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FORAGING BEHAVIOR OF THE PIKA (*OCHOTONA PRINCEPS*), WITH COMPARISONS OF GRAZING VERSUS HAYING

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ABSTRACT.—Pikas (*Ochotona princeps*) inhabit areas with talus and forage on surrounding vegetation. Their foraging behavior was consistent with several predictions of central place foraging theory. Intensity of foraging decreased with distance from talus, whereas selectivity increased. Plant abundance and species richness increased with distance from talus. Differences between grazing (direct consumption of plants) and haying (harvesting and caching plants) behaviors appear to reflect differences in costs and benefits between these activities. Higher proportions of forbs and tall grasses were hayed than grazed. When haying, pikas traveled significantly farther into the meadow from the talus border than when grazing. Pikas grazed year round, but hayed only during a restricted time (July through September) when plant biomass had peaked.

North American pikas (*Ochotona princeps*) are small, diurnal, herbivorous mammals that inhabit high altitudes and latitudes. They are invariably associated with talus (rock slides and boulder piles), where individuals hold territories from which they forage. Consequently, pikas are central place foragers (sensu Andersson, 1978; Covich, 1972; Orians and Pearson, 1979; Schoener, 1979); costs associated with foraging will vary with distance from talus. While most central place foraging models have expressed distance-dependent costs in terms of travel time, we believe that risk of predation varies with distance from talus and is a major cost influencing pika foraging. Pikas have distinct alarm-calls and retreat to talus in response to terrestrial predators; they are at considerably greater risk when away from talus (Conner, 1983, 1985; Ivins and Smith, 1983). When small rockpiles were provided near talus, pikas extended their foraging range and grazed around these, suggesting that distance to cover constrained foraging. The models of Rosenzweig (1974), Covich (1976), and Lima et al. (1985) explicitly consider predation as a foraging cost.

Although optimal foraging models have been successfully applied to analysis of foraging of many taxa (e.g., Kamil and Sargent, 1981; Krebs and McCleery, 1984; Pyke, 1984; Pyke et al., 1977), analyses of foraging of generalized herbivores have been relatively unsuccessful. The diets of generalized herbivores tend to be considerably broader than predicted from models (Lacher et al., 1982; Owen-Smith and Novellie, 1982; Westoby, 1974). This may in part reflect nutrient balancing constraints, which can be addressed using models of imperfectly- or non-substitutable resources (e.g., Covich, 1972; Pulliam, 1975; Rapport, 1980; Tilman, 1982). However, given the large number of locally present species and the large inter- and intraspecific variability in plant chemistry, modeling of herbivore foraging is probably intractable if each plant species must be regarded as a unique resource.

Alternatively, it may be possible to reduce specific herbivore biology to a few simple but realistic constraints and to group plants into categories that are relevant to these. This approach has been taken by Belovsky (1978) in his analysis of moose (*Alces alces*) foraging and in recent studies of other mammals (Belovsky, 1984a, 1984b, 1984c). Here, we compare foraging of the North American pika with several predictions of central place foraging theory. We consider the plants as groups defined by life form and growth rate, which are correlated with pika feeding

preferences (Huntly, 1985). We then compare the behavior of pikas while directly grazing with that while harvesting and caching plants.

Predictions for central place foraging pikas.—If foraging costs increase with distance from talus, two predictions follow as to allocation of foraging effort and selectivity among alternative foods (e.g., Andersson, 1981). A pika is expected to forage most near talus, where the cost of foraging is lowest. Also, as costs for a given plant type rise with distance while benefits remain constant, the selectivity of a pika is expected to increase with distance from talus.

These predicted patterns of foraging will, in turn, affect the distribution of vegetation used by pikas. If foraging intensity decreases with distance from talus, a gradient of plant abundance will be produced (Andersson, 1981). Reduction of vegetation will be greatest near talus and decrease with distance. Furthermore, a gradient from high to moderate grazing will produce a corresponding gradient in plant diversity (Connell, 1979; Lubchenco, 1978). Plant species richness is expected to increase with distance from talus, paralleling the gradient in grazing intensity.

