Talus fragmentation mitigates the effects of pikas, *Ochotona princeps*, on high alpine meadows

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North American pikas (*Ochotona princeps*) are central-place foragers that are restricted to talus slopes in the mountains of western North America. They graze meadows surrounding talus producing a gradient of grazing pressure extending out from the talus edge. We asked: 1) how does the physical structure of the talus slope affect pika foraging behavior? and 2) how do differences in foraging behavior affect the relative abundance of different plant functional groups?
Pikas at three talus-meadow interfaces differed in the distances they traveled for forage, depending upon the structure of the talus slope. Pikas fed preferentially on vegetation within the talus, ventured into the surrounding meadow when intra-talus vegetation was rare, and ranged farther when haying than when grazing. They ventured into the surrounding meadow less when talus fields were more fragmented and intra-talus vegetation was more abundant.
We tested the effects of pikas on meadow vegetation by excluding pikas from small plots located at various distances from talus edges. When habitat structure forced pikas to venture out from the talus to forage, they decreased total vegetative biomass by as much as 80% and increased the relative importance of cushion plants and sedges. These effects were undetectable at distances beyond one meter. These patterns appear to result from a change in the relative performance of different plant functional groups caused by herbivory.

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Central place foragers venture out from fixed locations (e.g. dens and other refuges) when foraging and return after each bout (Covich 1976, Orians and Pearson 1979). The relative benefits and costs associated with a given foray determine where an animal forages. Food quantity and quality are the most obvious benefits whereas travel time, handling time, and predation risk are among the more important costs (Jenkins 1980, Krebs 1980, Suhonen 1993, Chase 1998). Predation risk, in particular, is expected to increase with distance. Because the costs associated with a foraging bout increase with the distance traveled, consumers should minimize this distance while becoming more choosy when farther from their central place (Jenkins 1980, Lima and Dill 1990). Optimal foraging models and empirical studies have demonstrated that many animals reduce predation risk by limiting the time they spend in more distant areas (Brown 1988, 1992, Longland 1991, Brown et al. 1992, Hughes and Ward 1993, Suhonen 1993, Chase 1998). Consumers may further reduce predation risk by concentrating on more profitable items that can be carried to cover for consumption (Lima et al. 1985, Huntly et al. 1986, Lima and Valone 1986, Kieffer 1991, Dearing 1996). As a result of their reluctance to travel far for food, central place foragers often strongly limit the resources in the vicinity of their dens and refuges. In addition, consumers may increase the frequency of anti-predator behaviors like vigilance as risk increases (Krebs 1980).

Habitat structure as well as distance from centrally located refugia may influence foraging patterns. Numerous studies have shown that the success of predators like piscivorous fish (Hixon and Beets 1993), insectivorous fish (Power 1992), and owls (Longland and Price 1991) declines when their prey can forage in more structurally complex habitats. Prey may lower their predation risk by concentrating their foraging in areas that reduce predator efficiency. The resulting spatial variation in foraging intensity can have important implications for the distribution and abundance of prey resources. For example, rodents in the Negev Desert forage from and retreat to shelters as they consume their favorite prey, the desert snail *Trochoidea seetzenii*. Since the abundance of shelters for rodents depends upon the prevailing geology, the distribution of the snails is indirectly determined by the physical structure of the larger habitat (Abramsky et al. 1990).

In this paper, we report the results of a study examining how habitat structure affects the foraging behavior of North American pikas (*Ochotona princeps*) and, in turn, how pikas influence the structure of a high alpine meadow. Huntly (1987) demonstrated that pikas are an important determinant of the plant composition and biomass of subalpine meadows and that the intensity of their effects declines with distance from talus. Pikas are also common in the alpine (Smith and Weston 1990), but their impact on alpine vegetation has not been studied.

Pikas are small (121–176 g; Smith and Weston 1990), herbivorous lagomorphs that inhabit high altitudes and latitudes. As pikas are not equipped to physically defend themselves against predators, they invariably are associated with talus slopes and hide in the interstices between the rocks when threatened. Individuals are territorial and relatively long-lived, often occupying the same site for as many as seven years (Millar and Zwickel 1972a, Smith and Ivins 1983, Smith and Weston 1990). During the growing season pikas collect two distinct diets from the vegetation surrounding talus fields (Huntly et al. 1986, Dearing 1996). The summer diet is immediately consumed, whereas the winter diet is cached in haypiles in the talus. Pikas forage from these haypiles throughout the winter, during which they remain active (Millar and Zwickel 1972b, Conner 1983, Dearing 1997a). Although pikas are generalized herbivores and eat a wide variety of plant species (Huntly 1987, Dearing 1996), they nevertheless feed selectively (Millar and Zwickel 1972b, Huntly 1987, Dearing 1996, 1997b). Because the requirements of the winter diet are narrower (Dearing 1996, 1997b), pikas often are willing to accept more risk when haying than when grazing (Huntly et al. 1986).

