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Demography and Metapopulation Dynamics of Collared Pikas (*Ochotona collaris*) in the Southwest Yukon

by

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Demography and Metapopulation Dynamics of Collared Pikas (*Ochotona collaris*) in the Southwest, Yukon, submitted by Renee Joline Franken in partial fulfillment of the requirements for the degree of Master of Science in Environmental Biology and Ecology.

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Abstract

I conducted the first demographic analysis of collared pikas in the southwest Yukon. Individual growth rates were best described using a Gompertz model, and these rates were higher than those reported from southern latitudes. Parturition dates were asynchronous and weakly related to snow accumulation. Over-winter survival was low (34% adults; 25% juveniles), and juvenile survival was not related to dispersal, patch density, or parturition date. Survival was not sex-biased but varied depending on year of birth, aspect and other habitat variables, the latter showing considerable variation among years. A minimum of 34% of juveniles made inter-patch movements (mean of 332m); and both sexes dispersed with equal frequency. Pikas settled towards neighbors of the opposite sex, but males were more likely to recolonize unoccupied patches than females. Patch size and isolation only partly explained patterns of recolonization and extinction of talus patches by pikas. Habitat quality was also important in these processes.

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Chapter 1: General Introduction: Life history, demography, and metapopulation dynamics of collared pikas in Yukon Territory, Canada

Introduction

Many species are able to persist in fragmented landscapes by living in a network of populations called a metapopulation (Levins 1969, Hanski 1999). The movement or dispersal of individuals between these populations is an essential process that can facilitate local population persistence and species stability over large geographic areas (Gaines and McClenaghan 1980). Dispersal provides individuals and new genes to a population, which decreases the chance of population extinction due to environmental stochasticity or inbreeding effects (Gilpin 1987; Hanski 1991). An understanding of dispersal rates and behaviors is an important factor for the effective conservation of a species and their habitat.

Animals may disperse for a number of reasons such as, lack of resources including food and shelter, an absence of suitable mates, or competition from surrounding animals (Gaines and McClenaghan 1980). There may also be intrinsic factors that strongly influence dispersal behavior. For example, dispersal decisions in some animals may be innate to prevent inbreeding (Greenwood 1980). There are, however, costs associated with dispersing through unfamiliar and unfavorable terrain, including risk of predation or not finding a suitable patch or mate, and these costs may be exacerbated when animals live in fragmented habitats.

How habitat patches are organized spatially in a landscape may influence the dispersal of organisms between these habitat patches. Many natural habitats are becoming increasingly fragmented into smaller and more isolated patches as a result of habitat destruction, climate change, and other types of anthropogenic disturbance. The remaining suitable habitat fragments are separated by large expanses of relatively unsuitable habitat where individuals cannot survive. This isolation can have a number of effects on population structure, including loss of genetic and phenotypic diversity, and inbreeding depression (Morrison et al. 1998). A number of studies (e.g. Brown 1971; Sjögren Gulve 1994; Gustafson and Gardner 1996; Hanski et al. 1996; Saari 1998; Peltonen and Hanski 1991; Jansson and Angelstam 1999), including those on pikas (Smith 1974, 1980, 1987, 1988; Smith and Gilpin 1997), have shown that animals in smaller and more isolated patches are more prone to extinction and that recolonization of these patches is less likely than for larger, closer patches.

Theoretical metapopulation models (e.g. Hanski 1994, 1999; Moilanen and Hanski 1998) have attempted to describe population persistence based on patch size and isolation between patches. While most metapopulation models and empirical studies have considered the spatial arrangement of patches in predicting colonization and extinction processes, few have incorporated the effects of interpatch variability in habitat quality. It has also been suggested that the empirical application of metapopulation models to vertebrates has been constrained by inadequate data on dispersal (Doak and Mills 1994; Van Vuren 1998). Incorporating habitat quality and dispersal abilities of animals into metapopulation models, will likely make them more realistic and increase their predictive ability (e.g. Roslin 2002).

Research on the American pika (*Ochotona princeps*) has suggested that studies of metapopulation dynamics are tractable with this animal for a number of reasons (Smith and Ivins 1983; Peacock and Smith 1997; Moilanen et al. 1998). Pikas are territorial animals that live in spatially distinct or naturally fragmented landscapes (Smith 1974), disperse short distances and therefore will be affected by the spatial structure of the landscape (Moilanen et al. 1998), and local populations are largely asynchronous, which prevents simultaneous extinction of local populations (Moilanen et al. 1998). As well, pikas are highly visible (active diurnally) and are easy to catch, allowing the entire population to be marked. Based on these reasons pikas are considered a model organism to conduct studies on dispersal, colonization, metapopulation dynamics and species persistence.

Very little research has been conducted on the collared pika (*O. collaris*), and therefore most of what we assume about the collared pika is based on data collected from its southern relative, the American pika. There are, however, important differences between these two species, which are addressed in this thesis.

Biology of Collared Pikas

There are 25 extant species of pikas worldwide, most of them occurring in Asia (Smith 1990). Within this group of Lagomorphs, relatively little is know about the main population parameters, including natality, mortality, immigration and emigration. Most work has focused on foraging and territorial behaviour of these organisms.

Pikas are known from the Nearctic since at least the Pliocene (5.4-2.4 million years ago) (Hafner and Sullivan 1995). The collared pika (Family Lagomorph: *Ochotona collaris*) (Figure 1-1) is one of two species of pikas living in the New World. Its relative, the American pika (*O. princeps*), lives in southwestern Canada and the western U.S. It is believed that *O. princeps* dispersed south along cordilleran routes during early glacial stages and was separated from *O. collaris* to the north during the Wisconsin glaciation (Guthrie 1973; Hafner and Sullivan 1995) (Figure 1-2). The collared pika and the American pika are very similar in many life history traits, but the collared pika likely experiences additional stress by living in a high latitude environment.

Collared pikas are generalist alpine herbivores, inhabiting boulder fields (talus) in the mountains of central and southeastern Alaska, the Yukon, and northwestern British Columbia (MacDonald and Jones 1987). Pikas are territorial and will actively defend a home range. Each home range contains a haypile where they store collected vegetation for winter use (Figure 1-3).

Pikas reproduce at one year of age and gestation is 30 days (Severaid 1950). They have 1-2 litters per year with post-partum estrus (Millar 1973; Smith 1978; Smith and Ivins 1983), litters contain 1-4 individuals, but usually only one litter is weaned (Millar 1973; Smith 1978). Timing of reproduction is highly seasonal and the initiation of first litter is a compromise between two demands: (1) females needs to wean offspring early in season so young can secure territories (Smith 1978; Smith and Ivins 1983), and (2) energy requirements during lactation are high and therefore, they should delay reproduction to take advantage of peaks in vegetative growth (Millar 1972; Smith 1978).

Juveniles are the primary dispersers in pika populations, while adult pikas show a

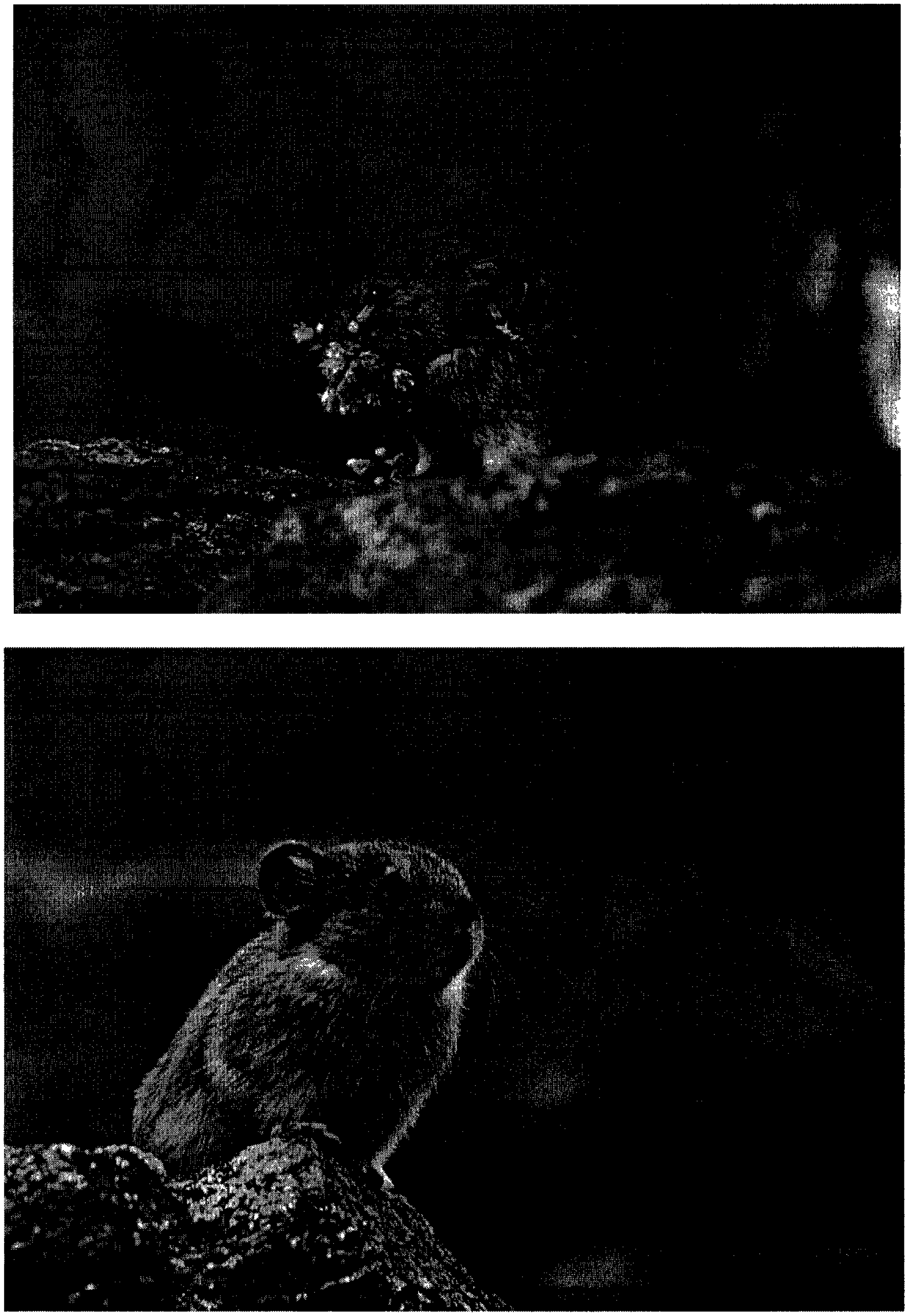
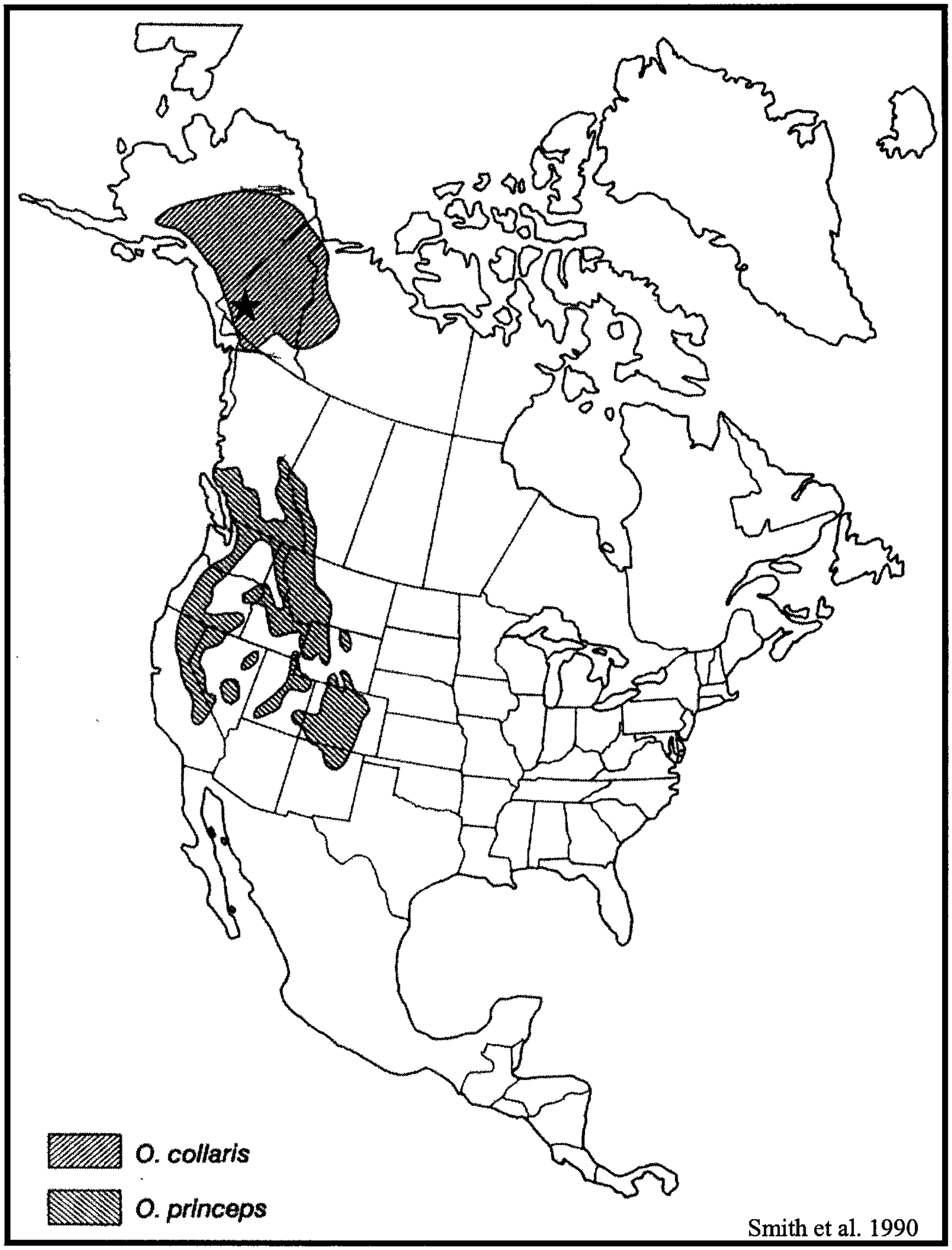


Figure 1-1. Photographs of collared pikas (*Ochotona collaris*).



Smith et al. 1990

Figure 1-2. Distribution of the collared pika (*Ochotona collaris*) and the American pika (*Ochotona princeps*) in North America. Study site in the Ruby Ranges, Yukon indicated by ★.

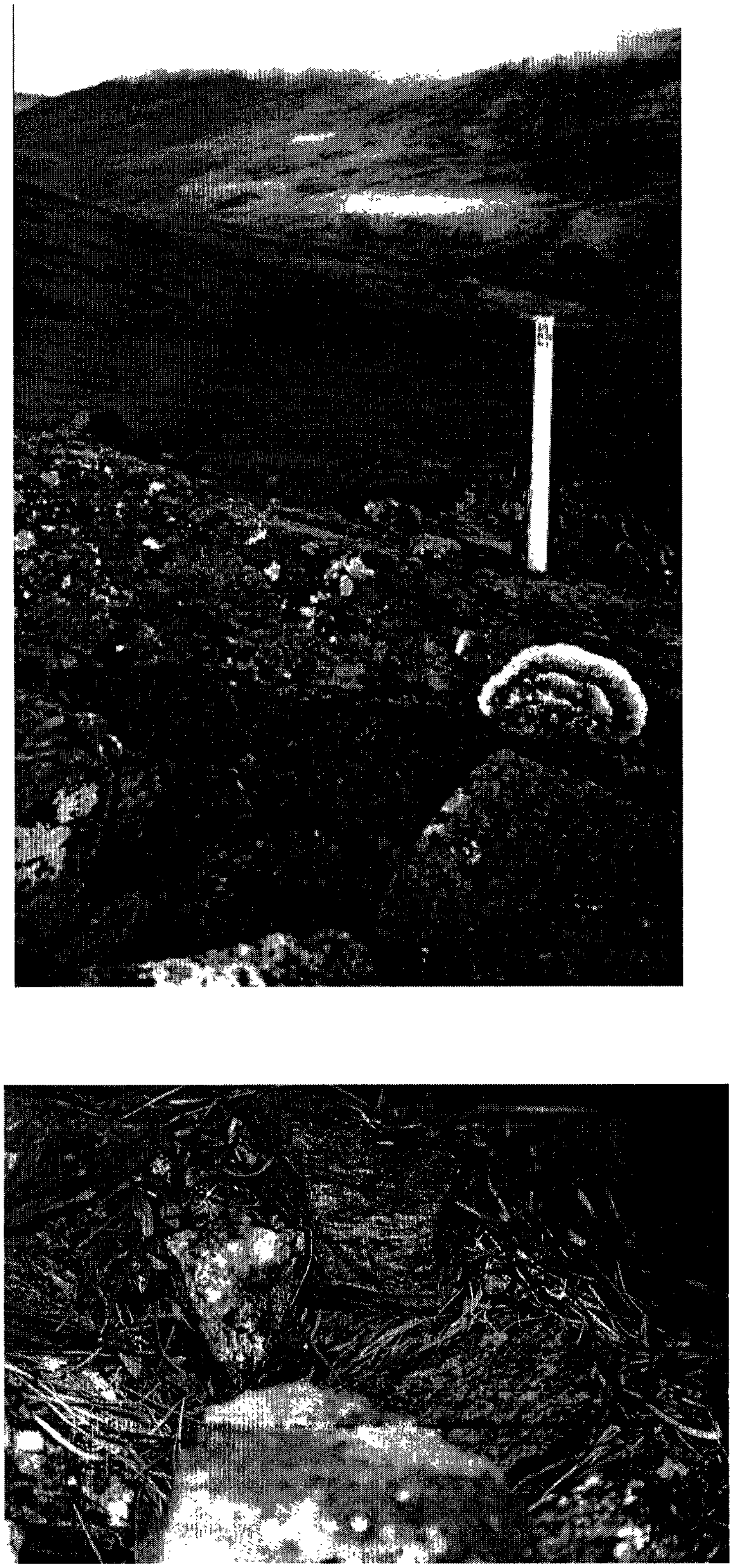


Figure 1-3. Photographs of pika haypiles in the talus.

high level of philopatry (Smith 1974). Timing of dispersal in pikas is related to the reproductive season, with juveniles dispersing in mid-summer after territories become saturated with young individuals. Peacock and Smith (1997) suggested that dispersal in pikas supports a resource competition hypothesis, where the predominate resource is territory. Dispersal distances of up to 3 km have been observed in the American pika (Tapper 1973) and it is believed that the maximum dispersal distance for individual pikas is probably between 10-20 km (Hafner 1994; Hafner and Sullivan 1995).

Pikas do not hibernate during the winter months, but rather rely on eating vegetation that they stored in haypiles during the summer (8-12 weeks). Pikas are active during the winter and are occasionally seen year-round (Hock and Cottini 1966). It is believed that haypiles rarely contain sufficient energy or protein to provide adequate resources for winter survival (Johnson and Maxwell 1966; Millar and Zwickel 1972; West 1980) and therefore pikas must forage on other materials such as lichens under the snowpack (Conner 1983; Gessaman and Goliszek 1989). Haypiles may be critical to survival during early spring when conditions are unpredictable due to late snow melt or early spring storms that can prevent surface foraging and vegetative growth (Conner 1983).

Pika movements away from the talus are inhibited due to increased chances of predation (Lutton 1975; Ivins and Smith 1983; Huntly et al. 1986; Holmes 1991). Pikas will rarely move >6m from the talus edge to forage, even though forage quality might be better further out (Huntly 1987, Roach et al. 2001, McIntire and Hik 2002). This suggests that movements among talus patches, which are separated by expanses of meadow, are rare. As a result, pikas are likely to spend the majority of their adult life on one patch. This spatially distinct landscape provides an excellent system to examine the metapopulation dynamics of collared pikas.

Most information on pikas has been based on the American pika, while there is sparse knowledge on the collared pika (MacDonald and Jones 1987). Previous studies of collared pikas have described aspects of their geographic range, foraging ecology, parasites, and behaviour (e.g. review in MacDonald and Jones 1987, Rausch 1962; Hock and Cottini 1966; Holmes 1991, McIntire 1999, Andruchow 2000, McIntire and Hik 2002, Tait 2002). Broadbrooks (1965) provided some basic biology on an unmarked population of pikas in Alaska, however, was unable to describe the population demography or survival of the collared pika.

Climate change and pikas

Summer temperatures in the Yukon are increasing, with an expected 3°C increase in parts of the Yukon over the next 50 years (YSOER 1999). Temperature increases of this kind will likely have dramatic effects on a number of species endemic to the Yukon. A 3°C increase in temperature may result in a 100 m shift of a species distribution upslope on mountains (Peters 1992). This could have dramatic effects on pikas that are restricted to mountaintops. McDonald and Brown (1992) developed a model predicting the extinction of boreal mammals on isolated mountaintops with increases in global temperatures of 3°C; pikas are no exception. Pikas are susceptible to temperature increases, as they cannot effectively regulate their body temperature (Smith 1974, Yang et al. 1988); this can essentially create a barrier to pika dispersal at low elevations. Smith (1974) has suggested that warmer temperatures at lower elevations are a major stress on dispersing pikas and short distances (<300m) constitute major dispersal barriers. With predicted increases in summer temperatures in the Yukon, pikas may become even more isolated on mountaintops, resulting in low dispersal of pikas among populations.

Winter temperatures in the Yukon are becoming more variable, with no clear trend (YSOER 1999), which may also affect pika survival. Climate models are predicting increases in precipitation for this area, which could potentially benefit pikas if it comes in the form of snow during the winter; over-winter survival of pikas is higher with greater snowpack (Smith 1988). It is possible, however, that a higher snowpack will also result in later snowmelt, which would shorten the growing season for pikas. Because climate models are also predicting more variability, this may result in periods of melt-freeze during the winter, exposing pikas to cooler temperatures and perhaps limiting access to vegetation if it ices up. Although, it is not clear what the results of climate change will be, it is predicted to be stronger in higher latitudes and will, therefore, likely affect the distribution and survival of pikas. Because collared pikas are susceptible to these changes in climatic conditions, they could potentially act as an indicator mammalian species to the effects of climate change. Therefore, it is critical to understand how these organisms persist in their environment.

Study site

This study was conducted in the Ruby Ranges, southwest Yukon (61°12’N, 138°16’W). This alpine site (elevation ~1800-2000 m a.s.l.) consists of talus patches (0.07 ha to 15.7 ha) separated by meadows ranging in distance from 15 m to 1140 m in a

4 km^2 study area (Fig 1-4 and 1-5). These talus patches are surrounded by expanses of meadow, essentially creating a system of spatially distributed patches. This site is characterized by alpine tundra vegetation and is dominated by *Dryas octopetala*, *Salix reticulata*, graminoids and lichens. The growing season (snow-free season) usually lasts approximately 10 weeks from mid-June to the end of August. The study site has been divided into 3 main sections, the East slope, the West slope and South slope. The East and West slopes have been trapped since 1995 and South slope trapped starting in 1998.

Objectives

Several novel topics are developed throughout this thesis, including (1) the first detailed study of *O. collaris* demography, with comparisons to its southern relative, *O. princeps*; (2) an explicit incorporation of habitat quality into an assessment of colonization/extinction dynamics. Few studies have successfully done this, although its importance has been implied in a number of studies; and (3) the opportunity to utilize small mammals, such as collared pikas, as indicators of potential climate impacts in northern alpine ecosystems.

In Chapter 2, I examined the variation in timing of parturition and how growth was affected by living in a northern environment. A number of organisms living in northern environments have faster growth rates because of the shorter growing season (e.g. Case 1978; Jensen et al. 2000; Merila 2000). Collared pikas also live in a northern environment, where individuals must grow to an adult body size before the onset of winter (Whitworth and Southwick 1981; Golian and Whitworth 1985). Initially, I developed a growth model for the collared pika and then compared the growth rate of

Figure 1-4. Talus patches at the Ruby Range, Yukon study site. Shaded areas represent talus surrounded by meadow (white), lines are creeks.

