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Changes in habitat and in quality of food intake after a summer of grazing by fenced voles (*Microtus pennsylvanicus*)

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Nutritional components of individual plant species such as protein, nonstructural carbohydrates, neutral detergent fibers and total phenolics are commonly used to assess the quality of vole habitats and food selection. Although voles act individually on each plant species of their habitat, I question the use of such variables for following habitat manipulation by this small herbivore after a summer of grazing. I tested the reliability of using chemical analyses of green biomass from quadrat samples, and fecal matter of meadow voles (*Microtus pennsylvanicus*) for determining changes in habitat quality and food quality by confined animals. Voles were introduced into fenced plots during early summer and reached peak numbers of 350 animals/ha. Green biomass did not vary among the grazed plots, nor between grazed and ungrazed (control) plots after a summer of grazing activity. Chemical components of green biomass did not differ significantly between grazed and ungrazed plots. As a whole, green biomass samples were unreliable for detecting habitat quality changes after vole grazing. Food habit determinations from fecal remains showed that five herbaceous species were selected by confined voles. Moreover, fecal matter contained significantly more carbohydrates, total phenolics, and neutral detergent fibers in the heavily grazed plot compared with samples collected in lightly grazed areas, indicating that consequences of heavy grazing could be detected from such analyses. I conclude that chemical analyses of fecal matter rather than green biomass represent a better way of measuring out changes in food quality of vole habitats. Further studies are needed to know which categories of animals make up the fecal dropping samples in the field, and how much information is lost when samples are collected directly from animals or on bi-weekly or monthly schedules from dropping boards.

1. Introduction

Meadow voles (*Microtus pennsylvanicus*) show high selectivity for herbaceous plants (Batzli 1985). Nutritional ecologists have labored over comparisons of chemical constituents characterizing selected (consumed) and avoided (non-consumed) plants to identify specific nutrients in-

volved in food selection. High content of protein and nonstructural carbohydrates and low values of total phenolics and crude fibers characterize preferred plants (Servello *et al.* 1985, Bergeron & Jodoin 1987, Marquis & Batzli 1989). Voles fed selected plants ate more and grew better than animals maintained in the laboratory on avoided plants. This led Batzli and Lesieutre (1991) to consider the selected plants as high-quality food resources and to use these variables to define high- and low-quality rodent habitats. However, selection and palatability of plants vary between habitats (Batzli 1985, Caron *et al*. 1985) owing to local growing conditions (Fajer *et al.* 1992). Most of our knowledge on the quality of food and habitat of small herbivores is based on post-hoc chemical analyses of individual plant species after extensive use/availability studies and palatability experiments that serve to construct selection and ranking indices of food resources. Both processes are informative but extremely time consuming for extensive studies of vole habitats because they need to be performed in each studied habitat.

Intense grazing by voles reduces biomass of selected plants (Batzli & Pitelka 1970, Myllymaki 1977, Noy-Meir 1988, Bergeron & Jodoin 1993) although there are contradictory results as well (Andersson & Jonasson 1986, Moen 1990, Oksanen 1990). I argue that if voles make intensive use of high-quality plants which are known to contain more nutrients (protein, carbohydrates) and less digestibility inhibitors (phenolics, fibers), the plants remaining in intensively grazed habitats should be those with more phenolic and fiber contents. These variables could be detectable from samples of either biomass, or fecal matter. Changes in habitat quality or food quality after a summer of intense grazing could perhaps be assessed from chemical analyses of either the remaining plants, or of the vole feces. I also wanted to measure habitat quality through chemical analyses of fecal matter. Feces of non-ruminant mammals have been used for rapid and accurate diagnosis of quality of food intake. Fecal protein of snowshoe hares (*Lepus americanus*) and pocket gophers (*Thomomys bottae*) are highly correlated with dietary protein (r = 0.94, Loeb & Schwab 1989; r = 0.96, Sinclair *et al*. 1982). A recent study (Bergeron & Jodoin 1995) showed that feces of voles from intensively grazed plots during winter yielded significantly higher dosages of total nonstructural carbohydrates and total phenolics, which was thought to be indicative of low-quality food use. Using confined populations of meadow voles, I measured nutritional constituents (protein, carbohydrates, phenolics, fibers) of green biomass, and of fecal matter to evaluate changes of habitat and food quality in plots that were intensively grazed. My working hypothesis was that heavily grazed plots will show low nutrients and high defensive compounds in the remaining green biomass while feces of voles will yield high values of carbohydrates and phenolics which are indicative of low-quality food use.