Comparison of grazing and haying economics.—Pikas remain active year-round, feeding during winter on stored vegetation and from snow-tunnels (Krear, 1965; Markham and Whicker, 1973; Severaid, 1955). Pikas are therefore of particular interest as foragers because they both graze plants directly and gather and store vegetation (hay) in caches (haypiles) among the rocks. These two behaviors contribute in different ways to the fitness of a pika. Grazing must supply current metabolic requirements for maintenance and reproduction; haying contributes primarily to winter survival and successful initiation of reproduction in early spring (Smith and Ivins, 1983a). Constraints on these behaviors will therefore differ and will be reflected in the economics of grazing and haying. We compare grazing and haying with regard to vegetation selection, distance traveled to forage, and time investment.

METHODS

Pika foraging was studied 1979–1981 at two sites near the Rocky Mountain Biological Laboratory, Gothic, Gunnison County, Colorado, USA. Data were gathered in Copper Creek Valley (3,200 m elev.) and in Virginia Basin (3,400 m elev.). At Virginia Basin, pika population density was 4 to 7 animals per 100 m talus frontage. For detailed descriptions of the study sites see Smith and Ivins (1983a, 1983b) and Huntly (1985).

Vegetational abundance and grazing damage were measured in mid-July 1980 along transects perpendicular to the talus-meadow interface at Virginia Basin. Two 0.25×0.25 -m plots were censused by species for percent cover at 0.5, 1, 2, 3, 4, and 5 m distances along each of 10 transects. Cover was estimated using a 0.25×0.25 -m frame divided into a 10×10 grid; the number of squares in which a given plant species occurred was used to estimate cover. Grazing damage was estimated as percent vegetational cover showing removed leaves, flowers, or stems. All grazing damage was attributed to pikas. No other mammalian herbivores were observed or trapped near talus where pikas grazed (1979 through 1981), although pocket gophers (*Thomomys talpoides*) and voles (primarily *Microtus montanus*) were common in the meadow farther from talus. Because rock-covered area was assumed to be unavailable to plants, total rock cover was also measured and subtracted from 100 to estimate total available area for each quadrat. Cover was expressed relative to this corrected total area.

Plant species were grouped for analyses as grasses (including sedges), forbs (excluding cushion plants), and cushion plants. Cushion plants are forbs which grow as low matted clusters of basal rosettes with a common root system (e.g., *Sedum groenlandicum*, *Saxifraga bronchialis*, *Silene acaulis*). This growth form is most characteristic of alpine environments and includes many wintergreen species.

Data on foraging behavior of individual pikas were collected at 8 sites within Copper Creek Basin. At each locality all plant types were available. Data were collected during a two-week period of August 1981, when animals of both sexes were actively grazing and haying. Only adult resident animals observed for at least 10 grazing and 10 haying trips were included in the sample. Animals were observed from a position near the area used for foraging. The presence of an observer had no apparent effect on pika behavior.

Activity (haying or grazing), distance to point of foraging, and plant type taken were recorded for each foraging bout. Perpendicular distances from meadow-talus interface to the point of foraging were estimated to the nearest meter by comparison to previously established reference points. Plants harvested were further classified as tall or short grasses, forb leaves or flowering stalks, or woody plants. These were generally identified using binoculars while an animal was foraging. Occasionally inspection of the meadow was