Pikas are central-place foragers and produce a gradient that extends out from the talus edge (Huntly et al. 1986, Huntly 1987). Pikas are known to be wary of a number of predators including weasels (Ivins and Smith 1983), pine martens (Ivins and Smith 1983), ermine (Holmes 1991, W. J. Roach pers. obs.), and hawks (W. J. Roach pers. obs.), and temporarily reduce their activity after sighting a predator (Holmes 1991, Ivins and Smith 1983, W. J. Roach pers. obs.). Holmes (1991) effectively demonstrated that habitat structure influences the behavior of collared pikas, *Ochotona collaris*. He constructed talus 'fingers' which extended from larger talus slides into previously un-utilized meadows. These 'fingers' provided refugia and extended the distance from the main talus to which pikas were willing to forage.

Huntly (1987) developed and tested a mechanistic model that predicts effects of pikas on three functional plant groups in a subalpine meadow surrounding a talus slope. Specifically, her model states that near talus, herbivory reduces plant growth leading to dominance by unpalatable and/or grazing tolerant plants; in particular, grazing tolerant graminoids and cushion plants thrive. Farther from talus herbivory decreases, plant biomass increases, and competition among plants increases. As a result, cushion plants, whose prostrate growth form makes them poor competitors for light, perform best where pikas graze heavily enough to limit the biomass of their competitive dominants (Huntly 1987).

We also considered effects of habitat structure, which influences predation risk and, hence, foraging behavior. Talus slopes often differ in their degree of fragmentation, and pikas living on more broken slopes can forage in relative safety on plants growing within talus. Thus, we expected that the effects of the pikas on the surrounding meadows would be reduced when the availability of intra-talus vegetation was high.

We tested this model with an experiment that modified pika foraging behavior. Pikas were prevented from foraging on patches of vegetation in the meadows surrounding three talus slopes that differed in their degree of fragmentation and thus in the availability of intra-talus vegetation. At each slope, we collected data on the foraging behavior of pikas and on the effects of pika herbivory on the vegetation of the adjacent meadows. This experiment addressed two hypotheses:

1) Pikas in alpine environments forage as predicted for central place foragers that minimize predation risk while maximizing resource yield. Based on this hypothesis, we predicted that (1a) pikas would produce a gradient of foraging pressure extending from the talus edge into the surrounding meadow; (1b) the extent of this gradient would depend upon the vegetation available within the talus; (1c) pikas would accept more risk when haying than when grazing and would travel farther when haying; (1d) vigilance would increase as the distance traveled increased; and (1e) pikas would have little effect on meadows surrounding fragmented talus slopes with abundant intra-talus vegetation.

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2) In the alpine, as has been shown in the more productive subalpine, meadow plant communities will be structured mainly by competition for light and nutrients when herbivory is low, but will be dominated by plants that are tolerant of herbivory or are less palatable when grazing pressure is high. Based on this hypothesis we predicted that (2a) cushion plants and sedges would dominate in areas where grazing pressure is high; and (2b) more palatable forbs would be most abundant in areas where grazing pressure was low.

Methods

This study was conducted on the Beartooth Plateau, a high-alpine area northeast of Yellowstone National Park in Park County, Wyoming, USA. The study area was located at ~ 3000 m elevation on a large butte with a $\sim 45°$ slope. Although a homogeneous talus field covered much of the slope, the talus on other portions was more broken with large patches of vegetation interspersed between the rocks, creating a mosaic of meadow and talus. The meadows surrounding the talus were dominated by forbs and graminoids. Ross' avens (*Acomastylis rossii*, previously *Geum rossii*) was the most abundant forb, though alpine bluebells (*Mertensia alpina*), alpine daisy (*Erigeron simplex*), numerous cinquefoils (*Potentilla* spp.), snow gentian (*Gentiana algida*), and twice-hairy groundsel (*Senecio fuscatus*) were also common. Graminoids were well represented by sedges (*Carex* spp.), short bluegrasses (*Poa* spp.) and fescues (*Festuca* spp.). Mat-like cushion plants such as moss campion (*Silene acaulis*) and stonecrop (*Sedum lanceolata*) also were locally important.

Habitat characterization

We focused our efforts on three talus slides (sites). At each site, we estimated the relative abundance of the available intra-talus vegetation using photographs taken from the opposite slope. We used a digitizing palette and Sigma-Scan version 3.90 to develop estimates of the area of each talus field and of the major vegetation patches within the talus, and estimated what percentage of each slope was covered by intra-talus vegetation. We used these estimates to rank the three sites according to the amount of intra-talus vegetation.

