1994. A practical model of metapopulation dynamics. Journal of Animal Ecology 63: 151 – 162.

Hayhoe, K.A. 2010. A standardized framework for evaluating the skill of regional climate downscaling techniques. Ph.D. Thesis. University of Illinois at Urbana-Champaign.

Hodgson, J.A., A. Moilenan and C.D. Thomas. 2009. Metapopulation responses to patch connectivity and quality are masked by successional habitat dynamics. Ecology 90(6): 1608 – 1619.

Hudson, J. M. G., S.F. Morrison, and D.S. Hik. 2008. Effects of leaf size on forage selection by collared pikas, *Ochotona collaris*. Arctic, Antarctic and Alpine Research 40 (30: 481 – 486.

Huntly, N.J., A.T. Smith and B.L. Ivins. 1986. Foraging behavior of the pika (*Ochotona princeps*) with comparisons of grazing versus haying. Journal of Mammalogy 67(1): 139 – 148.

Jeffress, M.R., T.J. Rodhouse, C. Ray, S. Wolff, and C.W. Epps. 2013. The idiosyncrasies of place: geographic variation in the climate-distribution relationships of the American pika. Ecological Applications 23(4): 864 – 878.

Jentsch, A., J. Kreyling, and C. Beierkuhnlein. 2007. A new generation of climate-change experiments: events, not trends. Frontiers in Ecology and Environment 5(7): 365 – 374.

Knape, J. and P. de Valpine. 2011. Effects of climate and climate on the dynamics of animal population time series. Proceedings of the Royal Society B 278: 985 – 992.

Knapp, R.A., K.R. Matthews, H. K. Preisler, and R. Jellison. 2003. Developing probabilistic models to predict amphibian site occupancy in a patch landscape. Ecological Applications 13(4): 1069 – 1082.

Krebs, C.J. and D. Berteaux. 2006. Problems and pitfalls in relating climate variability to population dynamics. Climate Research 32: 143 – 149.

Lanier, H.C. and L.E. Olson. 2012. Deep barriers, shallow divergences: reduced phylogeographical structure in the collared pika (Mammalia: Lagomorpha: *Ochotona collaris*). Journal of Biogeography 40:466 – 478.

MacDonald, S.O. and C. Jones. 1987. *Ochotona collaris*. Mammalian Species No. 281: 1 – 4.

Mantua, N.J. 2002. Pacific-Decadal Oscillation (PDO). Pages 592 – 594 in M.C. MacCracken and J.S. Perry editors. Encyclopedia of Global Environmental Change: Volume 1, The Earth system: physical and chemical dimensions of global environmental change. John Wiley and Sons, Ltd., Chichester, England.

Matter, S.F., M. Ezzedine, E. Duermit, J. Mashburn, R. Hamilton, T. Lucas and J. Roland. 2009. Interactions between habitat quality and connectivity affect immigration but not abundance or population growth of the butterfly, *Parnassius smintheus*. Oikos 118: 1461 – 1470.

McIntire, E.J.B. and D.S. Hik. 2005. Influences of chronic and current season grazing by collared pikas on above-ground biomass and species richness in subarctic alpine meadows. Oecologia 145: 288 – 297.

Millar, J.S. 1974. Success of reproduction in pikas, *Ochotona princeps* (Richardson). Journal of Mammalogy 55: 527 – 542.

Moilenan, A., and I. Hanski. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. Ecology 79(7): 25-3 – 2515.

Moilenan, A., A.T. Smith, and I. Hanksi. 1998. Long-term dynamics in a metapopulation of the American pika. The American Naturalist 152(4): 530 – 542.

Morrison, S.F., L. Barton, P. Caputa, and D.S. Hik. 2004. Forage selection by collared pikas, *Ochotona collaris*, under varying degrees of predation risk. Canadian Journal of Zoology 82: 533 – 540.

Morrison, S.F. and D.S. Hik. 2007. Demographic analysis of a declining pika *Ochotona collaris* population: linking survival to broad-scale climate patterns via spring snowmelt patterns. Journal of Animal Ecology 76: 899 – 907.

Morrison, S.F., and D.S. Hik. 2008. Discrimination of intra- and inter-specific forage quality by collared pikas (*Ochotona collaris*). Canadian Journal of Zoology 86: 456 – 461.

Morrison, S.F. , G. Pelchat, A. Donahue, and D.S. Hik. 2009. Influence of food hoarding behavior on the over-winter survival of pikas in strongly seasonal environments. Oecologia 159: 107- 116.

Moore, J.E., and R.K. Swihart. 2005. Modeling patch occupancy by forest rodents: incorporating detectability and spatial autocorrelation with hierarchically structured data. Journal of Wildlife Management 69(3): 933 – 949.

Mysterud, A., N.G. Yoccoz, R. Langvatn, M. Pettorelli, and N.C. Stenseth. 2008. Hierarchical path analysis of deer responses to direct and indirect effects of climate in northern forest. Philosophical Transactions of the Royal Society B 363: 2359 – 2368.

Neilsen, A., N.G. Yoccoz, G. Steinheim, G.O. Storvik, Y. Rekdal, M. Angeloff, N. Pettorelli, Ø. Holand, and A. Mysteryd. 2012. Are responses of herbivores to environmental variability spatially consistent in alpine ecosystems? Global Change Biology 18(10): 3050 – 3062.

O'Brien, C.M., M.S. Crowther, C.R. Dickman, and J. Keating. 2008. Metapopulation dynamics and threatened species management: Why does the broad-toothed rat (*Mastacomys fuscus*) persist? Biological Conservation 141: 1962 – 1971.

Olofsson, J. H., Tømmervik, and T.V. Callaghan. 2012. Vole and lemming activity observed from space. Nature Climate Change. Published online 27 May 2012.

Patil, V.P. 2010. The interactive effects of climate, social structure and life history on the population dynamics of hoary marmots (*Marmota caligata*). M.Sc. Thesis, University of Alberta, Edmonton.

Pellet, J., G. Maze, and N. Perrin. 2006. The contribution of patch topology and demographic parameters to population viability analysis predictions: the case of the European tree frog. Population Ecology 48: 353 – 361.

Pettorelli, N., J.O. Vik, A. Mysterud, J-M. Gaillard, C.J. Tucker and N.C. Stenseth. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology and Evolution 20(9): 503 – 510.

Pettorelli, N., S. Ryan, T. Mueller, N. Bunnefeld, B. Jędrzejewska, M. Lima and K. Kausrud. 2011. The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. Climate Research 46: 15 – 27.

Pita, R., P. Beja, and A. Mira. 2007. Spatial population structure of the Cabrera vole in Mediterranean farmland: The relative role of patch and matrix effects. Biological Conservation 134: 383 – 392.

Previtali, M.A., M. Lima, P.L. Meserve, D.A. Kelt, and J.R. Gutierrez. 2009. Population dynamics of two sympatric rodents in a variable environment: rainfall, resource availability, and predation. Ecology 90(7): 1996 – 2006.

Prugh, L.R., K.E. Hodges, A.R. Sinclair, and J.S. Brashares. 2008. Effect of habitat area and isolation on fragmented animal populations. PNAS 2105 (52): 20770 – 20775.

Robles, H. and C. Cuidad. 2012. Influence of habitat quality, population size, patch size and connectivity on patch-occupancy dynamics of the middle spotted woodpecker. Conservation Biology 26(2): 284 – 293.

Roland, J. and S.F. Matter. 2013. Variability in winter climate and winter extremes reduces population growth of an alpine butterfly. Ecology 94(1): 190 – 199.

Schooley, R.L., and L.C. Branch. 2009. Enhancing the area-isolation paradigm: habitat heterogeneity and metapopulation dynamics of a rare wetland animal. Ecological Applications 19(7): 1708 – 1722.

Smith, A.T. and B.L. Ivins. 1983. Colonization in a pika population: dispersal vs. philopatry. Behavioral Ecology and Sociobiology 13: 13 – 47.

Stenseth, N.C., and A. Mysterud. 2005. Climate packages: finding the right scale and composition of climate in ecology. Journal of Animal Ecology 74: 1195 – 1198.

Thornton, D.H., L.C. Branch and M.E. Sunquist. 2011. The influence of landscape, patch and within-patch factors on species presence and abundance: a review of focal patch studies. Landscape Ecology 26: 7 – 18.

Walther, G-R. 2010. Community and ecosystem responses to recent climate change. Philosophical Transactions of the Royal Society B 265: 2019 – 2024.

Wang, T., Hamann, A., Spittlehouse, D., and Murdock, T. N. 2012. ClimateWNA - High-Resolution Spatial Climate Data for Western North America. Journal of Applied Meteorology and Climatology 61: 16-29.

Wiegand, T. K.A. Moloney, J. Naves, and F. Knauer. 1999. Finding the missing link between landscape structure and population dynamics: a spatially explicit perspective.   The American Naturalist 154(6): 605-627.

Wiegand, T., J. Naves, M. F. Garbulsky, and N. Fernández. 2008. Animal habitat quality and ecosystem functioning: exploring seasonal patterns using NDVI. Ecological Monographs 78:87–103

Wilkening, J.L., C. Ray, E,A, Beever, and P.F. Brussard. 2011. Modeling contemporary range retraction in Great Basin pikas (*Ochotona princeps*) using data on microclimate and microhabitat. Quaternary International 235: 77 – 78.

With, K.A. 2004. Metapopulation dynamics: perspectives from landscape ecology.Pages 23 – 44 in I. Hanski and O.E. Gaggiotti, editors. Ecology, Genetics and Evolution of Metapopulations. pp 23 – 44. Reed Elsevier, New York.

Zgurski, J. M. 2011. The mating habits, dispersal behavior and genetic structure of a collared pika (*Ochotona collaris*: Ochotonidae) population in the southwest Yukon, and a phylogeny of the genus Ochotona. Ph.D. thesis, University of Alberta, Edmonton.

Zgurski, J. and D.S. Hik. 2012. Polygandry and even-sexed dispersal in a population of collared pikas, *Ochotona collaris*. Animal Behaviour 83: 1075 – 1082.

CHAPTER 2 Making hay where the sun shines: occupancy dynamics of collared pikas at multiple spatial scales

INTRODUCTION

Talus-dwelling pikas, such as the collared pika (*Ochotona collaris*) and American pika *(Ochotona princeps)*, are among the best mammalian examples of a metapopulation, which is an assemblage of local populations that are spatially separated but able to interact (Moilenan and Hanski 1998; Baguette and Mennechez 2004). Collared pikas are central-place foragers inhabiting landscapes naturally fragmented into talus patches and surrounded by a matrix of alpine meadow. Individuals establish and defend territories approximately 900 m^2 in size that comprise an area of talus and surrounding vegetation. They spend the entire growing season foraging and collecting plant material to cure and cache beneath the talus in 'haypiles' to act as a source of food and insulation in the winter months, as they do not hibernate (MacDonald and Jones 1987; Franken 2002; Morrison et al. 2009). Pikas rarely venture more than 10 m from the margin of the talus due to predation risk (Morrison et al. 2004), however both males and females will disperse up to 500m to establish new territories or to find mates (Zgurski and Hik 2012).

Early studies of American pika primarily defined the dynamics of pika metapopulations in terms of patch configuration i.e., patch area and connectivity between patches (Hanski 1994; Moilanen et al. 1998). This relationship, coined the 'area-isolation paradigm' is a foundational concept, along with island biogeography theory (MacArthur and Wilson 1967), in studies of the vulnerability of plant and animal species to fragmentation of landscapes and habitats.

Subsequent studies of various animal species have evaluated the assumptions behind the area-isolation paradigm (e.g., Clinchy et al. 2002; Moilenan and Nieminen 2002; Pellet et al. 2007; Kindlmann and Burel 2008; Prugh et al. 2008). One of the main criticisms relates to the simplicity of the concept; it does not consider other factors influencing population dynamics, in particular habitat quality (Fleishman et al., 2002; Franken 2002; Franken and Hik 2004b; Franzen and Nillson 2010; Robles and Ciudad 2012). Studies of the role of habitat quality on metapopulation dynamics include the impact of landscape heterogeneity (Holt et al. 2004; Visconti and Elkin 2009), successional dynamics (Hodgson et al. 2009; Donner et al. 2010), and the quality of the matrix (Wiegand et al. 1999; Schooley and Branch 2009). For collared pikas, patch configuration (area, perimeter and connectivity between occupied patches) explains a small percentage of the variability in occupancy. There are often strong correlations between occupancy and various indicators of habitat quality, however specific relationships may vary from year to year (Franken 2002; Franken and Hik 2004b).

Various metrics have been used to describe connectivity between patches. The ‘incidence function model’ (IFM) is an area-based measure scaled by distance between patches (Moilenan and Hanski 1998; Moilanen and Nieminen 2002). Recent studies comparing the IFM to simpler nearest neighbour measures have shown that the minimum distance to the nearest occupied source patch (NS*i*) performs as well or better at predicting species occupancy and colonization than more complex measures such as the IFM (Prugh 2009; Duggan et al. 2011). Aside from its simplicity, benefits of the nearest neighbor method are that (a) it requires fewer parameters than the IFM; and (b) it allows the covariate of ‘area’ to be more distinct from connectivity in metapopulation analyses as it is not embedded in the connectivity equation (Prugh 2009).

One of the criticisms of the metapopulation concept is that it fails to recognize the different scales (spatial and temporal) at which organisms use resources (Weigand et al. 1999; Baguette and Mennechez 2004). With regard to spatial scale, the dynamics of pika metapopulations have typically been analyzed based on the number of patch colonization and extirpation events among talus patches using presence/absence data and simple metrics of patch occupancy (occupied/not occupied). There are fewer studies (Franken and Hik 2004a; Franken and Hik 2004b; Morrison and Hik 2007) that incorporate data on population structure (age and sex) or occupancy dynamics within patches and for individual pika territories.

Metapopulation biology and landscape ecology are integrated to study local populations in the context of their habitat composition, structure and function across multiple spatial scales (Weigand et al. 1999; Baguette and Mennechez 2004; With 2004; Thornton et al. 2011). Studies of species' responses to landscape, patch and within-patch variables have shown that a multi-level approach is "often necessary for understanding species response in patch systems" (Thornton et al. 2011, pg. 7). For example, habitat selection by yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) is scale-dependent, so studies at a single scale might mask the complexities of selection behaviour (Orians and Wittenberger 1991). Also, patterns of distribution and abundance of breeding forest birds appear to be influenced more strongly by within-patch variables such as vegetation structure compared to indicators at a coarser scale (Cushman and McGarigal 2004).

The metapopulation dynamics of collared pikas can be considered at four spatial scales: range or region (multiple populations), the metapopulation as a whole, talus patches and pika territories (Figure 2-1). Studies have examined phylogeographical variation throughout the known range of the species (Lanier and Olson 2009, 2012). At the metapopulation scale, climate, as manifested by local climate (temperature, precipitation and length of growing season) has a strong influence on the population dynamics of both collared and American pikas (Morrison and Hik 2007; Beever et al. 2010; Erb et al. 2011; Wilkening et al. 2011, Jeffress et al. 2013). At the patch scale, patch configuration and habitat quality influence colonization and extinction of local populations (Hanski 1994; Moilanen et al. 1998; Franken 2002; Franken and Hik 2004b). At the territory scale, local site characteristics, such as vegetation and micro-topography, are linked to the persistence of occupancy by American pikas (Kreuzer and Huntly 2003; Wilkening et al. 2011; Jeffress et al. 2013).

In this study, I used data on marked individuals over 11 years to assess the relationship between the dynamics of a metapopulation of collared pikas and various metrics of habitat quality across two spatial scales: patch and territory. My hypotheses are that occupancy dynamics at the patch scale are influenced by the quality of habitats experienced by individual pikas at the territory scale and that a multi-scale approach more fully explains the variability in occupancy than a single scale. Based on this hypothesis, I predicted the following:

1. Response variables at the resolution of territories within a patch would explain variability in occupancy more effectively than presence/absence data for whole patches.
2. Habitat quality at the patch scale would comprise multiple interacting variables, in particular vegetation quality within and adjacent to the patch and aspect. Habitat quality and patch configuration would interact to positively influence occupancy.

3. Territory selection would be non-random and would be, at least in part, based on the quality of habitats as indicated by insolation, topography, and the quality of vegetation and talus.

4. The quality of habitat within a territory would contribute to pika survival.

METHODS

Study area

The study area was located in the Ruby Range, Yukon, at 61°12'N and 138°16'W to the east of Kluane Lake and the St. Elias Mountains. The elevation of the 4 km^2 study site extends from 1500m to 2000m. The orientation of natural landforms divides this steep-sided valley into sub-areas based on a north, south, east and west orientation and separated by 1 – 2 m wide creeks and continuous alpine meadow (> 100 m). Each slope is a mosaic of talus boulderfields within a matrix of alpine tundra vegetation. Pika haypiles are rarely established on north-facing aspects. Pikas on south, east and west-facing slopes area have been considered as separate sub-population units (Morrison and Hik 2007), however they are similar genetically (Zgurski and Hik 2012).

Alpine vegetation is dominated by graminoids (sedges, rushes and grasses), forbs, mosses and lichens with some low shrubs. Talus patches range in size from 0.13 ha - 10.0 ha. Collared pikas are sympatric with hoary marmots (*Marmota caligata*) and Arctic ground squirrels (*Urocitellus parryii*) within proximity of talus patches. The snow-free growing season is approximately 10 weeks from mid-June to the end of August, but timing at both ends of the season is highly variable (Williamson et al., unpublished data).

Pika data

Pikas were live-trapped and ear-tagged each summer from June to August between 1997 and 2009 using Tomahawk live-traps baited with fresh vegetation from the study site. Trapped animals were assessed for sex, age, body weight and condition at each capture. Researchers and field technicians were trained and followed University of Alberta animal care protocols throughout. Animals were released immediately if they exhibited signs of stress and mortality due to trapping was minimal.

Surveys occurred throughout the seven week field season. A final survey of all haypiles was completed in mid-late August each year, at which time all haypile activity was well underway. Trapping and tagging was discontinued after 2009 as part of a shift to non-invasive sampling methods since presence/absence information was considered adequate for future studies.

Indictors and Assumptions

Response and predictor variables used in these analyses are listed by spatial scale in Tables 2-1 and 2-2. My assumptions were:

- A *patch* was defined as contiguous area of talus (less than 15m separation by alpine vegetation); < 1830m maximum elevation; and having a distinct dominant aspect.
- *Territories* were estimated by placing a 50m diameter circle centred on groupings of haypiles known to be occupied by one pika. This size of circle was used because it best captured areas of talus and vegetation within the 10m buffer around patches while minimizing overlap with adjacent territories.
- All pikas in the study site were surveyed each year and any pikas surveyed in year t and not in year t+1 have died or emigrated (detection probability = 1). This assumption is reasonable given that collared pikas and their haypiles are highly visible in the active season and adults are philopatric to their territories (Franken 2002). Estimates of survey effort in my study area indicate that less than 0.5% of pikas were undetected in any given year on average (i.e., were marked in year t-1, not detected in year t and re-captured in year t+1 (Morrison and Hik 2007).

Response variables: indices of patch occupancy, colonization and extirpation

Indicators of occupancy dynamics at each spatial scale are listed in Table 2-1 and described in more detail below. Where the identity of individual pikas was not required, occupancy data was used for the 14 years of surveys 1998 – 2011. Where the identity of individual pikas was needed, only 11 years of tag and release surveys were used (1999 – 2009).

a. Whole patches

(i) Number of years a patch is occupied 1998 - 2011; and

(ii) Number of years a patch is unoccupied 1998 – 2011.

b. Territories within patches

(i) *Density of territories:* Number of territories/area of the patch (ha)

(ii) *Average occupancy of territories within a patch* 1998 – 2011 was calculated based on the total number of occupied territories per patch / number of years a patch is occupied during that period.

(ii) *Colonization index* 1999 – 2009 is, for each patch, the average colonization of individual territories within a patch over the survey period (= total number of territory colonizations/number of territories in a patch) multiplied by the number of years of occupancy. A colonization event occurred when a territory in the patch was either (a) empty in year t-1 and occupied in year t, or (b) occupied by a different individual in year t-1 than in year t. To quantify the number of colonization and extirpation events, I needed to know the identity of individual pikas and, therefore, only used survey data for 1999 -2009.

(iii) *Extirpation index* 1999 – 2009 is, for each patch, the average number of times individual territories were vacated over the survey period (= total number of times territories were vacated/number of territories in a patch) multiplied by the total number of years a patch was unoccupied. An extirpation event occurred when a territory was either (a) occupied in year t-1 and unoccupied in year t or (b) occupied by a different individual in year t-1 compared to year t.

Three patches were not included in calculating the indices of colonization and extirpation because they were continually occupied throughout the study period (i.e., there were no colonization or extirpation events). These patches were included in the other patch scale measures.

c. Territories

(i) Total years occupied 1998 – 2011.

(ii) Total number of colonizations 1999 – 2009 i.e., the number of times a territory was colonized by a different pika over the survey period.

(iii) Average survival 1999 – 2009 i.e., the number of years the occupying pika survived / the number of colonization events.

Predictor variables: patch configuration, topography and habitat quality

Spatial analyses were conducted in ArcGIS 10.0 (ESRI 2011) using Quickbird satellite imagery at 2.4 m resolution from July 31 2007 (http://www.digitalglobe.com/). The metrics for predictor variables, which are listed in Table 2-2, varied according to the scale of analysis (patch vs. territory) thereby maintaining the independence of hierarchical data.

Patch configuration

Patch configuration was estimated by hand-digitizing a vector layer of patch boundaries in ArcGIS 10 and using that layer to estimate patch area and perimeter and distance between patches. To calculate connectivity between patches, I applied the connectivity measure $NS_i = \min d_{ij} * k$ as the minimum distance to the nearest occupied source patch, where d_{ij} is the distance between focal patch i and source patch j and k is the occupancy status of patch j (1 = occupied, 0 = unoccupied) (Prugh 2009).

Topography

Slope and elevation were derived using 3D Analyst tools in ArcGIS on a raster digital elevation model (DEM) using Canadian Digital Elevation Data Level 1 (NRC-G 2007) at 16m resolution.

Habitat quality

Metrics of summer and winter insolation were derived using 3D Analyst tools in ArcGIS 10 on the 16m raster digital elevation model (DEM) described in the previous section. Two seasonal intervals were defined: summer insolation = June 1 to Sept 30; and winter insolation = Oct 1 to May 31. Aspect was not used as a variable due to its strong collinearity with insolation.

Values for the normalized difference vegetation index (NDVI) were derived from a single Quickbird image from July 31 2007 using spectral reflectance measurements in the visible (red; VIS) and near-infrared (NIR) spectral regions using the Image Analysis tool in ArcGIS 10 (calculation: NDVI = (NIR - VIS)/(NIR + VIS)). Late July is the period of peak vegetation biomass near talus at this site (McIntire and Hik 2005). The overall Quickbird image for the study area is clear, however territories and patches from one high elevation area and one mid-talus area were removed from the analyses due to cloud cover that can degrate NDVI images (Foster 1984; Petorelli et al. 2005). The quality of the imagery, taken at 20:53h at the height of summer, did not appear to be negatively impacted by shadow from the surrounding mountains.

Based on visual differences in talus and vegetation in the image, talus rock was estimated to have NDVI values between 80 and 125 and alpine vegetation to have values between 125 and 183. Separate talus and vegetation layers were used to calculate an 'NDVI' value for the two habitats separately. Because pikas are thought to mainly forage within 10m of the talus due to predation risk (Morrison et al. 2004) and the need to retreat to the talus to thermoregulate (Smith 1974), vegetation quality was estimated separately for two areas: (i) within each patch, and (ii) in a 10m buffer adjacent to the patch.

My assumption of NDVI as a measure of vegetation quality was validated by comparing NDVI values to above-ground biomass for vegetation communities in the vicinity of talus patches with active or inactive haypiles (Appendix A).

I tested for multicollinearity of predictor variables using the Pearson correlation function in Ri386 2.15.2 (RFSC 2012). Regressions for summer and winter insolation were conducted individually to examine differences in strength of response between seasons, however both were not included in the same multiple regression model due to their strong collinarity. Likewise, insolation and NDVI value for vegetation were strongly collinear and were not included together in multiple regression models.

Statistical methods

a. Multivariate analysis

I used non-metric multi-dimensional scaling (NMDS) in Ri386 2.15.2 (RFSC 2012) to assess primary relationships between response and predictor variables before conducting more in-depth statistical analyses. NMDS is robust to non-normally distributed data (Manly 1994). These analyses used indirect gradient analysis, ordinating the population (response) variables and overlaying the output with the spatial and environmental variables. I selected a 'gower' distance measure using a rankindex tool in R. Gower is an index of dissimilarity that is commonly used with mixed (continuous and categorical) data (Gower 2005).

b. Generalized linear regression

I tested the statistical relationship between response variables and patch and territory metrics using generalized linear model (GLM) regression with a negative binomial distribution. A negative binomial distribution was considered appropriate because the observations are based on counts and the variance exceeds the population mean (Krebs 1999). I adjusted the significance level using the Bonferroni equation where $\alpha = 0.05/8 = 0.006$ for 8 predictor variables and $\alpha = 0.05/10 = 0.005$ for 10 predictor variables.

To cross-validate my results at the territory scale, I randomly partitioned response variables into three sets of equal size and reran the GLM regressions to assess whether predictor and response variables were correlated due to analysis design rather than an actual relationship (Fielding and Bell 1997). The outcome of these cross-validations confirmed the basic patterns of relationship seen with the dataset as a whole. I was unable to do this exercise at the patch scale due to the small number of patches.

Akaike Information Criteria

I used the glmulti package in Ri386 2.15.2 (RFSC 2012) to determine the most parsimonious models for a set of predictor variables. I fine-tuned the result by running the recommended models in a multiple GLM regression with a negative binomial distribution using the extractAIC function.

RESULTS

The outputs of GLM regressions and multivariate analyses, summarized below, demonstrate relationships between indicators of occupancy dynamics and habitat quality at the patch and territory scales. Unless stated otherwise, all results described in the following sub-sections were statistically significant at a Bonferroni-adjusted p-value of less than 0.005. Biologically-significant results (p-value of less than 0.05 but greater than 0.005) were also reported because they were informative of patterns even though they lacked statistical rigour. More detailed regression outputs are provided in Appendix B.

a. Patch scale: whole patches

At the scale of whole patches, the number of years occupied and number of years unoccupied were primarily influenced by seasonal insolation (summer and winter) and biomass (within patch and buffer) (Table 2-3). The most significant p-values were observed for regressions involving the number of years unoccupied.

The number of years unoccupied were negatively correlated with insolation in summer and winter (p = 0.0001 and 0.0003, respectively). The years unoccupied were also negatively correlated with within-patch and buffer biomass and positive correlated with the distance to the nearest occupied patch (p-values = biologically significant). Results for the number of years occupied were opposite in sign for each predictor variable and the p-values for the regressions were less significant. There was no evident relationship between the number of years occupied or unoccupied and topography.

