The Influence of High Quality Food on Habitat Use by Arctic Microtine Rodents

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We used laboratory feeding trials to test the palatability and quality of 25 species of vascular plants for two common species of microtine rodents, the tundra vole (*Microtus oeconomus*) and the singing vole (*M. miurus*), in northern Alaska. Tundra voles ate more (high palatability) and grew better (high quality) on sedges that were most abundant in the low, wet habitats favored by tundra voles; singing voles ate more and grew better on shoots of forbs and leaves of deciduous shrubs that were most abundant in the more mesic habitats preferred by singing voles. These results coincide with the diet composition for these voles in the field and support the hypothesis that each species selectively forages on food that is higher quality for it. Multiple regression analyses indicated that availability of high quality food items, or vegetational components associated with high quality food, accounted for 98% of the variability in the relative abundance of both species of voles in eight habitat types. We used these regression equations to predict the relative abundance of the voles at previously unsampled sites and found that predicted values were strongly correlated with observed values (r = 0.89 for tundra voles, r = 0.80 for singing voles). All of these results support the hypothesis that the availability of high quality food largely determines the relative abundance of voles in different habitats.

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Mammalian herbivores in general show strong habitat preferences, preferences usually thought to be associated with the availability of food, shelter from physical conditions or escape from predators or parasites (Crawley 1983). However, evaluation of the causes of habitat preference is not simple because a single habitat characteristic, such as vegetation, can provide food, shelter and escape. In this paper we examine the role of food, particularly the availability of high quality food, as a determinant of habitat preferences of herbivorous microtine rodents.

Within a given habitat, mammals generally select their food from a wide variety of available plants, but different herbivores show markedly different abilities (nutritional adaptations) to utilize particular plants (Crawley 1983, Robbins 1983, Hume 1985). Different

nutritional adaptations occur even within closely related species, as documented for microtine rodents by Batzli and Cole (1979) and by Jung and Batzli (1981). These observations and studies on the nutritional ecology of a variety of species led us to the working hypothesis that the availability of high quality food largely determines the patterns of habitat use by microtine rodents (Cole and Batzli 1979, Batzli and Jung 1980, Batzli et al. 1980, 1983, Lindroth and Batzli 1986).

The testing of our hypothesis requires good measures of food quality and habitat use. Physiological performance, such as growth of young animals, provides a simple measure of food quality, and relative density provides a simple measure of habitat use. Habitat use is not necessarily the same as habitat suitability, which is best measured by fitness parameters (Van Horne 1983). Un-

fortunately, habitat use (relative density) may vary through time. The ideal-free distribution, proposed by Fretwell and Lucas (1970), has been accepted as a partial explanation for patterns of habitat use (Partridge 1978, Krebs and Davies 1981, Rabenold and Bromer 1989) and predicts changing habitat use as overall population density changes. In such circumstances, factors controlling habitat use can not be studied separately from factors controlling population dynamics. However, consistent habitat preferences do occur in at least some fluctuating populations of microtine rodents, including lemmings and voles in northern Alaska (Batzli et al. 1983, Batzli and Henttonen 1990) and voles in Illinois (Cole and Batzli 1979), and this facilitates the analysis of habitat use by these animals.

In this paper we report a test of our hypothesis using previously unstudied populations of microtine rodents near Toolik Lake, Alaska. To do so, we first documented the relative densities (measured by a trapping index) and food habits of two species of voles in different habitats and found that the highest densities of each species occurred in habitats that contained the greatest abundance of their preferred food (Batzli and Henttonen 1990). If this correspondence between food habits and distributional patterns represents cause and effect as stated in our hypothesis, we expect: 1) that foods selected by voles in the field will be the most palatable when fed in the laboratory, 2) that the most palatable foods will be the highest quality (as measured by physiological performance) when fed in the laboratory, 3) that most of the variance in relative abundance of the two species of voles in different habitats can be accounted for by availability of high quality food and 4) that the relative abundance of voles can be predicted for previously unsampled habitat patches based upon the availability of high quality food.