2. Materials and methods

Six contiguous enclosures were located in a meadow reclaimed 10 years ago from agriculture. Each fenced plot was 10 m wide and 20 m long (0.02 ha) and was constructed of 1.6-mm thick galvanized metal sheets that extended 70 cm above ground and 30 cm belowground. Strips of vegetation 0.25 m wide were cleared three years prior to the present study from both sides of the fence with Simazine® as an herbicide. Clearing of vegetation was necessary to prevent and detect digging and inter-plot movements. The dominant plant species censused in all grids were timothy (*Phleum pratense*), red fescue (*Festuca rubra*), coughgrass (*Agropyron repens*), cowvetch (*Vicia cracca*), Kentucky blue grass (*Poa pratensis*), Virginia strawberry (*Fragaria virginiana*), and goldenrods (*Solidago* spp.).

Two of the six plots (nos. 4 and 6) were stocked with two pairs each of adult toe-clipped meadow voles (density 200/ha) in early summer (30 May) to simulate low grazing pressure. Four pairs of adult voles were released in two other plots (nos. 1 and 5) to simulate higher grazing pressure (400/ha). The last two plots (nos. 2 and 3) did not contain any voles, and were used as control grids. There was no attempt after this period to replace any missing vole or to modify their reproductive activity or population density. These voles came from our laboratory-reared colony, and were acclimated by pairs to the early summer conditions one month prior to their introduction in the fenced plots. Bi-weekly trapping was performed throughout summer until early fall (mid-October) with pitfall traps prebaited with a few drops of liquid commercial peanut butter extract 2 days prior to each trapping session. Since pitfalls underestimate the adult portion of unrestrained vole populations (Boonstra & Rodd 1984), I also used Sherman live traps in the last four trapping sessions to evaluate the bias for confined voles. Pitfalls and Sherman traps were equally spaced in each grid to offer 10 trap locations, and were protected by trap shelters. Traps were visited twice daily for two consecutive days to estimate the minimum number of voles alive. Peanut butter

and apples were used as bait in live traps while cotton served as bedding material. Sherman and Havahart traps were operated outside the fenced grids to catch escaping voles or to stop small to medium-size mammalian predators from coming in. Ungrazed plots were also trapped at every trapping session to prevent any grazing activity. A final removal trapping using Museum Special snap-back traps to make an absolute count of all animals present in each plot began in mid-October and lasted 10 days.

The quality of habitat and food were defined and measured as follows. Changes in vegetation were estimated from chemical constituents (protein, carbohydrates, phenolics, fibers) of green biomass samples collected before (early May) and after (early November) the summer grazing period in each plot. Green biomass was randomly collected from 7 quadrats of 100 cm^2 per grid (0.03% of the grid surface) which provides a good representation of plant biomass in qualitative and quantitative comparisons within fenced plots (Bucyanayandi 1991). Vegetation was cut 1 cm above ground, dried in a forced-air oven at 60°C for 48 h, weighed, ground to 1 mm in a Brinkmann mill, and stored at – 20°C until analysed. Plant utilization was determined from monthly samples of feces collected on 10 dropping boards spaced at 3-m intervals in each grazed plot. Two slides were prepared for each fecal sample following the procedures of Neal *et al.* (1973). Identifiable epidermal fragments were counted in 10 random fields for each slide. Counts for each plant species were transformed into relative frequencies by dividing such counts by the total number of identified fragments for all species. I did not apply any correction measures related to differential digestibility of plants from fecal analyses because I was using these data sets only for qualitative comparisons. Quality of food intake was evaluated from chemical analyses of vole feces collected from the 10 dropping boards of each plot before each trapping session. Empty boards gave rise to unequal sampling size. Feces were dried and ground in a mortar with pestle prior to analysis. Each green biomass sample was separated into three sub-samples and every fecal sample into two sub-samples to determine mean values of the sample within one enclosure for every chemical constituent tested.

