Effects of geophagy on food intake, body mass, and nutrient dynamics of snowshoe hares (Lepus americanus)

S.B. Worker, K. Kielland, and P.S. Barboza

Abstract: Geophagy is thought to have several physiological benefits to animals, including mineral supplementation and adsorption of toxins. However, these benefits have rarely been demonstrated experimentally. Using soil from a known lick in northern Alaska, we investigated the effect of geophagy on food intake and mass loss in captive snowshoe hares (Lepus americanus Erxleben, 1777) fed a formulated ration of feltleaf willow leaves (Salix alaxensis [Andersson] Coville), a preferred forage of snowshoe hares. Lick soil contained 4.8% clay, 12.5% carbonates, and had more available Na (72.7 mg·kg−1) than willow leaves. Hares fed willow leaves consumed more soil (15.2 ± 2.0 g·kg−0.75·d−1) than those fed formulated ration (9.3 ± 1.3 g·kg−0.75·d−1). Hares had higher willow intake when offered soil (45.8 ± 2.0 g·kg−0.75·d−1) than those without soil (35.0 ± 2.1 g·kg−0.75·d−1), and willow-fed hares offered soil lost less body mass (P < 0.001) than those without soil. Soil availability resulted in higher digestible intakes of N, Ca, Mg, Na, and K, but not P. These results suggest that the availability of mineral licks may alter forage use and functional response of this generalist herbivore in interior Alaska.

Key words: geophagy, Lepus americanus, mineral lick, plant secondary metabolites, salt lick, snowshoe hare, sodium.

Introduction

Geophagy, the consumption of mineral soil, has been reported in a wide range of species, including birds, ungulates, and primates, and is particularly prevalent among generalist herbivores (Johns 1990). Geophagic behaviors among vertebrates have been attributed primarily to the acquisition of mineral nutrients and detoxification of plant secondary metabolites (PSMs) and may also have a role in the control of diarrhea and in pH adjustment of the gut (Krishnamani and Mahaney 2000; Slamova et al. 2011; Young et al. 2011).

Soil consumption can augment mineral intakes when plants provide insufficient supplies of minerals. In particular, sodium (Na) deficit is often reported as a cause of geophagy (e.g., Ayotte et al. 2006; Young et al. 2011; Dudley et al. 2012). Herbivores may seek Na from salt licks or other sources, particularly during times of high physiological demand (Hui 2004) and in mesic habitats far from the coast where Na concentrations of plants are low. Many licks have been shown to serve as concentrated sources of Na, as well as of calcium (Ca), magnesium (Mg), and potassium (K) (Tracy and McNaughton 1995; Wilson 2003; Ayotte et al. 2006). Although soil ingestion is often beneficial, this behavior may also have detrimental effects resulting from mineral interactions and imbalances (Abrahams 2005).

Consumption of mineral soil may also have a role in counteracting the negative effects of toxins such as phenolics and other PSMs (Krishnamani and Mahaney 2000). In particular, soils high in clay are thought to adsorb toxins, facilitating elimination through feces and preventing toxic effects. This may be particularly relevant for generalist herbivores, such as rodents and lagomorphs, which routinely cope with a range of PSMs.

PSMs are produced by many plant species as a defensive mechanism against herbivory (Freeland and Janzen 1974; Glendinning 2007). The ubiquity of PSMs in nature means that many herbivores are forced to consume them, at a physiological cost (Glendinning 2007). Furthermore, the process of browsing often increases the concentrations of PSMs in plants, so increased browsing intensity may decrease the forage quality for herbivores (Bryant et al. 1991).

Received 27 August 2014. Accepted 26 February 2015.

S.B. Worker,* K. Kielland, and P.S. Barboza. Department of Biology and Wildlife, and Institute of Arctic Biology, University of Alaska Fairbanks, P.O. Box 757000, Fairbanks, AK 99775, USA.

Corresponding author: Suzanne Worker (e-mail: sbworker@alaska.edu).

