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Foraging Ecology and Population Dynamics of Collared Pikas in Southwestern Yukon

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THE FORAGING DECISIONS MADE BY HERBIVORES influence population dynamics through their effects on energy gain, energy expenditure, and ultimately, survival (McNamara and Houston, 1997). In turn, foraging by herbivores may influence the amount of vegetation available for the future. Therefore, herbivores and vegetation often are coupled in a strong reciprocal relationship: the abundance of one affects the abundance of the other through time (e.g., Caughley, 1976).

This interaction is particularly important for herbivores living in seasonal environments where food abundance and quality vary dramatically between growing and winter seasons. Herbivores must adapt their foraging behaviour to contend with these changes and survive until the following growing season (Owen-Smith, 2002). In addition to seasonal effects, daily foraging decisions are constrained by a number of other factors, which may be classified as either internal (such as energetic or nutritional needs), or external (such as predation risk or interspecific interactions). These constraints limit the availability of food items to the herbivore and explain why most species exhibit some degree of diet selectivity. Most species, therefore, must balance trade-offs associated with these constraints such as obtaining enough food while minimizing predation risk (Lima and Dill, 1990), or decisions about selecting species with differing degrees of nutritional value (Stephens and Krebs, 1986).

I am using a combination of descriptive and experimental methodologies, combined with modelling techniques, to increase our understanding of plant-herbivore interactions and their influence on herbivore population dynamics, using the collared pika (*Ochotona collaris*) as a model species. Pikas are small (~160 g) lagomorphs that live in alpine talus slopes. Pikas are asocial and each individual collects vegetation for two distinct diets: a summer diet that is consumed immediately, and a winter diet that is stored in haypiles under boulders (Millar and Zwickel, 1972; Conner, 1983). Because of predation risk, pikas rarely venture more than 10 m from talus into meadows to collect vegetation (Holmes, 1991), and this behaviour creates a strong gradient of grazing pressure, with most foraging activity occurring within 3 m of talus (Huntly, 1987; McIntire and Hik, 2005). Insatiable hoarders of vegetation (McKechnie et al., 1994), pikas provide an opportunity to test experimentally hypotheses regarding diet selection as a function of various constraints. Since 1995, most individuals (> 95%) within the study area have been captured, weighed, sexed, and marked with uniquely coloured ear tags. This detailed, long-term demographic dataset will provide context for this study and a means of validating population models.

A collared pika (Ochotona collaris) with white ear tag for identification. Photo: S. Morrison.

The objectives for this project are 1) to determine how collared pikas make foraging decisions with respect to predation risk and forage quality, 2) to incorporate these constraints into a plant-herbivore modelling approach to determine their effects on population dynamics, and 3) to compare the plant-herbivore model to spatial demographic models of population dynamics.

STUDY AREA

The project is being conducted in a 4 km^2 alpine valley near Kluane Lake in the southwestern Yukon. The valley

Alpine boulder fields interspersed with meadow are typical pika habitat. Photo: S. Morrison.

is an alpine meadow interspersed with talus slopes. Collared pikas, hoary marmots (*Marmota caligata*), and arctic ground squirrels (*Spermophilus parryii*) are the dominant herbivores in the valley and have been studied there since 1995 (Hik et al., 2001). Predation on pikas within the valley is relatively low (Franken, 2002), suggesting that pika populations are more influenced by food resources and environmental conditions than by predation, a relationship similar to that observed for marmots in this study area (Karels and Hik, 2003).

METHODS AND PRELIMINARY RESULTS

The main components of this study are described below with respect to underlying theory, methodology, and progress to date.

Foraging Behaviour in Relation to Predation Risk

Predators may affect prey population dynamics either directly, through mortality, or indirectly, through changes in prey behaviour or physiology in response to predation risk (Lima and Dill, 1990; Sinclair and Arcese, 1995). These sub-lethal effects often are independent of actual predation (Lima, 1998) and may have large effects on prey populations (Schmitz et al., 1997).

