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The use of seedling bark by voles sustained by high proteinic content of food

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Meadow voles (*M. pennsylvanicus*) are known to select herbaceous plants with high protein contents and low phenolic values. However, they eat the bark of coniferous and deciduous seedlings with low dosages of protein and high phenolic contents. We tested the hypothesis that voles can use bark of red oak seedlings (*Q. rubra*) when their regular diet contains high proteinic components (> 8% dry matter). Three groups of 10 non reproducing female meadow voles were maintained on 15%, 8%, and 4% protein diets supplemented with red oak seedlings during two weeks. Variations in body mass, total food intake, ingestion of bark and the assigned diets, chemical constituents of fecal matter, protein digestibility, and phenolic recovery rates in fecal matter were compared between the experimental groups. Animals of all groups used extensively the bark of red oak seedlings. Ingestion of bark tissues explained 46% and 20% of the body mass variation of voles maintained on the 15% and 4% protein diets, respectively. Fecal matter yielded significantly higher contents of phenolics and total nonstructural carbohydrates and lower dosages of protein for voles maintained on the 4% proteinic diet. The opposite was true for animals maintained on the 15% proteinic diet. Protein digestibility was similar for every treatment which indicates that voles maintained on a 4% proteinic diet can keep an excellent proteinic balance if they have access to seedlings with high proteinic values in bark. Phenolic recovery rates from fecal matter varied between 12 and 23% for the three vole categories but were not statistically different. These results suggest that low proteinic content of food does not regulate the use of bark by voles. Bark tissues during short periods can be added to the vole diet without any apparent costs.

1. Introduction

Voles of the genus *Microtus* are classified as generalist herbivores, but they are also known for their high selectivity toward particular herbaceous plant species (Batzli & Pitelka 1971, Hansson 1971, Bergeron & Juillet 1979, Batzli 1985). For several non-ruminant herbivores, food choice has been associated with high protein contents of plants (Sinclair *et al.* 1988, Bergeron & Jodoin 1989), high levels of neutral detergent solubles, low values of crude fibers (Servello *et al.* 1985, MacPherson *et al.* 1988, Bergeron *et al.* 1990), high levels of nonstructural carbohydrates (Servello *et al.* 1984, Bucyanayandi *et al.* 1990) or low total phenolic contents of available plants (Bergeron & Jodoin 1987, Marquis & Batzli 1989). In general, plants with high selectivity indices contain more nutrients (protein, nonstructural carbohydrates) and less digestibility-reducing factors (total phenolics, fibers) than plants with low selectivity indices. Bergeron and Jodoin (1989) found a positive correlation between selection indices of the preferred plants and their protein contents. Female meadow voles (*M. pennsylvanicus*) have a lower fitness when maintained on 8% or lower protein diets (Lindroth *et al.* 1986) and are known to produce fewer young of lower quality (Bondrup-Nielsen 1993). Preferred plants by voles tend to have high protein values (> 15% dry matter) and low phenolic contents (< 3% DM) (Bergeron & Jodoin 1987). Phenolics in diets increase the basal metabolic rate of voles by 20% (Thomas *et al.* 1988) which puts a further burden in terms of food input requirements for such small animals.

During peak population densities of voles, animals supplement their winter diet with bark of seedlings and young trees (Hansson 1991). Bucyanayandi *et al.* (1992) showed that bark of many coniferous species used in reforestation in Canada, and by voles during winter, contained low levels of protein (< 8% DM) and high concentrations of phenolics (> 3% DM) in winter in spite of available green plants with a higher nutritive quality. Jodoin (1994) found that red oak seedlings (*Quercus rubra*) were heavily debarked in experiments where voles were offered both the seedlings and high proteinic diets. The best paradigm that can explain both series of results is that access to high proteinic food resources permits voles to detoxify bark phenols without very much costs.