*Present address: U.S. Fish and Wildlife Service, 1011 East Tudor Road, Anchorage, AK 99503, USA.
Tannins, a class of polyphenolic compounds, are particularly common in plants and are often found in high concentrations in browse species. Tannins interact with proteins to form insoluble complexes, which may reduce dietary protein absorption, inhibit digestive enzymes, or cause erosion of the intestinal epithelium, resulting in loss of Na, K, and other minerals (Bernays et al. 1989). If geophagy is an effective mechanism for binding toxins or mediating physiological effects of PSMs, then geophagy might allow higher intakes of chemically defended browse, and directly or indirectly affect growth, survival, and reproduction, which have important ecological consequences.

Snowshoe hares (Lepus americanus Erxleben, 1777; henceforth simply referred to as hares) are generalist herbivores that consume a variety of forage species. During fall and winter, hares browse the twigs, buds, and bark of deciduous shrubs and trees, as well as some evergreen species (Wolff 1978). Winter browse has reduced nitrogen (N) concentration compared with summer forages (Kubota et al. 1970), but contains high concentrations of secondary compounds, which may reduce intake and may increase nutrient requirements. During the summer months, hares typically feed on herbaceous vegetation and the leaves of deciduous shrubs. Browse typically exhibits rapid decreases in N concentrations over the summer with concomitant increases in PSM concentrations (McArt et al. 2009), which accelerates the reduction of diet quality during the reproductive season.

Local observations suggest that hares near Wiseman, Alaska (67.41°N, 150.11°W), consume mineral soil at several licks. Observers report that hare populations in areas with known licks appear to reach higher densities during the population high compared with areas where there is no known lick. These observations provided the motivation for the present study to examine the nutritional ecology of hares in the context of geophagy.

We relied on captive hares to explore the relationship between geophagy and diet composition and to investigate the physiological consequences of geophagy. Specifically, we examined intake rates, body mass, and nutrient digestibility in the presence and absence of geophagy to test the hypothesis that this behavior confers physiological benefits. We hypothesized that hares with access to soil would be able to sustain higher daily food intake and gain more mass than those without access to soil. We predicted that these effects would be more pronounced in hares fed a natural forage of feltleaf willow (Salix alaxensis (Andersson) Coville) leaves, which are not balanced for minerals and contain PSMs, compared with those fed a balanced experimental ration without PSMs.

## Materials and methods

### Animals

Ten hares were captured between 8 October and 5 November 2010 in the boreal forest at the Bonanza Creek Long-Term Ecological Research site (64.70°N, 148.28°W), approximately 20 km southwest of Fairbanks, Alaska. This site is located in the boreal forest and provides hare habitat similar to that adjacent to the Wiseman lick. Hares were captured and transported in wire-cage traps (model 106; Tomahawk Live Trap, Tomahawk, Wisconsin, USA). All animals were housed individually at the University of Alaska Fairbanks (UAF) Biological Reserve in 1 m × 2 m outdoor pens. The pens were covered and partially enclosed, so they were protected from precipitation but subject to natural temperature and light conditions. Pens had wood shavings on the floor and each hare had access to a 46 cm × 60 cm × 33 cm metabolism cage and a 40 cm × 26 cm × 18 cm plastic hutch for cover. Pens included a 45 cm high solid barrier at ground level so that hares had visual contact with one another only when they sat on top of the metabolism cages. During all nonexperimental periods, hares were maintained on a pelleted herbivore ration devoid of PSMs (Barboza and Parker 2006) and were provided small amounts of fresh willow (species of the genus Salix L.) and birch (Betula neoalaskana Sarg.) browse daily. Hares had ad libitum access to food and water. All procedures were approved by the University of Alaska Fairbanks Animal Care and Use Committee (protocol No. 175963-6).

### Lick soil

Soil was collected from a lick known by locals to be used by hares and other herbivores. The lick is located on the southern flank of the Brooks Range, approximately 10 km north of Wiseman, Alaska (67.49°N, 150.05°W). It is composed of a bluff situated at the edge of a small river (Fig. 1a) and is covered in a mineral precipitate (Fig. 1b). Approximately 20 kg of loose soil was collected from the lower edge of the bluff for use in captive trials. This area of the bluff is used by small mammals, and our observations at licks in interior Alaska indicate that hares seek the complete soil matrix, not just the mineral precipitate.

