SUMMER DIET AND FEEDING LOCATION SELECTION PATTERNS OF AN IRRUPTING MOUNTAIN GOAT POPULATION ON KODIAK ISLAND, ALASKA

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Abstract: The introduced mountain goat (*Oreamnos americanus*) population on Kodiak Island, Alaska, exhibited 60 years of rapid growth, resulting in an irruptive wave that expanded across the island from the initial introduction site. This unusual situation provided a rare opportunity to quantify and compare mountain goat summer diet and feeding location selection patterns at different stages along an irruptive growth cycle for an ungulate population. Diet composition analyses (via microhistological analyses of fecal pellets) indicated a temporal shift in summer mountain goat diets, which was likely driven by the onset of alpine plant growth following snowmelt. Sedges and forbs were important forage items and were increasingly consumed throughout the summer (June–August). Fern rhizomes were important in June (>16% of pellets), but less so (<1% of pellets) in July and August. Shrubs, mosses, and lichens were consistently consumed in small quantities (<5% of pellets), and therefore likely do not represent favored mountain goat summer forage on Kodiak Island. Consistent with our predictions, areas on Kodiak where mountain goats had completed an irruptive cycle (initial rapid population growth, decline to a lower abundance, and stabilization at a stochastic carrying capacity) had less forage cover at a lower diversity. However, contrary to our expectations, we found no evidence that feeding location selection patterns varied among goat subpopulations at different stages of irruptive growth, suggesting that this factor was independent of population history. Instead, we found that the area where mountain goats were at the highest density had the highest forage diversity and the most long-awned sedge (*Carex macrochaeta*) cover (i.e. the highest quality forage), which suggests that mountain goats there may not have reached carrying capacity yet. Mountain goats selected feeding locations close to escape terrain with abundant long-awned sedge, regardless of subpopulation density or history. Overall, our work is among the first to quantify mountain goat diets and feeding location selection on Kodiak Island and will guide management and research of the growing population.

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In 1952 and 1953, eighteen mountain goats (*Oreamnos americanus*) were introduced to Kodiak Island, Alaska, a large, geographically isolated island on which native large mammalian herbivores were historically absent (Paul 2009). By 2011, the population had grown exponentially to approximately 2,500 and had expanded to all known available habitats on the island. This process led to conservation concerns because introduced ungulates can cause detrimental landscape-level effects by altering vegetation structure and composition, soil system functioning, and chemical processes (Hobbs 1996, Spear and Chown 2009). Additionally, impacts can be especially severe on island and alpine ecosystems that are less resilient to disturbance (Courchamp et al. 2003). Therefore, empirical data about mountain goat foraging ecology on

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Kodiak Island are needed to understand potential impacts to native flora and to focus future research priorities.

Mountain goat diets are not well understood compared to other North American ungulates and it is unclear how the species' diets may vary across populations. Available habitats in southeastern Alaska contain diverse subalpine coniferous forests that are absent, and alpine plant community assemblages that differ, from Kodiak Island, which could lead to differences in mountain goat diet selection. Microhistological analysis of fecal pellets is a common technique for estimating mountain goat diets, but has yet to be applied to Kodiak. An observational study conducted in the 1970s at the initial introduction site (Hjeljord 1973) provided baseline dietary information and, through comparison with an updated assessment of diets, a unique opportunity to understand whether diets have changed in response to subsequent variation in population density, and whether the diets differ spatially across the island.

To more fully understand potential impacts of non-native mountain goats, it is critical to quantify not only diet, but also feeding location selection. Mountain goat habitat selection has been well-documented (Von Elsner-Schack 1986, Laundre 1994, Gross et al. 2002, Poole and Heard 2003), but mountain goat feeding location selection has received little attention (Hjeljord 1973). Quantifying the physical and forage-related attributes associated with mountain goat feeding locations provides a crucial link between their diets and spatial ecology, and is a first step toward developing an understanding of nutritional-based carrying capacity.

Mountain goat densities and the relative duration of occupancy at a particular location vary spatially across Kodiak Island as a function of their relative distances to the initial introduction site (Cobb 2011). This unusual ecological state offers a rare research opportunity to quantify variations in diet and feeding location selection patterns among spatially distinct mountain goat subpopulations with different densities and histories of occupancy. Annual surveys show that mountain goats at the initial introduction site have undergone a complete irruptive population growth cycle: an initial growth phase (phase 1), a subsequent decline to a lower abundance (phase 2), and a final "post-decline" population stochastic carrying capacity at a lower abundance (phase 3; sensu Caughley 1970). During the 1970s (approximately 10–20 years following introduction), mountain goat subpopulations colonized habitats surrounding the initial introduction site, increased in density (phase 1), and are predicted to follow the same trend of decline and stabilization (phases 2 and 3) exhibited at the initial introduction site (Cobb 2012). Subpopulations located on the current periphery of the population's range established in the 1990s are at low densities, but are predicted to follow a similar pattern as the other regions.

If the irruptive growth cycle observed on Kodiak Island has resulted in declines in plant diversity and preferred forage abundance, as predicted by Caughley's (1970) model, then we expect these changes to result in observable differences in plant community composition and related differences in diet and feeding location selection patterns across a spatial gradient related to distance from the initial introduction site. Specifically, we predict that more recently established mountain goat subpopulations (closer to the initial introduction site and in earlier phases of the irruptive growth cycle) will have greater availability of preferred forage, show a narrower diet breadth (more diet selection), and exhibit stronger evidence for feeding location selection than longer established subpopulations in later phases of the irruptive growth cycle.

