

Geophagic behavior in the mountain goat (*Oreamnos americanus*): support for meeting metabolic demands

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Abstract: Geophagy, the intentional consumption of earth or earth matter, occurs across taxa. Nutrient and mineral supplementation is most commonly cited to explain its adaptive benefits; yet many specific hypotheses exist. Previous research on mountain goats (*Oreamnos americanus* (Blainville, 1816)) broadly supports nutrient supplementation as the adaptive benefit of geophagy. Here, we use data from an undisturbed population of mountain goats inhabiting a geologically distinct coastal mountain range in southwestern British Columbia to test the hypothesis that geophagic behavior is a proximate mechanism for nutrient supplementation to meet metabolic demands. Our population, observed for over 30 consecutive years, returned each year with high fidelity to the same geophagic lick sites. Logistic regression demonstrated an overall effect of sodium and phosphorus, but not magnesium and calcium, on lick preferences. These data, in conjunction with field observations, provide support for the hypothesis that geophagy provides nutrient supplementation and that geophagy may be an obligate behavior to meet necessary metabolic demands within this population. The implications of our results suggest the necessity to preserve historically important habitats that may be necessary for population health.

Key words: geophagy, mountain goat, *Oreamnos americanus*, mineral supplementation.

Résumé : La géophagie, la consommation intentionnelle de terre ou de substances de la terre, est observée chez de nombreux taxons. L'explication de ses avantages adaptatifs fait le plus souvent appel à la supplémentation de nutriments et de minéraux, bien qu'il existe de nombreuses hypothèses distinctes. Des travaux antérieurs sur la chèvre des montagnes Rocheuses (*Oreamnos americanus* (Blainville, 1816)) appuient généralement l'hypothèse selon laquelle l'avantage adaptatif de la géophagie serait la supplémentation de nutriments. Nous utilisons des données sur une population non perturbée de chèvres des montagnes Rocheuses résidant dans une chaîne de montagnes côtières distincte sur le plan géologique dans le sud-ouest de la Colombie-Britannique pour vérifier l'hypothèse voulant que le comportement géophage soit un mécanisme immédiat de supplémentation de nutriments pour répondre à des demandes métaboliques. La population à l'étude, observée pendant plus de 30 années consécutives, retournait chaque année, de manière très fidèle, aux mêmes sites de blocs à lécher. La régression logistique démontre un effet global du sodium et du phosphore, mais non du magnésium et du calcium, sur les préférences en matière de blocs à lécher. Ces données, combinées à des observations de terrain, appuient l'hypothèse selon laquelle la géophagie assurerait une supplémentation de nutriments et qu'elle pourrait constituer un comportement obligatoire pour répondre à des demandes métaboliques nécessaires dans cette population. Nos résultats pointent vers la nécessité de préserver des habitats importants qui pourraient être nécessaires à la santé des populations. [Traduit par la Rédaction]

Mots-clés : géophagie, chèvre des montagnes Rocheuses, *Oreamnos americanus*, supplémentation de minéraux.

Introduction

Geophagy, the intentional consumption of earth or earth matter, is a behavior observed in a variety of organisms including ungulates (Hebert and Cowan 1971; Field and Ross 1976; Robbins 1993; Howell et al. 1996; Mincher et al. 2008), primates (Mahaney et al. 1990; Ketch et al. 2001), and parrots (Brightsmith and Muñoz-Najar 2004). Individuals frequent dry and wet licks created by natural deposition and concentration of dissolved elements and (or) clays and display preferences for specific lick and soil deposits (Jones and Hanson 1985; Klaus et al. 1998; Brightsmith and Muñoz-Najar 2004; Ayotte et al. 2006, 2008; Young et al. 2011). Preference among soil types (e.g., clay, mud, and dry soils) has been shown to vary across species and study sites. This variation could result from species-specific periods of elemental deficiencies and imbalances, and (or) site-specific variation of nutrient availability in forage (Cowan and Brink 1949; Jones and Hanson 1985; Ayotte et al. 2008).

Although the causal mechanism behind geophagic behavior varies from system to system, geophagy is generally considered to be beneficial (Kreulen 1985; Klaus et al. 1998; Ayotte et al. 2006, 2008; Gomes and Silva 2007; Slamova et al. 2011; Young et al. 2011; Starks and Slabach 2012). Benefits are broadly attributed to nutrient supplementation, which can aid in meeting requirements of specific metabolic demands such as antler osteogenesis, pregnancy, and lactation (Meschy 2000; Ayotte et al. 2006, 2008; Young et al. 2011) and can establish optimal levels of essential elements in times of mineral stress or imbalance (Jones and Hanson 1985; Kreulen 1985). Nutrient supplementation can also alleviate symptoms caused by gastrointestinal stress such as acidosis (Jones and Hanson 1985; Kreulen 1985; Ayotte et al. 2006, 2008). To identify specific causal mechanisms throughout populations and understand the evolutionary history of the behavior, this spectrum of benefits has been differentiated into four specific hypotheses: (1) detoxification of secondary plant compounds (Kreulen 1985; Müller-Schwarze 1991; Wilson 2003; Young et al. 2011), (2) allevia-