Pikas are classical central-place foragers, in that they venture out from a fixed location (a haypile) while foraging and repeatedly return with food for winter storage. The costs of increased travel time and predation risk must be balanced against the benefit of obtaining better-quality forage. To reduce the costs of travel time and predation risk, central-place foragers are predicted to become more selective as distance from the haypile increases.

Pikas appear to be very sensitive to predation risk (Holmes, 1991), and the hypothesis that this risk affects the selection of individual forage species was tested in 2000 and 2002. Selection was measured by using a cafeteria-style arrangement of six potential forage species at five levels of predation risk. Predation risk was manipulated by placing the "cafeteria" in the meadow at increasing distances from the talus. Contrary to expectations, pikas did not switch preferences for forage species as predation risk increased (Morrison et al., 2004). However, the total amount of vegetation removed was inversely related to risk, indicating that pikas removed less vegetation from the treatments furthest from talus cover. The addition of talus cover at treatments of greatest potential risk reduced the negative effects of higher predation risk.

Nutritional Constraints on Diet Selection

Multiple nutritional constraints often determine an herbivore's preference for certain forage species (Belovsky, 1978), and this selection process leads to a diet composition that is not proportional to the availability of its component species within the environment. Several factors have been hypothesized to explain how pikas select forage species, including nitrogen content (Millar, 1971; Holmes, 1991) and water content (Smith, 1974).

I experimentally tested these hypotheses by manipulating the nitrogen and water content of two commonly selected forage species (*Polygonum bistorta* and *Carex* spp.) and using a cafeteria-style arrangement as described previously. Nitrogen content was manipulated by adding fertiliser, and water content was manipulated by partially drying vegetation. Preliminary results suggest that pika forage preferences are more complex than previously reported. In addition to species-specific characteristics, pikas also appear to be making subtle intra-specific decisions based on nitrogen and water content interactions.

Plant – Herbivore Relationships

Results of the experiments described above, activity budgets, and fine-scale foraging observations are being used to develop a plant-herbivore population model similar to those described by Caughley (1976) and further developed by Owen-Smith (2002). This plant-herbivore modelling approach differs from traditional demographic models in that it incorporates pika foraging behaviour,

Pikas spend many hours collecting and storing vegetation to eat during winter. Photo: S. Morrison.

metabolism, and mortality components to model pika and vegetation biomass. Further, it allows for the integration of foraging behaviour into population dynamics while accounting for variation in habitat quality as a consequence of climate variability and change.

Because this family of models focuses on the environmental, rather than demographic, determinants of population dynamics, it is a particularly relevant approach for the southern Yukon, where temperature increases have averaged 2˚C per decade since the 1960s, and recent winters have been over 5˚C warmer than in previous decades (Zhang et al., 2000). The effects of such warming on alpine systems could include changes in growing season length, increased variability in precipitation frequency and type (snow vs. rain), or nutrient availability. All of these possibilities could have important effects on pika population abundance and stability through their effects on forage quality and quantity.

Pika Population Dynamics as a Function of Demography and Space

Long-term census data at our site show that pika populations tend to vary dramatically from year to year (Franken, 2002). The reasons for this yearly variation are currently unknown, but may reflect the influence of a variety of factors, including age-specific mortality or environmental conditions. Further, the importance of these factors may have a spatial component: south-facing slopes tend to have better survival than east- or west-facing slopes.

We are using age-based matrix population models (Caswell, 2001) to conduct a life table response experiment (LTRE) to decompose the variation in population growth rate into contributions from demographic vital rates. Results thus far strongly suggest that the vital rate that contributes most to the observed variance in growth rate differs according to subpopulation. Adult fecundity was most important in some areas, whereas variation in adult survival was most important in others. These results indicate that adult females have played the largest role in historical variation in population growth, but that the specific influence of adult females varied across distances as short as 200–300 metres.

