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Grizzly bear diet shifting on reclaimed mines

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ABSTRACT

Industrial developments and reclamation change habitat, possibly altering large carnivore food base. We monitored the diet of a low-density population of grizzly bears occupying a landscape with open-pit coal mines in Canada. During 2009–2010 we instrumented 10 bears with GPS radiocollars and compared their feeding on reclaimed coal mines and neighboring Rocky Mountains and their foothills. In addition, we compared our data with historical bear diet for the same population collected in 2001–2003, before extensive mine reclamation occurred. Diet on mines ($n = 331$ scats) was dominated by non-native forbs and graminoids, while diets in the Foothills and Mountains consisted primarily of ungulates and *Hedysarum* spp. roots respectively, showing diet shifting with availability. Field visitation of feeding sites ($n = 234$ GPS relocation clusters) also showed that ungulates were the main diet component in the Foothills, whereas on reclaimed mines bears were least carnivorous. These differences illustrate a shift to feeding on non-native forbs while comparisons with historical diet reveal emergence of elk as an important bear food. Food resources on reclaimed mines attract bears from wilderness areas and bears may be more adaptable to landscape change than previously thought. The grizzly bear's ready use of mines cautions the universal view of this species as umbrella indicative of biodiversity.

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1. Introduction

Occurrence and persistence of many wildlife populations are largely determined by the availability and distribution of food and habitat resources (Manly et al., 2002; Stephens et al., 2007). To avoid starvation, animals must be able to track information on food distribution (Dall and Johnstone, 2002; Dall et al., 2005). Locating adequate food resources can be challenging when original habitat is altered by human-caused landscape change. As human populations rise, so does the consumptive footprint (Houghton, 1994) even at lowered population growth rates (Ehrlich et al., 1999), leading to habitat change through conversion of natural areas to agriculturally and industrially modified landscapes (DeFries et al., 2004; Foley et al., 2005).

Open-pit (surface) mining provides a clear-cut example of habitat modification due to resource exploitation by humans. Following closure of open-pit mines, often a principal goal of mine reclamation is provision of habitat for wildlife (Erickson, 1995; Kennedy, 2002). In this context, reclaimed mines are accepted as dynamic landscapes colonized by species from

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nearby undisturbed areas (Hobbs and Harris, 2001; Choi et al., 2008). Colonization of mines by focal species is commonly used as a measure of reclamation success (Scott et al., 2001; Cristescu et al., 2012a). Terrestrial focal species chosen to monitor reclamation effectiveness are typically plants, invertebrates, amphibians, reptiles and birds (McCoy and Mushinsky, 2002; Cristescu et al., 2012a). Small mammals (Larkin et al., 2008) and ungulates (e.g., Jansen et al., 2009) are less commonly selected, although in natural systems foraging by ungulates can slow ecological succession (Mysterud, 2006) and substantially alter ecological processes (Frank, 1998). On reclaimed mines, ungulate foraging also slows or even prevents ecological succession to a more natural vegetation community, especially when combined with harsh abiotic conditions characteristic of mined landscapes (Smyth, 1997; Paschke et al., 2003; del Moral et al., 2007) and low dispersal and competitive abilities of native plants compared to non-natives (Holl, 2002; Zipper et al., 2011).

If ungulates are killed by large carnivores on reclaimed mines, then carnivores could facilitate ecological succession thus helping conversion of mines back to a more natural ecosystem state. Monitoring carnivores on and near mines could therefore provide valuable information for gauging reclamation success. However, data on large carnivore diet on reclaimed mines are absent from the peer-reviewed literature.

Canada is no exception to the global conservation crisis, with habitat loss being the single most important threat to species persistence (Venter et al., 2006). Extractive industries such as open-pit mining are forecasted to expand substantially in response to high demand from rapidly growing world economies (MiHR, 2010). To provide insights into large carnivore adaptation to industrially exploited and subsequently reclaimed landscapes, the Foothills Research Institute designed a monitoring program on grizzly bears in west-central Alberta, Canada, working in collaboration with universities and industry in Canada. Low grizzly bear population estimates found along with ongoing human activities led to grizzly bear designation as threatened in Alberta in 2010 (Festa-Bianchet, 2010).