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tion of gastrointestinal stress (Kreulen 1985; Wilson 2003; Ayotte et al. 2006, 2008; Young et al. 2011), (3) nutrient supplementation to meet metabolic demands (Jones and Hanson 1985; Kreulen 1985; Wilson 2003), and (4) remedying of osmotic imbalances in the digestive tract (Jones and Hanson 1985; Wilson 2003). These hypotheses are founded on the potential digestive benefits of consuming clay particles, carbonate salts, and (or) essential minerals, and in many instances are not mutually exclusive (Krishnamani and Mahaney 2000). Differentiating among specific nutrients that animals may be seeking has proven difficult because of geologic colocalization of elements and the physiological interrelationships of relevant nutrient pathways.

To understand the potential role of geophagy in population persistence, it is important to differentiate proposed hypotheses to better elucidate proximate causation. Understanding potential proximate causes will provide insight into movement patterns, habitat requirements, and how habitat alterations could impact population persistence through reduced body condition, decreased reproductive output, and (or) survival. For instance, if nutrients obtained from sites are required for proper fetal growth, impediment of travel routes to sites could increase nutritional stress on mothers. This physiological stress could have negative implications on both fetal growth and maternal fecundity or survival. Several studies have discussed the role of forage quality on movement patterns, growth, and reproductive success of ungulates (Festa-Bianchet 1988; Mduma et al. 1999; Cook et al. 2004; Hamel et al. 2010; Zweifel-Schielly et al. 2012). Species that inhabit alpine ranges, where the concentration of soil nutrients is typically poor, are presumably more greatly affected by small differences in nutrient concentrations found in forage (White 1983); geophagic nutrient supplementation may therefore be more important for these species. Quantifying these effects, and identifying species-specific nutrients of importance, is a daunting task, particularly in wild systems. Yet by integrating the natural history of populations, the areas they inhabit, along with soil and behavioral analyses, we can provide a more holistic depiction of the role of geophagic behavior.

We investigated the function of geophagic behavior in an isolated population of mountain goats (*Oreamnos americanus* (Blainville, 1816)) in the Coast Range of southwestern British Columbia, Canada. A variety of studies have documented geophagic behavior within this species, highlighting either individual movement patterns to specific lick sites or the nutrient composition of preferred licks (Jones and Hanson 1985; Poole and Heard 2003; Poole et al. 2010; Rice 2010) or discussed its potential role in home-range limitations (Hebert 1965; Festa-Bianchet 1988). We aimed to understand what specific nutrients goats were seeking at lick sites. Over the course of a 30+ year longitudinal ethological study, Dane (1977, 2002) observed the same herd of mountain goats return annually to the same lick, grazing, and bedding sites in their summer range. We took advantage of the opportunity to analyze the mineral content and soil texture of these licks.

Existing literature suggests that minerals of interest for ruminant nutrition include calcium (Ca), sodium (Na), phosphorus (P), and magnesium (Mg) (Jones and Hanson 1985; Kreulen 1985; Klaus et al. 1998; Ayotte et al. 2006, 2008). We focused on the analyses of those four nutrients to determine whether these minerals were specifically enriched at the lick sites. Alpine forage is typically depleted in Na and high in potassium (K) (Poole et al. 2010). Therefore, we predict that preferred soils will contain elevated Na concentrations to rectify this metabolic imbalance.

The study population included both sexes and all ages; lactating, nutritionally stressed females with kids or yearlings usually led the herd between bedding sites and grazing or lick sites (Dane 2002). We therefore predict elevated concentrations of P and Ca—essential elements in lactation, growth, and development—in lick soils if geophagy serves to meet both specific and general metabolic demands in this population. Six other minerals (K, iron (Fe),

manganese (Mn), aluminum (Al), copper (Cu), and zinc (Zn)) were analyzed for comparison.

The Pacific Coast Range is a remote area that is difficult to access and therefore has been left primarily undisturbed by human interference. Thus, our longitudinal behavioral data provides a unique opportunity to understand causative agents of geophagy in the absence of exogenous anthropogenic factors, providing insight into the importance of these specific sites to the ecology of the population, as well as the health and overall persistence of the herd. This information is not only important to understand geophagy as an adaptive response to meet metabolic demands, but to further our understanding of potential implications of anthropogenic disturbance on natural landscapes.

