Richard B. Harris[1], and **Clifford G. Rice,** Wildlife Program, Washington Department of Fish and Wildlife, 600 Capital Way, Olympia, Washington 98501

and

Adam G. Wells, 3927 NE 47th Avenue, Portland, OR 97213

Influence of Geological Substrate on Mountain Goat Forage Plants in the North Cascades, Washington State

Abstract

We addressed three questions relevant to patterns of mountain goat abundance in Washington's North Cascades: 1) What are forages used by mountain goats during summer? 2) Is canopy cover of mountain goat forage species predicted by geological substrates? and 3) Are indices of nutritional quality and digestibility of two mountain goat forage species predicted by geological characteristics? These questions were motivated by observations that historical abundance of mountain goats in Washington, accounting for habitats generally documented as suitable for them, was greater over some geological substrates than others. Mountain goats ate primarily sedges, secondarily rushes, and made surprisingly little use of grasses. Mountain goats ate a wide variety of forbs, with none showing overwhelming use. Despite their abundance in many landscapes near mountain goat escape terrain, *Vaccinium* spp. were rarely consumed, and other shrubs in Ericaceae were avoided entirely. Geological substrate explained only a small proportion of variability in mountain goat forage availability. Categorized by geological origin, sedges had higher canopy cover when over sedimentary and shale substrates than when over plutonic substrates. Categorized by geochemistry, sedges had higher canopy cover when over sedimentary rocks than over potassium-feldspar substrates. Sodium-rich substrates generally supported less vegetation than other substrates across all forage categories. Neither nutrients nor digestibility of the two focal species were predicted by geological type. Our study suggests that geological substrates in the North Cascades vary slightly in their production of forage plants valued by mountain goats, but do not affect the nutritional quality of two key forage plants.

Keywords: diet, geological substrate, mountain goat, nutritional quality, *Oreamnos americanus*

Introduction

Mountain goats (*Oreamnos americanus*), an emblematic species of Washington's North Cascades and the primary large mammal of North Cascades alpine zones, are estimated to have declined some 70% relative to historic abundance levels (Rice and Gay 2010, WDFW 2014). Because mountain goats recolonize slowly and natural rates of increase are slow, an inter-agency group of stakeholders was organized in 2009 as the North Cascades Mountain Goat Restoration Group (NCMGRG), with the goal of conservation planning and implementing reintroductions. The NCMGRG identified a number of candidate reintroduction sites, and ranked them based on patch size, proximity to other mountain goat core areas, estimates of previous abundance, implementation logistics, potential conflicts with other land-uses, and a qualitative, expert-opinion assessment of biological capacity. The NCMGRG also completed a quantitative assessment of all past mountain goat reintroductions within North American native range. That investigation (Harris and Steele 2014) concluded that reintroductions with larger numbers of seed animals were more likely to succeed than those with fewer, and that habitat quality was likely responsible for most residual variation in success.

Most scientists studying mountain goats (Hamel and Côté 2007, Festa-Bianchet and Côté 2008) have taken the view that although summer habitat selection is critical in that the animals must obtain nutrition to support them through the entire year in only a few months' time, mountain goats are flexible with regard to the specific plants they se-

[1] Author to whom correspondence should be addressed. Email: richard.harris@dfw.wa.gov

lect. Habitat analyses have emphasized proximity to escape terrain, aspect, and seasonality (Beus 2010; Wells et al. 2011, 2012), but have largely assumed that mountain goats consume the best available forage.

These topographically based habitat models generally seemed to perform well at delineating mountain goat habitat, in that, over much of their range in Washington, areas defined as mountain goat habitat generally supported substantial mountain goat populations, or at least were thought to have done so in the past. Consequently, these portrayals of the extent of habitat are of critical importance in evaluating areas for possible translocation or for use in other management decisions. However, these habitat models fail to predict accurately abundance patterns of mountain goats in some portions of the North Cascades (particularly in and around North Cascades National Park [NCNP]). There, models suggest that extensive rugged terrain should be considered good mountain goat habitat, but evidence suggests that few mountain goats occupy them at present and that abundance has similarly been low during recent decades. To evaluate potential reasons for this, we examined a proxy for historical mountain goat abundance: accumulated records of recreational harvest (1948–70, when mountain goats were still abundant throughout their native range in Washington, and largely before NCNP was established), adjusted by size of area. We supplemented this with examination of recent helicopter surveys in both NCNP, the Mount Baker-Snoqualmie National Forest, and the Gifford Pinchot National Forest (conducted in 2000, 2002, 2012, 2013 and 2014), which showed very similar geographical patterns of relative abundance. These supplementary data provided confidence that geographic patterns suggested by the historic harvest data were not strongly biased by patterns of access or historic hunting management, but largely reflected overall abundance.

Abundance patterns of mountain goats in the North Cascades evinced some striking anomalies: in large areas that appeared suitable for mountain goats (based on elevation and topography) but were underlain by specific geologic types, abundance

was much lower than over other geological substrates (Figure 1). Even allowing for imprecision in definitions and geographic locations of historical harvest, it seems clear that some geologic types were associated with larger mountain goat populations than others. In particular, geological types summarized into the broad category plutonic, common in NCNP, supported few mountain goats (using harvest as a proxy), whereas more mountain goats were harvested over other geological substrates.