Pika behavior

We conducted focal animal observations during the summer of 1996, during which we collected 1083 min of direct behavioral observations. After a brief period of acclimation, pikas readily accept human observers (Ivins and Smith 1983, Huntly et al. 1986, Holmes 1991). We recorded the time spent running, scanning, perching, walking, grazing, haying, depositing hay, vocalizing, socializing, and missing from sight as well as the distance pikas traveled during each foraging bout. A pika's distance from the talus edge was estimated by comparing its location to that of known markers. Pikas were recorded as being within the talus, at the talus edge, or at one of four distances from the talus edge (0–1 m, 1–2 m, 3–4 m, and >4 m). These data allowed us to estimate the percentage of trips pikas made to each distance when grazing and haying as well as the percentage of time pikas spent being vigilant.

Meadow vegetation

We compared the composition and biomass of vegetation on plots in which pikas were prevented from foraging to that on control plots that were available to pikas. During the summer of 1995, we established six transects (two at each site) that extended from talus slides into the surrounding meadows. Sites were separated by large distances, relative to the size of pika territories, and were inhabited by different groups of pikas. Thus, site becomes a factor in the experimental design with two transects located at each of three sites. Transects at each site were true replicates since each pair was separated by a distance great enough to ensure that they were in distinct pika territories.

Each transect consisted of three paired plots located at fixed distances from the talus edge. At each distance one plot from each pair was randomly assigned the pika removal treatment while the other served as the control. The transects were each 3.5 m long with the three paired plots centered on distances of 0.25 m, 1.25 m and 2.25 m. The plots were 0.5×1.0 m, with the long axis paralleling the talus edge. Pikas were excluded from the removal plots by small cages 0.5 m tall constructed from 2.5-cm mesh chicken-wire fencing stretched around a frame of 1.27-cm PVC pipes. Control plot corners were marked with nails. Control plots and exclosures were located so as to minimize the amount of bare rock included within the plots.

In August 1995, during peak biomass and immediately after the plots were established, one 10×25-cm strip of vegetation was clipped at ground level from each plot, sorted to species, dried in an oven for a minimum of 12 h, and weighed on an electronic balance. Since it was not always possible to identify sedges, grasses, and *Potentilla* to the species level on the basis of leaves alone, these plants were sorted to genus. Samples then were lumped into functional groups (forbs, sedges, grasses and cushion plants) for analysis. During peak biomass in August of 1996 and 1997 all plots were re-sampled; however, in each of these years four smaller 10×10-cm subsamples within each plot were clipped, dried, and weighed. The sampling

methodology was changed because the 1996 data suggested that plant species had a patchy distribution within plots. Sample locations were changed each year. When rocks comprised more than 20% of a subplot, the plot's location was systematically moved in order to avoid sampling areas where it was impossible for plants to grow. Statistical analyses from these two years were based on the average biomass of the four subplots from each plot.

Although marmots (*Marmota flaviventris*) and mountain goats (*Oreamnos americanus*) were briefly observed at the study site each year, they were not seen foraging near any of the transects. Other vertebrate herbivores frequent the Beartooth Plateau, but none were observed near our study sites. All transects were located within the foraging area of a pika, and pikas actively grazed in the general vicinity during each year of the experiment. Consequently, all effects of exclosure fences are ascribed to the removal of grazing by pikas.

Statistical analyses

The overall shapes of the grazing and haying distributions were compared to an even distribution using a chi-square analysis. The distances pikas traveled when haying were compared with the distances traveled when grazing using a chi-square contingency table analysis. This procedure was used to compare differences between sites in the distance pikas traveled when haying and when grazing. The average expected frequencies for all contingency tables were at least 6.0 when α was 0.05 and at least 10.0 when α was 0.01 (Zar 1996: 502).

A three-way ANOVA (site by distance by treatment [+ pikas, − pikas]) was performed on the 1995 total plant biomass. This pretreatment analysis indicated a highly significant interaction between site and distance ($F = 15.0$, df = 2, 30, $P < 0.001$). This suggests that the effect of pikas is not consistent across sites, perhaps because of differences in habitat structure. Consequently, all subsequent analyses evaluated each site independently using a repeated measures factorial analysis of treatment by distance. Analyses were run on total biomass and functional group biomass as well as the biomass of *A. rossii*, a species which has previously been shown to be an extremely important component of the winter diet of pikas (Dearing 1997a, b). Analyses were also run on the percent biomass of the four functional groups and *A. rossii*. Where necessary, two-way ANOVAs (distance by treatment) were performed to elucidate the effects suggested by the repeated measures analysis. Because each site had to be analyzed separately, the sample size was reduced from 6 to 2, resulting in a substantial loss of statistical power. As a result, although we adopted a traditional α level of 0.05, we also report P values ≤ 0.1 so that the reader can assess the importance of each effect.