The grizzly bear's distribution is driven primarily by foods and human persecution (Mattson and Merrill, 2002; Laliberte and Ripple, 2004; Proctor et al., 2012). The carnivorous digestive system and relatively poor ability to digest plant matter (Schwab et al., 2009, 2011) suggest that although bears can consume vegetation extensively, meat is an important component in their diet. In Yellowstone National Park, grizzly bears have greater impacts on elk calf survival than wolves and other predators (Barber-Meyer et al., 2008), and substantial predatory impact by grizzly bears has been documented in Alaska (Boertje et al., 1988) and Yukon (Larsen et al., 1989). In addition, grizzly bears frequently scavenge on wolf, cougar and human hunter-killed ungulates.

Our objective was to investigate bear diet in relation to availability of foods on a landscape with natural habitats and open-pit mining industrial disturbance. The research was carried out on and adjacent to two coal surface mines of west-central Alberta, where Munro et al. (2006) found that grizzly bears consumed a variety of food items. However that study occurred during 2001–2003, when mine reclamation had lower extent; did not explicitly address bear diet on reclaimed mines or differences in food consumption on vs. outside mines; and did not provide a detailed assessment of food availability on mines, in the mountains and foothills. Nonetheless, the Munro et al. (2006) study offered a unique opportunity to investigate differences in diet for the same bear population, which we studied during 2009–2010, once the mines had been largely reclaimed. Given the threatened status of grizzly bears in Alberta and continuing industrial development, documenting how bears have adapted to modification in the availability of foods associated with mine reclamation is informative for the conservation of this species.

2. Methods

2.1. Study area

The 3200 km² study area was located in the province of Alberta (53°15'N 118°30'W), at the eastern edge of the current distributional range of grizzly bears in Canada (Proctor et al., 2012) (Fig. 1). The entire province is virtually a coal-bearing basin (Cameron and Smith, 1991) and Alberta is the largest coal-producing and coal-consuming province in Canada (World Energy Council, 2010). Elevation and ruggedness are greater in the western section of the study area which is located on the Eastern Slopes of the Rocky Mountains, with the eastern section being characterized by a rolling landscape in the Foothills. The main natural land cover in the region is coniferous forest dominated by white spruce (*Picea glauca*) and lodgepole pine (*Pinus contorta*) with deciduous forest composed of balsam poplar (*Populus balsamifera*) and trembling aspen (*P. tremuloides*) also present at lower elevations and on sunny south and east facing slopes.

Mountainous areas include protected lands and generally have less human activity than the Foothills. The study area is sparsely populated and the primary human activity is open-pit coal mining, with other activities including oil and gas development, forest harvesting and recreation. The area encompasses two adjacent reclaimed open-pit coal mines (Luscar and Gregg River) located at the interface between the Rocky Mountains and their foothills near the coal mining town of Cadomin (population 60) and an active mine located approximately 20 km South of Cadomin. During the active mining phase, trees and other vegetation are removed, with blasting and excavating occurring to extract coal. Following mine closure, a combination of native non-native forbs and graminoids are sown as part of mine reclamation resulting in a predominantly open landscape with scattered forest fragments left undisturbed during active mining. The total combined mine disturbance area for the two mines under study is 3635 ha (Karmacharya et al., 2011). During the study period human activity was absent from one mine and restricted to <17% of the area of the second mine.