The soil was sifted through a 2 mm mesh, mixed, sampled for chemical analysis, and frozen until needed for the feeding trials. Soil samples were air-dried and subsampled to determine clay content, pH, calcium carbonate equivalent (CaCO₃), cation exchange capacity (CEC), available mineral (Na, K, Ca, Mg), and total mineral content (Na, K, Ca, Mg, phosphorus (P), iron (Fe), manganese (Mn), zinc (Zn), copper (Cu), cobalt (Co), chromium (Cr), molybdenum (Mo)).

Clay content was determined by dispersing soil in sodium pyrophosphate solution and measuring density with a hydrometer at 40 s and 2 h (Klute 1986). Water suspensions were used for pH determinations, following the Long-Term Ecological Research standards (Robertson et al. 1999). Concentrations of CaCO₃ were estimated by acid neutralization (USDA 1954). Cation exchange capacity and available minerals were determined by extraction in ammonium acetate adjusted to pH 7 (Page 1982). To approximate the acidic conditions of the gastric stomach, some authors advocate the use of acidic extracting solutions such as Mehlich 3 to estimate available minerals (e.g., Ayotte et al. 2006; Brightsmith et al. 2008). Mehlich 3 extraction has the same extraction efficiency as ammonium acetate for Na and K, but Mehlich 3 yields 1.10 times more Ca and Mg than ammonium acetate (Ziadi and Tran 2008), so we adjusted the latter values accordingly. To determine total mineral concentration, samples were digested in a mixture of sulfuric, nitric, hydrochloric, and perchloric acids (Coltrane and Barboza 2010) and assayed by direct coupled plasma spectrometry (Iris DCP; Thermo Elemental, Cheshire, UK). Total N was determined using an elemental analyzer (TruSpec C/N; LECO, St. Joseph, Michigan, USA).

### Feeding trial

Ten hares were housed individually in 46 cm × 60 cm × 33 cm metabolism cages from 18 June to 18 August 2011. The cages remained inside the 1 m × 2 m outdoor pens and the solid barrier at ground level prevented visual contact among hares during the trial. Cages had 1 cm mesh floors and fine mesh subfloors to separate feces and urine. Water was offered ad libitum in cage bottles. Hares were acclimated to the cages for 14 days, until daily food intake exceeded 50 g·kg⁻⁰·⁷⁵, which was within 10 g·kg⁻⁰·⁷⁵ of the mean pretrial intake of 60 g·kg⁻⁰·⁷⁵.

Treatments consisted of two diets and two soil regimes. Diets were either 100% formulated diet (D-ration; Alaska Pet and Garden, Anchorage, Alaska, USA), a high-protein, high-energy diet formulated to be similar to willow leaves, or 100% feltleaf willow leaves (henceforth, simply referred to as willow). Gross energy content of the diets were 18.36 kJ·g⁻¹ (Barboza and Parker 2006) and 19.0 kJ·g⁻¹ (Thompson and Barboza 2014), respectively. Fresh, juvenile-form leaves were collected daily for feeding and sampled for chemical analysis. Both diets were offered ad libitum and were offered sequentially, separated by a transition period (Fig. 2). Soil regimes were (+) soil or (−) soil. During each of two trials, half the hares had access to soil (Fig. 2). Soil was offered in bricks to prevent the hares from scattering the soil, allowing us to calculate
soil intake as the loss of mass from the brick. Soil bricks were prepared by adding gelatin (Knox brand; Kraft Foods, Tarrytown, New York, USA) to soil at 1% by mass, which increased the soil N concentration from 0.08% to 0.23%. Each hare received one soil brick (approximately 35–40 g) per day during the treatment periods. Refused food and soil were collected daily to calculate intake. Feces were collected daily. Hares were weighed to the nearest gram at the beginning, middle, and end of each treatment to calculate the percent change in body mass (SP4001; Ohaus Corporation, Parsippany, New Jersey, USA).