Microtine rodents near Toolik Lake

Five species of microtine rodents occur near Toolik Lake, Alaska, which lies in the northern foothills of the Brooks Range (latitude 68°38'N, elevation 720 m). Of these, only two species are widespread and abundant, the tundra vole *Microtus oeconomus* and the singing vole *M. miurus* (Batzli and Henttonen 1990). Within preferred habitats the population densities of these two species vary synchronously, at least they did so over four summers during which densities differed by a factor of ten (5–50 per ha).

The relative abundance of voles in different habitat types and the vegetational composition of those types are given in Batzli and Henttonen (1990: Table 1 and Fig. 8). Here we briefly summarize those results. Tundra voles concentrate in low, wet habitats (meadows and watercourses), which have high abundance of rhizomatous sedges (particularly *Eriophorum angustifo-*

lium); whereas singing voles concentrate in mesic habitats (low slopes, steep slopes and rocky flats), which have high abundance of horsetails (*Equisetum arvense*), palatable forbs and/or deciduous shrubs (particularly *Vaccinium uliginosum* and *Salix glauca*). Both species occur at lower densities in transitional habitats between the wet and mesic habitats, but neither species occurs in the driest habitat (heath).

Stomach content analyses indicate that sedges form most of the summer diet for tundra voles (Batzli and Henttonen 1990), whereas dicotyledons and horsetails contribute most to the summer diet for singing voles. As winter approaches, the aboveground parts of monocotyledons and horsetails die back. Tundra voles then use roots and rhizomes of sedges as well as green stem bases, and singing voles take more dicotyledon leaves and green bases of grass shoots. These differences in food selection appear to reflect strong dietary preferences because they are maintained in the transitional habitats where both species occur.

Methods

Feeding trials

During June of 1985 and 1986 we collected animals from the field near Toolik Lake and set up breeding colonies in a large tent. Ambient temperatures prevailed in the tent, but it provided protection from wind and rain. All animals were kept in standard shoebox cages with dried *Sphagnum* spp. as bedding. Voles do not eat this moss (pers. obs.). We housed animals as breeding pairs (with unweaned young) or as groups of weaned siblings. Young were weaned when 20 d old. All animals received ad libitum rabbit chow, water and a daily supplement of fresh natural food when not in an experiment. During an experiment voles were housed individually and given restricted diets.

To determine palatability of plants, young adult voles (28 to 40 g) received at least 20 g of freshly cut, green shoots (herbaceous plants) or leaves (woody plants) of a single species of test plant for 12 h. Each day that a plant species was fed to voles, two 10-g samples were dried at 60°C to determine water content. During the trial, rabbit chow and water continued to be freely available, so the voles could maintain their mass without consuming any of the test plant. This procedure reduced any effect that hunger (voles can starve to death in 24 h) might have on consumption of the test plants. At the end of 12 h all remnants of the plants were collected, dried and weighed so that the amount consumed could be determined by difference. Substantial amounts of the test plants remained at the end of every trial.

All palatability trials took place during peak standing crop of the tundra vegetation, mid-July to mid-August of 1985, and each animal was fed the 25 different species

300

of plants on successive days. The 25 plants chosen were the most abundant species near Toolik Lake (uncommon species could not be collected in sufficient amounts to conduct trials). To minimize bias in consumption caused by order of presentation we varied the order in which we fed the plants to each vole.

During late July and early August of 1986 we examined the effect of plants with different palatability on growth rates of the voles to test the hypothesis that the plants most palatable to each vole species were also the highest quality for that species. Using palatability ratings from the previous summer's feeding trials, we chose the following grouping of plants to represent diets of decreasing quality: 1) Highly palatable diet – *Carex bigelowii, Eriophorum angustifolium Equisetum arvense, Er. vaginatum,* and *Polygonum bistorta* for tundra voles; *E. arvense, Petasites frigidus, P. bistorta, Salix glauca,* and *S. reticulata* for singing voles. 2) Moderately palatable diet – *Arctostaphylos rubra, Boykinia richardsoni, C. aquatilis, Epilobium latifolium,* and *S. pulchra* for both species of voles. 3) Slightly palatable diet – *Potentilla fruticosa, Pyrola grandiflora, Rubus chamaemorus, Vaccinium uliginosum,* and *V. vitis-idaea* for both species of voles. 4) Unpalatable diet – *Betula nana, Cassiope tetragonum, Empetrum nigrum, Ledum palustre,* and *Rhododendron lapponicum* for both species of voles. Identification and nomenclature for vascular plants follows Hultén (1968). Voucher specimens have been deposited with the Herbarium of the Dept of Plant Biology of the Univ. of Illinois at Urbana-Champaign.