STUDY AREA

Kodiak Island (9,375 km^2), Alaska, separated from mainland Alaska by the Shelikof Strait, is the largest island in the Kodiak Archipelago. The island is approximately 160 km long and varies in width from 15 km to 130 km. The Kodiak National Wildlife Refuge encompasses 6,803 km^2 of Kodiak Island, or 73%. Topography is primarily mountainous, with elevations ranging from sea-level to 1,362 m. The sub-arctic maritime climate on Kodiak Island is characterized by long wet winters with alternating snow and rain events, and cool wet summers. Average annual precipitation between 2006 and 2011 was 195 cm (Kodiak airport weather station). Summer precipitation averaged 12 cm in June, 9 cm in July, and 13 cm in August. The average annual temperature was 4.9° C, and ranged from -1.2° C in January to 12.9° C in August. Summer temperatures averaged 9.8° C in June, 12.4° C in July, and 12.9° C in August. The summer growing season in the alpine generally runs from early June to late September.

Native terrestrial mammals sympatric with mountain goats included Kodiak brown bear (*Ursus arctos middendorffi*), red fox (*Vulpes vulpes*), short-tailed weasel (*Mustela erminea*), and tundra voles (*Microtus oeconomus*). Introduced sympatric mammals included Sitka black-tailed deer (*Odocoilus hemionus sitkensis*) and snowshoe hare (*Lepus americanus*). Levels of predation on mountain goats were unknown, but believed to be insignificant, due to few observations of bear-goat interactions and only a limited number of confirmed bear kills on mountain goats (J. Crye, Alaska Department of Fish and Wildlife, personal communication). Kodiak was the most popular mountain goat hunting destination in Alaska, and hunting occurred island-wide from 20 August to 25 October. Between 2007 and 2011, hunters harvested an average of 159 goats annually (Van Daele and Crye 2010).

We selected three study sites (Hidden Terror, Uyak, and Hepburn) on Kodiak Island (Fig. 1) based on their distance from the initial introduction site, their duration of occupancy by mountain goats, and their histories of population growth (Cobb 2012). Aerial surveys by the Alaska Department of Fish and Game (ADFG) and the U.S. Fish and Wildlife Service (FWS) provided annual estimates of subpopulation sizes (FWS, unpublished data). The Hidden Terror study site (76 km^2) was located in northeastern Kodiak Island and encompassed the initial introduction site. The subpopulation there peaked in density in 1985 (2.09/km^2 or 167 goats) and then declined to 1.21/km^2 (66 goats) in 2011. Elevations ranged from sea-level to 1,130 m. The Uyak study site (48 km^2) was centrally-located on Kodiak Island (48 km from the introduction site). Mountain goats colonized the site in the 1970s and then increased annually to a record high density in 2011 (2.54/km^2, 122 goats). Elevations ranged from sea-level to 1,320 m. The Hepburn study site was a 62 km^2 peninsula in southeastern Kodiak Island, 74 km from the initial introduction site. Mountain goats colonized this site in the mid-1990s and were still at low densities in 2011 (0.75/km^2 or 47 goats). Elevations ranged from sea-level to 700 m.

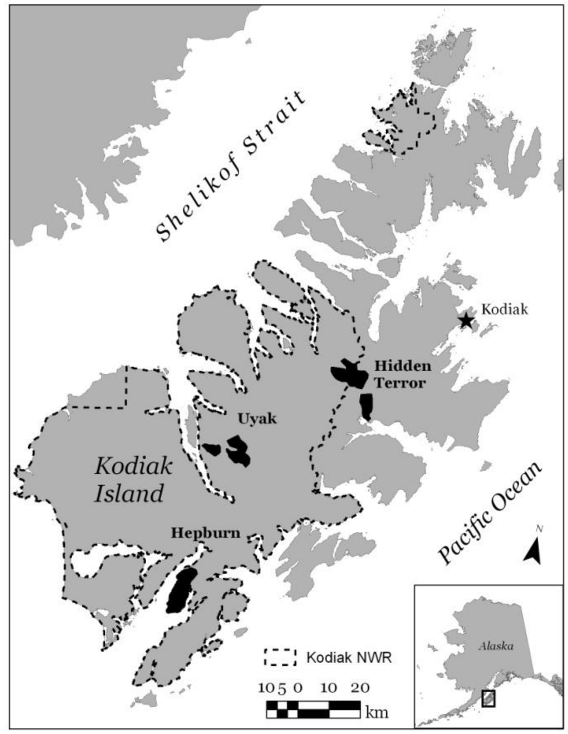

Fig. 1. Locations of study sites on Kodiak Island, Alaska.