I set up a short term experiment (2 weeks) where three groups of voles were maintained on low (4% DM), medium (8% DM) and high (15% DM) proteinic diets supplemented with red oak seedlings. I aimed to show the relationships between body mass variations and total food input (g of lab. chow and bark) and output (g of fecal matter), total nitrogen and phenolics input and output, and seedling losses due to bark use. My hypothesis is that voles maintained on higher proteinic diets will register higher bark use indices on seedlings than animals fed low protein rations.

2. Materials and methods

Three groups of ten laboratory-reared meadow vole females were fed diets under standardized photoperiod (10L + 14D), temperature (18–20°C), and relative humidity (40–60%). Food and water were given *ad libitum*. Animals were first acclimatized during one month to their future experimental conditions. Individual voles were kept in double 5 gal. polypropylene pails with the nesting material on one side and food in terms of experimental diets, seedlings and water in the other. During the first two weeks of the pre-test period each vole received a weekly ration composed of 100 g of their familiar Purina Rabbit Laboratory Chow (RLC) supplemented by 100 g of their assigned experimental diet. RLC was decreased to 50 g per week during the two last weeks of this period and supplemented by 150 g of the assigned diet category. Food was given to all groups of voles in stainless feeding troughs with small openings at the top to permit feeding and to prevent spillage or contamination.

After one month pre-test period, each group was maintained on its designated diet for two weeks. Voles were weighed before and after each weekly interval. Diet categories consisted of 15% protein Purina RLC, 8% protein diet (ICN Biochemical Co.), and a 4% protein diet which had to be supplemented by an ICN low renal load ration to prevent kidney damage. Two voles of the 15% protein group died the first day of the experiment, and were not replaced due to the logistic problems associated to the pre-trial period. Groups of voles were made of subadult and adult non reproducing females with body mass of 36.5 g ± 9.3 for those maintained on the 15% proteinic diet, 32.5 g ± 8.2 for the 8%, and 31.3 g ± 8.5 for the 4% treated category.

Each experimental treatment consisted of a weekly ration of 200 g dry mass of food (plus 100 g of ICN renal supplement for voles on the 4% protein diet) and 7 dormant red oak seedlings previously weighed. The two yr-old seedlings came from the Quebec Government nursary. Their growing conditions consisted of one year spent in the laboratory under standardized room-controlled conditions, followed by one year outdoor to prepare them to overwinter. Winterized seedlings were used in this experiment. Food intake was estimated by mass differences between initial and final weight measurements on dry pellets transformed into a g/g animal basis. Bark intake was corrected for water loss using 10 seedlings left unused near the experimental set up. Total food intake included both measurements on a g/g animal basis.

Bark use indices followed the procedures of Hansson (1985). Each seedling was assigned the following damage category:

0: if the trunk was not barked,
1: if the bark was missing on less than 25% of the trunk diameter,
2: if it was missing on 25–50%,
3: if it was missing on 50–75%,
4: if more than 75% of the trunk was debarked.

Mean debarking indices (± *S.E.*) were established for each vole and each treatment.

Fecal matter was collected at weekly intervals, weighed, dried for 48 h at 50°C, ground with a mortar and pestle and stored at – 20°C until analysis. Samples ($n = 8$) of each diet category and bark of individual seedlings ($n = 10$) followed the same procedures, although bark had to be ground to 1 mm in a Brinkmann mill. Chemical analyses were made for each diet category and fecal remains from individual voles using duplicate samples. Protein content (N × 6.25; Robbins 1983) was determined by a micro-Kjeldahl technique developed by Lang (1958). Total phenolics were estimated from the colorimetric procedure of Singleton and Rossi (1965) as modified by Gartlan *et al.* (1980) using the Folin-Ciocalteu reagent and gallic acid as a standard. Total nonstructural carbohydrates were measured following enzymatic digestion with amyloglucosidase (Da Silveira *et al.* 1978) and hydrolysis into monomers with a 0.2 N solution (0.1 M) of sulfuric acid (Smith 1969). Results are expressed as percentages of dry mass.