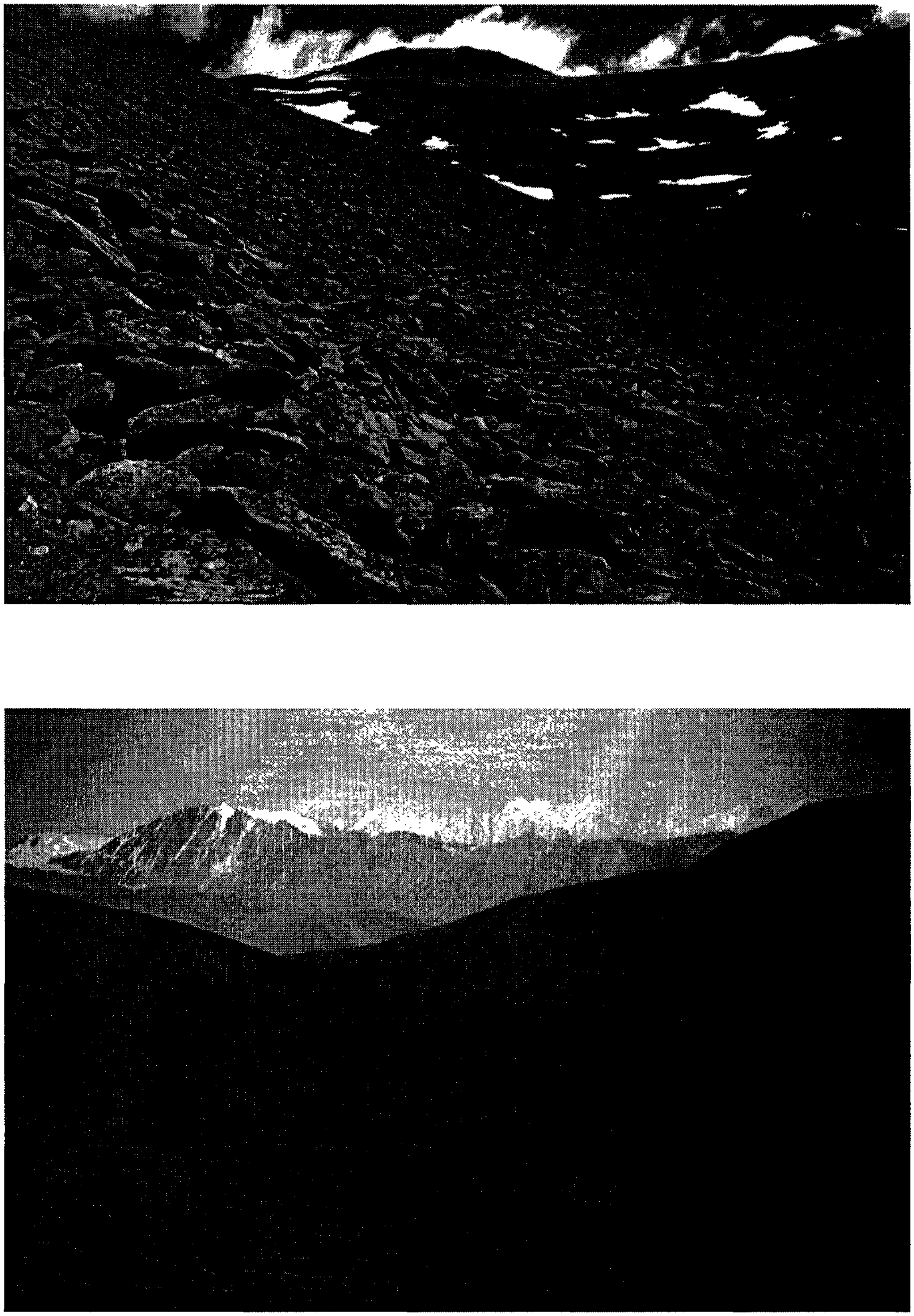


Figure 1-5. Photographs of the study site, Ruby Ranges, Yukon, Territory.

pikas at different latitudes to see the response to shorter growing seasons. I also addressed how variation in snow accumulation and snowmelt affected the timing of parturition and if changes in the date of birth affected survival of juvenile pikas at this site.

In Chapter 3, I described the patterns of survival, dispersal, and settlement of collared pikas in the southwest Yukon. Information on pikas is based on a few studies that have mainly examined the foraging and territorial behavior of the American pika, and very little is known about the survival or population dynamics of pikas (see Smith 1988; Smith et al. 1990). Most studies of collared pikas have been based on counts and observations rather than on a marked population. Pikas at our study site have been trapped since 1995 providing seven continuous years of data, which is unique for any *Ochotona* species. By using mark-recapture and radio-telemetry techniques, I was able to quantify dispersal and survival of the collared pika. I determined which pikas were dispersing, how far they were dispersing and where they were choosing to settle. I also determined what biotic and abiotic factors influenced the survival of adult and juvenile pikas at this site. Basic population parameters, such as survival, immigration and emigration provided necessary information to address metapopulation dynamics.

In Chapter 4, I addressed some of the factors that influenced colonization, extinction and occupancy of talus patches by pikas. Pikas have been described as a "classical metapopulation", but this is based on evidence from a single study (Moilanen et al. 1998). I addressed how the commonly used measures of isolation and patch size influenced the colonization, extinction and occupancy of talus patches. I also included measures of habitat quality to address their importance in these processes, something that has been largely overlooked in previous studies but increasingly recognized as being relevant (Thomas 2001; Roslin 2002).

References

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355-366.

Andruchow, J. 2000. Foraging preferences of collared pikas in alpine meadows in the southwest Yukon. B.Sc. thesis, University of Alberta, Edmonton, Canada.

Brown, J. H. 1971. Mammals on mountaintops: non-equilibrium insular biogeography. The American Naturalist 105:467-478.

Case, T. J. 1978. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. Quarterly Review of Biology 53: 243-282.

Conner, D. A. 1983. Seasonal changes in activity patterns and the adaptive value of haying in pikas (*Ochotona princeps*). Canadian Journal of Zoology 61:411-416.

Doak, D. F. and L. S. Mills. 1994. A useful role for theory in conservation. Ecology 75:615-626.

Gaines, M. S. and L. R. Jr. McClenaghan. 1980. Dispersal in small mammals. Annual Review of Ecological Systematics 11:163-196.

Gessaman, J. A. and A. G. Goliszek. 1989. Marmot scats supplement hay pile vegetation as food energy for pikas. Great Basin Naturalist 49:466-468.

Gilpin, M. E. 1987. Spatial structure and population vulnerability. In Soulé, M. E. (Ed), Viable Populations for Conservation. Cambridge University Press, Cambridge.

Golian, S. C. and M. R. Whitworth. 1985. Growth of pikas (*Ochotona princeps*) in Colorado. Journal of Mammalogy 66: 371-374.

Grayson, D. K. 1977. On the Holocene history of some northern Great Basin lagomorphs. Journal of Mammalogy 54:507-513.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behavior 28:1140-1162.

Gustafson, E. J. and R. H. Gardner. 1996. The effect of landscape heterogeneity on the probability of patch colonization. Ecology 77:94-107.

Guthrie, R. D. 1973. Mummified pika (*Ochotona*) carcass and dung pellets from Pleistocene deposits in interior Alaska. Journal of Mammalogy 54:970-971.

Hafner, D. J. 1994. Pikas and permafrost: post-Wisconsin historical zoogeography of Ochotona in the southern Rocky Mountains USA. Arctic and Alpine Research 26:375-382.

Hafner, D. J. and R. M. Sullivan. 1995. Historical and ecological biogeography of Nearctic pikas (Lagomorpha: Ochotonidae). Journal of Mammalogy 76:302-321.

Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. Biological Journal of Linnean Society 42:17-38.

Hanski, I. 1999. Metapopulation Ecology. Oxford University Press, Oxford.

Hanski, I., A. Moilanen, T. Pakkala, and M. Kuussaari. 1996. The quantitative incidence function model and persistence of an endangered butterfly metapopulation. Conservation Biology 10:578-590.

Hansson, L. 1991. Dispersal and connectivity in metapopulations. Biological Journal of the Linnean Society 42:89-103.

Harper, S. J., E. K. Bollinger, G. W. Barrett. 1993. Effects of habitat patch shape on population dynamics of meadow voles (*Microtus pennsylvanicus*). Journal of Mammalogy 74:1045-1055.

Hock, R. J. and V. Cottini. 1966. Mammals of the little Susitna Valley, Alaska. American Midland Naturalist 76:325-339.

Howard, W. E. 1960. Innate and environmental dispersal of individual vertebrates. The American Midland Naturalist 63:152-161.

Jansson, G. and P. Angelstam. 1999. Threshold levels of habitat composition for the presence of the long-tailed tit (*Aegithalos caudatus*) in a boreal landscape. Landscape Ecology 14:283-290.

Jensen, A. J., T. Forseth, and B. O. Johnsen. 2000. Latitudinal variation in growth of young brown trout *Salmo trutta*. Journal of Animal Ecology 69:1010-1020.

Johnson, D. R. and M. H. Maxell. 1966. Energy dynamics of Colorado pikas. Ecology 57:1059-1061.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237-240.

MacDonald, S. O. and C. Jones. 1987. *Ochotona collaris*. Mammalian Species 281:1-4.

McDonald, K. A. and J. H. Brown. 1992. Using montane mammals to model extinctions due to global change. Conservation Biology 6:409-415.

McIntire, E. J. B. 1999. The effects of collared pika grazing on alpine tundra vegetation in southwestern Yukon, Canada. M. Sc. Thesis, University of Toronto.

McIntire, E. J. B. and D. S. Hik. 2002. Grazing history versus current grazing: leaf demography and compensatory growth of three alpine plants in response to a native herbivore (*Ochotona collaris*). Journal of Ecology 90:348-359.

Merila, J., A. Laurila, A. T. Laurila, K. Rasanen, and M. Pahkala. 2000. Plasticity in age and size at metamorphosis in *Rana temporaria* - comparison of high and low latitude populations. Ecography 23:457-465.

Millar, J. S. 1973. Evolution of litter size in the pika, *Ochotona princeps* (Richardson). Evolution 27:134-143.

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

Moilanen, A., A. T. Smith, and I. Hanski. 1998. Long-term dynamics in a metapopulation of the American pika. American Naturalist 152:530-542.

Moilanen, A. and I. Hanski. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. Ecology 79:2503-2515.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1998. Wildlife-Habitat Relationship: Concepts and applications, 2nd edition. University of Wisconsin Press, Madison.

Peacock, M. M. and A. T. Smith. 1997. The effect of habitat fragmentation on dispersal patterns, mating behavior, and genetic variation in a pika (*Ochotona princeps*) metapopulation. Oecologia 112:524-533.

Peltonen, A. and I. Hanski. 1991. Patterns of island occupancy explained by colonization and extinction rates by shrews. Ecology 72:1698-1708.

Peters, R.L. 1992. Conservation of biological diversity in the face of climate change. Pages 15-30 In Global Warming and Biological Diversity (Eds. R.L. Peters and T.E. Lovejoy). Yale University Press, New Haven.

Roslin, T. 2002. Who said that size is all that matters? Trends in Ecology and Evolution 17:10-11.

Saari, L., J. Aberg, and J. E. Swenson. 1998. Factors influencing the dynamics of occurrence of the Hazel Grouse in a fine-grained managed landscape. Conservation Biology 12: 586-592.

Severaid, J. H. 1955. The natural history of the pika (Mammalian genus *Ochotona*). Ph.D. thesis. University of California, Berkeley. 820 p.

Sjögren Gulve, P. 1994. Distribution and extinction patterns with a northern metapopulation of the pool frog (*Rana lessonae)*. Ecology 75: 1357-1367.

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

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

Smith, A. T. 1980. Temporal changes in insular populations of the pika (*Ochotona princeps*). Ecology 61:8-13.

Smith, A. T. 1987. Population structure of pikas: dispersal versus philopatry. In: Chepko-Sade, B. D. and A. T. Halpin (Eds), Mammalian dispersal patterns: the effects of social structure on population genetics. The University of Chicago Press, Chicago.

Smith, A. T. 1988. Patterns of pika (Genus *Ochotona*) life history variation. In: Boyce, M.S. (Ed) Evolution of Life Histories: Theory and Patterns from Mammals. Yale University Press.

Smith, A. T. and M. Gilpin. 1997. Spatially correlated dynamics in a pika metapopulation. Pages 407-428. In : Hanksi, I. A. and W. E. Gilpin (Eds), Metapopulation Biology: Ecology, Genetics and Evolution. Academic Press Inc., San Diego.

Smith, A. T. and B. L. Ivins. 1983. Reproductive tactics of pikas: why have two litters? Canadian Journal of Zoology 61:1551-1559.

Smith, A. T., N. A. Formozov, R. S. Hoffmann, Z. Changlin, and M. A. Erbajeva. 1990. The Pikas. In: Chapman and Flux (Eds), Rabbits, Hares and Pikas: Status Survey and Conservation Action Plan. International Union for Conservation of Nature and Natural Resources. Oxford, U. K.

Southwick, C. H., S. C. Golian, M. R. Whitworth, J. C. Halfpenny, and R. Brown. 1986. Population density and fluctuations of pikas (*Ochotona princeps*) in Colorado. Journal of Mammalogy 67:149-153.

Tait, M. 2002. Effects of climate change and herbivory on photosynthesis and growth of alpine plants in the Yukon. MSc thesis, University of Alberta.

Tapper, S. C. 1973. The spatial organization of pikas (*Ochotona*) and its effect on population recruitment. Ph. D. Thesis, University of Alberta, Edmonton, 154 pp.

Thomas, J. A., N. A. D. Bourn, R. T. Clarke, K. E. Stewart, D. J. Simcox, G. S. Pearman, R. Curtis, and B. Goodger. 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. Proceedings Royal Society London, Series B, Biological Sciences 268:1791-1796.

Turner, I. M. 1996. Species loss in fragments of tropical rain forest: A review of the evidence. Journal of Applied Ecology 33:200-209.

Van Vuren, D. 1998. Mammalian dispersal and reserve design. In: Caro, T. (Ed), Behavioral ecology and conservation biology. Oxford University Press, New York.

Wauters, L., P. Casale, and A. Dhondt. 1994. Space use and dispersal of red squirrels in fragmented habitats. Oikos 69:140-146.

Whitworth, M. R. and C. H. Southwick. 1981. Growth of pika in laboratory confinement. Growth 45: 66-72.

Yang G-J, T. Matsumoto, M. Kosaka, M. Yamauchi, and N. Ohwatari. 1988. Poor heat loss ability of pika (whistle rabbit). Tropical Medicine 30: 45-48.

Yukon State of the Environment Report 1999. Yukon Department of Renewable Resources, Whitehorse, Yukon.

Chapter 2: Variation in timing of parturition and growth of collared pikas (*Ochotona collaris*) in the southwest Yukon (1995-2001)

Abstract

Growth rates and timing of parturition of collared pikas (*Ochotona collaris*) were examined from 1995-2001 in the Ruby Ranges, Yukon. Growth of pikas was best described using a Gompertz growth model, when the asymptotic mass (determined from the average male and female weights) was 157g, K (the growth rate constant) was 0.0557, and I (age at inflection) was 18.12 days, when the initial birth weight was 10g. The growth rate was higher than the rate for *O. princeps,* reflecting the shorter summer season at higher latitudes. Ninety percent of pikas were born in a 2-month period from the beginning of May until the end of June. Parturition date varied significantly among years and was significantly later in 1999 and 2000 compared to all other years. While delayed parturition may reflect high snow accumulation and late spring snowmelt, parturition date did not significantly affect the over-winter survival of juveniles.

Introduction

The environment in which a species lives can affect a number of life history parameters, including number and size of litters born, timing of parturition and the growth rate (Ricklefs 1967, Case 1978, Roff 1992, Charnov 1993). Timing of parturition in arctic and seasonal alpine environments is particularly critical for mammalian herbivores because the snow-free season is very short. The young must be born late enough to avoid unsuitable conditions, such as snow or low quality food resources, but they also must be born early enough in the summer to allow growth to a size at which they are able to acquire the resources necessary for over-winter survival. Depending on the species, this strategy may involve accumulating fat stores for hibernation (e.g. marmots) or migration (e.g. caribou), and/or the acquisition of territories and hoarding of food prior to the onset of winter (e.g. collared pikas).

Birthing tends to be synchronous in strongly seasonal environments (Rachlow and Bowyer 1991), with the majority of all offspring being born in a short period of time when conditions are optimum for growth. Reproductive synchrony may result from individuals selecting similar times for reproduction in relation to climate, however, the temporal pattern of reproduction may also be a result of other ecological processes, such as predation or timing of food availability (Ims 1990). Some research has shown that mammals may use changes in photoperiod and some secondary compounds in newly emerging vegetation as predictors for breeding season (Bronson 1985).

The timing of initiation of first litters is a compromise between having young early enough, so they can be weaned early and have an advantage securing a territory, and having them late enough to ensure that the mother can meet the energetic demands of weaning a litter (Smith 1978). Generally it is assumed to be an advantage to be born earlier in a growing season (Roff 1992) and this has been shown in some species (e.g. marmots, Armitage et al. 1976; snowshoe hares, Gillis 1998). For territorial species, being born early may be critical when finding and securing a territory are necessary for survival. As well, individuals born earlier may have an advantage in terms of vegetation quality and availability. Because forage quality starts high and declines over the season, young that are born later have less time to adequately prepare for winter (e.g. Dall sheep - Rachlow and Bowyer 1991; ground squirrels - Rieger 1996). Also, because lactation is more energetically demanding than pregnancy, it is advantageous for an adult female to have lactation coinciding with early emerging vegetation, which has higher protein content (Millar 1977; Rachlow and Bowyer 1991; Rubin et al. 2000).

Seasonal environments not only affect the timing of parturition, but can also influence growth rates of animals. Northern latitudes, in general, may be associated with faster growth rates because organisms must reach an optimal size during a shorter growing season. A number of studies have shown that growth rates are, in part, affected by latitude (Arctic ground squirrel, Case 1978; sturgeon, Power and McKinely 1997; bass, Brown et al. 1998; brown trout, Jensen et al. 2000; frogs, Merila 2000; moose, Ferguson 2002), with animals having faster growth rates in northern parts of their range. Increases in post-natal growth rates are usually only found in animals that are restricted to a short breeding season, however, some animals may use physiological and behavioral adaptations to counteract the short growing season without major increases in growth rates (Case 1978).

One group of species that are affected by a short growing season are talus dwelling pikas (Lagomorpha: *Ochotonidae*). Their life history variation has been summarized by Smith (1988). This group of pikas are generalist herbivores that live in boulderfields (talus) in alpine environments that are often characterized by short summers. They are territorial and do not hibernate during the winter, but rather forage below the snow and on vegetation that was collected and stored in a haypile at the end of the summer. There is high over-winter mortality of pikas especially in their first winter. They breed at one year of age, with average litter sizes of 3 (range 1-4) individuals, and an average of 2 individuals being weaned. Pikas generally produce one litter a year, but have a post-partum estrus allowing for a possible second litter. Breeding usually takes place while there is still snow on the ground and gestation is approximately 30 days. The litters are born in the talus (rock piles) and weaning occurs 3-4 weeks after birth.

The collared pika (*Ochotona collaris*) is found in Alaska, the Yukon Territory, the Northwest Territories and northern British Columbia (MacDonald and Jones 1987). Little is known about this species, and most of what we infer has come from work on its southern relative, the American pika (*O. princeps*). Both species have similar life history strategies, however, the length of summer growing season is longer for the American pika. There is a gap in the distribution of these two species, with the American pika inhabiting mountain areas in western North America from 35°N to 54°N and the collared pika's distribution ranging from 59°N to 68°N. A few studies have described the growth of the American pika in both wild populations (Alberta - Millar and Tapper 1973; Colorado - Golian and Whitworth 1985) and captive populations (Whitworth and

Southwick 1981). These studies have shown the importance of a rapid growth rate to ensure pikas reach an adult weight prior to the onset of winter.

This paper had two primary objectives. First, we developed a growth model for the collared pika and compared growth rates of pika populations in North America. Second, we used the growth equation to estimate dates of parturition of juvenile pikas at our study site and examined how parturition date affected survival and how variation in spring conditions influenced the growth rate and timing of parturition of collared pikas.

Methods

The growth rate and timing of parturition of collared pikas was examined in the Ruby Range Mountains, Yukon Territory (61°12'N, 138°16'W; 1800-2000 m a.s.l.). The snow-free season generally extends from mid-June to early September. Pikas were live-trapped mid-June to the end of August from 1995-2001, using Tomahawk live traps baited with native vegetation. Animals trapped for the first time were marked with numbered metal ear tags (Monel #1) and a unique color combination of thin wire. Age (adult or juvenile), sex, and weight (to the nearest 5 g using a 600 g Pesola balance) were recorded for all trapped individuals. Since pika nests are nearly impossible to access, juveniles were only weighed at first capture upon emergence.

Sigmoidal growth curves have been used in numerous studies to describe the growth of organisms. We determined which of three sigmoidal growth models (Gompertz, von Bertalanffy, and the logistic equations) best described pika growth. Relative to the logistic curve, the Gompertz curve has a slower more prolonged growth rate during the later stages of growth, and the von Bertalanffy shows this to even a greater extent (Ricklefs 1967; Day and Taylor 1997). Different studies have used various equations to examine growth, and while biological assumptions may be important, they are often overlooked. Nevertheless, once a growth curve has been established for an organism, the curve can be used to predict an organism's age at certain weights. It is also possible to predict the date of birth (parturition date) of individuals. This latter application is very useful for species where the birth date cannot be known exactly.

These sigmoidal growth equations required the asymptotic mass (A = mean adult weight) at a given age (t = days). We estimated the growth-rate constant K, and the inflection point I, using the equations in Table 2-1. Birth weight of pikas was set at 10 g, based on other studies of *O. princeps* in captivity (Millar 1972; Millar and Tapper 1973; Whitworth and Southwick 1981; Golian and Whitworth 1985). The asymptotic mass (A) was determined by calculating the average adult mass for all individuals at our study site.

Since specific ages for juveniles were unknown, a growth curve was developed from weight gain over known intervals in a method similar to the one used by Millar and Tapper (1973) and Golian and Whitworth (1985). Initial weights (first capture weights) were grouped into 10-g intervals and the mean initial weight for each interval was taken. The second and subsequent captures provided weight changes over known time intervals. We only used captures that occurred within 10 days of each other, to avoid the likelihood that weight gain decreased over time. The mean growth rate between intervals was calculated and a growth curve was constructed using the mean rate of growth from one mean interval weight to the next. Although we were able to calculate the total elapsed time we still needed to determine how old individuals were at 70 g (our earliest weight interval). We selected eight initial reference points (to scale the rest of our data) of 70 g from 20 – 27 days, and fit these to the three growth curves. Curves were fitted using non-linear regression in S-PLUS, with iterative least squares criterion (MathSoft 1999), and the best model was chosen when the residual standard error of the equation was minimized.

To compare the growth rate of the collared pika to other pika populations, the growth rate constant K(day^{-1}) was converted to maximum growth rate (g/day) by multiplying K by A*e^{-1} (estimated mass at inflection point) (Zullinger et al. 1984). From this we were able to compare growth rates of pikas at different latitudes. We refit growth rates of Alberta and Colorado (wild) pikas to a Gompertz growth curve, so comparisons among populations could be made using a standard curve.

We estimated the parturition date and age of all juveniles at our study site using the best fit curve (Zullinger et al. 1984), described by W=A*exp(-exp(-K(t-I))), where A is the asymptotic mass (g) at age t (days), K is a growth-rate constant (day^{-1}), and I is age at the inflection point (days). To determine if the mean parturition date among years was different, a single factor ANOVA was used. Tukey's test (S-Plus, Mathsoft 1999) was used to determine which years were significantly different from each other. For each year we compared the parturition date for juvenile pikas that survived, to those that did not, using logistic regression.

Two measures of abiotic conditions were used to examine if climate and weather may affect the timing of parturition of pikas: (1) the snow accumulation on Mt. Logan (same latitude, 120 km W) measured as water equivalent mass (1994/95 - 1999/2000, Moore et al. 2002; 2000/01 Gerry Holdsworth, pers. comm), and (2) the best estimate of snow free dates on plots at our study site based on dataloggers and field records (D. Hik, unpublished data). These abiotic measures were correlated with the average parturition date for the corresponding year.

Results

Mass of adult male pikas was 157.3 ± 12.5 (SE) g (range, 130-185 g; n=97); adult females were 157.4 ± 13.7 g (range, 130-200 g; n=126). When all years were combined, weight was not significantly different between the sexes (t=0.0853, df=221, P=0.9321), so we combined males and females from 1995 to 2001 to calculate a mean adult asymptotic mass of 157.4 g (n=223).

Based on the three growth equations and parameter estimates (Table 2-1), the best fit model was the Gompertz growth equation when pikas weighed 70 g at 22 days. The best fit curve is described by $W=157*e^{-\exp(-0.0557(t-18.12))}$, where 157 is the asymptotic weight in grams of adult pikas, 0.0557 is the growth rate constant (K) and 18.12 is the age (days) at inflection (I) (Fig. 2-1). We were not able to capture pikas in the first 21 days after birth, and therefore extrapolated this part of the curve from the Gompertz equation.

To compare growth rates of different populations of pikas we used the maximum growth rate per day (g/day). The maximum growth rate per day increased with an increase in latitude (Table 2-2).

We used the Gompertz growth equation to determine the approximate date of birth for all juveniles that were captured and weighed at our site. Dates are not exact because we had to estimate a starting reference point based on the best fit of the model, however, we estimate that the dates are likely correct to within 3 days. When all years were combined, most juveniles were born late June (Fig. 2-2). However, depending on year, the average parturition date of the majority of juveniles varied significantly over a three month period (*F*=9.592, *df*=6, 152, *P*<0.0001) (Fig. 2-3). Five years (1995, 1996, 1997, 1998, 2001) were not significantly different from each other and the average parturition date for these years was early to mid-June. Both 1999 and 2000 had later average dates of parturition compared to all other years: 1999 was significantly different from 1995, 1996, 1998 and 2001, and 2000 was significantly different from 1995 and 1996. We also determined the average date of conception (late May) by subtracting 30 days from the date of birth, since gestation is 30 days in the American pika (Severaid 1950; Millar 1973).

The snow-free dates at our study site were partially correlated with the net snow accumulation on Mt. Logan (r^2=0.40, *df*=6, *P*=0.13), with later snow-free dates in years with higher snow accumulation. The average parturition date for each year was positively correlated with the net snow accumulation on Mt. Logan (r^2=0.56, *df*=6, *P*=0.051), but not with the snow-free dates at our study site (r^2=0.10, *df*=6, *P*=0.50).

When all years were pooled, we found that juvenile survival did not vary with parturition date (logistic regression: coefficient =-0.00998, *SE*=0.00975, *P*=0.3109, *df*=122). Similarly, parturition date did not affect survival when years were examined individually (logistic regression: all p-values >0.05: Table 2-3), and no general trend was observed in terms of earlier born individuals having greater survival.

Synchrony of parturition varied among years. In 1995, 1997, 2000, and 2001, the greatest proportion of juveniles were born in late June and births after this dropped off steeply (Fig. 2-3). Only in 1999, did the number of births increase after late June. In 1996 and 1998 pikas births were distributed more evenly across the summer months, with no strong peaks. Within any given year, 90% of all juveniles were born in a two-month period from the beginning of May to the end of June.