A multivariate ordination using NMDS of relationships between response and predictor variables at the scale of whole patches was consistent with results of regression analyses (Figure 2-2(a)).

b. Patch scale: territories within a patch

Analyses at the scale of territories within patches used data on occupancy and colonization of territories by individual pikas rather than presence/absence of pikas on whole patches.

Density of territories

The density of territories was most highly correlated with biomass in the 10m buffer around a patch ($p < 0.0001$; Table 2-4). Territory density was also positively correlated with insolation (summer and winter) and within-patch biomass and a negatively correlated with the distance to the nearest occupied patch. There were no correlations between territory density and topographic variables.

Average occupancy

Average occupancy (total occupancy of territories within a patch / number of years the patch was occupied) was positively correlated with patch area and negatively correlated with connectivity (distance to the nearest occupied patch) (Table 2-4), consistent with classic metapopulation theory (area-isolation paradigm). As predicted, the p-values for these relationships were more significant when considered together in a multiple regression model (Prugh 2009).

Average occupancy was also positively correlated with elevation, slope and insolation (p-values = statistically significant). There was a positive correlation with within-patch biomass and a negative correlation with the average NDVI value for talus (p-values = biologically significant).

Colonization index

Colonization (# of times territories in a patch was colonized/ # of territories x number of years the patch was occupied) was positively correlated with both summer and winter insolation and within-patch and buffer biomass and negatively correlated with distance to the nearest occupied patch (all p-values statistically significant; Table 2-4).

Extirpation index

Extirpation (# of times territories in a patch was vacated/ # of territories x number of years the patch was unoccupied) was negatively correlated with insolation (Table 2-4).

c. Territory scale

Analyses at the territory scale used measures based on individual territories within the overall study area (Table 2-6). Measures of patch configuration were not applicable at the territory scale.

The *number of years of occupancy* was positively correlated with insolation (summer and winter) ($p < 0.0001$). There were also positive correlations with slope, biomass, and the length of talus perimeter and a negatively correlation with distance to vegetation having the highest NDVI values (p-values = biologically significant).

The *number of colonization events* was positively correlated with topography (average elevation and slope) and insolation (p-values = statistically significant). There was a positive correlation with biomass and a negative correlation with distance to vegetation having the highest NDVI values (p-values = biologically significant).

The *average years of survival* was positively correlated with the length of talus perimeter ($p < 0.0001$).

A multivariate ordination of response and predictor variables at the territory scale using NMDS was consistent with regression outputs (Figure 2-2(b)).

Models of occupancy and habitat quality

Models at the patch scale had lower AIC values overall (lowest AIC = 65.48) compared to models at the territory scale (lowest AIC = 275.10) (Tables 2-5 and 2-7).

Insolation and biomass were not included in the same multiple regression models due to their high level of correlation (Pearson's correlation coefficient = 0.70 for winter insolation and buffer biomass. Therefore two models are shown for each response variable in Table 2-5 (patch scale models) and Table 2-7 (territory scale models): one that includes winter insolation and the other that includes biomass.

Patch scale

With the exception of territory density, insolation emerged as a strong predictor of occupancy for all of the response variables at the patch scale (Table 2-5). Insolation and area were positive covariates in the model for average occupancy. Insolation and connectivity were negative covariates in the model for extirpation.

Biomass was a key variable in most of the models where insolation was omitted. Buffer biomass was the strongest predictor of territory density and was a positive covariate with elevation in the model of number of years occupied. Within-patch biomass was a positive covariate with elevation and area in the model for colonization.

The preferred model for average occupancy included connectivity, area and slope, but did not include biomass.

Models of the number of years occupied and unoccupied (= scale of whole patches) had the lowest AIC values of all response variables (Table 2-5). Models of the colonization index had the highest AIC values. For all response variables, models containing insolation had lower AIC values than models containing biomass, although the change in AIC was very small so there was little support of one model over another.

Territory scale

The most parsimonious models at the territory scale contained only one or two variables (Table 2-7). Winter insolation and biomass were run separately.

The best-fitting model for the number of years of occupancy had a single variable of within-territory biomass. There were two models for colonization with similar AIC values, one with insolation as a variable and the other with biomass as a variable. The model for the average years of survival included both talus perimeter and slope and had the lowest AIC of all models at the territory scale.

DISCUSSION

The responses of animal populations to patch and landscape variables are influenced by the life history traits and the scale of assessment, which should be appropriate to the size and characteristics of each study species (Prugh et al. 2008; Thornton et al. 2011). Collared pikas provide effective models of metapopulation dynamics at multiple spatial scales because each pika establishes and defends one size-limited territory (approximately 900 m^2) throughout their life, their territories occur in local populations that are clearly defined by the talus patches in which they occur and the metapopulation itself is a more-or-less geographically discrete entity. Different processes affect population dynamics at each of these spatial scales (Figure 2-1).

A number of studies have demonstrated the influence of within-patch variables, including habitat quality, on metapopulation dynamics (Fleishman et al. 2002; Franken and Hik 2004b; Schooley and Branch 2009; Thornton et al. 2011; Robles and Ciudad 2012). Comparative analyses across spatial scales indicate that variance at a scale with which individuals interact most directly with their environment (i.e., plot level measures) may predict abundance and distribution patterns more effectively than more coarse scale measures (Wiegand et al. 1999; Cushman and McGarigal 2004; Thornton et al. 2011). However, any comparison of effects across spatial scales must consider the potential for scale interactions (Cushman and McGarigal 2004). My results indicate that patch scale measures are better predictors of the occupancy dynamics of collared pikas than territory scale measures. This may be due to greater potential for error when quantifying habitat quality within an estimated 50m diameter territory compared to a patch.

Results at the patch scale

My results demonstrate that seasonal insolation and above-ground biomass within and adjacent to patches, where pikas are most likely to forage and harvest vegetation for their haypiles, have a significant influence on occupancy at both the patch and territory scales. At the patch scale, patch configuration (area and/or connectivity) interacts with habitat quality to explain more variability in occupancy, colonization and extinction compared to individual variables. The interactive effects of habitat quality and connectivity have been shown to positively influence immigration and colonization of individuals of other species in patchy landscapes (Jacquiéry et al. 2008; Matter et al. 2009). One anomaly in my results is a negative relationship between connectivity and extirpation which implies that a smaller distance between patches promotes extirpation (Table 2-5). If so , an explanation may be that nearer patches allow young pikas to more readily disperse away from a patch if habitat quality is poorer, although this explanation has not been tested.

Insolation is strongly correlated with aspect. Abundance of collared pikas was consistently higher, and the number of years of occupancy greater, on south and southwest-facing slopes compared to east- and west-facing slopes, particularly during downturns in the population (Figures 2-3 and 2-4). The timing of snow release and length of growing season can be assumed to vary by dominant aspect, as well as exposure to solar radiation on a daily basis while pikas are harvesting and drying hay in the summer months (Morrison and Hik 2007; Morrison et al. 2009). In the winter months, exposure to shortwave radiation enhances snowmelt in the early summer because visible light penetrates the snowpack, causing thawing from below and promotes early seed germination, plant emergence and photosynthesis beneath the snow (Walker et al. 2001). Germination and emergence beneath the snow may be an important growth strategy for plants in locations with short growing seasons in which to mature, flower and senesce (Walker et al. 2001). Plant emergence beneath the snow may also be important for mammalian herbivores, such as collared and American pikas, who are believed to forage within the sub-nivean space between snow and soil (Conner 1983; Aitchison 2001; Hudson et al. 2008).

The effect of insolation on occupancy by collared pikas is contrary to that of the American pika, with its more southern range. American pikas are vulnerable to heat stress and low precipitation and therefore the probability of occurrence is higher on cooler, north-facing slopes (Jeffress et al. 2013). In my study area, the north-facing slopes are devoid of territories, likely due to these aspects having longer periods of snow cover and less vegetation growth. Also, poor growing conditions on these aspects results in dominance by plant species that are less preferred as forage (Franken 2002).

Results at the territory scale

The results of analyses at the territory scale indicate that individual pikas are making choices about territory location based on insolation, quality of vegetation, and topographic factors that may be linked to microclimate. Territories having greater levels of insolation and above-ground biomass, and located at a higher elevation and slope, are colonized with a greater frequency and are occupied for more years.

Animals integrate information about a number of factors when dispersing to, and establishing a territory (Clobert et al. 2009). For collared pikas, these could include habitat quality, predation risk, and proximity to other pikas (Franken 2002; Franken and Hik 2004b; Morrison et al. 2004; Zgurski and Hik 2012). The results of previous studies of collared pikas at

Pika Valley are consistent with the strong relationship seen here between occupancy of territories and the quality of vegetation and exposure to solar radiation. Males and females both spend a large proportion of the active summer season foraging or gathering vegetation to cache for the winter (Hudson et al. 2008; Morrison et al. 2009). As central place foragers, collared pikas select larger sized plants when haying which helps to maximize their energy/effort ratio (Hudson et al. 2008). Forage preferences are unaffected by the level of predation risk although the amount of forage removed is inversely related to risk (Morrison et al. 2004). Survival of individuals is linked to the timing of spring snowmelt and, therefore the length of the growing season (Morrison and Hik 2007) and is greatest when haying commences earlier in the season (Morrison et al. 2009).

Pika survival is higher when there is greater length of talus perimeter providing a combination of ready access to vegetation and escape from predation. The talus-non-talus interface may also be a factor months when pikas forage on vegetation adjacent to talus under the snow (Hudson et al. 2008).

Neither talus quality nor percent vegetation cover were correlated with occupancy dynamics. Talus spacing and the amount of vegetation in a talus patch has been linked to probability of colonization in certain years (Franken 2002; Franken and Hik 2004b). Consequently, NDVI might not be effective as a proxy for talus quality and site-specific measures may be better indicators. Alternatively, pikas in my study area usually colonize pre-existing territories having the requisite structure, boulder size and spacing so comparisons among occupied territories may reveal few differences.

Comparison of occupancy models across spatial scales

Contrary to my predictions, models of occupancy based on data about individual pika territories did a poorer job of explaining variability in occupancy dynamics compared to simpler models at the scale of whole patches. This result does not negate the value of using territory data to describe occupancy. Hierarchical approaches to modeling can reveal relationships at more detailed spatial scales that might be masked at larger scales (Orians and Wittenberger 1991; Jeffress et al. 2013). In my study, an examination of relationships at the territory scale provides a more rounded understanding of pika habitat selection than would have been possible just looking at the patch scale.

Working with a relatively small number of patches (16) limited my ability to effectively detect responses to variables at different spatial scales or to deal with the variability in inputs (Quinn and Keough 2002; Thorton et al. 2011). The additional resolution provided by territory data at the scale of territories within patches detected effects of predictor variables despite the small number of patches in my study area.

My results affirm the value of long-running datasets that enable analysis of individual pikas as well as local populations and metapopulations over time. For collared pikas and other small mammals whose populations have a large range of inter-annual variability, the number of years of data, the seasons for which data is collected and the specific period studied can influence the outcome of analyses of population dynamics (Morrison and Hik 2008; Previtali et al. 2009). For example, studies based on a single year of data, or on data gathered intermittently over a number of years may not provide a fully accurate representation of local population dynamics (Hodgson et al. 2009). Indeed, a minimum of five years of continuous data is needed before population dynamics of collared pikas can be quantified with confidence (Morrison and Hik 2008).

Future research applications

- Little is known about the occurrence of collared pikas outside of commonly accessed areas. There is potential to use remote sensing and spatial analysis to apply my findings over larger areas in order to identify potential habitats and distribution of the species or to further investigate spatio-temporal relationships involving this and other pika metapopulations.
- A study of the effects of social dynamics on occupancy would provide additional perspective at the patch and territory scales. Collared pikas tend to establish territories within proximity of a pika of the opposite sex (Franken 2002, Zgurski and Hik 2012). Unlike juvenile males, juvenile females do not colonize unoccupied patches and usually establish their territory in patches occupied by at least some males (Franken 2002).

  Patches with less suitable habitat appear to be occupied by a higher proportion of juveniles (unpublished data). Demography may interact with habitat quality in interesting ways that merits further investigation.

- These results might be extended to integrate the effects of climate and habitat quality across spatial scales. Local site characteristics have been shown to affect survival of American pikas and to moderate macro-scale predictions of the vulnerability to climate change (Kreuzer and Huntly 2003; Wilkening et al. 2011; Jeffress et al. 2013). Pika populations can fluctuate greatly in my study area, particularly on east- and west-facing slopes in the study valley (Figure 2-3) and the dynamics of this population has been linked to climate, as manifested by local climate conditions and regional trends (Morrison and Hik 2007; Chapter 3). Linking climate and habitat quality is a logical next step.

CONCLUSION

Consistency in analysis outcomes across spatial scales supports my hypothesis that occupancy of territories by collared pikas is non-random and influenced by habitat quality. Assessing occupancy-habitat relationships across multiple scales provides a robust and informative picture of the relationship between habitat quality and occupancy. Not surprisingly, collared pikas ‘follow the sun’ when making choices about where to establish their territories. There are other factors that come into play, but insolation and above-ground biomass are two of the most significant. These results are consistent with what we know about the biology of pikas and reflect the importance of habitat quality and microclimatic conditions.

TABLES AND FIGURES

Table 2-1. Response variables used in analyses listed by spatial scale of analysis (whole patch, territories within a patch, and territory).

Scale	Response variables
Whole patch	• Number of years occupied • Number of years unoccupied
Territories within a patch	• Territory density: Number of territories / patch area (ha) • Average occupancy: Total occupancy of territories within a patch / number of years the patch is occupied • Colonization index: (# of times territories in a patch are colonized/ # of territories) x number of years the patch is occupied • Extirpation index: (# of times territories in a patch are vacated/ # of territories) x number of years the patch is unoccupied
Territories	• Total number of years occupied • Number of times a territory is colonized by a different pika • Average survival: Number of years the occupying pika survived/ number of colonization events

Table 2-2. Predictor variables used in analyses listed by spatial scale of analysis (whole patch, territories within a patch, and territory).

Patch scale (whole patches and territories within patches)
• **Patch configuration** i. area (m^2) ii. connectivity (distance to nearest source pop (m)) • **Quality of habitat** i. average summer and winter insolation (Watt hrs/m^2) ii. quality of vegetation (average NDVI index >125) (a) within patch; and (b) in a 10m buffer around the patch iii. talus NDVI value (average NDVI index (80 - 125)) iv. proportion of vegetation in a patch (%)
Territory scale
• **Topography** i. average elevation (m) ii. average slope (degrees) • **Quality of habitat** i. average summer and winter insolation (Watt hrs/m^2) ii. quality of vegetation (average NDVI index >125) iii. talus NDVI value (average NDVI index (80 - 125)) iv. length of talus perimeter within a territory (m) v. distance from territory centre to highest NDVI class vegetation (m) vi. proportion of vegetation in a territory (%)

Table 2-3. Occupancy as a function of patch configuration, topography and habitat quality at the scale of whole patches.

Statistical significance: $\alpha \leq 0.005$, biological significance: $\alpha \leq 0.05$ (*), d.f. = 14, n= 16 patches.
NS = not significant to $\alpha \leq 0.05$. The sign of the slope is shown in brackets after the p-value.
More detailed results are shown in Appendix B.

Indicator[□]	**# of years occupied**	**# of years unoccupied**
Patch configuration		
Connectivity (distance to nearest occupied patch)	NS	p = 0.031* (+)
Area	NS	NS
Habitat quality		
Average summer insolation	p = 0.010* (+)	p = 0.00030** (-)
Average winter insolation	p = 0.0087* (+)	p = 0.00012** (-)
Average NDVI for vegetation: within patch	p = 0.039* (+)	p = 0.0078* (-)
Average NDVI for vegetation: buffer around patch	p = 0.039* (+)	p = 0.0093* (-)

[□] The unit of measurement for each of these indicators is indicated in Table 2-2.

Table 2-4. Occupancy as a function of patch configuration, topography and habitat quality at the scale of territories within patches.

Statistical significance: $\alpha \leq 0.005$, biological significance: $\alpha \leq 0.05$ (*), d.f. = 14, n= 16 patches and 127 territories. NS = not significant to $\alpha \leq 0.05$. The sign of the slope is shown in brackets after the p-value. More detailed results are shown in Appendix B.

Indicator□	**Territory density**	**Average occupancy**	**Colonization index**	**Extirpation index**
Patch configuration				
Connectivity (in multiple regression model with area)	p = 0.0019** (-)	p = 0.00052** (-)	p = 0.0023** (-)	NS
Area (in multiple regression model with connectivity)	Not applicable	p <0.0001** (+)	NS	NS
Habitat quality				
Average summer insolation	p = 0.0019** (+)	p = 0.024* (+)	p = 0.00014** (+)	p = 0.0013** (-)
Average winter insolation	p = 0.0048** (+)	p = 0.0048** (+)	p < 0.0001** (+)	p = 0.0011** (-)
Average NDVI for vegetation: within patch	p = 0.0020** (+)	p = 0.043* (+)	p = 0.0010** (+)	NS
Average NDVI for vegetation: buffer around patch	p < 0.0001** (+)	NS	p = 0.0029** (+)	NS
Average NDVI for talus	NS	p = 0.032* (-)	NS	NS

□ The unit of measurement for each of these indicators is indicated in Table 2-2.

Table 2-5. Best-fitting models of relationships between response and predictor variables at the scales of patch and territories within patches, listed by AIC value.

Scale	Response variable	Best models	AIC	Equivalent d.f.
Whole patch	Number of years unoccupied	1 - (1.61E-05 * WINTER_SOLAR)	65.48	2
		1 – (0.010 * ELEVATION) – (0.104 * BUFFER_VEG)	67.96	3
	Number of years occupied	1 + (5.41E-06 * WINTER_SOLAR)	73.63	2
		1 + (0.0041 * ELEVATION) + (0,041 * BUFFER_VEG)	74.91	3
Territories within patches	Extirpation index	1 – (0.0079 * CONNECTIVITY) – (2.34e-05 * WINTER_SOLAR)	72.52	3
	Average occupancy	1 + (1.83E-05 * AREA) + (8.26E-06 * WINTER_SOLAR)	81.21	3
		1 – (0.0068 * CONNECTIVITY) + (1.77E-05 * AREA) + (0.047 * SLOPE)	82.75	4
	Territory density	1 + (6.05E-05 * BUFFER_VEG)	88.76	2
		1 – (0.010 * CONNECTIVITY) – (0.011 * ELEVATION) + (0.067 * SLOPE)	91.71	4
		1 + (1.08E-05 * WINTER_SOLAR) – (0.033 * ELEVATION)	92.96	3
	Colonization index	1 – (2.01E-05 * AREA) + (0.0098 * ELEVATION) + (0.16 * PATCH_VEG)	102.49	4
		1 + (1.04E-05 * WINTER_SOLAR)	103.81	2

Table 2-6. Occupancy as a function of topography and habitat quality at the territory scale.

Statistical significance: $\alpha \leq 0.005$, biological significance: $\alpha \leq 0.05$ (*), d.f. = 125, n= 127 territories. NS = not significant to $\alpha \leq 0.05$. The sign of the slope is shown in brackets after the p-value. More detailed results are shown in Appendix B.

Indicator[□]	**Number of years occupied**	**Number of colonization events**	**Average years of survival**
Topography			
Average elevation	NS	p = 0.0031** (+)	NS
Average slope	p = 0.0098 (+)	p = 0.0020** (+)	NS
Habitat quality			
Average winter insolation	p <0.0001** (+)	p <0.0001** (+)	NS
Average summer insolation			
Length of talus perimeter	p = 0.034* (+)	NS	p <0.0001** (+)
Average NDVI for vegetation	p = 0.017* (+)	p = 0.0082* (+)	NS
sqrt(Distance to highest quality vegetation)	p = 0.017* (-)	p = 0.0090* (-)	NS

[□] The unit of measurement for each of these indicators is indicated in 2-2.

Table 2-7. Best-fitting models of relationships between response and predictor variables at the territory scale.

Response variable	Best models	AIC	Equiv d.f.
No. of years of occupancy	1 + (0.022 * VEG_QUALITY)	641.30	2
No. of colonization events	1 + (5.07E-06 * WINTER_SOLAR)	453.52	2
	1 + (0.028 * VEG_QUALITY)	454.92	2
Average years of survival	1 + (0.0036 * TALUS_PERIMETER) – (0.016 * SLOPE)	275.10	3

Figure 2-1. Factors influencing metapopulation dynamics of collared pikas at three spatial scales: metapopulation (4 km^2 in this study area), patch (0.13 - 10 ha in this study area), and territory (900 m^2 approx.)

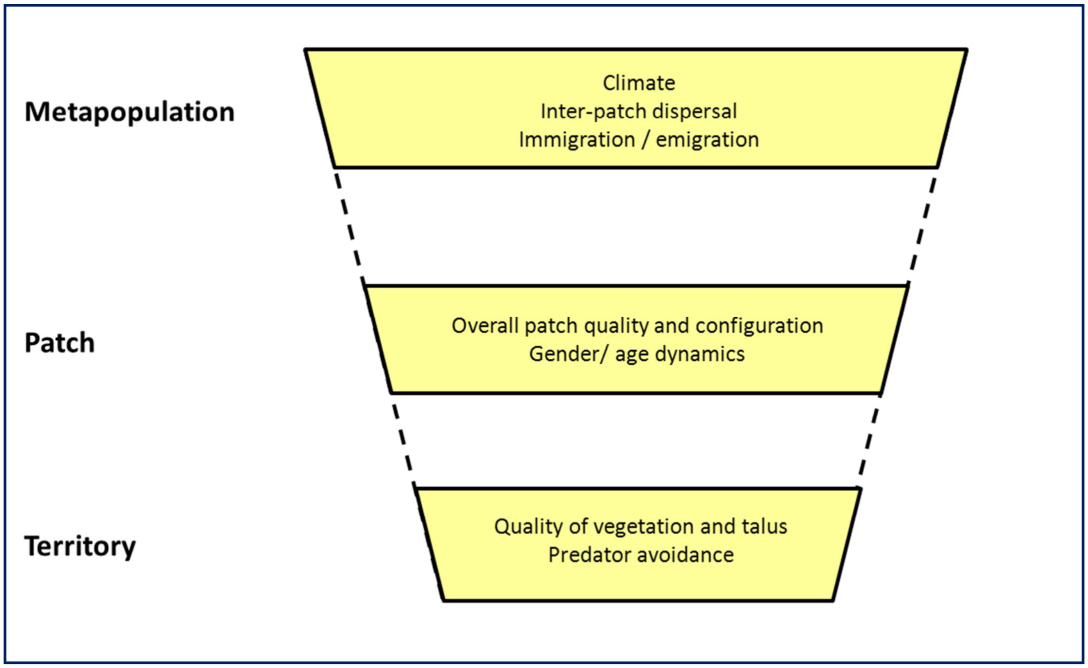


Figure 2-2. Relationship between predictor and response variables at two spatial scales (a) whole patches and (b) territories (shown in red and circled). Predictor variables are patch configuration (red), topography (blue), and habitat quality (green). Ordination uses non-metric multi-dimensional (NMDS) scaling with a Gower distance measure.

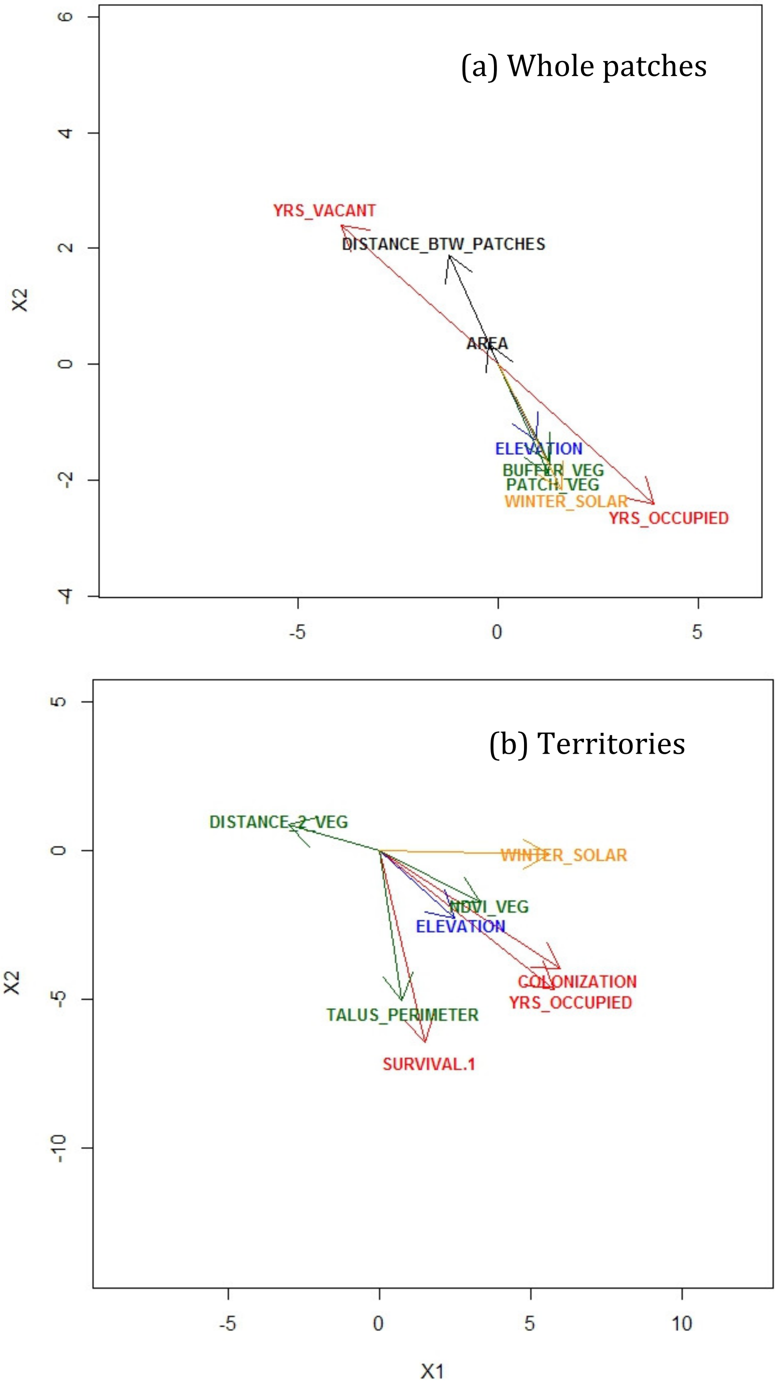


Figure 2-3. Population of collared pikas in the Ruby Range study area 1998 – 2011, showing variability in total numbers based on a seasonal census of all known individuals. Values are shown for the study area as a whole and for each dominant aspect.