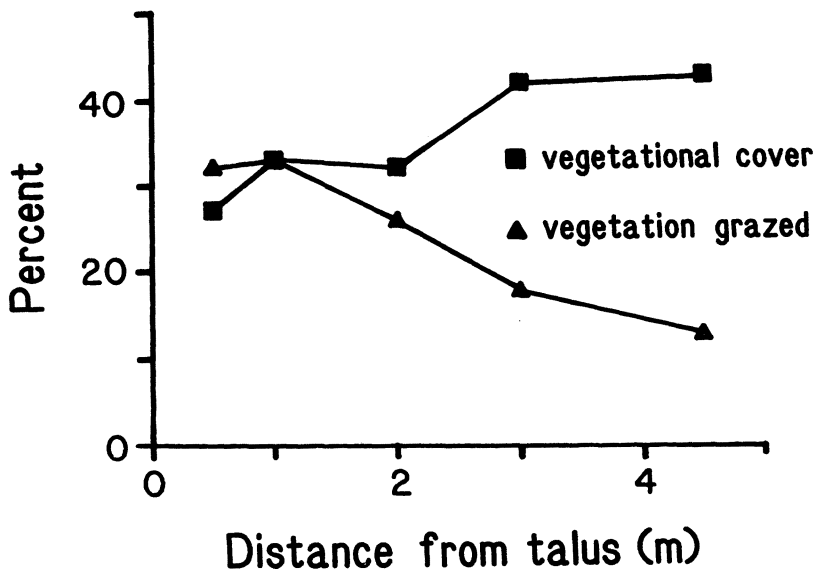


FIG. 1.—Distributions of percent vegetational cover and percent vegetation grazed at increasing distances from talus at Virginia Basin. Percent vegetation cover increases with distance from talus (Spearman $R = 0.9$, $P < 0.05$); percent vegetation grazed decreases with distance (Spearman $R = -0.9$, $P < 0.05$).

necessary to verify identification. When unambiguous identification could not be accomplished, these data were eliminated from the vegetation selection analysis (22 of 1,028 observations).

Seasonal patterns of pika foraging were determined from observations of marked individual pikas of known sex and age over two growing seasons (May through September, 1980 and 1981) at Cooper Creek. Behaviors were recorded at one minute intervals using focal animal sampling (Altmann, 1974). We calculated time spent haying and grazing for adult pikas of each sex by month.

RESULTS

Predictions From Central Place Foraging Theory

Distributions of percent vegetational cover and percent vegetation grazed showed that foraging intensity was highest near talus and decreased with distance (Fig. 1). As grazing decreased with distance from talus, total vegetational cover increased.

Near talus, all plant types were grazed by pikas. Cushion plants, however, were grazed only near talus and were rarely used, while forbs and grasses were used throughout the grazed area (Fig. 2). Use of forbs was highest overall across the transects, despite the relative rarity of this group near talus. Graminoid use declined more strongly with distance.

Plant species richness increased with distance from talus (Fig. 3). Species only occurring at greater distances were those preferred by pikas, particularly forbs.

Comparisons of Haying and Grazing Foraging Choices

Vegetation selection.—Grazing pikas tended to harvest different plant types than did haying pikas (Fig. 4). Relatively more grasses were grazed than hayed, and much of the difference between grazing and haying could be attributed to frequent grazing of short grasses. Forbs contributed a higher proportion of hayed vegetation, with flowering stalks contributing significantly more to total forb use in haying than in grazing.

Distance traveled to forage.—Pikas grazed closer to the talus than they hayed. For all observations ($n = 1,017$), the average grazing distance was 2.19 m ($SD = 2.13$), whereas the average haying distance was 7.49 m ($SD = 5.05$) (Mann-Whitney $t = 20.09$, $P < 0.001$). For all animals ($n = 24$), average grazing distance was 2.07 m ($SD = 0.90$), and average haying

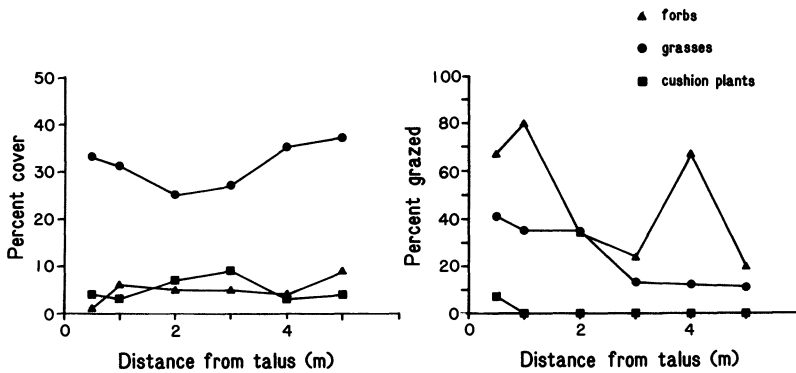


FIG. 2.—Distributions of percent cover and percent grazed for three categories of plants as functions of distance from talus at Virginia Basin.

distance was 7.07 m ($SD = 2.78$) (Mann-Whitney $t = 5.63$, $P < 0.001$). Although average grazing and haying distance varied among individuals, average distance traveled to graze was less than that traveled to hay for each pika observed. In addition, in 112 of 1,017 observations (11%), a pika both grazed and hayed during the same foraging bout. A pika hayed from the same distance as it grazed 49 times (43%); 62 times one traveled farther from talus before haying (55%); and only 2 times did one hay closer to talus (2%; $\chi^2 = 55.42$, $P < 0.001$). There were no significant differences between males and females in foraging distances (Mann-Whitney $t = 9$, $P > 0.90$, grazing; $t = 6$, $P > 0.41$, haying).