Discussion

Northern latitudes have both short and unpredictable growing seasons. Two strategies for coping with this uncertainty are (1) faster growth rates, and (2) variation in parturition dates among years to take advantage of the best conditions for growth. Collared pikas at our study site appeared to use both of these strategies to deal with the highly seasonal environment.

Of the three sigmoidal curves, the Gompertz curve fit our data best. This equation has also been used to describe the growth rates of many mammalian species (Zullinger et al. 1984). The growth rates of pikas are among the fastest for lagomorphs (Golian and Whitworth 1985), and the growth rates of collared pikas at our study site were even higher than those of its southern relative, the American pika. Faster growth rates at higher latitudes are likely an adaptation to shorter growing seasons. It is also possible that the difference in growth rates may be a difference between the two species, however given the similarity between these species it is probable to assume that latitude is an important factor. In this alpine environment, pikas must attain adult weights, establish territories, and begin collecting vegetation for their haypile before the onset of winter (Whitworth and Southwick 1981; Golian and Whitworth 1985).

Pikas not only have high growth rates in response to the highly seasonal environment in which they live, but they were also found to confine their reproduction to a short period, when periods are favorable for rearing offspring. Ninety percent of all births occurred at our study site between the beginning of May and the end of June. Compared to other populations of the American pika in southern Canada and the US, this is a much shorter period (i.e. compare to 95% of all births in 3.5 months in California) (Smith 1978). This suggests that although the actual timing may vary among years, pikas in northern latitudes may have adapted to a shorter growing season in part by limiting their reproduction to a narrower period. Smith (1978) also reported a similar trend, with pikas in Alberta born in a shorter period of time (more synchronous within a year) compared to those in California and Colorado.

American pikas can have two litters per year with the first litter conceived early summer, usually under snow-cover (Millar 1972; Millar and Tapper 1973; Smith 1978; Smith and Ivins 1983) allowing parturition to coincide with snowmelt and the onset of vegetative growth (Millar 1972; Smith 1978). Only one litter of pikas born per female was detected at our site, and the mean conception date was late May under snow cover. Similarly, Rausch (1961) found adult females to be pregnant late May to early June. However, these results were from collected individuals and would depend on the timing of the collection, as well, it is unknown if successful parturition would have followed. The average dates of conception for the collared pika are later than those reported for the

American pika (late March in California to late May in Alberta, see review in Smith 1978).

The timing of breeding in pikas at our site allows juveniles to be born at the start of vegetative growth when forage quality is high, even though peak biomass occurs later (late July) (Andruchow 2000). Due to the high energy demands of females during nursing, the higher quality of vegetation may be more important than having higher biomass. The timing of initiation of first litters is a compromise between having young early enough, so they can be weaned early and have an advantage securing a territory, and having them late enough to ensure that the mother can meet the energetic demands of weaning a litter (Smith 1978).

Smith (1978) suggested that a correlation existed within a population between the amount of variation in initiation of the first litter and the amount of variation in timing of snowmelt. He found pikas breeding asynchronously within a year and suggested this occurred because snowmelt varies among years and pikas are not able to predict snowmelt. Therefore, he suggests it may be advantageous to have asynchronous breeding to ensure some success. However, we suggest that parturition of pikas at our site was synchronous within a year, with the majority of individuals being born in a short period of time, even though snowmelt varied among years. Perhaps because of the constrained summer environment, breeding asynchronously within a year is unlikely. Instead, it appears that pikas may be able to use environmental cues to signal timing of snowmelt and adjust breeding accordingly.

Variation in the average parturition date among years, at our site, was partially correlated with net snow accumulation, with later dates of parturition following years of large snow accumulation. Similar results have been observed with pikas in Colorado, where the variation in initiation of first litters was positively correlated with snowmelt (Smith 1978; Smith and Ivins 1983). Pikas may delay breeding following winters with high snow accumulation in order to coincide parturition with vegetative growth. However, it is also possible that in years of late snow melt, pikas may lose litters or reabsorb litters and rebreed in post-partum estrus (Smith and Ivins 1983). We were unable to distinguish if this was occurring or if the pikas were choosing to breed later using environmental cues to signal the start of the breeding season. Studies have also shown a delay in the timing of parturition in other northern mammals following winters with deep or persistent snow-cover (caribou, Adams and Dale 1998), or when late spring storms create inhospitable conditions for young and limit forage availability (Dall sheep, Rachlow and Bowyer 1991). The early onset of spring conditions has allowed earlier parturition dates in some species (snowshoe hare, O'Donoghue and Krebs 1992).

Although the parturition date varied among years, there does not appear to be an advantage to being born early or late. Other studies have shown an advantage to individuals that are born earlier in the growing season, but our results suggest that this is not a critical factor in predicting survival. Because this population is at low densities, being born early to facilitate territory acquisition is not as strong a benefit as it would be at higher densities, when it is necessary to compete for territories and establish haypiles prior to winter. Even when a pika is born late in the growing season, due to their fast growth rate, they are still able to achieve near adult body size by fall and therefore timing of parturition does not seem to significantly influence the survival when living at low densities. The growth data and subsequently the parturition dates are based on individuals that have emerged from the nest, therefore, it is possible that timing may affect survival at earlier stages of life, before emergence, however, we were unable to detect this.

In this study we have only examined the growth rates and parturition dates, but it is possible that other life history factors, such as the number of litters, litter size and the age of first reproduction, may also be influenced by the shorter growing season. It is unknown if collared pikas at our site were able to conceive two litters per year. Some authors (Rausch 1961; Youngman 1975; R. Smith 1978) have indicated that collared pikas have two litters per year based on females being pregnant and lactating at the same time, however, this does not provide evidence that two litters are successfully weaned. At our site, we were not able to detect more than one litter born to a female per season. Although it is possible that juveniles may have emerged after we left the field site, very few unmarked individuals were found in the subsequent trapping season, suggesting that a possible second litter contributes little to the population. It is likely that this northern species only produces one litter per year, as a result of the latitudinal reduction in the length of breeding season. Similar patterns have been reported for land birds, with fewer broods produced at higher latitudes (Böhnig-Gaese et al. 2000).

Studies have reported that the litter size of collared pikas ranges from 1-4 pikas, averaging 2.2 - 3 (Dixon 1938; Raucsh 1961; 1970; Smith et al. 1990). Although, we could not determine average litter size for collared pikas in our study, it is expected that litter size is similar to other reported litter sizes. At this site litters of 4 individuals were observed upon emergence, however, this was not typical. Average number of successfully weaned juveniles was about one juvenile per female per year (based on number of juveniles and number of adult females at the site). It is possible, however, that the northern environment may influence litter size. In other lagomorphs (hares and rabbits), a direct correlation has been shown between latitude and litter size, with larger litters being produced where the growing season is the shortest (Conaway et al. 1974; Chapman and Flux 1990).

It is assumed that collared pikas are sexually mature at one year of age, however, female young of the year have been observed to copulate with adult males (personal observations). This does not indicate that they can successfully produce a litter, and even if a litter was produced these young would have very low chances of surviving because they would be born in the fall (Millar 1972).

Pikas in northern latitudes are constrained by the short-growing season, and timing of parturition may be affected by environmental conditions such as snowmelt. This pattern may, however, be disrupted by future climate change. In northern areas, such as the Yukon, heavier snow accumulations are predicted (Moore et al. 2002), which may result in a later snow free season and shorter growing season, as photo-period will not change. It is also predicted that weather patterns may become even more variable and the chance of having severe spring storms may increase (Houghton et al. 2001). Millar (1974) and Smith (1978) reported that in pikas, entire litters might be lost in response to severe weather storms during gestation. The implications of changing climate patterns on many animals is unknown, however, we suggest that the predicted climatic changes may adversely affect animals such as pikas that are constrained to a very short growing season already.

Comparisons of growth rates indicate that collared pikas in the Yukon have higher growth rates compared to the American pika. This is likely the result of living in a northern environment with short growing seasons, which forces an individual to reach an adult body size before the onset of winter. As well, our results suggest that the timing of parturition among years is asynchronous and adult pikas are likely using climatic cues to initiate the timing of breeding to enable juveniles to be born at the onset of vegetative growth.

References

Adams, L. G. and B. W. Dale. 1998. Timing and synchrony of parturition in Alaskan Caribou. Journal of Mammalogy 79:287-294.

Andruchow, J. 2000. Foraging preferences of collared pikas in alpine meadows in the southwest Yukon. B.Sc. thesis, University of Alberta, Edmonton, Canada.

Armitage, K. B., J. F. Downhower, and G. E. Svendsen. 1976. Seasonal changes in weights of marmots. American Midland Naturalist 96:36-51.

Böhnig-Gaese, K., B. Halbe, N. Lemoine, and R. Oberrath. 2000. Factors influencing the clutch size, number of broods and annual fecundity of North American and European land birds. Evolutionary Ecology Research 2:823-839.

Bronson, F. H. 1985. Mammalian reproduction: an ecological perspective. Biology of Reproduction 32:1-26.

Brown, J. J., A. Ehtisham, and D. O. Conover. 1998. Variation in larval growth rate among striped bass stocks from different latitudes. Transactions of the American Fisheries Society 127:598-610.

Case, T.J. 1978. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. Quarterly Review of Biology 53: 243-282.

Chapman, J. A. and J. E. C. Flux. 1990. Introduction and overview of lagomorphs. In: Chapman and Flux (Eds), Rabbits, Hares and Pikas: Status Survey and Conservation Action Plan. International Union for Conservation of Nature and Natural Resources. Oxford, U. K.

Charnov, E.L. 1993. Life history invariants. Oxford University Press, Oxford.

Conaway, C. H., K. C. Sadler, and D. H. Hazelwood. 1974. Geographic variation in litter size and onset of breeding in cottontails. Journal of Wildlife Management 38:437-481.

Day, T. and P.D. Taylor. 1997. von Bertalanffy's growth equation should not be used to model age and size at maturity. American Naturalist 149:381-393.

Dixon, J. S. 1938. Birds and mammals of Mount McKinley National Park, Alaska, U.S. National Park Service, Fauna Series, 3.

Ferguson, S. H. 2002. The effects of productivity and seasonality on life history: comparing age at maturity among moose (*Alces alces*) populations. Global Ecology and Biogeography 11:303-312.

Gillis, E. A. 1998. Survival of juvenile hares during a cyclic population increase. Canadian Journal of Zoology 76:1949-1956.

Golian, S. C. and M. R. Whitworth. 1985. Growth of pikas (*Ochotona princeps*) in Colorado. Journal of Mammalogy 66: 371-374.

Ims, R. A. 1990. The ecology and evolution of reproductive synchrony. Trends in Evolution and Ecology 5:135-140.

Houghton, J. T., Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, K. Maskell, and C. A. Johnson. 2001. Climate Change 2001: The Scientific Basis Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

Jensen, A. J., T. Forseth, and B. O. Johnsen. 2000. Latitudinal variation in growth of young brown trout *Salmo trutta*. Journal of Animal Ecology 69:1010-1020.

MacDonald, S. O., and C. Jones. 1987. *Ochotona collaris*. Mammalian Species 281:1-4.

MathSoft. 1997. S-PLUS 4 Guide to Statistics. MathSoft, Inc. Seattle.

Merila, J., A. Laurila, A. T. Laurila, K. Rasanen, and M. Pahkala. 2000. Plasticity in age and size at metamorphosis in *Rana temporaria* - comparison of high and low latitude populations. Ecography 23:457-465.

Millar, J. S. 1972. Timing of breeding of pikas in southwestern Alberta. Canadian Journal of Zoology 50: 665-669.

Millar, J. S. 1973. Evolution of litter-size in the pika, *Ochotona princeps* (Richardson). Evolution 27:134-143.

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

Millar, J. S. 1977. Adaptive features of mammalian reproduction. Evolution 31: 370-386.

Millar, J. S. and S. C. Tapper. 1973. Growth rates of pikas in Alberta. Canadian Field Naturalist 87: 457-459.

Moore, G. W. K., G. Holdsworth, K. Alverson. 2002. Climate change in the northern Pacific region over the last three centuries. Nature (in press).

O'Donoghue, M. and C. J. Krebs. 1992. Effect of supplemental food on snowshoe hare reproduction and juvenile growth at a cyclic population peak. Journal of Animal Ecology 61: 631-641.

Power, M. and R. S. McKinely. 1997. Latitudinal variation in lake sturgeons size as related to the thermal opportunity for growth. Transactions of the American Fisheries Society 126:549-558.

Rachlow, J. L. and R. T. Bowyer. 1991. Interannual variation in timing and synchrony of parturition in Dall Sheep. Journal of Mammalogy 72:487-492.

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

Ricklefs, R. E. 1967. A graphical method of fitting equations to growth curves. Ecology 48:978-983.

Rieger, J. F. 1996. Body size, litter size, timing of reproduction, and juvenile survival in the Uinta ground squirrel, *Spermophilus armatus*. Oecologia 107: 463-468.

Roff, D.A. 1992.The evolution of life histories: theory and analysis. Chapman and Hall, New York.

Rubin, E. S., W. M. Boyce, and V. C. Bleich. 2000. Reproductive strategies of desert bighorn sheep. Journal of Mammalogy 81:769-786.

Severaid, J. H. 1950. The gestation period of the pika (*Ochotona princeps*). Journal of Mammalogy 31:356-357.

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

Smith, A.T. 1988. Patterns of pika (Genus *Ochotona*) life history variation. In: Boyce, M.S. (Ed), Evolution of Life Histories: Theory and patterns from mammals. Yale University Press.

Smith, A. T. and B. L. Ivins. 1983. Reproductive tactics of pikas: why have two litters? Canadian Journal of Zoology 61:1551-1559.

Smith, A. T., N. A. Formozov, R. S. Hoffmann, Z. Changlin, and M. A. Erbajeva. 1990. The Pikas. In: Chapman and Flux (Eds), Rabbits, Hares and Pikas: Status Survey and Conservation Action Plan. International Union for Conservation of Nature and Natural Resources. Oxford, U. K.

Smith, R. 1978. The pika in Alaska. Wildlife Notebook Series, Alaska Dept. Fish and Game. Looseleaf.

Whitworth, M. R. and C. H. Southwick. 1981. Growth of pika in laboratory confinement. Growth 45: 66-72.

Youngman, P. M. 1975. Mammals of the Yukon Territory. Natural Museum of Canada, Publ. Zool. 10:1-192.

Zullinger, E. M., R. E. Ricklefs, K. H. Redford and G. M. Mace. 1984. Fitting sigmoidal equations to mammalian growth curves. Journal of Mammalogy 65: 607-636.

Table 2-1. Calculated parameter estimates for 3 growth curves fitted to collared pika post-natal growth. The best model is indicated by **. W is the weight at time t; t, age in days; A, asymptotic weight (calculated as 157g for collared pikas); I, inflection point, maximum growth rate.

Curve	**Equation**	**Parameter Estimates**				
Von Bertalanffy	$W_t=A(1-1/3e^{-K(t-I)})^3$					
Gompertz	$W_t=Ae^{-\exp(-K(t-I))}$					
Logistic	$W_t=A/(e^{-k(t-I)}+1)$	K	I	**Residual SE**	**AIC**	**loglik**
70g at 21 days	Von Bertalanffy	0.04890	13.3689	1.648	38.27	-16.13
	Gompertz	0.05647	17.34337	0.6508	21.55	-7.773
	Logistic	0.07774	24.8439	4.974	58.15	-26.08
70g at 22 days	Von Bertalanffy	0.04813	14.06	2.089	42.55	-18.27
	Gompertz**	0.05565	18.12	0.4181	13.59	-3.793
	Logistic	0.07679	25.73	4.600	56.75	-25.37
70g at 23 days	Von Bertalanffy	0.04745	14.78	2.511	45.85	-19.93
	Gompertz	0.05490	18.90	0.5361	18.06	-6.029
	Logistic	0.07589	26.63	4.244	55.30	-24.65
70g at 24 days	Von Bertalanffy	0.04691	15.55	2.909	48.50	-21.25
	Gompertz	0.05422	19.70	0.8409	26.16	-10.08
	Logistic	0.07504	27.52	3.905	53.80	-23.90
70g at 25 days	Von Bertalanffy	0.04657	16.40	3.279	50.65	-22.33
	Gompertz	0.05360	20.51	1.177	32.21	-13.10
	Logistic	0.07422	28.42	3.584	52.26	-23.13
70g at 26 days	Von Bertalanffy	0.04669	17.47	3.611	52.39	-23.19
	Gompertz	0.05306	21.35	1.508	36.67	-15.34
	Logistic	0.07345	29.32	3.280	50.66	-22.33

Table 2-2. A comparison of the growth curves and growth rates for different populations of pikas. Values in () are for the von Bertalanffy curve that was fitted by the authors of those studies; all other values are for the Gompertz growth curve.

Study	**Latitude : altitude**	**Growth curve**	**K**	**I (days)**	**A (g)**	**max growth rate (g/day)**
Colorado (*O. princeps*) (Golian and Whitworth 1985)	40°N: 3830m	Gompertz	0.0339	22	170	2.122
		(von Bertalanffy)	(0.0297)	(18)	(170)	(1.857)
Colorado (captive -*O. princeps*) (Whitworth and Southwick 1981)	40°N: 3450-3960m	Gompertz (Zullinger et al. 1984)	0.0376	25	160*	2.213
Alberta (*O. princeps*) (Millar and Tapper 1973)	51°N: 1370-2590m	Gompertz	0.0484	19	133	2.366
		(von Bertalanffy)	(0.0405)	(14)	(133)	(1.982)
Yukon (*O. collaris*) this study	61°N : 1800-2000 m	Gompertz	0.0557	18	157	3.238

* indicates A was estimated

Table 2-3. The average parturition date for all individuals in each year (± SD days) and the mean partition date for juveniles that survived and juveniles that did not survive (n). Results of logistic regression comparing the mean parturition dates of pikas that survived compared to juvenile pikas that did not survive their first winter.

Year	Mean parturition for all juveniles (± SD days)	Mean date of juveniles surviving (n)	Mean date of juveniles not surviving (n)	Coefficient (SE)	df	P
1995	5-June-95 (24.2)	8-June-95 (3)	5-June-95 (20)	0.0049 (0.028)	21	0.8554
1996	5-June-96 (16.9)	3-June-96 (10)	8-June-96 (11)	-0.0169 (0.027)	19	0.5282
1997	23-June-97 (6.3)	19-June-97 (3)	25-June-97 (8)	-0.1749 (0.132)	9	0.1416
1998	19-June-98 (13.5)	27-June-98 (5)	16-June-98 (18)	0.0753 (0.049)	21	0.0812
1999	3-July-99 (20.4)	28-June-99 (4)	4-July-99 (31)	-0.0123 (0.022)	33	0.5943
2000	27-June-00 (10.5)	23-June-00 (4)	29-June-00 (7)	-0.0724 (0.074)	9	0.2893
2001	15-June-01 (12.5)	na	na	na	na	na

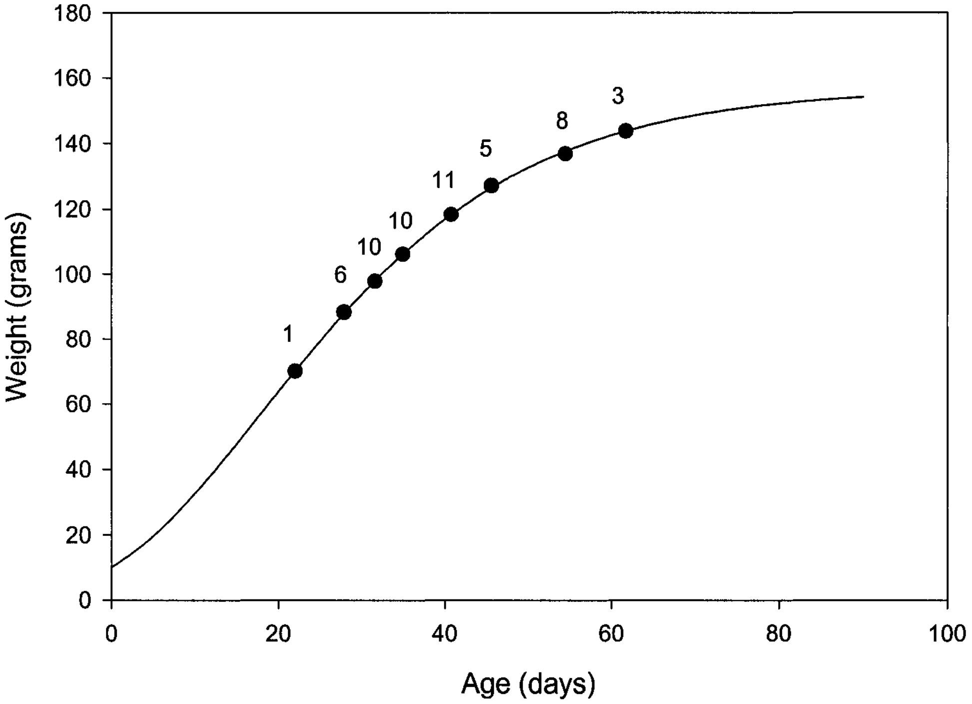


Figure 2-1. Predicted growth curve for collared pikas (*Ochotona collaris*) in the southwestern Yukon, from non-linear regression of the Gompertz growth curve, $W=157*e^{-exp(-0.0557(t-18.12))}$, using an initial starting weight of 10g and 70g at 22 days. Points are known weights with known growth rates between them. Sample sizes for each 10 g weight interval are indicated.

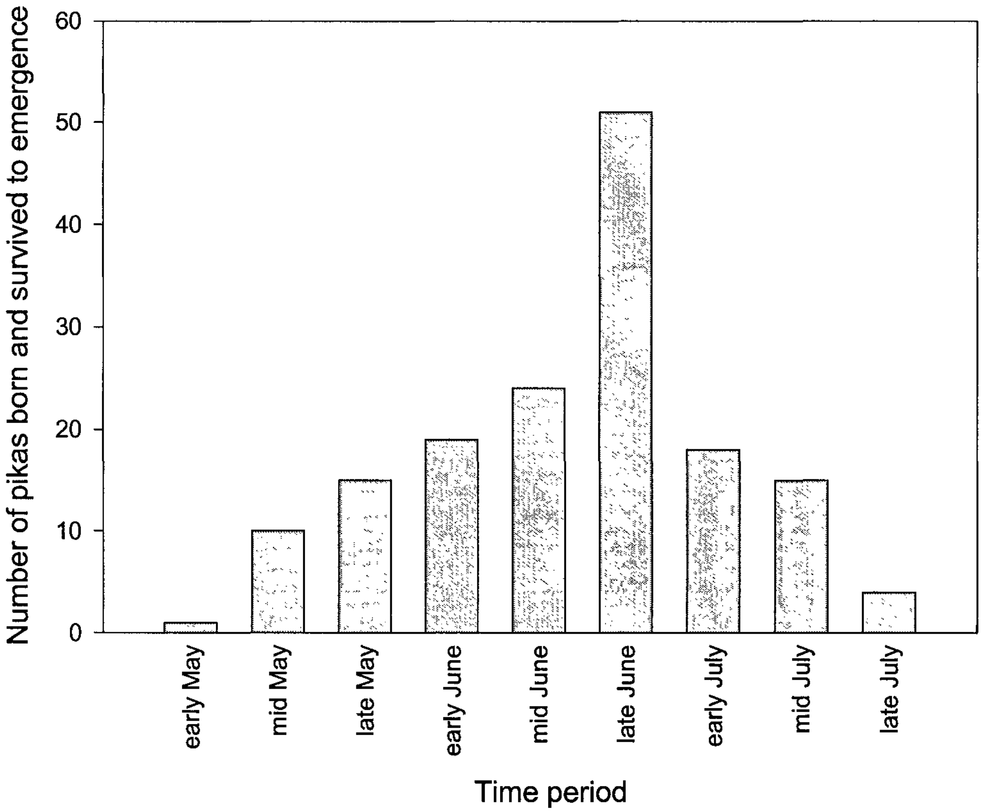


Figure 2-2. Proportion of juveniles born in each time period when all years (1995-2001) were combined.

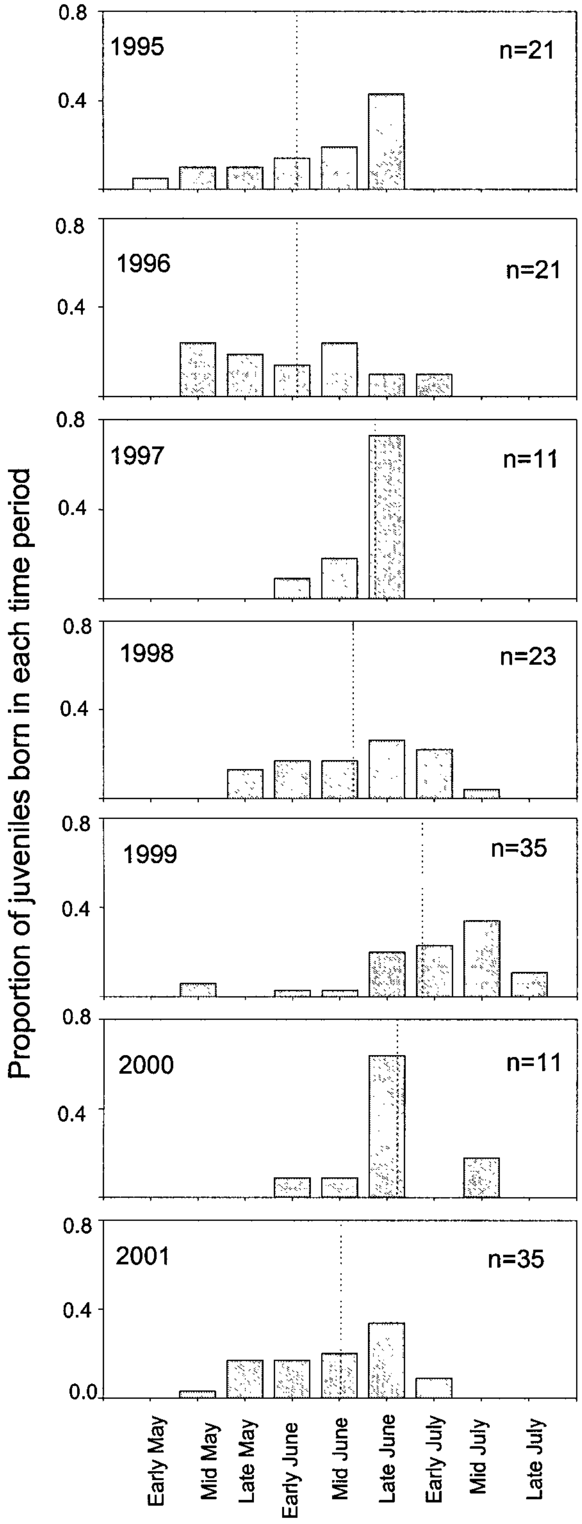


Figure 2-3. The proportion of juveniles born in each time period from 1995 to 2001. Dotted lines show the mean birth date for each year.