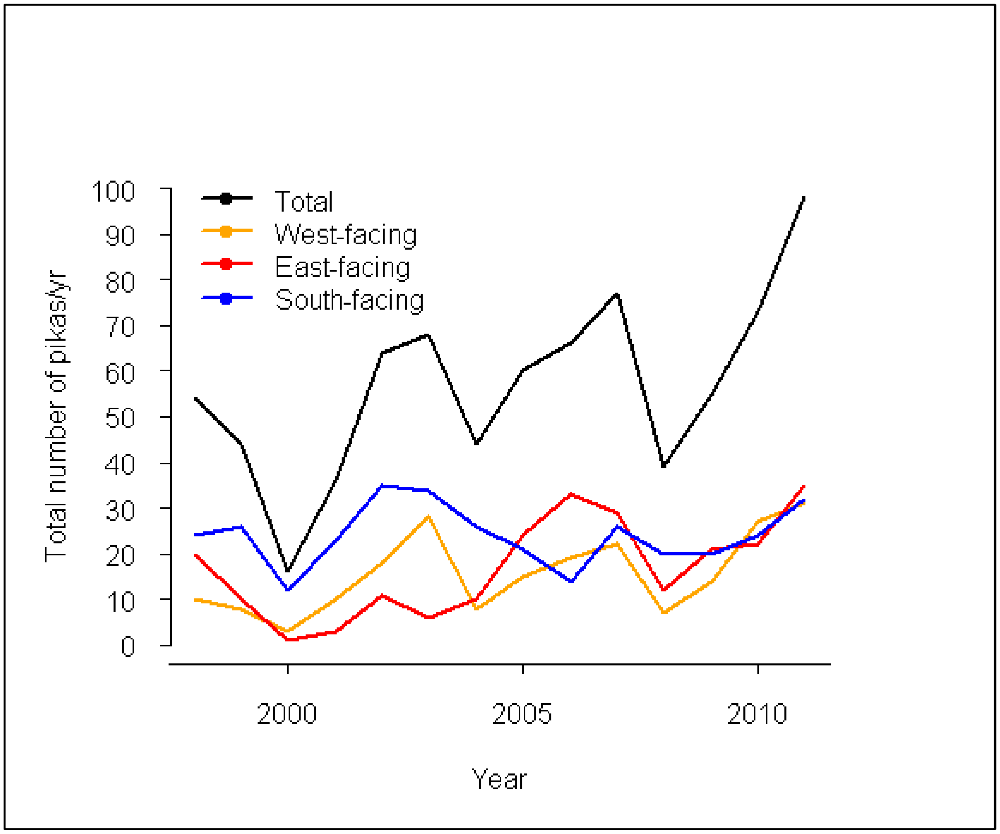
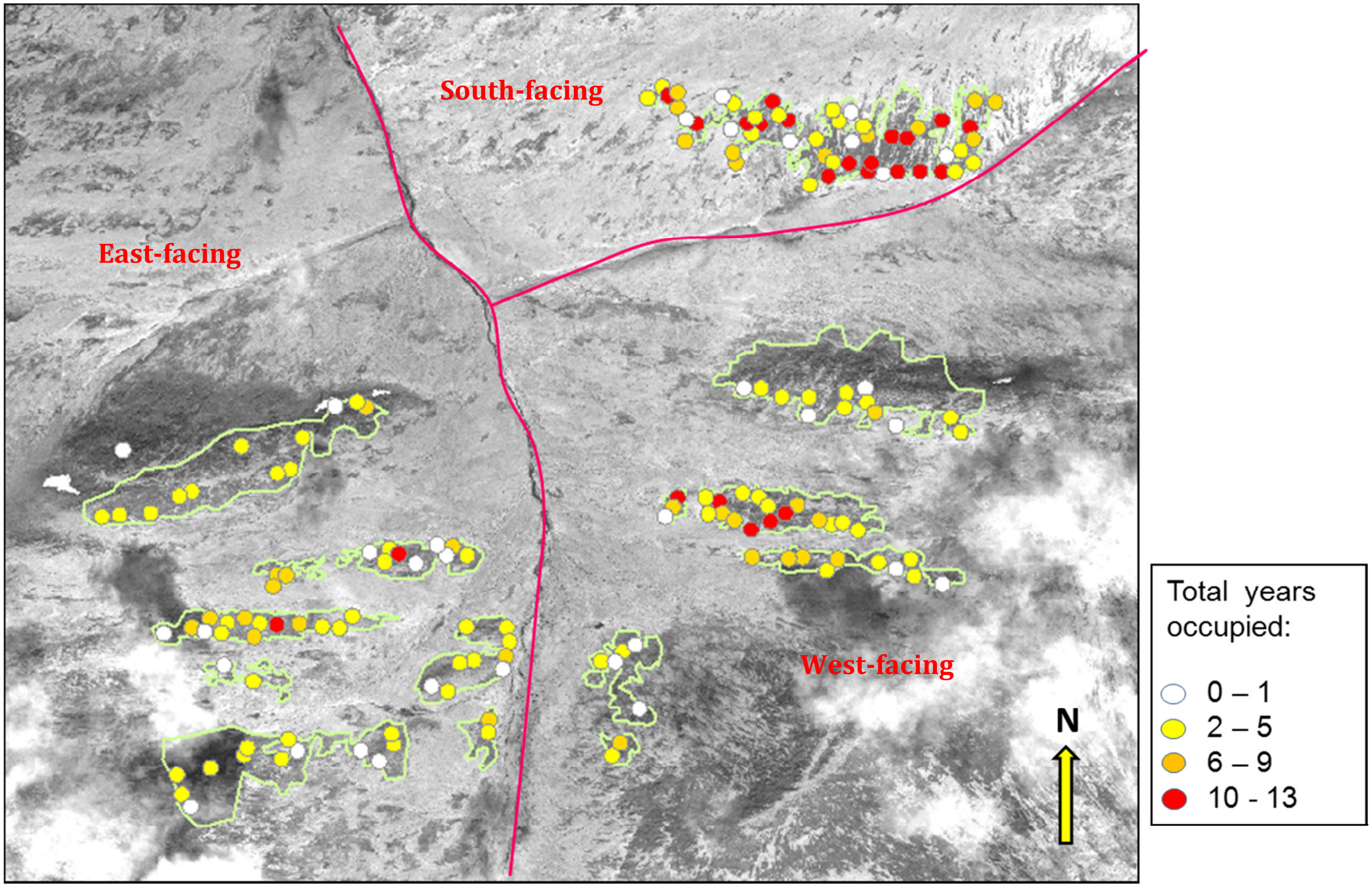


Figure 2-4. Total years of occupancy in each of three dominant aspects in this study area delineated by the red solid line. Talus patches are outlined in light green on a Quickbird satellite image from July 31 2007.



LITERATURE CITED

Aitchison, C.W. 2001. The effect of snow cover on small animals. *In* Snow Ecology: An Interdisciplinary Examination of Snow-Covered Ecosystems. (H.G. Jones, J.W. Pomeroy, D.A. Walker and R.W. Hoham eds). Cambridge University Press, Cambridge, U.K. pp 229 – 265.

Baguette, M. and G. Mennechez. 2004. Resource and habitat patches, landscape ecology and metapopulation biology: a consensual viewpoint. Oikos 106(2): 399 – 403.

Beever, E.A., C. Ray, P.W. Mote, and J.L. Wilkening. 2010. Testing alternative models of climate-mediated extirpations. Ecological Applications 20(1): 164 – 178.

Clinchy, M., D.T. Haydon, and A.T. Smith. 2002. Pattern does not equal process; what does patch occupancy really tell us about metapopulation dynamics? The American Naturalist 159 (4): 351 – 362.

Clobert, J., J-F le Galliard, J. Cote, S. Meylan and M. Massot. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecology Letters 12: 197 – 2009.

Cushman, S.A. and K. McGarigal. 2004. Hierarchical analysis of forest bird species-environment relationships in the Oregon Coast Range. Ecological Applications 14(4): 1090 – 1105.

Donner, D.M., C.A. Ribic, and J.R. Probst. 2010. Patch dynamics and the timing of colonization – abandonment events by male Kirtlands's Warblers in an early succession habitat. Biological Conservation 143: 1159 – 1167.

Duggan, J.M., R.L. Schooley, and E.J. Heske. 2011. Modeling occupancy dynamics of a rare species, Franklin's ground squirrel, with limited data: are simple connectivity metrics adequate? Landscape Ecology 26(10): 1477- 1490.

Erb, L.P., C. Ray, and R. Guralnik. 2011. On the generality of a climate-mediated shift in the distribution of the American pika (*Ochotona princeps*). Ecology 92(9): 1730 – 1735.

Fielding, A.H. and J.F. Bell, 1997. A review of methods for the assessment of prediction errors in conservation presence/ absence models. Environmental Conservation 24(1): 38 – 49.

Fleishman, E., C. Ray, P. Sjögren-Gulve, C.L. Boggs and D.D. Murphy. 2002. Assessing the roles of patch quality, area and isolation in predicting metapopulation dynamics. Conservation Biology 16(3): 706 – 716.

Franken, R.J. 2002. Demography and metapopulation dynamics of collared pikas (*Ochotona collaris*) in the southwest Yukon. M.Sc. Thesis. University of Alberta, Edmonton.

Franken, R.J. and D.S. Hik. 2004a. Interannual variation in timing of parturition and growth of collared pikas (*Ochotona collaris*) in the southwest Yukon. Integrative and Comparative Biology 44: 186 – 193.

Franken, R.J. and D.S. Hik. 2004b. Influence of habitat quality, patch size and connectivity on colonization and extinction dynamics of collared pikas, *Ochotona collaris*. Journal of Animal Ecology 73: 889 – 896.

Franzen, M. and S.G. Nilsson. 2010. Both population size and patch quality affect local extinctions and colonizations. Proceedings of the Royal Society B 277: 79 - 85.

Gower, J. C. 2005. Similarity, Dissimilarity, and Distance Measure. Encyclopedia of Biostatistics. John Wiley and Sons, Ltd., Mississauga, Ontario.

Hanski, I. 1994. A practical model of metapopulation dynamics. Journal of Animal Ecology 63: 151 – 162.

Hanski, I., and Gilpin, M.E. (eds). 1997. Metapopulation Dynamics: Ecology, Genetics, and Evolution. Academic Press, London, U.K.

Hodgson, J.A., A. Moilenan and C.D. Thomas. 2009. Metapopulation responses to patch connectivity and quality are masked by successional habitat dynamics. Ecology 90(6): 1608 – 1619.

Holt, A.R., P.H. Warren and K.J. Gaston. 2004. The importance of habitat heterogeneity, biotic interactions and dispersal in abundance – occupancy relationships. Journal of Animal Ecology 73: 841 – 851.

Hudson, J. M. G., S.F. Morrison, and D.S. Hik. 2008. Effects of leaf size on forage selection by collared pikas, *Ochotona collaris*. Arctic, Antarctic and Alpine Research 40 (30: 481 – 486.

Jacquiéry, J., J. Guélat, T. Broquet, L. Berset-Brändli, E. Pellegrini, R. Moresi, A.H. Herzel, and N. Perrin. 2008. Habitat quality effects on metapopulation dynamics in greater white-toothed shrew, *Crocidura russula.* Ecology 89(10): 2777 – 2785.

Jeffress, M.R., T.J. Rodhouse, C. Ray, S. Wolff, and C.W. Epps. 2013. The idiosyncrasies of place: geographic variation in the climate-distribution relationships of the American pika. Ecological Applications 23(4): 864 – 878.

Kindlmann, P. and F. Burel. 2008. Connectivity measures: a review. Landscape Ecology 23: 879 – 890.

Krebs, C.J. 1999. Ecological Methodology 2nd Edition. Adddison Wesley Longman Inc. Don Mills, Ontario.

Kreuzer, M.P. and N.J. Huntly. 2003. Habitat-specific demography: evidence for source-sink population structure in a mammal, the pika. Oecologia 134: 343 – 349.

MacArthur, R.H. and E.O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press, New Jersey.

MacDonald, S.O. and C. Jones. 1987. *Ochotona collaris.* Mammalian Species No. 281: 1 – 4.

Matter, S.F., M. Ezzedine, E. Duermit, J. Mashburn, R. Hamilton, T. Lucas and J. Roland. 2009. Interactions between habitat quality and connectivity affect immigration but not abundance or population growth of the butterfly, *Parnassius smintheus*. Oikos 118: 1461 – 1470.

Moilenan, A., and I. Hanski. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. Ecology 79(7): 25-3 – 2515.

Moilenan, A. and M. Nieminen. 2002. Simple connectivity measures in spatial ecology. Ecology 83(4): 1131 – 1145.

Morrison, S.F., L. Barton, P. Caputa, and D.S. Hik. 2004. Forage selection by collared pikas, *Ochotona collaris*, under varying degrees of predation risk. Canadian Journal of Zoology 82: 533 – 540.

Morrison, S.F. and D.S. Hik. 2007. Demographic analysis of a declining pika *Ochotona collaris* population: linking survival to broad-scale climate patterns via spring snowmelt patterns. Journal of Animal Ecology 76: 899 – 907.

Morrison, S.F. and D.S. Hik. 2008. When? Where? And for how long? Census design considerations for an alpine lagomorph, the collared pika (*Ochotona collaris*). Pages 103 – 113 in P.C. Alves, N. Ferrance and K. Hackănder, editors. Lagomorph Biology, Evolution , Ecology and Conservation. Springer-Verlag, Berlin, Germany.

Morrison, S.F. , G. Pelchat, A. Donahue, and D.S. Hik. 2009. Influence of food hoarding behavior on the over-winter survival of pikas in strongly seasonal environments. Oecologia 159: 107- 116.

Natural Resources Canada Geobase (NRC-G). 2007. Canadian Digital Elevation Data, Level 1, Product Specifications. Centre for Topographic Information. Sherbrooke, Quebec.

Orians, G.H.,and J.F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. The American Naturalist 137: S29 – S49.

Pellet, J., E. Fleishman, D.S. Dobkin, A. Gander, and D.D. Murphy. 2007. An empirical evaluation of the area and isolation paradigm of metapopulation dynamics. Biological Conservation 136: 483 – 495.

Previtali, M.A., M. Lima, P.L. Meserve, D.A. Kelt, and J.R. Gutierrez. 2009. Population dynamics of two sympatric rodents in a variable environment: rainfall, resource availability, and predation. Ecology 90(7): 1996 – 2006.

Prugh, L.R. 2009. An evaluation of patch connectivity measures. Ecological Applications 19(5): 1300 – 1320.

Prugh, L.R., K.E. Hodges, A.R. Sinclair, and J.S. Brashares. 2008. Effect of habitat area and isolation on fragmented animal populations. PNAS 2105 (52): 20770 – 20775.

Quinn, G.P. and M.J.Keough. 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, London. U.K.

R Foundation for Statistical Computing (RFSC). 2012. R: A Language and Environment for Statistical Computing, Vienna, Austria. http://www.r-project.org/

Robles, H. and C. Cuidad. 2012. Influence of habitat quality, population size, patch size and connectivity on patch-occupancy dynamics of the middle spotted woodpecker. Conservation Biology 26(2): 284 – 293.

Schooley, R.L., and L.C. Branch. 2009. Enhancing the area-isolation paradigm: habitat heterogeneity and metapopulation dynamics of a rare wetland animal. Ecological Applications 19(7): 1708 – 1722.

Smith, A.T. 1974. The distribution and dispersal of pikas: consequences of insular population structure. Ecology 55: 1112 – 1119.

Thornton, D.H., L.C. Branch and M.E. Sunquist. 2011. The influence of landscape, patch and within-patch factors on species presence and abundance: a review of focal patch studies. Landscape Ecology 26: 7 – 18.

Visconti, P. and C. Elkin. 2009. Using connectivity metrics in conservation planning – when does habitat quality matter? Diversity and Distributions 15: 602 – 612.

Walker, D.A., W.D. Billings and J.G. de Molenaar. 2001. Snow-vegetation interactions in tundra environments. *In* Snow Ecology: An Interdisciplinary Examination of Snow-Covered Ecosystems. (H.G. Jones, J.W. Pomeroy, D.A. Walker and R.W. Hoham eds). Cambridge University Press, Cambridge, U.K. pp 265 - 324.

Wiegand, T. K.A. Moloney, J. Naves, and F. Knauer. 1999. Finding the missing link between landscape structure and population dynamics: a spatially explicit perspective. The American Naturalist 154(6): 605-627.

Wilkening, J.L., C. Ray, E,A, Beever, and P.F. Brussard. 2011. Modeling contemporary range retraction in Great Basin pikas (*Ochotona princeps*) using data on microclimate and microhabitat. Quaternary International 235: 77 – 78.

With, K.A. 2004. Metapopulation dynamics: perspectives from landscape ecology. Pages 23 – 44 in I. Hanski and O.E. Gaggiotti, editors. Ecology, Genetics and Evolution of Metapopulations. pp 23 – 44. Reed Elsevier, New York.

Zgurski, J. and D.S. Hik. 2012. Polygandry and even-sexed dispersal in a population of collared pikas, *Ochotona collaris*. Animal Behaviour 83: 1075 – 1082.

CHAPTER 3 Vulnerability of collared pikas to climate varies by sex, age and aspect

INTRODUCTION

Climate has a strong influence on fitness and survival of animals in Arctic and alpine environments. Small mammalian herbivores living in alpine or Arctic environments are well-adapted to extreme and highly variable climatic conditions. Strategies include physiological (thick fur, high metabolic rate) and behavioural (hibernation, burrowing, caching food) adaptations (Aitchison 2001; Lovegrove 2003).

Climate, and its day-to-day manifestation as weather, has direct and indirect effects on abundance and survival of Arctic animals. During the growing season, summer temperature and precipitation may directly affect abundance and survival by providing more or less favourable conditions for foraging and gaining body mass in preparation for the long winter months ahead (Morrison and Hik 2007). For non-hibernating animals, winter climate can influence conditions beneath the snow (Aitchison 2001), timing of snowmelt (Morrison et al. 2007), and affect reproductive success (Millar 1972). Indirectly, climate can influence abundance and survival through its effect on productivity of vegetation and therefore forage quality (Walker et al. 2001; Forchhammer et al. 2005).

Large-scale climate indices such as the Pacific Decadal Oscillation (PDO) and North Atlantic Oscillation (NAO) are often used to examine species' responses to climate. As integrators of multiple climate variables (including temperature and precipitation), climate indices are often more effective predictors of ecological processes than specific climate variables (Hallett et al. 2004; Forchhammer et al. 2005; Stenseth and Mysterud 2005), although this is not always the case (Knape and de Valpine 2011; Nilsson et al. 2011; White et al. 2011). Climate acts most strongly on population dynamics through variations in local weather (Stenseth and Mysterud 2005; Nilsson et al. 2011) and the response of a species to a given climate index can vary spatially among populations (White et al. 2011; Neilson et al. 2012; Joly et al. 2012). It can also be a challenge with climate indices to determine specific mechanistic processes affecting observed dynamics (Krebs and Berteaux 2006; Knape and de Valpine 2011).

Limitations associated with local climate variables include the potentially large number of interactive and confounding variables associated with climate and ecology. There are also challenges with identifying which of many combinations of temperature, precipitation and season are most applicable to the study species and if climate effects are direct or indirect (Hallet et al. 2004; Stenseth and Mysterud 2005; Benton et al. 2006; Krebs and Berteaux 2006; Roland and Matter 2013).

Despite these various challenges, it is still important to understand how local climate interacts with species dynamics (Krebs and Berteaux 2006). An integrative index of local climate that incorporates multiple weather variables has been proposed as a better metric for studying relationships to ecological processes compared to large-scale indices like PDO (Hallet et al. 2004).

Environmental stresses can variably affect animals of different sex and age classes due to their distinct developmental and physiological demands and vulnerabilities (Benton et al. 2006). Young of the year allocate significant resources to growth, while adult females must balance survival and the energetic demands of reproduction. Adult males may need to defend a territory, mates or conspecifics. Studies have used large-scale climate indices or local climate or both to investigate specific biological mechanisms linking environmental variability to population dynamics. Examples include a study of the influence of winter and spring PDO on recruitment and predation of mountain caribou (*Rangifer tarandus*) in the Yukon Territory (Hegel et al. 2010); survival of different sex and age classes of mountain goats (*Oreamnos americanus*) in response to regional climate and seasonal PDO in coastal Alaska (White et al. 2011); links between NAO and the sex ratio and density of red deer (*Cervus elaphus*) in Scotland (Mysterud et al. 2000); and survival and fecundity of female collared pikas (*Ochotona collaris*) in relation to lagged PDO and spring snowmelt (Morrison and Hik 2007). These studies can help to identify key vulnerabilities and inform management and forecasting of responses among and within populations to climate change (White et al. 2011; Joly et al. 2012; Roland and Matter 2013).

Collared pikas have inhabited high elevation areas of Alaska and northwestern Canada since the early Pleistocene era (Lanier and Olson 2012) and are well-adapted to variable and extreme climate conditions (Morrison et al. 2009). Climate is considered to be one of the main influences on seasonal variability in habitat occupancy for populations of collared pikas in the southwest Yukon (Franken 2000; Franken 2002; Franken and Hik 2004b) and adult female survival has been correlated with positive winter PDO (Morrison and Hik 2007, Patil 2010). The effects of PDO at the local scale include depth of snow-pack and timing of snowmelt (Mantua 2002). Earlier snowmelt results in earlier green-up and a longer growing season, which may provide pikas with a survival advantage due to earlier access to spring vegetation and a longer season to collect vegetation for their overwinter haypiles (Morrison et al. 2009). However, a shallower snowpack also reduces the insulating effect of snow, potentially making pikas more vulnerable to freezing temperatures and rain events that potentially increase mortality due to exposure (Morrison and Hik 2007; Morrison et al. 2009).

Pikas do not hibernate in winter. They remain active beneath the talus and snowpack feeding primarily on vegetation cached during the summer. Mortality is high in the first winter after emergence (Franken and Hik 2004a; Morrison and Hik 2007; Patil 2010). The timing of parturition is correlated with snowmelt and emergence of spring vegetation but not correlated with the subsequent over-winter survival of juveniles (Franken and Hik 2004a). Juveniles must establish a territory, gain body mass and gather a haypile before the onset of winter conditions in October or November. Collared pikas become reproductively mature in their first winter, and, based on studies of American pikas *(Ochotona princeps)* (Millar and Zwickel 1972; Millar 1974; Smith 1978), their condition at the onset of winter likely influences their probability of survival and reproductive success. Mortality has been shown to be higher in American pikas in years of late snowmelt (Smith 1978).

By their second summer season, those pikas that survive are well-established in their territories. The average life expectancy for collared pikas in the Yukon is two years, but a few individuals live to five years (Franken 2002; Morrison and Hik 2007; Patil 2010).

This study expands previous research (Morrison and Hik 2007; Patil 2010) by examining the responses of a pika population in the southwest Yukon to a suite of seasonal climate variables. Effects of age and sex are considered using demographic data from 11 years of mark-recapture studies

(1999 – 2008). This study analyzes relationships between collared pikas and climate at a more detailed scale of resolution than has been previous investigated. This work is timely due to ongoing concern about the vulnerability of both collared and American pikas to rapid warming of high elevation and Arctic areas as a result of climate change. Two main questions are addressed:

1) What are the most appropriate temporal and spatial scales for assessing the response of a collared pika population to climate indicators? Are the large-scale climate index of Pacific Decadal Oscillation (PDO) or local climate variables more effective as predictors of population dynamics?
2) What is the relationship between recruitment and survival of collared pikas and climate indicators? Can these relationships be differentiated by age and sex?

I predicted that the strongest relationships would be observed between recruitment and survival and local climate variables. My rationale was that, once collared pikas established on a territory, they remain in their small (~900m^2) home range for their entire life (Franken 2002). Therefore they might be expected to have localized responses to climate conditions.

Four additional predictions were considered:

- The abundance of juveniles would be most strongly correlated with summer climate variables (temperature, precipitation and length of growing season) in the season after they are born. This is because juveniles of the year must disperse soon after emerging, establish a territory, build up body mass and harvest enough vegetation for their haypiles in one short growing season (Franken 2002; Morrison et al. 2009).
- Survival of Year 1 females would be correlated with winter and spring climate due to the high mortality of pikas in their first year (Franken 2002) and the energetic costs to females of gestation and nursing young (Millar 1974).
- Year 2 adults of both sexes would have a weaker relationship to climate compared to other age groups due to having already established a territory and haypile in the previous season.
- Responses to climate indicators would vary by dominant aspect. Correlations with lagged winter PDO vary by dominant aspect in this study area (Morrison and Hik 2007) and it is likely that this relationship extends across other seasons.

METHODS

Study Area

The Pika Valley study area is located in the Ruby Range, Yukon Territory, at 61°12’N and 138°16’W to the east of Kluane Lake and the St Elias Mountains. The 4 km^2 study valley extends from approximately 1500m to 2000m. The orientation of natural landforms of the valley provide distinct north, south, east and west-facing slopes, each with a mosaic of talus boulderfields in a matrix of alpine tundra vegetation. Vegetation is dominated by alpine graminoids (sedges, rushes and grasses), forbs, mosses and lichens with some low shrubs. Talus patches range in size from 0.13 ha - 10.0 ha. Collared pikas are sympatric with hoary marmots (*Marmota caligata*) and Arctic ground squirrels (*Urocitellus parryii*) within proximity of talus patches (Barash 1973). The snow-free growing season is approximately 10 weeks from mid-June to the end of August, but timing at both ends of the season is highly variable.

Pika Data

Pikas were live-trapped and tagged with a distinct eartag each summer during June to August 1997-2009 using Tomahawk live-traps baited with fresh vegetation from the study site (Franken 2002). Trapped animals were assessed for sex, age, body weight and condition at each capture.

Researchers and field technicians were trained and followed University of Alberta animal care protocols throughout. Animals were released immediately if they exhibited signs of stress and mortality due to trapping was minimal.

Surveys to determine the abundance of pikas occurred throughout the field season and a final survey of all haypiles was completed in mid-late August each year, at which time all haypile activity was well underway. Trapping and tagging was discontinued after 2009 as part of a shift to non-invasive sampling methods.

Indictors and Assumptions

A suite of response and predictor variables were used to determine pika recruitment and survival as a function of climate (Table 3-1). For these analyses, I assumed that all pikas in the study site were surveyed each year and that any pikas surveyed in year t and not in year t+1 have died or emigrated (detection probability = 0.95). This assumption is reasonable given that collared pikas and their haypiles are highly visible in the active season and adults are philopatric to their territories (Franken 2002; Morrison and Hik 2008). Previous estimates of survey effort indicate that less than 0.5% of pikas were missed in any given year on average (i.e., were marked in year t-1, not detected in year t and re-captured in year t+1 (Morrison and Hik 2008).