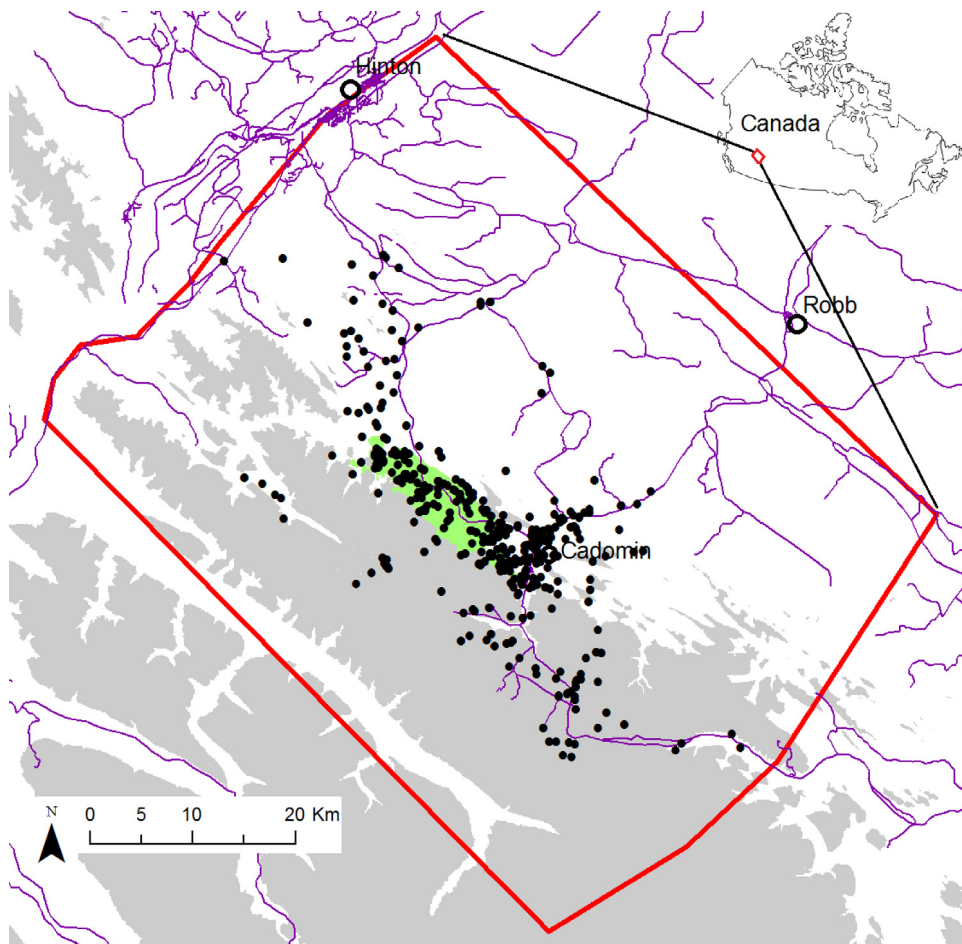


Fig. 1. Study area (red) in west-central Alberta, Canada, including major roads (purple), towns (empty dots) and reclaimed mines (green). Grizzly bear GPS location clusters with evidence of feeding ($n = 234$) and/or where scat was collected ($n = 331$) in 2009–2010 (black dots) are overlaid on Mountains (≥ 1700 m; gray) and Foothills (< 1700 m; white). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.2. Study animals

Grizzly bears persist at low density (4.79 bears/1000 km²) in the study area (Boulanger et al., 2005). In 2008–2010, we captured and attached remotely downloadable GPS radiocollars (Followit, Telus UHF, Sweden) on twelve adult grizzly bears in the study area. An effort was made to sample the bear population randomly on reclaimed mines, Foothills (elevation < 1700 m) and Mountains (≥ 1700 m), using aerial (helicopter darting) and ground capture methods (culvert traps and leg-hold snares). Two large male bears dropped their collars within a month from capture and were excluded from analyses. The remaining ten bears ($n_{\text{males}} = 4$; $n_{\text{females}} = 5$; $n_{\text{females with cubs}} = 2$) were monitored for a total of 55.6 bear-months (mean \pm standard deviation 5.6 ± 3.3). One female counted as a female with cubs in 2009 and single female in 2010 for statistical analyses. Radiocollars were set to acquire a location every hour during the active bear season (outside denning). This fix rate was chosen as a compromise between having sufficiently detailed tracking data and extending collar battery life. Each month we approached every bear on foot or via fixed-wing aircraft or helicopter and triggered its radiocollar to send GPS data remotely via VHF transmission.

2.3. Bear foraging at field-inspected sites

In 2008, a pilot study was conducted with two radiocollared grizzly bears to test the feasibility of GPS location cluster visitation for identifying bear foraging. Following the success of this pilot work, during April–October 2009 and 2010 we tracked a total of ten adult grizzly bears, eight of which used reclaimed mine sites. Clusters were identified by running a Python algorithm originally designed for cougar kill site identification (Knopff et al., 2009), which we modified to accommodate a 50 m seed cluster radius. During the main study period (2009–2010), only clusters with ≥ 3 telemetry relocations were visited in the field. Due to logistical limitations, for each bear during each month we attempted to visit the

Table 1

Grizzly bear diet composition in west-central Alberta, Canada, April–October 2009 and 2010. Diet was assessed by field visitation of GPS location clusters and scat analyses based on frequency of occurrence of food items relative to total items, total scats and taxonomically-identified total subitems.