Normality of distribution in the data sets was verified with a Kolmogorov-Smirnov test (SAS Institute 1989). Variations in body mass, food intake, debarking indices, and chemical constituents of fecal matter were compared with a one-way ANOVA followed by a Sheffé classification test. Some data sets had to be transformed to attain a normal distribution. When normality could not be reached, even after transformation, the non-parametric Kruskal-Wallis test was used. When the K-W test rejected the null hypothesis, we assigned a rank to the data to perform an ANOVA followed by a Scheffé classification test. ANOVAs used on ranked data are non parametric. Simple linear regressions were run using food intake as independent variables and the corresponding values in body mass or debarking indices on seedlings as dependent variables.

3. Results

Body mass varied significantly among the tested voles since animals maintained on the 4% diet increased their weight while those fed the 8% and 15% protein rations lost weight (Table 1). Total intake of dry matter (Table 1) did not vary among the vole categories. Regression analyses (Table 2) show that total food intake explains 81% of the body mass variation of animals maintained on the 15% protein diet, 66% for those on the 4% protein ration, but none for those on the 8% protein diet. Food rations were composed of laboratory chow and bark tissues. Ingestion of lab chow varied significantly among the treatments (Table 1) since voles maintained on the 15% RLC diet ingested more food than animals maintained on the ICN 8% ration. Intake of lab chow (Table 2) explains 57% and 45% of the body mass variation of animals maintained on the 15% and 4% protein diets, respectively. Ingestion of bark tissues did not vary among the vole categories (Table 1), nor did bark use indices that were extremely high in all groups. Seedlings had on average between 75% (index of 3.3 on a scale of 4) and 100% (index of 3.9) of their trunk diameter damaged by voles. Intake of bark (Table 2) explains only 46% and 20% of the body mass variation of animals fed the 15% and 4% protein diets, respectively.

The proportion of bark used by voles over the intake of lab chow varies from 22% for voles maintained on the 15% protein diet to 44% and 47% for those fed the 8% and 4% protein rations, respectively. Intake of lab chow has a very low predictive value (Table 3) on bark use indices of seedlings for all treatments. Rations made of higher proteinic components do not lead to a higher bark use by voles. This is contradicting my hypothesis so that more information on food intake processes is needed to understand why voles maintained on the lowest protein diet can manage to gain weight and use extensively bark tissues of red oak seedlings compared to

Table 1. Variation in body mass, food intake, and damage indices to seedlings between day 1 and 14 for voles maintained on three types of proteinic rations: 15%, 8% and 4%.

Body mass changes (g/g–animal) [a] Mean ± *S.E.*	*n*	Total food intake (g/g–animal) Mean ± *S.E.*	*n*	Food intake interms of lab. chow (g/g–animal) Mean ± *S.E.*	*n*	Amount of bark intake (g/g–animal) [b] Mean ± *S.E.*	*n*	Debarking indices [c] Mean ± *S.E.*	*n*
0.223 ± 0.099(4%)	10	1.320 ± 0.138(15%)	8	1.076 ± 0.111(15%)	8	0.388 ± 0.071(4%)	10	3.875 ± 0.125(15%)	8
– 0.016 ± 0.030(15%)	8	1.222 ± 0.095(4%)	10	0.834 ± 0.069(4%)	10	0.319 ± 0.075(8%)	10	3.350 ± 0.289(8%)	10
– 0.021 ± 0.012(8%)	10	1.035 ± 0.108(8%)	10	0.716 ± 0.057(8%)	10	0.244 ± 0.059(15%)	8	3.300 ± 0.374(4%)	10
$F_{2,25} = 4.60$ $P = 0.02$		$F_{2,25} = 1.64$ $P = 0.01$		$F_{2,25} = 5.22$ $P = 0.01$		$F_{2,24} = 0.36$ $P = 0.70$		$X = 1.85$ *d.f.* = 2 $P = 0.40$	