Results

Habitat structure

The structure of the talus slide varied dramatically from site to site. The talus at Site 1 was relatively homogeneous with few small intra-talus vegetation patches comprising a mere 2% of the slide. The slope at Site 2 also was relatively homogeneous, but its edge was much more convoluted than that of Site 1 and there was nearly twice as much intra-talus vegetation, with plants covering just over 4% of the total area. The talus at Site 3 was the most fragmented and had extensive patches of intra-talus vegetation comprising nearly 21% of the total area. Based on this assessment, we ranked the three sites according to their degree of fragmentation as follows: Site $3 \gg$ Site 2 > Site 1.

Pika behavior

Pikas foraged most frequently on vegetation found within and immediately adjacent to the talus, regardless of whether they were haying ($\chi^2 = 128$, df = 5, $P < 0.001$) or grazing ($\chi^2 = 208$, df = 5, $P < 0.001$). The number of trips decreased rapidly with distance from the talus edge (Fig. 1). This decline was most precipitous at Site 3 and most gradual at Site 1. Thus, the three sites define a gradient of foraging behavior with pikas venturing farthest into the meadow at Site 1 and foraging nearest the talus at Site 3 (Fig. 1, Table 1). Pikas ventured significantly farther when haying than when grazing at Sites 1 and 2, but not at Site 3 (Fig. 1, Table 2). At Site 2 pikas foraged most intensely in the abundant edge habitat (Fig. 1).

Pikas at all three sites were intensely vigilant. Pikas spent much of their total time scanning their surroundings (mean $\pm$ SE = 39% $\pm$ 5%). Pikas most often surveyed their surroundings from the safety of the talus and were often seen perching on rocks near their haypiles (Fig. 2). Neither the ratio of the time vigilant: time foraging nor the total number of looks per minute foraging increased as distance increased. In fact, at all three sites, pikas were in the talus for the vast majority (mean $\pm$ SE = 81% $\pm$ 2.1%) of the total time they spent being vigilant, repeatedly choosing the same perch to scan their surroundings. Once pikas left the talus, they tended to concentrate their efforts on foraging behavior with proportionally more time spent on first grazing and then haying as distance increased.

Effects of pikas on vegetation

In 1995, before exclusion of pikas, there were no significant differences in total vegetative biomass between controls and exclosures ($F = 0.234$, df = 1,18, $P > 0.5$). Total biomass varied with distance, but these effects

were not consistent across sites (Fig. 3). The initial distance effects were most pronounced at Site 1, where the biomass of vegetation increased markedly with
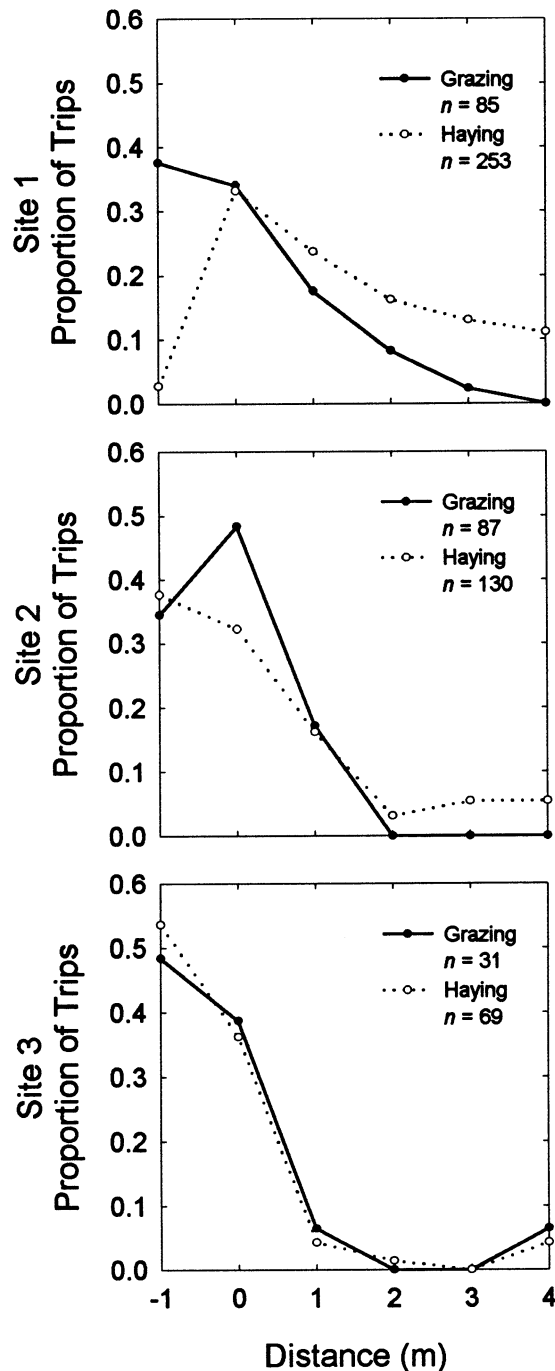

Fig. 1. Proportion of foraging trips made by pikas at each site to each of six distances when grazing and haying. The number of observations, n, for each distribution is provided in the upper right hand corner of each panel. Distance "0" indicates the talus-meadow interface and that distance "−1" indicates intra-talus vegetation patches.

