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Strategy of Food Plant Selection in the Siberian Northern Pika, *Ochotona hyperborea*

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Abstract

The rock-dwelling pikas of Asia and North America are suitable model species for studying foraging strategies of small generalist herbivores, because they collect and store green parts of plants for winter. In the past, contents of these stores were subjected to numerous studies but researchers differed in opinions on selective versus opportunistic plant-gathering by pikas. We analyzed plant species composition and their shares (%) in caches and in surrounding habitats in six territories of *Ochotona hyperborea* in Siberian mountains. We applied Ivlev's Electivity Index for assessing selectivity. We found that some plant species were evidently preferred and others avoided by caching pikas. Among the former, many were rich in secondary compounds, while among the latter, evergreen tuft-forming plants prevailed. Our data conform to earlier findings on selective foraging by the American pika *Ochotona princeps*, and prove great similarity in winter diet of both species. We discuss possible cues used by rock-dwelling pika species to choose which plants to collect, and suggest that their harvesting strategy is most economic in harsh high-mountain habitats.

Introduction

Pikas (*Ochotona* spp.) are important components of alpine zone ecosystems in Asian and North American mountain ranges. Both plants and animals of alpine habitats are now threatened by global warming (Krajick, 2004); therefore, ecological studies of these highly vulnerable species should be intensified in order to provide reference data (at the beginning of the climate change) and to predict and monitor ongoing changes in their populations. Moreover, pikas are ideal model animals for studying foraging strategies of small generalist herbivores. They are among the few mammal species that store green parts of plants for winter. During late summer (July–September) they simultaneously collect two different diets, one for immediate consumption and another for storing (Huntly et al., 1986; Dearing, 1996). The winter diet of mountain-dwelling pikas is especially interesting, for two reasons. First, their caches are easily accessible for investigators, and the content can be precisely analyzed. Second, transportation of plants from alpine meadows to storing sites is energetically costly and involves increased predation risk (Ivins and Smith, 1983). Therefore, the optimization in foraging should be evident in pikas selecting plants for transportation and long storage. But do pikas actively select plants for their winter stores?

Opinions of researchers studying Asian pikas, *O. hyperborea* and *O. alpina*, and those studying the American pika, *O. princeps*, differ considerably in this respect. In the studies of Asian rock-dwelling pikas, it was found that pikas were opportunistic folivores that did not display any evident selectivity in food choice (Krivoshayev, 1971; Khlebnikova, 1976; Yudin et al., 1976; Revin and Boeskorov, 1990). The number of plant species they utilized well represented the species composition of the surrounding meadows (Kapitonov, 1961; Travina et al., 2000) and the most readily eaten and collected were those plants which were most common in the area (Cherniavski, 1984; Voronov and Basarukin, 1992). While these observations concerned the majority of plants, some were preferred more than others (Travina et al., 2000), and some plant species were collected by pikas rarely, if at all (Kishchinski, 1969). In the case of the American pika, more recent studies generally indicated significant selectivity by pikas toward

plants offered by a surrounding habitat (Millar and Zwickel, 1972; Dearing, 1996; Roach et al., 2001). However, in older papers (e.g., Bailey, 1936; Broadbooks, 1965, and others cited by Millar and Zwickel, 1972), the opinion prevailed that American pikas utilized whatever plants were available. Is the difference in the results of studies of Asian and American pikas a matter of interspecific difference or of different research methods?

In order to solve this problem, we examined the composition of plants stored for winter in six territories of the northern pika, *O. hyperborea*, and in the immediate vicinity of storing places. We then assessed food selectivity by several means, including those used in the studies on American pikas. In particular, we tested with help of several indices the alternative hypotheses: (1) random (non-selective) versus selective plant gathering by pikas, (2) absolute versus relative selectivity. Additionally, we considered the existing hypotheses about bases for plant selection by caching pikas and proposed additional selection cues.

Study Area, Materials, and Methods

STUDY ANIMAL AND STUDY AREA

The northern pika, *O. hyperborea*, is a Palearctic counterpart of the American pika, *O. princeps*, and shares many similarities in morphological features, life history, behavior, and habitat characteristics with the latter (Cherniavski, 1984; Smith et al., 1990; Gliwicz et al., 2005). In the Siberian mountain ranges, they are common in subalpine and alpine zones, where they are associated with rock slides interspersed with meadows.

The study was conducted in the southern part of Eastern Siberia, in mountains surrounding Lake Baikal, in the Khamar-Daban Range (Baikal Nature Reserve) and Baikal Range (Baikal-Lena Nature Reserve), during two research expeditions undertaken in August 2000 and August 2001. Climate of the studied regions is of the continental type, with a growing period lasting 120–130 days. Mean temperature of the coldest month (January) in the Khamar-Daban Range is -22°C and in the Baikal Range is -24°C ; the mean

temperatures in the warmest month (July) are 16°C and 12°C, respectively. In each region, three areas inhabited by northern pikas were selected. All study sites were situated in protected areas, where the natural vegetation was well preserved. They were located in the strata of subalpine or alpine vegetation and composed of naked rock slides surrounded by meadows.