Frequency distributions of haying and grazing trips differed significantly (Fig. 5). Although both behaviors decreased in frequency with distance from talus, the decrease was more rapid for grazing. No grazing was observed beyond 10 m from talus in any locality sampled; haying was observed at up to 30 m.

Additionally, vegetation selection varied with distance from talus. Pikas hayed proportionately fewer grasses and more forbs from greater than 1 m from talus than from within 1 m ($\chi^2 = 19.06$, $d.f. = 2$, $P < 0.001$). Within forbs, proportionately more flowering stalks were hayed from the greater distances ($\chi^2 = 3.92$, $d.f. = 1$, $P < 0.05$).

Time investment.—Haying activity peaked in late summer to fall for both sexes (Fig. 6). Males, however, initiated a high level of haying prior to females. Total time spent foraging was similar for males and females from May through September (males: 5.10 min/h; females: 5.21 min/h), and represented a large proportion of a pika's total activity (Smith and Ivins, 1984). Females, however, allocated a higher proportion of foraging time to grazing than did males (74.6% versus 50.7%).

DISCUSSION

Central Place Foraging and its Influence on Vegetation

Pikas behaved as predicted by central place foraging theory. Intensity of foraging effort, measured either as percent vegetation grazed (Fig. 1) or percent trips per distance (Fig. 5), was highest near talus and decreased with distance. Consequently, a parallel gradient of vegetational abundance was expected. Percent vegetational cover did increase with distance from talus. Although an edaphic productivity gradient could also produce this distribution of plant abundance, experimental exclusion of pikas, using small wire mesh fences, resulted in significant increases in vegetation (Huntly, 1985). The increase in vegetation when pikas were excluded was largest near talus, as expected if pikas depress vegetation more near talus than at greater distances.

Foraging selectivity also varied as predicted from central place foraging theory. Within 1 m

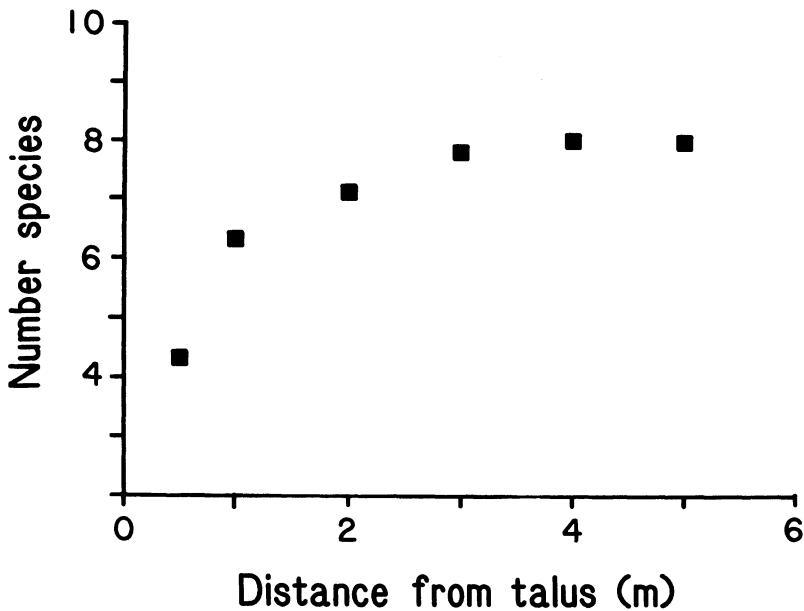


FIG. 3.—Average species richness (number species/area) for 0.25×0.25 -m plots within the area grazed by pikas at Virginia Basin. (Plots with greater than 20% rock cover were eliminated from calculation of means.)

of talus, all plant types, including the least preferred cushion plants, were used. With increasing distance from talus, pikas became more selective grazers: only forbs and the more preferred grasses were frequently harvested. Although neither absolute nor relative abundance of vegetation was constant along the distance gradient sampled, preference experiments in which pikas were offered choices among potted plants at each of several distances from talus supported this interpretation of preference and selectivity.