Crude protein content was determined from total nitrogen ($N \times 6.25$ for plant material — Allen 1974, Maynard *et al.* 1979) according to the micro-Kjeldahl method developed by Lang (1958). Total phenolics were measured by colorimetric procedures (absorbance read at 765 nm) with gallic acid as standard (Singleton & Rossi 1965). Determinations of total nonstructural carbohydrates followed the technique of Da Silveira *et al.* (1978) using amyloglucosidase (Sigma Chem. Co.) for digestion. After enzymatic digestion, hydrolysis of carbohydrates into monomers was completed with 0.1 M (0.2 N) sulfuric acid (Smith 1969). Neutral detergent fibers were evaluated with the procedures of Goering and Van Soest (1970). Results are expressed as percentages of dry mass, and reported as means ± *S.E.*

Tests for normality of distribution for vegetation and feces were performed on the pooled data sets from each sampling time period. I used "skewness" in Statview procedures (Abacus Concepts Statview II 1987) to see if distributions were significantly different from 0 using the t-distribution test (Sokal & Rohlf 1981). For green biomass samples, logarithmic transformations were made for phenolics. For chemical constituents of fecal samples, logarithmic transformations were also used for values of nonstructural carbohydrates. Effects of enclosure and time of sampling on the chemical constituents of green biomass samples, and fecal matter were tested in two-factor ANOVAs. ANOVAs were performed using type III sum of squares in Super ANOVA computing procedures (Abacus Concepts Super ANOVA 1989).

3. Results

Population density of voles fluctuated in the four grazed plots during summer (Table 1). There is evidence that reproduction occurred in all fenced plots containing voles and that introduced adults resided on their respective grids all summer. For unknown reasons, some marked voles were never captured by pitfall traps. Few of the marked young animals produced in the grids during June and July were recaptured later in summer. No marked voles were trapped outside the fenced areas by Sherman live traps spaced 7 m along the perimeter. One vole succeeded in entering each of the control plots but it was moved to its original grid. Predators were often seen near the fenced areas, which might explain partly the recapture problems encountered in certain grids. Short-tailed weasels (*Mustela erminea*) were caught outside the enclosures, while red foxes (*Vulpes fulva*), coyotes (*Canis latrans*), marsh hawks (*Circus cyaneus*), and common garter snakes (*Thamnophis sirtalis*) were seen or heard near the experimental areas. In spite of such potential mortality factors, voles reached maximum densities of 350 animals/ha at the end of summer (September) but did not maintain such densities thereafter. Sexually active animals in all grazed plots were heavy adults (mean vole weight of 12 females, 40 ± 4.69 g, mean weight of 8 males, 41 ± 7.25 g), which indicated that fenced cohorts behaved like unrestrained populations at or near peak densities (Taitt & Krebs 1985). Table 1 also shows the transformation of bi-weekly population estimates into vole grazing-days. Grid 1 sustained the highest number of grazing-days, plot 6 had the lowest, and plots 4 and 5 registered intermediate values.

Pitfall traps did not underestimate the adults living on fenced plots during the four tested periods of early fall (Table 2). Pitfalls caught more animals of all age class categories than did Sherman live traps near the end of the trapping season. However, by the end of October, only the Museum Special mouse traps were able to catch any voles, whereas both types of live traps failed to do so.

Biomass of green vegetation did not differ between ungrazed and grazed plots during summer (Table 3). I registered no significant effects of time, plots, or time and plot interactions on biomass estimates at such vole grazing pressure. No significant interactions of time and plots were detected in any of the chemical analyses performed on green biomass samples. Total nonstructural carbohydrates varied significantly in time because samples collected in May contained lower levels than those of October. There were no significant differences between plots. Time was an important factor involved in estimations of total phe-

Table 1. Minimum number of voles (*Microtus pennsylvanicus*) known to be alive in trapping grids during summer (density/ha).