Materials and methods

Study area and population

The study area is 48 km north of Mount Waddington in the Coast Range of southwestern British Columbia (see details in Dane 1977, 2002). The total area monitored for goat movements and specific behaviors is approximately 16 km long by 6.5 km wide; it consists of a high timberless plateau separated from 2300 to 2500 km mountains by an alpine valley. During the 33 years of the study period, the population varied between 6 and 48 animals (Dane 2002). The herd exhibited high site fidelity within the study range, allowing groups to be easily located for observation (Dane 1977, 2002). Behavior, including geophagy, was observed without interference from established observation posts at ranges of 100–1000 m. Individuals were reliably identified by horn structure for consecutive years (Dane 2002). Animals arrive in the study area from late June to early July and leave in September of each year. Although the main focus of the long-term study was social behavior and reproductive patterns in relation to population cycles (Dane 2002), geophagy was observed regularly at lick sites that were easily identified for sampling.

Soil sampling and analysis

Soil samples were obtained annually from 1987 to 1990 and 1992. Lick samples were collected from both dry and mud lick sites. Dry licks were defined as areas where goats had pawed and (or) scraped soil from dry terrain, whereas mud licks were defined as areas along stream banks where goats either ingested mud or muddy water (for a review of lick-type definitions see Dormaar and Walker 1996). All dry lick sites were approximately 50–100 cm in diameter and had been cleared of overlying gravel and any vegetation by goats' pawing, licking, and scraping over time, which resulted in shallow depressions. There were often several sites co-localized in the same general area. Control samples were collected haphazardly from undisturbed soils within 1–15 m of lick sites; a few control samples were taken from more distant areas in which the mountain goats were never observed consuming soil. Surface gravel was scraped away to simulate depressions typical of lick sites before collection of the control soil sample.

Soil samples were dried, pulverized, screened through 1 mm mesh and sent to the Analytical Laboratory in the Department of Plant and Soil Sciences at the University of Maine – Orono for soluble mineral analysis. Replicate samples were extracted 1:4 or 1:8 (m:v) for 15 min in 1 mol/L ammonium acetate buffered to pH 3.0 and filtered. Filtrates were analyzed for soluble Ca, K, Mg, P, Al, Cu, Fe, Mn, Zn, and Na. All elemental determinations were by plasma emission spectrometry, with the exception of Na, which was analyzed by flame emission, and K, which was also run by flame emission to verify plasma emission K values.

A subset of samples ($N = 14$ lick; $N = 16$ control soils) was analyzed for soil texture to determine the physical composition of samples. Soils ingested for detoxification or alleviation of gastrointestinal stress in both human and nonhuman vertebrates are

Table 1. Mean (\pm SE) mineral concentration (ppm, where 1 ppm = 1 mg/kg) by soil type (mud vs. dry) and by preference (lick vs. control).

	Control			Lick		
	Dry (N = 75)	Mud (N = 25)	Overall (N = 100)	Dry (N = 45)	Mud (N = 27)	Overall (N = 72)
Minerals of interest						
Calcium (Ca)	337.92 \pm 44.29	1126.01 \pm 216.12	534.94 \pm 71.46	850.24 \pm 101.62	2342.47 \pm 259.57	1409.83 \pm 143.53
Sodium (Na)	17.48 \pm 2.79	33.77 \pm 5.26	21.42 \pm 2.55	55.57 \pm 4.97	129.15 \pm 11.46	83.16 \pm 6.74
Magnesium (Mg)	37.03 \pm 6.08	72.82 \pm 17.53	45.98 \pm 6.46	86.55 \pm 7.21	101.85 \pm 10.02	92.29 \pm 5.89
Subsequent minerals analyzed						
Phosphorus (P)	4.41 \pm 0.28	8.54 \pm 1.08	5.44 \pm 0.38	9.42 \pm 1.21	6.85 \pm 0.94	8.46 \pm 0.84
Aluminum (Al)	261.62 \pm 20.74	367.57 \pm 51.55	288.10 \pm 20.58	75.09 \pm 10.53	464.85 \pm 44.50	221.26 \pm 28.57
Copper (Cu)	0.44 \pm 0.03	1.02 \pm 0.26	0.58 \pm 0.07	0.97 \pm 0.26	1.45 \pm 0.49	1.16 \pm 0.24
Iron (Fe)	13.59 \pm 3.81	78.02 \pm 17.07	29.69 \pm 5.80	11.95 \pm 6.29	72.61 \pm 31.64	34.17 \pm 12.71
Manganese (Mn)	4.05 \pm 0.73	16.61 \pm 3.18	7.19 \pm 1.10	4.02 \pm 0.70	10.72 \pm 3.49	6.53 \pm 1.42
Zinc (Zn)	0.54 \pm 0.04	1.17 \pm 0.19	0.69 \pm 0.06	0.54 \pm 0.08	1.82 \pm 0.37	1.02 \pm 0.16
Potassium (K)	42.01 \pm 4.29	99.01 \pm 16.61	56.26 \pm 5.76	64.66 \pm 12.35	198.81 \pm 50.02	114.96 \pm 21.49

Note: Samples were combined based on site (control vs. lick). Overall concentrations were used for the logistic regression analysis.

Table 2. Result of logistic regression model.