The plant diversity (species richness) gradient which existed across the talus-border meadow grazed by pikas was consistent with expectations from pika foraging. Species richness was lowest near talus, where pikas foraged most, and increased with distance from talus. This diversity pattern is consistent with the models of Lubchenco (1978) and Connell (1979) which postulate that 1) low levels of predation increase prey species diversity by suppressing dominance, and 2) heavy predation results in elimination of species. Experimental data also support the notion that pika foraging causes the observed gradient in species richness. Exclusion of pikas from grazed areas resulted in increased species diversity (Huntly, 1985).

Grazing and Haying Economics

Vegetation selection.—Pikas selected different classes of vegetation when haying than when grazing. Forbs and woody plants comprised a larger percentage of plants hayed than grazed. More flowering stalks were hayed than grazed, and tall bunch grasses were disproportionately represented among hayed versus grazed graminoids.

We suggest that vegetational characteristics which influence foraging economics cause the observed differences in plant preference between haying and grazing. Haying entails additional costs not present when grazing: hayed vegetation is transported to talus and undergoes a period of storage before being consumed. Both plant size and plant nutrient content could contribute to balancing these additional costs. Consumption rate while grazing is expected to be relatively independent of plant size. A haying pika, however, could increase harvest return rate by selecting larger plants. Suitability of vegetation for storage may involve either initial nutritional

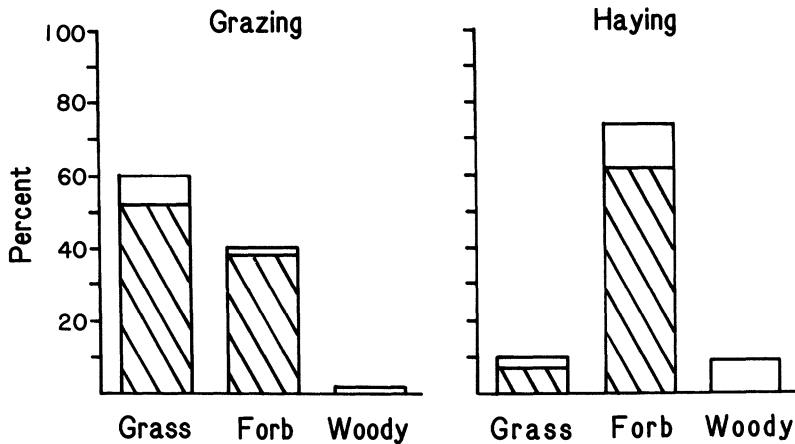


FIG. 4.—Proportions of total vegetation hayed and grazed belonging to each of five categories. Sample sizes: grazing = 418 trips; haying = 588 trips. Shaded portions of bars show short grasses and forb leaves; open portions show tall grasses and forb flowering stalks. Proportions of grasses, forbs, and woody plants ($\chi^2 = 198.87$, $d.f. = 2$, $P < 0.001$); short and tall grasses ($\chi^2 = 73.57$, $d.f. = 1$, $P < 0.001$); and forb leaves and flowering stalks ($\chi^2 = 15.58$, $d.f. = 1$, $P < 0.001$) differed between grazing and haying.

quality or rate of change in quality with time. Energy, vitamin, and protein contents of vegetation generally decline during storage (Stoddart et al., 1975; NRC, 1978). While we know of no data for relative decomposition rates of non-agricultural plants during open storage, haypiles show significantly lower nitrogen and carotene contents in spring than in fall (Paddock, 1961). Decomposition is apparent in spring.

Other studies support the generalization that plants hayed proportionately more often than grazed are larger or of higher nutrient content. Millar (1971) found that pikas selected different species when haying than when grazing, with haying preference correlated with plant size and/or local density. Also, pikas frequently harvest entire plants at ground level when haying; entire plants are rarely consumed when grazing. Higher protein, lipid, and energy contents were found in preferentially hayed plant species by Millar and Zwickel (1972) and West (1980). The higher variance in distance traveled to hay is consistent with our suggestion that pikas hay more selectively than they graze.

Distance traveled to forage.—Individual pikas hayed farther from talus than they grazed. This difference was true for each pika observed. Pikas therefore appeared regularly to travel farther than necessary when haying. Assuming that pikas are efficient foragers and that this behavior is adaptive, we suggest two factors that may be responsible for the discrepancy in grazing and haying distances.