Lower elevation habitats (sea-level to 300 m) consisted of a matrix of mixed forb meadows, open alder with forb meadows, and dense alder habitats (Fleming and Spencer 2007). The mixed forb meadow habitat consisted of Nootka lupine (*Lupinus nootkatensis*), woolly geranium (*Geranium erianthum*), fireweed *(Epilobium angustifolium)*, goldenrod (*Solidago lepida*), Jacob's ladder (*Polemonium acutiflorum*), paintbrush (*Castilleja unalaschcensis*), and burnett (*Sanguisorba stipulate*). The open alder with forb meadow habitat type consisted of patches of dense alder (*Alnus crispa*), often mixed with salmonberry (*Rubus spectabilis*) and elderberry (*Sambucus racemosa*), and patches of forbs such as fireweed, lupine, and cow-parsnip (*Heracleum lanatum*). Forb-dominated habitat types were more common, and alder-dominated habitats were less common, in lower elevation regions (<150 m) at the Hepburn and Hidden Terror study sites, but the inverse was observed at the Uyak study site. Alpine regions (>150 m) were composed of tundra, forb meadow, heath, prostrate shrub tundra, exposed bedrock, talus slopes, and snow-covered habitat types (Fleming and Spencer 2007). Common alpine plants included long-awned sedge (*Carex macrochaeta*), mosses, lichens, partridgefoot (*Luetkea pectinata*), and black crowberry (*Empetrum nigrum*). Snow was present at the study sites above approximately 600 m at the start of our field season (1 June) and was completely melted by mid-July.

METHODS

We visited each study site twice in 2011, during the growing season: once in the early summer (June–early July) and once in the late summer (late July–August). During each sampling occasion, we collected fresh mountain goat pellets and compared vegetation diversity and abundance between locations where goats were observed feeding ("feeding locations") and randomly selected areas in the alpine ("available locations").

Diet

We quantified mountain goat diets using microhistological analyses of fecal pellets (Hinnant and Kothmann 1988). To collect pellets, we observed a mountain goat group until at least one defecated. We then slowly approached the center of the group's location and searched for fresh pellets. We considered pellets to be fresh if they were moist, soft, had a slimy sheen, and were free of mold and insects. We collected approximately 25 mg (15 pellets) of fresh pellets from individual pellet groups and stored samples in a WhirlPak (Nasco, Ft. Atkinson, WI). We kept pellet samples in a cool dry location in the field and then we froze them upon returning to the office (1–12 days later). We randomly selected 9–10 pellet samples from each study site visit and submitted the samples to the Wildlife Habitat Nutrition Lab at Washington State University (Pullman, WA) at the conclusion of the field season for microhistological analyses to estimate the relative percent composition of forage classes that were comprised >5% of the sample (Level B, 50 views/sample).

We quantified the influence of the day of the year and study site on diets using linear regression (Zar 2009).

Habitat Availability and Feeding Location Selection

We located mountain goat groups by conducting ground-based and fixed-wing aerial surveys of the study sites. We defined feeding locations as the centroid of a mountain goat group observed feeding. We constrained selection of random locations to areas on Kodiak where mountain goats have been observed during summer aerial surveys (Kodiak Refuge, unpublished data) and typical mountain goat summer ranges (Hjeljord 1970, Von Elsner-Schack 1986, Fox et al. 1989, Poole and Heard 2003), which was composed of low willow, alpine tundra, heath, forb-graminoid meadows, snow/ice, and fragmented rock habitat types. We used a GIS land cover classification map of Kodiak to delineate the extent of these habitats within each study site (Fleming and Spencer 2007). Additionally, we limited available habitats to areas over 150 m above sea-level because we did not expect mountain goats to occupy areas below this elevation during the summer (Hjeljord 1973). We designated random locations by creating 100 random waypoints in available habitats, for each study site visit, using Spatial Analyst in ESRI® ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, CA). We included an inhibition distance (minimum allowable distance between random waypoints) of 100 m to eliminate potential overlap between transects (below) and to ensure a more even sampling distribution across study sites. We uploaded random waypoints into portable GPS units (Garmin® GPSmap 76CSx), which we used to locate random locations in the field.

Our methods for conducting plant surveys were the same at feeding and random locations. We inserted an aluminum stake into the ground at the location, selected a random compass bearing using a random number table, and extended a tape measure from the stake along the random bearing for 16 m in both directions. Starting from the stake, we placed a 50 cm by 20 cm plot frame to the right side of the tape measure at 2-m intervals, for a total of 17 plots per location (Daubenmire 1959). Within each plot, we defined cover as the percentage of the plot that was encompassed by the sum of imaginary minimum convex polygons

Table 1. Canopy cover classes with associated range of percent canopy covers used to quantify vegetation cover at mountain goat summer feeding and random locations, Kodiak Island, Alaska.

Code	Range	Mid
T	0-1%	0.50%
0	1-5%	3%
1	5-15%	10%
2	15-25%	20%
3	25-35%	30%
4	35-45%	40%
5	45-55%	50%
6	55-65%	60%
7	65-75%	70%
8	75-85%	80%
9	85-95%	90%
X	95-100%	97.5%

drawn on leaf tips of undisturbed canopies (ignoring inflorescences) and projected onto the ground (Kent 2012). We classified cover into 12 classes based on their relative percentages of a plot, following a modified Domin scale (Currall 1987; Table 1). For each plot, we estimated cover of forb and sedge species, and plant classes for other plants (grasses, rushes, ferns, lichens, mosses and willow; Studebaker 2010, USDA NRCS 2013).