Chapter 3: An assessment of factors influencing dispersal, settlement patterns, and survival of collared pikas (*Ochotona collaris*) in the southwest Yukon

Abstract

We present the first detailed field study on the collared pika (*Ochotona collaris*), a lagomorph inhabiting alpine areas in northwestern Canada and Alaska. From 1995 to 2001 420 individuals were trapped and marked in the Ruby Ranges, Yukon. Over-winter survival was low, with an average of 34% of adults and 25% of juveniles surviving. Survival was not sex-biased, but the year in which a pika was born, as well as slope aspect, significantly influenced how long a pika lived. Total density of pikas on a patch, the presence of adults, or parturition date did not influence juvenile survival. Both sexes dispersed between patches with equal frequency and a minimum of 34% of juveniles made inter-patch movements. Inbreeding avoidance and habitat selection are possible hypotheses for dispersal in the collared pika. In general, pikas settled closer to the opposite sex, however, juvenile males recolonized unoccupied patches, whereas juvenile females never did and usually settled in patches with the opposite sex. Densities were <8 individual/ha, and home range sizes were not significantly different between males (0.2 ha) and females (0.16 ha). Among years, different habitat characteristics were found to be important in over-winter survival. Collared pikas are similar to their southern relatives (*O. princeps*) in most respects, but differences are evident as a result of living in high latitude environments.

Introduction

Dispersal is an important process that affects population structure. Dispersal of individuals between local populations is critical to the maintenance and survival of populations, both on short-term demographic and longer-term evolutionary scales (Gaines and McClenaghan 1980; Stenseth1984). The patterns of dispersal are important in many aspects of species' ecology including social interactions and population dynamics (Horn 1984). Knowledge of dispersal barriers and rates is critical to understanding how populations are able to persist in a metapopulation structure, in which spatially distinct subpopulations are connected through dispersal (Levins 1969). Dispersal also involves organisms settling in new areas; these settlement patterns often reflect the social structure and mating systems of species. Although dispersal is thought to be an important parameter in population and conservation models, it is often poorly understood (Bowman et al. 2002).

The structure of a population is not only influenced by dispersal and settlement patterns of an organism, but also by survival. Survival of individuals is affected by a number of factors, both biotic (e.g. predation, population density) and abiotic (e.g. weather, habitat quality). Survival typically changes with age and can also be related to the sex of an organism. Dispersal, settlement, and survival are critical factors relating to population structure and persistence and understanding these is an essential prerequisite for a detailed assessment of metapopulation dynamics.

Very little is known about dispersal, settlement patterns and survival of the collared pika (*Ochotona collaris*), which inhabit alpine boulderfields in the mountains of northwestern North America (MacDonald and Jones 1987). Previous studies of collared pikas have described aspects of their geographic range, foraging ecology, parasites and behaviour (e.g. review in MacDonald and Jones 1987, Rausch 1962; Broadbrooks 1965; Hock and Cottini 1966; Holmes 1991, McIntire 1999, Andruchow 2000, McIntire and Hik 2002, Tait 2002). Although collared pikas are likely similar in most respects to the more southerly American pika (*O. princeps*), the collared pika experiences additional stress living in a northern environment with very short summers.

In this paper we provide the first detailed description and assessment of the patterns of survival, dispersal, and settlement of a population of collared pikas inhabiting alpine meadows in the southwest Yukon using seven years of demographic data. Comparisons to the American pika are made where possible. Both biotic and abiotic factors that may influence these patterns were assessed. This analysis forms the basis for an explicit assessment of metapopulation structure and dynamics (Chapter 4).

Methods

Study area and species

This study was conducted in the Ruby Range Mountains, Yukon (61°12'N, 138°16'W; 1800 – 2100 m) from 1995-2001. Numerous talus patches (boulderfields) inhabited by pikas are surrounded by extensive alpine meadows dominated by *Dryas octopetala, Salix reticulata*, and graminoid species (e.g. *Carex consimilis*). *Cassiope tetrogona* was common along the margin of the talus. Price (1971), McIntire (1999), and Hik et al. (2001) provide more detailed descriptions.

Our 4 km^2 study site had 27 distinct talus patches ranging in size from 0.07 ha to 15.7 ha and separated by 15 m to 1140 m of alpine vegetation. Pikas were located on three main slopes (Fig. 1), identified by their predominant aspect: East and West (1995 to 2001), and South (1998 to 2001).

From mid-June to the end of August, pikas were live-trapped using Tomahawk live traps baited with native vegetation. Animals captured for the first time were marked with numbered metal ear tags and a unique color combination of wires. All animals were sexed, weighed and aged. Age (adult or juvenile) for each animal was determined based on weight (see Chapter 2), as well as fur color and molt patterns. Occasionally, in order to minimize stress during handling, sex was not determined, so we do not know the sex of 31/420 individuals. A binomial test was used to determine if the population was sex-biased. Pikas are diurnal, have distinctive territorial calls, are highly visible and have distinguishable haypiles, permitting us to identify and capture all pikas resident within the study area. A permanent 50 m-interval grid system (±5 m accuracy) was used to determine locations of pikas within the study area.

The ecology of collared pikas was described in more detail in Chapter 1, and by McDonald and Jones (1987). Briefly, collared pikas are generalist herbivores, and coexist with hoary marmots (*Marmota caligata*) and arctic ground squirrels (*Spermophilus parryii plesius*) at this site. Pikas are territorial and defend a home range with cached vegetation (haypile) that is used during winter. Pikas are assumed to be facultatively monogamous, in which multiple mates are restricted due to ecological constraints (Kleiman 1981). Alternating sexes in adjacent territories along with the short summer reproductive season is thought to restrict access to multiple mates in pikas

(Smith and Ivins 1984). The collared pika lives in a non-continuous landscape and most literature suggests that long-distance dispersal of pikas between patches is rare (Smith and Ivins 1983; Smith 1974, 1987; Peacock 1997). Pikas survive long winters feeding under the snow and foraging on stored vegetation. In the spring, female pikas one year and older have 1-2 litters. The juveniles of these litters are thought to be philopatric and dispersal is thought to be due to competition for resources, where the primary resource is habitat.

Survival

Mark-recapture methods were used to determine survival by following marked individuals from birth to death or disappearance. Because adult pikas are philopatric (Smith and Ivins 1983; this study) and rarely disperse after establishing a territory, an adult pika was assumed dead if it was absent in a subsequent trapping session or season. Over-winter survival for both adult and juvenile pikas was determined for winters of 1995/1996 to 2000/2001.

Juvenile over-winter survival was analyzed using generalized linear models with binomial errors (survived/died) (SPLUS, MathSoft Inc. 1999). Variables included for analysis were: sex of the juvenile, whether the juvenile dispersed between patches or within patches, whether the juvenile was on a patch with adults, the parturition date of the juvenile, the number of days the juvenile was born before or after the average birth date of surviving juveniles in that year, and the total density of individuals on the patch where the juvenile settled.

A Cox's proportional hazards analysis (SPLUS, Mathsoft 1999) was used to examine what factors were important in determining how long a pika lived. This method allowed us to include individuals that were still alive in fall 2001, and was performed on all individuals with a known time of birth. Variables included in this analysis were sex, year of birth, and slope aspect (east, west, south).

To determine if spring and winter conditions affected the survival of pikas, we correlated Mount Logan annual snow accumulations and winter temperature deviations with average juvenile and adult over-winter survival.

Dispersal

During the summers of 1999-2001, we attempted to measure dispersal directly by radio-collaring juvenile pikas at their natal sites. Since pika nests are inaccessible in deep talus and juveniles cannot be marked while in the nest, we monitored the home ranges of lactating adult females in order to observe the emergence of juveniles. Maternity of juveniles was assumed through direct observation of young immediately after emergence in association with an adult female. Juveniles were fitted with radio collars (approximately 4 g) after emergence, and subsequently located at least once per day using handheld antennae and receivers. Tagged juveniles were monitored until a territory was obtained, death, or the end of field season. Juveniles were considered to have settled when they had a territory and were displaying territorial behaviors, such as, haypile building, vocalizations, scent marking, and defending territory by chasing others away.

Dispersal was also detected through mark and recapture if a juvenile was caught in one area and later settled in another area. In addition, pikas were known to have dispersed if they appeared on a talus patch that did not have a resident adult female. Because adult mortality during the summer is low, as well, due to intensive monitoring and trapping of adults before the emergence of juveniles, we are able to detect if adult females may have died after young are born.

Based on these inter-patch movements, we determined the minimum number of individuals successfully dispersing between patches and the minimum dispersal distance, measured as the straight-line distance to the nearest adult female when maternity was unknown. Chi-squared contingency analysis was used to test if the number of females and males dispersing between patches was different. Wilcoxon rank-sum test was used to determine if the minimum known dispersal distance differed between sexes. We also examined if pikas settled on patches that were unoccupied, occupied by adult males, or occupied by juveniles of the same and/or opposite sex. Unfortunately, pikas moving to patches with adult females could not be classified, as we were unable to determine if juveniles in these patches were born there or had dispersed.

Settlement

Previous literature on a similar species, the American pika (*O. princeps*), suggested that pikas tend to settle closer to individuals of the opposite sex (Smith and Ivins 1984; Brown et al. 1989). To examine settlement patterns, a home range center was determined for each pika, based on the Kernel fix (Worton 1989) of its mark-recapture and sighting locations. Distances between territorial pikas were then calculated as the straight-line distance between these centroids. A one-tailed Wilcoxon signed-ranked test was used to determine if males and females lived closer to the opposite sex, as well, if juveniles settled closer to the opposite sex (either adult or juvenile).

Maximum densities were determined for the three slopes in our site. The mean distance between range centers for all adults in 1998, 1999, 2000, and 2001 were also calculated.

The 95% kernel method with the Least Squares Cross Validation smoothing factor was used to calculate home range size (Worton 1989). Home range analyses were calculated in Ranges V (Kenward and Hodder 1995), using mark-recapture and sighting data. The minimum number of locations per animal necessary to give an accurate estimate of home range size was determined using incremental area analysis. The range size was considered a reliable estimate when home range size reached an asymptote with increasing number of locations.

Habitat Characteristics

We used generalized linear models (GLM, McCullagh and Nelder 1989) with binomial errors in S-PLUS (Mathsoft Inc., Seattle) to model the survival of pikas for each year with respect to the habitat characteristics. Terms were added in forward step-wise sequence starting with a null model (intercept only) and using the *Cp* statistic, until no additional variables improved model fit.

A total of nine habitat characteristics were measured at established haypile locations, including: patch aspect (converted to the sine of the radians to give a continuous variable), slope (degrees), rock size (small <15 cm; small-medium 0-60 cm; medium 15-60 cm; medium-large 15->60 cm; large >60 cm; mixed – all size classes), boulder spacing (the total number of gaps greater than 5 cm in diameter along two 30 cm x 5 m transects radiating from the haypile in cardinal directions), distance from the haypile to the nearest vegetation, level of the talus relative to the surrounding meadow (categorical: level with the slope grade, above-grade, or below-grade), and presence of lichen on boulders (categorical: > 10% cover or ≤10%). Transects were also run in the cardinal directions (NESW) to the nearest patch of vegetation that was at least 2 m x 2 m. Characteristics recorded included the distance from the haypiles to vegetation and the percent cover of *Dryas octopetala, Salix spp.*, graminoids, and *Cassiope tetragona.* Values from the four transects were averaged.

All variables had an a priori reason for being selected. Patch aspect provided an indication of plant productivity, with SW having higher productivity than NE facing slopes. Talus slope provided an indication of the stability of the talus with steeper talus slopes being less stable. Rock size and boulder spacing were thought to be important in terms of the amount of protection the rocks provide the pika, as well as the number of escape routes between the rocks. Spacing of rocks also may provide an indication of the depth of the talus; areas with higher spacing may have greater depth providing a buffer against pikas in extreme temperatures. Distance from the haypile to the meadow provided an indication of the distance a pika must travel to collect vegetation. The level of the talus relative to the surrounding meadow provided an indication of drainage. Transects provided information on the average distance to the meadow, which gives an approximation of the size of talus patch the pika lives in. Transects also provided information on the percent cover of three highly palatable vegetation species: *Dryas octopetala, Salix spp.*, and graminoides, and one species which is not preferred, *Cassiope tetragona.*

Classification trees (Steinberg and Colla 1997) were also used to determine which habitat variables were important for predicting annual survival (1995, 1996, 1998, 1999, 2000). Classification trees have commonly been used in medical research and are just starting to be used in ecology (De'ath and Fabricius 2000). Classification trees are constructed by repeatedly splitting the data into pairs. At each split the data are partitioned into two mutually exclusive groups, each of which is as homogenous as possible. Some advantages to classification trees are they can give easily interpretable results, handle a broad range of response variables and missing values in both the explanatory and response variables, ease and robustness of construction. Trees are invariant to monotonic transformations of numeric explanatory variables, it is a non-parametric procedure so does not require the specification of a functional form, variables can be selected several times, can detect complex interactions and is extremely robust with respect to outliers (Steinberg and Colla 1997; De'ath and Fabricius 2000; Vayssières et al. 2000). Some disadvantages of CART are that parametric analysis can better capture algebraic relationships between the response and a continuous variable and because of the dichotomous nature, later splits are based on fewer cases than the initial ones, therefore, parametric methods are generally more efficient for small data sets (Vayssières et al. 2000).

We used the Gini index as our splitting decision rule with a minimum of 10 samples being required in each parent node. Once the largest tree was grown, it was pruned back using cross-validation (10 fold), which essentially uses the data to create a test sample. The misclassification rate (the number of cases that were not classified correctly) is used to determine the best tree. The optimal tree was selected by using 1-SE rule suggested by Breiman et al. (1984), where the best tree is the smallest tree such that its estimated error rate is within one standard error of the minimum. The final tree is constructed from all the data. The same explanatory and response variables used in the GLMs were used in this analysis.

Results

A total of 420 pikas were captured from 1995 to 2001. The adult sex ratio was significantly biased towards females 1:1.34 (males:females) (n=225) ($Z_{0.05(2)}$=2.147, P=0.0327). The juvenile sex ratio was 1.12:1 (males:females) (n=157), in favor of males, but was not significantly different ($Z_{0.05(2)}$=0.71, P=0.5233) (Table 3-1).

Survival

Mean adult over-winter survival for all years was 34.3%, varying from 18.9% survival in 1999/00 to 43% in 2000/01 (Fig. 3-2). Over-winter survival of juveniles was lower than adult survival, and ranged from 10.3% in 1999/00 to 44% in 1996/97 (Fig. 3-2). In general, over-winter survival was low in 1998/99 and 1999/00, resulting in a sharp decline in adult population numbers on all three slopes (Fig 3-3).

The combined survival of pikas from all years with known birth dates indicated that only 25% (n=106/142) of individuals survived their first winter. Fourteen percent (n=20) of pikas at this site lived to age 1, 8% (n=11) lived to age 2, 3 % (n=4) lived to age 3, and <1% (n=1) lived to age 4, which was the oldest recorded known-age pika in this study. Using Cox proportional hazards we found that survival was not sex-biased; however, both the year that a pika was born and location within the valley influenced survival (Table 3-2). Pikas born in 1996 lived significantly longer than pikas born in 1995 (Table 3-2, Fig. 3-4). No other years differed significantly from 1995. It is important to note that three of the individuals born in 2000 were still alive at the end of the sampling period and therefore may live older than one year of age. Pikas living on the South-facing slope lived significantly longer than pikas on the west-facing slope (Table3-2, Fig. 3-5). Pikas living on the East-facing slope did not differ in survival compared to the West-facing slope (Table 3-2).

Juvenile over-winter survival was not influenced by the sex of the individual, whether the individual made an inter-patch movement, whether adults were present on the patch, the total density on the patch (both juveniles and adults), or parturition dates (GLM, Table 3-3).

Adult and juvenile over-winter mortality was not correlated with the Mount Logan snow accumulations (r=0.27, P=0.55; r=0.25, P=0.59 respectively) or the winter temperature deviations (r=-0.04, P=0.93; r=-0.07, P=0.89).

Dispersal and Settlement

Direct methods of determining dispersal of pikas were technically difficult (i.e. radio collaring and mark-recapture). Juveniles dispersed almost immediately upon emerging from their nest site and as a result most juveniles caught at this site were believed to have already dispersed when they were trapped because they were caught in areas without adult females. For these individuals, dispersal distances could not be determined because natal sites were unknown. Only one juvenile was successfully captured and radio-collared prior to dispersal from its natal site; it moved 606 m between patches. Five other juveniles were determined to have dispersed from their natal area based on mark-recapture and sighting records (one female moved within the patch 190 m, two females moved inter-patch: 307 m and 382 m, and three males moved inter-patch: 100 m, 283 m, 780 m).

Juveniles were the primary dispersers in our population, as no adults moved after establishing a territory and haypile. Thus, all juveniles on talus patches without an adult female must have dispersed there (i.e. they could not have been born there). From 1999 to 2001 there was low patch occupancy due to low over-winter survival, however this provided the opportunity to indirectly examine juvenile dispersal and settlement. In 1999, 2000, and 2001 a minimum of 32% (12/38), 50% (6/12), and 31% (11/36) of juveniles, respectively, made inter-patch movements. There was no difference in the proportion of females (12/33) or males (15/48) making inter-patch movement (X^2=0.2301, *df*=1, *P*=0.6314), nor was there a difference in the distance that females and males dispersed (*W*=168, *n*=12, *m*=15, *P*=1) when years were combined. On average males dispersed 375.2 ±71.0 m (standard error) and females dispersed 350.8 ±62.3 m. Two individuals of unknown sex were excluded from these analyses.

For juveniles that made inter-patch movements, we examined where these individuals choose to settle in relation to the other occupants of the patch (Fig. 3-6). Fifty-three percent (8/15) of males that made inter-patch movements settled on unoccupied patches, whereas, no females settled on unoccupied patches (0/12). Juvenile females never settled in patches that had only female juveniles as occupants (0/12). Instead, they settled in patches that had juvenile males (41%; 5/12), adult males (25%; 3/12) or both sexes of juveniles (25%; 3/12) as occupants. Besides settling on unoccupied patches, juvenile males also settled on patches with juvenile females (2/15) or patches with both sexes of juveniles (3/15) more often then on patches with only juvenile males (1/15). Juvenile males never settled on patches where adult males were the only occupants. All other juveniles were found on patches with adult females and therefore we cannot say whether they were born on this patch or had dispersed.

The maximum adult densities of pikas on South slope, East slope and West slope were 7.82, 6.82 and 7.6 pikas per hectare of talus. The total density of pikas (including juveniles) was higher, but these juveniles did not have established territories or haypiles, and therefore were not included. These are maximum densities that were observed on these three slopes, however, pikas generally existed at much lower densities than these maxima. The mean distance between range centers (another measure of density) of adults in 1998, 1999, 2000 and 2001 was 33 m, 57 m, 67 m, and 107 m respectively.

A minimum of 20 locations for adult males and females provided reliable estimates of home range size, and data from 1999, 2000 and 2001 were combined to determine mean home range sizes for each sex. The mean 95% kernel home range estimate was 0.2032 ±0.4 ha (n=12) for adult males and 0.1568 ±0.04 ha (n=10) for adult females. These home range areas were not significantly different (t=-0.7476, df=20, P=0.4634).

Using the range centers for all individuals at our study site, we determined that pikas do not settle randomly with respect to sex. When data from 1998 to 2001 were combined, adult males lived significantly closer to adult females than adult males (Z=4.5853, n=52, P<0.001) and adult females also lived significantly closer to adult males (Z=1.8521, n=67, P=0.032) (Fig. 3-7a). Both juvenile males and females settled significantly closer to juveniles of the opposite sex (Z=3.1727, n=88, P=0.0008) (Fig. 3-8b), but not significantly closer to adults of the opposite sex (Z=0.8692, n=94, P=0.1924).

Influence of Habitat Characteristics on Survival

In each year, different habitat variables were important in determining the survival of pikas (Table 3-4). In 1995/96, steeper slopes had lower survival, haypiles located closer to the meadow had lower survival and haypiles surrounded by more *Cassiope* had higher survival. Although these variables were important in predicting survival of pikas, the model only accounted for 30% of the variation observed. The results from CART also showed that slope could best explain the survival of pikas in 1995. Slopes >16.5° had high mortality with 81.5% (N=27) of cases being correctly classified (Fig. 3-8a).

In 1996/97, pika survival was higher in territories with: less cover of graminoids, and haypiles located further away from the talus on average. These two variables accounted for 22% of the variation in survival of pikas. The analysis from CART revealed that territories with ≤31.5% cover from graminoids had higher survival in 1996 (70.4% correctly classified, N=27) (Fig 3-8b).

Haypile locations were incomplete in 1997, therefore no habitat analysis was done for this year.

In 1998/99, survival was higher in territories with: haypiles with a SW aspect, greater spacing in between the rocks (> 5 cm diameter), and haypiles with a large outcrop rock (to store vegetation underneath). These 3 variables explained 33% of the variance. Results from CART also showed that the aspect was important and territories with the sine of radians ≤-0.451 had low survival (94.4% correctly classified, N=18) (Fig. 3-8c).

In 1999/00, survival was higher in territories with: more spacing, haypiles without outcrops, and higher percent cover of graminoids. These 3 variables explained 39% of the variance in this model. The CART results also showed spacing to be the most important variable. Pikas living in territories with ≤25.5 spaces along the transect did not survive (100% correctly classified, N=17) (Fig. 3-8d).

In 2000/01, survival was higher in territories with: higher amounts of *Cassiope*, haypiles located further away from talus (both the nearest distance and the average distance), and haypiles lacking outcrops. The four variables added into this model explained 65% of the variance. CART was unable to build the best tree that was within 1-SE using cross-validation methods, likely due to a small sample size. However, a minimum cost tree was built, and spacing was the most important variable; pikas living in territories with ≤45.5 spaces along the transect were more likely to survive (58.8% correctly classified, N=10) (Fig. 3-8e).

Discussion

Dispersal, settlement, and survival are critical factors relating to population structure and persistence. While settlement patterns of collared pikas were similar to the better known American pika, important differences were found in dispersal rates and mechanisms, as well as, differences in survival. These differences are likely associated with living in a strongly seasonal high latitude environment.

Sex ratio

The adult sex ratio of the collared pika at this site was significantly female biased, while there was no difference in the juvenile sex ratio. In the American pika the sex ratio is balanced (Tapper 1973; Smith 1981; Smith and Ivins 1983). The female biased sex ratio in our population is largely an artifact of higher proportions of females in the early years (1995-1998) and therefore it is possible to have survival not being sex biased (results from the Cox regression) and still have an overall female biased population.

Survival

Collared pikas appear to have lower survival and a shorter life span compared to the American pika. This may, in part, be due to the shorter summer season and more extreme environmental conditions in the Yukon. The average life span of pikas at our site was less than one year with the oldest known-age pika living to four years. The mean life expectancy is 1.7 years for the American pika, with pikas living up to 7 years of age (Millar and Zwickel 1972). Similar to our population, the highest age specific mortality rates in the American pika occurred between 0-1 years of age (Millar and Zwickel 1972), and at our site only 25% of juveniles survived to a reproductive age. The annual age-specific survivorship of American pika adults averages between 55% and 63% (Millar and Zwickel 1972; Smith 1978), but only 34% for adult collared pikas in the Yukon. The differences in survival between these two species could be due to the declining nature of our population resulting in lower survival rates, however, even when the population was stable, survival rates of the collared pika were still lower than those of the American pika. Collared pikas may also have lower survival rates if they are limited by food availability due to the shorter growing season.

Mortality of pikas during the summer months was very low and usually undetectable at our site, therefore most mortality occurred over-winter. Over-winter survival dramatically declined from 1998 to 2000. Similar trends in numbers were recorded for collared pikas located 40 km south-southwest in the nearby Front Ranges, Yukon (60°57'N, 138°32'W) suggesting that the observed decline in pikas in 1999 and 2000 may be more regional and likely a result of poor winter conditions, rather than predation (D. Hik, unpublished data).

Pika over-winter mortality tends to be high when there is little or no snow pack to provide insulation (Smith 1988). However, we did not find a correlation between Mt. Logan snow accumulation and winter temperature deviations with adult or juvenile survival. It is possible that shorter weather changes, which cannot be identified in annual averages, may affect pika survival. For example, data loggers at this site showed short periods of very warm temperatures (> 5° C) in December (D. Hik, unpublished data). These warm conditions likely created freeze-thaw patterns that may have inhibited foraging by pikas due to icing. As well, snow pack would have decreased during this time and subsequent cold periods may have left pikas exposed.