1. *Effects of prior grazing.*—The effects of prior grazing may influence the distance from talus pikas travel to hay. Because haying occurs at the end of the growing season for plants, earlier grazing could deplete vegetation near talus. Longer-term, grazing-induced decrease of vegetation near talus clearly occurs (Huntly, 1985). Biomass is decreased and species composition is changed such that energy and protein contents of plants are greater beyond the area grazed. However, pikas continue to graze near talus during the haying season. Thus, there must also be some difference in suitability of vegetation for haying versus grazing for prior foraging to cause the difference in distance. If higher quality vegetation is required to hay and is sufficiently rare near talus, then pikas must travel farther on average while haying than while grazing.

2. *Resource husbandry.*—Haying at greater distances from talus than grazing could result from selection for sustained yield of vegetation near talus (resource husbandry). Resource husbandry may evolve in sedentary, territorial foragers; and resource use which appears suboptimal on a short time scale, but which results in increased longer-term yield, can result (Katz, 1974;

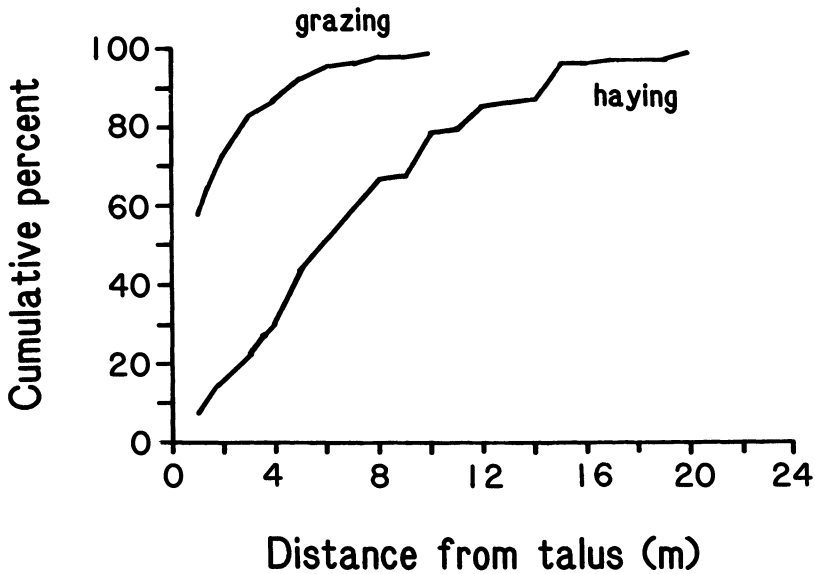


FIG. 5.—Cumulative frequency functions for haying and grazing at varying distance from talus at Copper Creek. Sample sizes: grazing = 440 trips; haying = 577 trips. Distributions differ significantly (two-sample Kolmogorov-Smirnov test, $d = 0.6$, $P < 0.005$).

Pyke et al., 1977). Pikas are good candidates for selection for long-term yield. Resident adult pikas are long-lived (Smith, 1978), most occupy a single area of talus for life (Smith and Ivins, 1983b), and the plant resources required by pikas are strongly influenced by previous local foraging (Huntly, 1985). Foraging patterns could evolve in which vegetation near talus was passed, while plants located farther from talus (and thus more expensive to harvest) were used.

Additionally, members of local pika populations are closely related (Glover et al., 1978), and kin selection could contribute to evolution of resource husbandry. If individual pikas do not reside on territories for sufficient time to experience resource depletion as a result of their own previous foraging, the inhabitants which do experience this will likely be closely related (Smith and Ivins, 1983a). Although the large overlap of grazing and haying distances (Fig. 5) does not suggest conservation of resources for grazing, further quantitative exploration of conditions under which pikas would evolve so as to optimize long-term yield is warranted.