[a] Arcsin transformations for normality
[b] In transformations for normality
[c] Kruskal-Wallis tests on non-normal data sets

other groups fed higher proteinic diets. I can hypothesize that fecal remains of animals maintained on the 4% protein diet should yield higher values of phenolics and lower ones in protein. Chemical constituents of vole fecal matter of this 4% proteinic diet category (Table 4) show significantly higher values of phenolics and lower ones in crude protein as one would expect if a tanin-binding protein process exists in this small herbivore to increase the efficiency of their protein metabolism. Vole fecal matter also showed a significantly lower percentage of nonstructural carbohydrates (Table 4) for animals maintained on the 15% protein diet and a significantly higher one for voles fed the 4% protein ration. However, all treatments yielded results leading to a similar apparent protein digestibility (Table 5). Although voles maintained on the 4 and 8% protein diets seemed to be more efficient, they did not vary significantly from animals fed the 15% protein ration ($F_{2,25} = 1.69$, $P = 0.20$). Even maintained

Table 2. Regression analyses between body mass variations in g/g animal (*y*) and food intake in g/g animal (*x*) for voles maintained on three types of proteinic diets.

y-body mass variation = *a* + *bx*-food intake variables (g/g–animal) (g/g–animal)	R^2	*P*	Diet category
$y = -0.279 + 0.199x$ (total food intake)	0.81	0.002	15%
$y = -0.022 + 0.001x$	0.0001	0.98	8%
$y = -0.817 + 0.851x$	0.66	0.004	4%
$y = -0.240 + 0.208x$ (intake of lab chow)	0.57	0.03	15%
$y = -0.040 + 0.027x$	0.02	0.72	8%
$y = -0.580 + 0.962x$	0.45	0.03	4%
$y = -0.101 + 0.350x$ (intake of bark)	0.46	0.06	15%
$y = -0.017 - 0.013x$	0.01	0.82	8%
$y = -0.021 + 0.629x$	0.20	0.20	4%

Table 3. Regression analyses between debarking indices (*y*) and food intake in g/g–animal (*x*) for voles maintained on three types of proteinic diets.

y-Debarking indices = *a* + *bx*-food intake variables (g/g–animal)	R^2	*P*	Diet category
$y = 2.516 + 0.940x$ (intake of lab chow)	0.03	0.63	4%
$y = 2.663 + 0.960x$ —"—	0.04	0.60	8%
$y = 4.211 - 0.312x$ —"—	0.08	0.51	15%

Table 4. Chemical constituents (%DM) of vole feces from animals maintained on three types of proteinic diets supplemented with red oak seedlings. ANOVAs were followed by Scheffé classification tests. Diet categories are in parentheses.

Total phenolics		Crude protein		Total nonstructural carbohydrates [a]	
Mean ± *S.E.*	*n*	Mean ± *S.E.*	*n*	Mean ± *S.E.*	*n*
2.25 ± 0.092(4%)	10	29.78 ± 1.78(15%)	8	4.4277 ± 0.6547(4%)	10
1.90 ± 0.071(8%)	10	21.63 ± 2.56(8%)	10	3.2118 ± 0.2141(8%)	10
1.72 ± 0.087(15%)	8	19.27 ± 1.15(4%)	10	1.1719 ± 0.2162(15%)	8
$F_{2,25} = 10.40$		$F_{2,25} = 7.26$		$F_{2,25} = 19.20$	
$P = 0.0005$		$P = 0.003$		$P = 0.0001$	

[a] ANOVA performed on non-parametric ranked data

on a 4% proteinic diet, voles can keep an excellent protein metabolism on a short-term basis by having access to bark of seedlings. Recovery rates of total phenolics in vole fecal matter are very low for all vole categories (Table 6) and not significantly different between animals fed high and low dietary protein ($F_{2,24} = 2.53, P = 0.10$).