We fed freshly cut samples of five species of plants (at least 5 g of each species) with similar palatability ratings to young voles (16 to 30 g) twice a day for three days, less time if they became lethargic or died. The appropriate experimental diet was added to the cages of each of the four treatment groups for five days before the beginning of the experiment, at which time rabbit chow was withdrawn. Substantial amounts of fresh food remained in all cages at the end of each day. We weighed each animal to the nearest gram at the beginning of each experiment and daily thereafter so that changes in mass could be used as a measure of physiological performance.

Sampling vole populations

Original measurements of the relative abundance of voles in different habitats were taken in July to September of 1984 and June of 1985 as part of a general survey of the microtine rodent community (Batzli and Henttonen 1990). We set Museum Special snap traps to sign in irregular lines in a wide variety of habitats around Toolik Lake and checked traps daily for three days before moving them to other habitat patches. During these 4867 trapnights we caught 208 tundra voles and 184 singing voles. Our purpose was to sample a maximum amount of terrain over a complete growing season. All

trap locations were marked by flagging tape and later classified by habitat type. These samples provided data for the dependent variables (number of voles per 100 trapnights as shown in Appendix 1) in multiple regression equations used to predict the relative abundance of voles in this paper.

The predictions from regression equations were tested by sampling previously untrapped vole populations in July and August of 1987 and August of 1988. In most cases we used patches of relatively uniform habitat that could hold a 0.25-ha grid (varying in dimensions from 25 × 100 m to 50 × 50 m); for three grids that contained mixed habitat types we assigned each trapping station to a particular habitat type. We established trapping stations at 5-m intervals, set one trap to sign near each station, and checked them daily for three days. We noted the location of all captured animals, identified them to species, weighed them, and necropsied them to determine reproductive condition (data on population structure and reproduction are reported in Batzli and Henttonen 1990).

Vegetation sampling

Using a combination of topography and vegetational composition, we previously classified eight major habitat types for voles along moisture gradients in the Toolik Lake region (Batzli and Henttonen 1990): 1. *Swales* – dense, wet sedge meadows in low areas with standing water; 2. *Watercourses* – willows and sedges in drainage areas with intermittent or permanent streams; 3. *Transition areas* – variable vegetation between wet and better-drained habitats; 4. *Low slopes* – moist, mossy slopes with shrubs, sedges, forbs and horsetails; 5. *Steep slopes* – better drained, shrubby slopes usually adjacent to low slopes; 6. *Rocky flats* – low areas, often by streams between lakes, with patches of shrubs and horsetails on large rocks; 7. *Tussock tundra* – upland tundra with continuous vegetation composed of sedges, shrubs, and forbs; 8. *Heaths* – upland tundra with sparse cover of evergreen shrubs and lichens on gravelly moraines.

To determine the vegetational composition within each habitat type we clipped 10–12 randomly placed quadrats (20 × 50 cm) at ground level during peak growing season – late July to early August. We then sorted the vascular plants by species as far as possible (vegetative parts of some congeneric species could not be separated), by leaf and stem for woody species, and by live and dead (litter) for non-woody material. All categories for each sample were then dried at 60°C and weighed to the nearest 0.1 g. We took the first set of samples in 1986 and used them to calculate independent variables (g dry mass per m² for each vegetational category) for the multiple regression equations that we used to predict vole abundance (calculations done using Stat View 512+ on a Macintosh IIcx computer). These samples came from the same habitat patches surrounding

Table 1. Palatability of 25 common plants to voles as measured by mean intake (g wet mass per 12 h) under standard conditions ($N = 6$). Ranks given in parentheses. Growth forms include rhizomatous monocotyledon (M), tussocky monocotyledon (T), forb (F), pteridophyte (P), deciduous shrub (D), and evergreen shrub (E).