How geologic substrate might affect mountain goat habitat suitability remains conjectural. One hypothesis is that landforms overlaying plutonic formations are less conducive than others to producing moist meadows that provide nutritious summer forage for mountain goats. Alternatively, nutrient levels of vegetation growing in soil derived from differing bedrock may vary due to substrate chemistry. Littke et al. (2011) found that soil overlaying sedimentary parent material had significantly greater N and C than those atop plutonic formations in Cascade Range Douglas-fir plantations. Morford et al. (2011) showed similar relationships from parent material, through soil, to plants.

In this study, we built on existing field and remote sensing analyses conducted by Wells et al. (2011, 2012) of mountain goat habitat suitability in the North Cascades, by adding 1) analysis of mountain goat diets, as sampled using plant fragments found in feces, 2) additional field plots to quantify vegetation, and 3) analyses of underlying geological substrates, obtained from existing digital sources. Our objectives were to elucidate connections between underlying geology, nutritional characteristics of plants, and historic abundances of mountain goat harvest, with the intent of assisting decision making by the NCMGRG in future management.

Methods

Study Area

Following Wells et al. (2012), we defined the study area as high elevation lands within the Cascade Mountain Range in Washington State, extending
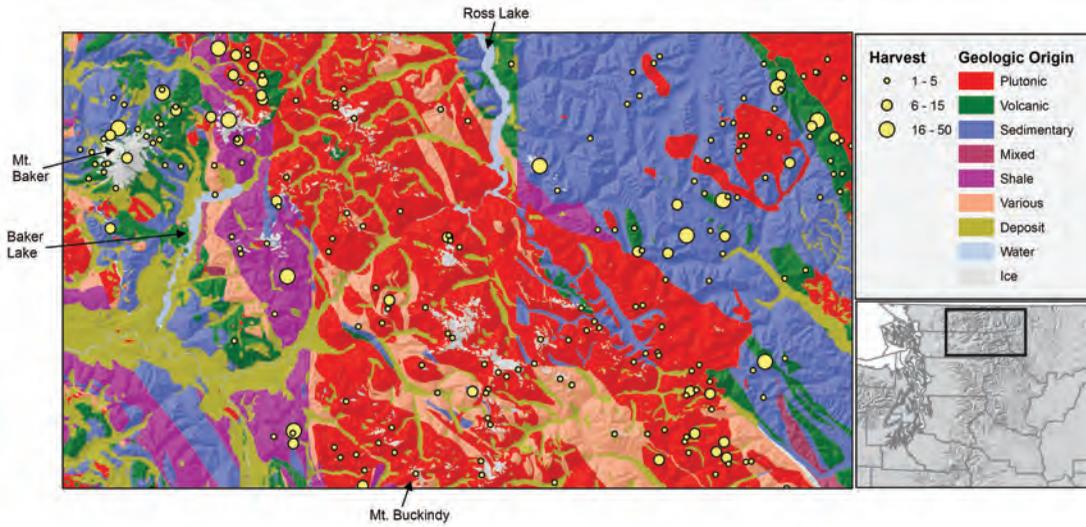
Figure 1. Geological types in the North Cascades region of Washington State, USA, summarized into broad categories, with approximate locations and number of mountain goats harvested during 1948-70 (size of yellow circles illustrates number of goats harvested).
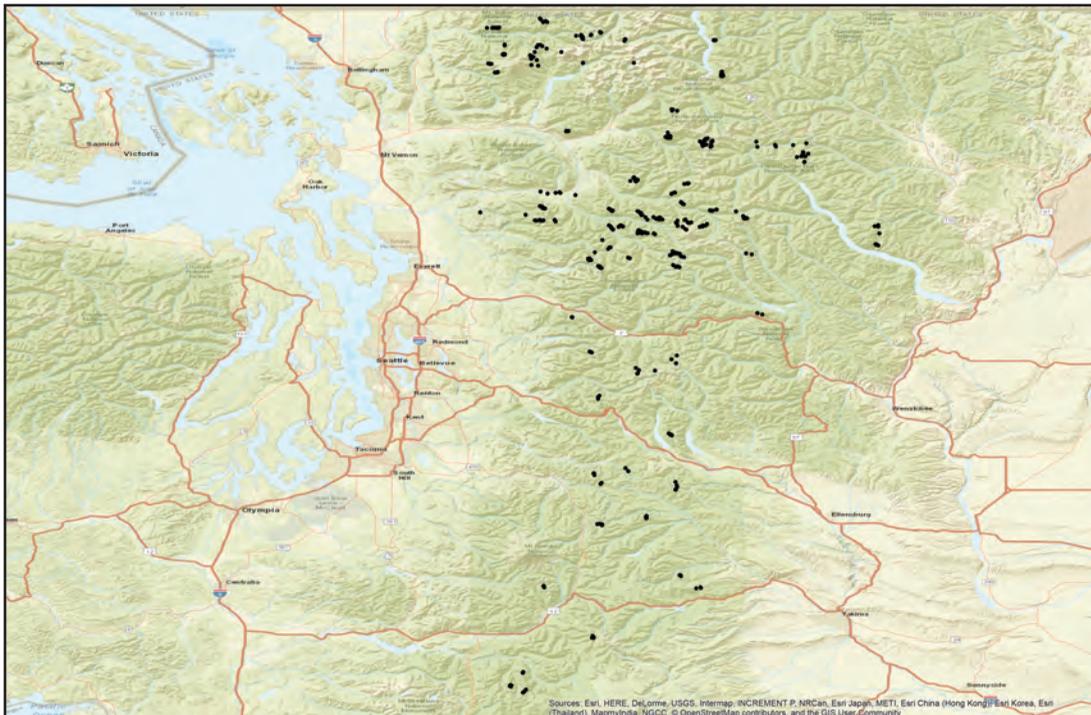