Independent variable	Parameter estimate	SE	Odds ratio (95% CI)	p
Intercept	-3.58	0.54	0.02 (0.01, 0.07)	0.0001
Mud	-3.01	0.83	0.04 (0.01, 0.22)	0.0001
Calcium (Ca)	0.001	0.001	1.00 (0.99, 1.00)	0.22
Magnesium (Mg)	-0.001	0.004	0.99 (0.98, 1.00)	0.70
Sodium (Na)	0.06	0.01	1.06 (1.04, 1.09)	0.0001
Phosphorus (P)	0.13	0.04	1.14 (1.04, 1.27)	0.001

Note: Lick sites served as the dependent variable because of the pre-existing preference for these sites. An overall main effect was found ($\beta = -3.58$, $p < 0.0001$; values set in boldface type) as expected because of the observed mountain goat (*Oreamnos americanus*) preference for lick sites. The concentration of mud ($\beta = -3.01$, $p < 0.0001$), Na ($\beta = 0.01$, $p < 0.0001$), and P ($\beta = 0.04$, $p < 0.001$) were also found to have a significant effect on goat preference (values set in italic type). This finding is further supported by the adjusted odds ratio for these variables, with increased presence of these minerals increasing the likelihood of goat preference by 4%–14%. It should be noted that the confidence intervals (CI) for Ca and Mg include 1.00, suggesting no causal relationship between the mineral concentrations of these nutrients and geophagic behavior.

commonly clay-rich. Certain clay types aid in ridding the body of chemicals or parasitic infections due to increased binding affinities (Young et al. 2011). Thus, increased clay content would suggest detoxification as one plausible explanation for geophagy in this population. Particle size was run on screened (1 mm) samples by the Bouyoucos or hydrometer method routinely used by the Analytical Laboratory at the University of Maine – Orono, Department of Plant and Soil Sciences. Texture classes are those stipulated by the U.S. Department of Agriculture Soil Conservation Services, reported as percent sand, percent silt, and percent clay.

Fecal-sample analysis

Fecal material, consisting of compact pellets of various sizes, was collected at random from frequently used goat bedding areas or along regularly used goat trails. Ash content was analyzed as a proxy for the amount of soil ingested by individual goats at various times. Loose fecal masses were neither observed in the study area nor observed during active defecation. Pellets were sprayed with shellac to minimize water absorption prior to determination of size by volume displacement. Fecal samples were sent to the Washington State University Wildlife Habitat Laboratory where they were dried, pulverized, and heated in a muffle furnace to determine percent ash as the residual noncombustible mass compared with the starting mass.

Statistical analyses

To assess the relationship between goat preference for lick sites and mineral concentrations, while controlling for confounding variables, logistic regression was used. Since a pre-existing bias of goat preference to licks is known, a logistic regression approach provided an indication of what factors (e.g., nutrient concentrations) effect the true probability of soil being ingested, or in other

Table 3. Analysis of fecal-pellet content from mountain goats (*Oreamnos americanus*).

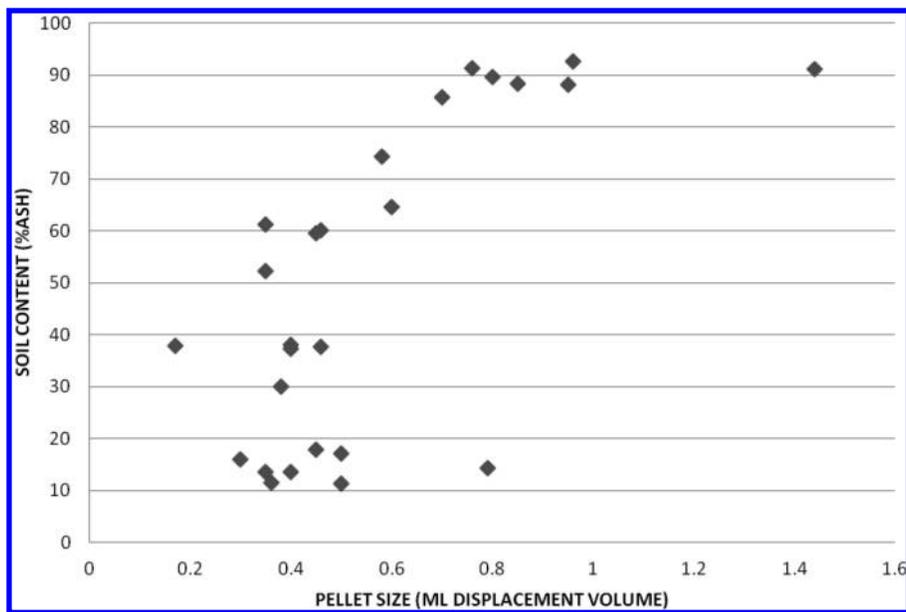
	Sand (%)	Silt (%)	Clay (%)
Lick (N = 14)	54.36 \pm 7.93	38.43 \pm 5.54	7.21 \pm 4.12
Control (N = 16)	62.88 \pm 14.48	33.00 \pm 14.32	4.12 \pm 2.23

Note: Analysis of soils in lick sites used by goats compared with control soils by texture type. Values are means \pm SD.

words, what nutrients were increasing the probability of sampled sites to be utilized as licks.