The relatively high 2000-2001 over-winter survival allowed for the population to slightly increase in summer 2001, however the population has not recovered to 1995/96 population numbers. The large crash in the population numbers at this site resulted in a small population size with many vacant territories and unoccupied patches. This allowed us to assess extinction and recolonization processes at this site (Chapter 4).

Several authors have reported pika populations to be relatively stable between years (Millar 1974; Smith 1978; Southwick et al, 1986; Smith et al. 1990), even given the highly variable environment in which they live. The collared pika, however, did not exhibit stable numbers at our study site, likely due to the extreme climatic conditions, especially during winter. It does not seem unusual to expect fluctuations in pika numbers, as fluctuations are a common characteristic observed in several rodent and lagomorph species, especially those in highly variable environments (Southwick et al. 1986; Yoccoz and Ims 1999).

Survival was independent of sex in both juveniles and adults. The total density of pikas on a patch did not influence survival of juveniles. Density dependent mortality in small mammals is most often related to space and social issues and the only stage that consistently shows density dependent mortality are juveniles (later stage) (Sinclair 1989). However, in the majority of the years, pikas were found at low densities and therefore, densities may not have been high enough to have an effect on survival. The presence of adults on a patch was thought to indicate high patch quality, however, juvenile survival did not appear to be influenced by this. Whether a juvenile made inter-patch dispersal movements or intra-patch dispersal movements did not influence their over-winter survival, however, it is possible there were too few samples to detect a difference. Juvenile over-winter survival was also not influenced by the timing of parturition (see Chapter 2 for more discussion on factors influencing parturition dates).

The year in which a pika was born did seem to have an influence on its lifetime survival, with pikas born in 1996 living to older ages. Juveniles born in 1996 had relatively high over-winter survival (44%) in their first year, which contributed to their longer life spans. However, it is unknown why juvenile survival was high from 1996-97, but may be related to better winter conditions. Pikas that lived on the South slope also tended to live to older ages compared to all other slopes. This may be partly explained by the southern aspect of this slope, where there is greater solar warming and higher plant productivity, which may lead to higher pika survival.

Dispersal

Early research on the American pika suggested that juvenile pikas were highly philopatric (Krear 1965; Tapper 1973; Smith and Ivins 1983) and it was only recently, using DNA analysis that researchers have shown that pikas are commonly dispersing intermediate distances, and occasionally dispersing long distances (2 km) (Peacock 1997). Previous literature further suggested that competition for resources is the main motivation for dispersal in pikas. Pikas disperse to find an available territory and avoid competing with relatives (Peacock 1997; Peacock and Smith 1997).

Dispersal at our site, however, suggests that there may be another mechanism involved. Of the dispersal events recorded at our site, all juveniles moved beyond the nearest available territory opening, ignoring one of the main assumptions of Waser's (1985) competition for resources model. As well, we observed the recolonization of a number of habitat patches, even when carrying capacity (measured as the maximum number of adult pikas that lived on a patch at one time) of other patches remained low. Peacock (1997) suggested territory availability explained both the short and long distance dispersal movements observed. However, in our population, other mechanisms such as inbreeding avoidance or habitat selection may explain the dispersal of pikas and it is possible that these hypotheses are not mutually exclusive (Greenwood 1980; Dobson 1982; Dobson and Jones 1985).

We observed low natal philopatry at this site and found a minimum of one-third to one-half of all juveniles making inter-patch movements in low-density years. This high voluntary emigration suggests that the cost of dispersal in pikas is low (Wolff 1994) and it is likely that pikas are capable of making large dispersal movements. The collared pika is also able to persist on nunataks (mountaintops) in the icefields of Kluane National Park (60°36'N, 139°25'W) located 100 km south-southwest of our study site. These small meadows (<1 ha) are surrounded by glaciers, separating the nearest population from 2-10 km (Krajick 1998; D. Hik et al., unpublished data). Therefore, it is expected that the dispersal abilities of these animals are likely greater than sometimes suggested.

In mammals, juvenile dispersal is often male-biased to reduce inbreeding depression especially among polygynous animals (Greenwood 1980; Dobson 1982). However, we did not observe any sex-biased dispersal of pikas at this site. Juvenile females and juvenile males made inter-patch movements with the same frequency. The results from the inter-patch movements are very similar to the known dispersals in terms of the number of males and females moving, as well as, the distances moved. Sex-biased dispersal may be more related to the permanence of the opposite-sex parent than resource availability (Wolff 1994). Because both adult males and females are territorial and keep these territories for life, it is not surprising that both juvenile males and females will disperse away from the natal territory to avoid breeding with the parent of the opposite sex. There was also no difference in the distance that juvenile males and female dispersed. It has been suggested that in monogamous species the dispersal distances should be similar for males and females (Wolff 1994). Although pikas may not be truly monogamous, because they establish permanent territories and have a social spacing pattern in which nearest neighbors are the opposite sex, this predicts no advantage to one sex dispersing further distances over the other.

Settlement

The inter-patch settlement patterns observed suggest that pikas may make decisions on where they settle based on the resident occupants of the patch. Dispersing between patches is thought to be risky, however, the presence of other animals on patches may yield information on the suitability of the patch and may attract conspecifics. This has been termed "conspecific attraction" (Stamps 1988). Juvenile female settlement does not appear to be random, but suggests that they may be attracted to patches where males or potential mates are occupants.

The settlement choices that females and males make appear to be different. Juvenile females always settled on patches that had the opposite sex (either adult males or juvenile males) and never settled on patches that were unoccupied or only had the same sex. This suggests that females are selecting patches based on conspecifics. Males do not appear to be as selective in the patches they settle on with respect to conspecifics, compared to females. There were a large number of recolonizations of unoccupied patches by males, suggesting that conspecific attraction is not as important. Males may settle on patches they perceive to be suitable habitat, or avoid competition for mates with other males, as they rarely settled on patches with only juvenile males as the only occupant and never settled on patches where adult males were the only occupant. The patterns of male settlement could also reflect inbreeding avoidance, in which males may be attempting to avoid mating with their sisters and thus are more likely to settle on unoccupied patches.

Nearest neighbor settlement of pikas was found to be non-random with respect to sex. Adjacent home ranges were more often occupied by the opposite sex, similar to results found for the American pika (Krear 1965; Sharp 1973; Tapper 1973; Smith and Ivins 1984; Brown et al. 1989). In the American pika, a strong sexual alternation of territories (i.e. nearest neighbor being the opposite sex) has been shown by several studies and this has been used to suggest that there are limited opportunities for access to multiple mates and thus leads to forced or facultative monogamy, as defined by Kleiman (1981; see Krear 1965; Sharp 1973; Tapper 1973; Svendsen 1979; Smith and Ivins 1983, 1984). However, Brown et al. (1989) noted that patterns of spacing should not be used to infer mating systems without supporting evidence (e.g. genetics).

At our study site, meadow occurs both at the periphery and interspersed throughout the talus patches, therefore, territories are not limited to talus edge and higher population densities may occur than if they were restricted to the edge (Brown et al. 1989). Brown et al. (1989) suggested that this spatial distribution of pikas in the talus, along with the asynchronous estrus of females, facilitates promiscuity by allowing a greater opportunity for mating with multiple individuals (Smith 1978). There has been little evidence in the past to support this, as female pikas were never observed to attract a number of males for mating (Krear 1965; Millar 1971; Sharp 1973; Tapper 1973; Svendsen 1979; Whitworth 1979). However, at our study site, males were observed to travel into the territories of several females within a short period of time (minutes) and therefore, mating may be more promiscuous than facultatively monogamous. Future genetic studies will be necessary to properly address this issue.

We determined the maximum density of pikas per hectare at our site ranged from 6.82 to 7.82, which is very similar to densities reported for a population of *O. collaris* in Alaska (6.4 – 7.2 animals per hectare, Broadbrooks 1965). However, the values reported at our site are maximum values and the average density observed from 1995-2001 was much lower. Talus dwelling pikas are thought to live at relatively low densities (<10 individuals/ha) compared to the burrowing pikas in Asia and the densities of talus dwelling pikas generally do not vary greatly with time (Southwick et al. 1986; Smith 1988; Angermann et al. 1990). In terms of spacing, our results prior to the population crash are very similar to those reported by Broadbrooks (1964) (30-70 m between neighbors), while post population crash, densities were lower.

Home range sizes observed for collared pikas at our site were similar to those reported for the American pika (Smith and Ivins 1984). However, home range size for collared pikas in Alaska, as reported by Broadbrooks (1965), was much smaller (0.032 ha). The smaller size is likely due to the methods used, which included making a number of short observations. Broadbrooks (1965) noted that because animals at his study site were not marked and could only be identified in association with a haypile, his estimates of home range sizes might be underestimates.

The home range size and spacing of pikas is thought to be related to having adequate food resources to survive over-winter (Millar 1971; Tapper 1973; Smith 1980; Whitworth and Southwick 1984; Smith and Ivins 1984). Male home ranges were slightly, but not significantly, larger than females. Although, we had too few samples to compare home range size within a year, it is expected the home range size will change with season, expanding during the breeding season and shrinking during the fall when pikas are spending the majority of their time haying and are more territorial, as observed in the American pika (Lutton 1975; Conner 1983; Smith and Ivins 1984; Huntly et al. 1986).

Complex relationships between habitat and survival?

The results from our habitat models indicate that among years, different habitat characteristics are important in predicting survival. This pattern suggests that this is a very dynamic system and there is little predictability based on the characteristics we measured. It is also possible that we were not able to correctly measure the variables that are important to the survival of pikas, or perhaps it is not even possible to measure these. Because the results of the GLMs and CART were similar, interannual variability is supported.

The higher survival with increases in amounts of *Cassiope* (1995 and 2000) was an unusual result, as preference studies indicate that *Cassiope* is not a preferred species in the pika diet (Andruchow 2000). However, other mammal species at this site (hoary marmot and arctic ground squirrel) also do not prefer *Cassiope* and may actively avoid these areas. Thus, areas with less *Cassiope* may less inter-specific competition with the pikas and may lead to higher pika survival.

In both 1998 and 1999, talus spacing was positively correlated with survival. This may be a result of two factors. First, more spaces within the talus allow for more escape routes for pikas, while moving in the talus around their haypile. Second, more spaces within the talus also indicate a greater depth to the talus, which could potentially allow for higher over-winter survival because pikas would be able to move deeper providing more buffer against the extreme winter temperatures (Bunnel and Johnson

1974). Slope was only found to be an important factor in 1995 when steeper slopes were found to have lower survival. This may be a result of steeper slopes having less stable talus or reduced snow cover.

Survival was higher as distance from the haypile to the meadow increased. As the average distance to meadow increases, so does the size of the talus patch. This suggests that pikas have higher survival in larger patches, even though they may have to travel further to obtain food. Larger talus patches would also have larger perimeters and therefore, more food for the pikas.

In 1998, 1999, and 2000, patches without outcrops had higher survival. Initially, outcrops were considered to provide a large area for pikas to store food under and they were thought to provide lookouts. However, it is possible that these outcrops allow stored vegetation to be exposed and more accessible to other pikas, as well as other species (e.g. ground squirrels and hoary marmots), which may not otherwise have access to the stored vegetation. Overall, the habitat characteristics that were measured varied in their importance on pika survival in different years.

The survival of pikas at this site was more related to abiotic habitat factors, such as aspect and perhaps weather, than biotic factors, such as density. Inter-patch movement at this site was high, suggesting dispersal may not be related to competition for resources as hypothesized for the American pika. The non-random settlement patterns of collared pikas were similar to the American pika, and reflects their social structure and mating system.

References

Andruchow, J. 2000. Foraging preferences of collared pikas in alpine meadows in the southwest Yukon. B.Sc. thesis, University of Alberta, Edmonton, Canada.

Angermann, R., J. E. C. Flux, J. A. Chapman, and A. T. Smith. 1990. Lagomorph classification. In: Chapman and Flux (Eds), Rabbits, Hares and Pikas: Status Survey and Conservation Action Plan. International Union for Conservation of Nature and Natural Resources. Oxford, UK.

Bowman, J., J. A. G. Jaeger, and L. Fahrig. 2002. Dispersal distance of mammals is proportional to home range size. Ecology 83:2049-2055.

Breiman, L., J. H. Friedman, R. A. Olshen, and C. G. Stone. 1984. Classification and Regression Trees. Wadsworth International Group, Belmont, California, USA.

Broadbrooks, H. E. 1965. Ecology and distribution of the pikas of Washington and Alaska. The American Midland Naturalist. 73:299-335.

Brown, R. N., C. H. Southwick, and S. C. Golian. 1989. Male-female spacing, territorial replacement, and the mating system of pikas (*Ochotona princeps*). Journal of Mammalogy 70:622-627.

Bunnel, S. D. and D. R. Johnson. 1974. Physical factors affecting pika density and dispersal Journal of Mammalogy 55:866-869.

Conner, D. A. 1983. Seasonal changes in activity patterns and the adaptive value of haying in pikas (*Ochotona princeps*). Canadian Journal of Zoology 61:411-416.

De'ath, G. and K. E. Fabricius. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81: 3178-3192.

Dobson, F. S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. Animal Behavior 30:1183-1192.

Dobson, F. S. and W. T. Jones. 1985. Multiple causes of dispersal. American Naturalist 126:855-858.

Gaines, M. S. and L. R. Jr. McClenaghan. 1980. Dispersal in small mammals. Annual Review of Ecological Systematics 11:163-196.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behavior 28:1140-1162.

Hik D. S., C. McColl, and R. Boonstra. 2001. Why are Arctic ground squirrels more stressed in the boreal forest than in alpine meadows? EcoScience 8:275-288.

Hock, R. J. and V. Cottini. 1966. Mammals of the little Susitna Valley, Alaska. American Midland Naturalist 76:325-339.

Holmes, W. G. 1991. Predator risk affects foraging behavior of pikas: observational and experimental evidence. Animal Behavior 42:111-119.

Horn, H. 1984. Some theories about dispersal. In: Swingland, I. R. and P. J. Greenwood (Eds), The Ecology of Animal Movement. Oxford University Press, Oxford.

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 67:139-148.

Kenward, R. E. and K. H. Hodder. 1995. Ranges V. An analysis system for biological location data. Institute of Terrestrial Ecology, Furzebrook Research Station, Wareham, UK.

Kleiman, D. G. 1981. Correlations among life history characteristics of mammalian species exhibiting two extreme forms of monogamy. In: Alexander, R. D. and Tinkle, D. W. (Eds), Natural Selection and social behavior. Chiron Press, New York.

Krajick, K. 1998. Nunataks. National Geographic194:60-71.

Krear, H. R. 1965. An ecological and ethological study of the pika (*Ochotona princeps saxitilis* Bangs) in the Front Range of Colorado. Ph.D. thesis. University of Colorado, Boulder. 329p.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237-240.

Lutton, L. M. 1975. Notes on territorial behavior and response to predators of the pika, *Ochotona princeps*. Journal of Mammalogy 56:231-234.

MacDonald, S. O., and C. Jones. 1987. *Ochotona collaris*. Mammalian Species 281:1-4.

MathSoft. 1997. S-PLUS 4 Guide to Statistics. MathSoft, Inc. Seattle.

McCullagh, P. and J. A. Nelder. 1989. Generalized Linear Models. 2nd ed. Monographs on Statistics and Applied Probability 37. Chapman and Hall, London.

McIntire, E. J. B. 1999. The effects of collared pika grazing on alpine tundra vegetation in southwestern Yukon, Canada. M. Sc. Thesis, University of Toronto.

McIntire, E. J. B. and D. S. Hik. 2002. Grazing history versus current grazing: leaf demography and compensatory growth of three alpine plants in response to a native herbivore (*Ochotona collaris*). Journal of Ecology 90:348-359.

Millar, J. S. 1971. Breeding of the pikas in relationship to environment. Ph. D. thesis, University of Alberta.

Millar, J. S. 1972. Timing and breeding of pikas in southwestern Alberta. Canadian Journal of Zoology 50:665-669.

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

Millar, J. S. and F. Zwickel. 1972. Determination of age, structure, and mortality of the pikas, *Ochotona princeps* (Richardson). Canadian Journal of Zoology 50:229-232.

Peacock, M. M. 1997. Determining natal dispersal patterns in a population of North American pikas (*Ochotona princeps*) using direct mark-resight and indirect genetic methods. Behavioral Ecology 8:340-350.

Peacock, M. M. and A. T. Smith. 1997. The effect of habitat fragmentation on dispersal patterns, mating behavior, and genetic variation in a pika (*Ochotona princeps*) metapopulation. Oecologia 112:524-533.

Price, L. W. 1971. Vegetation, microtopography, and depth of active layer on different exposures in subarctic tundra. Ecology 52:638-647

Rausch, R. 1962. Notes on the collared pikas, *Ochotona collaris* (Nelson), in Alaska. Murrelet 42:22-24.

Sharp, P. L. 1973. Behavior of the pika (*Ochotona princeps*) in the Kananaskis region of Alberta. M. Sc. thesis, University of Alberta, Edmonton.

Sinclair, A. R. E. 1989. Population regulation in animals. In: Cherrett, J. M. (Ed), Ecological Concepts, 29th Symposium of the British Ecological Society. Blackwell Scientific Publications, Oxford.

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

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

Smith, A. T. 1980. Temporal changes in insular populations of the pika (*Ochotona princeps*). Ecology 61:8-13.

Smith, A. T. 1981. Territoriality and social behavior of *Ochotona princeps*. In: Myers, K. and MacInnes, C. D. (Eds), Proceedings of the World Lagomorph Conference. Guelph Univ. Press, Guelph, Ontario. Pp. 310-323.

Smith, A. T. 1987. Population structure of pikas: dispersal versus philopatry. In: Chepko-Sade, B. D. and Z. T. Halpin (Eds), Mammalian Dispersal Patterns: the effects of social structure on population genetics.. University of Chicago Press.

Smith, A. T. 1988. Patterns of pika (Genus *Ochotona*) life history variation. In: Boyce, M.S. (Ed), Evolution of Life Histories: Theory and Patterns from Mammals. Yale University Press,

Smith, A. T., N. A. Formozov, R. S. Hoffmann, Z. Changlin, M. A. Erbajeva. 1990. The pikas. In: Chapman, J. A. and J. E. C. Flux (Eds), Rabbits, Hares and Pikas. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.

Smith, A. T. and M. Gilpin. 1997. Spatially correlated dynamics in a pika metapopulation. In : Hanksi, I. A. and W. E. Gilpin (Eds), Metapopulation Biology: Ecology, Genetics and Evolution. Academic Press Inc., San Diego.

Smith, A. T. and B. L. Ivins. 1983. Colonization in a pika population: dispersal vs. philopatry. Behavioral Ecology and Sociobiology 13:37-47.

Smith, A. T. and B. L. Ivins. 1983. Reproductive tactics of pikas: why have two litters? Canadian Journal of Zoology 61:1551-1559.

Smith, A. T. and B. L. Ivins. 1984. Spatial relationships and social organization in adult pikas: a facultatively monogamous mammal. Z. Tierpsychol. 66:289-308.

Southwick, C. H., S. C. Golian, M. R. Whitworth, J. C. Halfpenny, and R. Brown. 1986. Population density and fluctuations of pikas (*Ochotona princeps*) in Colorado. Journal of Mammalogy 67:149-153.

Stamps, J. 1988. Conspecific attraction and aggregation in territorial species. American Naturalist 131:329-347.

Steinberg, D. and P. Colla. 1997. CART - Classification and Regression Trees. Salford Systems, San Diego, California, USA.

Stenseth, N. 1984. Causes and consequences of dispersal in small mammals. In: Swingland, I. R. and P. J. Greenwood (Eds), The Ecology of Animal Movement. Oxford University Press, Oxford.

Svendsen, G. E. 1979. Territoriality and behavior in a population of pikas (*Ochotona princeps*). Journal of Mammalogy 60:324-330.

Tait, M. 2002. Effects of climate change and herbivory on photosynthesis and growth of alpine plants in the Yukon. MSc thesis, University of Alberta, Edmonton, Alberta.

Tapper, S. C. 1973. The spatial organization of pikas (*Ochotona*) and its effect on population recruitment. Ph. D. thesis, University of Alberta, Edmonton, 154 pp.

Vayssières, M. P., R. E. Plant, and B. H. Allen-Diaz. Classification trees: An alternative non-parametric approach for predicting species distributions. Journal of Vegetation Science 11:679-694.

Waser, P. M. 1985. Does competition drive dispersal? Ecology 66:1170-1175.

Whitworth, M. R. 1979. Population ecology of the pikas (*Ochotona princeps*) in relation to density and climate. M.Sc. thesis, The Johns Hopkins University, Baltimore.

Whitworth, M. R. and C. H. Southwick. 1984. Sex differences in the ontogeny of social behavior in pikas: possible relationships to dispersal and territoriality. Behavioral Ecology and Sociobiology 15:175-182.

Wolff, J. O. 1994. More on juvenile dispersal in mammals. Oikos 71:349-352.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164-168.

Yoccoz, N. G. and R. A. Ims. 1999. Demography of small mammals in cold regions: the importance of environmental variability. Ecological Bulletins 47: 137-144.

Table 3-1. Number of collared pikas captured in the Ruby Ranges, Yukon 1995-2001.

Year		**Total**		**Adult**		**Juvenile**		**Sex**
	n	**females**	**males**	**females**	**males**	**females**	**males**	**unknown**
1995	69	37	25	25	15	12	10	7
1996	65	34	23	23	13	11	10	8
1997	45	20	21	14	15	6	6	4
1998	77	41	29	31	19	10	10	7
1999	75	35	35	18	16	17	19	5
2000	35	15	19	11	12	4	7	1
2001	54	21	27	7	6	14	21	6
Total	**420**	**203**	**179**	**129**	**96**	**74**	**83**	**38**

Table 3-2. Influence of the year of birth, slope aspect, and sex on survival of pikas determined by Cox regression. Significant effects are indicated in bold.

Variable	Coefficient (SE)	*df*	Wald	*P*
Overall Model		**9**	**23.3**	**0.005**
Year born				
1996 vs. 1995	**-0.801 (0.30)**	**1**	**-2.687**	**0.007**
1997 vs. 1995	-0.476 (0.34)	1	-1.404	0.160
1998 vs. 1995	0.090 (0.32)	1	0.285	0.780
1999 vs. 1995	0.487 (0.29)	1	1.706	0.088
2000 vs. 1995	-0.232 (0.48)	1	-0.488	0.630
Aspect				
South vs. West	**-0.800 (0.45)**	**1**	**-2.935**	**0.003**
East vs. West	-0.115 (0.89)	1	-0.554	0.580
Sex				
Female vs. Male	-0.189 (0.83)	1	-0.964	0.330
Unknown vs. Male	0.182 (1.20)	1	0.629	0.530

Table 3-3. Model parameters tested for the over-winter survival of juvenile pikas. Terms were fit using step-wise addition of terms to a null model, based on the *Cp* statistic at each step. The *P* value is given for the change in deviance of the model by the inclusion of the term tested against a X^2 distribution.

Variable	df	Deviance (residual =131.44)	P for X^2-test on deviance
Presence of adults on patch	1	0.0482	0.8263
Parturition date	1	1.0607	0.3031
Sex (Male/Female/unknown)	2	3.2441	0.1975
Days different from average survival date	1	2.2288	0.1355
Total patch density`	1	0.1788	0.6724
Dispersal (inter/intra/unknown)	2	2.0974	0.3504

Table 3-4. Final models of the habitat variables important in determining pika survival for each year. Significant terms were added step-wise base on the *Cp* statistic at each step. The change in deviance of the model by the inclusion of the term is tested against a X^2 distribution

Year	Variables included in final model	Coefficient (SE)	Residual df	Change in deviance	P for X^2 - test on deviance
1995	null	1.496 (1.34)	41	54.75	-
	Slope	-0.220 (0.08)	40	47.21	0.0060
	Nearest dist. to meadow	0.809 (0.45)	39	41.20	0.0128
	% cover *Cassiope*	0.050 (0.03)	38	38.3	0.100
1996	Null	0.506 (1.06)	50	70.52	-
	% cover graminoids	-0.083 (0.03)	49	62.19	0.0039
	Avg. dist. to meadow	0.205 (0.09)	48	55.30	0.0087
1998	Null	-1.515 (1.10)	53	73.67	-
	Aspect	1.815 (0.66)	52	58.48	0.0000
	Spacing	0.052 (0.04)	51	55.87	0.1062
	Outcrop	-1.348 (0.63)	50	49.40	0.0110
1999	Null	-8.101 (2.93)	39	42.65	-
	Spacing	0.153 (0.07)	38	37.44	0.0225
	Outcrop	-1.452 (0.62)	37	30.12	0.0068
	% cover graminoids	0.054 (0.03)	36	26.13	0.0456
2000	Null	-16.91 (9.57)	21	30.32	-
	% cover *Cassiope*	0.722 (0.40)	20	25.04	0.0216
	Nearest dist. to meadow	2.794 (1.53)	19	20.72	0.0376
	Outcrop	-8.626 (5.05)	18	16.51	0.0402
	Avg dist to meadow	0.929 (0.57)	17	10.55	0.0146

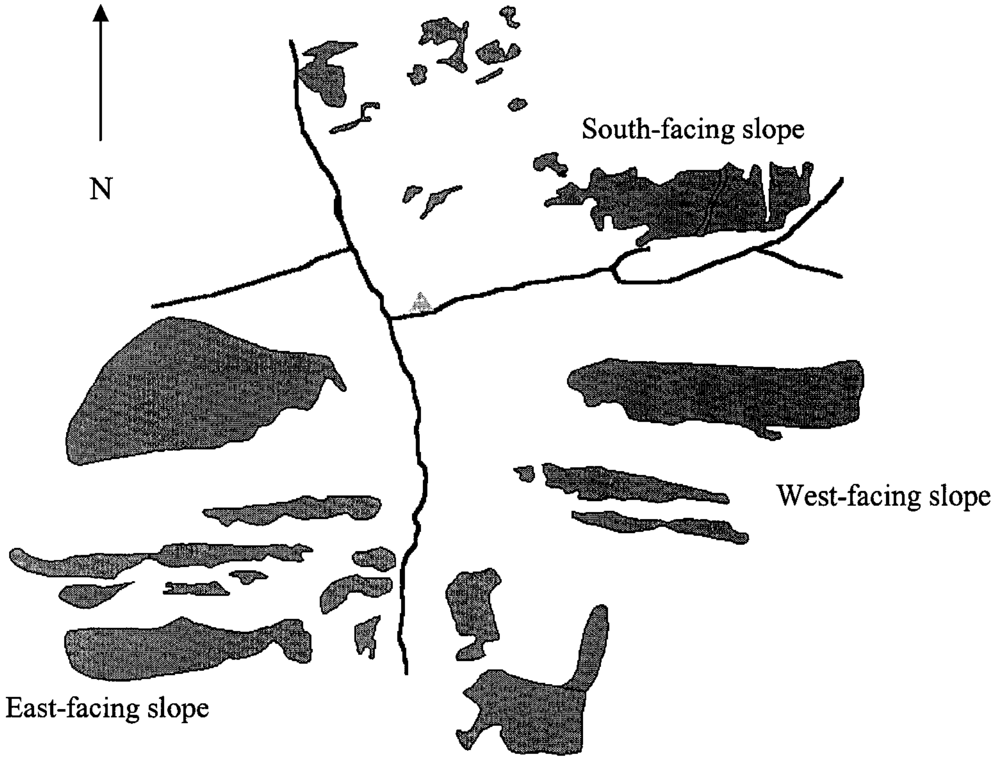


Figure 3-1. Talus patches at the Ruby Range, Yukon study site. Shaded areas represent talus surrounded by meadow (white), lines are creeks. ▲ represents the camp site.