Chemical analysis and calculations

Fecal samples were dried in a forced air oven at 55 °C. Willow samples were freeze-dried. Dried samples were ground in a Wiley Mill (20 screen). Soil samples were pulverized in a ball mill. Representative fecal samples were prepared for each animal by combining a proportionate mass from each daily sample into a 25 g analytical sample. Ash and total mineral concentration (Ca, Mg, Na, K, P, N) of food, soil bricks, and feces was determined as described above. Apparent digestible mineral intakes were calculated as the difference of each component in the diet and the feces. Ingestion of abrasives such as soil increases endogenous N losses (Young and Hume 2005), so we estimated metabolic fecal nitrogen (MFN) by running a neutral detergent fiber digest (NDF) on fecal samples to remove soluble N (Van Soest 1994). We then subtracted N in the NDF residue from the total fecal N to estimate MFN (Barboza and Parker 2006). Total phenolic concentration of willow was determined by reaction with Folin-Ciocalteau reagent, as described by Ainsworth and Gillespie (2007). Tannin concentration was assessed by measuring the protein binding capacity, using the radial diffusion method (Graça and Bärlocher 2005).

All statistical analyses were executed using R version 2.15.2 (R Core Development Team 2012). Repeated measures using mixed-effects models (Pinheiro et al. 2012) were used to compare daily food and mineral intakes and body mass change among diet and soil treatments. Pairwise contrasts for diet and soil treatments were corrected for multiple comparisons with a Bonferroni adjustment (Hothorn et al. 2008). Square-root transformations were applied to mineral intakes and mineral intake ratios to correct for unequal variance related to the mean, while arcsine of the square-root transformations were applied to data expressed as proportions (Quinn and Keough 2002). Values are reported as means ± SE. Statistical significance was determined at $\alpha < 0.05$.

Results

Mineral soil obtained from the lick was relatively low in clay (4.8%), contained 12.5% CaCO$_3$, and had a pH of 8.9 (Table 1). Although soil was high in total minerals, especially Fe, Ca, and Mg (Table 1), available minerals in soil were lower than in willow leaves, except for Na, which was higher in soil than leaves (Tables 2, 3). Hares that were fed willow leaves had significantly higher ($P = 0.008$) daily intake of soil (15.2 ± 2.0 g·kg$^{-0.75}$) than those fed the formulated diet (9.3 ± 1.3 g·kg$^{-0.75}$).

Compared with the formulated diet, willow leaves were lower in N, Na, and P, but contained approximately twice as much Ca. Consequently, the ratio of Ca:P in willows was greater than that of the formulated diet, while the ratio of Na:K was much lower than that of the formulated diet. Unlike the formulated diet, willow leaves also contained significant amounts of phenolic compounds and tannins (Table 3).

In hares fed the formulated diet, soil availability did not affect food intake (Fig. 3) or digestible dry matter (DM) intake (Table 4).
Table 1. Soil properties from a lick used by herbivores, including snowshoe hares (Lepus americanus), near Wiseman, Alaska (n = 5, except for CaCO3 where n = 3).

<table>
<thead>
<tr>
<th>Value (mean ± SE)</th>
<th>Value (mean ± SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>pH 8.9±0.0</td>
<td></td>
</tr>
<tr>
<td>CaCO3 (%) 12.5±0.4</td>
<td></td>
</tr>
<tr>
<td>Clay (%) 4.8±0.2</td>
<td></td>
</tr>
<tr>
<td>CEC (meq·(100 g)−1) 1.4±0.1</td>
<td></td>
</tr>
<tr>
<td>Na (mg·kg−1) 313±16</td>
<td></td>
</tr>
<tr>
<td>K (mg·kg−1) 6492±246</td>
<td></td>
</tr>
<tr>
<td>Ca (mg·kg−1) 1470±717</td>
<td></td>
</tr>
<tr>
<td>Mg (mg·kg−1) 145372±246</td>
<td></td>
</tr>
<tr>
<td>P (mg·kg−1) 802±12</td>
<td></td>
</tr>
<tr>
<td>Fe (mg·kg−1) 4713±428</td>
<td></td>
</tr>
<tr>
<td>Mn (mg·kg−1) 2338±31</td>
<td></td>
</tr>
<tr>
<td>Zn (mg·kg−1) 118±20</td>
<td></td>
</tr>
<tr>
<td>Cu (mg·kg−1) 30.8±1.2</td>
<td></td>
</tr>
<tr>
<td>Co (mg·kg−1) 14.2±4.7</td>
<td></td>
</tr>
<tr>
<td>Cr (mg·kg−1) 84±21.9</td>
<td></td>
</tr>
<tr>
<td>Mb (mg·kg−1) 0.02</td>
<td></td>
</tr>
</tbody>
</table>