Table 1. Results of chi-square analysis of contingency tables comparing the distributions of the distance pikas traveled when haying and when grazing. For both behaviors, the overall tests are reported first followed by the paired comparisons between sites. Degrees of freedom are calculated as (rows-1) × (columns-1). Cells with an expected number of observations equal to zero were excluded. For $P < 0.05$ the average expected frequency was at least 6.0 and for $P < 0.01$, the average expected frequency was at least 10.0.

Behavior	Null hypothesis[1]	df	χ^2	P
haying	Site 1 = Site 2 = Site 3	10	144.3	<0.01
	Site 1 = Site 2	5	94.4	<0.01
	Site 2 = Site 3	5	12.4	<0.05
	Site 1 = Site 3	5	133.8	<0.01
grazing	Site 1 = Site 2 = Site 3	10	28.9	<0.01
	Site 1 = Site 2	4	11.4	<0.05
	Site 2 = Site 3	5	9.1	<0.05
	Site 1 = Site 3	3	11.5	<0.05

[1] The null hypothesis indicates which sites are being compared.

distance. The reverse pattern was seen at Site 3, where initial biomass declined significantly as distance increased.

Excluding pikas resulted in a rapid reversal of the trend in total biomass observed in exclosures at Site 1 (Fig. 3). At the experiment's end, total vegetative biomass decreased with distance within exclosures while it continued to increase with distance in the control plots at Site 1, as suggested by the marginally significant repeated measures distance × treatment effect ($F = 4.95$, df = 1,8, $P = 0.057$). This interpretation is bolstered by a two-way ANOVA performed on the 1997 total biomass which indicated a significant interaction of distance and treatment ($F = 10.6$, df = 1,8, $P = 0.012$). There were no such effects of pika herbivory at Sites 2 and 3 (Fig. 3). Consequently, the remainder of our analysis focused on the patterns observed at Site 1.

Effects of pika removal on plant functional groups at Site 1

Pika exclusion resulted in a rapid increase in the biomass of forbs and sedges and, to a lesser extent,

Table 2. Results of chi-square analysis of contingency tables comparing pika grazing to pika haying behavior. The overall test comparing grazing to haying is reported first followed by paired comparisons comparing the grazing to the haying distribution at each site. For all four tests, the null hypothesis is that the distributions are the same for haying and for grazing. Degrees of freedom and expected values were calculated as in Table 1.

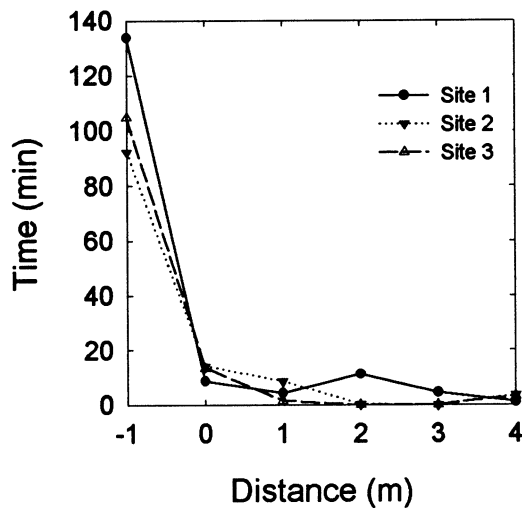| Site	df	χ^2	P
Overall	5	53.1	<0.001
1	5	87.4	<0.001
2	5	15.6	<0.01
3	4	1.0	>0.1

Fig. 2. Total time pikas at each site were observed being vigilant by distance. Distances as in Fig. 1.

grasses. In 1995, before the exclusion of pikas, the biomass of forbs was greater in plots more distant from talus. By the experiment's end, the exclusion of pikas caused a significant increase in the biomass of forbs in plots immediately adjacent to the talus (Fig. 4) as indicated by the marginally significant distance × treatment interaction ($F = 4.02$, df $= 1,8$, $P = 0.080$) and significant year × distance interaction ($F = 7.02$, df $= 2,16$, $P = 0.006$) of the repeated measures analysis. The majority of this increase was due to *A. rossii* (Fig. 4) which increased significantly in plots near the talus edge as indicated by the year × distance × treatment interaction ($F = 3.63$, df $= 2,16$, $P = 0.050$). However, there was not a significant change in the relative abundance of forbs or of *A. rossii* near the talus between 1995 and 1997.