To summarize available forage at each location, we quantified forage diversity and cover. We defined forage diversity as the sum of unique plant species and habitat classes observed in all plots at a location. We quantified forage cover (relative spatial cover of a plant species or class at a location) as the median percent value for a particular plant's cover class within a plot, averaged across all plots at a location.

Because mountain goats are associated with steep terrain that they use to escape from predators (Hamel and Côté 2007), we included a measure of distance to escape terrain as a predictor of feeding location selection. Escape terrain has been described as steep rocky slopes ranging from >25^{o} to >33^{o} (Adams and Bailey 1982, Gross et al. 2002). To be conservative, we considered escape terrain as slopes ≥33^{o}. We defined the distance to escape terrain as the distance (m) from random and feeding locations to the edge of the closest pixel of escape terrain, defined by a 30 m pixel USGS Digital Elevation Model (DEM) in GIS (ESRI 2012).

Habitat selection of northern ungulates, such as mountain goats, is affected by forage availability and thermodynamics, which are influenced by relative solar radiation (Keating et al. 2007). To determine if mountain goat feeding location selection was correlated with solar radiation, we estimated hypothetical solar illumination (12:00 pm, 1 July) across Kodiak Island using the ArcGIS's Hillshade function applied to the DEM. We then standardized hillshade values by converting to *z*-scores (Zar 2009), and then extracted standardized hillshade values at random and feeding locations.

We considered random and feeding locations as the sampling unit for statistical analyses. To avoid overfitting models and to simplify the results, our predictors included forage cover estimates for the top 8 forage classes (genera, if classified) in mountain goat summer diets (as determined above), and 4 additional habitat predictors (forage diversity, distance to escape terrain, hillshade, and study area) in statistical tests. The top-8 forage classes composed approximately 96% of the mountain goat pellets.

We tested for differences between pairs of study sites using Mann-Whitney *U* tests (Zar 2009). We quantified feeding location selection with logistic regression models using the same predictors. To assess relative correlation between predictors, we computed a Pearson product-moment correlation matrix. If pairs of predictors showed high correlation (>0.30; Zar 2009), we retained the predictor that had the greatest biological significance. To evaluate competing candidate models, we examined differences in ΔAIC_c (Akaike's Information Criterion) using a backwards, step-wise approach (Burnham and Anderson 2002). Finally, we calculated AIC_c weights (w) to determine relative support for each of the top models.

RESULTS

We visited each study area twice, between 2 June and 19 August 2011. Visits averaged 8 days long and ranged from 4 to 10 days.

Table 2. Major forage classes in mountain goat pellet samples (n = 59), quantified through microhistological analyses of pellet samples collected in summer 2011, Kodiak Island, Alaska.

Forage class	Average percent	Genus	Average percent	Common name
Sedges	34.5%	*Carex*	34.1%	Sedges
		Eriophorum	0.3%	Cottongrasses
		Eleocharis	<0.1%	Spikesedges
Forbs	22.2%	*Lupinus*	14.1%	Nootka lupine (only spp.)
		Geranium	7.0%	Woolly geranium (only spp.)
		Potentilla	0.3%	Cinquefoils
		Galium	0.2%	Bedstraws
		Taraxacum	0.2%	Dandelions
		Epilobium	<0.1%	Willowherbs
		Polygonum	0.1%	Bistorts
		Stellaria	<0.1%	Chickweeds & stitchworts
		Achillea	<0.1%	Yarrows
		Artemisia	<0.1%	Mugworts & wormwoods
		Astragalus	<0.1%	Vetches
		Campanula	<0.1%	Bellflowers
		Oxytropis	<0.1%	Locoweeds
		Pedicularis	<0.1%	Louseworts
		Penstemon	<0.1%	Beard-tongues
		Ranunculus	0.1%	Buttercups & spearworts
		Rumex	<0.1%	Sorrels & docks
		Saxifraga	0.1%	Saxifrages
Rushes	17.4%	*Juncus*	14.2%	Rushes
		Luzula	3.2%	Wood-rushes
Grasses	12.4%	*Alopecurus*	3.5%	Foxtails
		Calamagrostis	3.5%	Reedgrasses
		Poa	3.5%	Meadow-grasses, bluegrasses, tussocks & speargrasses
		Hordeum	2.4%	Barleys
		Hierochloe	0.5%	Sweetgrasses
		Phleum	<0.1%	Catstails & Timothy grasses
Ferns[a]	8.1%		8.1%	
Mosses[a]	5.8%		5.8%	
Lichens[a]	2.0%		2.0%	
Shrubs	1.2%	*Salix*	0.7%	Willows
		Empetrum	<0.1%	Crowberries
		Vaccinium	<0.1%	Cranberries & blueberries

[a] Not classified to genus level

Diet

We collected 97 pellet samples from Hidden Terror, 65 samples from Uyak, and 38 samples from Hepburn (n = 200). From these, we submitted 10 samples per study site, per visit, for microhistological analyses, except for the first Hepburn visit, for which we were only able to collect 9 samples because foul weather shortened our time in the field (n = 59).

Microhistological analyses revealed that mountain goats largely consumed sedges (34.5% of pellet biomass) followed by forbs (22.2%), rushes (17.4%), grasses (12.4%), ferns (8.1%), mosses (5.8%), lichens (2.0%), and shrubs (1.2%; Table 2). The most commonly consumed forbs were in the *Lupinus* (14.1%) and *Geranium* (7%) genera; the only species in these genera on Kodiak were Nootka lupine and woolly geranium.