Note: CEC, cation exchange capacity.

Table 2. Available minerals in lick soil (n = 5) used by herbivores, including snowshoe hares (Lepus americanus), near Wiseman, Alaska.

<table>
<thead>
<tr>
<th>Value (mean ± SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Na (mg·g−1) 0.07±0.001</td>
</tr>
<tr>
<td>K (mg·g−1) 0.03±0.002</td>
</tr>
<tr>
<td>Ca (mg·g−1) 3.17±0.03</td>
</tr>
<tr>
<td>Mg (mg·g−1) 1.93±0.02</td>
</tr>
</tbody>
</table>

Table 3. Mineral and plant secondary metabolite (PSM) constituents of experimental diets (n = 3 for minerals and n = 12 for PSMs) consumed by snowshoe hares (Lepus americanus).

<table>
<thead>
<tr>
<th>Formulated diet</th>
<th>Feltleaf willow (Salix alaxensis) leaves</th>
</tr>
</thead>
<tbody>
<tr>
<td>N (mg·g−1)</td>
<td>23.72±0.25 a</td>
</tr>
<tr>
<td>Na (mg·g−1)</td>
<td>1.09±0.12 a</td>
</tr>
<tr>
<td>K (mg·g−1)</td>
<td>10.18±0.11</td>
</tr>
<tr>
<td>Ca (mg·g−1)</td>
<td>5.78±0.11 a</td>
</tr>
<tr>
<td>Mg (mg·g−1)</td>
<td>1.77±0.01</td>
</tr>
<tr>
<td>P (mg·g−1)</td>
<td>5.09±0.18 a</td>
</tr>
<tr>
<td>Na:K</td>
<td>0.10±0.009 a</td>
</tr>
<tr>
<td>Ca:P</td>
<td>1.14±0.01 a</td>
</tr>
<tr>
<td>Total phenolics (mg·g−1)</td>
<td>69.5±14</td>
</tr>
<tr>
<td>Tannin (mg·g−1)</td>
<td>61.05±11.66</td>
</tr>
</tbody>
</table>

Note: Values are means ± SE. Different lowercased letters denote significant difference between diets (P ≤ 0.03).

There was no difference in change in body mass when hares were fed formulated diet with or without soil.

Nitrogen digestibility and digestible N intake were higher in hares fed the formulated diet than those fed willow leaves. Within diet, availability of soil had no effect of digestible N intake, but access to soil resulted in lower N digestibility in hares fed willow leaves (Tables 4, 5). Daily MFN, which ranged from 262 to 305 mg·kg−1, did not differ among treatments (P = 0.14). Within the willow diet, MFN consisted of a significantly lower proportion of total fecal N in hares with access to soil (0.38 ± 0.02 g·g−1) compared with hares without access to soil (0.45 ± 0.03 g·g−1; P = 0.03). By contrast, there was no difference in the MFN proportion between soil treatments (0.73 ± 0.01 g·g−1; P = 1) for hares fed the formulated diet.

In hares fed willow leaves, access to soil resulted in significantly higher digestible intakes of Na (P = 0.01) and K (P < 0.001) (Table 4). Mineral digestibility varied primarily with diet and was not significantly affected by the presence of soil except for K, which was more digestible in hares without access to soil (Table 5). Na:K intake was low for hares fed willow leaves, but access to soil resulted in doubling of this ratio. Soil had no effect on Na:K for hares fed the formulated diet (Table 6).