4. Discussion

Voles of this study were probably never subject to nutritional stresses in spite of the fact that treatments maintained voles on low (8%) and very low (4%) proteinic diets. Both of these low proteinic diets should have negatively affected growth and survival of voles as shown by Lindroth and Batzli (1984). Diet categories given to voles were tested to mimic field situations during winter when herbaceous species lose more than 50% of their fall protein content (Bergeron & Jodoin 1995). Alternate food supplies are not numerous at that period of the year but do exist if seedlings are present in vole habitats. Contrary to my working hypothesis, all vole categories used extensively bark tissues. Although not statistically different, data on voles maintained on the 4% proteinic diet had a tendency to show higher bark use relative to lab chow intake. Furthermore, this group of animals has increased body mass during the experiment. I first thought that the highest proteinic ration would sustain the highest use of bark by voles because bark of red oak seedlings contains 11% phenolics on a dry matter basis (Appendix). These phenolics are composed of 7% dry matter of

Table 5. Apparent protein digestibility for voles maintained on three types of proteinic diets.

Variables		15% protein diet *n* = 8 Mean ± *S.E.*	8% protein diet *n* = 10 Mean ± *S.E.*	4% protein diet *n* = 10 Mean ± *S.E.*
Total intake in protein (g/g animal x % protein DM)				
	lab chow	25.34 ± 2.60	6.72 ± 0.54	5.18 ± 0.43
	bark	3.87 ± 0.94	5.06 ± 1.19	6.16 ± 1.12
	Σ	29.21 ± 2.98	11.78 ± 1.45	11.34 ± 1.17
Total output in protein (g/g–animal x % protein DM)	feces	14.13 ± 1.66	3.95 ± 0.44	4.18 ± 0.32
Apparent protein digestibility [(input-output) ÷ input]		0.50 ± 0.06	0.63 ± 0.05	0.60 ± 0.04

Table 6. Total phenolics recovery rates from fecal matter for voles maintained on three types of diets.

Variables		15% protein diet *n* = 7 Mean ± *S.E.*	8% protein diet *n* = 10 Mean ± *S.E.*	4% protein diet *n* = 10 Mean ± *S.E.*
Total phenolics ingested (g/g–animal ×% phenol DM)				
	lab chow	0.98 ± 0.10	0.17 ± 0.01	0.07 ± 0.01
	bark	3.12 ± 0.62	3.57 ± 0.84	4.34 ± 0.79
	Σ	4.11 ± 0.61	3.74 ± 0.85	4.41 ± 0.79
Total phenolics excreted by feces (g/g–animal ×% phenol DM)		0.86 ± 0.14	0.38 ± 0.05	0.52 ± 0.07
Excreted/ingested ×100%		22.72 ± 4.29 [(a]	16.47 ± 4.82 [(a]	12.51 ± 1.87 [(a]

[(a] In transformation for normality and ANOVA condensed tanins with a variation between 4 and 13% DM (Jodoin 1994). According to the results of this study, voles were probably using the bark itself as their proteinic source to detoxify or neutralize the phenolics of their diets. Voles survived very easily on such food and registered a similar protein digestibility compared to animals maintained on the highest proteinic diet. If we use Milton's (1979) digestion-inhibition ratios to compare food quality of red oak seedlings to the most preferred plant species of voles (Bergeron & Jodoin 1987), the seedlings are yielding protein/phenolics ratios of 1^+ while the selected herbaceous species range between 4 and 11. Bark of red oak seedlings can indeed be classified among the food categories having a high potential to be used by voles since their protein/phenolics ratios are much alike those of Norway spruce (*Picea abies*) and Norway pine (Bucyanayandi *et al.* 1992) which are also used as food by meadow voles or to those of Sitka spruce (*Picea sitchensis*) also heavily damaged by Orkney voles (*Microtus arvalis orcadensis*) (Hartley *et al.* 1995).