An indirect benefit to heavy local grazing.—While pikas use vegetation nearest talus less heavily than they might, their grazing results in decreased plant biomass and increased occurrence of less nutritious plants (Huntly, 1985). Local depression of vegetation near talus may be advantageous to pikas by increasing visibility of diurnal terrestrial predators (e.g., weasels and martens). Pikas appear to avoid high vegetation and have been observed to pull up vegetation and produce open pathways in heavily vegetated enclosures (Markham and Whicker, 1973). Both avoidance of high vegetation and plant clipping not associated with foraging are also reported for prairie dogs, and there is evidence that they are subject to heavy predation when they cannot depress local vegetation (Hansen and Gold, 1977). Our observations of attempted predation on adult pikas have been exclusively of cases where the predator appeared from higher vegetation. The only cases of successful predation we have observed (2) occurred while a pika was beyond the grazed area (Ivins and Smith, 1983).

Time Investment

Seasonality.—While grazing occurs throughout the snow-free season, haying is strongly seasonal (Fig. 6). We suggest that seasonal change in vegetation which affects foraging economics may produce this pattern. Because haying entails additional costs not present when grazing,

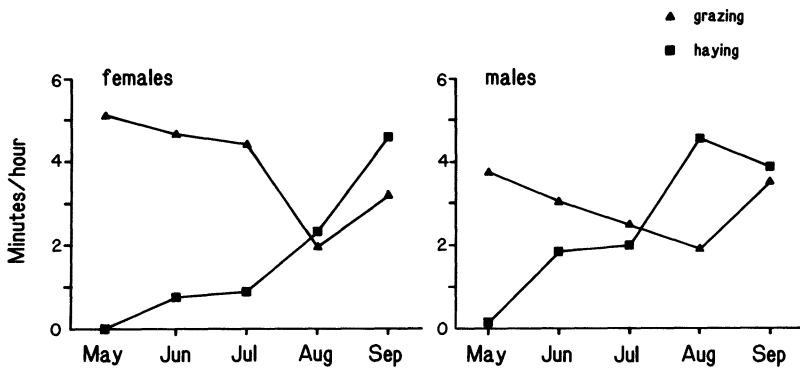


FIG. 6.—Allocation of time to haying and grazing for adult female and male pikas by month. Sample sizes (min): males = 1,254 grazing, 1,224 haying; females = 2,441 grazing, 833 haying.

haying may only be profitable given a threshold plant density or nutritional quality. Initiation of haying by pikas occurs as plant biomass and flowering peak (Millar, 1971; this study). In some managed prairies, both hay quality and long-term hay yield are maximized by cutting at a similar time, when significant nutrient translocation has not occurred and plant reaccumulation of reserves prior to winter is possible (Launchbaugh and Owensby, 1978).

Although haypiles rarely contain sufficient energy or protein to provide adequate sole resources for surviving winter (Johnson and Maxell, 1966; Krear, 1965; Millar and Zwickel, 1972; West, 1980), pikas cease haying before snowfall or obvious depletion of vegetation (Smith, 1974; this study). We suggest two factors which might cause early haying termination. First, vegetation quality may decrease with senescence until harvest and storage are less profitable than winter grazing from snow-tunnels. Reduction in food value could be produced by withdrawal of nutrients, particularly non-structural carbohydrate and nitrogen. Nutrient retranslocation from deciduous to perennating parts is well-documented, with large proportions of potentially limiting nutrients being seasonally redrawn (Chapin, 1980; Mattson, 1980; Rodin and Bazilevich, 1967). Second, the water content of vegetation decreases and haying becomes noisy at this time of year. A foraging pika in fall is thus conspicuous and may be more vulnerable to predation.

Comparison of males and females.—We found few sex-specific differences in foraging. Males and females did not differ in either diet selection or distance traveled to forage at the time of our observations. The proportional differences we observed in grazing and haying (Fig. 6) may be accounted for by the energetic costs of reproduction of females. All female pikas breed each year (Millar, 1974; Smith, 1978; Smith and Ivins, 1983a) and their high allocation of grazing time relative to males may be necessary to meet demands of lactation. Additionally, rate of haying by females may peak later than that of males because of the female's reproductive commitment earlier in the summer (Smith, 1978).

In conclusion, we have offered several hypotheses for the observed foraging of pikas. Our current data can only define, not test, these hypotheses; however, our suggestions are amenable to modeling and direct experimentation. We find this system particularly interesting because pika foraging both affects and is affected by local vegetation. Additionally, the behavior of the forager appears to be influenced by its predators. Further field studies are needed, in this and other plant-herbivore systems, which take account of both the influence of vegetation on foraging and the influence of foraging history on vegetation.

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