Food category	GPS						Scat																				
	Fth			Mt			Rmi			Fth						Mt			Rmi								
	# ^a	F		# ^a	F		# ^a	F		# ^b	F ^c	F ^d	# ^e	F ^f		# ^b	F ^c	F ^d	# ^e	F ^f		# ^b	F ^c	F ^d	# ^e	F ^f	
	165			65			71			502	502	179	4240	4240		200	200	91	1333	1333		164	164	61	1304	1304	
Plant																											
Herb	30	18.2	6	9.2	57	80.3	223	44.4	124.6	1535	36.2	73	36.5	80.2	559	41.9	116	70.7	190.2	940	72.1						
Berry	3	1.8	3	4.6	0	0.00	35	7.0	19.6	399	9.4	18	9.0	19.8	247	18.5	7	4.3	11.5	51	3.9						
Root	26	15.8	33	50.8	0	0.00	87	17.3	48.6	NA	NA	70	35.0	76.9	NA	NA	20	12.2	32.8	NA	NA						
Animal																											
Ungulate	98	59.4	16	24.6	13	18.3	77	15.3	43.0	1276	30.1	13	6.5	14.3	208	15.6	9	5.5	14.8	133	10.2						
Small mammal	6	3.6	3	4.6	0	0.00	51	10.2	28.5	522	12.3	17	8.5	18.7	138	10.4	6	3.7	9.8	80	6.1						
Bird	1	0.6	1	1.5	0	0.00	0	0.0	0.0	0	0.0	0	0.0	0.0	0	0.0	0	0.0	0.0	0	0.0						
Insect	1	0.6	3	4.6	1	1.4	29	5.8	16.2	508	12.0	9	4.5	9.9	181	13.6	6	3.7	9.8	100	7.7						
Total	165	100.0	65	100.0	71	100.0	502	100.0	280.4	4240	100.0	200	100.0	219.8	1333	100.0	164	100.0	268.9	1304	100.0						

^a Total number of items sampled from visitation of foraging clusters in the foothills (Fth; $n = 136$), mountains (Mt; $n = 58$) and reclaimed mines (Rmi; $n = 40$).

^b Total number of items sampled from scats collected from foothills (Fth; $n = 179$), mountains (Mt; $n = 91$) and reclaimed mines (Rmi; $n = 61$).

^c % occurrence of items relative to total items.

^d % occurrence of items relative to total number of scats.

^e Total number of taxonomically identifiable subitems in scat (i.e., total number of sampled berries, herbaceous fragments, ungulate/small hairs, bird feathers, and insects; roots were assumed to be *Hedysarum* spp.)

^f % occurrence of subitems relative to total number of subitems.

largest four GPS relocation clusters as well as randomly picked other clusters from the remaining cluster list as identified by the algorithm. This sampling scheme was designed as a trade-off between enhancing the probability of obtaining scat for diet estimation and sampling diverse bear behaviors across a range of cluster durations. The centroid of each cluster selected for field visitation was programmed into hand-held Wide Area Augmentation System (WAAS) enabled Garmin GPS Map 60CSx units with low error (5.31 ± 1.45 m). Based on the 2008 pilot study when we located bears on large ungulate kills within 3 weeks of cluster start date, for safety reasons, to avoid disturbing the animals and due to logistical constraints, we visited clusters 40.64 ± 15.45 days after the first fix in the cluster. Because clusters were not visited immediately after formation, it is possible that some evidence of bear feeding was missed or erroneously attributed to grizzly bears, especially regarding herbaceous and berry feeding. Crews recorded whether there was uncertainty in bear sign at a cluster site and bear behavior data associated with such sites were omitted from analyses.

Once at the cluster centroid, crews searched within a 50 m radius for any evidence of bear feeding on animal and plant matter following a similar protocol to Munro et al. (2006). Typical sites where bears had fed on animal prey included ungulate skeletal and hair remains, evidence of small mammal feeding such as diggings or displaced rocks and logs, or evidence of ant feeding such as split logs and excavated ant hills. Assigning mammalian prey to species was based on field evidence validated by laboratory microscopic identification of hair collected at kill sites as described in the 'Scat analysis' section. Sign of feeding on plant material included evidence of digging for *Hedysarum* spp. roots, foraging on berries and grazing on graminoids and forbs. With the exception of graminoids, we differentiated herbaceous and berry material by species based on identification keys (Johnson et al., 1995; Kershaw et al., 1998) and when necessary by laboratory keying of plant samples collected in field. We separated forbs into native and non-native (introduced) based on USDA, and NRCS (2012). Some cluster sites were assigned multiple foraging activities and for all sites we assigned activity by taking into account age of sign such as algal growth on carcass bones, plant growth inside root digs or greenness of grazed vegetation. For clusters with long duration, presence of specific food items in bear scat found at the site also was used to confirm feeding site assessments.

We summarized total number of food items classed into broad categories sampled from cluster visitation (Table 1) and calculated frequency of occurrence of each item relative to total items. Broad item grouping included plant (herbaceous, berry, root) and animal (ungulate, small mammal, bird, insect) matter.