Sedges increased markedly in response to exclusion of pikas (Fig. 4) as indicated by a significant year × distance interaction ($F = 8.52$, df $= 2,16$, $P = 0.003$) and a marginally significant year × treatment interaction ($F = 3.28$, df $= 2,16$, $P = 0.064$). The biomass of grasses also appeared to respond to removal of pikas (Fig. 4), increasing in exclosures near the talus edge, but this increase was not significant (distance × treatment $F = 0.118$, df $= 1,8$, $P = 0.7$). However, neither the relative abundance of sedges nor grasses changed significantly over time.

The biomass of cushion plants did not change with distance, nor did it respond to the removal of pikas (Fig. 4). However, the relative importance of cushion plants was affected by the exclusion of pikas from the experimental plots. As the biomass of the other three functional groups increased within the exclosures, the relative importance of cushion plants decreased. As a result, the initial pattern of declining importance of cushion plants with distance seen in 1995 was obscured.

By 1997, cushion plants were relatively unimportant in all plots at all distances (Fig. 5). This interpretation is supported by the significant repeated measures year × distance interaction ($F = 5.19$, df $= 2,16$, $P = 0.018$).

Discussion

Pikas behave as predicted by central place foraging theory

As seen in other studies (Huntly et al. 1986, Huntly 1987, Holmes 1991), pikas on the Beartooth Plateau produced a gradient of foraging pressure that decreased as distance from the talus edge increased. Pikas also were willing to extend their foraging farther into the meadow when haying than when grazing. Brown (1988, 1992) predicted that foragers should accept a higher degree of predation risk in order to harvest higher quality food items. Since pikas are more selective when haying (Huntly et al. 1986, Dearing 1996) they should be willing to increase their foraging effort to meet the needs of a more restrictive winter diet. This willingness to travel farther when haying was previously documented by Huntly et al. (1986). On the Niwot Ridge, Colorado, *A. rossii* is the pika's winter forage of choice, perhaps because of its ability to retard the decomposition of cached plant material over the course of the winter (Dearing 1997a). It comprises 60–77% of the pika's winter diet in this locale, far more that would be expected by its relative abundance in the environment (Dearing 1996). *A. rossii* is an important part of the winter diet of pikas on the Beartooth Plateau as well (H. McKim unpubl.) and our data show that pika's foraging efforts are responsible for reducing the biomass of *A. rossii* near the talus edge. We suspect that as the abundance of *A. rossii* and other preferred species declines, pikas are forced to travel farther to find the food items they need. These results are consistent with predictions (1a) and (1c) and provide strong support for our first hypothesis that pikas forage as predicted by central place foraging theory.

Pika foraging behavior varied significantly with habitat structure. As expected (prediction 1b), pikas infrequently foraged at distance when the availability of safer intra-talus vegetation was high. When intra-talus vegetation was abundantly available, pikas made fewer trips into the surrounding meadow. In fact, at Site 3, pika foraging was focused so completely on intra-talus vegetation that differences between distance-distributions of haying and grazing were undetectable. Conversely, at Site 1, where there were few opportunities to forage within the homogenous talus slide, pikas traveled much farther into the meadow to forage and ventured farther when haying than when grazing.

Pikas did not appear to increase their vigilance as the distance traveled increased (prediction 1d). This is

somewhat surprising considering the results of other studies of central place foragers. Hoary marmots (*Marmota caligata*), for example, increased their vigilance while foraging as their distance from refuges increased (Holmes 1984), as did yellow-bellied marmots (*Marmota flaviventris*) (Carey and Moore 1986), wild guinea pigs (*Cavia aperea*) (Cassini 1991), and blue tits (*Parus caeruleus*) (Lendrem 1983). Pikas appear to have adopted a slightly different strategy. We suspect that vigilance, which involves stillness, far from talus is too risky for pikas. Instead, pikas look more and longer from the safety of the talus and, when they enter the meadow, they move fast and forego vigilance, which minimizes time in the riskier habitat.

Foraging behavior and plant community responses depend on habitat structure

Consistent with prediction (1e), the effects of pikas on meadow vegetation were correlated with foraging activity. At Site 1, where foraging intensity was high, pikas reduced the total vegetational biomass and produced a predictable shift in the composition of the plant community that varied with distance. Conversely, at Sites 2 and 3, where foraging intensity in the meadow was moderate to low, the effects of pikas on the surrounding vegetation were negligible. However, we expect that their impact on the intra-talus plant community was severe.