Figure 2. Locations of 504 vegetation plots examined during 2008 and 2009 and used in this study ($n = 292$; Wells et al. 2012, and 2015 [present study], $n = 212$), in the Cascade Mountains of Washington State, USA. Shown are major highways and large cites in Washington.

south from the Canadian border to the Oregon state line along the Columbia River (49° N to 45° 30N, approximately 120° 10'E to 122° 30'E, Figure 2). Overall, this region encompasses parts of the Mount Baker-Snoqualmie, Okanogan-Wenatchee, and Gifford Pinchot National Forests, North Cascades and Mount Rainier National Parks, and Mount Saint Helens National Monument. During our 2015 sampling, we restricted our attention to polygons that had previously been mapped by Wells et al. (2011) as summer mountain goat habitat. We focused most sampling effort within the northern portion of this large study area and in areas of potential candidate reintroduction sites. This northern section of the Cascades is underlain by ancient sedimentary material, much of which has been at least partially metamorphosed, but which also features intrusions of large, plutonic batholiths (Franklin and Dryness 1973).

Definition and Identification of Geological Substrates

To identify and locate geological substrates, we used the surface geology layer managed by the Washington State Department of Natural Resources Division of Geology and Earth Resources (2010). We considered two typologies of geological substrate: one we termed "geologic origin", and one we termed "geochemistry". These two typologies reflect the two hypotheses concerning the mechanism by which geological features might affect habitat suitability for mountain goats. Geologic origin was chosen to reflect physiographic features that may affect vegetation communities (Franklin and Dyrness 1973), especially the distinctions between plutonic, sedimentary, and volcanic landscapes. Thus, given the lithologies in the original layer's classification, we recognized the geologic origin categories plutonic, volcanic, sedimentary, deposit (water or glacial), shale, and various.

Alternatively, geologic substrate may have chemical effects through resulting soils and plant chemistry. The link between geochemistry and lithology is primarily discernable for igneous rocks, for which we followed Abbott et al. (2000), resulting in sub-types sodium-rich (diorite, andesite), calcium-rich (gabbro, basalt), potassium-feldspar

(e.g., granite, rhyolite, obsidian), intermediate (dacite and monzonite), unknown, and unspecified volcanic.

To locate field plots within mapped geological substrates, we mapped feasible ground routes (i.e., hiking trails) that accessed patches of mountain goat habitat (Wells et al. 2011) that overlaid each of the geological types of interest. We established zones of potentially sampled areas for each geological type, ensuring that none was located > 500m from mountain goat escape terrain (i.e., likely to be available to mountain goats, Hamel and Côté 2007), and none was located on slopes > 45° (to maintain field crew safety). We then identified plot centers using ArcGIS, ensuring that each was no less than 200 m from a geological substrate boundary (to minimize the chance that either mapping or field error would result in the plot not corresponding to the intended geological type), and had field crews attempt to reach each. At each plot center, field crews established temporary vegetation sampling plots of 5 m radius (~ 79 m^2) using a flexible tape measure to delineate the outer boundary of the plot. We could not always control the selection of plots by other topographic attributes, and instead treated possible influences of slope and aspect (as well as the date of sampling) *a posteriori* by including these in statistical models.

Occurrence and Abundance of Vegetation by Species

Following Wells et al. (2012), at each plot we recorded slope, aspect, elevation, and visually estimated the canopy cover (which we used as our measure of abundance; Damgaard 2009, 2013) of each species. Crews made visual estimates of the proportion of vegetation consisting of categories grass (subdivided into the genera *Festuca* and *Poa*, documented as preferred by mountain goats in Washington [Pfitch and Bliss 1985, Fiedler and McKay 1984]), sedge (most of which was *Carex* spp.), and rush (primarily *Juncus* and *Luzula* spp.). Crews identified other plants to individual species, and estimated canopy cover for each (Anderson 1986). In analyses however, we categorized the remaining canopy cover estimates as ericaceous

shrubs (categorized as either *Vaccinium* spp., or heather [*Cassiope mertensiana, Phyllodoce empetriformis*, and *P. glanduliflora*]), other shrubs, forbs, and conifers.