Response variables

I used the identity of individual pikas over 11 years of late-summer surveys to stratify the data into three age groups: juveniles, Year 1 adults and Year 2 adults. I defined each age group as follows (Figure 3-1):

- Juveniles (surveyed late summer in the year of emergence):
  a. *Recruitment*: An index of recruitment based on the number of juveniles in year t divided by the total number of female pika surveyed in year t-1. For this study site, one juvenile is typically weaned per female in a census year (Franken and Hik 2004).
  b. *Abundance*: A count of juveniles in each census year.
- Percent survival of Year 1 adults:

  Number of Year 1 adults in year t divided by the number of juveniles in year t-1 and multiplied by 100. This metric assumes that all juveniles in year t-1 stay in the study area and survivors are identified in surveys in year t.
- Percent survival of Year 2 adults (Year 1 or newly tagged adult in year t-1 and alive in year t):

  The percent survival of Year 2 adults is a combination of two metrics:

  (1) The number of Year 2 adults in year t divided by the number of Year 1 adults in year t-1; and

(2) The number of adults who were untagged in year t-1 and were re-surveyed in year t. I assumed that an adult newly tagged in year t-1 was likely to be an immigrant to the area and a Year 1 adult for two reasons: (i) the rate of detection of pikas at the study site is > 99%; and (ii) collared pikas disperse in their first year and are philopatric once established on their territory (Zgurski and Hik 2012).

When data for Year 1 and Year 2 adults was stratified by both age and sex, the percent survival of each sex was estimated as the number of females/males in year t divided by the number of the corresponding sex in year t-1.

Pikas aged 3 and over were not included in this analysis. The average lifespan during this study period was 2.12 years and only a small number of pikas survived longer than 2 years (8% of all adults). An analysis of Year 2 adults fulfills the purpose of comparing the response of pikas in their first year with adult pikas that have survived a full year and are established on their territories.

Predictor variables

Pacific Decadal Oscillation

Monthly data on the Pacific Decadal Oscillation index was acquired from the Joint Institute for the Study of Atmosphere and Ocean (http://jisao.washington.edu/data/pdo/). PDO is an oscillating pattern of climate variability centered over the Pacific Ocean and western North America. This pattern is most variable in winter and spring and manifests locally as above- or below-average air temperature and precipitation (Mantua 2002).

I regressed my response variables against the average PDO index for autumn, winter, spring, and summer. The breaks for each season (Figure 3-1) were set to be consistent with seasonal breaks used in the ClimateWNA data for local climate (described below). I also ran analyses using the average PDO for October to March, the period when annual PDO fluctuations are most energetic (Mantua 2002). All analyses were run using PDO data for year t and t-1 to test for lag effects.

Local climate

Climate statistics were acquired from Climate WNA v4.62 (Wang et al. 2012), including indicators for average temperature (°C) and average precipitation (mm) for each of the four seasons and the number of frost-free days for the growing season in the two years leading up to the pika census in August of year t (Figure 3-1).

ClimateWNA combines interpolated historical weather data (Mitchell and Jones 2005) and downscaled monthly climate data generated by PRISM, a program that integrates climate station data, a digital elevation model and expert knowledge of climate patterns (Daly et al. 2002). The product is a set of scale-free point data for a suite of monthly, seasonal and annual climate variables (Wang et al. 2012). In using Climate WNA data I assumed that downscaled data reasonably reflect the climate conditions in the study area at a level of resolution that enables detection of seasonal differences. I acknowledge that the localized effects of climate may be specific to this one population and may be inconsistent with effects in other locations. Climate WNA was used because it was specifically designed for ease of use in research and resource management. The program provides high resolution, biologically-relevant data for use at multiple scales and locations, including mountainous regions (Wang et al. 2012).

Statistical Methods

a. Multivariate analysis

I used non-metric multi-dimensional scaling (NMDS) in Ri386 2.15.2 (RFSC 2012) to assess primary relationships between response and predictor variables before conducting more in-depth statistical analyses. NMDS is robust to data that is non-normally distributed (Manly 1994). These analyses used indirect gradient analysis, ordinating the population (response) variables and overlaying the output with the spatial and environmental variables. I selected a simple 'Euclidean' distance measure using a rankindex tool in R (RFSC 2012).

b. Generalized linear regression

I tested the statistical relationship between response and predictor variables using generalized linear model (GLM) regression in Ri386 2.15.2 (RFSC 2012) with a negative binomial distribution. A negative binomial distribution was considered appropriate because the observations are based on counts and the variance exceeds the population mean (Krebs 1999). A significance level of $\alpha = 0.05$ was conservatively adjusted based a Bonferroni adjustment of 0.05/9 variables = 0.006.

Where necessary, I used the glm.control function and substituted zero values with 1 in the response variables to control the number of iterations used to estimate maximum likelihood. Since the response variables are represented as percent values (0 – 100) the substitution of 0 for 1 was considered a reasonable correction to control for incompatibilities in the regression.

To cross-validate my results, I randomly partitioned data on survival of adult pikas into three equal sets and reran the GLM regressions to assess whether predictor and response variables were correlated due to analysis design rather than an actual relationship (Fielding and Bell 1997). The outcome of these cross-validation regressions confirmed the basic patterns of relationship seen with the entire dataset.

RESULTS

The outputs of GLM regressions are summarized below (Tables 3-2 to 3-6). Unless stated otherwise, all results described in the following sub-sections were statistically significant at a Bonferroni-adjusted p-value of less than 0.006. Biologically-significant results (p-value of less than 0.05 but greater than 0.006) are also reported because they were informative of patterns even though they lacked statistical rigour. More detailed regression outputs are provided in Appendix B.

Pacific Decadal Oscillation

Survival of Year 1 adults of both sexes and Year 2 females were correlated with lagged PDO (year t-1) but not PDO for year t. Data for Year 2 males was over-dispersed and it was not possible to estimate maximum likelihood and fit a model to the relationship.

More significant p-values were seen when adults were stratified by age (Table 3-2) compared to all adults of each sex, which only revealed two biologically significant relationships: male adults were negatively correlated with spring PDO for year t and female adults were positively correlated with lagged winter PDO. There were no significant relationships between juvenile recruitment or abundance and PDO for year t-1 or year t.

(a) PDO for October to March

There were strong positive correlations between lagged PDO for October to March and survival of Year 1 males and Year 2 females ($p < 0.0001$ and 0.00023 respectively, Table 3-2).

(b) Seasonal PDO

There was a positive correlation between survival of Year 1 females and lagged spring PDO ($p = 0.039$). There were also positive correlations between lagged PDO and survival of Year 1 males across all seasons, with particularly strong results for winter, spring and summer PDO ($p < 0.0001$, 0.00045 and 0.00021, respectively). There were strongly positive correlations between survival of Year 2 females and lagged PDO for autumn and winter ($p = 0.00019$ and 0.00037, respectively).

Local climate variables

Correlations were present between pika recruitment and survival and local climate variables for all age/sex groupings and across seasons, although the p-values for most results were biologically significant rather than statistically significant (Tables 3-3 and 3-4).

Recruitment and abundance of juveniles (Table 3-3):

Recruitment of females and all juveniles in year t was negatively correlated with the number of frost-free days in year t-1 ($p = 0.026$ and

0.010, respectively). Recruitment of males and all juveniles was negatively correlated with temperature in the autumn before conception ($p < 0.0001$ and $p = 0.0055$, respectively).

Juvenile abundance was positively correlated with temperature ($p = 0.021$) and negatively correlated with precipitation ($p = 0.045$) in the summer following their emergence and dispersal from their natal territory.

Survival of Year 1 adults (Table 3-4):

Survival of Year 1 females in year t was negatively correlated with spring precipitation in year t-1 ($p = 0.035$).

Survival of year 1 males in year t was positively correlated with winter and summer temperatures in year t-1 ($p = 0.0041$ and 0.014, respectively).

Survival of all Year 1 adults was positively correlated with winter temperature in year t-1 ($p = 0.031$) and negatively correlated with summer precipitation in year t ($p = 0.05$).

Survival of Year 2 adults (Table 3-4):

The survival of Year 2 males in year t was positively correlated with the number of frost-free days in year t-1 ($p = 0.05$ and 0.046, respectively).

Multivariate analyses using NMDS ordinations

The patterns of relationship identified through generalized linear regressions were supported by ordinations using NMDS (Figures 3-2). Juvenile recruitment and survival of Year 1 and Year 2 adults were all positively related to summer temperature and number of frost-free days and negatively related to summer precipitation for year t (Figure 3-2 (a) – (b)).

Interactions among local climate variables

The myriad of potential interactions among local climate variables is well-recognized as a confounding factor in studies of climate and ecology (Krebs and Berteaux 2006; Roland and Matter 2013). To test for the prevalence of interactions among local climate variables, I ran multiple regressions of (i) temperature + precipitation for each season (lagged and for year t), (ii) precipitation for all four seasons; and (iii) temperature for all four seasons. The most significant results are summarized in Table 3-5. These are only some of the possible combinations.

When seasonal precipitation and temperature for year t were included together in a multiple regression against survival of Year 1 or Year 2 adults, interactions among the climate variables resulted in strongly significant p-values ($p < 0.0001$; Table 3-5). Significant p-values were also observed when average precipitation in each the four seasons was run in a multiple regression against survival of Year 1 males and Year 2 females (Table 3-5).

Relationship with PDO by aspect

Pika Valley is oriented north-south and slopes on three distinct aspects (south, east and west) are occupied by pikas. Collared pikas rarely establish territories on north-facing slopes, possibly due to microclimate, delayed snowmelt and reduced forage availability. Exposure to solar radiation is a strong driver of occupancy of patches and individual territories and the amount of solar radiation is correlated with dominant aspect (Chapter 2).

Relationships between seasonal PDO and adult survival varied by dominant aspect (Table 3-6):

- On the south-facing slope, survival of both Year 1 and Year 2 adults in year t was positively correlated with PDO for winter in year t-1 ($p < 0.0001$ and $p = 0.0078$, respectively).
- On the west-facing slope, survival of Year 1 adults in year t was negatively correlated with autumn PDO ($p = 0.028$) and positively correlated with winter PDO for year t ($p = 0.0041$).
- On the east-facing slope, the survival of Year 1 adults in year t was positively correlated with PDO across all four seasons in year t-1 ($p < 0.0001$ for all seasons).

The survival of Year 1 adults in year t was influenced by the sign of PDO for year t-1, as shown in plots of Year 1 survival as a function of lagged PDO on the east-facing slope of the study area (Figure 3-3). Survival was zero on this aspect when PDO was negative but increased rapidly above zero to high levels when PDO was +1.0 or greater. These results appeared most pronounced for winter and summer PDO.

DISCUSSION

Collared pikas may be useful as an indicator species for studies of relationships between climate and population dynamics. Their home range is relatively small (900 m^2) and once they establish their territories they are highly philopatric so it is uncommon for them to move to another location (Franken 2002). This means that they experience climate at a localized scale, unlike more wide-ranging animals such as red deer (Mysterud et al. 2000), mountain caribou (Hegel et al. 2010), and mountain goats (White et al. 2011) that may be influenced across climatic and topographic gradients. Collared pikas appear to be neither forage-limited (Morrison et al. 2009) nor predation-limited (Franken and Hik 2004b) and adult survival is affected mainly by density-independent factors as territories are never fully saturated (Morrison and Hik 2007). For these reasons, there may be fewer confounding effects on population dynamics compared to other species.

My results showed that, with the exception of juvenile abundance, local climate variables perform relatively poorly in predicting population dynamics of collared pikas compared to PDO. This is likely due to the large number of interactions occurring among the local climate variables combined with the high level of variability in my population data (Figures 3-4 and 3-5). Nonetheless, the combined results for PDO and local climate provide a complementary and informative picture of relationships between climate and population dynamics for collared pikas. PDO, as an integrator of multiple climate variables, provides an effective metric for identifying broad patterns of relationship while local climate variables provide more detailed information about relationship between climate and abundance or survival in each age and sex class. The patterns of relationship seen with these results are robust to different analytical methods and are consistent with what is known of the biology of collared pikas. Seasonal vulnerabilities to local climate have been summarized in Table 3-7.

Relationships to PDO and local climate: juveniles

A positive relationship between summer temperature and precipitation and juvenile abundance was expected, given that juveniles have a relatively short growing season (approximately 10 weeks) in which to establish a territory, gain body mass to survive the winter and gather a haypile for a winter food supply (Franken 2002). My results infer that juvenile abundance is higher in summers that are warmer and drier. Warmer, drier summers in my study area, where average temperatures range from 5 to 10°C and average precipitation from 130mm to 300mm (Figure 3-6 (a) and (b)), may benefit juveniles by reducing the energetic costs of thermoregulation and providing a greater number of days suitable for foraging and gathering vegetation for haypiles.

Birth rates are higher for American pikas in habitats with earlier snowmelt (Kreuzer and Huntly 2003) inferring that a longer growing season can positively influence juvenile abundance. A predicted correlation between the number of frost-free days and juvenile abundance was not observed, perhaps because my study looked at variability in frost-free days across years rather than comparing sites within a metapopulation.

A consistent and unexpected result was a correlation between recruitment (not abundance) of juveniles and local climate in the summer and autumn before conception. These results suggest that maternal condition may influence recruitment, the so-called 'silver spoon effect' also seen in grizzly bears (*Ursus Arctos*) (Nielsen et al. 2013). A previous study of this population did not detect a link between reproduction and climate (Morrison and Hik 2007) however the earlier analysis was based on PDO and not on local climate measures. Studies of American pikas have shown that the fat content of females is the lowest during gestation and lactation and reproduction can be completely terminated during severe weather conditions, such as unusually heavy snowfall in spring (Millar 1974; Smith and Ivins 1983). As we have no information on reproductive success before collared pikas emerge from their haypiles in spring, it is not possible to draw definitive conclusions about maternal condition and reproductive success.

Relationships to PDO and local climate: adults

Stratification of adult collared pikas into one year olds (= ‘Year 1 adults’) and two year olds (= ‘Year 2 adults’) and by sex provided a better fit to climate data than analyzing data for all adults. Almost all results correlated adult survival with lagged climate indicators, suggesting a complicated relationship between pikas survival and the cumulative effects of environmental conditions.

In the southern Yukon, PDO was positively correlated with temperature in all seasons and winter and spring PDO were negatively correlated with snow depth and the date of the first snow-free day of the year (Morrison and Hik 2007; Hegel et al. 2010, Supporting Information). My results infer that survival of Year 1 males and Year 2 females was higher when temperatures are trending to warmer in winter and summer and when snow depths were lower and there was earlier snowmelt. The absence of a correlation between survival of Year 1 females and PDO was surprising. Female collared pikas become reproductively mature in their first year. Mortality is particularly high in the first winter (Franken 2002; Franken and Hik 2004a) and female American pikas are vulnerable to the energetic costs of giving birth and nursing young (Millar 1974, Smith 1978). It may be that differences in the response of Year 1 males and females are based on their behaviour during vulnerable periods. For example, in the spring months, when snow patterns can affect pika survival (Morrison and Hik 2007), females may spend more time within their haypiles with their young while males may be more active in the subnivean space or on the snow surface.

Another unpredicted result was the strong and unexpected relationship between the survival of Year 2 females and lagged PDO. By the time pikas have survived their first winter they are already established on a territory and have created one or more haypiles. One might therefore expect less vulnerability to climate compared to Year 1 females.

It is difficult to interpret these results directly by trying to identify specific mechanistic relationships between local climate variables and pika biology. What these results infer overall is that influences from previous seasons can manifest beyond the season of occurrence and that there are likely to be complexities in these relationships that extend beyond simple animal-climate relationships. Animals may be variably affected by an environmental effect at different life stages and this effect can take time to work its way through a life cycle, resulting in a lagged effect (Benton et al. 2006). For example, weather conditions in their first winter may affect the condition of Year 1 females but the effects on survival may not be observed until the following winter.

There can also be a lag as environmental conditions work through trophic levels. For example, soil moisture 'memory' is a well-documented phenomenon whereby soils ‘remember’ an anomalous wet or dry period long after atmospheric conditions have changed (Senevirante et al. 2006). Response of vegetation to climate can also have a ‘memory’ that extends back to conditions in previous months or seasons (e.g., Weiss et al. 2004) and this, in turn, can affect the behaviour and physiology of herbivores. There is recognition of the need to consider the connections of organisms within and across trophic levels in assessing responses to climate and “acknowledge that biotic interactions and feedback processes lead to highly complex, nonlinear and sometimes abrupt responses” (Walther 2010, pg. 2019).

Influence of aspect on climate relationships

There were clear differences in the relationship between the survival of adults and PDO on the three occupied aspects in this study area.

The relationship between survival and lagged PDO on the east-facing slope (Figure 3-3) showed a distinct effect of the value of PDO on survival. Survival was zero when the lagged PDO for winter, spring and summer was negative but survival in all four seasons increased rapidly above neutral PDO to high levels when PDO values equaled or exceeded +1.0. These results suggest that populations on the east-facing slopes may be particularly vulnerable during negative (“cool”) phase PDO.

During the study period there have been a number of shifts in the overall phase of PDO, which appears to have moved out of its previously observed decadal cycle. PDO went through cold phases from 1999 to 2002 and from 2007 to 2009 and a somewhat neutral phase from 2005 to 2007 (NFSC 2012). Following a brief positive signal during 2010, the PDO has been negative. The two periods of largest decline in pika numbers on the east and west-facing slopes occurred in the middle of the cold phases (in 2000 and 2008) (Figure 3-5).

The south-facing slope was continuously occupied (Figure 3-5) and this sub-population appears to act as a source to patches on other aspects following large declines in numbers (Zgurski and Hik 2013). Thus, the overall equilibrium of this metapopulation may also be maintained through dispersal and an influx of new pikas from neighbouring areas.

The vital rates of pikas vary by aspect, with south- and east-facing subpopulations responding differently to the west-facing sub-population in terms of links between adult female survival and fertility and projected population growth rate (Morrison and Hik 2007). This relationship may be driven by the timing of spring snowmelt due to correlations with winter PDO. My results suggest that a larger suite of interacting climate variables may be influencing vital rates of sub-populations across all four seasons. East- and west-facing slopes appear to have later snowmelt and lower vegetation biomass compared to south-facing slopes (D.S. Hik and T.J. Karels, unpublished data) and there may be other differences in the manifestations of climate that distinguish these aspects. For example, there may be differences in phenology and timing of peak biomass that influences over-winter survival (Morrison et al. 2009).

Collared pikas and climate change

The collared pika and its southern counterpart, the American pika, are believed to be particularly vulnerable to climate change due to the rapidly changing conditions in Arctic and alpine environments (Bruggerman 2009; Beever et al. 2010, COSEWIC 2011; Wilkening et al. 2011). In 2011, the Canadian Committee on the Status of Endangered Wildlife in Canada (COSEWIC) designated the collared pika as a species of Special Concern. This designation was applied because of the predicted vulnerability of collared pikas to climate change coupled with the species' poor dispersal ability due to populations being naturally fragmented into "alpine islands" (COSEWIC 2011).

My results affirm the sensitivity of this collared pika population to variability in climate but there is considerable uncertainty as to how interactions among changing climate variables will manifest and how pika populations will respond to those changes. For example, observed trends of earlier spring snowmelt in the Arctic (Derksen and Brown 2012) coupled with predicted increases in summer temperatures (AMAP 2012) may be beneficial to pikas in the near term due to increased length of growing season and warmer days for foraging and harvesting haypile vegetation. However, longer term effects might be negative due to untenable increases in ambient daytime temperatures and shrub encroachment resulting in reduced area of suitable habitat (Danby et al. 2011; Myer-Smith et al. 2011).

There is a high level of concern about the fate of American pikas to warming temperatures at high elevations due to the vulnerability of the species to heat stress (Bruggerman 2009; Beever et al. 2010, 2013). This specific concern may not be as relevant to collared pikas at this time. Evidence of this difference in the two species is that collared pikas colonize and occupy sunny south-facing slopes with higher frequency than other aspects (Chapter 2) and avoid north-facing slopes while American pikas preferentially occupy north-facing slopes, likely to avoid heat stress (Jeffress et al. 2013).

Positive correlations with lagged winter PDO across age groups at my study site imply that projected increases in winter temperatures (AMAP 2012) will also be beneficial to collared pikas. However, changes in the amount and duration of snow cover may also be detrimental to collared pika populations. Positive correlations between date of parturition and snow water equivalent and pika survival and spring snowmelt are well-documented at my study site (Franken and Hik 2004a; Morrison and Hik 2007; Patil 2010). It is uncertain, however, which specific characteristics of snow cover are of greatest impact on pika recruitment and survival. Potential negative effects for collared and American pikas of changed snow regimes could include an increase in rain-on-snow events, resulting in possible freezing of haypiles and reduced insulating effect (Smith 1978; Morrison and Hik 2007), delayed green-up, particularly for females who are low in fat stores following gestation and lactation (Millar 1974) ; Smith 1978; Franken and Hik 2004a; Morrison and Hik 2007; Patil 2010); and changes in the thermal character of the snow so that a 'hiemal threshold' of neutral temperature is not maintained in the subnivean layer between ground and snow layer and pikas are unable to forage effectively during winter (Aitchison 2001).

While alpine and Arctic species are well-adapted to variable and extreme climates, the frequency and magnitude of extreme and unpredictable climate events is increasing under climate change (Jentsch et al. 2007; AMAP 2012). Short-lived species with only one cohort per year, may be particularly vulnerable to extreme climate events due to lack of demographic buffering and the risk that an entire cohort will be lost (Roland and Matter 2013). Collared pikas appear to have only one litter per year (Franken and Hik 2004a) and animals at my study site have an average lifespan of 2.12 years so they are not well buffered to the loss of entire generations.

It is likely that it is not a single season but the interplay of conditions over multiple seasons that influence pika recruitment and survival. To-date, local populations at my study site appear to be able to recover and thrive 1 – 2 years after a period of adverse weather conditions (Figures 3-4 and 3-5).

Limitations of this analysis

There were challenges with comparing my dataset of 11 years of mark data with local climate variables. Although I identified patterns of relationship to local climate using ordinations that were affirmed using generalized linear regressions, there were not enough years of data to provide statistical power and to overcome the large amount of annual variability in pika numbers (Figures 3-4 and 3-5). A power analysis of minimum sample size revealed that, to reliably detect a 25% change in population means in each age group at an 80% confidence level for this population of pikas would require over 50 years of data. In the absence of this kind of long-term sampling effort, I acknowledge this lack of statistical power and assert that there is still useful information to be gained by looking at patterns of relationship that are robust to different analysis methods.

There may also be problems with extrapolating data from a few regional climate stations to my study area. A stronger fit to local population dynamics might have been achieved using local temperature and precipitation data, but the effort required to acquire this information would need to be weighed against the information that can be obtained using broader scale climate data.

Finally, there are limitations with drawing conclusions about ecological processes based on a single population. This one well-studied population of collared pikas has provided the largest and longest-running dataset for this species, however my findings would be strengthened by studies of populations in other areas to see if the same patterns of relationship hold true.

CONCLUSIONS

Despite the challenges of working with climate as an indicator, large-scale climate indices such as PDO and local climate variables can help to shed light on the biological mechanisms behind population dynamics, particularly if one considers individual life stages and sexes of the study species. Collared pikas are adaptable creatures, having persisted through variability and extremes in climate since the last Ice Age. However, they appear to be vulnerable to climate conditions at specific life stages, as demonstrated through a number of studies (Franken 2002; Franken and Hik 2004a; Morrison and Hik 2007; Patil 2010). This foundation of research and long-running dataset of an otherwise little-studied species could be used to further investigate relationships between climate and ecological processes such as the relationship between local site characteristics and survival under different climate regimes. At the same time, it is important to recognize the limitations of climate-population studies given the complexities of interactions between climate and ecology.

TABLES AND FIGURES

Table 3-1. Response and predictor variables used to analyze collared pika survival as a function of climate variables.

Analysis	Response variables	Predictor variables
All adults	• Number of surviving pikas in year t/ all pikas surveyed in year t-1	• Average local temperature by season: a. Autumn (Sept – Nov) b. Winter (Dec – Feb) c. Spring (Mar – May) d. Summer (Jun – Aug) • Average local precipitation by season • Length of growing season (number of frost-free days) • Pacific Decadal Oscillation (PDO) (i) by season and (ii) for October - March
Sex	• Surviving adult females in year t/ corresponding females in year t-1 • Surviving adult males in year t/ corresponding males in year t-1	
Age	• Juveniles: a. Recruitment: Juveniles in year t/ all females in year t-1 b. Abundance: Juveniles in year t • Year 1 adults: Adults 1 year old in year t/ juveniles in year t-1 • Year 2 adults: Adults 2 years old in year t + surviving adults from year t who were untagged in year t-1/ Year 1 and untagged adults surveyed in year t-1	

Table 3-2. Survival of year 1 and year 2 adult collared pikas in Pika Valley, Yukon Territory, during 1999 – 2009 as a function of average Pacific Decadal Oscillation (PDO) indices in autumn, winter, spring, summer of year t-1.

Statistical significance: $\alpha \le 0.006$ (**), biological significance $\alpha \le 0.05$ (*), d.f. = 9), n = 11 years. NS = not significant to $\alpha \le 0.05$. The sign of the slope is shown in brackets after the p-value. More detailed results are shown in Appendix B.

Period of average PDO for year t-1	**Year 1 Adults**			**Year 2 Females (n=41)**
	Females (n=24)	**Males (n=26)**	**All Year 1 (n=50)**	
Autumn PDO (ave Sept – Nov)	NS	$p = 0.0016$** (+)	NS	$p = 0.00019$** (+)
Winter PDO (ave Dec - Feb)	NS	$p < 0.0001$** (+)	NS	$p = 0.00037$**(+)
Spring PDO (ave Mar – May)	$p = 0.039$* (+)	$p = 0.00045$** (+)	$p < 0.0001$** (+)	NS
Summer PDO (ave Jun – Aug)	NS	$p = 0.00021$** (+)	$p = 0.039$* (+)	NS
October – March (period of most energetic PDO fluctuations (Mantua 2002))	NS	$p <0.0001$** (+)	$p = 0.022$* (+)	$p = 0.00023$** (+)

Table 3-3. Recruitment and abundance of juvenile collared pikas in Pika Valley, Yukon Territory during 1999 – 2009 as a function of seasonal climate (temperature, precipitation and number of frost-free days) for year t-1 and year t.

Statistical significance: $\alpha \leq 0.006$ (**), biological significance $\alpha \leq 0.05$ (*), d.f. = 9), n = 11 years. NS = not significant to $\alpha \leq 0.05$. The sign of the slope is shown in brackets after the p-value.
More detailed results are shown in Appendix B.

Climate variable	**Juveniles**□		
	Females (n=77)	**Males (n=84)**	**All juveniles (n = 161)**
Pre-conception			
Summer (Jun– Aug) year t-1			
Number of frost-free days	p = 0.026[R] (-)	Data over-dispersed	p = 0.010[R] (-)
Autumn (Sept – Nov) year t			
Average temperature(°C)	NS	p < 0.0001[R] (-)	p = 0.0055[R], (-)
Post-emergence			
Summer (Jun– Aug) year t			
Average temperature (°C)	NS	NS	p = 0.021[A] (+)
Average precipitation (mm)	NS	NS	p = 0.045[A] (-)

[R] Based on recruitment (ratio of juveniles in year t to no. of females in year t – 1)

[A] Based on abundance of juveniles in year t

Table 3-4. Survival of year 1 and year 2 adult collared pikas in Pika Valley, Yukon Territory during 1999 – 2009 as a function of climate (temperature, precipitation and number of frost-free days) during winter, spring or summer for years t-1 and year t.