The Osinovka study site was situated in the central part of the Khamar-Daban Range (51°31'N, 105°26'E) at an altitude of 1600 m, 8 km from the shore of Lake Baikal. The territories of three pairs of pikas (Os1, Os2, Os3) were investigated in August 2000. The territories Os1 and Os2 were situated above treeline and surrounded by alpine vegetation with a very rich forb community, and dwarf pine (*Pinus pumila*), alder (*Duschekia fruticosa*), and willow (*Salix* spp.). Territory Os3 was located below treeline, at the verge of taiga forest composed of *Pinus sibirica* and *Abies sibirica*. Floor-level vegetation was poor, dominated by ferns, grasses, *Bergenia crassifolia*, and *Rubus sachalinensis*.

The Izomrudne study site was located in the main part of the Baikal Range in the region of Solncepad Pass (54°40'N, 108°10'E) at an altitude of 1400 m. The territories of two solitary pikas (Iz1, Iz2) and one pair of pikas (Iz3) were investigated there in August 2001. The territories of Iz1 and Iz3 were situated in the subalpine zone and surrounded by a rich association of dwarf shrubs and shrubs and some herbaceous vegetation. The rock slide with Iz2 territory was located in the zone of larch forest-tundra, and was overgrown by lichens (*Cladonia*, *Cetraria*). Around the talus, vegetation was dominated by dwarf shrubs (*Vaccinium uliginosum*, *V. vitis-idaea*, *Ledum palustre*, and *Empetrum nigrum*).

FIELD METHODS

The study of plant species composition in the pikas' stores and in the surrounding habitats was carried out in the second half of August in six territories of individually recognized pikas (Gliwicz et al., 2005). August is the month of the most intense harvesting and storing in Siberian mountains, when pikas have been reported to make an average of 5.7 round trips with plant material per hour (Khlebnikova, 1976). Therefore, at the end of August in each of the studied territories, the storing sites were full of stored plants and numerous (4 caches in the Os1 territory, 13 caches in Os2, 7 in Os3, 6 in Iz1, 3 in Iz2, and 4 in Iz3). The contents of all caches were examined. The results of plant analysis of all caches in one territory were pooled. The items found in the stores were green parts of plants (and sometimes mushrooms). Each plant species was harvested by pikas in a characteristic manner, depending on the size of plant and on what part of it was collected. Usually these were stems of herbs and twigs of dwarf shrubs cut off at fixed length, bunches of grass or clumps of moss and lichens of a typical size, or single leaves. The prevailing form of a harvested item was used as a standard for counting plants found in caches and for assessment of the species availability in the habitat.

All plants were classified to species or one of the following higher taxonomic groups: sedges and grasses (graminoids), ferns, mosses, lichens, or fungi. The number of standardized specimens of each species or group was counted, and all plants were returned to the cache after analysis. Unidentified objects were numbered and collected for future identification. Exemplary specimens of identified plants were also collected. These were soaked in water, spread and dried for further confirmation of their taxonomic identity.

Our method of counting standardized specimens is equally as accurate as biomass measurements and, additionally, less invasive. Plant material found in caches is partly fresh and partly dry, so its mass cannot be measured *in situ*. Thus, it would be necessary to remove a substantial part of the pikas' stored food and take it to the lab (endangering pika winter survival), or alternatively, take only a small

sample of the storage (Millar and Zwickel, 1972). However, since the plant material in the piles is not homogenous but often stored in distinctive layers, the subsampling could cause a significant bias in the assessment.

Plants from the surrounding meadow were collected in places closest to the location of caches and/or in places where foraging pikas were observed. A wire ring of 40 cm in diameter was placed on the ground at a distance of 1–2 m from the rock/meadow interface, and all plants within the ring were cut. In each territory, plants from 10 to 38 circles were collected, depending on the length of the meadow strip visited by collecting pikas. Identification of plants and the counting of specimens were carried out according to the same protocol as cached plants.

The collected plants were identified by botanists on the staff of local nature reserves. The information on the content of tannins, toxins, and other secondary compounds in plant species collected by pikas comes from the book on chemical composition of most species of East Siberian forbs, shrubs, and mushrooms that may be of medical value (Telyatev, 1991).

STATISTICAL ANALYSIS

Plant species diversity in stores and in the environment was assessed by Simpson's Index (Krebs, 1989):

$$\frac{1}{D} = \frac{1}{\sum p_i^2}, \quad (1)$$

where $1/D$ = Simpson's reciprocal index and p_i = proportion of species i .