Plant species	Growth form	Tundra vole	Singing vole
Carex bigelowii	M	7.55 (1)*	1.73 (12)°
Polygonum bistorta	F	7.37 (2)*	3.51 (3)*
Eriophorum angustifolium	M	6.54 (3)*	3.46 (5)*
E. vaginatum	T	6.45 (4)*	1.28 (18)°
Equisetum arvense	P	6.35 (5)*	3.66 (1)*
Petasites frigidus	F	5.09 (6)+	3.53 (2)*
Salix glauca	D	4.38 (7)+	3.48 (4)*
Epilobium latifolium	F	4.32 (8)+	2.36 (9)+
Arctostaphylos rubra	D	4.20 (9)+	3.04 (7)*
Carex aquatilis	M	3.86 (10)+	1.31 (17)°
S. reticulata	D	3.70 (11)+	3.32 (6)*
Boykinia richardsonii	F	3.42 (12)+	1.62 (13)°
Dodecatheon frigidum	F	3.35 (13)°	2.05 (10)+
Rubus chamaemorus	F	2.90 (14)°	0.99 (19)°
Dryas integrifolia	E	2.81 (15)°	1.81 (11)°
S. pulchra	D	2.17 (16)°	2.34 (8)+
Potentilla fruticosa	D	2.05 (17)°	1.55(14.5)°
Vaccinium vitis-idaea	E	1.92 (18)°	1.44 (16)°
V. uliginosum	D	1.83 (19)°	1.55(14.5)°
Pyrola grandiflora	F	1.70 (20)°	0.91 (20)°
Betula nana	D	1.37 (21)°	0.42 (24)−
Ledum palustre	E	1.21 (22)−	0.83 (21)°
Empetrum nigrum	E	0.92 (23)−	0.51 (23)−
Rhododendron lapponicum	E	0.05 (24)−	0.29 (25)−
Cassiope tetragona	E	0.09 (25)−	0.74 (22)−
X±1 SD		3.42±2.20	1.91±1.11

*highly palatable ($> \bar{X} +1$ SD), + moderately palatable ($> \bar{X}$, $< \bar{X} +1$ SD),° slightly palatable ($< \bar{X}$, $> \bar{X} -1$SD), − unplatable ($< \bar{X} -1$SD).

Toolik Lake that had been trapped for voles in 1984–85 and are summarized in Appendix 1. The second set of samples, taken to test the predictions of the regression equations, were clipped immediately after trapping new habitat patches for voles in July and August of 1987 and 1988. In 1987 we sampled habitat types 1–4 and 6–7; in 1988 we sampled types 1, 3, and 5–7. Type 8 was never resampled because neither species of vole ever occurred there.

Results

Feeding trials

Tundra voles generally consumed more of each plant than did singing voles, except for the plants that were unpalatable (Table 1), but the amounts consumed by the two voles were positively correlated ($r = 0.71$, Pearson's product-moment correlation, d.f. = 23, p < 0.001). As a result, the rankings of plants by the two species were also similar (rho = 0.77, Spearman's rank correlation, d.f. = 23, p < 0.001). We present data for

wet mass consumption in Table 1 because stomach fill depends on wet mass consumed. Calculations based upon dry mass consumption changed the rank order of plants somewhat (rho = 0.84 for wet and dry mass consumption by tundra voles, and rho = 0.74 for wet and dry mass consumption by singing voles; d. f. = 23, p < 0.001 in both cases), but designation of the most palatable and least palatable species changed little.