Grid[a]	June 15	June 29	July 13	July 27	Aug 10	Aug 24	Sept 7[b]	Sept 21[b]	Oct 5[b]	Oct 19[c]	No. vole days of grazing
1 (400)	8 (400)	2 (100)	2 (100)	4 (200)	0	0	3 (150)	5 (250)	1 (50)	0	474
2 (0)	0	0	0	0	0	1 (50)	0	0	0	0	14
3 (0)	0	0	0	0	0	0	1 (50)	0	0	0	14
4 (200)	3 (150)	1 (50)	1 (50)	2 (100)	1 (50)	0	7 (350)	3 (150)	1 (50)	1 (50)	336
5 (400)	6 (300)	3 (150)	1 (50)	2 (100)	1 (50)	1 (50)	2 (100)	5 (250)	1 (50)	1 (50)	322
6 (200)	0	2 (100)	0	1 (50)	0	1 (50)	1 (50)	5 (250)	3 (150)	1 (50)	238

[a] (Initial density/ha late May).
[b] The figures include voles trapped in pitfalls and Sherman live traps.
[c] The figures include voles trapped in pitfalls, Sherman live traps and Museum Special snap-back traps.

Table 2. Number of voles (*Microtus pennsylvanicus*) trapped by pitfalls and Sherman live traps during the four last trapping sessions.

Type of trap	September 7	September 21	October 5	October 19[a]
Pitfall	11 1 juvenile 7 subadults 3 adults	15 6 juveniles 5 subadults 4 adults	5 2 juveniles 3 subadults	0
Sherman	3 3 adults[b]	1 1 adult[b]	1 1 juvenile	0

[a] 1 subadult and 2 adult voles were caught only by Museum Special traps in this period.
[b] 1 adult also caught in pitfall.

nolics since samples collected in May were significantly higher compared with estimates in October. There was also a significant plot effect since phenolics of green biomass in one control plot were significantly higher than those from the most heavily grazed plot (#1). Plot effects were noted for fibers as well. The green biomass of one control plot contained significantly less fibers than one of the slightly grazed plots (#6), although it did not differ from that of the highly grazed area.

Five plant species (*Agropyron*, *Festuca*, *Fragaria*, *Phleum*, *Vicia*) (Table 4) form the food resource base of voles throughout summer and early fall. However, each species is used differently in each grid according to their relative frequencies. Chemical constituents from fecal remains of voles represent an alternative method of measuring time and plot effects in relation to food selection. Protein was not used in this category of analyses because fecal protein could not be cor-

Table 3. Time and/or plot interactions on chemical constituents (mean % dry matter) of green biomass in grids over summer. Different letters represent significant differences according to Sheffé's or Duncan New Multiple Range tests ($P < 0.05$). Ungrazed plots: 2 and 3; lightly grazed plots: 4, 5 and 6; heavily grazed plot: 1.