Concentrations of many nutrients tend to be highly correlated, making it difficult to deduce a specific nutrient, or suite of nutrients, as the causative factor of the behavior (White 1979). Thus, linear relationships between nutrients were assessed via bivariate scatter plots and Pearson correlation coefficients prior to any further analyses. Many of the nutrient concentrations were strongly correlated. Due to a high instance of multicollinearity between minerals, variables of interest included in the final model were Ca, Na, and Mg. Samples were combined based on site (control vs. lick) and coded as a binary outcome. The variables “mud soil type” and “P” were also included because of their association with site preference and biological relevance. Other variables of interest were not predictive and thus were not included in the final model. Specific habitat locales (valley, plateau, etc.) and the soil variable “dry” were also not included because of their lack of association with site preference. Adjusted odds ratios for each variable are presented with 95% confidence intervals (CI). All data were log-transformed and points greater than three SD from the mean were considered outliers and excluded from the analysis. All statistical analyses were conducted using R Studio version 0.96.331 (RStudio 2012).

Fig. 1. Mountain goat (*Oreamnos americanus*) fecal pellets were collected and analyzed for size (proxy for animal age) and ash content (indication of amount of soil ingested). Data indicate that animals of different sizes (and thus ages) consume soil.



Results

Mineral analysis

Mineral concentration (ppm, where 1 ppm = 1 mg/kg) varied between lick and control sites, with lick sites demonstrating higher mean concentrations of all minerals except Al and Mn (Table 1). All variables of interest (Ca, Mg, Na) were found in higher concentrations at mud lick sites compared with all other sites (Table 1).

Logistic analysis

An overall association between lick sites and at least one regressor was found ($\beta = -3.58$, $p < 0.0001$). A negative relationship between mud soil type and lick preference was also found ($\beta = -3.01$, $p < 0.0001$); it was 90% less likely for soil to be ingested at mud sites compared with dry sites (Table 2). Na ($\beta = 0.06$, $p < 0.0001$) and P ($\beta = 0.13$, $p < 0.001$) were positively correlated with probability of soil ingestion; greater concentrations of both these micronutrients at lick sites increased the probability of soil ingestion by 6% and 14%, respectively. The presence of increased concentrations of Mg and Ca were not found to affect site preference (Table 2).

Soil texture

Differences in sand, silt, and clay contents between lick and control soils were not significant (Table 3). Clay content averaged less than 8% in both lick and control soils; all lick and control samples were classified as “sandy loam” or “loamy sand”.

Fecal soil content

Ash content of fecal pellets varied between 11% and 90% of mass, reflecting highly variable amounts of soil ingestion by individuals at different times (Fig. 1). To the extent that pellet size is a function of animal age, Fig. 1 also suggests that animals in all age classes, including kids of the year, ingest soil. The amount of soil ingested rather than animal age might account for some size variation of pellets. However, the fact that ash content in a narrow range of pellet size (approximately 0.35–0.45 mL) varied from 10% to 60% suggests that pellet size is not strictly correlated with amount of soil ingested and that very young animals may engage in geophagy.

Discussion

Our findings suggest that geophagy at lick sites in this study are driven by elevated Na and P concentrations. The overall differences in mineral concentrations found between lick and control sites are comparable with those previously reported (Jones and Hanson 1985; Dormaar and Walker 1996). The preference for these sites due to increased Na concentrations supports the conventional hypothesis that Na is the driving factor behind geophagic behavior, specifically in ungulates (Botkin et al. 1973; Belovsky 1978; Jones and Hanson 1985; Hebert and Cowan 1971; Ayotte et al. 2006). Our results represent an extension of a long-term behavioral study of an undisturbed population inhabiting a remote mountain range that is geologically different from those previously reported (Vaughan 1974; Singer 1975). More specifically, our findings provide evidence that geophagic behavior acts as an adaptive mechanism for nutrient supplementation to meet metabolic demands during the summer months in this population, further revealing the role of geophagy in wild populations.

As the largest North American mammalian species found at high altitudes (goats frequent altitudes as high as 4000 m), geophagic behavior as a response to Na deficiency was anticipated. Subalpine and alpine flora are commonly Na deficient (Hebert 1965; White 1979; Poole et al. 2010). Na requirements increase during late spring and early summer in response to increased K within forage, as well as during late pregnancy and lactation (Weeks and Kirkpatrick 1976; Jones and Hanson 1985; Atwood and Weeks 2002; Ayotte et al. 2006). Mountain goats give birth in late May and lactate throughout the summer. Our population included many lactating females, including biennial breeding females nursing yearlings, which acted as herd leaders (Dane 2002). Na concentrations at lick sites increased the probability of soil ingestion by 6% (Table 2).