We divided the plants into palatability categories based upon mean consumption values and standard deviations from the mean as shown in Table 1. Though arbitrary, these criteria provided an objective way of grouping the plants. The same species of plants tended to be unpalatable to both species of voles. Thirteen plants fell into the unpalatable and slightly palatable categories for tundra voles; 11 of these were in the same categories for singing voles, and the six least preferred plant species were the same for both voles. There were more discrepancies among the higher ranks, however. Only three species of plants (*Polygonum bistorta, Eriophorum angustifolium,* and *Equisetum arvense*) were highly palatable to both vole species. Of the five plants
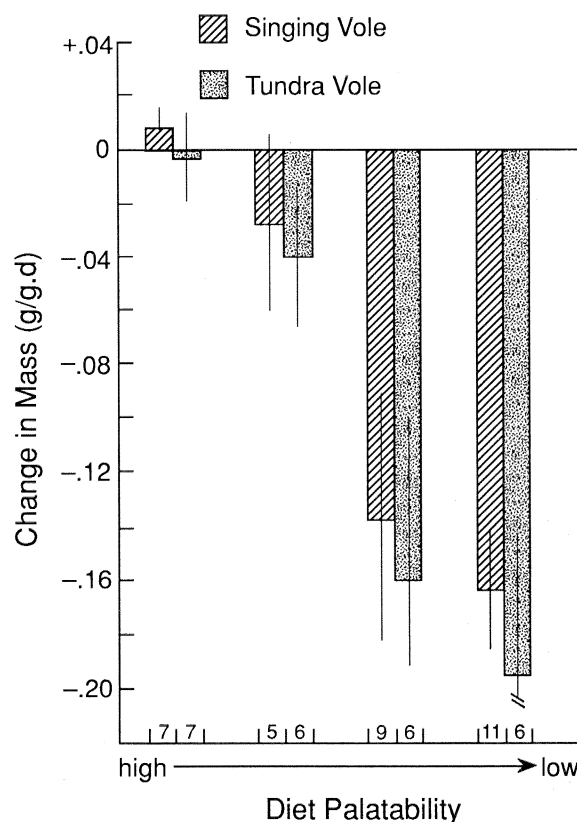

Fig. 1. Mean change in body mass (expressed as proportion per day) of young voles fed plants with different palatabilities (defined in Table 1). Vertical lines give 95% confidence intervals. Number of voles in each experimental group given at bottom of graph.

Table 2. Coefficients for multiple regression equations (d. f. = 7) used to predict abundance of two species of voles in different habitats. Dependent variable expressed as relative abundance of voles (captures/100 trapnights), and independent variables expressed as biomass (gm^{-2}) of green plant material.

Dependent variable	Independent variable	Regression coefficient	Significance level	Cumulative adjusted R^2
Tundra voles	*Eriophorum angustifolium*	0.366	<0.001	0.92
	Carex spp.	0.198	<0.005	0.98
	Intercept	−0.280		
Singing voles	*Vaccinium uliginosum*	0.274	<0.001	0.72
	Total forbs	0.582	<0.001	0.98
	Intercept	−1.242		

highly palatable to tundra voles, two (*Carex bigelowii* and *Eriophorum vaginatum*) were only sightly palatable to singing voles; and of the seven plants highly palatable to singing voles, four (*Petasites frigidus, Salix glauca, Arctostaphylos rubra*, and *Salix reticulata*) were only moderately palatable to tundra voles. Of the four monocotyledons tested, three were highly palatable and one moderately palatable to tundra voles, but only one was highly palatable and three were slightly palatable to singing voles. Of the five dicotyledons that were highly palatable to singing voles, only one was highly palatable and four were moderately palatable to tundra voles.

Changes in body mass of voles fed different groups of plants matched the palatability ratings of those groups (Fig. 1). Animals on the slightly palatable and unpalatable diets ate very little, lost body mass rapidly, and died or were removed from the experiment after one day. All voles on the highly palatable diet and all but two on the moderately palatable diets survived for three days,

but most of those on the moderately palatable diet slowly lost mass whereas most of those on the highly palatable diet maintained or gained mass.