As a measure of preference, the Ivlev's Electivity Index (Krebs, 1989) was used:

$$E_i = \frac{r_i - n_i}{r_i + n_i}, \quad (2)$$

where E_i = Ivlev's electivity measure for species i , r_i = percentage of species i in the store, and n_i = percentage of species i in the environment.

Results

NON-SELECTIVE VERSUS SELECTIVE COLLECTION

Species composition and quantitative distribution of plants in hay stores of pikas were assessed in six territories and compared with species composition and percentage distribution of plants available on meadows surrounding each territory. The list of species and their share in the stores ("collected") and on the meadow ("available") are presented in Appendix A.

If pikas, when food storing, randomly choose plants available to them in a nearby meadow, we would expect the following: (1) there would be a significant correlation between diversity of plants growing on nearby meadows and those found in the hay stores; (2) numerical distributions of species present in stores and on the meadow (assessed for each territory separately) would not differ significantly; and (3) plants encountered most often in the stores would be those most common in the meadow.

The first prediction was tested by means of Simpson Index of species diversity, calculated separately for species composition found in stores in each territory, and for plant diversity in the adjacent meadow (Appendix A). No consistent relationship was found between those two values; in some cases species diversity in stores was much lower than in the habitat (e.g., 1.81 and 4.94, respectively, in Iz1), and in some higher (e.g., 5.57 and 3.37, respectively, in Iz2). Overall correlation between values of those two indices for all six territories

was not significant ($R^2 = 0.25$, $n = 6$, $P = 0.31$), indicating that plants were not collected randomly.

The second prediction was tested by comparing distributions of plants collected versus those available by chi-square test, for each territory. The test indicated highly significant differences ($P < 0.0001$ or $P < 0.00001$) between compared values in all six cases (Appendix A), supporting conclusion of non-random selection.

However, since the less common plants could be neglected by opportunistic pikas, the third test concerned only plants that were the most common in the food stores and in the habitat. We checked whether the three most abundant species in each territory (written in a bold font in Appendix A) were among the plant species most common in the neighboring meadows. We considered a plant species to be common if its share in vegetation was above 10%. Among the 18 plant species (3 species \times 6 territories) which were analyzed, 9 were not common in the habitat surrounding the territory, and 9 were common. Among the latter ones, pikas selected some species even more frequently than by random choice. Such active selection of the most common plants was evident in five cases out of nine (the food item no. 2 on the list in the territory Os1; and the food items no.1 in the territories Os2, Os3, Iz1, and Iz3; Appendix A).

The hypothesis of non-selective collection of plants by food-caching pikas was not supported, although the result of the last test indicated that high abundance of a plant in the vicinity may be the reason for including it in the diet.

SELECTIVITY: ABSOLUTE OR RELATIVE?

Positive or negative selection for each plant species in each territory separately was assessed by Ivlev's Index of Electivity (Appendix A). Index values E range from +1 (full preference) to -1 (full rejection). After grouping plants with similar values of the Electivity Index into 10 classes, three discrete categories of preference emerged (Fig. 1). Based on this distribution, we considered the species with E below -0.4 to be avoided by pikas, those with values -0.4 to +0.4 to be neutral, and those with E above +0.4 to be positively selected by pikas.

To assess how much pikas were intentional in their choice or rejection of plant species, we examined a consistency in plant selection among territories. The analysis included 10 plant species or groups that were available in more than one territory (Table 1a). Some plants were consistently avoided or consistently preferred (the absolute selectivity), whereas others were preferred in one territory and avoided in another (the relative selectivity). Pikas demonstrated absolute preference for three plants, relative preference/avoidance for two, and consistent strong avoidance for five.

Additional information about *Ochotona* preferences was extracted from the analysis of plants that were positively selected by pikas only in one territory, but had the highest values of Electivity Index (0.75–1.0), or were found in the cache in a very high proportion (above 20%) (Table 1b). In the last category, the single most collected species was *Pentaphylloides fruticosus*, making up 73% of the hay stored in one territory, while its frequency in the nearby habitat was 15% ($E = 0.67$).