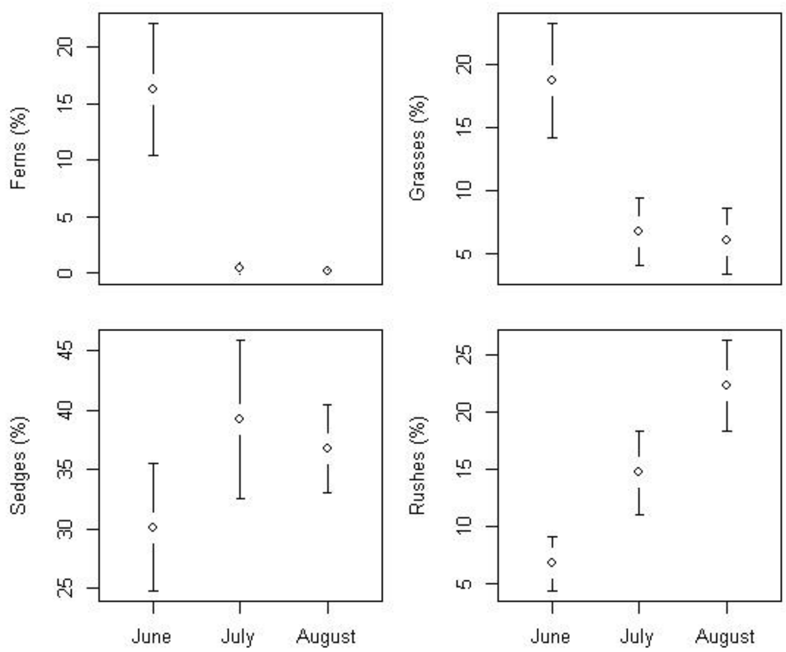

Fig. 2. Percent composition of ferns, grasses, sedges, and forbs in mountain goat summer diets by month, 2011, Kodiak Island. The percent composition of lichens and shrubs did not vary significantly over time. Diets were estimated by microhistological analyses of pellet samples. Circles indicate average percent compositions and bars extend to 95% confidence intervals.

Mountain goats consumed more sedges and rushes, and less ferns and grasses, as the season progressed, according to regression analyses (Fig. 2). More specifically, from June to July, mountain goats significantly increased their sedge consumption ($P = 0.02$), from 30.2% (SE = 1.16) to 39.2% (SE = 1.68) and forbs ($P < 0.01$), from 18.9% (SE = 1.43) to 24.8% (SE = 2.34). Rush consumption increased significantly each month ($P < 0.01$), from 6.8% (SE = 1.16) in June, to 14.7% (SE = 1.68) in July, and 22.3% (SE = 1.84) in August. In contrast, from June to July mountain goats significantly decreased their consumption of grasses ($P < 0.01$) from 18.7% (SE = 2.23) to 6.7% (SE = 1.25), and ferns ($P < 0.01$) from 16.2% (SE = 2.84) to 0.4% (SE = 0.23). Mountain goats did not vary their consumption of moss, lichen, and willow over the summer.

After accounting for monthly variation, regression results indicated that mountain goat diets, as estimated by pellet sample composition, varied among study sites (Fig. 3). Goats at the Uyak study site (the highest density subpopulation) consumed 6.9% more sedge on average than those at Hidden Terror (SE = 3.97, $P = 0.09$) and 8.0% more than those at Hepburn (SE = 3.97, $P = 0.05$). Goats at the Hidden Terror study site (the introduction site) ate 5.2% more forbs on average than goats at Uyak (SE = 2.67, $P = 0.05$) and 6.8% more than those at Hepburn (SE = 3.0, $P = 0.03$). However, goats at the Hidden Terror study site also consumed 10% less ferns than goats at Uyak (SE = 3.32, $P < 0.01$) and 14.0% less than those at Hepburn (SE = 3.78, $P < 0.01$). Goats at the Hepburn study site (newly established subpopulation) ate 7.6% more moss (SE = 0.95, $P < 0.01$) than goats at Uyak and 9.0% more than those at Hidden Terror (SE = 1.09, $P < 0.01$). Alternatively, we found no evidence that fern, forb, lichen, or shrub consumption varied among study sites.

Habitat Availability and Feeding Location Selection

We recorded 161 unique plant species and habitat classes at 298 locations (72 feeding and 226 random). The most common plant species were moss spp. and long-awned sedge, which occurred at 86% and 74% of locations, respectively. Other common plants included partridgefoot (49%), arctic daisy (*Dendranthema arcticum*; 47%), black crowberry (40%), and variegated sedge (*Carex stylosa*; 37%).

The eight most common mountain goat forage items identified in diet analyses were: long-awned sedge, variegated sedge, woolly geranium, Nootka lupine, rushes, grasses, ferns, and moss. We did not include forage diversity in feeding location selection modeling because it was correlated (>0.30) with other predictors.