Digestible Ca and Mg intakes were higher for hares fed willow leaves than those fed the formulated diet and access to soil resulted in further increased digestible intake rates for both Ca (P = 0.002) and Mg (P < 0.001). Hares were in negative P balance when fed willow leaves (Table 4). Digestible intakes of P were positive on the formulated diet, but reduced by the provision of soil (P = 0.05). Increasing soil intake resulted in higher dietary Ca:P ratios across diets (P = 0.02). Ca:P intake was different among all treatments (P < 0.001; Table 6) and was higher for hares on the willow diet.

By contrast, in hares fed willow leaves, access to soil resulted in a 30% increase in food intake (Fig. 3) and a similar increase in digestible DM intake (Table 4). For both diets, total DM digestibility decreased when soil was consumed, but soil consumption did not change organic matter digestibility (Table 5). Between diets, there was no difference in food intake for hares with access to soil (Fig. 3), though hares had higher digestible DM intake when fed the formulated diet (Table 4).

The mean (±SE) pretrial body mass of hares was 1317 ± 15 g. All hares maintained or gained mass during the trials, except for those on the willow diet with no soil, which lost 4.4% of their body mass over the 6-day trial (Fig. 4). Within the willow diet, hares without access to soil lost significantly more mass than those offered soil (P < 0.001). Among hares not offered soil, those fed willow leaves lost more mass than those fed the formulated diet.

Discussion

Physiological effects

Many lick soils associated with PSM detoxification contain high concentrations of clay, which confer a high adsorption capacity and potential for binding with tannins to reduce the formation of tannin–protein complexes (Kreulen 1985; Johns and Duquette 1991), resulting in increased N digestibility. Soil used in this experiment was several-fold lower in clay than many licks discussed in the scientific literature (e.g., Klaus et al. 1998; Gilardi et al. 1999; Wilson 2003; Ayotte et al. 2006; Brightsmith et al. 2008) and there is no evidence to suggest that access to soil improved retention of...
Rabbits may compete with tannins for the protein substrate (Kreulen 1985), as clay soils are capable of binding proteins (Shan 2011). If these complexes remain insoluble, it would result in a reduction of digestible N. This process may explain the reduction of N digestibility in hares fed soil. Hindrance of N utilization is a detrimen-
to free-ranging herbivores, but is apparently outweighed by the other benefits conferred by geophagy, including increased forage intake and mineral acquisition.

Our MFN data show that soil consumption was neither harmful nor beneficial with regard to preserving endogenous N. Increased fecal N observed in hares fed willow leaves is of dietary origin, which is likely composed of fiber-bound N in plant cell walls.

Although high roughage diets—or those containing soil—can have an abrasive effect on the GI tract and result in endogenous N loss (Young and Hume 2005), our results do not support this conclusion. Similarly, the idea that the formation of tannin–soil complexes might prevent endogenous N loss by preventing tannin–epithelial protein interactions (Freeland et al. 1985) is inconsistent with our findings.

Terrestrial vegetation is generally low in Na and its net uptake can be impaired by excess K (Underwood and Suttle 2001; Barboza et al. 2009). PSMs, including tannins, are known to induce Na depletion in herbivores (Pehrson 1983; Freeland et al. 1985; Foley et al. 2009). Na concentrations of willow leaves were still lower than the general Na guide-
lines for wildlife of 9.6 mg·kg–0.75 for an animal weighing 1300 g (Robbins 1993).

Access to soil increased ingested Na:K (Table 6) for hares fed willow leaves, though these ratios remained well below 0.33, the recommended dietary Na:K ratio for domestic rabbits (National Research Council 1977). Pehrson (1983) reported that Na loss coincides with mass loss in hares. Likewise, dietary Na restriction can

### Table 4. Digestible intakes of snowshoe hares (*Lepus americanus*) fed formulated diet or feltleaf willow (*Salix alaxensis*) leaves, with and without access to lick soil (*n* = 10).