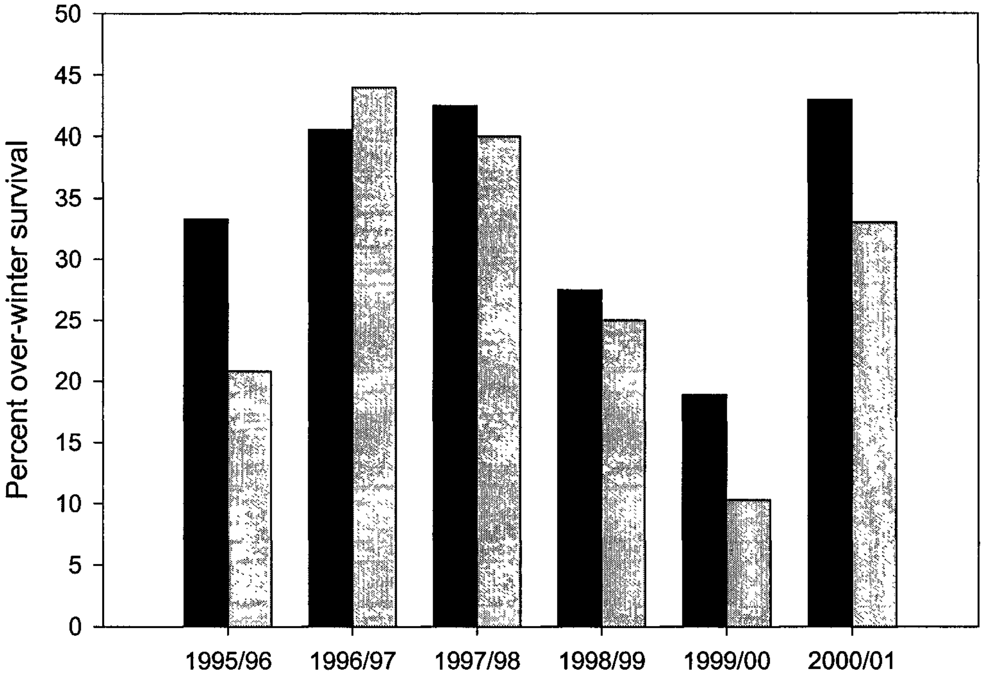


Figure 3-2. The mean over-winter survival of adult (black) and juvenile (grey) pikas on the East, West, and South slopes combined.

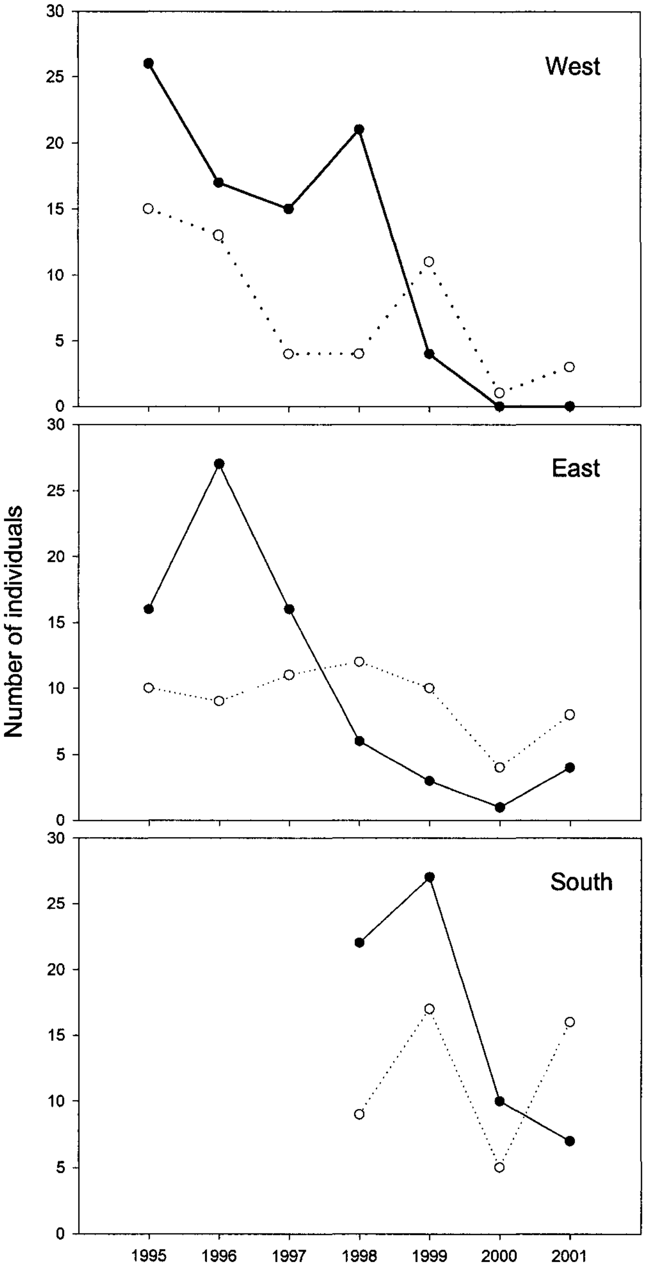


Figure 3-3. Number of adults (solid line) and juveniles (dotted line) censused on West, East and South slopes in the Ruby Ranges, Yukon.

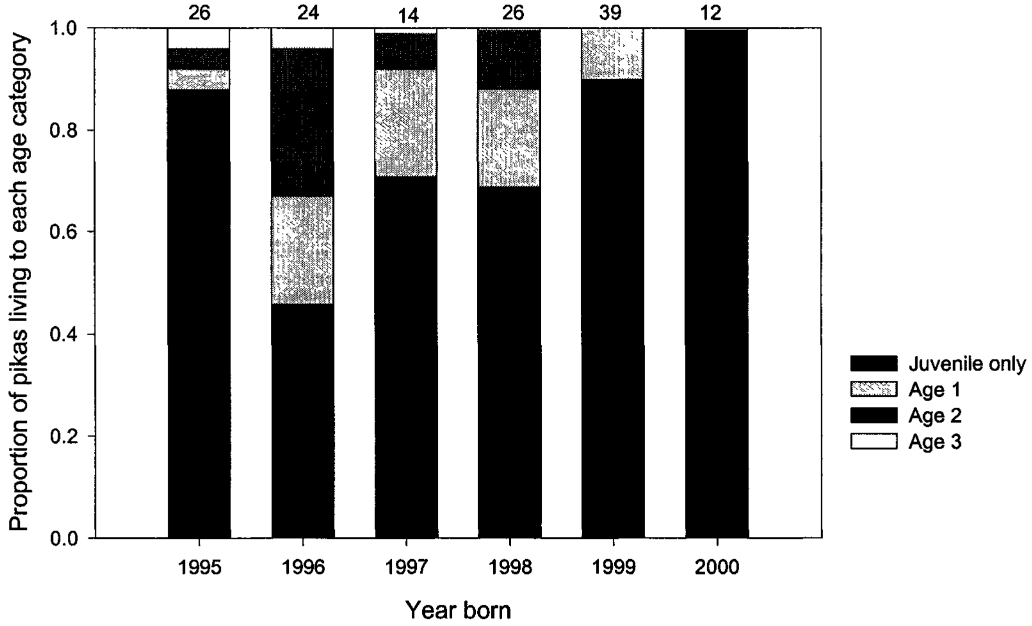


Figure 3-4. The proportion of pikas with known birth dates, surviving to each age class. Sample sizes are indicated above the bars.

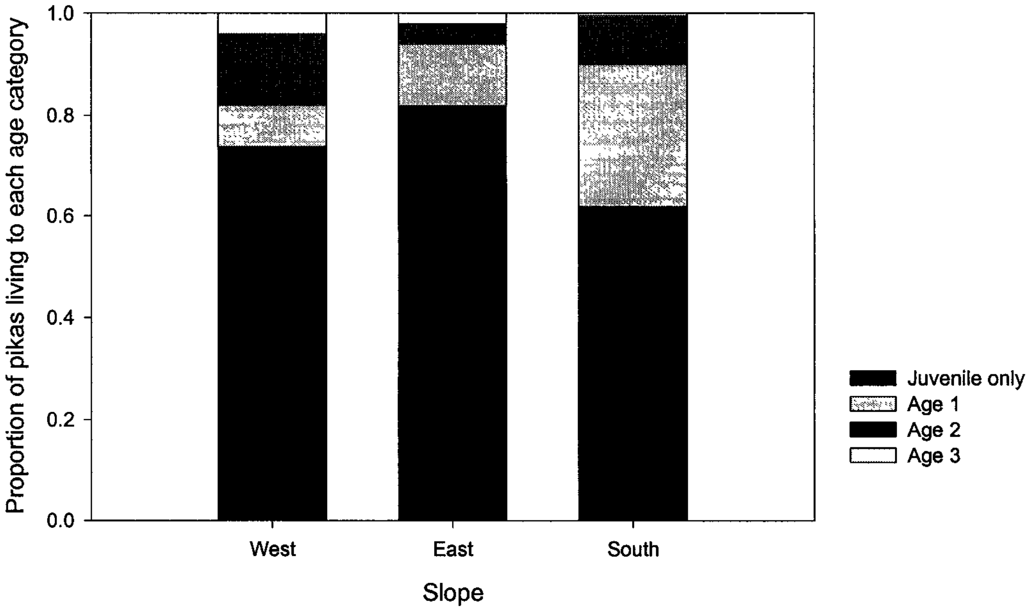


Figure 3-5. The proportion of pikas (with known birth dates) living in different parts of the study area surviving to each age category.

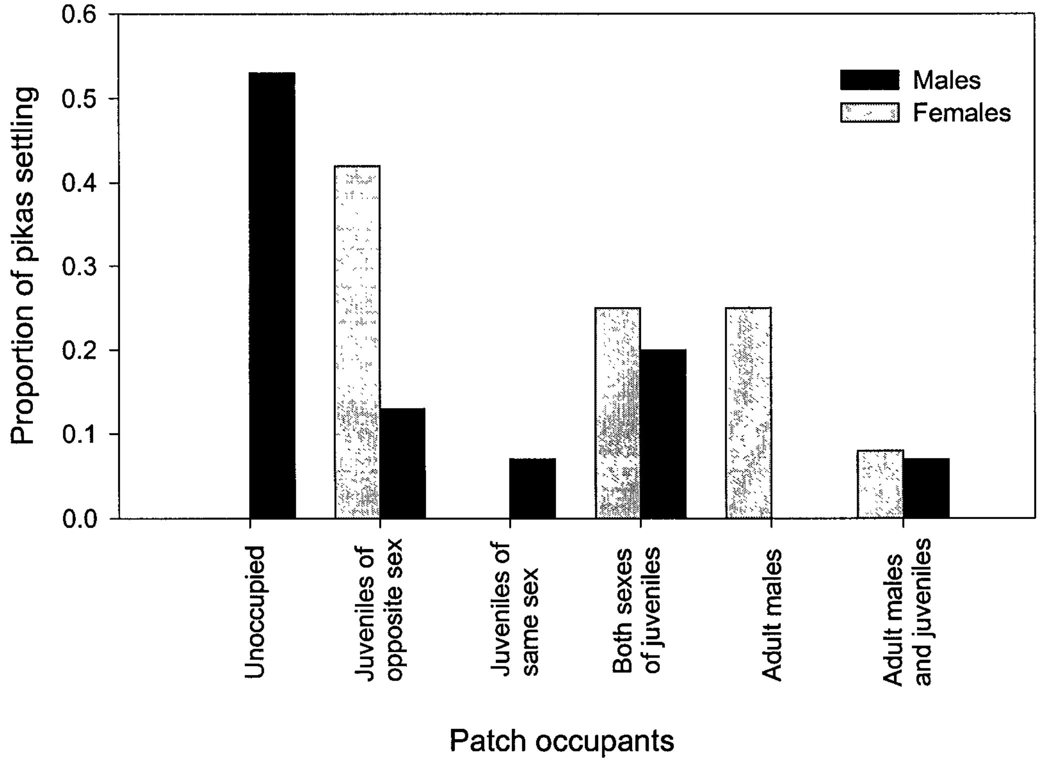


Figure 3-6. The proportion of pikas settling in relationship to the occupants of the patch, following dispersal.

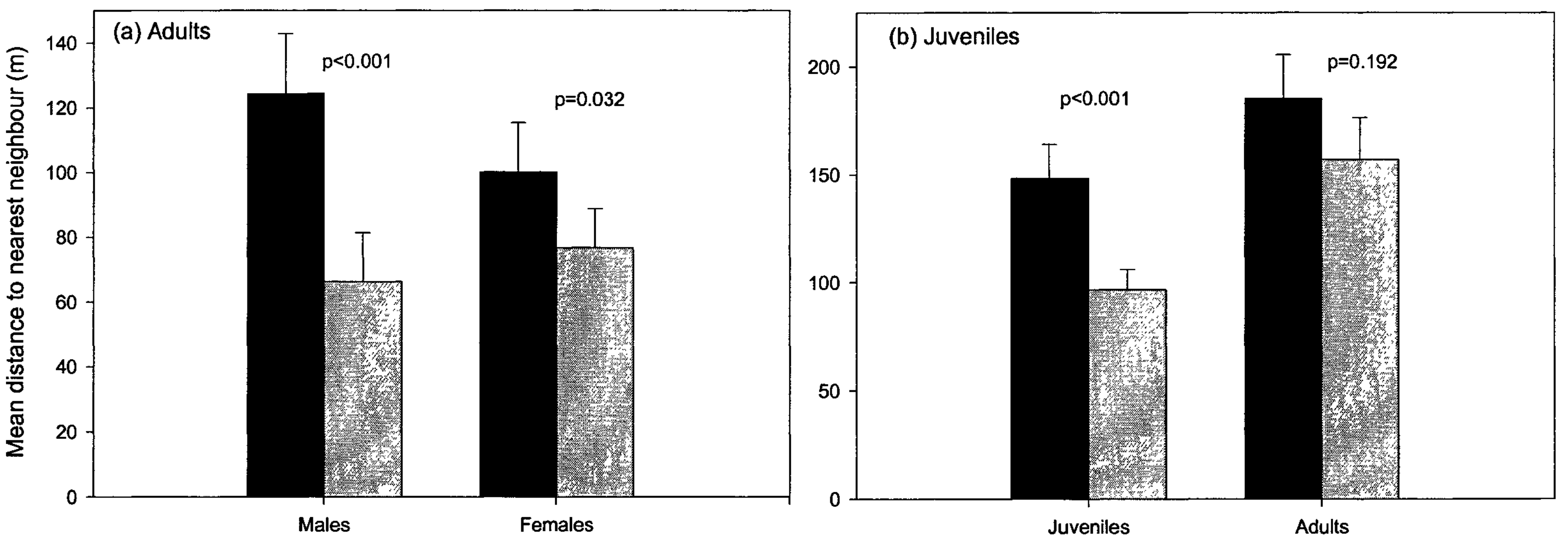


Figure 3-7. The mean nearest neighbor distance to the same sex (black) and opposite sex (grey) for (a) adults, and (b) juveniles.

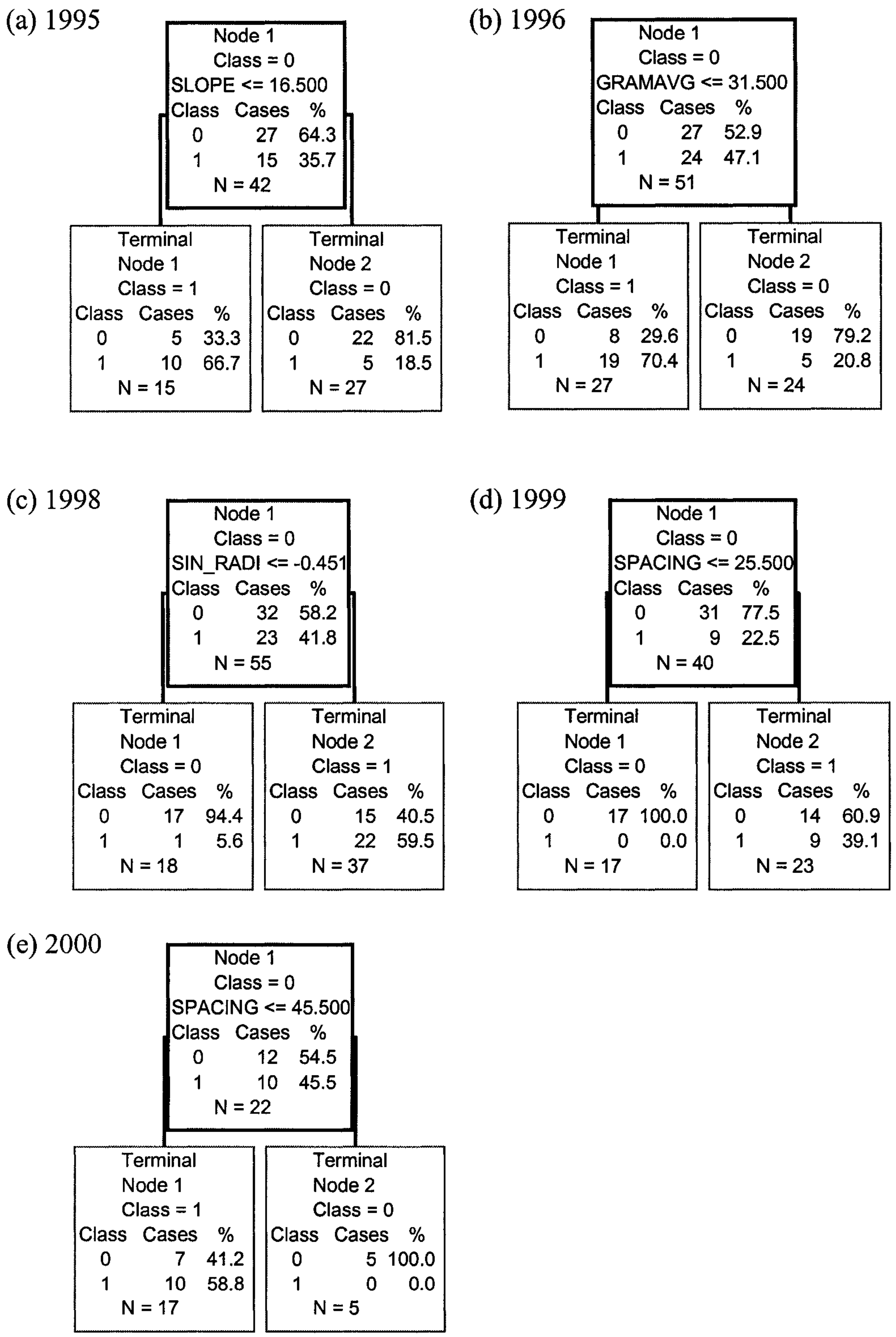


Figure 3-8. Results from CART - classification trees showing the habitat factors important in pika survival. The branching (parent) nodes feature the split variable, its split value and the number of samples to be split. The child nodes indicate the class (0- did not survive, 1-survived), the number of cases (pikas) in each class and the percent correctly classified. Nodes branching to the left are values less than or equal to the splitting value, and the branches on the right are values greater than the splitting value.

Chapter 4: Influence of habitat quality, patch size, and connectivity on colonization and extinction dynamics of collared pikas (*Ochotona collaris*)

Abstract

The effects of habitat quality, patch size, and connectivity between patches on patterns of local extinction and colonization of collared pikas were studied over seven years in alpine meadows in the southwest Yukon. While adult population size was found to independently have a significant influence on patch extinction, its influence was minimal when other variables were included in generalized linear models. Instead, an index of habitat quality and the connectivity of a patch were found to be the best predictors of pika extinction. Similarly, patch connectivity only partly explained the recolonization of talus patches by pikas. Other patch characteristics, including aspect, amount of vegetation within the patch, and an index of habitat quality based on survival of pikas also had a significance influence on recolonization. These results suggest that the influence of patch quality on local extinction and recolonization need to be more fully incorporated into metapopulation models.

Introduction

High rates of habitat loss and fragmentation as a result of habitat destruction, climate change, and other types of anthropogenic disturbance have potentially serious consequences for maintenance of biodiversity (e.g. Sinclair et al. 1995; Moilanen and Cabeza 2002). Fragmented habitat patches are often separated by large expanses of relatively unsuitable habitat where individuals of some species cannot survive, and once restricted to small and isolated patches, some species will rapidly disappear (Turner 1996). Nevertheless, many species naturally persist in a network of isolated populations or a "metapopulation", in which smaller subpopulations are connected by dispersal or the movement of individuals (Levins 1969; Hansson 1991, Hanski 1999).

Metapopulation models examining the effects of patch size and isolation on rates of extinction and recolonization have been well studied (e.g. Hanski 1994; Hanski et al. 1996; Moilanen and Hanski 1998). Larger population sizes, often approximated by patch area, are believed to be less prone to extinction resulting from demographic stochasticity (MacArthur and Wilson 1967), while the colonization probability of an empty patch is largely determined by its isolation to other surrounding populations. These models have tended to assume that patch size and isolation are sufficient for predicting extinction and colonization of local populations over time.

A few studies have begun to incorporate measures of habitat quality into metapopulation models (e.g. Thomas et al. 2001; Fleishman et al. 2002), but in at least one case (Moilanen and Hanski 1998), habitat quality was not found to improve the predictive ability of the models. Nevertheless, habitat quality is likely an important determinant of persistence for some populations (Harrison 1991; Sjögren 1991; Verboom et al. 1991; Klok and DeRoos 1998), and Roslin (2002) has suggested that habitat quality is the missing third parameter in metapopulation dynamics. However, there are still too few studies to fully evaluate the relative importance of habitat quality on metapopulation dynamics.

Previous work suggests that talus-dwelling pikas (Lagomorpha: Ochotonidae) represent a "classical" metapopulation structure (Smith 1980, 1987; Smith and Ivins 1983; Hanski and Gilpin 1991; Gilpin and Smith 1997; Peacock and Smith 1997; Moilanen et al. 1998), however these dynamics have only been adequately quantified in one population of the American pika (*Ochotona princeps)* (Moilanen et al. 1998). The metapopulation dynamics of pikas are generally tractable because, (1) they are territorial and live in spatially distinct or naturally fragmented landscapes (talus or boulderfields separated by meadows) (Smith 1974); (2) dispersal rates are low and individuals that disperse tend to move short distances, suggesting that the spatial configuration (or isolation) of the habitat patches will influence the dynamics of the populations (Moilanen et al. 1998); and (3) the overall population size is thought to be relatively stable (Southwick et al. 1986), and even though subpopulations may experience extinctions and colonizations, these dynamics are largely asynchronous, which appears to prevent extinction of all subpopulations simultaneously (Moilanen et al. 1998).

Our primary objectives were (1) to test the assumption of general metapopulation models that patch size is largely responsible for predicting patch extinction, and isolation is the best predictor of colonization events, and (2) to explicitly examine the relative importance of patch size, isolation, connectivity, and a few attributes of habitat quality on patch occupancy, local extinction, and recolonization rates in a population of collared pikas (*Ochotona collaris*) in the southwest Yukon over seven years (1995-2001).

Methods

Collared pikas are generalist alpine herbivores endemic to the mountains of central and southeastern Alaska, the Yukon, and northwestern British Columbia (MacDonald and Jones 1987). They are territorial animals that live in a naturally patchy landscape consisting of isolated talus patches separated by expanses of alpine meadows, which is homogenous. Our study site was located in the Ruby Ranges, Yukon (61°12'N, 138°16'W; 1700-2100 m), and included 27 discreet talus patches ranging in size from 0.07 ha to 15.7 ha and separated by meadow ranging in distance of 15 m to 1140 m within a 4 km^2 study area (Fig. 4-1 and Table 4-1). A 50 m x 50 m grid system covering the study site allowed us to map the talus patches. The size and isolation of the patches were calculated using ArcView (Environmental Systems Research Institute, Inc. 1999).