Cover of these vegetation categories, expressed in percent, was non-normally distributed, with the most common value being zero in almost all cases. Such distributions were unlikely to be successfully transformed statistically; rather, we interpreted them as resulting from two related but separate processes, one determining whether or not the taxon would be present at all, the other determining the taxon's canopy cover if present. That is, some habitat characteristics may have been simply unsuitable for the species, resulting in its absence. If suitable, other habitat characteristics might further have determined the species' abundance. We thus examined relationships between vegetation and geology in two steps: First, we used logistic regression to test associations with plant species occurrence in the plot. If present, we used conventional linear models to test associations of abundance, defined as the natural logarithm of canopy cover (i.e., excluding plots in which the taxon was absent entirely). In both approaches, we included the Julian date of sampling, plot elevation, plot elevation squared, and plot aspect (defined as the absolute value of the deviation from 180° [due south] in degrees) in all models to account for temporal and plot-level effects other than geological substrate. To account for spatial autocorrelation, we used generalized least squares methods, fitting a variance-covariance matrix based on the non-independence of spatial observations (Dormann et al. 2007) as implemented by the gls function of R package nlme (Pinheiro et al. 2011) for continuous responses (cover), and using the glmmPQL function of R package MASS (Ripley et al. 2013). Statistical analyses were conducted using JMP 11.2.0 (SAS Institute Inc., Cary, NC.). Acknowledging that our study was exploratory, and to minimize the possibility of erroneous inference arising from multiple unplanned comparisons, we considered associations worthy of serious consideration only when $P < 0.01$.

Mountain Goat Diets

We collected freshly deposited fecal pellets from maternal groups we observed in two areas (Ptarmigan Ridge near Mt. Baker, and Three Fingers), combining pellets that appeared to come from 6–8 animals into a single composite sample. We sampled at Ptarmigan Ridge, a spur extending northeast from Mt. Baker, because recent surveys had indicated the mountain goat population there had recovered to what we considered a healthy density (WDFW 2016); the ease with which we encountered large groups of mountain goats in this area while collecting samples corroborated our surveys. Samples collected in the Three Fingers area, southwest of the small town of Darrington, WA, were designed to represent a newly recovering population; this area had few mountain goats in the early 2000s, but surveys since 2013 have indicated 100–150 mountain goats in the area (WDFW 2016). Samples collected in early July 2015 were considered to represent early-summer diets; samples collected in late August or early September 2015 were considered to represent late-summer diets. Pellets were placed in paper bags, refrigerated, and analyzed using microhistological fragment analyses at the Wildlife Habitat Nutrition Laboratory, Washington State University, Pullman, WA. Plants were identified to the finest possible taxon; percent volume was calculated from 100 views on each slide. We made no attempt to correct for differential digestibility among taxa.

We declined to make formal statistical inference on differences between abundances of plants in mountain goat diets and of those same plants on the landscapes (e.g., in a use vs. availability framework) for a number of reasons. First, dietary percentages were expressed in relative volume, whereas species-specific abundances were measured in relative cover; we had no way to reformulate vegetation metrics to a biomass basis. Secondly, our vegetation plots were designed to characterize vegetation types (Wells et al. 2011) or, in 2015, of vegetation as a function of geological types. Although we associated mountain goat fecal pellets with vegetation types based on collection location, we had no way of knowing

where the mountain goats producing these pellets actually consumed the vegetation. Thus, we had only an approximate spatial matching of diets with landscapes. Thirdly, differences between forage used and forage available can be informative, but can also be misleading (Johnson 1980). Although it is reasonable to assume importance to the animal when a species uncommon on the landscape is common in the diet, the reverse logic may not hold. Animals may elect to spend time where a preferred (or even critically important) plant species is abundant, and if so, there may be little or no difference between use and availability at the 4th order of selection (Johnson 1980). Instead, we simply report data on forages used and plant species cover generally, and temper our interpretations accordingly.

Nutritive Value of Two Mountain Goat Forage Species by Geology

We clipped and collected stems and leaves of two species used as forage by mountain goats: *Carex spectabilis* and *Polygonum bistortoides* (Fiedler and McKay 1984, Pfitch and Bliss 1985). Vegetation samples were typically collected on the final day of field-trips to minimize time between collection and refrigeration. Samples were subsequently shipped overnight, packed in coolers with ice packs, to the Wildlife Habitat and Nutrition Laboratory at Washington State University, Pullman, Washington. There, samples were dry-frozen, ground and processed. Samples were analyzed separately for each location and date for percent crude protein, percent in vitro dry matter digestibility (IVDMD), percent acid detergent fiber (ADF), percent neutral detergent fiber (NDF), acid insoluble ash, and acid determent lignin (ADL; Hamel and Côté, 2007).

We examined linear models with data from both species aggregated, using species as a fixed factor. We investigated possible associations with dependent variable geological substrate at the same two levels of resolution as used in examining species-specific occurrence and cover; i.e., categorized by geologic origin, and by geochemistry. To account for temporal and plot effects other than geological substrate, we included Julian date, elevation,

elevation squared, and aspect as explanatory fixed factors in all models. Statistical analyses were conducted using JMP 11.2.0 (JMP 2013).