SELECTION CUES

The attempt was made to identify cues used by pikas when selecting plants for collection. When looking for those features of plants which could be attractive or repelling for pikas, we considered plant morphological form, its chemical contents (based on the literature), and whether it was evergreen or seasonal; in plants being positively selected by pikas in one area and rejected in another, the presence of other types of plants was taken into consideration (Table

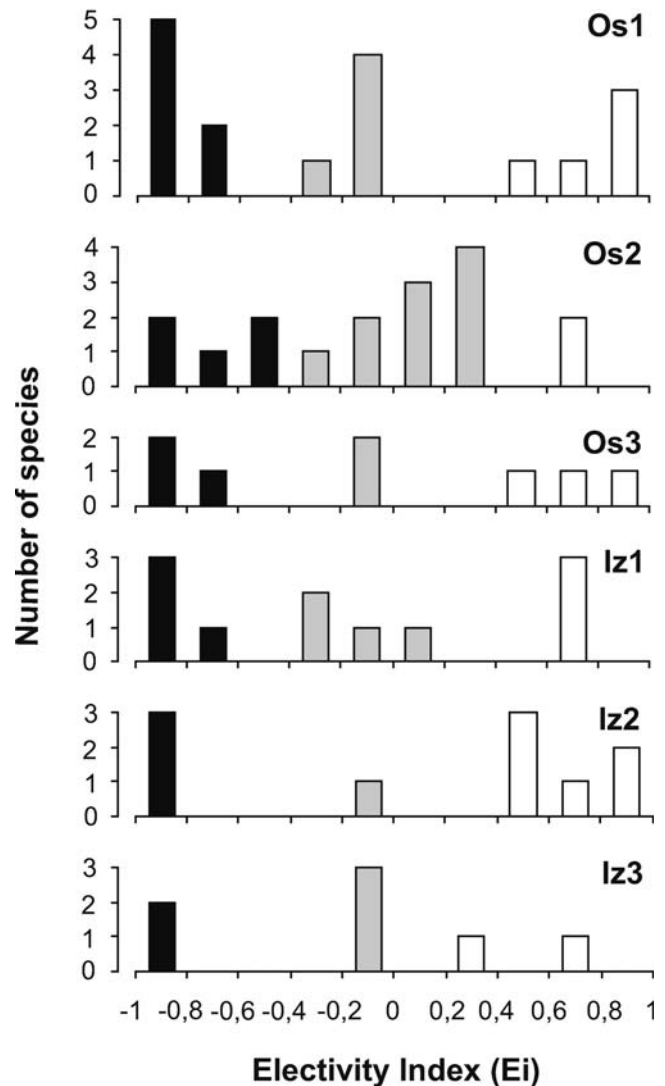


FIGURE 1. Distribution of plant species with different values of Ivlev's Electivity Index (E) found in six territories of the northern pika, *Ochotona hyperborea*. Three groups of plants were distinguished: avoided ($E < -0.4$; black bars), neutral (E between -0.4 and $+0.4$; gray bars), and preferred ($E > 0.4$; white bars). For the list of species and their Electivity Index values, see Appendix A.

1). The most obvious results of this search are the following characteristics: (1) the most consistently rejected species were growing in the form of cushions or were evergreen (non-seasonal); (2) among those relatively selected were dwarf shrubs and monocotyledons, and their utilization could depend negatively on the local richness of dicotyledonous forbs; and (3) many species positively selected by pikas are known as plants containing tannins and other secondary compounds, including durable toxins.

Discussion

Our data confirm the hypothesis about non-random selection of plants available to *O. hyperborea* in the surrounding habitat. They show that despite earlier published results, this species is equally as selective as its close relative *O. princeps* when caching. However, among plants collected by northern pikas in the highest quantities quite often were those most common in the surroundings; sometimes they

TABLE 1

Characteristics of plants toward which pikas were strongly selective, (a) in several studied localities, and (b) in a single locality. Data about secondary compounds and chemical proprieties of plants from Telyatev (1991).

Species or group	Electivity <i>E</i>	Morphology	Relevant characteristics
(a) Plants present in several localities			
Plants consistently avoided (absolute negative selectivity)			
<i>Bergenia crassifolia</i>	-1, -1, -1, -0.08	herb	rich in tannins
<i>Empetrum nigrum</i>	-1, -1	dwarf shrub	evergreen, contains toxin (andrometoxin)
Mosses	-1, -1	tuft-forming	evergreen
Lichens	-0.94, -0.92	tuft-forming	evergreen
Conifers: <i>Pinus pumila</i> , <i>Picea obovata</i>	-1, -1	dwarf or young trees	evergreen
Plants positively or negatively selected (relative selectivity)			
<i>Vaccinium myrtillus</i>	0.87, 0.78, -0.17, -0.60, -0.69	dwarf shrub	avoided in the areas rich in forbs (Os1, Os2); rich in tannins and glycosides
Grasses and sedges	0.46, 0.23, -0.52, -0.78, -0.91	herbs (in clumps)	avoided in the areas rich in forbs (Os1, Os2, Iz2)
Plants consistently preferred (absolute positive selectivity)			
<i>Rhaponicum chamarense</i>	0.89, 0.75	herb	rich in tannins and other secondary compounds
<i>Rubus spp.</i>	0.73, 0.73	shrub	rich in tannins
Mushrooms	0.93, 0.75, 0.73, 0.40, 0.20	solitary	rich in tannins
(b) Plants positively selected in a single locality			
<i>Filipendula ulmaria</i>	1	herb	rich in tannins
<i>Caltha palustris</i>	1	herb	contains toxin (proanemonin)
<i>Aconitum septentrionale</i>	0.77	herb	contains toxin (aconitine)
<i>Pentaphylloides fruticosa</i>	0.67 (73% in Iz1) ¹	shrub	rich in tannins and alkaloids ("Kurilian tea")
<i>Solidago virgaurea</i>	0.43 (26% in Os1) ¹	herb	
<i>Lonicera pallasii</i>	0.41 (22% in Iz2) ¹	shrub	rich in glycosides