Forage cover and habitat predictors differed between study sites, according to Mann-Whitney *U* tests (Table 3). Hidden Terror (introduction site) had lowest forage diversity ($P < 0.01$) and the least long-awned sedge, moss, grass, fern, and moss

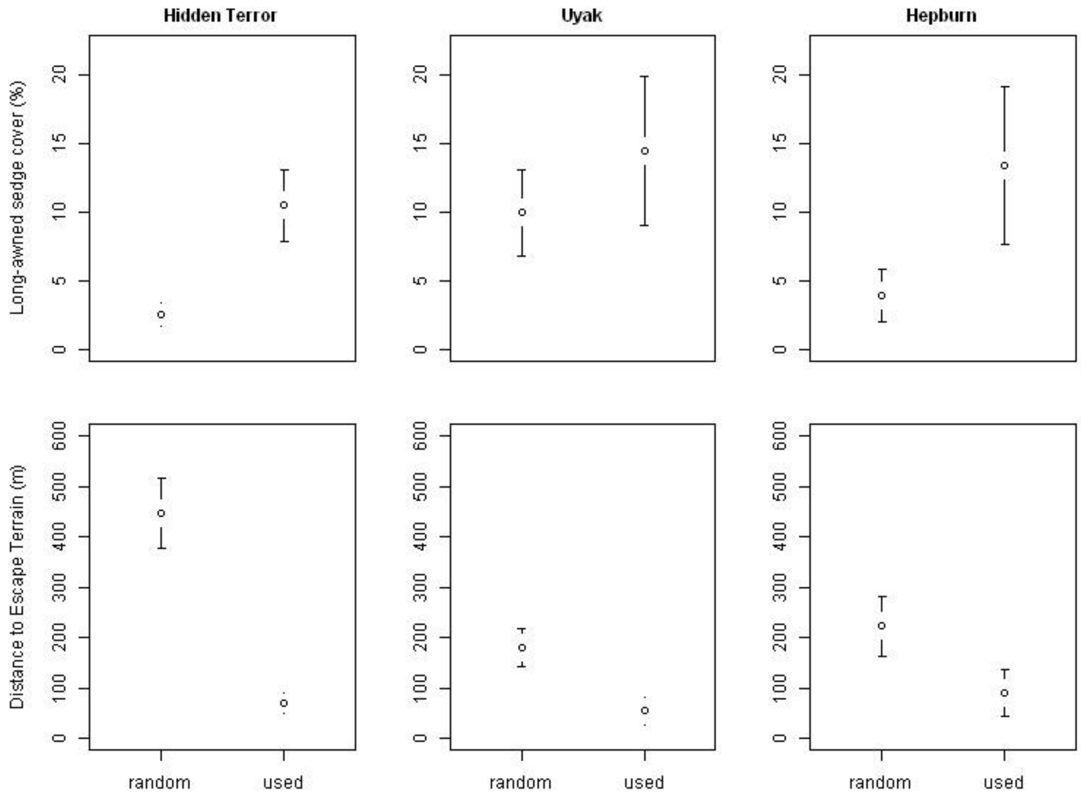

Fig. 3. Percent cover of long-awned sedge (*Carex macrochaeta*) and distance to escape terrain (m) at random and feeding locations, by study site during summer 2011, Kodiak Island. Circles indicate average percent covers and bars extend to 95% confidence intervals.

cover. Alternatively, Uyak (highest mountain goat densities) had the highest forage diversity (P = 0.01) and the most long-awned sedge cover (P < 0.01). Hepburn (lowest mountain goat densities and most recently colonized) had more moss cover than other study sites (P = 0.02).

The most parsimonious model for feeding location selection included nine predictors: long-awned sedge, woolly geranium, Nootka lupine, rush, grass, fern, and moss cover; hillshade, and distance to escape terrain (Table 4). Variegated sedge and study site were not in the top three most parsimonious models. According to this model, mountain goats selected feeding locations that were closer to escape terrain and had abundant long-awned sedge, rush and moss cover; and little woolly geranium, Nootka lupine, grass, and fern cover. The most significant covariate associated with feeding location selection, based on ΔAIC_c values, was distance to escape terrain, followed by long-awned sedge cover (Table 5, Fig. 3).

DISCUSSION

We predicted that areas on Kodiak where mountain goats have completed an irruptive growth cycle (i.e. established, then peaked in density, and finally declined to a lower ecological carrying capacity) would have less preferred forage cover at a lower diversity than areas occupied by mountain goats that are at earlier stages of colonization. Our results lend some support for this prediction. The Hidden Terror study site, where mountain goats were introduced to Kodiak and have completed an irruptive growth cycle, had lower forage diversity and less long-awned sedge, woolly geranium, grass, fern, moss, and lichen cover than other study sites. However, there was not a consistent relationship between site occupancy and forage: forage diversity and cover were generally lower at the Hepburn site than the Uyak site, despite mountain goats having colonized Hepburn approximately 20 years after Uyak. Although the irruptive growth of Kodiak's

Table 3. Results of Mann-Whitney *U* tests for differences in mountain goat forage cover and habitat predictors between pairs of study sites, 2011, Kodiak Island. Study sites with significantly larger values (*P* ≤ 0.05) are listed. Ties (*P* > 0.05) are indicated with a dashed line.