Results

Mountain Goat Diets

Mountain goats in both sample areas consumed primarily sedges (family Cyperaceae, genus *Carex*), and secondarily rushes (family Juncaceae) during both early and late summer, 2015. A diverse variety of dicots (forbs), grasses, ferns, leaves from shrubs, and mosses rounded out their summer diets (Tables 1, 2). Early summer (July) samples taken from the recovered population near Mt. Baker (Ptarmigan Ridge, Table 1) consisted, on average, of 57.1% from the genus *Carex* (about half of which could be identified as the *C. spectabilis*, the other half could be identified only as *Carex* of other species). Taken as a group, sedges and rushes constituted > 80% of diets by volume for Ptarmigan Ridge samples. Similarly, July diets of the recovering mountain goat population in the Three Fingers area (Table 2) were 57.0% sedges and rushes.

Grasses as a category made up only 1.6% of July diets on Ptarmigan Ridge, but constituted 8.2% of July diets for Three Fingers mountain goats (and of Three Fingers diets, 72% of grasses were from the genus *Poa*). Dicots as a group (consisting of 27 uniquely identified species or genera) constituted 14% of summer diets at Ptarmigan Ridge, and 17.7% at Three Fingers; individually, most were < 1% of diets. Despite their abundance on the landscape, vegetation in the family Ericaceae was relatively rare in July mountain goat diets. Leaves and stems from *Vaccinium* spp. together comprised 3.0% of diets at Ptarmigan and 3.3% at Three Fingers. No fragments from heathers (e.g., *Phyllodoce* spp. and *Cassiope* spp.) were documented, despite their relative abundance in both study areas (Tables 1, 2).

Early fall diets of mountain goats (in late August at Three Fingers and early September at Ptarmigan Ridge) were largely similar to July diets. At Ptarmigan Ridge, proportion of diets consisting of *Carex* spp. declined slightly (to 47.1%), of rushes increased (from 21.3% to 29.5%), and

TABLE 1. Diets of mountain goats in the Ptarmigan Ridge area, near Mt. Baker, Washington, 2015 from fecal micro-histological fragment analysis. Shown are dietary proportions of major forage categories for early (column b) and late (column c) summer diets, and cover (expressed in percent) of the same taxa as estimated from vegetation plots in the Ptarmigan Ridge area (column d). Goat diets are expressed in mean percent volume and each contains pellets from ~ 6–8 different animals; vegetation availability metrics are expressed in cover (and thus can sum to > 100%); not detected in plots = nd.

a	b	c	d
	Early Summer Mountain Goat	Late Summer Mountain Goat	Early Summer Canopy Cover
Vegetation Category			
	Diets		
	Graminoids		
Carex spp.	57.1	47.1	13.3
Rushes[1]	23.1	29.5	3.6
Poa spp.	1.2	4.2	nd
Other grasses	0.4	0.8	3.1
	Ericaceae Shrubs		
Vaccinium spp.	3.5	0.8	21.8
Heather[2]	0.0	0.0	29.3
	Dicotyledons		
Anemone occidentalis	0.0	0.0	nd
Epilobium angustifolium	0.8	0.0	nd
Erigeron spp.	0.4	0.0	0.3
Fragaria vesca	0.6	1.9	nd
Hieracium gracile	0.4	1.3	1.4
Luetkea pectinata	0.8	0.0	16.2
Lupinus spp.	0.8	0.8	12.1
Penstemon spp.	3.9	0.8	0.6
Phacelia hastata	2.1	1.3	nd
Phlox diffusa	0.0	0.0	5.9
Polygonum bistortoides	1.4	1.3	3.9
Saxifraga spp.	0.2	0.4	1.9

[1]*Juncus* and *Luzula* spp.
[2]*Cassiope* and *Phyllodoce* spp.

use of grasses (mostly *Poa* spp.) increased to 5%. At Three Fingers, use of *Carex* spp. increased (to 68.1%), and use of forbs (aggregated as a category) declined to 3.6%. Use of *Vaccinium* spp. declined in early fall to 0.8% at Ptarmigan Ridge, and undetected levels at Three Fingers.

Physical and Vegetative Characteristics of Sample Plots

We quantified 504 plots in terms of both vegetation and geology. Elevation of plots averaged 1723 m (SD = 288 m), slopes averaged 28.8° (SD = 13.6), and aspects (defined as absolute difference from due south) averaged 67.9° (SD = 48.0). Presence of sedges was not associated with elevation, slope, or aspect; where present, however ($n = 180$), canopy cover of sedge was negatively associated with elevation ($\beta = -0.001$, SE = 0.0001, $P = 0.017$). Presence of rushes was negatively associated with steepness (odds ratio = 0.9572, CI = 0.9378–0.9769), but where present ($n = 63$) cover was not further predicted by physical characteristics. Presence of heather species was negatively associated with slope (odds ratio = 0.9766, CI = 0.9612–0.9923, $P = 0.004$), and positively associated with difference from due south (odds ratio = 1.0109, CI = 1.006–1.0159, $P < 0.001$); where present ($n = 250$) heather canopy cover was not associated with topographic variables. We found no associations between any of

TABLE 2. Diets of mountain goats in the Three Fingers area, Washington, 2015 from fecal micro-histological fragment analysis. Shown are dietary proportions of major forage categories for early (column b) and late (column c) summer diets, and cover (expressed in percent) of the same taxa as estimated from vegetation plots in the Three Fingers area (column d). Goat diets are expressed in mean percent volume and each contains pellets from ~ 6–8 different animals. Vegetation availability metrics are expressed in cover (and thus can sum to > 100%); not detected in plots = nd.