¹ The most often collected species in a given territory, making up high proportion of the hay stored.

were selected even more frequently than by random choice. Perhaps the high frequency of encountering a given item in a habitat helped animals to develop the best technique of harvesting and carrying the plant, and therefore to reduce the handling time, making this food type more profitable (Stephen and Krebs, 1986). As the pika caches frequently contained the most abundant of the meadow's plant species, some authors concluded that pikas were non-selective. However, when more precise methods of assessment of distribution of plant species present in the pika caches and in the habitat were introduced (Millar and Zwickel, 1972), selectivity of pikas became obvious.

There are three existing hypotheses about factors affecting winter diet selection by pikas: high nutrient contents, plant morphology facilitating transportation (both proposed by Millar and Zwickel, 1972), and high contents of secondary compounds (proposed by Dearing, 1996, 1997a, 1997b). Our data may be useful for testing only the latter two hypotheses, as we have no information on nutritive value of cached plants. Our results give support for the claim that pikas preferentially store plants rich in secondary compounds. To make the support stronger it would be necessary to measure the exact amount of tannins and other secondary metabolites in the species found in caches of the northern pika, as did Dearing (1997a, 1997b) for the American pika. He suggested that this preference arises from either better preservation of such plants in the cache or the increase in their palatability or digestibility after they dry. In the case of tannins, which were found to be very common in plants stored by pikas (Dearing, 1996, 1997b; our Table 1), it is well known that their negative effects—unpalatability and decreased digestibility of proteins and carbohydrates—are reduced by drying. Even farmers are advised to dry forage rich in tannins before they feed it to cattle. However, plants with high contents of other secondary compounds, especially toxins, may be unsuitable for consumption even after drying, because some toxins remain active, e.g., those present in *Aconitum*, *Veratrum*, in Ranunculaceae, and in some mushrooms, all of which were reported

from pika caches (Kishchinski, 1969; Khlebnikova, 1976; Travina et al., 2000). Khmelevskaya (1961) and Dearing (1996) specifically stressed the fact of high frequency of plants toxic to mammals in *Ochotona* caches. If those plants were toxic to pikas as well and could not be eaten even after they had dried up, then why were they collected? We suggest that pikas collect for winter mostly those plants that are untasty and therefore cannot be eaten immediately. Since a great majority of them become edible after drying, this strategy is still profitable for pikas, even if some stored plants remain useless. The other possible function of plants rich in secondary compounds indicated by Dearing (1996), better preservation of cached material, cannot be excluded. This possibility, however, became less attractive (as an explanation for caching definitely inedible plants) when experiments did not support preservative effects of such species on other plants present in caches (Dearing, 1997b). Our suggestion requires further research, including feeding experiments, which would allow testing of actual unpalatability and toxicity of some collected species.

As for plant morphology, Millar and Zwickel (1972) and Huntly et al. (1986) proposed that pikas should collect larger species, avoiding smaller plants like cushion plants as less profitable and difficult to transport. Utilizing shrubs and clumped herbs, pikas would maximize the amount of vegetation stored per unit of energy spent. We did not find a marked preference for specific forms of plants, except that dwarf shrubs and graminoids were collected less frequently in habitats rich in dicotyledons. A similar observation was made by Revin and Boeskorov (1990) and Dubrovski et al. (2000). On the other hand, negative selectivity towards cushion plants, mosses, and lichens was unanimously reported by all researchers from Asia and America. These data might support the suggestion about their low profitability for harvesting. However, when Dearing (1996) experimentally facilitated their harvesting, pikas still did not incorporate them into the winter stores, implying that the plants were excluded for other reasons. We

propose that the reason for their absence among stored plants is their evergreenness and availability in winter. Thus, it is not profitable to spend energy in summer for transporting plants which are equally available later. Pikas must supplement their winter diet with growing vegetation (Millar and Zwickel, 1972), and they are known to harvest evergreen forbs and lichens in winter (Conner, 1983). Moreover, pikas avoided storing other evergreen plants like conifers, which were available at ground level (Millar and Zwickel, 1972; Voronov and Basarukin, 1992; our Table 1a).