Pikas were live-trapped in summer 1995 to 2001 using Tomahawk traps baited with native vegetation. Animals trapped for the first time were marked with numbered metal ear tags and a unique combination of colored wires to allow for subsequent observation and identification of individuals without handling. The age and sex of each individual was also determined (see Chapter 2). Since pikas are diurnal, vocal, and build large distinctive haypiles, we were able to determine the number and location of all pikas in the study area with confidence.

Each summer talus patches were surveyed to determine the occupancy (presence or absence) of pikas on a patch. A patch was considered to be recolonized if pikas were absent the previous summer and present the current summer. Clinchy (2002) suggested that because juveniles are the main dispersers and they tend to have lower survival than adults, that there would be a higher probability of extinction following recolonization events. To avoid this problem, we defined a patch as becoming extinct if adult pikas were present in the previous summer, but absent in the subsequent summer. Because adults are philopatric (*O. princeps* - Smith 1974; O. *collaris* - this study; see Chapter 3), we assumed that the absence of adult pikas from previously occupied patches indicated death rather than dispersal.

Several of the patches in the study area were only surveyed in the more recent years (1998-2001) and therefore population sizes and connectivity to these patches was not included in the early surveys (1995-1998). It is possible that this may have underestimated the importance of connectivity with respect to extinction, however, it likely will not affect the importance of connectivity on recolonization, as most patches were recolonized in the more recent years. Three common parameterization errors discussed by Moilanen (2002: inaccurate measurement of patch area, unknown patches, inaccurate patch occupancy) were not applicable to our study. Pikas are present throughout the Ruby Ranges, and although we were unable to assess the influence of long distance dispersal onto our study site (i.e. edge effects) our core area (Fig 4-1) was relatively isolated from other large talus patches occupied by pikas (>400m).

A patch was defined as the area with a population of pikas in which most of behavioral interactions occur within the patch rather than among patches (Harrison 1991).

We were able to define populations, and thus patches, using mark-recapture studies. It is possible that pikas may have made brief movements to these other patches for mating, however, pika movements away from the talus are inhibited due to the threat of predation (Lutton 1975; Huntly et al. 1986, Ivins and Smith 1983; Holmes 1991). Pikas will rarely move greater than 6 m from the talus edge to forage, even though forage availability might improve further out (Huntly 1987, Roach et al. 2001, McIntire and Hik 2002), suggesting that movements between talus patches separated by expanses of meadow are rare. The smallest distance between our patches was 15 m and more often this distance was much larger.

In metapopulation models, patch size and population size are assumed to be correlated and therefore patch size is often used as a surrogate for population size because it is easier to measure. At our study site, we were able to determine both the population size and the patch size. We used population size in determining the probability of extinction, and patch size when determining the probability of recolonization. Patch size was measured as both the total area (hectares) and the perimeter of a talus patch (meters). Previous work on pikas has used perimeter as an indication of habitat because pikas tend to live and forage at the patch edge (Smith 1974). We correlated patch area and perimeter with population size to determine which was better at describing the relationship between patch size and population size.

Connectivity was measured two ways. First, because juveniles are the only dispersers in this population, we measured the distance from the patch edge to a source of potential colonists and refer to this as isolation or the nearest neighbor method. Therefore, isolation was the minimum distance to a talus patch with an adult female whose offspring could be colonists. Secondly, we used a measure of connectivity described by Hanski (1994), which takes into account distances to all potential source populations and their population size. This connectivity measure is determined based on the movement ability of individuals in a spatially structured landscape (Moilanen and Hanski 2001):

$$S_i = \sum_{j \neq i} \exp(-\alpha d_{ij}) N_j$$

where S_i is a measure of connectivity for patch "i" to other potential source populations "j", α scales the effect of distance to migration ($1/\alpha$ is the average migration distance), d_{ij} is the distance from patch i to j, and N_j is the population size of the potential source population. This second measure of connectivity is referred to as the IFM measure because it was originally used in the Incidence Function Model (IFM; Hanski 1994). The IFM measure has been shown to be a better measure for estimating connectivity in fragmented landscapes compared to the nearest neighbor method of isolation, as it takes into consideration the movement abilities of the animals, as well as, the distance to and the sizes of the source populations (Moilanen and Nieminen 2002).

We initially tested the significance of size (perimeter) and isolation (NN) and connectivity (IFM) on the patch dynamics in our study site. We used univariate logistic regression to model the probability of occupancy, recolonization and extinction using these measures. We then used generalized linear models (GLM, McCullagh and Nelder 1989) with binomial errors (Splus - Mathsoft Inc., 1999) to model extinction and recolonization of talus patches by pikas incorporating both size and connectivity measures, as well as other patch characteristics. Terms were added in a forward step-wise sequence starting with a null model (intercept only) and using the Cp statistic as the criteria for addition of terms, until no additional variables improved model fit significantly. Additional non-linear effects were tested for by fitting splines to the variables using generalized additive models (GAM: Hastie and Tibshirani 1990). These additional non-linear effects did not, however, improve model fit significantly, therefore the results from the GLM were used. Whether a patch went extinct and whether it was recolonized was modeled as a function of (1) patch size (population size for extinction and perimeter for recolonization), (2) connectivity - using the IFM measure of S_i, (3) aspect - measured as the sine of radians, (4) amount of meadow within the talus, (5) year (1995-2000), and (6) average survival (habitat quality); all variables are described in more detail below.

We attempted to determine the quality of each patch by correlating a number of measured habitat variables with survival, however, different habitat characteristics were important in different years and we were unable to develop a set of characteristics that could be used to predict quality for all the years (see Chapter 3). While it is possible that we were not measuring the correct habitat characteristics, there is likely real variation in the resources that are important for survival from one year to the next. Consequently, we determined the fate of all individuals and used average survival values over all years as an index of habitat quality for a patch. This provided an indication of patch quality, since we assumed that patches with higher survival rates indicated better quality. While it is possible that this measure is circular when used to predict extinction, it was considered to be the best option because of the variability in individual habitat characteristics.

We also used two other potential measures of habitat quality: talus aspect and the amount of meadow within a patch. The aspect of the patch was measured in degrees and then converted to a sine wave by taking the sine of the radians to linearize aspect. Observations suggest that SE facing slopes have higher pika survival due to the increased solar exposure and plant productivity and therefore was set equal to 1. Patches with a NW aspect were considered least productive and were set to –1; all other aspects fell between 1 and –1. We also examined the proportion of meadow within the patch that would provide foraging opportunities. We estimated the percent of meadow located within a talus patch based on photos taken of each patch.

The above variables were used to predict patch occupancy, recolonization and extinction. None of these variables were correlated with each other. All patches that were measured in the study site had indications of previous pika use (old haypiles or pellets), however, we only used patches in the analysis if adults had lived there during our study. This allowed us to determine average survival of pikas in the patch.

Results

Adult population size and total population size were more correlated with perimeter (r^2=0.33, P<0.001; r^2=0.38, P<0.001 respectively), than to patch area (ha) (r^2=0.06, P=0.004; r^2=0.071, P<0.001 respectively). Therefore, perimeter was used as our size measure for recolonization and occupancy analyses. There were a total of 18 colonization events and 15 extinction events from 1995-2001 (Table 4-1). The majority of these events occurred from 1998 to 2001 when the population density was low (Chapter 3).

A high proportion (minimum of 31-50%) of juveniles at this site made inter-patch movements and there was no significant difference between the number of males and females moving, nor the distance that the different sexes moved (see Chapter 3). The majority of pikas at our site moved short distances from their natal territories, with a few pikas making larger movements. The average minimum dispersal distance moved by juvenile pikas at this site was 332m (n=35) (for more detail on dispersal movements see Chapter 3). This value was used to calculate α (the effect of distance to dispersal), which was set to 3.0. This is similar to the value of α (2.5) used by Moilanen et al. (1998) for the American pika.

The results of the univariate logistic regression showed that isolation, connectivity, and the perimeter of a patch (Table 4-2) significantly influenced the probability of a patch being occupied. Patches were more likely to be occupied if they were less isolation, had higher connectivity and were larger in perimeter. Although these variables were important, very little of the total variation was explained; connectivity only explained approximately 11% of the variation in occupancy. The probability of a patch being recolonized was significantly influenced by the connectivity among patches, where more connected patches had a greater probability of being colonized (Table 4-2). However, although this logistic regression was significant, it was only able to explain approximately 17% of the variation in colonization.

The probability of a patch going extinct was significantly influenced by the adult population size, with smaller populations having greater probability of going extinct (Table 4-2). However, this was only able to explain approximately 7% of the variation in extinction. These results from the univariate logistic regression suggest that there are likely other variables that could explain the patch dynamics of pikas at this site besides patch size (population size) and connectivity.

Factors affecting recolonization

Aspect, connectivity, average survival and the amount of meadow were all important in predicting the probability of recolonization of a patch by pikas (Table 4-3). Aspect had a large effect on which patches were recolonized. This was the first variable added to the model; all other terms were assessed after holding the effect of aspect constant. Patches oriented southwest had a higher probability of being recolonized (Table 4-3, Fig. 4-2a). Connectivity, measured as the proportion of surrounding patches that could contribute colonizing individuals, also had significant effects on whether a patch was recolonized or not. Patches that had high connectivity were more likely to be recolonized (Table 4-3, Fig. 4-2b). The recolonization of a patch was also significantly affected by the average survival of individuals in the patch (as a measure of habitat quality); patches where the average survival of individuals was higher were also more likely to be recolonized (Table 4-3, Fig 4-2c). The proportion of meadow within a patch also affected the probability of recolonization of a patch; patches with less meadow interspersed throughout the talus had a higher probability of being recolonized (Table 4-3, Fig 4-2d). Year (1995-2001) and the size or perimeter of a patch did not contribute significantly when added to the model and were subsequently excluded from it. Aspect, connectivity, average survival and amount of meadow within the talus explained approximately 41% of the variation in recolonization.

Factors affecting extinction

The average survival and the connectivity of the talus patch were both important in predicting the probability of a patch going extinct (Table 4-3). Average survival of the patch had a strong influence and was added into the model first. All other terms were therefore assessed after holding the effect of average survival constant. Patches were less likely to go extinct if they had higher average survival, as well as higher connectivity (Table 4-3, Fig. 4-3b). The talus aspect, amount of meadow within a talus patch, population size and year (1995-2001) did not contribute significantly to the model. Average survival and connectivity explained approximately 26% of the total variance in extinction events.

Discussion

Several studies have examined the influence of patch size, which is assumed to be correlated with population size and isolation on the persistence of populations (e.g. Smith 1980; Peltonen and Hanski 1991; Sjögren Gulve1994; Hanski et al. 1995; Saari 1998; Forys and Humphreys 1999; Jansson and Angelstam 1999; Skelly et al. 1999), and many have shown that smaller, more isolated patches are more subject to extinction and less likely to be recolonized than larger, closer patches. Our results, however, suggest that population size is only marginally important in predicting extinction of pikas, and connectivity only partially explains colonization of patches at our site. Other habitat quality features such as aspect, amount of meadow, and average survival (a proxy measure of patch quality) were also found to be important in terms of pika persistence. Although our population declined from 1998-2000 (Chapter 3), there was still a balance between the number of colonization and extinction events suggesting evidence of equilibrium metapopulation structure (Hanski 1991, 1999).

Recolonization of patches is largely dependent on the dispersal abilities of organisms (Hansson 1991). Knowledge of dispersal barriers and dispersal rates is necessary for understanding the effects of habitat fragmentation on metapopulation persistence, however dispersal is often poorly understood and difficult to measure (Gaines and Bertness 1993). The dispersal of individuals and recolonization of habitat patches following extinction can facilitate local population persistence and species stability over large geographic areas (Gaines and McClenaghan 1980; Henderson et al. 1985). Numerous studies have shown that shorter distances between habitat patches increases the colonization probabilities (e.g. Smith 1980; Sjögren 1991; Gustafson and Gardner 1996; Skelly et al. 1999). Similarly, recolonization of talus patches by pikas at our site was higher when there was greater patch connectivity, as measured by a number of neighboring populations with potential colonists within dispersal distance. Connectivity takes into account distances to all potential source populations and their population sizes, and is also based on the movement ability of individuals in a spatially structured landscape (Moilanen and Nieminen 2002). For these reasons, connectivity is a much better predictor of recolonization compared to the nearest neighbor isolation method, which only measures the distance to one other patch and does not include information on the potential number of colonists that patch has.

Connectivity was also important in preventing local extinctions of pikas. Other empirical evidence has also shown that as populations become more isolated, the risk of extinction increases (e.g. Smith 1980; Fahrig and Merriam 1985; Sjögren 1991). Patches that are highly connected have less chance of going extinct due to the "rescue effect" (Brown and Kodric-Brown 1977), where immigrating individuals decrease the probability of local extinction (Gilpin 1987; Hanski 1991).

A number of studies have shown patch size to be an important factor affecting extinction rates (Brown 1971; Saari et al. 1998; Crooks et al. 2001). Larger patches, which tend to have larger populations, are less likely to go extinct from stochastic events (Shaffer 1981). We did not observe a strong relationship with population size and extinction, which has also been observed in other studies (e.g. Weddell 1991). Although univariate analysis indicated that population size had a significant influence on extinction, little variation was explained. When other variables were included in the analysis, adult population size did not appear to be important in predicting extinction. Although larger populations are less susceptible to extreme stochastic events, patches that went extinct at our site were not large enough to avoid these extreme events. There were, however, large patches that remained occupied during the entire study. It is possible that we did not see an affect of population size on extinction because of a low variation in the sizes of populations. Also, because of the low over-winter survival of pikas at this site and moderate to high inter-patch movement rates (Chapter 3), it is possible that the effect of population/patch size on extinction would be weakened. High mortality and high dispersal rates could result in relatively large population being more likely to go extinct than expected if these removals from the population were not balanced by immigration.

Clinchy et al. (2002) argued that spatial patterns of patch occupancy may be related to processes other than dispersal, such as weather, anthropogenic changes and predation. They found that spatially correlated extinctions of American pikas in California are likely not a result of the rescue effect, but may be explained by predation. They argued that there was very little dispersal in their population of pikas and therefore, another mechanism explained the recolonization and extinction patterns. However, at our site, there are few predators (Hik et al. 2001) and inter-patch dispersal is common and seems to be an important process in both the recolonization and extinction patterns observed.

We were fortunate to have accurate population sizes for every patch in the study area. This is often difficult information to obtain and therefore patch size is often used in metapopulation models as a surrogate of population size (Hanski 1994, 1999). Although, patch area and patch perimeter were both correlated with population size, patch perimeter had a higher r^2-value, while patch area actually explained very little variation in population size. Because pikas often establish haypiles along the edge of the talus patch (Smith 1974), it is not surprising that population size would be correlated with perimeter. It is important, therefore, to have an understanding of how patch area correlates with population sizes for the organisms of interest before applying the results of metapopulation models for conservation purposes.

The assumption that population size correlates with patch size may be risky in a conservation situation if large patches of poor habitat are conserved over small patches of high quality habitat. One patch (snowplot – Fig. 4-1 and Table 4-1), the largest patch in terms of area and perimeter, was never occupied by pikas during our study. There are two possible reasons to explain absence of pikas from this site. Pikas may not have colonized this area because of lack of conspecifics, which suggests that animals will disperse to patches where conspecifics are located and will avoid unoccupied patches regardless of quality (Stamps 1988; Smith and Peacock 1990). However, unoccupied patches were often recolonized at our site, suggesting that conspecific attraction may not be the only factor determining recolonization (Chapter 3). It is more likely that this patch may not be able to support pikas because of low habitat quality and persistent late season snow cover.

Thomas et al. (2001) and Fleishman et al. (2002) found habitat quality contributed more to species persistence than area or isolation. Although habitat quality is more difficult to measure than area and isolation, Roslin (2002) has suggested its importance in metapopulation modeling. We used average survival as a measure of habitat quality, as well as amount of meadow within a patch and talus aspect. Patches that had higher values of survival were more likely to be recolonized and less likely to go extinct over time. As well, patches that had less meadow and a SW aspect were more likely to be recolonized.

Pikas were more likely to recolonize patches with more talus and less meadow interspersed. The main foraging opportunities for pikas are on the talus-meadow interface (perimeter) (Huntly 1987; Holmes 1991), and although meadow interspersed within the talus patch may be beneficial in terms of shorter travel distance to forage, there may be greater threat of predation. More meadow within a patch means less continuous talus, which may be important for escape terrain from their main predators such as weasels and birds of prey (Lutton 1975; Ivins and Smith 1983; Smith and Ivins 1983; Holmes 1991).

Talus aspect was also important in recolonization of patches; pikas recolonized patches that were southwest facing more often then patches that were northeast facing. The length of growing season and the quality of vegetation surrounding the talus patches may explain this. Patches facing north and east are more likely to have longer periods of snow cover and less vegetation growth. More significantly, lichens and *Cassiope* dominated these slopes, which have fewer nutrients and are less preferred compared to *Dryas octopetala* and *Salix spp.* (Andruchow 2000), which are more common on the south and west facing slopes.

Average survival was important in determining the recolonization of talus patches, and therefore, may be a suitable proxy measure at this site because survival of individuals is the most direct measure of quality. This suggests that possibly pikas can assess patches where they are more likely to survive and will recolonize these sites. Average survival was a significant predictor for recolonization, and provided a useful measure of habitat quality in this system.

Patch size and isolation are the primary features used in metapopulation models such as the incidence function model (Hanski 1994). These models can be used to predict the persistence of some populations, but modeling based mainly on these factors may not be useful or predictive for all organisms. We found patch size and isolation to be only marginally important predictors of the dynamics in this pika population, while features such as aspect, and amount of meadow, were found to be important in terms of pika persistence. Habitat quality plays a very important role in persistence of populations, and others have found that populations are more likely to persist when living on patches with higher habitat quality (Verboom et al. 1991; Klok and DeRoos 1998; Thomas et al. 2001; Fleishman et al. 2002). There may be a compensatory effect between habitat quality and population size, whereby populations on small patches high in habitat quality survive, while local extinctions occur on large patches low in quality (Kindvall 1996). Habitat quality may be equally important and more useful when combined with patch size and isolation to predict population persistence (Thomas et al. 2001, Roslin 2002), and thus unless these additional components can be added into metapopulation models, the models will poorly predict occupancy patterns for some species.

This research also suggests that there are implications beyond the use of area and isolation in theoretical metapopulation models. In much of conservation planning, managers are conserving habitats based on area and isolation alone (ref). However, our results and others suggest that large areas and even large population sizes are not secure from extinction risks. Connectivity played an important role in both recolonization and extinction. Ebenhard (1991) has suggested that, "unless the regional persistence of a species is ensured by large, more or less permanent source patches, the colonization ability of a species will be crucial to its survival in a patchy habitat". Therefore, it is necessary to ensure that in reserve design, habitat patches should be close enough together to allow the dispersal of organisms between patches. Our results have also suggested that habitat quality must also be considered in conservation planning to ensure populations have a chance at persisting. Understanding the factors that are important to the persistence of an organism is critical to effectively conserve its habitat (e.g. Moilanen and Cabeza 2002).

References

Andruchow, J. 2000. Foraging preferences of collared pikas in alpine meadows in the southwest Yukon. BSc. thesis, University of Alberta, Edmonton, Canada.

Brown, J. H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. The American Naturalist 105:467-478.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58: 445-449.

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? American Naturalist 159:351-362.

Crooks, K. R., A. V. Suarez, D. T. Bolger and M. E. Soulé. 2001. Extinction and colonization of birds on habitat islands. Conservation Biology 15:159-172.

Delin, A. E. and H. Andrén. 1999. Effects of habitat fragmentation on Eurasian red squirrel (*Sciurus vulgaris*) in a forest landscape. Landscape Ecology 14:67-72.

Ebenhard, T. 1991. Colonization in metapopulations: a review of theory and observations. Biological Journal of the Linnean Society 42:105-121.

Environmental Systems Research Institute. 1999. ArcView GIS 3.2. Environmental Systems Research Institute, Inc.

Fahrig, L. and G. Merriam. 1985. Habitat patch connectivity and population survival. Ecology 66:1762-1768.

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

Forys, E. and S. R. Humphreys. 1999. The importance of patch attributes and context to the management and recovery of an endangered lagomorph. Landscape Ecology 14:177-185.

Gaines, S. D. and M. Bertness. 1993. The dynamics of juvenile dispersal: why field ecologists must integrate. Ecology 74:2430-2435.

Gaines, M. S. and L. R. Jr. McClenaghan. 1980. Dispersal in small mammals. Annual Review of Ecological Systematics 11:163-196.

Gilpin, M. E. 1987. Spatial structure and population vulnerability. In Soulé, M. E. (Ed), Viable Populations for Conservation. Cambridge University Press, Cambridge.

Gustafson, E. J. and R. H. Gardner. 1996. The effect of landscape heterogeneity on the probability of patch colonization. Ecology 77:94-107.

Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. Biological Journal of Linnean Society 42:17-38.

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

Hanski, I. 1999. Metapopulation Ecology. Oxford University Press, Oxford.

Hanski, I. and M. E. Gilpin. 1991. Metapopulation dynamics: brief history and conceptual domain. Biological Journal of the Linnean Society 42:3-16.

Hanski, I., A. Moilanen, T. Pakkala, and M. Kuussaari. 1996. The quantitative incidence function model and persistence of an endangered butterfly metapopulation. Conservation Biology 10:578-590.

Hanski, I., T. Pakkala, M. Kuussaari, and G. Lei. 1995. Metapopulation persistence of an endangered butterfly in a fragmented landscape. Oikos 72:21-28

Hansson, L. 1991. Dispersal and connectivity in metapopulations. Biological Journal of the Linnean Society 42:89-103.

Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. Biological Journal of the Linnean Society 42:73-88.

Hastie, T. J. and R. J. Tibshirani. 1990. Generalized Additive Models. Chapman and Hall, London.

Henderson, M. T. G. Merriam and J. Wegner. 1985. Patchy environments and species survival. Biological Conservation 31:95-105.

Hik, D.S., C. McColl, and R. Boonstra. 2001. Why are Arctic ground squirrels more stressed in the boreal forest than in alpine meadows? EcoScience 8: 275-288.

Holmes, W. G. 1991. Predator risk affects foraging behavior of pikas: observational and experimental evidence. Animal Behavior 42:111-119.

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

Huntly, N. J. 1987. Influence of refuging consumers (Pikas: *Ochotona princeps*) on subalpine meadow vegetation. Ecology 68: 274-283.

Ivins. B. L. and A. T. Smith. 1983. Responses of pikas (*Ochotona princeps*, Lagomorpha) to naturally occurring terrestrial predators. Behavior Ecology and Sociobiology 13:277-285.

Jansson, G. and P. Angelstam. 1999. Threshold levels of habitat composition for the presence of the long-tailed tit (*Aegithalos caudatus*) in a boreal landscape. Landscape Ecology 14:283-290.

Kindvall, O. 1996. Habitat heterogeneity and survival in a bush cricket metapopulation. Ecology 77:207-214.

Klok, C. and A. M. DeRoos. 1998. Effects of habitat size and quality on equilibrium density and extinction time of *Sorex araneus* populations. Journal of Animal Ecology 67:195-209.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237-240.

Lutton, L. M. 1975. Notes on the territorial behavior and response to predators of the pika, *Ochotona princeps*. Journal of Mammalogy 56:231-234.

MacArthur R. H. and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton.

MacDonald, S. and C. Jones. 1987. *Ochotona collaris*. In: Mammalian Species No. 281 pp.1-4. The American Society of Mammalogists.

MathSoft. 1997. S-PLUS 4 Guide to Statistics. MathSoft, Inc. Seattle.

McCullagh, P. and J. A. Nelder. 1989. Generalized Linear Models. 2nd ed. Monographs on Statistics and Applied Probability 37. Chapman and Hall, London.

McIntire, E. J. B. and D. S. Hik. 2002. Grazing history verses current grazing: leaf demography and compensatory growth of three alpine plants in response to a native herbivore (*Ochotona collaris*). Journal of Ecology 90:348-359.

Moilanen, A. 2002. Implications of empirical data quality to metapopulation model parameter estimation and application. Oikos 96:516-530.

Moilanen, A., and I. Hanski. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. Ecology 79: 2503-2515

Moilanen, A., and I. Hanski. 2001. On the use of connectivity measures in spatial ecology. Oikos 95:147-151.

Moilanen, A. and M. Cabeza. 2002. Single-species dynamic site selection. Ecological Applications 12:913-926.

Moilanen, A. and M. Nieminen. 2002. Simple connectivity measures in spatial ecology. Ecology 83:1131-1145.

Moilanen, A., A. T. Smith, and I. Hanski. 1998. Long-term dynamics in a metapopulation of the American pika. The American Naturalist 152:530-542.

Peacock, M. M. and A. T. Smith. 1997. The effect of habitat fragmentation on dispersal patterns, mating behavior, and genetic variation in a pika (*Ochotona princeps*) metapopulation. Oecologia 112:524-533.

Peltonen, A. and I. Hanski. 1991. Patterns of island occupancy explained by colonization and extinction rates by shrews. Ecology 72:1698-1708.

Roach, W. J., N. Huntly, and R. Inouye. 2001. Talus fragmentation mitigates the effects of pikas, *Ochotona princeps*, on high alpine meadows. Oikos 92:315-324.

Roslin, T. 2002. Who said that size is all that matters? Trends in Ecology and Evolution 17:10-11.

Saari, L., J. Aberg, and J. E. Swenson. 1998. Factors influencing the dynamics of occurrence of the Hazel Grouse in a fine-grained managed landscape. Conservation Biology 12: 586-592.

Shaffer, M. L. 1981. Minimum viable population sizes for species conservation. BioScience 31:131-134.