a	*b*	*c*	*d*
Vegetation Category	Early Summer Mountain Goat	Late Summer Mountain Goat	Early Summer Canopy Cover
	Diets		
Graminoids			
Carex spp.	46.3	68.1	18.6
Rushes[3]	10.7	18.2	1.4
Poa spp.	3.8	3.0	nd
Other grasses	4.3	5.7	10.6
Ericaceae shrubs			
Vaccinium spp.	4.1	0.0	28.7
Heather[4]	0.0	0.0	43.6
Dicotyledons			
Anemone occidentalis	3.5	1.0	nd
Erigeron spp.	0.0	0.2	2.1
Fragaria vesca	0.1	0.4	nd
Hieracium gracile	0.0	0.0	1.9
Luetkea pectinata	0.0	0.0	22.6
Lupinus spp.	0.0	0.0	12.2
Penstemon spp.	0.0	0.0	nd
Phlox diffusa	0.0	0.0	1.8
Polygonum bistortoides	3.8	1.7	13.7
Saxifraga spp.	0.0	0.0	nd
Valeriana sitchensis	0.0	0.0	3.2

[3] *Juncus* and *Luzula* spp.

[4] *Cassiope* and *Phyllodoce* spp.

our geologic categorizations and elevation, aspect, or slope of our sample plots.

Forage Plants Relationships with Geology

Geological Origin—The logistic regression model accounting for Julian date, elevation, and aspect predicted that sedge was more likely to occur on sedimentary than most other types (Figure 3; see Table S1 for odds ratios). Among plots where sedge was present, geologic origin did not further explain its canopy cover. For the sedge *C. spectabilis*, occurrence was more likely on shale than volcanic or plutonic substrates (Figure 3 and Table S2). Presence of heather was not associated with geologic origin class. However, on plots with heather present, canopy cover of heather was lower on sedimentary and volcanic

than other substrates (*P* = 0.002, Figure 4). We found no significant associations of either presence or canopy cover of rushes, *P. bistortoides*, *Poa arctica,* or *Penstemon* spp. by geologic origin. Figure 3 presents predicted occurrence of each taxon by geologic type adjusted for covariates.

Geological Type Chemistry—Logistic regression models accounting for Julian date, elevation, and aspect indicated that sedge was more likely to occur on sedimentary and shale, and less likely to occur on potassium-feldspar and sodium rich substrates than other types (Figure 5, Table S3). Among plots where sedge was present, geochemical subtype did not further explain its canopy cover. For the sedge *C. spectabilis*, occurrence was less likely on potassium-feldspar and sodium rich substrates than other types (Table S4). Among plots where
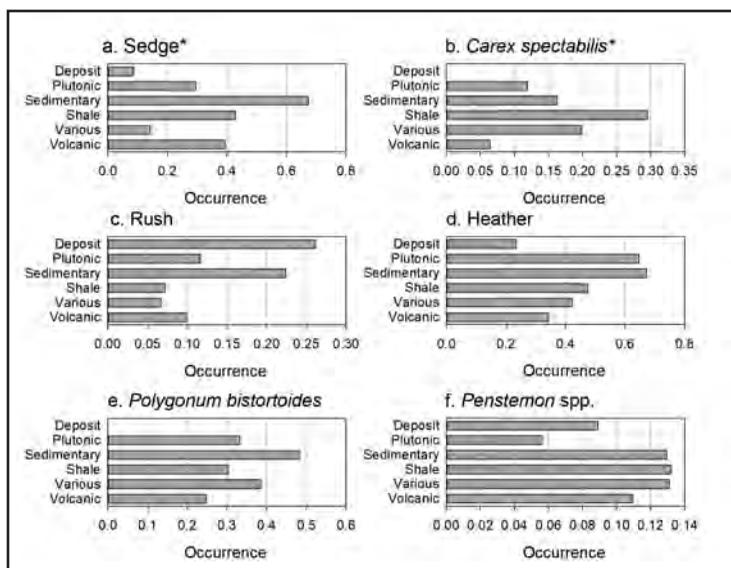
Figure 3. Histograms showing proportional predicted occurrence of 6 plant taxa of importance to mountain goats by geological origin subtype, as estimated from 504 79 m^2 vegetation plots inspected during summers 2008-2015. Subtype sample sizes: deposit = 12, plutonic = 177, sedimentary = 45, shale = 70, various = 24, volcanic = 176. Symbol "*" represents significant predictor, P < 0.01 from logistic regression model incorporating geological origin, Julian date, elevation, and aspect.
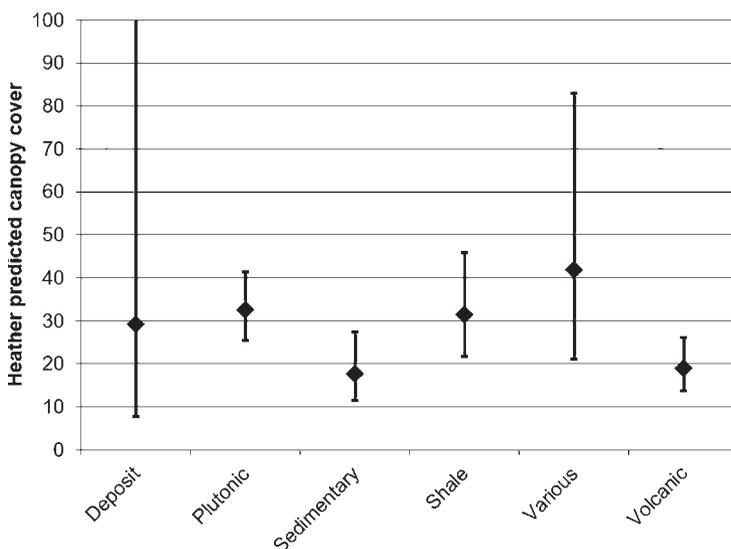