In summary, we propose that pikas, when selecting food plants, use very simple cues. In summer, they eat whatever is edible when fresh, while for winter they store whatever is non-edible in summer (possibly anticipating its improvement with time), and they do not store what will be accessible in the habitat in winter. We suggest that such an energetically economic strategy should be most rewarding in harsh high-mountain habitats of rock-dwelling *Ochotona* species, where food resources are scarce both in summer and in winter. For perfecting such a strategy, the experience of at least one successful wintering is needed. Therefore, we predict that the caches of young pikas will contain a smaller percentage of tannin-rich plants and a larger percentage of winter-green plants than the caches of older, more experienced pikas in the same habitat.

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References Cited

- Bailey, V., 1936: The mammals and life zones of Oregon. *North American Fauna*, 55: 112–117.
- Broadbooks, H. E., 1965: Ecology and distribution of the pikas of Washington and Alaska. *American Midland Naturalist*, 73: 299–335.
- Chemiavski, F. B., 1984: [*Mammals of Siberia's Far Northeast*]. Moscow: Izdatelstvo Nauka (in Russian).
- Conner, D. A., 1983: Seasonal changes in activity patterns and adaptive value of haying in pikas (*Ochotona princeps*). *Canadian Journal of Zoology*, 61: 411–416.
- Dearing, M. D., 1996: Disparate determinants of summer and winter diet selection of a generalist herbivore, *Ochotona princeps*. *Oecologia*, 108: 467–478.
- Dearing, M. D., 1997a: The function of haypiles of pikas (*Ochotona princeps*). *Journal of Mammalogy*, 78: 1156–1163.
- Dearing, M. D., 1997b: The manipulation of plant toxins by food-hoarding herbivore, *Ochotona princeps*. *Ecology*, 78: 774–781.
- Dubrovski, V. Yu., Ashchekina, Yu. A., and Shakhunyanc, L. A., 2000: The comparative analysis of food storages of two *Ochotona* species—*hyperborea* and *alpina* in northwest of the Putorana Plateau. *Byulletin Moskovskogo Obshchestva Ispytatelej Prirody, Otdiel Biologii*, 105: 38–42.
- Gliwicz, J., Witczuk, J., and Pagacz, S., 2005: Spatial behaviour of the rock-dwelling pika, *Ochotona hyperborea*. *Journal of Zoology*, 267: 113–120.
- Huntly, N. J., Smith, A. T., and Ivins, B. L., 1986: Foraging behavior

- of the pika (*Ochotona princeps*), with comparisons of grazing versus haying. *Journal of Mammalogy*, 67: 139–148.
- Ivins, B. L., and Smith, A. T., 1983: Responses of pikas (*Ochotona princeps*, Lagomorpha) to naturally occurring terrestrial predators. *Behavioral Ecology and Sociobiology*, 13: 277–285.
- Kapitonov, V. I., 1961: [Ecological observations on *Ochotona hyperborea* Pall. in the lower part of the Lena River]. *Zoologicheskij Zhurnal*, 40: 922–932 (in Russian, English summary).
- Khlebnikova, I. P., 1976: [Plant biomass used and stored by the northern pika in burned Siberian pine forests of Western Sayan Mts.]. *Ekologia*, 2: 99–102 (in Russian).
- Khmelevskaya, N. V., 1961: [On the biology of *Ochotona alpina* Pallas.]. *Zoologicheskij Zhurnal*, 40: 1583–1585 (in Russian, English summary).
- Kishchinski, A. A., 1969: [The pika (*Ochotona alpina hyperborea* Pall.) in the Kolyma Highlands]. *Byulletin Moskovskogo Obshchestva Ispytatelej Prirody, Otdiel Biologii*, 74: 134–143 (in Russian, English summary).
- Krajick, K., 2004: All downhill from here? *Science*, 303: 1600–1602.
- Krebs, Ch. J., 1989: *Ecological methodology*. New York: Harper-Collins Publishers.
- Krivoshcheyev, V. G., 1971: [*Ochotona alpina* Pallas (1773)—the Altai or northern pika]. In [*Mammals of Yakutia*]. Moscow: Izdatelstvo Nauka, 115–127 (in Russian).
- Millar, J. S., and Zwickel, F. C., 1972: Characteristics and ecological significance of hay piles of pikas. *Mammalia*, 36: 657–667.
- Revin, Yu. V., and Boeskorov, G. G., 1990: [Distribution and ecology of the northern pika (*Ochotona hyperborea* Pall.) in southern Yakutia]. *Byulletin Moskovskogo Obshchestva Ispytatelej Prirody, Otdiel Biologii*, 95: 48–60 (in Russian).
- Roach, W. J., Huntly, N., and Inouye, R., 2001: Talus fragmentation mitigates the effects of pikas, *Ochotona princeps*, on high alpine meadows. *Oikos*, 923: 315–324.
- Smith, A. T., Formozov, N. A., Hoffman, R. S., Zheng, Ch., and Erbaeva, M. A., 1990: The pikas. In Chapman, J. A., and Flux, J. E. C. (eds.), *Rabbits, Hares and Pikas*: 14–60. Gland, Switzerland: IUCN.
- Stephen, D. W., and Krebs, J. R., 1986: *Foraging Theory*. Princeton: Princeton University Press.
- Telyatev, V. V., 1991: [*Medicinal Treasures*]. Irkutsk: Vostochno-sibirskoe Knizhnoe Izdatelstvo (in Russian).
- Travina, I. V., Derviz, D. G., and Dmitriev, P. P., 2000: [Interactions between pikas (*Ochotona*, Mammalia) of Tuva and vegetation]. *Ekologia*, 1: 41–47 (in Russian).
- Voronov, G. A., and Basarukin, A. S. M., 1992: [The northern pika (Lagomorpha, Lagomyidae) on Sakhalin]. *Vestnik Zoologii*, 6: 58–63 (in Russian).
- Yudin, B. S., Galkina, L. I., and Potapkina, A. F., 1976. [*Mammals of the Altai-Sayan mountain country*]. Novosibirsk: Izdatelstvo Nauka (in Russian).