Cover class	Hidden Terror: Uyak	*P*-value	Hidden Terror: Hepburn	*P*-value	Uyak: Hepburn	*P*-value
Long-awned sedge	Uyak	>0.01	Hepburn	0.18	Uyak	<0.01
Variegated sedge	--	0.14	--	0.07	Hepburn	0.01
Woolly geranium	Uyak	<0.01	Hepburn	<0.01	--	0.20
Nootka lupine	Uyak	<0.01	--	0.06	--	0.15
Rushes	Hidden Terror	<0.01	Hidden Terror	<0.01	--	0.66
Grasses	Uyak	<0.01	Hepburn	<0.01	--	0.09
Ferns	Uyak	<0.01	Hepburn	<0.01	--	0.43
Mosses	Uyak	<0.01	Hepburn	<0.01	Hepburn	0.02
Forage diversity	Uyak	<0.01	Hepburn	<0.01	Uyak	0.01
Distance to escape terrain	Hidden Terror	>0.01	Hidden Terror	<0.01	--	0.20
Hillshade	--	0.06	--	0.24	--	0.60

goats may have led to the observed differences in forage, as documented in introduced ungulate populations elsewhere (Caughley 1970), we cannot completely rule out that observed differences in vegetation diversity and cover among study sites may have existed prior to the arrival of goats because the composition of plant communities prior to goat colonization is unknown.

The study site with the highest mountain goat density on Kodiak (Uyak) also had the highest forage diversity and the most forage cover, for all forage classes except mosses and rushes. This was an unexpected result because irrupting nonnative ungulate populations are typically known as threats to biodiversity and forage abundance through herbivory, rooting, digging, and trampling (Spear and Chown 2009). As stated earlier, it is possible that habitats with the highest densities of mountain goats had greater forage biodiversity and cover than other areas prior to the arrival of mountain goats, and which then led to a rapid increase in mountain goat subpopulation densities. By 2011, mountain goat densities at the highest density study site (Uyak, 2.54/km^2) had already exceeded the maximum mountain goat density at the Hidden Terror (2.09/km^2) site, before the subpopulation there subsequently crashed to a lower density. Pre-introduction carrying capacities at Hidden Terror and Uyak may have differed, and it is possible that the Uyak subpopulation had yet to reach carrying capacity. Despite the apparent lack of impacts to forage from the highest density goat subpopulation, future impacts by growing

Table 4. Logistic regression model output for the top candidate model evaluating mountain goat feeding location selection, summer 2011, Kodiak Island, Alaska.

Predictor	Estimate	SE	*p*-value
(Intercept)	-1.04	0.39	<0.01
Distance to escape terrain	-0.01	<0.01	<0.01
Long-awned sedge cover	0.14	0.03	<0.01
Fern cover	-1.67	0.61	<0.01
Woolly geranium cover	-0.21	0.07	<0.01
Rush cover	1.21	0.35	<0.01
Nootka lupine cover	-0.29	0.11	<0.01
Moss cover	0.03	0.01	<0.01
Hillshade	-0.16	0.09	0.06
Grass cover	-0.09	0.60	0.12

Table 5. Top ten candidate models for feeding location selection. The final model included nine predictors that were removed individually for comparison. K is the number of predictors in the model. Distance to escape terrain (m) was the strongest predictor of a mountain goat feeding location selection, followed by long-awned sedge cover (%), and then fern cover.

Model	k	AIC_c	ΔAIC_c	*w*
Full[a]	10	187.16	0	0.44
(-Grass cover)	9	187.81	0.65	0.32
(-Hillshade)	9	188.71	1.55	0.20
(-Moss cover)	9	193.04	5.88	0.02
(-Nootka lupine cover)	9	196.49	9.33	0.00
(-Rush cover)	9	197.73	10.57	0.00
(-Woolly geranium cover)	9	198.75	11.59	0.00
(-Fern cover)	9	201.93	14.77	0.00
(-Long-awned sedge cover)	9	205.94	18.78	0.00
(-Distance to escape terrain)	9	235.24	48.08	0.00

[a] Full model = Intercept + Distance to escape terrain + Long-awned sedge + Fern + Woolly geranium + Rush + Nootka lupine + Moss + Hillshade + Grass

mountain goat subpopulations at Uyak and Hepburn are likely if population growth rates remain unchanged. Therefore, continued monitoring of forage diversity, abundance, and quality is needed.

Mountain goats in areas on Kodiak that have completed an irruptive growth cycle were predicted to have a broader diet (show less selection for certain forage items) because declines in preferred forage would increase the energetic cost of locating and consuming such forages, and cause goats to seek alternative food items (MacArthur and Pianka 1966). Contrary to our predictions, we did not find a consistent correlation between mountain goat summer diets and their stage along the irruptive growth cycle. Although we found no consistent correlation between mountain goat diets and irruptive growth, we found that mountain goats on Kodiak in the highest density subpopulation consumed more sedge than any other subpopulation, which is viewed as a high quality summer forage for northern ungulates (Fox 1991). This finding is likely because sedge was most abundant at that site. In contrast, mountain goats in the lowest density subpopulation consumed the most moss, which is seen as a low quality forage for northern ungulates (Ihl and Barboza 2007).