Figure 4. Predicted canopy cover of heather species on 504 vegetative plots in the North Cascades, Washington, by geologic substrate. Shown are point estimates (diamonds) and 95% confidence intervals (vertical bars). See text for explanation of underlying model.

C. spectabilis was present, geologic subtype origin did not further explain its canopy cover. Presence of heathers (other than *Vaccinium* spp.) was unrelated to geologic substrate chemistry. We found no significant associations of either presence or abundance of rushes, *P. bistortoides*, or *Penstemon* spp. by geochemical type. Figure 5 presents predicted occurrences of each taxon by geochemical type adjusted for covariates.

Nutritive Characteristics of Two Species of Mountain Goat Forage

Crude protein of *C. spectabilis* ($\bar{x} = 11.8$, $n = 34$) did not differ from *P. bistortoides* ($\bar{x} = 11.0$, $n = 27$; $t = 1.25$, $P = 0.218$). As expected, crude protein declined with time over the growing season (β [Julian date] $= -0.08$, SE = 0.02, $t = -3.41$, $P = 0.001$). However, we found no significant associations of crude protein with geological substrate at either level of categorization. Similarly to crude protein, IVDMD did not differ between *C. spectabilis* ($\bar{x} = 44.3$) and *P. bistortoides* ($\bar{x} = 44.0$; $t = 0.28$, $P = 0.778$), and declined as the season progressed (β [Julian date] $= -0.16$, SE = 0.04, $t = -2.60$, $P = 0.012$). Neutral detergent fiber was higher in *C. spectabilis* ($\bar{x} = 61.1$, SE = 0.50) than *P. bistortoides* ($\bar{x} = 40.6$, SE = 0.99; $t = 16.9$, $P < 0.01$), but was not associated with geological types. Lignin was greater in *P. bistortoides* ($\bar{x} = 10.4$, SE = 0.28) than *C. spectabilis* ($\bar{x} = 3.46$, SE = 0.25), but did not vary with time ($t = -0.02$, P
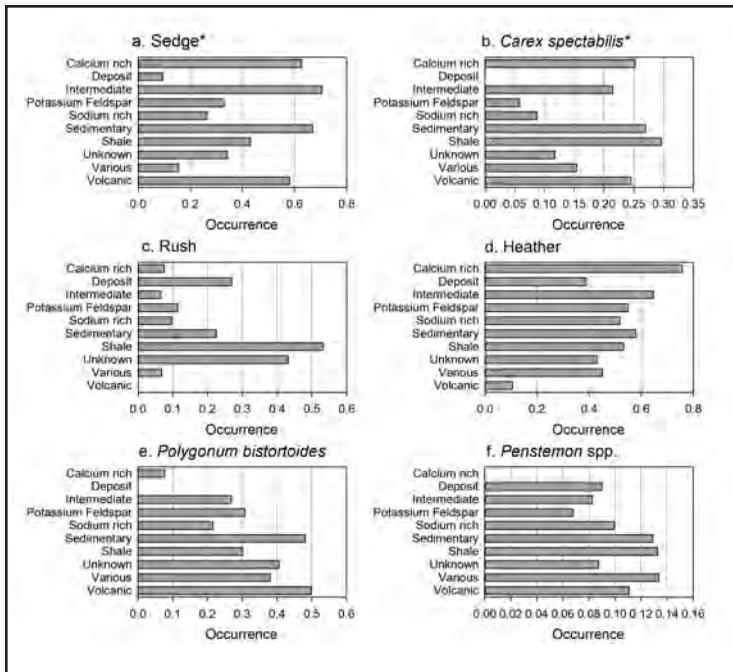
Figure 5. Histograms showing proportional predicted occurrence of 6 plant taxa of importance to mountain goats by geological origin chemistry subtype, as estimated from 504 79 m^2 vegetation plots inspected during summers 2008-2015. Subtype sample sizes: Calcium-rich 11; Deposit 12; Intermediate 11; Potassium-Feldspar 124; Sodium-rich 131; Sedimentary 45; Shale 70; Unknown 57; Various 24; Volcanic 19. Symbol "*" represents significant predictor, $P < 0.01$ from logistic regression model incorporating chemistry, Julian date, elevation, and aspect.

= 0.021). We quantified no other associations of nutritive indices with geological substrate.