Total g dry matter/ 100 cm^2	% Proteins	% Carbohydrates	% Phenolics[1]	% Fibers
Plot effects:	Plot effects:	Time effects:	Plot effects:	Plot effects:
Grid *n* Mean *S.E.*	Grid *n* Mean *S.E.*	Time *n* Mean *S.E.*	Grid *n* Mean *S.E.*	Grid *n* Mean *S.E.*
6 14 1.80 0.23^a	5 14 13.22 ± 0.84^a	May 42 18.29 ± 0.48^a	6 14 1.48 ± 0.10^a	2 14 43.05 ± 0.87^a
4 14 1.83 0.22^a	3 14 13.85 ± 0.80^a	Oct 42 22.90 ± 0.76^b	1 14 1.64 ± 0.13^a	5 13 45.29 ± 1.45^{ab}
2 14 2.12 0.26^a	1 14 14.09 ± 0.77^a		4 14 1.78 ± 0.19^a	3 14 46.52 ± 0.89^{ab}
5 14 2.17 0.26^a	2 14 14.22 ± 0.84^a		3 14 1.82 ± 0.14^a	1 13 46.90 ± 0.75^{ab}
1 14 2.35 0.35^a	6 14 14.69 ± 0.88^a		5 14 2.21 ± 0.18^b	4 14 48.34 ± 1.58^{ab}
3 14 2.45 0.16^a	4 14 15.01 ± 0.76^a		2 14 2.66 ± 0.27^b	6 12 49.37 ± 0.77^{bc}
$F_{5,72}$ = 1.127	$F_{5,72}$ = 0.607	$F_{1,82}$ = 26.06	$F_{5,77}$ = 9.914	$F_{5,74}$ = 4.016
P = 0.354	P = 0.695	P = 0.0001	P = 0.0001	P = 0.0028
Time effects:	Time effects:	Plot effects:	Time effects:	Time effects:
			Time *n* Mean *S.E.*	
$F_{1,72}$ = 2.449	$F_{1,72}$ = 0.098	$F_{5,72}$ = 0.725	May 42 2.33 ± 0.11^a	$F_{1,68}$ = 1.232
P = 0.122	P = 0.755	P = 0.607	Oct 42 1.53 ± 0.08^b	P = 0.271
			$F_{1,77}$ = 59.949	
			P = 0.0001	
Time × plot interactions:	Time × plot interactions:	Time × plot interactions:	Time × plot interactions:	Time × plot interactions:
$F_{5,72}$ = 1.209	$F_{5,72}$ = 1.375	$F_{5,72}$ = 0.938	$F_{5,72}$ = 0.743	$F_{5,68}$ = 0.518
P = 0.314	P = 0.244	P = 0.462	P = 0.594	P = 0.762

[1] Values transformed by log-phenols + 1; classification by Duncan New Multiple Range test.

Table 4. Food habits of fenced voles (% frequencies of plant species in feces) in grids 1 (heavily grazed plot), 4, 5 and 6 (lightly grazed grids) during summer.

	June				July				August				September				October			
Plant Species	1	4	5	6	1	4	5	6	1	4	5	6	1	4	5	6	1	4	5	6
Agropyron repens	10	7	7	17	8	4	5	13	7	0	0	10	16	3	3	–	20	23	–	–
Agrostis sp.	0	2	0	0	0	0	0	0	7	0	17	0	0	6	0	–	0	0	–	–
Anthoxanthum odoratum	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	–	0	0	–	–
Carex sp.	10	0	7	2	11	22	0	3	0	0	0	0	3	0	0	–	0	0	–	–
Festuca rubra	28	30	59	23	19	27	10	42	24	15	22	65	60	85	73	–	80	77	–	–
Fragaria virginiana	0	0	0	0	3	9	0	3	4	0	0	0	0	0	3	–	0	0	–	–
Phleum pratense	22	54	16	36	5	31	17	39	7	9	35	25	0	0	0	–	0	0	–	–
Solidago sp.	0	0	0	8	0	0	0	0	10	0	0	0	0	0	0	–	0	0	–	–
Stellaria graminea	5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	–	0	0	–	–
Vicia cracca	25	7	7	14	54	7	68	0	17	64	4	0	13	0	18	–	0	0	–	–
Unknown	0	0	0	0	0	0	0	0	24	9	22	0	8	6	3	–	0	0	–	–

related properly with dietary protein (unpublished data). Total nonstructural carbohydrates from vole feces (Table 5) varied significantly between grids and between sampling periods. Time effects ($F_{7,38}$ = 9.02, P = 0.0001) were involved because carbohydrates in samples of late August and late September were significantly higher than those estimated from early July and early August. Plot effects were significant ($F_{3,38}$ = 3.03, P = 0.04) since the lowest carbohydrate determinations originated from feces collected in one plot that was lightly grazed and the highest ones in the most intensively grazed area. Total phenolics were also affected by time and plot factors. Phenolics varied significantly in time ($F_{8,102}$ = 11.61, P = 0.0001) because feces collected in late July contained significantly more phenolics than samples collected at other collection periods. Phenolics of fecal matter differed significantly among plots ($F_{3,102}$ = 41.10, P = 0.0001). Feces collected in the heavily grazed plot (#1) had significantly higher dosages than those sampled in the lightly grazed area. Neutral detergent fibers in feces were only influenced by a plot factor ($F_{3,43}$ = 7.34, P = 0.0004). Fibers in feces were significantly lower in samples of lightly grazed plots compared with those of the heavily grazed area.