<table>
<thead>
<tr>
<th>Diet treatment</th>
<th>Formulated diet</th>
<th>Feltleaf willow leaves</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No soil</td>
<td>Soil</td>
</tr>
<tr>
<td>Dry matter (g·kg–0.75·d–1)</td>
<td>32.8±1.3 a</td>
<td>34.2±1.1 a</td>
</tr>
<tr>
<td>N (g·kg–0.75·d–1)</td>
<td>1.00±0.04 a</td>
<td>1.05±0.03 a</td>
</tr>
<tr>
<td>Ca (mg·kg–0.75·d–1)</td>
<td>93.1±16.9 a</td>
<td>166.7±30.2 a</td>
</tr>
<tr>
<td>Mg (mg·kg–0.75·d–1)</td>
<td>39.4±7.4 A,a</td>
<td>107.8±22.8 B,a</td>
</tr>
<tr>
<td>P (mg·kg–0.75·d–1)</td>
<td>59.4±9.8 a</td>
<td>25.6±6.0 a</td>
</tr>
<tr>
<td>Na (mg·kg–0.75·d–1)</td>
<td>47.1±4.3 A</td>
<td>48.8±3.7 a</td>
</tr>
<tr>
<td>K (mg·kg–0.75·d–1)</td>
<td>429.4±15.0 A,a</td>
<td>427.8±11.3</td>
</tr>
</tbody>
</table>

**Note:** Values are means ± SE. Different uppercased letters denote significant difference between soil treatments within diet (*P* ≤ 0.01). Different lowercased letters denote significant difference between diet treatments within soil (*P* ≤ 0.01).

### Table 5. Daily digestibilities (digestive efficiency) of dietary constituents in snowshoe hares (*Lepus americanus*) fed formulated diet or feltleaf willow (*Salix alaxensis*) leaves, with and without access to lick soil (*n* = 10).

<table>
<thead>
<tr>
<th>Diet treatment</th>
<th>Formulated diet</th>
<th>Feltleaf willow leaves</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No soil</td>
<td>Soil</td>
</tr>
<tr>
<td>Dry matter</td>
<td>0.69±0.01 A,a</td>
<td>0.58±0.02 B,a</td>
</tr>
<tr>
<td>Organic matter</td>
<td>0.70±0.01 a</td>
<td>0.69±0.01 a</td>
</tr>
<tr>
<td>N</td>
<td>0.87±0.01 a</td>
<td>0.87±0.01 a</td>
</tr>
<tr>
<td>Ca</td>
<td>0.31±0.05 a</td>
<td>0.38±0.04 a</td>
</tr>
<tr>
<td>Mg</td>
<td>0.45±0.04 a</td>
<td>0.47±0.04 a</td>
</tr>
<tr>
<td>P</td>
<td>0.23±0.03 a</td>
<td>0.09±0.02 a</td>
</tr>
<tr>
<td>Na</td>
<td>0.86±0.03 a</td>
<td>0.84±0.03 a</td>
</tr>
<tr>
<td>K</td>
<td>0.86±0.01 A,a</td>
<td>0.77±0.01 B</td>
</tr>
</tbody>
</table>

**Note:** Values are means ± SE. Different uppercased letters denote significant difference between soil treatments within diet (*P* ≤ 0.001). Different lowercased letters denote significant difference between diet treatments within soil (*P* ≤ 0.04).

![Fig. 4. Change in body mass of snowshoe hares (*Lepus americanus*) without access (open bars) or with access (solid bars) to lick soil over a 6-day experimental period (*n* = 10). Bars are means ± SE.](image-url)

Published by NRC Research Press
result in decreased apparent dry matter and crude protein digestibility (Chamorro et al. 2007). These findings are consistent with our observations. Given the importance of Na to physiological processes and the interactive constraint with PSMs, enhanced Na nutrition likely explains, at least in part, the benefits of soil consumption. It may also help explain the high daily soil intake rates. Although estimates of soil ingestion in free-ranging mammals are scarce, soil generally constitutes <10% of the diet of small herbivores (Beyer et al. 1994). This is well below our observations for hares eating willow leaves, where soil constituted nearly 25% of total DM intake.