Statistical significance: $\alpha \leq 0.006$ (**), biological significance $\alpha \leq 0.05$ (*), d.f. = 9), n = 11 years. NS = not significant to $\alpha \leq 0.05$. The sign of the slope is shown in brackets after the p-value.
More detailed results are shown in Appendix B.

Climate variable	Year 1 Adults			Year 2 Adults	
	Females (n=24)	**Males (n=26)**	**All Year 1 (n=50)**	**Females (n=41)**	**Males (n=47)**
YEAR t – 1					
Winter (Dec – Feb)					
Average temperature (°C)	NS	p = 0.0041** (+)	p = 0.031* (+)	NS	NS
Spring (Mar – May)					
Average precipitation (mm)	p = 0.035* (-)	NS	NS	NS	NS
Summer(Jun– Aug)					
Average temperature (°C)	NS	p = 0.014* (+)	NS	NS	NS
Number of frost-free days	NS	NS	NS	p = 0.05*(+)	p = 0.046*(+)
YEAR t					
Summer (Jun - Aug)					
Average precipitation (mm)	NS	NS	p = 0.050*(-)	NS	NS

Table 3-5. Survival of year 1 and year 2 adult collared pikas in Pika Valley, Yukon Territory during 1999 – 2009 as a function of interacting local climate variables for year t-1 and year t

Climate variable	**Year 1 Adults**		**Year 2 Adults**	
	Females (n=24)	**Males (n=26)**	**Females (n=41)**	**Males (n=47)**
YEAR t – 1				
Seasonal precipitation			Autumn precip ($p = 0.052$) - Spring precip ($p = 0.0016$) - Summer precip ($p = 0.019$)	
YEAR t				
Seasonal precipitation		Spring precip ($p < 0.0001$) - Autumn precip ($p < 0.0001$) - Winter precip ($p < 0.0001$)	Spring precip ($p = 0.0073$) + Summer precip ($p = 0.11$) - Autumn precip ($p = 0.01$) - Winter precip ($p = 0.045$)	
Summer temperature + precipitation	- Summer temp ($p < 0.0001$ - Summer precip ($p < 0.0001$)			Frost-free days ($p < 0.0001$) - Summer temp ($p < 0.0001$)

Table 3-6. Survival of year 1 and year 2 adult collared pikas in Pika Valley, Yukon Territory during 1999 – 2009 as a function of seasonal Pacific Decadal Oscillation (PDO) by dominant aspect for year t-1 and year t.

Statistical significance: $\alpha \leq 0.006$ (**), biological significance $\alpha \leq 0.05$ (*), d.f. = 9), n = 11 years. NS = not significant to $\alpha \leq 0.05$. The sign of the slope is shown in brackets after the p-value.
More detailed results are shown in Appendix B.

Period of PDO	Year 1 adults			Year 2 adults
	South- facing (n=106)	West-facing (n=26)	East-facing (n=41)	South-facing (n=46)
Year t – 1 (lagged PDO effect)				
Autumn PDO (ave Sept – Nov)	NS	NS	$p < 0.0001$** (+)	NS
Winter PDO (ave Dec - Feb)	$p < 0.0001$** (+)	NS	$p < 0.0001$** (+)	$p = 0.0078$*(+)
Spring PDO (ave Mar – May)	$p = 0.043$* (+)	NS	$p < 0.0001$** (+)	NS
Summer PDO (ave Jun – Aug)	NS	NS	$p < 0.0001$** (+)	NS
Year t				
Autumn PDO (ave Sept – Nov)	NS	$p = 0.028$*(-)	NS	NS
Winter PDO (ave Dec - Feb)	NS	$p = 0.0041$** (+)	NS	NS

Table 3-7. Potential vulnerabilities of collared pikas in the Southwest Yukon in each season of activity. References are shown for studies of collared and American pikas.

Season	Local climate 1999 - 2009	Pika activity	Potential vulnerabilities	References
Autumn (Sep – Nov)	Temperature: -2 to – 9 °C Precipitation: 89 to 165 mm	Haying completed; Foraging before snow cover; Defense of territories	Slow freeze-up results in freezing rain or wet haypiles. Early snowfall or freeze-up shortens haying and foraging time.	
Winter (Dec – Feb)	Temperature: -13 to – 19 °C Precipitation: 65 – 125 mm	Foraging beneath the snow	Shallow snow lacks insulation. Warm mid-winter climate results in freezing rain.	Smith 1978; Hudson et al. 2008
Spring (Mar – May)	Temperature: -1 to – 7 °C Precipitation: 30 – 83 mm	Parturition and rearing of young Timing of parturition adjusted to climate conditions.	Delayed snowmelt shortens growing season and delays green-up for forage.	Franken 2002; 2004(a) Kreuzer and Huntly 2003 Morrison and Hik 2007
Summer (Jun – Aug)	Growing season Temperature: 6 – 10 °C Precipitation: 128 – 307 mm Frost-free days: 63 - 85	Mainly foraging prior to peak biomass, then haying.	Continuous precipitation impedes curing of vegetation and foraging activity.	Morrison et al. 2009

Figure 3-1. Timeline of seasons used to analyze the relationship between recruitment and survival of collared pikas in Pika Valley, Yukon Territory and seasonal climate variables.

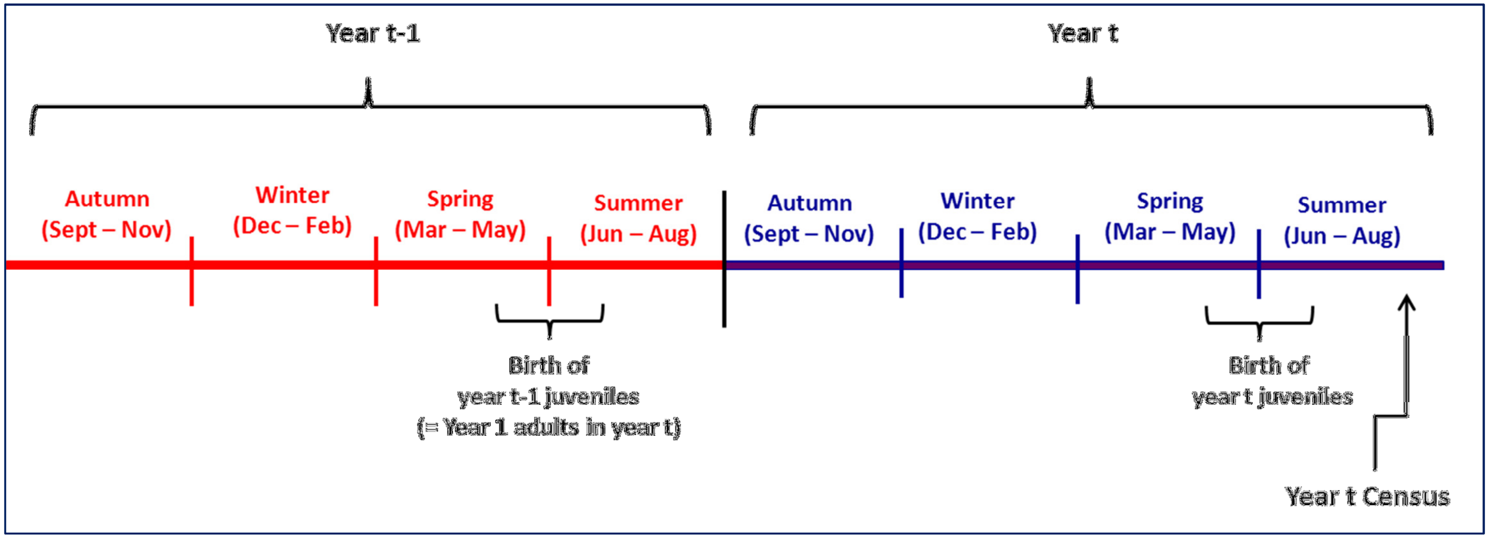
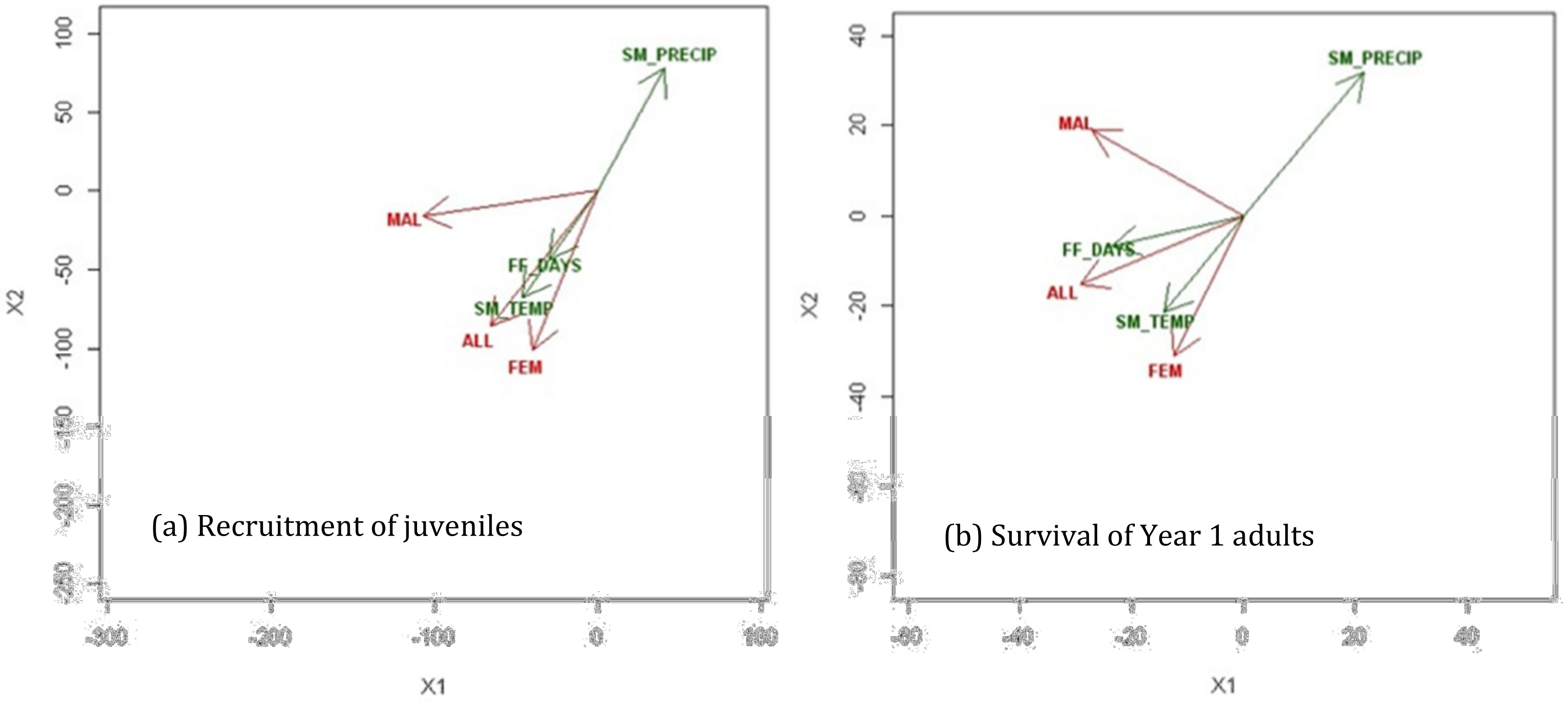


Figure 3-2. Ordinations using non-metric multi-dimensional scaling with a Euclidean distance showing the relationship between indicators of summer climate in year t (temperature, precipitation and number of frost-free days; green) and (a) recruitment of juveniles and (b) survival of Year 1 adults (red). Ordinations were run for females (FEM), males (MAL) and all individuals in each age group. Similar results were observed for survival ofYear 2 adults.


(a) Recruitment of juveniles

(b) Survival of Year 1 adults

Figure 3-3. Scatterplots of percent survival of Year 1 adult collared pikas in the , Yukon Territory, as a function of lagged seasonal PDO for the east – facing slope of the study area. The red vertical line indicates the point of neutral PDO.

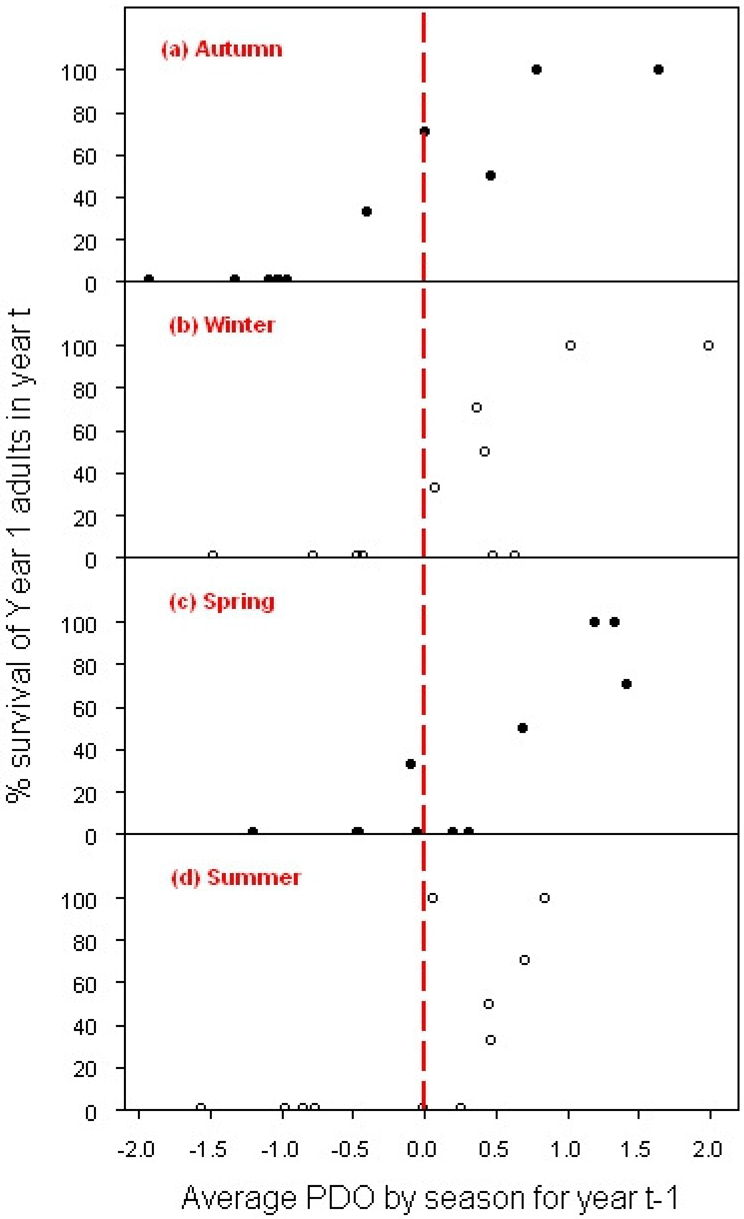


Figure 3-4. Number of collared pikas per year 1999 – 2009 by age group in the Pika Valley, Yukon Territory.

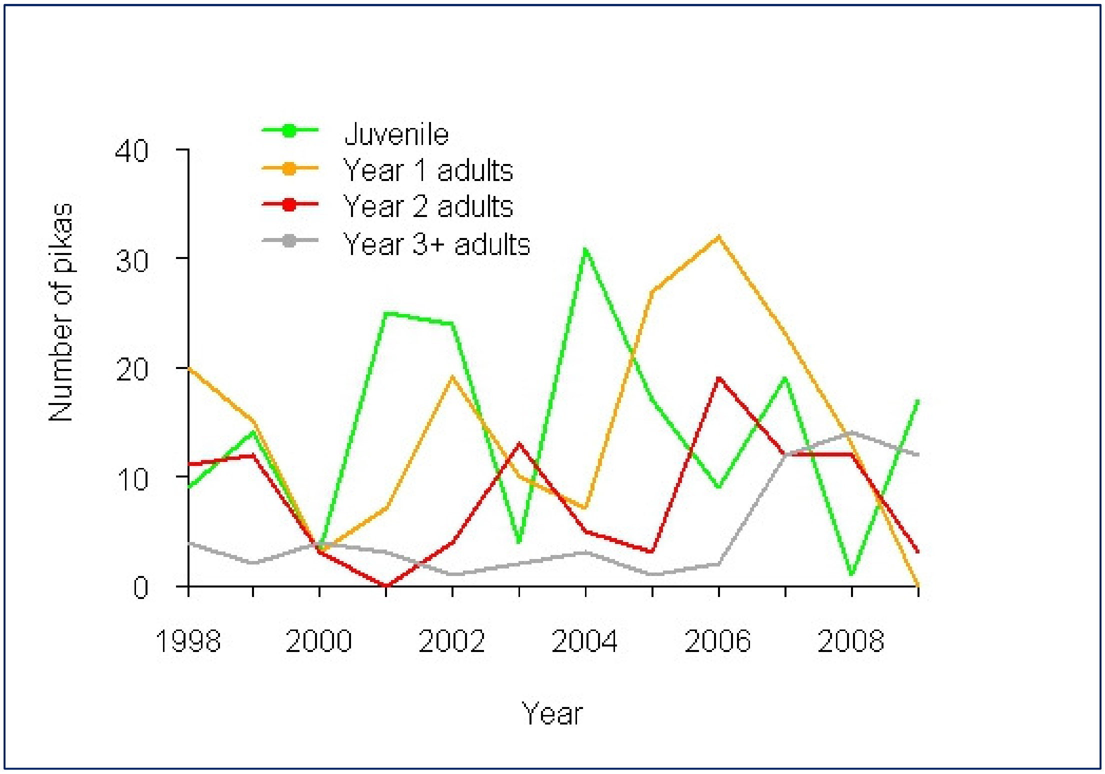


Figure 3-5. Number of collared pikas per year 1998 – 2011 in Pika Valley, Yukon Territory by dominant aspect and showing relationship to phase of PDO (red = warm; blue = cool)

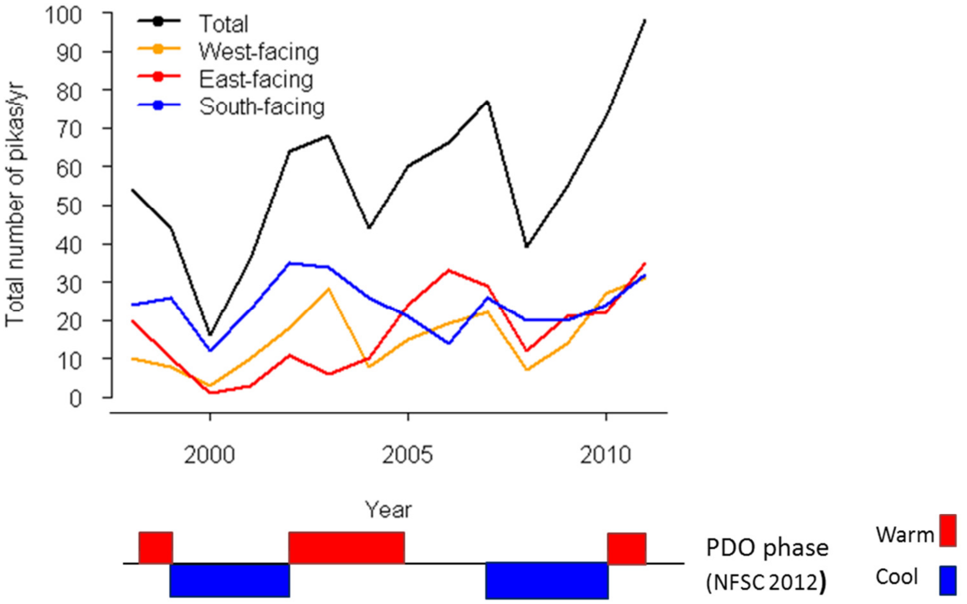
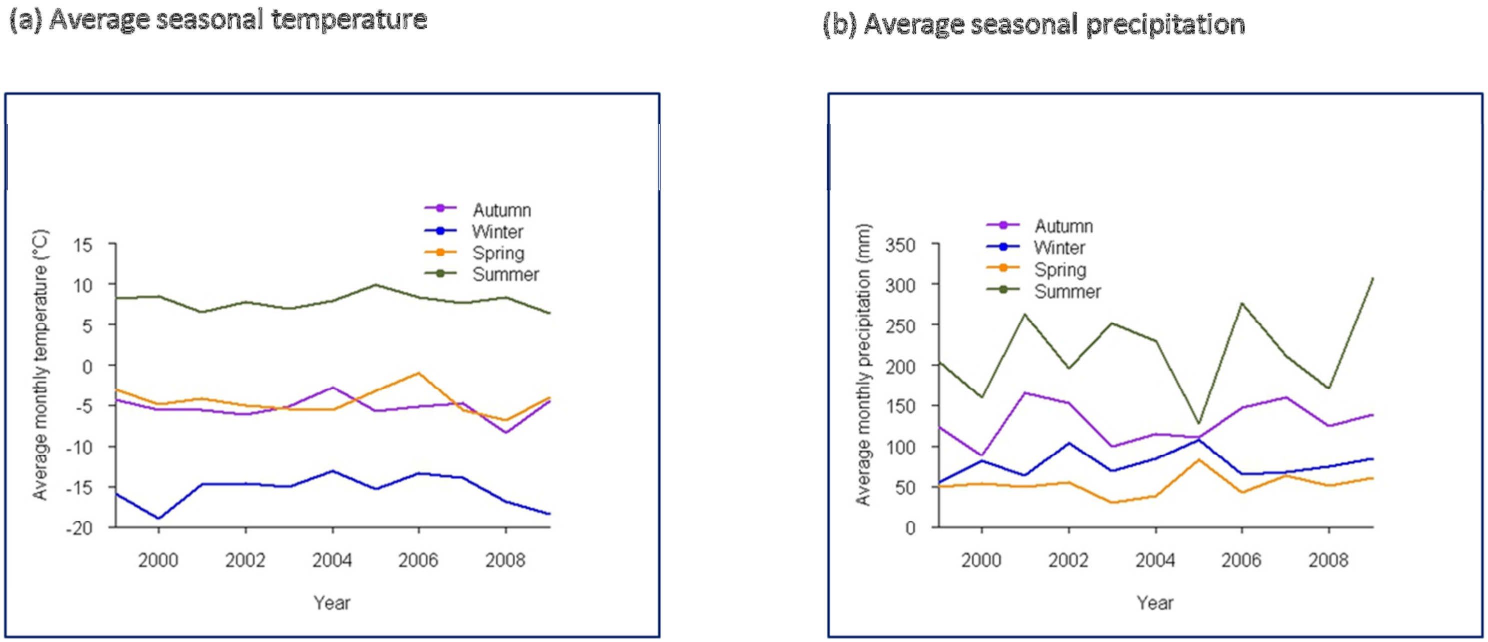


Figure 3-6. Average seasonal temperature (°C) and precipitation (mm) 1998 - 2009 for Pika Valley, Yukon Territory (data from Climate WNA v4.62 (Wang et al. 2012). This data was used as local climate variables in analyses of the relationship between recruitment and survival of collared pikas and climate.


(a) Average seasonal temperature

(b) Average seasonal precipitation

LITERATURE CITED

Aitchison, C.W. 2001. The effect of snow cover on small animals. *In* Snow Ecology: An Interdisciplinary Examination of Snow-Covered Ecosystems. (H.G. Jones, J.W. Pomeroy, D.A. Walker and R.W. Hoham, eds.). Cambridge University Press, Cambridge, U.K. pp 229 – 265.

AMAP (Arctic Monitoring and Assessment Programme). 2012. Arctic Climate Issues 2011: Changes in Arctic Snow, Water, Ice and Permafrost. SWIPA 2011 Overview Report.

Barash, D.P. 1973. Habitat utilization in three species of subalpine mammals. Journal of Mammalogy 54(1): 247 – 250.

Beever, E.A., C. Ray, P.W. Mote, and J.L. Wilkening. 2010. Testing alternative models of climate-mediated extirpations. Ecological Applications 20(1): 164 – 178.

Beever, E. A., S. Z. Dobrowski, J. Long, A. R. Mynsberge, and N. B. Piekielek. *In press*. Understanding relationships among abundance, extirpation, and climate at ecoregional scales. Ecology.

Benton, T.G., S.J. Plaistow, and T.N. Coulson. 2006. Complex population dynamics and complex causation: devils, details and demography. Proceedings of the Royal Society B 273: 1173 – 1181.

Bruggerman, J.E. 2010. Pilot Study on Factors Affecting Pika Populations in the North Cascades Ecosystem: Final Report. Beartooth Wildlife Research, Farmington, Minnesota.

COSEWIC. 2011. COSEWIC assessment and status report on the Collared Pika, *Ochotona collaris,* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa.

Daly, C., W.P. Gibson, G.H. Taylor, G.L. Johnson, P. Pasteris. 2002. A knowledge-based approach to the statistical mapping of climate. Climate Research 22: 99 - 113.

Danby, R.K., S. Koh, D.S. Hik, and L.W. Price. 2011. Four decades of plant community change in the alpine tundra of Southwest Yukon, Canada. AMBIO 40: 660 – 671.

Derksen, C. and R. Brown. 2012. Spring snow cover extent reductions in the 2008–2012 period exceeding climate model projections. Geophysical Research Letters 39: L19504 (6 pages).

Fielding, A.H. and J.F. Bell, 1997. A review of methods for the assessment of prediction errors in conservation presence/ absence models. Environmental Conservation 24(1): 38 – 49.

Forchammer, M.C., E. Post, T.B.G. Berg, T.T. Høye, and N.M. Schmidt. 2005. Local-scale and short-term herbivore-plant spatial dynamics reflect influences of large-scale climate. Ecology 86(10): 2644 – 2651.

Franken, R.J. 2000. Size isn't everything: a preliminary examination on the effect of habitat patch size and isolation on pika persistence. Proceedings of the 6th National Student Conference on Northern Studies, Université Laval, May 5 – 7 2000.

Franken, R.J. 2002. Demography and metapopulation dynamics of collared pikas (*Ochotona collaris*) in the southwest Yukon. M.Sc. Thesis. University of Alberta, Edmonton.

Franken, R.J. and D.S. Hik. 2004a. Interannual variation in timing of parturition and growth of collared pikas (*Ochotona collaris*) in the southwest Yukon. Integrative and Comparative Biology 44: 186 – 193.

Franken, R.J. and D.S. Hik. 2004b. Influence of habitat quality, patch size and connectivity on colonization and extinction dynamics of collared pikas, *Ochotona collaris*. Journal of Animal Ecology 73: 889 – 896.

Hallet, T.B., T Coulson, J.G. Pilkington, T.H. Clutton-Brock, J.M. Pemberton, and B.T. Grenfell. 2004. Why large-scale climate indices seem to predict ecological processes better than local climate. Nature 430: 71 – 75.