Increased intake of P and Ca are also necessary during pregnancy. P levels in ruminant milk have been found to remain constant despite variable amounts in traditional forage (Cohen 1980). The metabolic diversion of P and Ca necessary for successful pregnancy and lactation could result in demineralization of bones in does in response to loss of P via lactation. P concentrations at lick sites increased the probability of ingestion by 14% (Table 2). Ca concentrations at lick sites did not affect the probability of soil ingestion (95% CI for odds ratio: 0.99, 1.00; Table 2), yet Ca levels at

lick sites were much greater than Ca levels at control sites (Table 1). Supplementing these minerals through geophagy could act to slow bone demineralization.

Although soil samples were only collected for a subset of years, the documented continual return of the herd to licks during certain seasonal time periods, the amount of soil found in fecal matter, and the low clay content of lick soils all provide further support for the hypothesis that geophagic behavior is a proximate mechanism for nutrient supplementation in this population. Previous studies of mountain goat geophagic behavior have yielded similar conclusions; yet different nutrients were cited as causative factors (e.g., Ca and Mg; Vaughan 1974; Singer 1975). The study locale, the Coast Range of southwestern British Columbia, is geologically dissimilar from all other reported geophagic studies on this species (Hebert 1965; Vaughan 1974; Singer 1975; Ayotte et al. 2006). Differences in causative nutrients could therefore be explained by the geologic differences in study locales.

Many nutrient concentrations are highly correlated, as we found here, therefore making it difficult to deduce if a specific nutrient, or suite of nutrients, are causative factors of the specific sites that are consumed (White 1979). Studies have suggested that the presence of elevated Na concentrations could be acting as an indicator to organisms that additional beneficial nutrients are present (Sclafani 1991). Evidence has shown that ungulates can differentiate between Na and other nutrients across age classes (Ceacero et al. 2010). Thus, individuals have the ability to differentiate—to a certain extent—necessary nutrients providing additional evidence for geophagic behavior as an adaptive mechanism.

The focus of Dane's long-term studies (Dane 1977, 2002) was social behavior and population dynamics, and thus lacks empirical data sufficient to correlate specific lick use (e.g., time spent licking, frequency of visits, or number of goats at a lick) with visibility or quality of escape terrain. However, observations suggest that goats show high fidelity to these lick and grazing sites, even when they are vulnerable to predators (Dane 2002). Early studies hypothesized that home range of ungulates is constrained by location of lick sites given these sites provide vital nutrients necessary for survival and fecundity (Jones and Hanson 1985; Festa-Bianchet 1988). Yet, individuals will utilize multiple lick sites within their home range if available (Poole et al. 2010; Rice 2010). The availability of other lick sites to individuals in this population was not observed. High site fidelity, particularly in the presence of predators, suggests that individuals are not only constrained by these sites, but may have no additional resources to gather necessary nutrients.

In conclusion, previous studies support the hypotheses that geophagy in mountain goats is adaptive through the alleviation of gastrointestinal distress and supplementation of essential nutrients (Jones and Hanson 1985; Kreulen 1985; Ayotte et al. 2006, 2008). Findings for our population of mountain goats suggest that they preferentially select soil based on key mineral content. In concert with behavioral observations at lick sites, the leadership of herd movements by reproductively active females, low clay content of lick soils, fecal-pellet integrity and soil content, and high fidelity to these lick sites long term lead to the conclusion that the principal advantage of geophagy in this population is supplementation of minerals to meet metabolic demands. These minerals are principally Na, P, and Ca. Further investigation comparing goat forage preferences with the mineral quality of various forbs could provide insight into the relative importance of grazing and geophagy for the acquisition of nutritionally important minerals in alpine environments.