Soil used for this study was relatively high in Ca and Mg, similar to soil from many licks (Klaus et al. 1998; Wilson 2003; Abrahams 2005; Ayotte et al. 2006). For hares fed willow leaves, soil ingestion resulted in digestible Ca and Mg intakes at least double that of hares not offered soil (Table 4). However, it is unclear to what degree these minerals are metabolized. Rabbits and hares are known to tolerate high serum levels of Ca, much of which is absorbed, regardless of dietary Caintake rates (Beyer et al. 1994). This is well below our observations for hares eating willow leaves, where soil constituted nearly 25% of total DM intake.

Soil used for this study was relatively high in Ca and Mg, similar to soil from many licks (Klaus et al. 1998; Wilson 2003; Abrahams 2005; Ayotte et al. 2006). For hares fed willow leaves, soil ingestion resulted in digestible Ca and Mg intakes at least double that of hares not offered soil (Table 4). However, it is unclear to what degree these minerals are metabolized. Rabbits and hares are known to tolerate high serum levels of Ca, much of which is absorbed, regardless of dietary intake rates (Beyer et al. 1994). This is well below our observations for hares eating willow leaves, where soil constituted nearly 25% of total DM intake.

Ecological implications

We have shown that geophagy results in trade-offs among improved forage intake rates, enhanced Na acquisition, reduced N digestibility, and accelerated P depleting resulting from excess Ca ingestion. Despite the potential detrimental effects of this behavior, soil ingestion provides an overall benefit to hares feeding on natural summer diets that contain little Na, are high in K, and also contain tannins. Physiological demands for energy and protein intake for reproductive animals, as do requirements for mineral nutrients, including Na, K, Ca, and P (National Research Council 1977; Barboza and Parker 2006). In winter, hares switch to woody browse, which is low in energy, high in PSMs, and may become scarce during high hare densities. This situation, coupled with increased thermoregulatory demands at low temperatures, results in nutritional challenges for hares. If geophagy results in higher forage consumption rates or more efficient nutrient assimilation, this behavior likely represents an important adaptive response for reproduction and survival.

Changes in hare reproduction and survival also may have implications ecosystem-wide (Kielland et al. 2006). Hares are considered a keystone species of the boreal forest and their abundance affects both vegetation communities and predator densities (Bryant et al. 1991; Rohner 1995; Stenseth et al. 1997; O’Donoghue et al. 1998; Krebs et al. 2001). Given that food resources play a role in regulating hare population cycles (Bryant 1981; Krebs et al. 2001) and the potential for geophagy to alter use of food resources, licks may represent an important resource on the landscape. Whereas the particular lick we studied is prominent, it is likely that many smaller, undetected licks exist in this area. It is unknown how prevalent these licks are, how they affect animal movement and spatial use of the food resources, and whether the benefits shown in our study are likely to be localized or widespread. Notwithstanding these uncertainties, the abundance and distribution of licks may be an important factor controlling the local abundance and distribution of snowshoe hares in interior Alaska.

Acknowledgements

K. Olson provided assistance with forage collection, animal care, and sample analysis. L. Oliver assisted with sample analysis. Funding for this project was provided by UAF Long-Term Ecological Research and the National Park Service.

References


Worker et al. 2009. Summer dietary nitrogen availability as a potential bottom-up con-

Hässig, M., and Hatt, J.-M. 2012. Influence of diet on calcium metabolism, minerals and


Freeland, W.J., Calcott, P.H., and Geiss, D.P. 1985. Allelochemicals, minerals and


Brower, M. 2003. Clay mineralogical and related characteristics of geophagic

Worker et al. 329


Young, V., and Hume, I.D. 2005. Nitrogen requirements and urea recycling in an


USDA. 1954. Alkaline-earth carbonates from acid neutralization. In Diagnosis and


USDA. 1994. Alkaline-earth carbonates from acid neutralization. In Diagnosis and


USDA. 1994. Alkaline-earth carbonates from acid neutralization. In Diagnosis and


USDA. 1994. Alkaline-earth carbonates from acid neutralization. In Diagnosis and


USDA. 1994. Alkaline-earth carbonates from acid neutralization. In Diagnosis and


USDA. 1994. Alkaline-earth carbonates from acid neutralization. In Diagnosis and