Hegel, T.M., A. Mysterud, T. Ergon, L.E. Loe, F. Huettmann, and N.C. Stenseth. 2010. Seasonal effects of Pacific-based climate on recruitment in a predator-limited large herbivore. Journal of Animal Ecology 79: 471 – 482.

Jeffress, M.R., T.J. Rodhouse, C. Ray, S. Wolff, and C.W. Epps. 2013. The idiosyncrasies of place: geographic variation in the climate-distribution relationships of the American pika. Ecological Applications 23(4): 864 – 878.

Jentsch, A., J. Kreyling, and C. Beierkuhnlein. 2007. A new generation of climate-change experiments: events, not trends. Frontiers in Ecology and Environment 5(7): 365 – 374.

Joly, K., D.R. Klein, D.L. Verbyla, T.S. Rupp, and F.S. Chapin III. 2011. Linkages between large-scale climate patterns and the dynamics of Arctic caribou populations. Ecography 34: 345 – 352.

Knape, J. and P. de Valpine. 2011. Effects of climate and climate on the dynamics of animal population time series. Proceedings of the Royal Society B 278: 985 – 992.

Krebs, C.J. 1999. Ecological Methodology, 2nd Edition. Benjamin Cummings, San Francisco.

Krebs, C.J. and D. Berteaux. 2006. Problems and pitfalls in relating climate variability to population dynamics. Climate Research 32: 143 – 149.

Lanier, H.C. and L.E. Olson. 2009. Inferring divergence times within pikas (*Ochotona* spp.) using mtDNA and relaxed molecular dating techniques. Molecular Phylogenetics and Evolution 53: 1 - 12.

Lanier, H.C. and L.E. Olson. 2012. Deep barriers, shallow divergences: reduced phylogeographical structure in the collared pika (Mammalia: Lagomorpha: *Ochotona collaris*). Journal of Biogeography 40:466 – 478.

Lovegrove, B.G. 2003. The influence of climate on the basal metabolic rate of small mammals: a slow-fast metabolic continuum. Journal of Comparative Physiology B 173: 87 – 112.

Manly, B.F.J. 1994. Multivariate statistical methods: a primer. Chapman and Hall, London, U.K.

Mantua, N.J. 2002. Pacific-Decadal Oscillation (PDO). Pages 592 – 594 in M.C. MacCracken and J.S. Perry editors. Encyclopedia of Global Environmental Change: Volume 1, The Earth system: physical and chemical dimensions of global environmental change. John Wiley and Sons, Ltd., Chichester, England.

Millar, J.S. 1974. Success of reproduction in pikas, *Ochotona princeps* (Richardson). Journal of Mammalogy 55: 527 – 542.

Millar, J.S and F.C. Zwickel. 1972. Characteristics and ecological significance of hay piles of pikas. Mammalia 36(4): 657 – 667.

Mitchell, T.D., and P.D. Jones. 2005. An improved method of constructing a database of monthly climate observations and associated high-resolution grids. International Journal of Climatology 25: 693 – 712.

Morrison, S.F. and D.S. Hik. 2007. Demographic analysis of a declining pika *Ochotona collaris* population: linking survival to broad-scale climate patterns via spring snowmelt patterns. Journal of Animal Ecology 76: 899 – 907.

Morrison, S.F., G. Pelchat, A. Donahue, and D.S. Hik. 2009. Influence of food hoarding behavior on the over-winter survival of pikas in strongly seasonal environments. Oecologia 159: 107 – 116.

Myers-Smith, I.H., B.C. Forbes, M. Wilmking, M. Hallinger, T. Lantz, D. Blok, K.D. Tape, M. Macias-Fauria, U. Sass-Klaassen, E. Lévesque, S. Boudreau, P. Ropars, L. Hermanutz, A. Trant, L. Siegwart Collier, S. Weijers, J. Rozema, S.A. Rayback, M. M. Schmidt, G. Schaepman-Strub, S. Wipf, C. Rixen, C.B. Menard, S. Venn, S. Goetz, L. Andreu-Hayles, S. Elmendorf, V. Ravolainen, J. Walker, P. Grogan, H.E. Epstein and D.S. Hik. 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. Environmental Research Letters 6 (4): 045509

Mysterud, A., N.G. Yoccoz, N.C. Stenseth, and R. Langvatn. 2000. Relationships between sex ratio, climate and density in red deer: the importance of spatial scale. Journal of Animal Ecology 69" 959 – 974.

Neilsen, A., N.G. Yoccoz, G. Steinheim, G.O. Storvik, Y. Rekdal, M. Angeloff, N. Pettorelli, Ø. Holand, and A. Mysteryd. 2012. Are responses of herbivores to environmental variability spatially consistent in alpine ecosystems? Global Change Biology 18(10): 3050 – 3062.

Nielsen, S.E., M.R.L. Cattet, J. Boulanger, J. Cranston, G.J. McDermid, A.B.A. Schafer, and G.B. Stenhouse. 2012. Environmental, biological and anthropogenic effects on grizzly bear body size: temporal and spatial considerations. BMC Ecology 13: 31.

Nilsson, A.L.K., E. Knudsen, K. Jerstad, O.W. Røstad, B. Walseng, T. Slagsvold and N.C. Stenseth. 2011. Climate effects on population fluctuations of the white-thrated dipper *Cinclus cinclus*. Journal of Animal Ecology 80: 3235 – 243.

Northwest Fisheries Science Centre (NFSC) website. 2012. Pacific Decadal Oscillation (PDO).

http://www.nwfsc.noaa.gov/research/divisions/fe/estuarine/oeip/ca-pdo.cfm, accessed June 22 2013.

Patil, V.P. 2010. The interactive effects of climate, social structure and life history on the population dynamics of hoary marmots (*Marmota caligata*). M.Sc. Thesis, University of Alberta, Edmonton.

R Foundation for Statistical Computing (RFSC). 2012. R: A Language and Environment for Statistical Computing, Vienna, Austria. http://www.r-project.org/

Roland, J. and S.F. Matter. 2013. Variability in winter climate and winter extremes reduces population growth of an alpine butterfly. Ecology 94(1): 190 – 199.

Seneviratne, S.I., R.D. Koster, Z. Guo, P.A. Dirmeyer, E. Kowalczyk, D. Lawrence, P. Liu, C-H. Lu, D. Mocko, K.W. Oleson, and D. Verseghy. 2006. Soil moisture memory in AGCM simulations: analysis of global land-atmosphere coupling experiment (GLACE) data. Journal of Hydrometeorology 7: 1090 – 1112.

Smith, A.T. 1978. Comparative demography of pikas (*Ochotona*): Effect of spatial and temporal age-specific mortality. Ecology 59: 133 – 139.

Smith, A.T. and B.L. Ivins. 1983. Colonization in a pika population: dispersal vs. philopatry. Behavioral Ecology and Sociobiology 13: 13 – 47.

Smith, A.T., W. Li, and D.S. Hik. 2004. Pikas as harbingers of global warming. Species 41: 4 - 5

Stenseth, N.C., and A. Mysterud. 2005. Climate packages: finding the right scale and composition of climate in ecology. Journal of Animal Ecology 74: 1195 – 1198.

Walker, D.A., W.D. Billings and J.G. de Molenaar. 2001. Snow-vegetation interactions in tundra environments. *In* Snow Ecology: An

Interdisciplinary Examination of Snow-Covered Ecosystems. (H.G. Jones, J.W. Pomeroy, D.A. Walker and R.W. Hoham eds). Cambridge University Press, Cambridge, U.K. pp 265 - 324.

Walther, G-R. 2010. Community and ecosystem responses to recent climate change. Philosophical Transactions of the Royal Society B 265: 2019 – 2024.

Wang, T., Hamann, A., Spittlehouse, D., and Murdock, T. N. 2012. ClimateWNA - High-Resolution Spatial Climate Data for Western North America. Journal of Applied Meteorology and Climatology 61: 16-29.

Weiss. D.L., D.S. Gutzler, J.E. Allred Coonrod, and C.N. Dahm. 2004. Seasonal and inter-annual relationships between vegetation and climate in central New Mexico, USA. Journal of Arid Environments 57: 507 – 534.

White, K.S., G.W. Pendelton, D. Crowley, H.W. Griese, K.J. Hundertmark, T. McDonough, L. Nichols, M. Robus, C.A. Smith, and J.W. Schoen. 2011. Mountain goat survival in coastal Alaska: effects of age, sex and climate. The Journal of Wildlife Management 75 (8): 1731 – 1744.

Wilkening, J.L., C. Ray, E.A. Beever, and P.F. Brussard. 2011. Modeling contemporary range retraction in Great Basin pikas (*Ochotona princeps*) using data on microclimate and microhabitat. Quaternary International 235: 77 – 78.

Zgurski, J. M. 2011. The mating habits, dispersal behavior and genetic structure of a collared pika (*Ochotona collaris*: Ochotonidae) population in the southwest Yukon, and a phylogeny of the genus *Ochotona*. Ph.D. thesis, University of Alberta, Edmonton.

Zgurski, J. M and D.S. Hik. 2012. Polygamy and even-sexed dispersal in a population of collared pikas, *Ochotona collaris*. Animal Behaviour 83: 1075 – 1082.

Zgurski, J.M. and D.S. Hik. 2013. Gene flow and the restoration of genetic diversity in a fluctuating collared pika (*Ochotona collaris*) population. Conservation Genetics online publication (01 September 2013), doi: 10.1007/s10592-013-0519-2.

CHAPTER 4 General Discussion and Conclusions

It was Aldo Leopold who eloquently captured the concept of an organism-centric view of ecological study in his passage on “thinking like a mountain” in Sand County Almanac (1949). Animals interact with their environment at multiple spatial and temporal scales in a complex interplay of life history attributes and underlying ecological processes. My research examined multi-scalar relationships for a small, alpine herbivore that is adapted highly variable and extreme climatic conditions at high elevations in the Arctic. Collared pikas (*Ochotona collaris*) have many distinct and intriguing characteristics: their effort put into curing and caching haypiles (Morrison et al. 2009); long distance dispersal from their natal home range shortly after emergence (Frankin and Hik 2004a; Zgurski and Hik 2012), promiscuous mating behaviour (Zgurski and Hik 2012), and potentially facilitative interactions with sympatric alpine mammals (Patil 2010; Barrio et al. 2013) . The outcomes of this study provide new information regarding habitat selection by collared pikas and influences on their survival and population dynamics.

I used a long-running dataset of marked individuals to investigate relationships with environmental influences at different spatial and temporal scales. At the metapopulation scale, I identified relationships between recruitment and juvenile abundance and survival of adult pikas with different indicators of seasonal climate and PDO (Chapter 3). Lagged PDO (year t-1) provided the strongest predictor of adult survival, particularly for Year 1 males and Year 2 females. Recruitment and juvenile abundance were correlated with lagged summer and autumn climate and current summer temperature, inferring that both maternal condition and current growing season influence reproductive success and fitness. Relationships with climate varied by dominant aspect and may be linked to exposure to sun and timing of snowmelt.

At the scale of talus patches and territories, my research spatially defined occupancy - habitat relationships. I used a remote sensing image in ArcGIS 10 to map the location of pika territories within patches and linked them to metrics of patch configuration, topography, and the quality of talus and vegetation using Normalized Difference Vegetation Index (NDVI) (Chapter 2). My results, consistent across spatial scales, were that colonization by pikas occurs more frequently, and occupancy lasts for longer, in areas of higher solar radiation and above-ground biomass of vegetation. This relationship is seen for metrics of habitat quality within territories and patches and in a 10m grazing buffer around patches. Data based on territories within patches provided predictors of relationship across a broader array of predictor variables compared to presence/absence information for whole patches, but models derived from the latter were more parsimonious (had lower AIC values with fewer variables).

These results highlight the complexity of factors influencing pika abundance, survival and occupancy in one metapopulation, building on previous studies at this study site. My research methods demonstrated that GIS and remote sensing can be used effectively to study habitat-occupancy dynamics at the scale of collared pika territories, including the use of NDVI as a proxy for above-ground biomass. It also affirmed the value of using long-running datasets that can provide information about individual pikas for examining mechanistic links between occupancy and population dynamics and environment.

Integration of research outcomes

Collared pikas appear to be integrating information on a number of habitat-related factors when selecting and establishing their territories, as indicated by the strong correlations found between colonization and length of occupancy with indicators of habitat quality. The implications of choosing a territory are not trivial. The accessibility and biomass of vegetation affects the energetic cost of harvesting for haypiles (McIntire and Hik 2005; Hudson et al. 2008; Morrison et al. 2009). The spatial configuration of patches in a site influences ease of dispersal and physical capacity for territories, and therefore, affects social interaction and proximity of potential mates (Franken and Hik 2004b; Zgurski and Hik 2012). The influence of survival and fecundity on local populations varies with microclimates (Morrison and Hik 2007).

Specific life history traits increase the probability of survival of collared pikas regardless of territory choice. The timing of parturition varies with snowmelt and vegetation green-up (Franken and Hik 2004a). Haying provides a buffer against variable winter conditions (Morrison et al. 2009) by creating a source of food large enough to last through long and climatically variable Arctic winters, supplemented by grazing in the autumn and likely, also, under snow cover in the winter and spring (Hudson et al. 2008; Morrison et al. 2009).

In this study, exposure to solar radiation was revealed as an integrating theme across spatial scales and seasons, with winter insolation being a stronger predictor of occupancy than summer insolation. There are many reasons why this might be the case. There was a positive correlation in my study area between the amount of solar radiation and above-ground biomass of vegetation territories, inferring that sunnier areas also have higher vegetation quality. Exposure to sun in the summer influences ambient temperature and timing of green-up. It may beneficial to juveniles to sun themselves while they are grazing and building body mass. In winter, exposure to sun can affect the depth and quality of snow as well as emergence of alpine vegetation beneath the snow (Walker et al. 2001).

Suggestions for future research

One of the limitations of this research is that it examines only one population occupying a single valley. Confidence in these results would be increased by gathering data in other locations and seeing if the same patterns hold. For example, these results indicate specific relationships between life stage, sex and climate but correlations between climate indicators and population dynamics can vary by location (Joly et al. 2011; Neilsen et al. 2012) and with local site characteristics (Wilkening et al. 2011; Jeffress et al. 2013). Site-specific climate data such as temperature, precipitation and snow depth and duration can provide more reliable indicators of climate-population correlations compared with data averaged and downscaled across the region from distant climate stations (Nielsen et al. 2013a).

Future studies of occupancy dynamics should include information about social dynamics. Although mating behaviour and sexual alternation of territories by collared pikas (Zgurski and Hik 2012) is not as rigidly maintained as it is for American pikas (Smith and Ivins 1983), social dynamics still play an important role in occupancy (Franken 2002). Nearest-neighbour analysis using data on pika sex and age may reveal informative links with habitat selection and quality.

New information about correlations between habitat quality and occupancy could be applied to further examine relationships between population dynamics (recruitment, abundance, survival, fecundity) and indicators of habitat quality, such as solar radiation and vegetation quality. Existing data on body mass could be used to further my understanding of these relationships.

The results of parentage analysis from this site could be used with spatial data on habitat quality to investigate factors influencing dispersal. Juvenile collared pikas disperse shortly after emergence in the spring and have a strong time constraint to dispersal in that they must find and establish a territory quickly to be able to gain body mass and amass a haypile in their first growing season. Once settled in a territory, they are unlikely to disperse further (Franken 2002; Franken and Hik 2004a; Zgurski and Hik 2012). Kin relationships for American pikas facilitate settlement of adjacent territories by offspring (Smith and Ivins 1983) and may increase probability of survival of juveniles (Smith 1974) but this dynamic has not been fully examined for collared pikas, who disperse sooner and further (Zgurski and Hik 2012). Red squirrels (*Sciurus vulgaris*) (Haughland and Larsen 2004; Clobert et al. 2009) and grizzly bears (*Ursus arctos*) (Nielsen et al. 2013b) settle in territories based on similarities with their natal territories rather than the intrinsic quality of the habitats. Juvenile collared pikas may also be using environmental cues to move across the landscape and settle on a suitable territory.

CONCLUSIONS

These research findings provide further confirmation that habitat quality is important to occupancy dynamics and survival of collared pikas. All patches are not created equal; pikas are making choices about where they establish their territories based on environment cues.

Climate is an important driver of pika demography but may be buffered by habitat quality (Franken and Hik 2004b; Wilkening et al. 2011; Jeffress et al. 2013) and social dynamics (Franken 2002; Franken and Hik 2004a; Zgurski and Hik 2012) and more investigation is needed in these areas.

Long-term demographic data are invaluable for increasing our understanding of the mechanisms linking population dynamics to ecological processes (Hallett et al. 2004; Previtali et al. 2009; Hegel et al. 2010; Roland and Matter 2013). These processes are often highly complex, interacting across numerous environmental factors at multiple spatial and temporal scales (Benton et al. 2006; Walther 2010; Thornton et al. 2011). 'Thinking like a pika' requires us to apply what we know of the biology of this endearing species at scales where individuals interact most directly with their environment

(Wiegand et al. 1999; Thornton et al. 2011). Increases in the accuracy and resolution of spatial and climate data will provide ongoing opportunities to explore these relationships.

LITERATURE CITED

Beever, E. A., S. Z. Dobrowski, J. Long, A. R. Mynsberge, and N. B. Piekielek. *In press*. Understanding relationships among abundance, extirpation, and climate at ecoregional scales. Ecology.

Benton, T.G., S.J. Plaistow, and T.N. Coulson. 2006. Complex population dynamics and complex causation: devils, details and demography. Proceedings of the Royal Society B 273: 1173 – 1181.

Barrio, I. C.; Hik, D. S.; Bueno, C. G.; and J.F. Cahill. 2013. Extending the stress-gradient hypothesis - is competition among animals less common in harsh environments? Oikos 122 (4): 516-523.

Clobert, J., J-F. Le Galliard, J. Cote, S. Meylan, and M. Massot. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecology Letters 12: 197 – 209.

Franken, R.J. 2002. Demography and metapopulation dynamics of collared pikas (*Ochotona collaris*) in the southwest Yukon. M.Sc. Thesis. University of Alberta, Edmonton.

Franken, R.J. and D.S. Hik. 2004a. Interannual variation in timing of parturition and growth of collared pikas (*Ochotona collaris*) in the southwest Yukon. Integrative and Comparative Biology 44: 186 – 193.

Franken, R.J. and D.S. Hik. 2004b. Influence of habitat quality, patch size and connectivity on colonization and extinction dynamics of collared pikas, *Ochotona collaris*. Journal of Animal Ecology 73: 889 – 896.

Hallet, T.B., T Coulson, J.G. Pilkington, T.H. Clutton-Brock, J.M. Pemberton, and B.T. Grenfell. 2004. Why large-scale climate indices seem to predict ecological processes better than local climate. Nature 430: 71 – 75.

Haughland, D.L., and K.W. Larsen. 2004. Exploration correlates with settlement: red squirrel dispersal in contrasting habitats. Journal of Animal Ecology 76: 1024 – 1034.

Hegel, T.M., A. Mysterud, T. Ergon, L.E. Loe, F. Huettmann, and N.C. Stenseth. 2010. Seasonal effects of Pacific-based climate on recruitment in a predator-limited large herbivore. Journal of Animal Ecology 79: 471 – 482.

Hudson, J. M. G., S.F. Morrison, and D.S. Hik. 2008. Effects of leaf size on forage selection by collared pikas, *Ochotona collaris*. Arctic, Antarctic and Alpine Research 40 (30: 481 – 486.

Jeffress, M.R., T.J. Rodhouse, C. Ray, S. Wolff, and C.W. Epps. 2013. The idiosyncrasies of place: geographic variation in the climate-distribution relationships of the American pika. Ecological Applications 23(4): 864 – 878.

Joly, K., D.R. Klein, D.L. Verbyla, T.S. Rupp, and F.S. Chapin III. 2011. Linkages between large-scale climate patterns and the dynamics of Arctic caribou populations. Ecography 34: 345 – 352.

Leopold, A. 1949. A Sand County Almanac with Essays on Conservation from Round River. Oxford University Press, U.K.

McIntire, E.J.B. and D.S. Hik. 2005. Influences of chronic and current season grazing by collared pikas on above-ground biomass and species richness in subarctic alpine meadows. Oecologia 145: 288 – 297.

Morrison, S.F. and D.S. Hik. 2007. Demographic analysis of a declining pika *Ochotona collaris* population: linking survival to broad-scale climate patterns via spring snowmelt patterns. Journal of Animal Ecology 76: 899 – 907.

Morrison, S.F. , G. Pelchat, A. Donahue, and D.S. Hik. 2009. Influence of food hoarding behavior on the over-winter survival of pikas in strongly seasonal environments. Oecologia 159: 107- 116.

Neilsen, A., N.G. Yoccoz, G. Steinheim, G.O. Storvik, Y. Rekdal, M. Angeloff, N. Pettorelli, Ø. Holand, and A. Mysteryd. 2012. Are responses of herbivores to environmental variability spatially consistent in alpine ecosystems? Global Change Biology 18(10): 3050 – 3062.

Nielsen, S.E., M.R.L. Cattet, J. Boulanger, J. Cranston, G.J. McDermid, A.B.A. Schafer, and G.B. Stenhouse. 2012. Environmental, biological and anthropogenic effects on grizzly bear body size: temporal and spatial considerations. BMC Ecology 13: 31.

Nielsen, S.E., A.B.A. Shafer, M.S. Boyce, and G.B. Stenhouse. 2013b. Does learning or instinct shape habitat selection? PLoS ONE 8(1): e53721. doi:10.1371/journal.pone.00053721

Patil, V.P. 2010. The interactive effects of climate, social structure and life history on the population dynamics of hoary marmots (*Marmota caligata*). M.Sc. Thesis, University of Alberta, Edmonton.

Previtali, M.A., M. Lima, P.L. Meserve, D.A. Kelt, and J.R. Gutierrez. 2009. Population dynamics of two sympatric rodents in a variable environment: rainfall, resource availability, and predation. Ecology 90(7): 1996 – 2006.

Roland, J. and S.F. Matter. 2013. Variability in winter climate and winter extremes reduces population growth of an alpine butterfly. Ecology 94(1): 190 – 199.

Smith, A.T. 1974. The distribution and dispersal of pikas: influences of behavior and climate. Ecology 55: 1368 – 1376.

Smith, A.T. and B.L. Ivins. 1983. Colonization in a pika population: dispersal vs. philopatry. Behavioral Ecology and Sociobiology 13: 13 – 47.

Thornton, D.H., L.C. Branch and M.E. Sunquist. 2011. The influence of landscape, patch and within-patch factors on species presence and abundance: a review of focal patch studies. Landscape Ecology 26: 7 – 18.

Walker, D.A., W.D. Billings and J.G. de Molenaar. 2001. Snow-vegetation interactions in tundra environments. *In* Snow Ecology: An Interdisciplinary Examination of Snow-Covered Ecosystems. (H.G. Jones, J.W. Pomeroy, D.A. Walker and R.W. Hoham eds). Cambridge University Press, Cambridge, U.K. pp 265 - 324.

Walther, G-R. 2010. Community and ecosystem responses to recent climate change. Philosophical Transactions of the Royal Society B 265: 2019 – 2024.

Wiegand, T. K.A. Moloney, J. Naves, and F. Knauer. 1999. Finding the missing link between landscape structure and population dynamics: a spatially explicit perspective. The American Naturalist 154(6): 605- 627.

Wilkening, J.L., C. Ray, E,A, Beever, and P.F. Brussard. 2011. Modeling contemporary range retraction in Great Basin pikas (*Ochotona princeps*) using data on microclimate and microhabitat. Quaternary International 235: 77 – 78.

Zgurski, J. and D.S. Hik. 2012. Polygandry and even-sexed dispersal in a population of collared pikas, *Ochotona collaris*. Animal Behaviour 83: 1075 – 1082.

APPENDIX A. Forage biomass is correlated with NDVI in alpine meadows used by collared pikas

INTRODUCTION

The relationship between values of the Normalized Difference Vegetation Index (NDVI) and phytomass in Arctic and alpine ecosystems has been demonstrated in a number of studies (e.g. Walker et al. 2003; 2005; Tamstorf et al. 2007; Raynolds et al. 2012). NDVI, derived from spectral remote sensing, is useful as a proxy for vegetation productivity and distribution because live green plants strongly absorb visible light and reflect at near-infrared, giving a positive NDVI value that varies with the physical characteristics of plants (e.g., leaf structure and amount of chlorophyll) and the density of the vegetation layer (Tucker and Sellers 1986; Neigh et al. 2008). Rock and ice, on the other hand, have NDVI values closer to zero.

NDVI has proven useful for tracking changes in tundra vegetation over time, in particular as this relates to climate change (e.g., Pouliot et al. 2009; Bhatt et al. 2010). Spectral measures have typically been used to characterize and quantify vegetation at large spatial scales, such as circumpolar classification of tundra bioclimate zones (Walker et al. 2005; Raynolds et al. 2012) and mapping of vegetation at regional scales (e.g. Arctic Refuge Coastal Plain, Griffiths et al. 2002). There are fewer examples of NDVI being used to measure Arctic and alpine vegetation at more local scales, particularly since these ecosystems tend to be of lower productivity and difficult to differentiate using remote imagery. However, improved resolution of remote sensing instruments is increasing the utility of NDVI at these more detailed scales (Petorelli et al. 2011). Examples include the use of NDVI to investigate changes in seasonal growth dynamics of dry, mesic and wet vegetation types within a single high Arctic valley (Tamstorf et al. 2007) and to assess biophysical influences on Arctic tundra vegetation (Laidler et al. 2008).

NDVI is also an effective and useful tool for quantifying relationships between the productivity and distribution of vegetation cover and the dynamics and distribution of animals (Petorelli et al. 2005; Petorelli et al. 2011). It has been used to relate vegetation distribution and the dynamics of large mammals, such as tundra caribou (*Rangifer tarandus*) (Griffith et al. 2002; Bårdsen and Tveraa 2012); red deer (*Cervus elaphus*) (Mysterud et al. 2008); and grizzly bear (*Ursus arctos*) (Wiegand et al. 2008). Recent studies linking NDVI values to the dynamics of small mammalian herbivores include the effect of changes in plant cover on fluctuations in populations of grass and vesper mice (*Akodon azarae; Calomys venustus*) in agricultural lands (Andreo et al. 2009) and microtine rodents in a sub-Arctic ecosystem (Olofsson et al. 2012). Ongoing advances in the resolution of remote imagery is making it increasingly possible to use NDVI at spatial scales pertinent to small mammals (Petorelli et al. 2011), although assumptions of large-scale changes in biomass based on NDVI must be validated by ground-based surveys of changes in plant species composition (Olofsson et al. 2012).

Collared pikas (*Ochotona collaris*) inhabit high-elevation valleys in the Arctic that are naturally fragmented into talus patches and surrounded by a matrix of alpine meadow. They establish and defend territories that comprise an area of talus, in which they establish 'haypiles' or overwinter food caches collected from adjacent meadows (MacDonald and Jones 1987, Franken 2002, Morrison et al. 2009). The quality of vegetation within and around each patch is positively linked to colonization and length of occupancy by the species (Franken 2002; Chapter 2).