Relative abundance of voles and composition of vegetation

Using biomass data (gm^{-2}) for the most palatable species of plants and for total litter, woody stems, monocotyledon shoots, forb shoots, leaves of deciduous shrubs, and leaves of evergreen shrubs as independent variables (see Appendix 1), we calculated step-wise multiple regression equations for the relative abundance (number captured per 100 trapnights) of each species of vole. A single independent variable, green biomass of the sedge *E. angustifolium*, explained 92% of the adjusted variance in tundra vole abundance among the eight habitat types (Table 2). The addition of

Table 3. Observed frequency, expected frequency (based on current vegetation and densities of voles in 1984–85), and adjusted expected frequency (based on current densities of voles) for captures of voles in a variety of habitats.

| Habitat type	Tundra Vole			Singing Vole		
	Observed (O)	Expected (E)	Adjusted (E×T$_o$/T$_e$)	Observed (O)	Expected (E)	Adjusted (E×T$_o$/T$_e$)
1987						
1	6	27.9	3.9	0	0	0
1–2	5	30.9	4.3	0	0.6	0.1
2–3	1	12.5	1.7	0	2.7	0.6
3	1	11.1	1.5	0	3.1	0.7
4–5	0	3.1	0.4	11	24.0	5.7
6	0	3.9	0.5	4	32.0	7.6
7	0	4.9	0.7	0	1.2	0.3
Totals(T)	13	94.3	13	15	63.6	15
1988						
1A	20	175.3	30.1	1	0.2	0.1
1B	29	109.6	18.0	0	0	0
3	2	19.6	3.4	0	0	0
5	1	1.4	0.2	9	0	0
6	3	14.4	2.5	16	54.8	22.9
7	1	5.2	0.9	0	7.2	3.0
Totals(T)	56	325.5	56	26	62.2	26
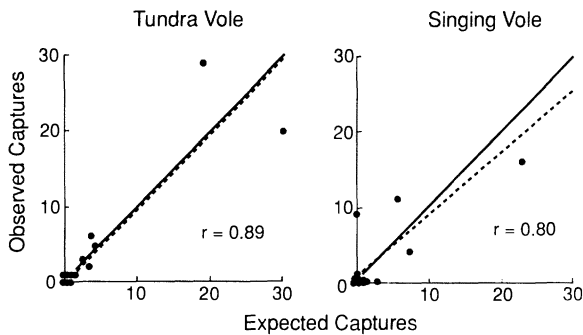
Fig. 2. Expected (adjusted for current density) and observed number of captures for two species of voles in a variety of habitats over two summers (1987 and 1988). Solid lines give expected position of points if expected and observed abundances coincided; dashed lines give regressions for the actual results. Correlation coefficients highly significant (d. f. = 11, p < 0.001 for tundra voles; d. f. = 11, p = 0.001 for singing voles).

a second significant variable, green biomass of other sedges (*Carex* spp.), increased the cumulative variance explained to 98%. For singing voles a single independent variable, green biomass of *V. uliginosum* leaves, explained 72% of the adjusted variance. Addition of a second significant variable, total green biomass of forbs, again increased the cumulative variance explained to 98%. No other combination of two independent variables, and we tried them all, gave R^2 values close to these.

We tested the general application of these regression equations to the Toolik Lake region by applying them to new sites that we sampled in 1987 and 1988. To do this we calculated the number of expected captures (predicted relative density from regression equations X number of trapnights for each habitat) and compared them with the observed number of captures. Because the absolute densities of voles varied by as much as ten-fold between the summers of 1984–85 and 1987–88 (Batzli and Henttonen 1990), we adjusted the expected number of captures for each habitat by multiplying with the ratio of total observed captures to total expected captures for each year. These adjustments made the totals for expected captures match the totals for observed captures (Table 3), which allowed direct comparison of the two.

Because expected frequencies were low we combined wetter habitats with more rhizomatous sedges (1–3) in one category and mesic habitats with more forbs and/or shrubs (4–7) in another before testing for significant differences among expected and observed frequencies. Some expected values were still low, so we used Yate's correction for continuity and found no significant differences (χ^2 = 0.87, d. f. = 1, p > 0.55 for tundra voles in 1987; χ^2 = 0.002, d. f. = 1, p > 0.90 for tundra voles in 1988; χ^2 = 0.64, d.f. = 1, p > 0.60 for singing voles in

1988; χ^2 = 1.61, d. f. = 1, p > 0.15 for singing voles in 1988).