Discussion

We found that mountain goats in two recently recovered populations ate primarily sedges and rushes in mid- and late-summer. Where studied elsewhere, mountain goats in summer have shown a preference for graminoids (Brandborg 1955, Hibbs 1967; Pfitsch and Bliss 1985, Houston et al. 1994) although in some areas, forbs have been preferred over graminoids (Dailey et al. 1984). Equally noteworthy, we found that these mountain goats make almost no use of species within the family Ericaceae, which likely account for more canopy cover than any other plant within substantial portions of North Cascades mountain goat habitat (Douglas 1972, Franklin and Dyr-

ness 1973:255). It is likely that heathers, in addition to being quite fibrous, contain secondary compounds that reduce the nutritional quality otherwise available to mountain goats (Gonzalez-Hernandez et al. 2003; see also McArthur et al. 1993). Villamuelas et al. (2016) found that Pyrenean chamois (*Rupicapra pyreniaca*), closely related to mountain goats, tended to avoid the fibrous plant common heather (*Culluna vulgaris*).

Our estimates of mountain goat diets were developed entirely from fecal micro-histological fragment analyses, and we had no way to correct for differential digestion by plant species (Holechek et al. 1982). Most controlled studies have found biases in diet estimation to be modest (Vavra and Holechek 1980, Gill et al. 1983, Alipayo et al. 1992, Chapuis et al. 2001), with many finding that dicot forbs tend to be underestimated in fecal diets due to more complete digestion (Vavra and Holechek 1980, Shrestha and Wegge 2006). Leslie et al. (1983), working with a selection of plants species from the Washington's Olympic Peninsula, found that *Carex deweyana* was slightly over-represented in fecal diets of black-tailed deer (*Odocoileus hemionus columbianus*) and Roosevelt elk (*Cervus elaphus roosevelti*). Our estimates may thus overestimate the importance of sedges in diets of North Cascades mountain goats, but we see no reason to suspect that our failure to detect plants from Ericaceae was caused by differential digestion (if anything, these fibrous shrubs would probably be over-represented, Leslie et al. 1983).

Our study was also designed to assess the hypothesis that patterns evident in historic mountain goat abundance that were correlated with underly-

TABLE 3. Summary of statistical tests of association between major vegetation categories in North Cascade mountain goat habitat sample plots, 2008-2015, and geologic categories "origin" and "chemistry". Presence columns reflect results of logistic regressions; canopy cover columns reflect results of linear models using only sample plots containing the plant species. The symbol "+" indicates a positive association ($P < 0.01$) and the symbol "-"indicates a negative association ($P < 0.01$). See text for modeling details.

Plant	Geologic Origin		Geological Chemistry	
	Presence	Canopy Cover	Presence	Canopy Cover
Sedge	+ Sedimentary	None	+ Sedimentary + Shale - K-feldspar - Na-rich	None
C. spectabilis	+ Shale	None	- K-feldspar - Na-rich	None
Rush	None	None	None	None
Heather	None	- Sedimentary Plutonic > Volcanic	None	None
P. bistortoides	None	None	None	None
Penstemon spp.	None	None	None	None
Poa arctica	None	None	None	None

ing geology could be explained on the basis of presence, abundance, or nutritive quality of highly used forage species. We found some indication that sedges, the single most utilized forage class by mountain goats in summer, were more likely to be present on sedimentary than plutonic or volcanic formations (Table 3), although effect size was not large and the total variability explained by our best statistical models was small. We found a weak signal that Ericaceous species were associated with plutonic substrates. However, we failed to find meaningful associations between any nutrient characteristics of the two species we sampled and geological substrate. Taken together, our results are suggestive that forage valued by mountain goats is more common on sedimentary and shale than on plutonic geologic origins, and that plutonic formations characterized by potassium-feldspar chemistry (e.g., granite, rhyolite, obsidian) and sodium chemistry diorite, andesite) were particularly unlikely to support these species. That said, our results also suggest that our hypothesis was inadequate to explain satisfactorily the distributional of mountain goat patterns we have observed in recent years.

Sedimentary parent material underlying coniferous forests were found by Littke et al (2011) to have greater nitrogen and carbon content than those of glacial or igneous origins. Contrary to our expectations, we found no difference in crude protein in our plant sample among any geological types. In contrast, Kranabetter and Banner (2000) found lower nitrogen concentrations in forest soils atop limestone than schist or gneissic diorite. Unlike Littke et al (2011), we were unable to analyze soils as well as geology; thus we do not know if there were important differences in the chemical composition among bedrocks we examined, if any differences did not extend to soils, or if differences in soils did not extend to the two plant species we sampled. Notable in this regard are the findings of Castle and Neff (2009), who found differences in a number of macro- and micronutrient concentrations in bedrocks, but not in the foliage of either aspen (*Populus tremuloides*) and two conifer species examined.

Our results suggest some rationale for mountain goat populations to be smaller and have slower growth rates on plutonic substrates than sedimentary, shale, or some volcanic geological formations, but likely explain only part of the patterns we observed. Ultimately, studies that combine detailed examination of habitat characteristics with long-term demographic responses from individually monitored mountain goats are needed to fully understand patterns in population performance (e.g., Garshelis 2000).

Acknowledgments

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