The composition of plant communities associated with the alpine tundra inhabited by collared pikas is driven by micro-topographic gradients and their influence on soil moisture, nutrient availability, snow cover, and exposure to sun (Laidler et al. 2008; Nagy and Grabherr 2009; Perez 2012). Snow gradients, in particular, have an important influence on patterns of alpine vegetation (Walker et al. 2001). In areas of talus, surface boulders create micro-topographic conditions that are distinct from the surrounding deep-soiled meadow. Geomorphic processes are at work in and around talus that affect edaphic conditions, such as frost-heaving, talus movement and deposition of sediment and debris (Perez 2012). The movement of moisture along topographic gradients influences productivity due to transport of nutrients from upper slopes and concentrating them at slope bottoms (Yano et al. 2010). The timing of snow release also influences moisture levels and vegetation growth (Walker et al. 2001). The result is a predictable pattern of plant communities associated with micro-topography. For example, *Dryas*-dominated communities are typically located on the upper crest or near-sides of talus patches where snow releases early in the spring and moisture levels are lower (Jónsdóttir et al. 1999; Tamstorf et al. 2007). Wetter areas include more productive graminoid and *Salix*–dominated communities (Tamstorf et al. 2007), and *Cassiope*-dominated communities typically occur in depressions that retain snow for longer periods than other sites (Walker et al. 2001).

Previous studies of alpine vegetation in the southwest Yukon have used plot data based on ground-based surveys and transects (e.g. Franken 2002; McIntire and Hik 2005; Danby et al. 2011) but these have not been linked to remote sensing. In this study, I mapped and measured the species composition and peak season above-ground biomass for plant communities around 18 talus patches occupied by collared pikas and compared this information to the NDVI values for each community type. I predicted that NDVI (resolution of 2.4 m) would be a reliable predictor of above-ground biomass in the territories of collared pikas. These results were used to validate NDVI as a proxy for vegetation quality when assessing the relationship between habitat quality and occupancy by collared pikas at different spatial scales (Chapter 2).

METHODS

Study area

The Pika Valley study area is located in the Ruby Range, Yukon Territory, at 61°12'N and 138°16'W to the east of Kluane Lake and the St Elias mountain range. The elevation of the 4 km^2 study site ranges from 1500m to 2000m. The orientation of natural landforms divides this valley into sub-areas with north, south, east and west aspects, separated by 1 – 2 m wide creeks. Each slope is a mosaic of talus boulderfields within a matrix of alpine tundra vegetation.

Vegetation adjacent to boulderfields is dominated by alpine graminoids (sedges, rushes and grasses), forbs, mosses and lichens with some low shrubs. Hoary marmots (*Marmota caligata*) and Arctic ground squirrels (*Urocitellus parryii*) are other resident mammalian herbivores.

Vegetation data

Vegetation surveys around occupied talus patches

Plant species composition was measured within three 1m x 1m quadrats and one 2m x 3m ‘macro’ plot located randomly within visibly distinct plant communities in the vicinity of the 18 talus patches having evidence of occupancy by collared pikas (currently or previously active haypiles present). I used this approach rather than transects due to high levels of variability in micro-topography around talus.

For each plant community (see Table A-1), I recorded the species composition and noted the slope, land shape (flat, convex, concave), ‘rockiness’, moisture, soil depth and height of vegetation. I also cut a 10cm x 10cm sample of each community and recorded its composition and dry weight to calculate above-ground biomass (g/m^2). Vascular plants were identified to the species level (whenever possible) following nomenclature in *Flora of the Yukon Territory, 2nd edition* (Cody 2000). Bryophytes were categorized as moss (‘*Raconitrum* spp.’ or ‘Other’) or lichen (Pojar and MacKinnon 2004).

I measured the location and extent of each plant community relative to the talus patch and haypiles in the patch.

I classified plant communities in two different ways and compared the results:

<u>Method 1</u>: Field identification of 13 different plant communities, each having a visibly distinct plant species composition as well as similar soil depth, soil moisture and location relative to the talus patch (Table A-1; Figure A-1). Each community was readily identifiable based on plant associations, with one or two characteristically dominant species and commonly associated minor species.

<u>Method 2</u>: Cluster analysis of plot data using using K-means Cluster Analysis in R i386 2.15.2 (RFSC 2012). Plot data consisted of % cover of each ground cover types in the plot (with the exception of bareground-rock). Plant composition data was grouped as follows prior to the cluster analysis to reduce the number of variables to a number that the analysis could handle:

- Mosses and lichens: all mosses; all lichens
- Graminoids: all *Carex* spp.; other graminoids (grasses, sedges and rushes);
- Forbs: *Silene acaulis*; *Petasites frigida; Polygynum bistort; Saxifrage bronchiatus; S. davorica;* all other forbs;
- Deciduous shrubs: *Salix arctica; S. polaris; S. reticulata*; *Vaccinium* spp.; *Dryas* spp.; and
- Evergreen shrubs: *Cassiope tetragona.*

Mid-talus vegetation was removed from the cluster analysis and manually added later; this community is mainly bareground and rock with scattered and diverse plant species and therefore did not separate out as a distinct community using cluster analysis.

Normalized difference vegetation index (NDVI) data

I digitized the spatial extent of each surveyed community using ArcGIS 10. To reduce bias in my characterization of polygons, I separated the talus and vegetation layers in the Quickbird imagery and only displayed the talus layer during the digitization process. NDVI values were derived from a single Quickbird image taken on July 31 2007 using spectral reflectance measurements in the visible (red; VIS) and near-infrared (NIR) spectral regions using the Image Analysis tool in ArcGIS 10 (calculation: NDVI = (NIR – VIS) / (NIR + VIS). The Quickbird image was taken during the height of summer and hence, peak vegetation biomass near talus at this study site (McIntire and Hik 2005; Tamstorf et al. 2007). The overall image was very clear, however territories and patches from one high elevation area and one mid-talus area were removed from the analyses due to cloud cover, which falsely decreases NDVI values (Petorelli et al. 2005; Williamson et al. 2013). Shadow was not considered a confounding factor in this wide valley. The image was not atmospherically corrected so NDVI values were compared as relative, rather than absolute, amounts.

Based on visual differences in talus and vegetation in the Quickbird image, talus was estimated to have NDVI values between 80 and 125 and alpine vegetation to have values between 125 and 183. All pixels having an NDVI value of more than 125 were extracted into a separate raster layer for vegetation. The vegetation layer and polygons of digitized plant communities were overlaid to determine the average NDVI value for each community type.

In using the Quickbird image for a single date (July 31 2007), I assumed the following:

- an image at the peak of the growing season reflects the above-ground biomass for the site; and
- relative NDVI values for vegetation in this alpine environment are constant from year to year at the scale of resolution for the image.

Statistical analysis

Average NDVI values for each of the plant communities were compared to the above-ground biomass for that community using linear regression in R i386 2.15.2 (RFSC 2012). Separate linear regressions were run for communities identified using each of the two types of classification methods described above (field identification versus cluster analysis).

Cassiope tetragona and *Sphagnum* spp. were excluded from the regressions for two reasons: (1) their above-ground parts are reddish in colour rather than green and therefore were not expected to reflect light in the same way as green plants; and (2) these plants are only rarely harvested by pikas (Hudson et al. 2008). Additionally, there was only one sample of *Sphagnum* and there was a risk that the single sample might skew the analysis results.

Vaccinium spp. are also somewhat brown in colour but were included in the regression because they are utilized as forage by pikas (Rausch 1961; Hudson et al. 2008).

RESULTS

Analysis of NDVI values for plant communities

NDVI differentiated plant communities in a manner consistent with the moisture levels of the site and position relative to the talus patch (Figure A-2). Average NDVI and above-ground biomass were greater for plant communities that were expected to be more productive based on their plant species composition and position relative to the talus. For example, forb-rich receiving sites at the bottom of talus patches and alpine meadow had higher NDVI values. Conversely, drier ecosystems such as *Dryas*-dominated communities at the top of talus patches and mid-talus mixed plant communities had comparatively low NDVI values (Table A-1; Figure A-2).

There was a linear relationship between peak season above-ground biomass and the average NDVI value for plant communities derived through both Method 1: field identification (Figure A-3; n=94, r^2=0.52, p=0.013) and Method 2: communities identified using cluster analysis (Figure A-4; n=94, r^2=0.53, p=0.027).

The linear formulae for the two classifications were similar:

Method 1: Field identification: y = 3.75 + 0.037 (x);

Method 2: Cluster analysis: y = 2.44 + 0.035 (x)

As expected, communities where *Cassiope* and *Sphagnum* moss were the dominant species were anomalous, with average NDVI values similar to dry ecosystems even though they both grow in moist conditions. Exclusion of the NDVI values for *Vaccinium* spp. from the regression resulted in a closer fit to the data (r^2 = 0.73, p = 0.0017).

DISCUSSION

NDVI is an effective proxy for the productivity of vegetation communities within and adjacent to talus in alpine meadows. Correlations between NDVI values and peak season above-ground biomass and plant species composition were robust to different classification and analysis methods. Cluster analysis was less precise, in part because the automated lumping of communities was unable to distinguish very dry mid-talus communities. The cluster analysis also did not take into account the position of the community relative to the talus and therefore lumped together rich communities such as meadow and forb-rich receiving sites. This issue could be addressed by weighting some communities according to their position relative to the talus.

Just over 50% of the variability in average NDVI was explained by the relationship with above-ground biomass (Figures A-3 and A-4), leaving a large amount of variance unexplained. The r^2 value can be increased to 73% by removing *Vaccinium* spp. from the linear regression, since the plants have reddish, rather than green leaves and would therefore be expected to have lower NDVI values. The remaining variance could be due to lack of precision in digitally mapping the plant communities as well as the large amount of variability in the biomass for each community (Table A1).

These results are consistent overall with expected patterns of plant communities in the proximity of talus patches, with drier to mesic dwarf shrub communities on the ridge of talus, wetter and somewhat more productive *Salix*-dominated communities along the side slopes and highest productivity mixed graminoid and forb-dominated communities in moist sites at the base of the talus and further into the meadow (Jónsdóttir et al. 1999; Tamstorf et al. 2007).

Plant composition and above-ground biomass adjacent to talus may be more effectively characterized by mapping individual plant communities rather than random sampling or transect lines since the latter fails to account for the high amount of variability in topography and, therefore, in plant communities. At the same time, accurate mapping of individual plant communities can be challenging and more prone to error than simple transects. My results demonstrate that remote sensing imagery can be used to estimate vegetation productivity with high resolution in alpine landscapes having high variability in community composition. This method has potential for broader-scale application to extrapolate the productivity of alpine habitats over broad spatial scales.

The 'plant morphology hypothesis' states that central place foragers, such as pikas, will collect larger forage to maximize energy-effort ratios (Millar and Zwickel 1972; Huntly et al. 1986; Gliwicz et al. 2006). Consistent with this hypothesis, collared pikas preferentially select larger leaves from graminoids and deciduous shrubs in proportions that exceed the availability of these plant life forms within their territories (Hudson et al. 2008; Morrison and Hik 2008). They will not switch food preferences even when predation risk is increased (Morrison et al. 2004). Given the short growing season in the Arctic alpine (approximately 3 months), harvesting larger plant forms can reduce energetic costs and increase efficiencies associated with gathering haypile materials to sustain the pikas through the long winter months (Huntly et al. 1986; Morrison et al. 2009).

Plant communities with larger plant forms and greater biomass are associated with more productive growing sites. Therefore, we might expect habitat occupancy to be higher in and around talus patches where vegetation productivity is higher, as estimated using NDVI. It should be noted that, in my study area, plant communities adjacent to talus reach peak biomass late in July and they begin to senesce soon after (McIntire and Hik 2005). These areas are heavily grazed by alpine herbivores (collared pikas, hoary marmots and Arctic ground squirrels) particularly late in the summer. Therefore remote imagery from peak growing season (end of July) is the most suitable time to estimate vegetation cover.

CONCLUSION

These results validate my assumptions about the relationship between NDVI and the peak season above-ground biomass of vegetation in this study area, supporting my use of NDVI as a proxy for vegetation quality in analyses of occupancy dynamics and habitat (Chapter 2). These results also provide further evidence of utility of NDVI for evaluating alpine vegetation at the scale of small mammalian herbivores.

TABLES AND FIGURES

Table A-1. Description of plant communities surveyed around talus patches in Pika Valley, Yukon Territory July – August 2010.

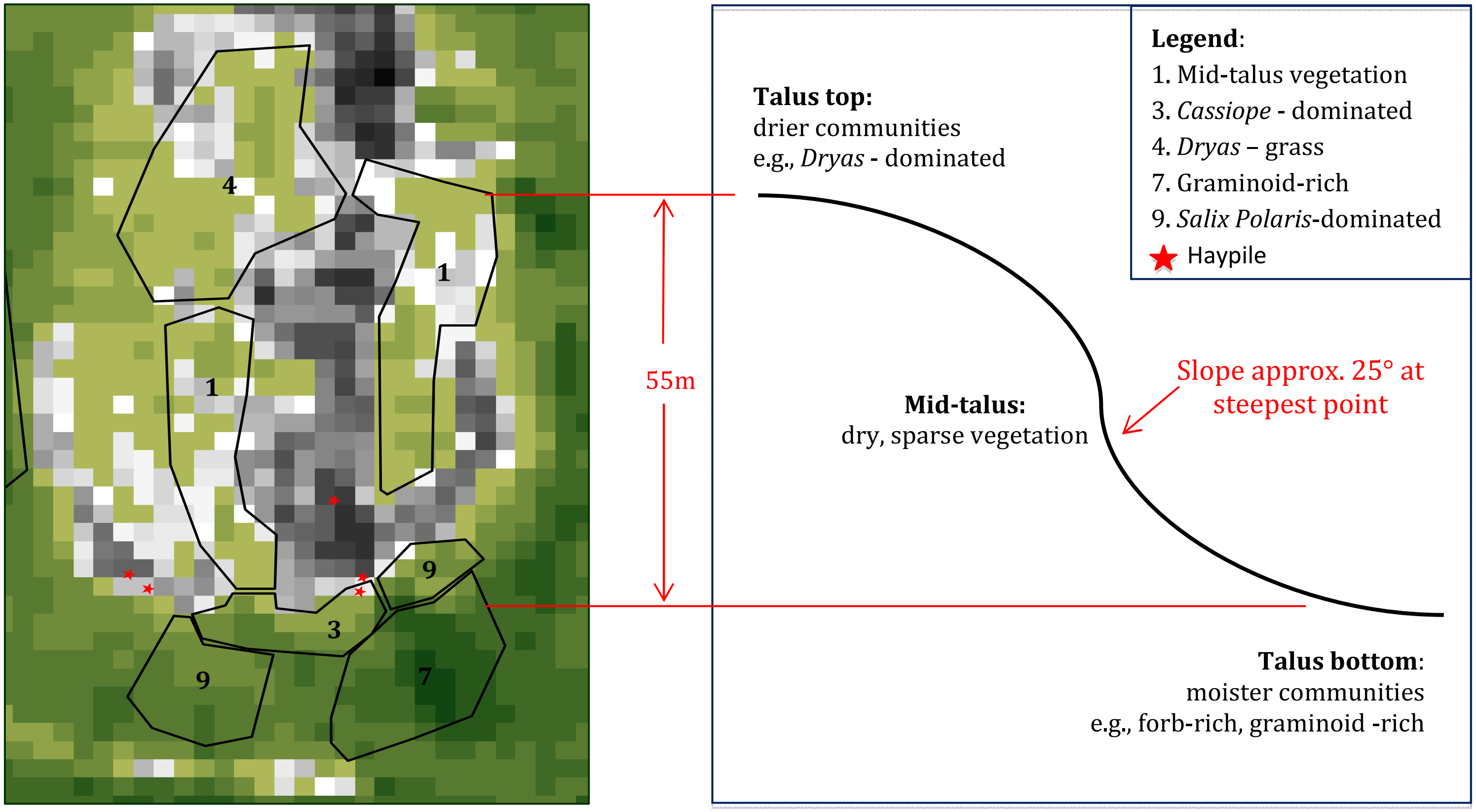
Plant communities were characterized in the field based on plant species composition (dominant and commonly associated species), soil depth and moisture, and location relative to the talus patch. Above-ground biomass (g/m2) was based on the average dried weight of samples taken from each study site. Average NDVI was derived from polygons drawn of each community based on measurements taken the field.

Plant community	Dominant plant species	Associated plant species	Moisture	Soil depth	Location relative to talus	Average biomass (g/m^2)	Average NDVI value
1. Mid-talus vegetation	Moss and lichens	*Silene acaulis*, *S. bronchialis*, *Carex* spp., *Festuca*, Dry grass species (*Heirochloe, Kobresia*), *Salix* spp.	Xeric – sub-xeric	Mixed	Rocky mid-talus tongues	140 ± 92 (n=5)	131.7 ± 3.1 (n=8)
2. Sphagnum	*Sphagnum* moss	*Carex* spp., *Trisetum*, *Anenome* spp., *Mertensia*, *Petasites frigida, Salix polaris, Cassiope*	Moist	Mid-deep	Bottom, receiving sites	480 (n=1)	132.7 ± 5.2 (n=2)
3. Cassiope	*Cassiope tetragona*, *Dryas* spp., Lichens	*Salix polaris, Salix reticulata Carex spp., Festuca, Anenome, Arnica griscomii, Silene acaulis, Petasites, Polygynum bistort, S. bronchialis, S. davorica, Sausseria, Raconitrum* and other mosses	Sub-xeric - moist	Mixed	Sides and bottom; concave topography	780 ± 462 (n=18)	138.0 ± 5.9 (n=31)
4. Dryas-grass	*Dryas* spp.	Mosses and lichens, *Carex* spp., *Heirochloe, Kobresia*, Other grass spp., *Silene acaulis, Oxytropis nigriscens, Pyrola*	Xeric – sub-xeric	Mixed: Shallow - deep	Top of talus, immediately adjacent	340 ± 150 (n=19)	138.3 ± 5.3 (n=35)

Plant community	**Dominant plant species**	**Associated plant species**	**Moisture**	**Soil depth**	**Location relative to talus**	**Average biomass (g/m²)**	**Average NDVI value**
		grandii, S.bronchialis, Salix arctica, Salix reticulata					
5. Vaccinium	*Vaccinium uglinosum, Vaccinium vitae, Dryas* spp.	*Carex* spp., Mosses and lichens	Sub-xeric	Deep	Side of talus	510 ± 283 (n=2)	139.9 ± 6.4 (n=5)
6. Dryas – S. arctica	*Dryas* spp., *Salix arctica*	*Carex* spp., *Kobresia* and *Festuca* on drier sites, Lichens	Sub-xeric	Med - deep	Side of talus, above Cty 8	350 ± 61 (n=3)	142.0 ± 7.2 (n=5)
7. Graminoid -rich	*Carex* spp., *Festuca*, Mosses	*Trisetum, Poa alpina, Salix reticulata,* Mixed forbs (*Petasites frigidis, Gentiana algida, Artemesia norvegica*).	Moist – Very wet	Deep	Rich receiving sites at bottom of talus	470 ± 151 (n=8)	142.5 ± 5.2 (n=10)
8. Dryas – S. reticulata	*Dryas* spp., *Salix reticulata, Raconitrum* moss	*Polygynum bistort, Silene acaulis, Salix arctica, Carex* spp., *Kobresia* and *Hierochloe* on drier sites	Sub-xeric – Very moist	Mid – very deep	Side of talus, below Cty 6	450 ± 177 (n=8)	143.4 ± 7.6 (n=11)
9. S. polaris dominant	*Salix polaris, Carex* spp., *Raconitrum* and other mosses	*Petasites frigidis, Salix reticulata*, Lichens, *Luzula* spp., *Vaccinium vitis-idaea, Cassiope*	Xeric - moist	Mixed, not v rocky	Bottom of talus on level ground	300 ± 127 (n=6)	143.7 ± 5.4 (n=6)
10. Grassy slope	*Festuca, Carex* spp., Other grass	*S. bronchialis, Anenome spp., Artemesia norvegica, Raconitrum* moss	Xeric - moist	Mixed	Steep slopes to edge or side of talus	410 ± 191 (n=2)	146.4 ± 2.4 (n=4)

Plant community	Dominant plant species	Associated plant species	Moisture	Soil depth	Location relative to talus	Average biomass (g/m²)	Average NDVI value
	spp.						
11. Forb-rich	*Petasites frigida*, *Carex* spp., Mosses, *Salix polaris*.	Mixed forbs (all lush: *Artemesia norvegica, Mertensia, Polygynum bistort, Polemonium*), *Festuca, Arctogrosis, Poa alpina, Salix reticulata*	Moist – wet	Mid – Very deep	Rich receiving sites at toe of talus	490 ± 114 (n=4)	148.6 ± 5.9 (n=5)
12. Alpine meadow	*Carex* spp., *Salix reticulata* (wetter sites), *Salix polaris* (drier sites), *Raconitrum* moss	*Dryas* spp., *Polygynum bistort, Gentian algida, Artemesia norvegica, Petasites frigida*	Moist - wet	Very deep	More than 10m from talus into meadow	450 ± 157 (n=10)	149.5 ± 5.8 (n=18)
13. S. reticulata – Carex species	*Carex* spp., *S. reticulata*	*Dryas* spp., *Raconitrum* and other mosses, *Festuca, Arctogrosis, Polygynum bistort, Salix arctica, Salix polaris*	Moist - wet	Very deep	Between drier communities adj to talus and the meadow	490 ± 133 (n=7)	151.5 ± 8.2 (n=7)

Figure A-1. Planimetric view of plant communities surrounding a patch of talus on the east-facing slope of Pika Valley, Yukon Territory. Vegetation is driest and least productive adjacent to the talus top and side and becomes moister and more productive with distance from talus and at the bottom of the slope in moisture-receiving sites.



(a) GIS map of plant communities. Grey-shaded pixels are talus and green-shaded pixels are vegetation. Darker green pixels have higher NDVI values.

(b) Slope profile (not to scale)

Figure A-2. Average NDVI value for each of the plant community types sampled (see Table A-1).

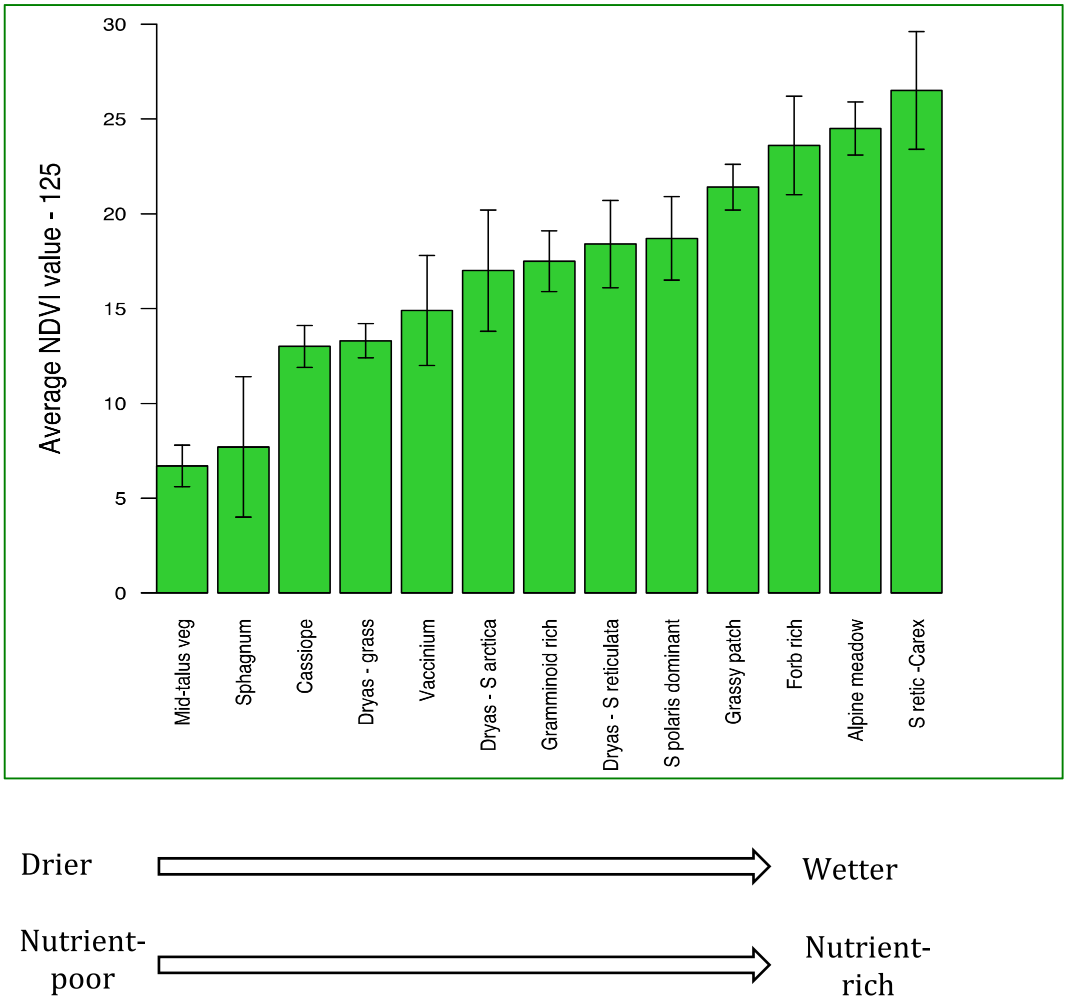


Figure A-3. Results of a linear regression of NDVI as a function of above-ground biomass for alpine plant communities in Pika Valley, Yukon Territory, in 2010. Plant communities were identified based on dominant species and location relative to talus (n = 94).