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Appendix A

List of plant species (or groups), their numerical and percentage distributions in the hay stores in six territories of the northern pika *Ochotona hyperborea* (collected), and in the samples of vegetation taken from nearby meadows (available). The most abundant species in stores in each territory are in bold.

On the basis of these data, Ivlev's Electivity Index for each plant species in each territory was calculated, as well as Simpson's Index of Diversity of plant species in the stores and on the meadow in each territory. Additionally, distributions of plants collected and available were statistically compared by chi-square test in each territory and found significantly different in all six studied locations.

TABLE A1
Territory Os1.

Species	Collected		Available		Electivity Index (<i>E</i>)
	<i>n</i>	%	<i>n</i>	%	
Ferns	346	28.2	409	34.4	-0.10
<i>Solidago virgaurea</i>	317	25.8	124	10.4	0.43
<i>Rhaponticum chamarense</i>	288	23.4	17	1.4	0.89
<i>Aconitum septentrionale</i>	75	6.1	10	0.8	0.77
<i>Caltha palustris</i>	47	3.8	0	0.0	1.00
<i>Swertia baicalensis</i>	45	3.7	53	4.5	-0.10
<i>Geranium krylovii</i>	25	2.0	43	3.6	-0.29
<i>Filipendula ulmaria</i>	14	1.1	0	0.0	1.00
<i>Cardamine macrophylla</i>	15	1.2	19	1.6	-0.14
<i>Saussurea</i> sp.	11	0.9	14	1.2	-0.14
Grasses and sedges	10	0.8	202	17.0	-0.91
<i>Cirsium heterophyllum</i>	4	0.3	39	3.3	-0.83
<i>Vaccinium myrtillus</i>	3	0.2	13	1.1	-0.69
<i>Galium boreale</i>	2	0.2	14	1.2	-0.71
<i>Rumex acetosa</i>	1	0.1	55	4.6	-0.96
<i>Duscheckia fruticosa</i>	1	0.0	47	3.9	-0.95
<i>Bergenia crassifolia</i>	0	0.0	122	10.2	-1.00
Other	27	2.2	10	0.8	0.47
Total	1231	100	1191	100	
Simpson's Index	4.81		5.65		
chi-square = 883.1; df = 16; <i>P</i> < 0.0001					

TABLE A2
Territory Os2.

Species	Collected		Available		Electivity Index (<i>E</i>)
	<i>n</i>	%	<i>n</i>	%	
<i>Geranium krylovii</i>	1198	24.6	509	14.2	0.27
<i>Anemone</i> sp.	1077	22.1	728	20.3	0.04
<i>Origanum vulgare</i>	759	15.6	326	9.1	0.26
<i>Rhaponticum chamarense</i>	443	9.1	46	1.3	0.75
<i>Galium boreale</i>	195	4.0	135	3.8	0.03
<i>Trollius asiaticus</i>	143	2.9	111	3.1	-0.03
<i>Thalictrum simplex</i>	126	2.6	57	1.6	0.24
<i>Saussurea</i> sp.	124	2.5	65	1.8	0.16
<i>Bupleurum longifolium</i>	118	2.4	173	4.8	-0.33
Grasses and sedges	95	2.0	227	6.3	-0.52
<i>Euphrasia pectinata</i>	90	1.8	30	0.8	0.38
<i>Tanacetum vulgare</i>	89	1.8	67	1.9	-0.03
Mushrooms	33	0.7	3	0.1	0.75
<i>Vaccinium myrtillus</i>	22	0.5	73	2.0	-0.60
Ferns	24	0.5	90	2.5	-0.67
<i>Maianthemum bifolium</i>	3	0.1	76	2.1	-0.91
<i>Bergenia crassifolia</i>	1	0.0	56	1.6	-1.00
Other	331	6.8	807	22.7	-0.54
Total	4871	100	3579	100	
Simpson's Index	6.58		7.55		
chi-square = 829.8; df = 16; <i>P</i> < 0.0001					