CONCLUSIONS

My dissertation examines the relationship between the foraging behavior of pikas and their population dynamics. The experimental and observational data necessary for the foraging components (parts 1 and 2, above) were collected from 2002 to 2005 and are now being analyzed. These results will parameterize the plant-herbivore model (part 3) to examine the effects of food resources on the abundance and stability of pika populations. The data required for the demographic models (part 4) have been gathered as part of long-term research at this site and data collection will continue indefinitely. My data-driven population models (3 and 4) will allow us to understand the observed declines in pika abundance and to make predictions about the future of these populations in a changing and variable environment. More broadly, the combined aspects of my project will advance our understanding of climate-plant-herbivore interactions in alpine ecosystems.

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REFERENCES

BELOVSKY, G.E. 1978. Diet optimization in a generalist herbivore: Moose. Theoretical Population Biology 14:105–134.

CASWELL, H. 2001. Matrix population models, 2nd ed. Sunderland, Massachusetts: Sinauer Associates.

CAUGHLEY, G. 1976. Plant-herbivore systems. In: May, R.M., ed. Theoretical ecology. Philadelphia: Saunders. 94–113.

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.

FRANKEN, R.J. 2002. Demography and metapopulation dynamics of collared pikas (*Ochotona collaris*) in the southwest Yukon. MSc thesis, University of Alberta, Edmonton, Alberta, Canada.

HIK, D.S., McCOLL, C.J., and BOONSTRA, R. 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 Behaviour 42:111–119.

HUNTLY, N.J. 1987. Influence of refuging consumers (pikas - *Ochotona princeps*) on sub-alpine meadow vegetation. Ecology 68:274–283.

KARELS, T.J., and HIK, D.S. 2003. Demographic responses of hoary marmots (*Marmota caligata*) to environmental variation. In: Ramousse, R., Allaine, D., and Leberre, M., eds. International Marmot Network. 167–168.

LIMA, S.L. 1998. Nonlethal effects in the ecology of predator–prey interactions: What are the ecological effects of anti-predator decision-making? Bioscience 48(1):25–34.

LIMA, S.L., and DILL, L.M. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. Canadian Journal of Zoology 68:619–640.

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

McKECHNIE, A.M., SMITH, A.T., and PEACOCK, M.M. 1994. Kleptoparasitism in pikas (*Ochotona princeps*): Theft of hay. Journal of Mammalogy 75:488–491.

McNAMARA, J.M., and HOUSTON, A.I. 1997. Currencies for foraging based on energetic gain. American Naturalist 150: 603–617.

MILLAR, J.S. 1971. Breeding of the pika in relation to the environment. PhD Dissertation. University of Alberta, Edmonton, Alberta, Canada.

MILLAR, J.S., and ZWICKEL, F.C. 1972. Characteristics and ecological significance of haypiles of pikas. Mammalia 36: 657–667.

MORRISON, S., BARTON, L., CAPUTA, P., and HIK, D.S. 2004. Forage selection by collared pikas, *Ochotona collaris*, under varying degrees of predation risk. Canadian Journal of Zoology 82(4):533–540.

OWEN-SMITH, N. 2002. Adaptive herbivore ecology. Cambridge: Cambridge University Press.

SCHMITZ, O.J., BECKERMAN, A.P., and O'BRIEN, K.M. 1997. Behaviorally mediated trophic cascades: Effects of predation risk on food web interactions. Ecology 78(5):1388–1399.

SINCLAIR, A.R.E., and ARCESE, P. 1995. Population consequences of predation-sensitive foraging: The Serengeti wildebeest. Ecology 76(3):882–891.

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

STEPHENS, D.W., and KREBS, J.R. 1986. Foraging theory. New Jersey: Princeton University Press.

ZHANG, X., VINCENT, L.A., HOGG, W.D., and NIITSOO, A. 2000. Temperature and precipitation trends in Canada during the 20th century. Atmosphere-Ocean 38:395–429.

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