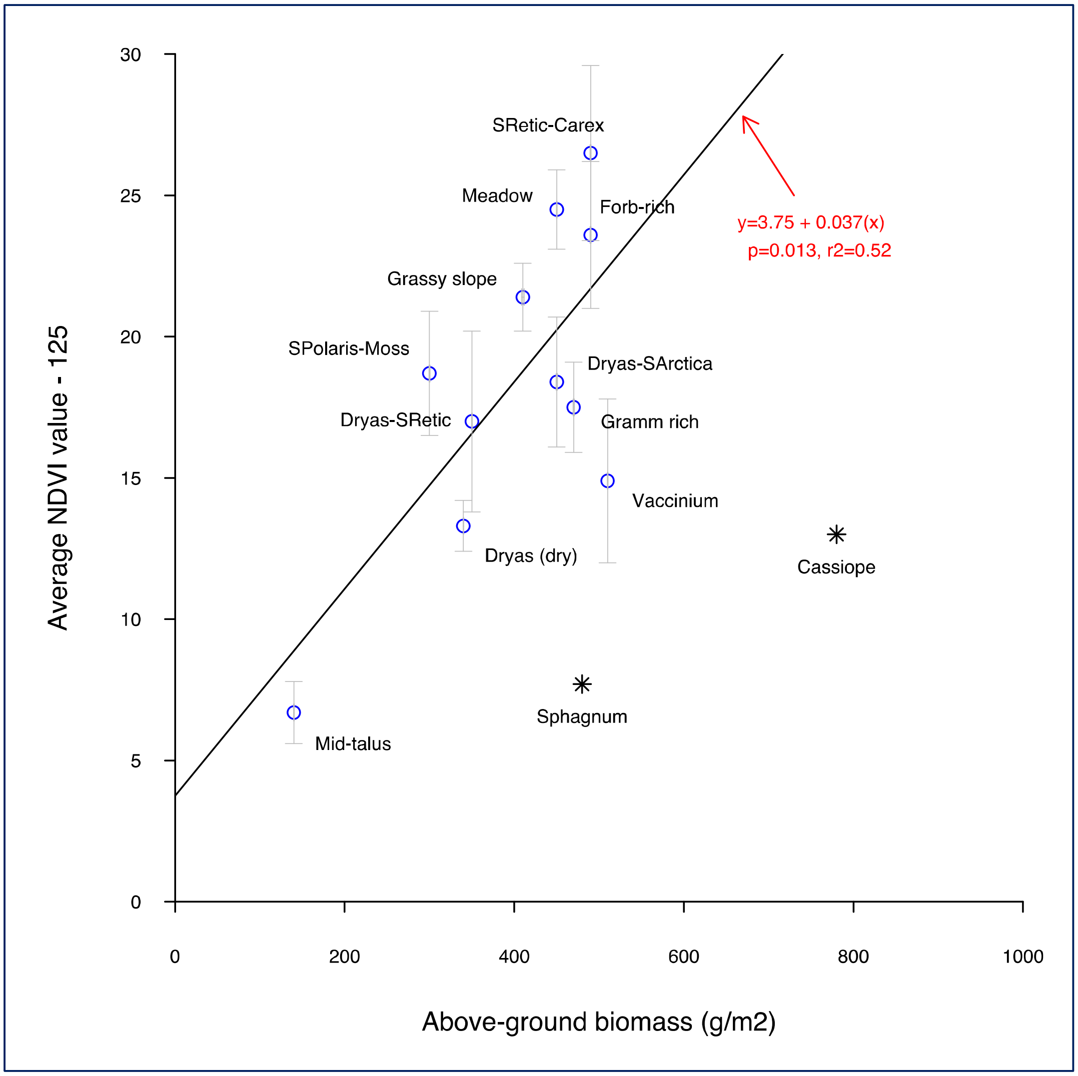
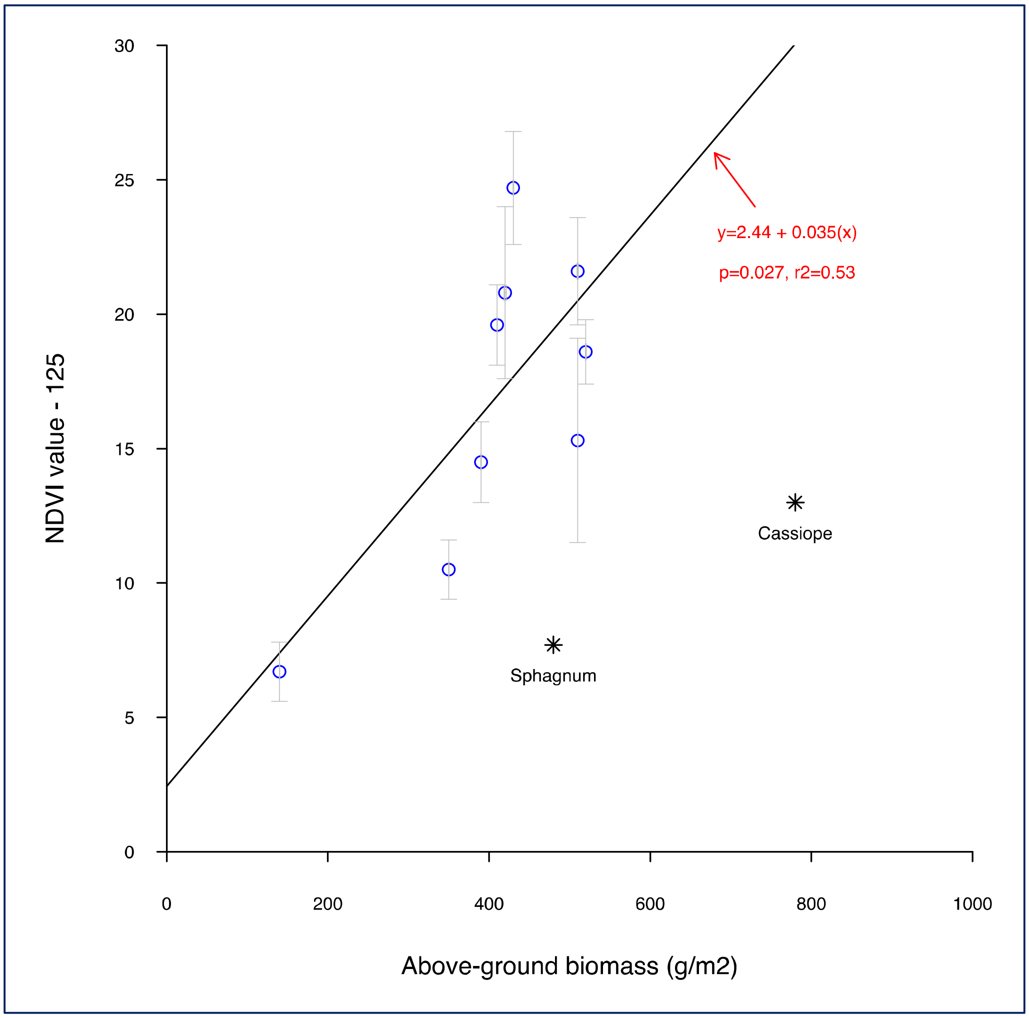


Figure A-4. Results of a linear regression of NDVI and above-ground biomass for alpine plant communities in Pika Valley, Yukon Territory in 2010. Plant communities were identified based on cluster analysis of plant species composition (n = 94).



LITERATURE CITED

Andreo, V., M. Lima, C. Provensal, J. Priotto, and J. Polop. 2009. Population dynamics of two rodent species in agro-ecosystems of central Argentina: intra-specific competition, land-use and climate effects. Population Ecology 51: 297 – 306.

Bårdsen, B-J., and T. Tveraa. 2012. Density-dependence vs. density-independence – linking reproductive allocation to population abundance and vegetation greenness. Journal of Animal Ecology 81: 264 – 376.

Bhatt U.S., D.A. Walker, M.K. Raynolds, J.C. Comiso, H.E. Epstein, G. Jia, R. Gens, J.E. Pinzon, C.J. Tucker, C.E. Tweedie, and P.J. Webber. 2010. Circumpolar Arctic tundra vegetation change is linked to sea ice decline. Earth Interactions 14(8): 1 – 20.

Bliss, L.C. 1956. A comparison of plant development in microenvironments of arctic and alpine tundra. Ecological Monographs 26(3): 303 – 337.

Cody, W.J. 2000. Flora of the Yukon Territory (2nd Edition). National Research Council Research Publications, Ottawa, Ontario.

Danby, R.K., S. Koh, D.S. Hik and L.W. Price. 2011. Four decades of plant community change in the alpine tundra of southwest Yukon, Canada. Ambio 40: 660 – 671.

Franken, R.J. 2002. Demography and metapopulation dynamics of collared pikas (*Ochotona collaris*) in the southwest Yukon. M.Sc. Thesis. University of Alberta, Edmonton.

Gliwicz, J., S. Plagacz, and J. Witczuk. 2006. Strategy of food plant selection in the Siberian northern pika, *Ochotona hyperborea*. Arctic, Antarctic and Alpine Research 38: 54 – 59.

Griffith, B., D. C. Douglas, N. E. Walsh, D. D. Young, T. R. McCabe, D. E. Russell, R. G. White, R. D. Cameron, and K. R. Whitten. 2002. The Porcupine caribou herd. Pages 8-37 *in* D. C. Douglas, P. E. Reynolds, and E. B. Rhode, editors. Arctic Refuge coastal plain terrestrial wildlife research summaries. U. S. Geological Survey, Biological Resources Division, Biological Science Report USGS/BRD/BSR-2002-0001. http://alaska.usgs.gov/BSR-2002/index.html

Hudson, J.M.G., S.F. Morrison and D.S. Hik. 2008. Effect of leaf size on forage selection by collared pikas, *Ochotona collaris*. Arctic, Antarctic and Alpine Research 40(3): 481 – 486.

Huntly, N.J., A.T. Smith and B.L. Ivins. 1986. Foraging behavior of the pika (*Ochotona princeps*) with comparisons of grazing versus haying. Journal of Mammalogy 67(1): 139 – 148.

Jónsdóttir, I.S., R. Virtanen, and I. Kärnefelt. 1999. Large-scale differentiation and dynamics in tundra plant populations and vegetation. Ambio 28(3) 230 – 238.

Laidler, G.J., P.M. Treitz, and D.M. Anderson. 2008. Remote sensing of Arctic vegetation: relationship between the NDVI, spatial resolution and vegetation composition on Boothia Peninsula, Nunavut. Arctic 61(1): 1 – 13.

MacDonald, S.O. and C. Jones. 1987. *Ochotona collaris.* Mammalian Species No. 281: 1 – 4.

McIntire, E.J.B. and D.S. Hik. 2005. Influences of chronic and current season grazing by collared pikas on above-ground biomass and species richness in subarctic alpine meadows. Oecologia 145: 288 – 297.

Millar, J.S. and F.C. Zwickel. 1972. Characteristics and ecological significance of hay piles of pikas. Mammalia 36: 657 – 667.

Morrison, S.F., L. Barton, P. Caputa, and D.S. Hik. 2004. Forage selection by collared pikas, *Ochotona collaris*, under varying degrees of predation risk. Canadian Journal of Zoology 82: 533 – 540.

Morrison, S.F., and D.S. Hik. 2008. Discrimination of intra- and inter-specific forage quality by collared pikas (*Ochotona collaris*). Canadian Journal of Zoology 86: 456 – 461.

Morrison, S.F. , G. Pelchat, A. Donahue, and D.S. Hik. 2009. Influence of food hoarding behavior on the over-winter survival of pikas in strongly seasonal environments. Oecologia 159: 107- 116.

Mysterud, A., N.G. Yoccoz, R. Langvatn, M. Pettorelli, and N.C. Stenseth. 2008. Hierarchical path analysis of deer responses to direct and indirect effects of climate in northern forest. Philosophical Transactions of the Royal Society B 363: 2359 – 2368.

Nagy, L. and G. Grabherr. 2009. The Biology of Alpine Habitats. Oxford University Press, Oxford, England.

Neigh, C.S.R., C.J. Tucker, and J.R.G. Townshend. 2008. North American vegetation dynamics observed with multi-resolution satellite data. Remote Sensing of Environment 112: 1749 – 1772.

Olofsson, J. H., Tømmervik, and T.V. Callaghan. 2012. Vole and lemming activity observed from space. Nature Climate Change. Published online 27 May 2012.

Perez, F.L. 2012. Biogeomorphological influence of slope processes and sedimentology on vascular talus vegetation in the southern Cascades, California. Geomorphology 138(1): 29 – 48.

Pettorelli, N., J.O. Vik, A. Mysterud, J-M. Gaillard, C.J/ Tucker and N.C. Stenseth. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology and Evolution 20(9): 503 – 510.

Pettorelli, N., S. Ryan, T. Mueller, N. Bunnefeld, B. Jędrzejewska, M. Lima and K. Kausrud. 2011. The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. Climate Research 46: 15 – 27.

Pojar, J. and A. MacKinnon. 2004. Plants of the Pacific Northwest Coast: Washington, Oregon, British Columbia & Alaska. Lone Pine Publishing, Edmonton, Alberta.

Pouliot, D., R. Latifovic, and I. Olthof. 2009. Trends in vegetation NDVI from 1 km AVHRR data over Canada for the period 1985 – 2006. International Journal of Remote Sensing 30(1): 149 – 168.

Rausch, R.L. 1961. Notes on the collared pika, *Ochotona collaris* (Nelson) in Alaska. The Murrelet 42(2): 22 – 24.

Raynolds, M.K., D.A. Walker, H.E. Epstein, J.E. Pinzon, and C.J. Tucker. 2012. A new estimate of tundra-biome phytomass from trans-Arctic field data and AVHRR NDVI. Remote Sensing Letters 3(5): 403 – 411.

R Foundation for Statistical Computing (RFSC). 2012. R: A Language and Environment for Statistical Computing, Vienna, Austria. http://www.r-project.org/

Tamstorf, M.P., L. Illeris, B.U. Hansen and M. Wisz. 2007. Spectral measures and mixed models as valuable tools for investigating controls on land surface phenology in high arctic Greenland. BMC Ecology 7: 9 – 25.

Tucker. C.J. and P.J. Sellers. 1986. Satellite remote sensing of primary production. International Journal of Remote Sensing 7(11): 1395 – 1416.

Walker, D.A., W.D. Billings and J.G. de Molenaar. 2001. Snow-vegetation interactions in tundra environments. *In* Snow Ecology: An Interdisciplinary Examination of Snow-Covered Ecosystems. (H.G. Jones, J.W. Pomeroy, D.A. Walker and R.W. Hoham eds). Cambridge University Press, Cambridge, U.K. pp 265 - 324.

Walker, D.A., H.E. Epstein, G.J. Jia, A. Balser, C. Copass, E.J. Edwards, W.A. Gould, J. Hollingsworth, J. Knudson, H.A. Maier, A. Moody, and M.K. Raynolds. 2003. Phytomass, LAI and NDVI in northern Alaska: Relationships to summer warmth, soil pH, plant functional types, and extrapolation to the circumpolar Arctic. Journal of Geophysical Research 108 (D2): 8169 – 8184.

Walker, D.A., M.K. Raynolds, F.J.A. Daniëls, E. Einarsson, A. Elvebakk, W.A. Gould, A.E. Katenin, S.S. Kholod, C.J. Markon, E.S. McInikov, N.G. Moskalenko, S.S. Talbot, B.A. Yurtsev and the other members of the CAVM Team. 2005. The Circumpolar Arctic Vegetation Map. Journal of Vegetation Science 16: 267 -282.

Wiegand, T., J. Naves, M. F. Garbulsky, and N. Fernández. 2008. Animal habitat quality and ecosystem functioning: exploring seasonal patterns using NDVI. Ecological Monographs 78:87–103

Williamson, S.N., D.S. Hik, J.A. Gamon, J.L. Kavanough, and S. Koh. 2013. Evaluating cloud contamination in clear-sky MODIS Terra daytime land surface temperatures using ground-based meteorology station observations. Journal of Climate 26: 1551–1560.

Yano, Y., G.R. Shaver, A,E. Giblin, E.B. Rastetter and K.J. Nadelhoffer. 2010. Nitrogen dynamics in a small arctic watershed: retention and downhill movement of ^{15}N. Ecological Monographs 80(2): 331 – 351.

APPENDIX B: Detailed statistical results

The following tables contain detailed statistical outputs from generalized linear model regressions shown in Chapters 2 and 3.

Tables from Chapter 2

Table B-1. (Cross-reference = Chapter 2, Table 2-3). Occupancy as a function of patch configuration, topography and habitat quality at the scale of whole patches.

Statistical significance: $\alpha \leq 0.005$, biological significance: $\alpha \leq 0.05$(*), d.f. = 14, n= 16 patches. NS = not significant to $\alpha \leq 0.05$, RD = residual deviance.

Indicator	# of years occupied	# of years unoccupied
Patch configuration		
Connectivity (distance to nearest occupied patch)	NS	p = 0.031* β = + 0.0076 RD = 21.10
Habitat quality		
Average summer insolation	p = 0.010* β = + 5.11E-06 RD = 9.00	p = 0.00030** β = -1.36R-05 RD = 19.73
Average winter insolation	p = 0.0087* β = + 5.41E-06 RD=8.78	p = 0.00012** β = -1.61E-05 RD = 19.48
Average NDVI for vegetation: within patch	p = 0.039* β = + 0.077 RD = 11.18	p = 0.0078* β = -0.22 RD = 21.11
Average NDVI for vegetation: buffer around patch	p = 0.039* β = + 0.04 RD = 11.07	p = 0.0093* β = -0.095 RD = 21.45

Table B-2. (Cross-reference = Chapter 2, Table 2-4). Occupancy as a function of patch configuration, topography and habitat quality at the scale of territories within patches.
Statistical significance: $\alpha \leq 0.005$, biological significance: $\alpha \leq 0.05$ (*), d.f. = 14, n= 16 patches and 127 territories. NS = not significant to $\alpha \leq 0.05$, RD = residual deviance.

Indicator	Territory density	Average occupancy	Colonization index	Extirpation index
Connectivity (in multiple regression model with area)	p = 0.0019** β = - 0.0093 RD = 15.36	p = 0.00052** β = - 0.0089 RD = 15.23	p = 0.0023** β = - 0.0093 RD = 17.22	NS
Area (in multiple regression model with connectivity)	Not applicable	p < 0.0001** β = + 2.69E-05 RD = 15.23	NS	NS
Average summer insolation	p = 0.0019** β = + 9.25E-06 RD = 14.51	p = 0.024* β = + 6.47E-06 RD = 15.89	p = 0.00014** β = + 9.81E-06 RD = 17.60	p = 0.00013** β = - 1.26E-05 RD = 21.48
Average winter insolation	p = 0.00048** β = + 9.07E-06 RD = 14.79	p = 0.0049** β = + 7.88E-06 RD = 16.00	p < 0.0001** β = + 1.04E-05 RD = 17.61	p = 0.0011** β = - 1.47E-05 RD = 21.23
Average NDVI for vegetation: within patch	p = 0.0020** β = + 0.16 RD = 15.88	p = 0.043* β = + 0.12 RD = 15.16	p = 0.0010** β = + 0.17 RD = 16.76	NS
Average NDVI for vegetation: buffer around patch	p < 0.0001** β = + 0.094 RD = 16.04	NS	p = 0.0029** β = + 0.081 RD = 16.95	NS
Average elevation (m)	NS	p = 0.0011** β = + 0.011 RD = 14.60	NS	
Average slope (°)	NS	p = 0.0056* β = + 0.084 RD = 15.30	NS	
Average NDVI for talus	NS	p = 0.032* β = - 0.20 RD = 14.84	NS	NS

Table B-3. (Cross-reference = Chapter 2, Table 2-6). Occupancy as a function of topography and habitat quality at the territory scale.

Statistical significance: $\alpha \leq 0.005$, biological significance: $\alpha \leq 0.05$ (*),
d.f. = 125, n= 127 territories. NS = not significant to $\alpha \leq 0.05$,
RD = residual deviance.

Indicator[□]	**Number of years occupied**	**Number of colonization events**	**Average years of survival**
Topography			
Average elevation	NS	$p = 0.0031$** $\beta = + 0.0040$ RD = 134.89	NS
Average slope	$p = 0.0098$* $\beta = + 0.023$ RD = 131.24	$p = 0.0020$** $\beta = + 0.023$ RD = 135.25	NS
Habitat quality			
Average winter insolation	$p < 0.0001$** $\beta = + 4.76\text{E-}06$ RD = 131.82	$p < 0.0001$** $\beta = + 5.07\text{E-}06$ RD = 135.78	NS
Average summer insolation	$p < 0.0001$** $\beta = + 4.57\text{E-}06$ RD = 131.00	$p < 0.0001$** $\beta = + 4.72\text{E-}06$ RD = 135.73	NS
Length of talus perimeter	$p = 0.034$* $\beta = + 0.00098$ RD = 131.13	NS	$p = < 0.0001$** $\beta = + 0.0035$ RD = 127.03
Average NDVI for vegetation	$p = 0.017$* $\beta = + 0.022$ RD = 130.85	$p = 0.0082$* $\beta = + 0.028$ RD = 133.74	NS
sqrt(Distance to highest quality vegetation)	$p = 0.017$* $\beta = - 0.079$ RD = 130.74	$p = 0.0090$* $\beta = - 0.10$ RD = 134.35	NS

[□] The unit of measurement for each of these indicators is presented in 2-2.

Tables from Chapter 3

Table B-4. (Cross-reference = Chapter 3, Table 3-2). Survival of year 1 and year 2 adult collared pikas in Pika Valley, Yukon Territory, during 1999 – 2009 as a function of average Pacific Decadal Oscillation (PDO) indices in autumn, winter, spring, and summer of year t-1.

Statistical significance: $\alpha \leq 0.006$ (**), biological significance $\alpha \leq 0.05$ (*), d.f. = 9, n = 11 years. NS = not significant to $\alpha \leq 0.05$. RD = residual deviance.

Period of average PDO for year t-1	**Year 1 Adults**			**Year 2 Females (n=41)**
	Females (n=24)	**Males (n=26)**	**All Year 1 (n=50)**	
Autumn PDO (ave Sept – Nov)	NS	$p = 0.0016$** $\beta = +0.85$ RD =12.40	NS	$p = 0.00019$** $\beta = +0.54$ RD = 13.77
Winter PDO (ave Dec - Feb)	NS	$p = < 0.0001$** $\beta = +1.31$ RD = 12.09	NS	$p = 0.00037$** $\beta = +0.63$ RD = 13.22
Spring PDO (ave Mar – May)	$p = 0.039$* $\beta = +0.80$ RD = 12.48	$p = 0.00045$** $\beta = +1.16$ RD = 12.38	$p < 0.0001$** $\beta = +0.96$ RD = 12.40	NS
Summer PDO (ave Jun – Aug)	NS	$p = 0.00021$** $\beta = +1.32$ RD = 12.25	$p = 0.039$* $\beta = +0.65$ RD = 12.20	NS
October – March (period of most energetic PDO fluctuations (Mantua 2002))	NS	$p <0.0001$** $\beta = +2.49$ RD = 12.49	$p = 0.022$* $\beta = +3.36$ RD = 12.42	$p = 0.00023$** $\beta = +3.72$ RD = 13.72

Table B-5. (Cross-reference = Chapter 3, Table 3-3). Recruitment and abundance of juvenile collared pikas in Pika Valley, Yukon Territory during 1999 – 2009 as a function of seasonal climate (temperature, precipitation and number of frost-free days) for year t-1 and year t.

Statistical significance: $\alpha \leq 0.006$, biological significance $\alpha \leq 0.05$, d.f. = 9, n = 11 years. NS = not significant to $\alpha \leq 0.05$. RD = residual deviance.

Climate variable	**Juveniles□**		
	Females (n=77)	**Males (n=84)**	**All juveniles (n = 161)**
Pre-conception			
Summer (Jun– Aug) year t-1			
Number of frost-free days	$p = 0.026^R$ $\beta = - 0.093$ RD = 13.33	Data over-dispersed	$p = 0.010^R$ $\beta = - 0.10$ RD = 12.31
Autumn (Sept – Nov) year t			
Average temperature(°C)	NS	$p < 0.0001^R$ $\beta = - 1.32$ RD = 12.68	$p = 0.0055^{R,}$ $\beta = - 0.67$ RD = 12.52
Post-emergence			
Summer (Jun– Aug) year t			
Average temperature (°C)	NS	NS	$p = 0.021^A$ $\beta = + 0.47$ RD = 12.24
Average precipitation (mm)	NS	NS	$p = 0.045^A$ $\beta = - 0.0077$ RD = 12.23

[R] Based on recruitment (ratio of juveniles in year t to no. of females in year t – 1)

[A] Based on abundance of juveniles in year t.

Table B-6. (Cross-reference = Chapter 3, Table 3-4). Survival of year 1 and year 2 adult collared pikas in Pika Valley, Yukon Territory during 1999 – 2009 as a function of climate (temperature, precipitation and number of frost-free days) during winter, spring or summer for years t-1 and year t.

Statistical significance: $\alpha \leq 0.006$ (**), biological significance $\alpha \leq 0.05$ (*), d.f. = 9), n = 11 years. NS = not significant to $\alpha \leq 0.05$, RD = residual deviance.

Climate variable	Year 1 Adults			Year 2 Adults	
	Females (n=24)	Males (n=26)	All Year 1 (n=50)	Females (n=41)	Males (n=47)
YEAR t – 1 (lagged climate effect)					
Winter (Dec – Feb)					
Average temperature (°C)	NS	$p = 0.0041^{**}$ $\beta = + 0.48$ RD = 12.22	$p = 0.031^{*}$ $\beta = + 0.27$ RD = 12.25	NS	NS
Spring (Mar – May)					
Average precipitation (mm)	$p = 0.035^{*}$ $\beta = - 0.051$ RD = 12.50	NS	NS	NS	NS
Summer(Jun– Aug)					
Average temperature (°C)	NS	$p = 0.014^{*}$ $\beta = + 0.86$ RD = 12.41	NS	NS	NS
Number of frost-free days	NS	NS	NS	$p = 0.05^{*}$ $\beta = + 0.054$ RD = 12.73	$p = 0.046^{*}$ $\beta = + 0.054$ RD = 12.95
YEAR t					
Summer (Jun - Aug)					
Average precipitation (mm)	NS	NS	$p = 0.050^{*}$ $\beta = - 0.0086$ RD = 12.30	NS	NS

Table B-7. (Cross-reference = Chapter 3, Table 3-6). Survival of year 1 and year 2 adult collared pikas in Pika Valley, Yukon Territory during 1999 – 2009 as a function of seasonal Pacific Decadal Oscillation (PDO) by dominant aspect for year t-1 and year t.

Statistical significance: $\alpha \leq 0.006$ (**), biological significance $\alpha \leq 0.05$ (*), d.f. = 9, n = 11 years. NS = not significant to $\alpha \leq 0.05$, RD = residual deviance.

Period of PDO	**Year 1 adults**			**Year 2 adults**
	South- facing (n=106)	**West-facing (n=26)**	**East-facing (n=41)**	**South-facing (n=46)**
Year t – 1 (lagged PDO effect)				
Autumn PDO (ave Sept – Nov)	NS	NS	$p < 0.0001$** $\beta = +1.91$ RD = 10.32	NS
Winter PDO (ave Dec - Feb)	$p < 0.0001$** $\beta = +1.08$ RD = 12.26	NS	$p < 0.0001$** $\beta = +1.76$ RD = 11.78	$p = 0.0078$* $\beta = +0.51$ RD = 13.13
Spring PDO (ave Mar – May)	$p = 0.043$ $\beta = +0.75$ RD = 12.46	NS	$p < 0.0001$** $\beta = +1.84$ RD = 11.57	NS
Summer PDO (ave Jun – Aug)	NS	NS	$p < 0.0001$** $\beta = +2.30$ RD = 11.36	NS
Year t				
Autumn PDO (ave Sept – Nov)	NS	$p = 0.028$* $\beta = -1.33$ RD = 12.85	NS	NS
Winter PDO (ave Dec - Feb)	NS	$p = 0.0041$** $\beta = +1.44$ RD = 12.63	NS	NS