As expected, the summer diets of mountain goats on Kodiak consisted largely of alpine sedges and forbs, as reported elsewhere for coastal Alaska (Hjeljord 1973, Fox et al. 1989, White et al. 2012). Introduced goats in Montana and Colorado primarily consumed grasses, sedges, and rushes in the summer (Saunders and Saunders 1955, Hibbs 1967) and fall (Varley 1994). Although this suite of plants tend to dominate goat diets, browse plants have been found to be a primary summer food in Montana and South Dakota (Casebeer 1948, Richardson 1971). Like other ungulates, summer forage intake by mountain goats is largely driven by the need for rapid growth and weight gain to counterbalance annual weight loss over the winter due to nutritional deprivation. By consuming sedges and forbs mountain goats on Kodiak focused on high quality forage, which has high cellular content, little cell wall material, and minimal secondary compounds (Fox et al. 1989). Alpine plants contain more nitrogen (i.e. higher quality) than their counterparts at lower elevations and continue to emerge from areas adjacent to receding snow banks throughout much of the summer (Fox 1991), which provides goats with highly nutritious new growth over an extended time period.

Mountain goats on Kodiak Island shifted their diets between June and August by consuming more sedges and forbs, and less ferns and grasses, as the summer progressed. This dietary shift, most pronounced between June and July, was consistent across all study sites and was likely linked to increased availability of new alpine vegetative growth following snowmelt. Higher elevations on Kodiak Island were still largely snow-covered through most of June, which presumably presented limited forage that was more similar to winter conditions. Seasonal dietary shifts by mountain goats have been observed on Kodiak (Hjeljord 1971) and elsewhere (Hjeljord 1973, Varley 1994, Degano and Catan 2002), and have been tied to changes in forage availability and quality (Pfitsch and Bliss 1985). The only previous mountain goat diet study on Kodiak found that mountain goats in the Hidden Basin area (a portion of this study's Hidden Terror study site) utilized tall rigid grasses and sedges during the winter, especially Altai fescue (*Festuca altaica*) and coiled sedge (*Carex circinata*), which maintain an upright structure and green tissue even on snow-covered slopes (Hjeljord 1971). Hjeljord (1971) observed mountain goats spending much of their feeding time digging through litter to consume lady fern (*Athyrium filix-femina)* rhizomes in the winter, and blue-joint (*Calamagrostis canadensis*) and fern rhizomes in early spring (May). Our results expanded upon these findings by showing that ferns and grasses are still important components of Kodiak's mountain goat diets well into summer (late June) and this dietary pattern appears to be independent of population density and a history of irruptive growth.

Our feeding location selection models indicated that proximity to escape terrain was the most critical element of mountain goat feeding location selection on Kodiak, as previously identified in other areas (Gross et al. 2002, Poole and Heard 2003, Hamel and Côté 2007). However, unlike other populations that are vulnerable to predation by wolves (*Canis lupus*), black bear (*U. americanus*), and brown bears (Fox and Streveler 1986), mountain goats on Kodiak are only at risk of predation by brown bears, golden eagles (*Aquila chrysaetos*), and humans (Côté and Beaudoin 1997, Demarchi et al. 2000). Levels of bear and eagle predation on mountain goats were unknown on Kodiak, but thought to be minimal because observed interactions between the species and discoveries of mountain goat predation events were rare. Despite increasingly liberal hunter harvest pressure (5–10% targeted kill rates in 2010), the goat population has exponentially grown for over 60 years (Van Daele and Crye 2010). It is unlikely that this observed rate of mountain goat population increase would have been possible in combination with heavy bear and eagle predation.

Our feeding location selection models indicated that mountain goats on Kodiak selected feeding locations that had abundant and homogeneously distributed long-awned sedge, a highly nutritious forage throughout summers in Alaska (Fox 1991). Like many northern ungulates, mountain goats are considered selective feeders and display seasonal preferences for specific classes and species of forage (Festa-Bianchet and Côté 2008). This selective feeding behavior typically manifests itself in selection for specific habitat types that harbor the greatest abundance of preferred forage items. Mountain goat feeding locations have been described as alpine meadows near cliffs (Von Elsner-Schack 1986). Confirming our findings, Hjeljord (1971) found that mountain goats in the Hidden Basin region selected sedge meadows and slopes as feeding locations during the summer in the 1970s, where their preferred forage was also long-awned sedge. Our microhistological results of mountain goat pellets collected at feeding locations also confirmed the importance of sedges in the summer diets of mountain goats.

Long-awned sedge was also found to be heavily used by Kodiak bears in the spring (Atwell et al. 1980). Given overlapping dietary preferences, the potential exists for forage competition between bears and mountain goats. Bears have been observed congregating at high densities (0.85/km^2) on localized patches of long-awned sedge, presumably because it is fast growing, nutritious, and one of the first to emerge following snowmelt, but before salmon spawning (Atwell et al. 1980). Although the potential for competition exists, we did not directly observe interactions between bears and mountain goats to support this hypothesis.

Understanding the diet, feeding location selection and behavioral patterns of a growing Kodiak mountain goat population is a critical first step for developing empirically-driven harvest management strategies. Our results show that mountain goat feeding location selection is driven by access to high quality sedges and forbs, and proximity to escape terrain. This finding was universal, regardless of goat population densities or history. If Kodiak's mountain goat population continues to grow it will likely exceed its nutritional carrying capacity and cause a reduction in their preferred forage species, which could in turn affect other species such as bears, which also rely on these forage species. Additional work is therefore needed to further understand the relationship between the resource selection patterns, population dynamics, and harvest management options for mountain goats on Kodiak Island.

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