TABLE A3
Territory Os3.

Species	Collected		Available		Electivity Index (<i>E</i>)
	<i>n</i>	%	<i>n</i>	%	
Grasses and sedges	137	34.0	45	12.7	0.46
<i>Rubus sachalinensis</i>	134	33.3	18	5.1	0.73
<i>Vaccinium myrtillus</i>	80	19.9	5	1.4	0.87
Ferns	27	6.7	132	37.4	-0.70
<i>Sambucus sibirica</i>	13	3.2	12	3.4	-0.03
Mushrooms	3	0.7	1	0.3	0.40
<i>Picea obovata</i>	0	0.0	12	3.4	-1.00
<i>Bergenia crassifolia</i>	0	0.0	120	34.0	-1.00
Other	9	2.2	8	2.3	-0.02
Total	403	100	353	100	
Simpson's Index	3.68		3.61		
chi-square = 402.1; df = 7; <i>P</i> < 0.00001					

TABLE A4
Territory Iz1.

Species	Collected		Available		Electivity Index (<i>E</i>)
	<i>n</i>	%	<i>n</i>	%	
<i>Pentaphylloides fruticosa</i>	490	73.5	147	14.7	0.67
<i>Rubus</i> sp.	56	8.4	13	1.3	0.73
<i>Lonicera pallasii</i>	38	5.7	71	7.1	-0.11
<i>Rosa acicularis</i>	32	4.8	11	1.1	0.63
<i>Betula fruticosa</i>	17	2.6	42	4.2	-0.24
<i>Salix</i> sp.	10	1.5	32	3.2	-0.36
Grasses and sedges	7	1.1	86	8.6	-0.78
Lichens	3	0.5	113	11.3	-0.92
Mushrooms	1	0.2	1	0.1	0.20
<i>Empetrum nigrum</i>	0	0.0	29	2.9	-1.00
Mosses	0	0.0	384	38.3	-1.00
Other	13	2.0	74	7.4	-0.58
Total	667	100	1003	100	
Simpson's Index	1.81		4.94		
chi-square = 815.1; df = 10; <i>P</i> < 0.0001					

TABLE A5
Territory Iz2.

Species	Collected		Available		Electivity Index (<i>E</i>)
	<i>n</i>	%	<i>n</i>	%	
<i>Vaccinium vitis-idaea</i>	139	26.9	21	2.7	0.82
<i>Lonicera pallasii</i>	111	21.5	72	9.1	0.41
<i>Betula fruticosa</i>	85	16.4	45	5.7	0.48
<i>Ledum palustre</i>	66	12.8	103	13.1	-0.01
Mushrooms	59	11.4	3	0.4	0.93
<i>Sorbaria pallasii</i>	24	4.6	13	1.6	0.48
<i>Vaccinium myrtillus</i>	17	3.3	3	0.4	0.78
Lichens	9	1.7	400	50.7	-0.94
<i>Pinus pumila</i>	0	0.0	30	3.8	-1.00
<i>Empetrum nigrum</i>	0	0.0	55	7.0	-1.00
Other	7	1.4	43	5.5	-0.59
Total	517	100	788	100	
Simpson's Index	5.57		3.37		
chi-square = 615.8; df = 9; <i>P</i> < 0.0001					

TABLE A6
Territory Iz3.

Species	Collected		Available		Electivity Index (<i>E</i>)
	<i>n</i>	%	<i>n</i>	%	
Grasses and sedges	169	59.3	120	37.4	0.23
<i>Vaccinium myrtillus</i>	50	17.5	80	24.8	-0.17
<i>Bergenia crassifolia</i>	30	10.5	40	12.4	-0.08
<i>Rhododendron</i> sp.	25	8.8	28	8.7	0.01
Mushrooms	11	3.9	2	0.6	0.73
Mosses	0	0.0	19	5.9	-1.00
<i>Pinus pumila</i>	0	0.0	33	10.2	-1.00
Total	285	100	322	100	
Simpson's Index	2.48		4.21		
chi-square = 71.4; df = 6; <i>P</i> < 0.00001					