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References

- Atwood, T.C., and Weeks, H.P., Jr. 2002. Sex- and age-specific patterns of mineral lick use by white-tailed deer (*Odocoileus virginianus*). *Am. Midl. Nat.* **148**: 289–296. doi:10.1674/0003-0031(2002)148[0289:SAASPO]2.0.CO;2.
- Ayotte, J.B., Parker, K.L., Arocena, J.M., and Gillingham, M.P. 2006. Chemical composition of lick soils: functions of soil ingestion by four ungulate species. *J. Mammal.* **87**: 878–888. doi:10.1644/06-MAMM-A-055R1.1.
- Ayotte, J.B., Parker, K.L., and Gillingham, M.P. 2008. Use of natural licks by four species of ungulates in northern British Columbia. *J. Mammal.* **89**: 1041–1050. URL: 10.1644/07-MAMM-A-345.1.
- Belovsky, G.E. 1978. Diet optimization in a generalist herbivore: the moose. *Theor. Popul. Biol.* **14**: 105–134. doi:10.1016/0040-5809(78)90007-2. PMID:741393.
- Botkin, D.B., Jordan, P.A., Dominski, A.S., Lowendorf, H.S., and Hutchinson, G.E. 1973. Sodium dynamics in a northern ecosystem. *Proc. Natl. Acad. Sci. U.S.A.* **70**: 2745–2748. doi:10.1073/pnas.70.10.2745. PMID:16592111.
- Bowell, R.J., Warren, A., and Redmond, I. 1996. Formation of cave salts and utilization by elephants in the Mount Elgon region, Kenya. *Environ. Geochem. Health.* **113**: 63–79. doi:10.1144/GSL.SP.1996.113.01.06.
- Brightsmith, D.J., and Muñoz-Najar, R.A. 2004. Avian geophagy and soil characteristics in southeastern Peru. *Biotropica*, **36**: 534–543. doi:10.1111/j.1744-7429.2004.tb00348.x.
- Ceacero, F., Landete-Castillejos, T., García, A.J., Estévez, J.A., and Gallego, L. 2010. Can Iberian red deer (*Cervus elaphus hispanicus*) discriminate among essential minerals in their diet? *Br. J. Nutr.* **103**: 617–626. doi:10.1017/S0007114509992091. PMID:19860987.
- Cohen, R.D.H. 1980. Phosphorus in rangeland ruminant nutrition: a review. *Livestock Prod. Sci.* **7**: 25–37. doi:10.1016/0301-6226(80)90046-9.
- Cook, J.G., Johnson, B.K., Cook, R.C., Delcurto, T., Bryant, L.D., and Irwin, L.L. 2004. Effects of summer–autumn nutrition and parturition date on reproduction and survival of elk. *Wildl. Monogr.* **155**: 1–61.
- Cowan, I.M., and Brink, V.C. 1949. Natural game licks in the rocky mountain national parks of Canada. *J. Mammal.* **30**: 379–387. doi:10.2307/1375213.
- Dane, B. 1977. Mountain goat social behavior: social structure and play behavior as affected by dominance. In *Proceedings of the First International Mountain Goat Symposium*, Kalispell, Mont., 19 February 1977. Edited by W. Samuel and W.G. Macgregor. Province of British Columbia, Ministry of Recreation and Conservation, Fish and Wildlife Branch, Victoria. pp. 92–106.
- Dane, B. 2002. Retention of offspring in a wild population of ungulates. *Behaviour*, **139**: 1–21. doi:10.1163/15685390252902247.
- Dormaar, J.F., and Walker, B.D. 1996. Elemental content of animal licks along the eastern slopes of the Rocky Mountains in southern Alberta. *Can. J. Soil Sci.* **76**(4): 509–512. doi:10.4141/cjss96-063.
- Festa-Bianchet, M. 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. *Oecologia*, **75**: 580–586. doi:10.1007/BF00776423.
- Field, C.R., and Ross, I.C. 1976. The savanna ecology of Kidepo Valley National Park. II. Feeding ecology of elephant and giraffe. *East Afr. Wildl. J.* **14**: 1–16. doi:10.1111/j.1365-2028.1976.tb00148.x.
- Gomes, C.S.F., and Silva, J.B.P. 2007. Minerals and clay minerals in medical geology. *Appl. Clay Sci.* **36**: 4–21. doi:10.1016/j.clay.2006.08.006.
- Hamel, S., Côté, S.D., and Festa-Bianchet, M. 2010. Maternal characteristics and environment affect the costs of goat reproduction in female mountain goats. *Ecology*, **91**: 2034–2043. doi:10.1890/09-1311.1. PMID:20715626.
- Hebert, D. 1965. Natural salt licks as a part of the ecology of the mountain goat. M.Sc. thesis, The University of British Columbia, Vancouver.
- Hebert, D., and Cowan, I.M. 1971. Natural salt licks as a part of the ecology of the mountain goat. *Can. J. Zool.* **49**(5): 605–610. doi:10.1139/z71-097. PMID:5557898.
- Jones, R.L., and Hanson, H.C. 1985. Mineral licks, geophagy, and biochemistry of North American ungulates. Iowa State University Press, Ames.
- Ketch, L.A., Malloch, D., Mahaney, W.C., and Huffman, M.A. 2001. Comparative microbial analysis and clay mineralogy of soils eaten by chimpanzees (*Pan troglodytes schweinfurthii*) in Tanzania. *Soil Biol. Biochem.* **33**: 199–203. doi:10.1016/S0038-0717(00)00129-2.
- Klaus, G., Klaus-Hügi, C., and Schmid, B. 1998. Geophagy by large mammals at natural licks in the rain forest of the Dzanga National Park, Central African Republic. *J. Trop. Ecol.* **14**: 829–839. doi:10.1017/S0266467498000595.
- Kreulen, D.A. 1985. Lick use by large herbivores: a review of benefits and banes of soil consumption. *Mammal Rev.* **15**: 107–123. doi:10.1111/j.1365-2907.1985.tb00391.x.
- Krishnamani, R., and Mahaney, W.C. 2000. Geophagy among primates: adaptive significance and ecological consequences. *Anim. Behav.* **59**: 899–915. doi:10.1006/anbe.1999.1376. PMID:10860518.
- Mahaney, W.C., Watts, D.P., and Hancock, R.G.V. 1990. Geophagia by mountain gorillas (*Gorilla gorilla beringei*) in the Virunga Mountains, Rwanda. *Primates*, **31**: 113–120. doi:10.1007/BF02381034.
- Mduma, S.A.R., Sinclair, A.R.E., and Hilborn, R. 1999. Food regulates the Serengeti wildebeest: a 40-year record. *J. Anim. Ecol.* **68**: 1101–1122. doi:10.1046/j.1365-2656.1999.00352.x.