4. Discussion

In this study, I aimed to compare two methods to qualify food and vole habitats using the same sets of variables. I assumed that selective feeding by animals transforms the biomass and plant composition of meadows more rapidly than natural processes of re-growth maintains it. Bergeron and Jodoin (1993) showed in another study that unusually high vole densities (1 000/ha) could significantly reduce summer biomass, although plant quality of the remaining green biomass was not affected. Grazing intensity in the present experiment varied between 238 and 474 vole grazing-days per pen, which is much lower than the 1 000 grazing-days previously reported. Differences in green vegetation between grazed and ungrazed plots were not detected after a summer of grazing by voles at densities often associated with peak numbers (350 voles/ha, Taitt & Krebs 1985). The first series of results in the present study, which is based only on biomass variations between spring and fall samples, suggests that all the tested grids could maintain high vole densities with no significant impact on vegetation. Chemical analyses of the green biomass differed among plots and time of year. I had also assumed that the highest

Table 5. Time and plot interactions related to chemical constituents (mean % dry matter) found in feces of fenced voles in grids over summer. Different letters represent significant differences according to Scheffé's post-hoc tests (P < 0.05). Lightly grazed plots: 4, 5 and 6; heavily grazed plot: 1.

% Carbohydrates[1]				% Phenolics				% Fibers			
Time effects:				Time effects:				Time effects:			
Time	*n*	Mean	*S.E.*	Time	*n*	Mean	*S.E.*	Time	*n*	Mean	*S.E.*
Early Aug.	5	1.94	0.33^{a}	Early Sept.	14	1.30	0.09^{a}	Late Oct.	4	46.88	2.95^{a}
Early July	3	2.02	0.13^{ab}	Early Aug.	6	1.41	0.07^{ab}	Early Sept.	6	47.92	2.51^{a}
Early June	17	2.80	0.18^{b}	Early July	18	1.47	0.09^{ab}	Late July	12	48.05	0.54^{a}
Early Sept.	5	2.81	0.33^{b}	Late Sept.	14	1.50	0.11^{ab}	Early July	8	48.22	0.95^{a}
Late June	16	3.17	0.06^{b}	Late June	22	1.57	0.05^{ab}	Early Aug.	5	49.35	0.41^{a}
Late Sept.	3	3.88	0.71^{c}	Early June	20	1.65	0.05^{bc}	Late Aug.	10	49.71	0.58^{a}
Late July	9	3.94	0.54^{d}	Late Aug.	16	1.69	0.08^{bc}	Early June	9	52.01	1.21^{a}
Late Aug.	4	4.30	1.43^{e}	Early Oct.	8	1.83	0.11^{bc}	Late June	13	52.65	1.22^{a}
				Late July	18	1.91	0.05^{d}	Late Sept.	8	53.64	2.35^{a}
Plots effects:				Plots effects:				Plots effects:			
Grid	*n*	Mean	*S.E.*	Grid	*n*	Mean	*S.E.*	Grid	*n*	Mean	*S.E.*
6	5	2.74	0.25^{a}	6	22	1.20	0.09^{a}	4	20	48.84	0.63^{a}
5	23	2.88	0.28^{ab}	5	42	1.58	0.04^{b}	6	11	48.94	1.55^{a}
4	21	3.27	0.29^{bc}	1	36	1.68	0.04^{bc}	5	24	49.94	0.96^{ab}
1	13	3.37	0.24^{bc}	4	36	1.80	0.05^{cd}	1	20	52.46	0.97^{bc}

[1] Values transformed by log-carbohydrates for Anova.

quality biomass should be found in ungrazed plots, but none of the variables used in this study from both control pens were consistently different from those of the grazed areas. Phenolics were significantly lower in green biomass samples of 3 grazed plots, which is the opposite of my original hypothesis that selective feeding by voles would leave low-quality plants on the plots, hence, plants with high phenolic content. This may indicate that grazing by voles forces re-growth and production of new shoots having low phenol content. My experimental design did not permit the measurement of new growth in October but the green vegetation sampled in October had significantly fewer phenolics (1.53% DM) than the May samples (2.33% DM). As a whole, however, chemical analyses from green vegetation of grazed and ungrazed plots were almost similar, which is showing that grazing has no effect on nutritive constituents of plants during a summer of high vole population density.