Comparison of expected and observed results by simple linear regression gives a better indication of how well predictions and observations agreed (Fig. 2). Because this regression was meant to be descriptive rather than predictive, we used the geometric mean procedure to indicate the trend (Krebs 1989: 458). Data for 1987 and 1988 were combined because the slopes and intercepts of the regressions for each year were not significantly different (p > 0.05) for either vole. The high product-moment correlations indicated a strong relationship between the expected and observed captures (r = 0.89 for tundra voles and r = 0.80 for singing voles). Furthermore, the values for the intercepts (a) and the values for the slopes (b) did not differ significantly from 0 and 1, respectively (a ± 95% CL = 0.001 ± 2.655, b = 0.997 ± 0.305 for tundra voles; a = 0.519 ± 2.079, b = 0.836 ± 0.334 for singing voles). Given that the predictive equations were based on data from earlier years, the expected and observed results matched remarkably well.

Discussion

Our results provide strong support for the hypothesis that the availability of high quality food largely determines the pattern of habitat use by microtine rodents, which implies that shelter and escape play much less important roles. For both species of voles the food items preferred in the field were also the most palatable in the laboratory (Table 1). Only highly palatable plants consistently supported maintenance or growth in young animals (Fig. 1), which indicated that they were also the highest quality. Multiple regression equations that best explained the variability in relative abundance of tundra voles in different habitats included only highly preferred food items or vegetational components associated with highly preferred foods (Table 2). Furthermore, observed relative densities of tundra voles in newly sampled habitats closely matched those predicted by the multiple regression equations (Fig. 2). These results occurred largely because of the very high correlation between the abundance of tundra voles and *Eriophorum angustifolium* (r = 0.93), which confirmed our intuitive conclusion, arrived at after several years of trapping, that this sedge serves as an indicator species for the presence of tundra voles near Toolik Lake.

Though observed densities were significantly correlated with expected densities for singing voles as well (Fig. 2), the results were not as clearly supportive of our hypothesis. The independent variable that explained most of the variance in relative abundance, leaves of blueberry (*V. uliginosum*), was not a highly preferred food (Table 1). However, in August these shrubs produce highly palatable berries, which captive singing

voles readily eat and which are found in stomachs collected from the field (pers. obs.). The availability of these berries may have influenced the distribution of singing voles. Furthermore, the distribution of the blueberry was highly correlated (r = 0.67) with one other plant species, the willow *S. glauca*, whose leaves were highly palatable to singing voles. Finally, the second independent variable in the predictive equation (total forbs) was composed largely of species highly palatable to singing voles. Thus we view both blueberry leaves and total forbs as variables associated with availability of high quality food. An alternative view might be that blueberries and associated shrubs provide cover for the singing voles, particularly since the abundance of blueberry leaves was strongly correlated with total shrub leaves (r = 0.69) and total wood (r = 0.86) in the vegetation samples.

Given that *Equisetum* formed so much of the summer diet (Batzli and Henttonen 1990) and was a highly preferred food, the weak correlation between the abundance of *Equisetum* and singing voles (r = 0.38) surprised us. Indeed, after several years trapping we had come to look upon *Equisetum arvense* as an indicator species for the presence of singing voles in the Toolik lake area. The low correlation occurred primarily because we found no *Equisetum* in habitat 5 (steep, shrubby slopes) even though singing voles were abundant there. Habitat 5 occurred in narrow bands (10–50 m wide), almost always adjacent to habitat 4, which did contain *Equisetum*. It may be that singing voles living in narrow strips of habitat 5 had access to *Equisetum* in habitat 4 and that our statistical analysis of singing voles' relationship to *Equisetum* is misleading.