- Meschy, F. 2000. Recent progress in the assessment of mineral requirements of goats. *Livestock Prod. Sci.* **64**: 9–14. doi:10.1016/S0301-6226(00)00171-8.
- Mincher, B.J., Ball, R.D., Houghton, T.P., Mionczynski, J., and Hnilicka, P.A. 2008. Some aspects of geophagia in Wyoming bighorn sheep (*Ovis canadensis*). *Eur. J. Wildl. Res.* **54**: 193–198. doi:10.1007/s10344-007-0128-9.
- Müller-Schwarze, D. 1991. The chemical ecology of ungulates. *Appl. Anim. Behav. Sci.* **29**: 389–402. doi:10.1016/0168-1591(91)90263-W.
- Poole, K.G., and Heard, D.C. 2003. Seasonal habitat use and movements of mountain goats, *Oreamnos americanus*, in east-central British Columbia. *Can. Field-Nat.* **117**: 565–576.
- Poole, K.G., Bachmann, K.D., and Teske, I.E. 2010. Mineral lick use by GPS radiocollared mountain goats in southeastern British Columbia. *W. N. Am. Nat.* **70**: 208–217. doi:10.3398/064.070.0207.
- Rice, C.G. 2010. Mineral lick visitation by mountain goats, *Oreamnos americanus*. *Can. Field-Nat.* **124**(3): 225–237.
- Robbins, C.T. 1993. *Wildlife feeding and nutrition*. Academic Press, San Diego, Calif.
- RStudio. 2012. RStudio: integrated development environment for R. Version 0.96.122 [computer program]. RStudio, Boston, Mass. Available from <https://www.rstudio.com/> [accessed 20 May 2012].
- Sclafani, A. 1991. Conditioned food preferences. *Bull. Psychon. Soc.* **29**: 256–260. doi:10.3758/BF03335250.
- Singer, F.J. 1975. Behavior of mountain goats, elk, and other wildlife in relation to U.S. Highway 2, Glacier National Park. Report for Federal Highway Administration, Denver, Colo.
- Slamova, R., Trckova, M., Vondruskova, H., Zraly, Z., and Pavlik, I. 2011. Clay minerals in animal nutrition. *Appl. Clay Sci.* **51**: 395–398. doi:10.1016/j.clay.2011.01.005.
- Starks, P.T.B., and Slabach, B.L. 2012. The scoop on eating dirt. *Sci. Am. Mag.* **306**: 30–32. doi:10.1038/scientificamerican0612-30.
- Vaughan, M.R. 1974. Aspects of mountain goat ecology, Wallowa Mountains, Oregon. Master's thesis, Oregon State University, Corvallis.
- Weeks, H.P., Jr., and Kirkpatrick, C.M. 1976. Adaptations of white-tailed deer to naturally occurring sodium deficiencies. *J. Wildl. Manage.* **40**: 610–625. doi:10.2307/3800555.
- White, R.G. 1979. Nutrient acquisition and utilization in arctic herbivores. In *Comparative mechanisms of cold adaptation*. Edited by L.S. Underwood, L.L. Tieszen, A. Callahan, and G.E. Folk. Academic Press, New York. pp. 13–50. doi:10.1016/B978-0-12-708750-4.50006-4.
- White, R.G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. *Oikos*, **40**: 377–384. doi:10.2307/3544310.
- Wilson, M.J. 2003. Clay mineralogical and related characteristics of geophagic materials. *J. Chem. Ecol.* **29**: 1525–1547. doi:10.1023/A:1024262411676. PMID:12921434.
- Young, S.L., Sherman, P.W., Lucks, J.B., and Pelto, G.H. 2011. Why on earth?: Evaluating hypotheses about the physiological functions of human geophagy. *Q. Rev. Biol.* **86**: 97–120. doi:10.1086/659884. PMID:21800636.
- Zweifel-Schielly, B., Leuenberger, Y., Kreuzer, M., and Suter, W. 2012. A herbivore's food landscape: seasonal dynamics and nutritional implications of diet selection by a red deer population in contrasting Alpine habitats. *J. Zool.* **286**: 68–80. doi:10.1111/j.1469-7998.2011.00853.x.