Repeated measures	
treatment	*P* = .017
distance	*P* = .079
distance*treatment	*P* = .057
year	*P* = .001
year*distance	*P* = .001

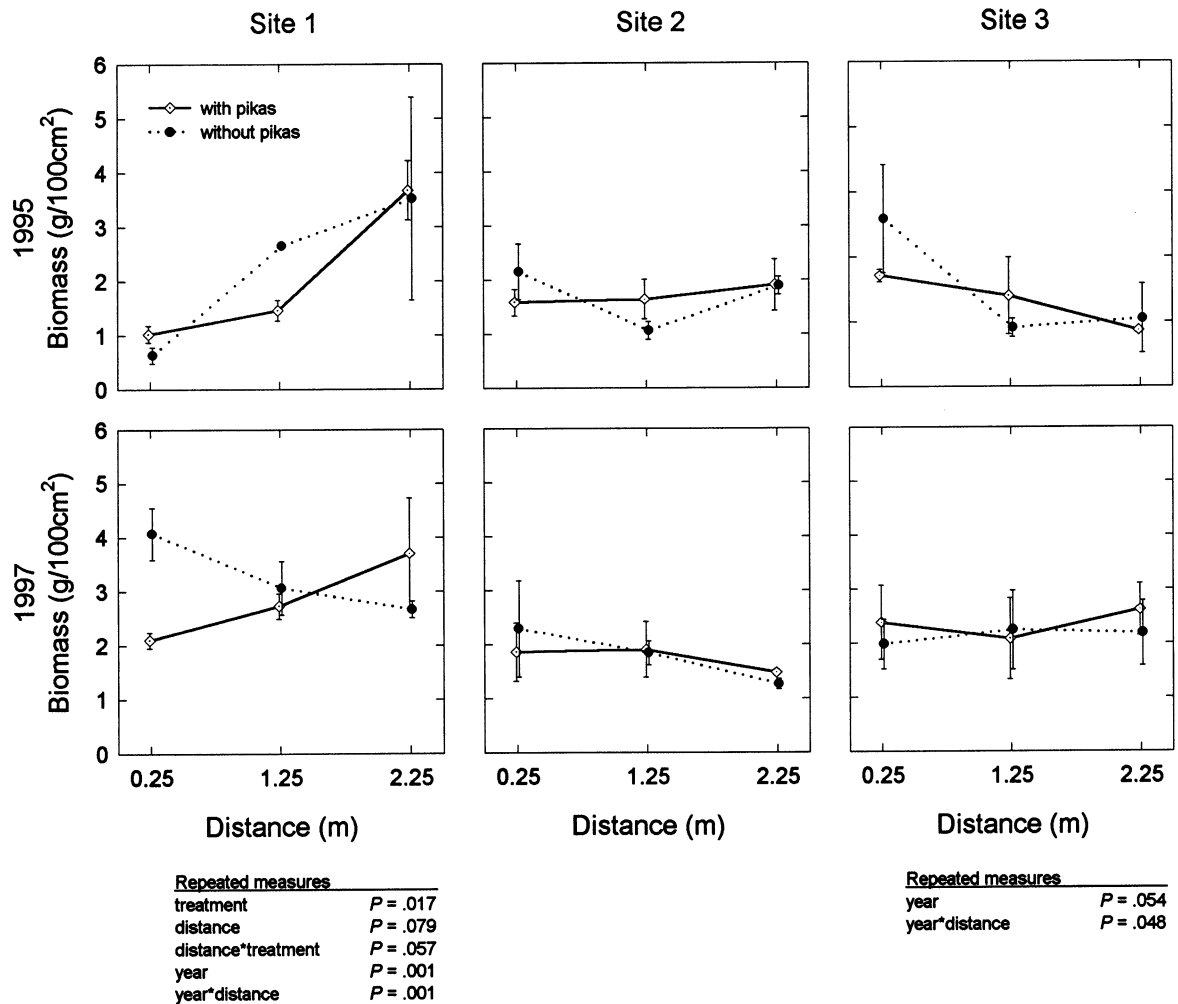| Repeated measures	
year	*P* = .054
year*distance	*P* = .048

Fig. 3. Average biomass of all plants by site in pika exclosures (without pikas) and their controls (with pikas) during the summers of 1995 and 1997. The 1995 data represent pre-treatment conditions as plants were sampled immediately after the exclosures were established. The 1997 data show the effects of excluding pikas for two years. Bars represent standard errors. *P* values reported below each pair of graphs are the results of the repeated measures analysis for all three years (df = 1, 8 for all between-subjects effects and df = 2, 16 for all within-subjects effects).