Sinclair, A.R.E., D.S. Hik, O.J. Schmitz, G.G.E. Scudder, D.H. Turpin and N.C. Larter. 1995. Biodiversity and the need for habitat renewal. Ecological Applications 5:579-587.

Sjögren, P. 1991. Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*). Biological Journal of the Linnean Society 42:135-147.

Sjögren Gulve, P. 1994. Distribution and extinction patterns with a northern metapopulation of the pool frog (*Rana lessonae).* Ecology 75: 1357-1367.

Skelly, D. K., E. E. Werner and S. A. Cortwright. 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. Ecology 80:2326-2337.

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

Smith, A. 1980. Temporal changes in insular populations of the pika (*Ochotona princeps*). Ecology 60: 8-13.

Smith, A. T. 1987. Population structure of pikas: dispersal versus philopatry. In: Chepko-Sade, B. D. and Halpin, A. T. (Eds), Mammalian dispersal patterns: the effects of social structure on population genetics. University of Chicago Press, Chicago. Pp. 128-142.

Smith, A. T. and B. L. Ivins. 1983. Reproductive tactics of pikas: why have two litters? Canadian Journal of Zoology 61:1551-1559.

Smith, A. T. and M. M. Peacock. 1990. Conspecific attraction and the determination of metapopulation colonization rates. Conservation Biology 4:320-323.

Southwick, C. H., S. C. Golian, M. R. Whitworth, J. C. Halfpenny, and R. Brown. 1986. Population density and fluctuations of pikas (*Ochotona princeps*) in Colorado. Journal of Mammalogy 67:149-153.

Stamps, J. A. 1988. Conspecific attraction and aggregation in territorial species. American Naturalist 131:329-347.

Thomas, J. A., N. A. D. Bourn, R. T. Clarke, K. E. Stewart, D. J. Simcox, G. S. Pearman, R. Curtis, and B. Goodger. 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. Proceedings Royal Society London, Series B, Biological Sciences 268:1791-1796.

Turner, I. M. 1996. Species loss in fragments of tropical rain forest: A review of the evidence. Journal of Applied Ecology 33: 200-209.

Verboom, J., K. Lankester, and J. A. J. Metz. 1991. Linking local and regional dynamics in stochastic metapopulation models. Biological Journal of the Linnean Society 42:39-55.

Verboom, J., A. Schotman, P. Opdam, and J. A. J. Metz. 1991. European nuthatch metapopulations in a fragmented agricultural landscape. Oikos 61:149-156.

Weddell, B. J. 1991. Distribution and movements of Columbian ground squirrels (*Spermophilus columbianus* (Ord)): are habitat patches like islands? Journal of Biogeography 18:385-394.

Table 4-1. Patch area, perimeter, number of years surveyed, number of times occupied by adults, number of times went extinct, number of times recolonized, range in population size and connectivity measure (S_i) for each patch shown in Fig. 4-1.

Patch	Area (m^2)	Perimeter (m)	No. years Surveyed	Adult pop range	Times occupied	Times recolonized (years)[1]	Times extinct (years)[2]	Range of connectivity
CCk	78201	2744	4	13-29	4	na[3]	0	3.6-8.8
E GH	100177	1830	7	1-13	7	2 (99, 00)	1 (98)	10.5-27.0
snowplot	156875	1801	7	0	0	0	na	4.9-20.8
W O	31712	1704	7	0-15	6	1 (01)	1 (99)	3.5-22.3
GILL	59741	1663	2	7-9	2	na	0	3.0-15.4
WS	63897	1488	7	0-7	5	0	1 (99)	3.5-23.8
EK9	23954	1060	7	3-16	7	na	0	7.6-20.9
W M	19374	992	7	0-7	4	0	1 (98)	5.2-30.5
EM8	14063	956	7	0-6	6	4 (97,98,99,01)	1 (96)	10.0-28.4
E P-T	19973	734	7	0-8	5	0	1 (99)	10.1-25.0
OBL	12561	656	2	0-4	2	1 (01)	1 (00)	3.6-10.9
HAW	7797	623	3	1-4	3	na	0	7.3-16.25
WPQ2	8793	480	7	0-4	5	1 (99)	1 (98)	5.4-31.4
WQ17	6481	421	4	0	0	0	na	1.1-14.2
WQ12	3871	405	7	0-2	0	0	1 (98)	2.0-27.9
WHH3	1775	378	4	0	0	0	na	7.8-12.5
WS3	3661	334	7	0-3	5	0	1 (99)	5.5-25.8
E LL4	3571	319	3	0-2	2	1 (01)	1 (99)	8.0-16.1
FF7	2557	290	4	1-2	4	na	1 (00)	14.5-42.5
WO3	4504	277	7	0-4	6	2 (99, 00)	1 (98)	4.7-31.62
WP9	1793	220	7	0	0	1 (95)	na	2.7-31.4
ENN4	1184	175	3	0-1	2	1 (01)	1 (99)	6.5-15.2
KK0	1571	172	2	0-2	1	1 (01)	na	7.6-15.8
EK5	1316	156	7	0-2	6	4 (98, 99, 00, 01)	1 (97)	7.5-33.2
E JJ3	654	152	3	0	0	0	na	6.7-16.7
EII5	949	117	3	0	0	0	na	9.4-25.7

[1] A patch was considered to be recolonized if pikas were absent the previous summer and present the subsequent summer.

[2] A patch was defined as becoming extinct if adult pikas were present in the previous summer, but absent in the subsequent summer. A patch was not considered ‘extinct’ if the recolonizing individual did not survive the winter; therefore it is possible to have a patch being recolonized more often then it going extinct.

[3] "na" indicates that the patch was either never unoccupied to be recolonized, or never occupied to become extinct. Patches never occupied during our study were not included in the analysis.

Table 4-2. Results from univariate logistic regression in predicting patch occupancy, recolonization and extinction based on patch size (adult population and perimeter) and patch isolation (nearest neighbor and IFM connectivity).

Patch process	**Coefficient**	**SE**	**Deviance explained of total (df)**	**P (Chi)**
Occupancy				
Isolation	-0.0022	0.0008	7.46/181.86 (135)	0.0063
Connectivity	0.1121	0.0273	20.26/181.86 (135)	0.0000
Perimeter	0.0008	0.0003	7.98/181.86 (135)	0.0047
Recolonization				
Isolation	-0.0026	0.0016	3.40/79.23 (65)	0.0650
Connectivity	0.0928	0.0431	5.04/79.23 (65)	0.0248
Perimeter	0.0000	0.0005	0.0045/79.23 (65)	0.9460
Extinction				
Isolation	-0.0026	0.0029	1.15/68.05 (60)	0.2840
Connectivity	-0.0278	0.0389	0.52/68.05 (60)	0.4727
Adult population size	-0.2537	0.1431	4.89/68.05 (60)	0.0270
Perimeter	-0.0009	0.0005	3.26/68.05 (60)	0.0711

Table 4-3. Final model of recolonization and extinction. Significant terms were added step-wise base on the *Cp* statistic at each step. The change in deviance of the model by the inclusion of the term was tested against a X^2 distribution

Model	Variables included in final model	Coefficient (SE)	Residual df	Change in deviance	P for X^2 -test on deviance
Recolonization	null	-2.835 (1.31)	47	64.44	-
	aspect	1.057 (0.62)	46	51.93	0.0004
	Connectivity (Si)	0.2698 (0.09)	45	45.51	0.0113
	Average survival	8.375 (3.66)	44	41.69	0.051
	meadow	-7.744 (4.15)	43	38.03	0.0556
				R=0.41	
Extinction	Null	3.994 (1.80)	60	68.05	-
	Average survival	-8.962 (2.83)	59	53.89	0.0002
	Connectivity (Si)	-0.0907 (0.06)	58	50.59	0.0832
				R=0.26	

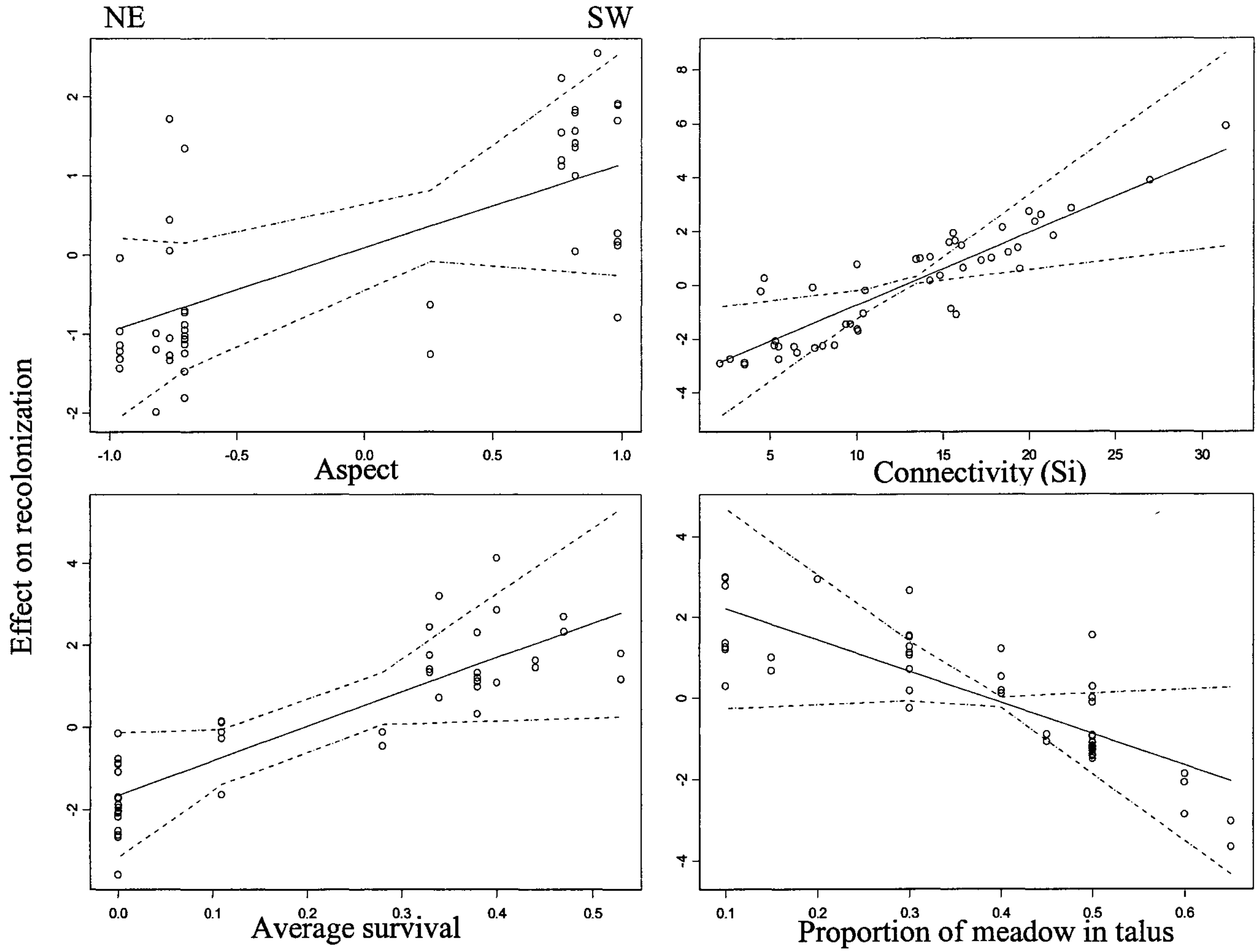


Figure 4-2. Effects of aspect, connectivity, average survival and amount of meadow within the talus patch on the recolonization of talus patches by collared pikas. Plots show the additive effect of each variable on whether a talus patch was recolonized. Standard errors are indicated.

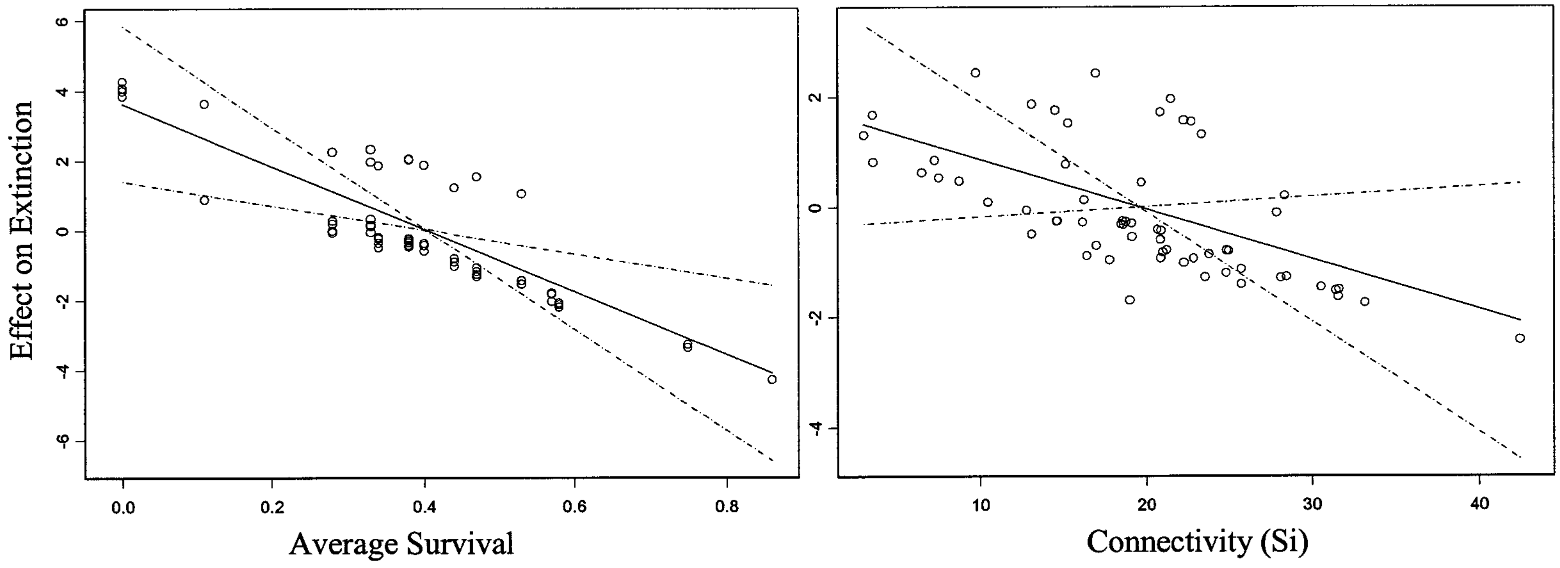


Figure 4-3. Effects of average survival (habitat quality) and connectivity on extinction of pikas on talus patches. Plots show the additive effect of each variable on whether a talus patch went extinct. Standard errors are indicated.

Chapter 5: General Discussion

This study has provided the first detailed assessment of population ecology of the collared pika (*Ochotona collaris*). Pikas are generally a poorly known group of mammals, even though they are widely distributed in the mountains of Asia and North America (Smith et al. 1990). Previous studies of pikas have provided intriguing insights into a number of ecological problems including metapopulation dynamics, foraging behaviour, predation risk, and adaptation to extreme environments, but most of this work has been conducted on just one species (*O. princeps*), and at only a few sites.

The analyses presented in this thesis greatly expand our general knowledge of talus-dwelling pikas, and will hopefully provide a basis for further research of these intriguing mammals. Population ecologists are interested in determining the relative importance of various factors on population dynamics, including density-dependent and density independent factors, and the roles of food, predation, disease, habitat quality and climate variability. It has even been suggested that population regulation is fundamental in most ecological problems of interest (Sinclair 1989, Murdoch 1994), and may be especially true in terms of understanding how best to conserve a species or habitat.

In the following sections I have summarized the main contributions of my thesis, some limitations of these results, and potential directions for new studies.

Demography of Collared Pikas

Collared pikas and American pikas have a number of similar life-history traits, but there are also some important differences (Table 5-1). These differences likely reflect

Table 5-1. Demographic Characteristics of the collared pika (*Ochotona collaris*) and the American pika (*Ochotona princeps)*

Characteristic	Collared pika	American pika
Average litter size	2.2 - 3 (Rausch 1962)	2.3-3.7 (Smith 1990)
Litters/year	1 (this study); 2 (Rausch 1962)	2 (Smith 1988)
Mean date of conception of first litter	late May (this study; Rausch 1962)	late April (Millar 1972)
Reproductive maturity	yearling (this study)	yearling (Smith 1988)
Average adult weight	157g (this study)	133 g (Millar and Tapper 1973); 150g (Whitworth and Southwick 1981); 170 g (Golian and Whitworth 1985)
Oldest recorded age (years)	4 (this study)	7 (Millar and Zwickel 1972; Smith 1978)
Average annual mortality	66-75% (this study)	37-46% (Millar and Zwickel 1972; Smith 1978)
Sex ratio	1:1 (1998-2001 this study)	near unity (Smith 1981b)
Density/ha	6.4-7.2 animals/ha (Broadbrooks 1965)	6-10 animals/ha (Smith 1990)
Home range	0.20 ha (males), 0.16 ha (females); 0.032 ha (Broadbrooks 1965)	0.22 ha (males), 0.18 ha (females) Smith and Ivins 1984
Nearest neighbor	opposite sex; 30-70 m (Broadbrooks 1965); 33-107 m (this study)	opposite sex; range 14 m (Smith and Ivins 1984) to 32.6 m (Broadbrooks 1965)
Natal philopatry or dispersal	minimum 34% juveniles disperse inter-patch	philopatric
Sex-biased dispersal?	no (this study)	no (Smith 1987; Smith and Ivins 1983b)
Dispersal hypothesis	inbreeding avoidance and/or habitat selection (this study)	competition for resources (Peacock 1997)

differences in their environment, with collared pikas experiencing more extreme conditions in northern environments. Collared pikas are found to have faster growth rates than the American pika and they likely only produce one litter a year, which is conceived in late May. Collared pikas also make more inter-patch dispersals than the American pika and inbreeding avoidance and habitat selection are possible dispersal hypotheses. The collared pika has higher annual mortality and lives to a younger age than the American pika.

Because pikas are born within the talus a number of life history parameters are difficult to assess, including post-natal growth rates, litter size, and dispersal. One possible way to do this would be to raise pregnant females in captivity until they have a litter, then take the weights of juveniles over known time intervals. This would also provide information on litter size, and the number of young that live to weaning; both of these are unknown for *O. collaris*. As well, a more accurate assessment of dispersal could be made if the mother-offspring relationship is known. Some alternative methods to effectively examine dispersal in pikas include: using genetics markers or using of some kind of marker in pregnant females and testing blood in the juveniles to determine maternal linkages. We were restricted at our site, in part, due to the large drop in overall numbers and not wanting to risk using intrusive methods with the remaining pikas.

Most of the work on dispersal and settlement patterns of *O. collaris* occurred in low density years and therefore the results may be different when pikas exist at higher populations.

Habitat Quality and Metapopulation Dynamics

I have provided a detailed assessment of how habitat quality contributes to metapopulation dynamics for collared pikas. Some authors have shown that habitat quality is important in terms of species persistence (Verboom et al. 1991; Kindvall 1996; Klok and DeRoos 1998; Tomas et al. 2001; Fleishman et al. 2002). It has been suggested that habitat quality is the missing third parameter in metapopulation models (Roslin 2002), although very few studies have tested this. We found habitat quality to be equally or more important for pika persistence than patch size and isolation. This result suggests that unless these additional components are added into metapopulation models, the models will poorly predict occupancy patterns for some species. These results are also important for species conservation and suggest that habitat managers should not only be concerned with managing patches based on their size and connectivity, but they must also consider the quality within the remaining habitat patches.

Fleishman et al. (2002) have also recently emphasized this point for understanding the dynamics of the butterfly *Speyeria nokomis* in riparian areas of the Great Basin. Their results are in broad agreement with our conclusion that extinction and colonization events are closely related to multiple aspects of habitat quality, and that the ability of various habitat characteristics to explain these dynamics varies among years. While Hanski et al. (1996) and Moilanen (1999, 2002) suggest that metapopulation models can be parameterized with data pooled over several years to minimize the effects of interannual variation, this approach ignores the role of temporal variation on metapopulation dynamics. More research is needed to fully understand the role of habitat on metapopulation processes (e.g. Roslin 2002), but our studies of collared pikas should help to encourage more work in this area.

Pikas as Indicators of Climate Change

Through this thesis I have addressed how climate may be impacting the timing of parturition, growth, survival, dispersal and ultimately the metapopulation structure of collared pikas. Although this population of collared pikas is not at risk of increased habitat fragmentation due to anthropogenic causes, they may be at risk of fragmentation resulting from climate change. Predicted temperature increases as a result of climate change could result in smaller areas of suitable habitat with greater isolation between populations. Although, the effects of climate variability and change on collared pikas were not assessed in detail, the results here suggest that abiotic processes play a significant role in population dynamics. I have suggested that pikas could potentially act as an indicator of climate change, because they are highly susceptible to changes in temperature. As well, collared pikas live at high latitudes in northwestern North America where significant climate warming is occurring.

We cannot know with absolute certainty why collared pika populations in the southwest Yukon have collapsed since 1998, but the most parsimonious explanation is that insulation in winter declined and reached a critical level. Similar events have undoubtedly occurred in the past (climate records), however the cumulative effect of consecutive years of warmer winters may prevent these populations from recovering to their former levels.

While the sensitivity of hibernating species such as yellow-bellied marmots (*Marmota flaviventris*) to climate change has recently been noted (Inouye et al. 2000), it is likely that species that do not hibernate will be even more sensitive to interannual and directional changes in climate. McDonald and Brown (1992) have also suggested that montane mammals would provide an early indication of global climate change impacts in the western USA, and that *O. princeps* in particular would be adversely affected by changes in habitat associated with long-term increases in atmospheric CO_2.

Very rapid climate-induced demographic changes are well known in populations of rodents in arid environments in response to rainfall and drought (e.g. Newsome and Corbett 1975, Brown and Heske 1990, Dickman et al. 1999, Lima et al. 1999). Weather conditions may also influence population dynamics of small mammals in Arctic and alpine environments, although it is unclear that these changes are as predictable as in arid environments (Hansson and Hentonen 1985, Scott 1993, Reid and Krebs 1996, Yoccoz and Ims 1999).

We have shown that the potential for rapid extinction events may occur much more rapidly if they are a consequence of changes in critical environmental conditions. Since climate is difficult to manipulate at a scale relevant to pikas, only long-term studies of population dynamics will be able to adequately address these questions.

References

Brown, J.H. and E.J. Heske. 1990. Temporal changes in a Chihuahuan Desert rodent community. Oikos 59:290-302.

Dickman, C.R., P.S. Mahon, P. Masters and D.F. Gibson. 1999. Long-term dynamics of rodent populations in arid Australia: the influence of rainfall. Wildlife Research 26:389-403.

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

Hanski, I., A. Moilanen, T. Pakkala, and M. Kuussaari. 1996. The quantitative incidence function model and persistence of an endangered butterfly metapopulation. Conservation Biology 10:578-590.

Hansson, L. and H. Henttonen. 1985. Gradients in density variations of small rodents: the importance of latitude and snow cover. Oecologia 67:394-402.

Inouye, D.W., B. Barr, K.B. Armitage and B.D. Inouye. 2000. Climate change is affecting altitudinal migrants and hibernating species. Proceedings National Academy of Science, USA. 97:1630-1633.

Kindvall, O. 1996. Habitat heterogeneity and survival in a bush cricket metapopulation. Ecology 77:207-214.

Klok, C. and A. M. DeRoos. 1998. Effects of habitat size and quality on equilibrium density and extinction time of *Sorex araneus* populations. Journal of Animal Ecology 67:195-209.

Lima, M., P.A. Marquet and F.M. Jakisc. 1999. El Nino events, precipitation patterns, and rodent outbreaks are statistically associated in semiarid Chile. Ecography 22:213-218.

McDonald, K.A. and J.H. Brown. 1992. Using montane mammals to model extinctions due to global change. Conservation Biology 6:409-415.

Moilanen, A. 1999. Patch occupancy models of metapopulation dynamics: efficient parameter estimation using implicit statistical inference. Ecology 80:1031-1043.

Moilanen, A. 2002. Implications of empirical data quality to metapopulation model parameter estimation and application. Oikos 96:516-530.

Murdoch, W. W. 1994. Population regulation in theory and practice. Ecology 75:271-287.

Newsome, A.E. and L.K. Corbett. 1975. Outbreaks of rodents in semi-arid and arid Australia: causes, preventions, and evolutionary considerations. In 'Rodents in Desert Environments'. (Eds. I. Prakash and P.K. Ghosh.). pp. 117-153. Junk, The Hague.

Reid, D.G. and C.J. Krebs. 1996. Limitations to collared lemming population growth in winter. Canadian Journal of Zoology 74:1284-1291.

Roslin, T. 2002. Who said that size is all that matters? Trends in Ecology and Evolution 17:10-11.

Scott, P.A. 1993. Relationship between the onset of winter and collared lemming abundance at Churchill Manitoba, Canada: 1932-1990. Arctic 46:293-296.

Sinclair, A.R.E. 1989. Population regulation in animals. Pp. 197-241. In Ecological Concepts (Ed. J.M. Cherrett). Blackwell Scientific Publications, Oxford.

Thomas, J. A., N. A. D. Bourn, R. T. Clarke, K. E. Stewart, D. J. Simcox, G. S. Pearman, R. Curtis, and B. Goodger. 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. Proceedings Royal Society London, Series B, Biological Sciences 268:1791-1796.

Verboom, J., A. Schotman, P. Opdam, and J. A. J. Metz. 1991. European nuthatch metapopulations in a fragmented agricultural landscape. Oikos 61:149-156.

Yoccoz, N.G. and R.A. Ims. 1999. Demography of small mammals in cold regions: the importance of environmental variability. Ecological Bulletins 47:137-144.