Availability and distribution of preferred plants have been correlated with vole densities so that high-quality habitats are those maintaining high food quality and high vole numbers (Batzli & Henttonen 1990, Batzli & Lesieutre 1991). Voles of this study used mainly five plant species among the 10 species censused from fecal analyses. The impact of vole grazing on plants was particularly evident in fall because new growth could be seen in most plots (pers. obs.). This is probably the main reason explaining the time effects registered from carbohydrates and phenolics analyses. Fall samples were higher in carbohydrates and lower in phenolics than those of early summer. These results are surprising and are contrary to the common assumption that quality of vegetation declines with the onset of winter. This suggests that voles (herbivores) may begin winter on high-quality diets and so be best able to prepare body condition for the winter stress. Since plant biomass did not vary among grazed and ungrazed plots between the two sampling periods analysed, the data do not fit the overcompensation biomass models of McNaughton (1986), and are more closely related to the normal regrowth patterns after herbivory of Belsky *et al.* (1993).

Feces of voles could perhaps represent the best indicator of habitat manipulation by voles, hence of habitat quality changes. Chemical analyses of feces in this study were influenced by time and plot factors similar to those recorded from fecal matter of voles using bark tissues of seedling in plantations (Bergeron 1996). Feces collected in the highly grazed plot yielded significantly more phenolics, carbohydrates and fibers than those collected from one of the three lightly grazed areas. Voles producing feces with 1.20–1.58% DM phenolics, 2.74–2.88% DM carbohydrates and 48.0–50.0% DM fibers are characteristic of animals living in lightly grazed habitats (Table 5). Opposite to this, feces yielding > 1.80% DM phenolics, > 3.37% DM carbohydrates, and > 52% DM fibers are produced by voles from the heavily grazed plot. Since green biomass quantity and quality did not vary between grazed plots, fecal matter was the alternate habitat variable of this study which shows consistent and significant differences in fibers, phenolics and carbohydrates between the highly grazed and the lightly grazed plot. Further studies are needed to replicate these results since my experimental design failed to do so. Bergeron and Jodoin (1995) found similar results from feces collected from wintering voles in fenced plots where bark use occurred on wild shrub species. Girdling by voles was not noticed in the present study, performed in the summer season, so that other factors are probably involved to explain the differences in chemical constituents of vole feces between the highly and lightly grazed plots.

Separation of vole habitats into qualitative categories has progressed over the years. Birney *et al.* (1976) found that open fields with more than 400–550 g DM/m^2 of biomass could be defined as high-quality habitats because they were harboring vole communities with multi-year cycles. Batzli and Lesieutre (1991) correlated high vole densities with high biomass of the most palatable plant species ($R^2 = 0.98$). Optimum vole habitats were defined by them in terms of high biomass of the sedge *Equisetum angustifolium* for tundra voles (*M. oeconomus*) and of the deciduous shrubs *Vaccinium uliginosum* for singing voles (*M. miurus*). However, growth, reproductive performance, and survival of voles also are related to nutrients and digestion-inhibition factors in food (Lindroth & Batzli 1984, Lindroth *et al.* 1986). Perhaps habitat quality can be defined equally well from chemical analyses of vole feces. High-quality habitats

should maintain a high-quality food base, and my prediction would be that chemical analyses of feces should always yield low values of phenolics, carbohydrates and fibers in such habitats. Feces of voles sampled from lightly grazed plots (high-quality habitats) tended to have significantly lower contents of phenolics, carbohydrates, and fibers than that of the highly grazed area. We need however more studies of this sort to better understand the relationships between constituents of vole feces and food intake. Future studies directed toward this idea of using vole feces to assess habitat quality must determine the chemical composition of fecal matter by age classes, sex, and reproductive categories. We also need some information on chemical constituents losses with time, since feces of voles can be sampled directly from animals or collected on bi-weekly, monthly or a seasonal basis from dropping boards.

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