Fig. 4. Average biomass from Site 1 of the four functional groups (forbs, sedges, grasses, and cushion plants) as well as the common forb *Acomastylis rossii* in pika exclosures (without pikas) and their controls (with pikas) during the summers of 1995 and 1997. Symbols as in Fig. 3.
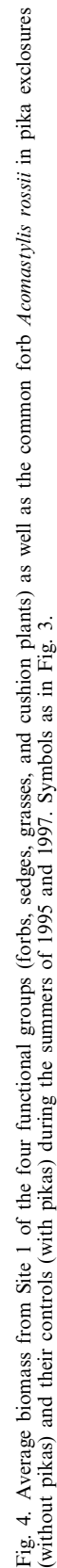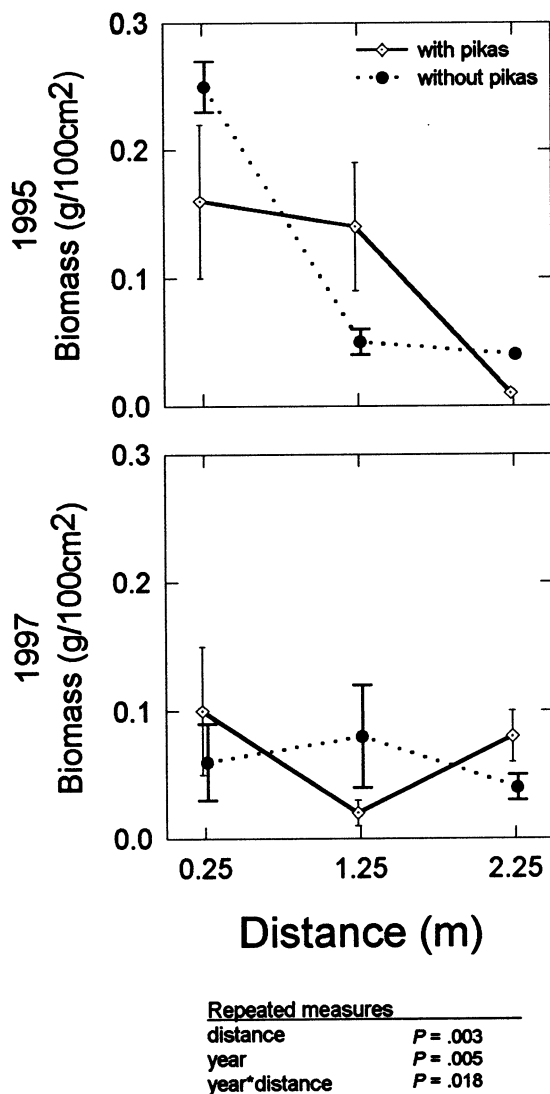
Fig. 5. Proportional biomass of cushion plants from Site 1 in pika exclosures (without pikas) and their controls (with pikas) during the summers of 1995 and 1997. Symbols as in Fig. 3.

The observed responses of plant functional groups to pika herbivory supported the hypothesis that cushion plants and sedges gain a competitive advantage when grazing pressure is high (prediction 2a), while forbs tend to dominate in the absence of herbivory (prediction 2b) when there is a premium on competition for resources (Tilman 1990). Although it would be necessary to manipulate the plant populations to demonstrate competition directly, the fact that pikas produced a shift in community structure similar to that observed previously (Huntly 1987) suggests that grazing acts to mediate competitive interactions in an alpine meadow.

These results parallel findings by Chase (1998) who demonstrated a gradient in trophic structure surrounding stumps in California meadows. He found that west-ern fence lizards, which are central place foragers, had less impact on their primary prey, grasshoppers, as the distance from the stumps they lived in increased. As predation pressure on the grasshoppers decreased, grazing pressure by grasshoppers increased, and plant biomass decreased. These two studies suggest habitat structure frequently causes spatial variation in trophic interactions and that the relative importance of predation and competition is likely to vary across any given landscape.

Implications for the importance of trophic dynamics in alpine systems

The alpine is a harsh environment, characterized by low water availability, cold short growing seasons, strong desiccating winds, intense ice-crystal abrasion, and limited nutrient supplies. Tundra plants often show rapid shoot growth after snow melt and are capable of metabolizing, growing and reproducing at low temperatures (Billings and Mooney 1968). Additionally, many species have low, prostrate growth forms and compact morphologies that allow them to take advantage of the more favorable microclimate near the ground (Callaghan and Emanuelsson 1985, Carlsson and Callaghan 1991). Some authors hypothesize that positive plant-plant interactions such as the provision of more favorable germination sites by existing "nurse-plants" (Carlsson and Callaghan 1991, Brooker and Callaghan 1998) are the key interspecific interactions in the alpine (but see Moen 1993 and Olofsson et al. 1999).

Although we do not dispute that positive-positive plant interactions may be important in some instances, we believe that the effects of grazing and of competition are often more important determinants of alpine community composition. This study demonstrates that herbivory by pikas has a strong effect on the biomass and species composition of alpine meadows and suggests that competition between plant species may be important when herbivory pressure is low.

Conclusions

This study shows how physical habitat structure and herbivore behavior can interact to shift the competitive balances and spatial patterns of an alpine plant community. We documented that habitat structure and the availability of intra-talus vegetation influences where pikas are willing to forage and, consequently, the degree to which pikas influence the structure of alpine meadows. Specifically, we demonstrated that pikas play a more important role in structuring the alpine meadows surrounding contiguous talus slopes where intra-talus vegetation is scarce. Similarly, we expect that

pikas also have a strong impact on the composition of intra-talus vegetation patches.

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