Given that our results indicate a strong influence of the availability of high quality food on spatial patterns of voles, it is tempting to extend our results to temporal patterns (population dynamics) of voles. The consistent habitat preferences shown by tundra voles and singing voles in spite of large population fluctuations through time (10-fold differences in density occurred over four summers, Batzli and Henttonen 1990) suggest environmental factors had similar effects on the populations in all habitats. If not, the relative abundances of voles among habitats would have differed among years. While synchronous changes in quality of available food in different habitats are possible, recent experimental results indicate that densities of microtine rodent populations respond to multiple environmental factors, including at least food and predation (Taitt et al. 1981, Taitt and Krebs 1983, Desy and Batzli 1989). Batzli and Henttonen (1990) also noted a negative relationship between the densities of predators and of microtine rodents near Toolik Lake.

A more likely extension of our results is to larger patterns of geographic distribution. High quality food has its major impact on vole populations via reproductive success (Batzli 1985, 1986, Desy and Batzli 1989), which spurs population growth even though negative factors such as predators and disease continue to take their toll. The main reason that habitats with more high quality food have greater population densities is because voles in these habitats maintain higher birth rates for any given density. When availability of high quality food in a habitat is so low that reproduction can not overcome losses, the population can not persist there (assuming no immigration). Thus the availability of high quality food may be a major factor affecting patterns of distribution for microtine rodents. Pitelka and Batzli (1991) have suggested a correspondence between distributional patterns of microtine rodents and their preferred foods on the North Slope of Alaska.

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Appendix 1. Data used for multiple regression equations summarized in Table 2. Vole trapping indices based on number of trapnights given in parentheses; mean values for vegetation based on 10 or 12 sampling quadrats.

	Habitat type							
	1 (729)	2 (478)	3 (891)	4 (613)	5 (389)	6 (511)	7 (954)	8 (292)
Dependent variables (captures/100 trapnights)								
Tundra voles	15.2	6.5	5.9	1.1	0	0.4	0.4	0
Singing voles	0	0.8	3.5	10.0	11.1	8.0	0.4	0
Independent variables (gm^{-2})								
Equisetum spp.	0.3	0.4	2.1	2.4	0	4.0	0	0
Carex spp.	16.0	9.1	21.5	4.5	2.4	2.1	10.8	0.5
Eriophorum angustifolium	34.2	12.2	3.6	0.2	0	0	0	0
E. vaginatum	0.7	<0.1	0	1.0	3.7	<0.1	12.0	0.8
Total Monocotyledons	50.9	24.4	26.8	7.5	6.8	3.6	22.8	1.4
Arctostaphylos spp.	0	0	1.5	9.1	0.2	0.4	0	21.2
Salix glauca	0	0	10.7	0	23.6	2.4	0	0
S. pulchra	3.0	67.6	11.9	2.7	0	15.9	0.6	0
S. reticulata	0	0	6.4	5.9	0	0	<0.1	0
Total *Salix*	5.8	72.4	30.3	11.3	32.8	32.4	0.7	1.8
Vaccinium uliginosum	<0.1	0	7.4	14.1	39.1	33.7	<0.1	0.4
Total deciduous shrubs	6.0	79.2	50.6	46.0	97.6	69.8	7.3	55.6
Total evergreen shrubs	0	<0.1	12.4	12.4	13.2	42.8	58.4	11.4
Boykinia richardsonii	0	0	0	0	2.5	0	0	0
Dodecatheon frigidum	0	0	0	0	0.4	0	0	0
Epilobium latifolium	0	0	0	1.2	0.6	0	0	0
Petasites frigidus	0.4	0.2	0.5	0	0	0	0.4	0
Polygonum bistorta	0	0	0.4	1.1	<0.1	0.3	1.1	0.1
Total forbs	0.9	2.5	5.6	12.1	2.4	0.8	4.2	0.3
Total green biomass	58.2	106.5	97.4	80.4	119.8	120.9	92.8	68.7
Herbaceous litter	546.4	159.2	221.8	168.7	502.8	453.8	240.7	169.6
Wood	29.9	331.1	174.3	81.8	695.2	546.2	116.6	102.0
Total litter	576.3	490.3	396.1	250.5	1198.0	1000.1	357.3	275.6