When voles are using extensively red oak seedlings with high phenolic contents, they certainly need physiological adaptations to reduce the metabolic costs associated to the ingestion of such food resources which are far from the chemical and nutritional composition of their usual selected herbaceous species. Dietz *et al.* (1994) were unable to identify any tanin-binding proteins from salivary glands of meadow voles arguing that the quebracho extracts used in their study might not have been the proper product to challenge their salivary glands. The present study brings indirect evidence that such a mechanism is probably existing in voles since the treated vole categories using extensively bark tissues with low proteinic diets were able to maintain protein digestibility similar to that of animals fed higher protein rations. Fecal matter of treated voles yielded significantly more phenolics and carbohydrates and less protein as one would expect if tanin-binding proteins were present in salivary glands to sequester phenolics through their passage in the digestive system. In the process, less endogenous protein is lost (showed in Table 4) which permits voles to perform better against the negative digestion inhibitors of bark. However, the low phenolic recovery rates from fecal matter suggest that voles might have used other detoxification mechanisms as well. Voltura and Wunder (1994) were unable to stimulate in the Mexican woodrat (*Neotoma mexicana*) any tanin-binding proteins in salivary glands due apparently to the high proteinic ration used (22% crude protein). The alternative to using tanin-binding proteins to sequestre phenolics from food is to use liver and kidneys to detoxify secondary metabolites. However, this is probably done with higher metabolic costs as showed by Thomas *et al.* (1988).

Chemical constituents of fecal matter of meadow voles are perhaps good indicators of dietary shifts in favor of bark tissues. In a recent study, Bergeron and Jodoin (1995) showed that higher contents of phenolics and nonstructural carbohydrates in vole fecal matter coincided with bark use of wild shrubs during winter by fenced voles. Similar results are registered in the present study since voles of both the 4% and 8% proteinic diets yielded fecal matter with significantly higher dosages of phenolics and nonstructural carbohydrates. Reasons to explain such changes in food selection are not known yet. Use of bark occurs in sapling plantations of Québec (Canada) during winter at times of high population density of voles. Whatever the causes, the consequences are always impressive. Damage by vole is so extensive since 1990 on the newly established hardwood plantations that reforestation incitatives are at their lowest and foresters might have to abandon the idea of re-introducing hardwoods in southern Québec for the time being.

If red oak seedlings are introduced into open habitats able to sustain fluctuating populations of meadow voles, these seedlings are representing an alternate food supply of high quality that voles can use in times of food scarcity. Foresters are thus perpetuating two errors while trying to introduce certain coniferous or deciduous species in reclaimed lands from agriculture. First, most of these lands have the potential to be occupied by fluctuating populations of meadow voles especially from the mid-succession to the old-field community stages which are probably optimum vole habitats. Second, they are introducing on those lands high quality food for voles that will be eventually used when needed. Seedling species with no potent defensive compounds such as monoterpenes found in unpalatable coniferous species (Bucyanayandi *et al.* 1990) should not be introduced into open habitats unless protected by chemical or mechanical protection measures. Tree losses is not a vole problem. Rather, it is a management problem that appeared a few decades ago when some people thought that reforestation would be successful if one could introduce the right seedling species into the right type of soil. Meadow voles are masters of open lands. Ostfeld and Canham (1993) think they are the keystone species of this habitat category and represent thus a key element to consider if we want to be more successful in our reforestation effort.

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Appendix

Nutritional and chemical components of the three diet categories used in the present study to construct parts of Table 5 and Table 6.

Dietery items	Crude protein (% DM)		Total phenolics (% DM)		Total non-structural carbohydrates (%DM)	
	Mean ± *S.E.*	*n*	Mean ± *S.E.*	*n*	Mean ± *S.E.*	*n*
15% protein diet	23.55 ± 0.51	8	0.87 ± 0.01	8	24.33 ± 0.31	8
8% protein diet	9.38 ± 0.16	8	0.23 ± 0.004	8	75.39 ± 1.98	8
4% protein diet	6.22 ± 0.11	8	0.08 ± 0.01	8	77.64 ± 0.51	8
Bark of seedlings	15.87 ± 0.73	10	11.20 ± 0.26	10	19.22 ± 0.32	10