We used bear behavior sign, time bear spent at the site based on GPS cluster information, and maximum daily intake rates for bears of different body sizes to estimate dry biomass ingested at each site. Intake rates were taken from the literature on bears in captive trials feeding on ungulates (Mattson, 1997), small mammals (Pritchard and Robbins, 1990; Berkes et al., 1994), birds (Bissett, 1974), insects (Brian, 1978), roots (Hamer, 1999), herbaceous material (Rode et al., 2001) and berries (Welch et al., 1997). Whenever available, species-specific food item estimates were used. For ungulates, estimates were sex and age-specific based on mean body sizes of ungulates in Alberta (Knopff et al., 2010) and were corrected for ungulate skeletal, rumen and water weights (Mattson, 1997). If evidence of bear bedding was detected at a foraging site, we assigned one hour for each of the following feeding activities: digging (roots, small mammals, insects), feeding (birds, herbaceous, berries), with the remainder of time the bear had spent at the site assigned to bedding. This hourly allocation to feeding behavior was meant to standardize bear food intake based on the maximum resolution of the GPS collar data (1 GPS fix

per hour), while taking into account the fact that the bear also had bedded at the site. For example, if a site where a GPS-radiocollared bear had spent 5 h had evidence of digging for roots, grazing and bedding, then we assumed that the bear spent 1 h foraging on roots, 1 h feeding on vegetation and 3 h bedding. If the bear had not bedded at the site, we assumed that it spent the entire time engaged in foraging, therefore biomass calculations reflected the entire cluster duration. For sites where bears spent long time periods, primarily at ungulate carcasses, we assumed that bears fed on the ungulate for 16 h in every 24 h cycle, based on known bedding duration for the sampled bears (7.7 ± 4.7 h).

2.4. Scat collection and analysis

Crews searched each cluster location for bear scat and collected approximately 50 ml each of 1–2 scats. When multiple scats were found, only scats whose age matched the actual date when the bear was present at the site were collected (Wasser et al., 2004). If all scats appeared of the same relative freshness, scats were selected randomly for collection. To avoid pseudoreplication in dietary inferences because of oversampling scats from the same bear, or collecting more scats at locations where bears had spent longer time (ungulate carcasses), only one scat per site was retained for diet analysis (Bacon et al., 2011). While this sampling scheme might undersample meat consumption, the diet composition data from scat analyses are still comparable between land designations, because the sampling protocol was maintained in the foothills, mountains and on reclaimed mines. Further, the results from scat sampling are also comparable in a relative sense to those from the GPS cluster method, given that protocols for both methods were identical across the study area.

Thirty ml of each sample were autoclaved and rinsed through a 0.5 mm metal sieve to remove small soil and sand particles. Samples were air dried overnight in a fume hood and transferred to wide diameter petri dishes of one standard size. The sample was spread flat over the dish using tweezers and a dissecting microscope, grouping together broad food items defined as roots, herbaceous material, berries, ungulates, small mammals, birds, insects, as well as miscellaneous non-foods (soil, rock, wood). A grid of 2×2 -cm squares was placed below the dish and used to estimate the percentage of each broad food item relative to total fecal sample excluding miscellaneous material. This technique allowed estimation of proportion of various food items in scat for the same standardized sample volume (Schwab et al., 2011).

We identified species consumed by bears whenever possible, by attempting to take 20 subitems (mode 20) per scat sample for each broad food item. Subitems were either herbaceous material fragments, berries or berry seeds, mammalian hairs, and insects or insect fragments. All roots were assumed to be *Hedysarum* spp. (Munro et al., 2006). Herbaceous samples were assessed based on leaf morphology (lamina, apex and base shape, margin, gland position) and epidermal characteristics (stomatal complex and trichomes) (Dilcher, 1974; Riegert and Singh, 1982). Berries were identified based on morphological differences of seeds (size, aspect, color, surface aspect). For herbaceous material and berries, we collected samples in the study area and created seed and herbaceous reference collections as well as microscopy slides based on *a priori* knowledge of foods consumed by bears in western Canada (Nielsen et al., 2003; Munro et al., 2006) to which we added *Melilotus* spp. planted on reclaimed mines. All vegetation other than roots items were validated against three reference collections (University of Alberta Herbarium, Edmonton, Alberta; Foothills Research Institute Grizzly Bear Program, Hinton, Alberta; our own seed and herbaceous collection of bear foods). Mammals were identified to North American species based on hair medulla and scales/cuticula identification (Moore et al., 1974; Teerink, 1991; Jones et al., 2009). Insects were classified into Formicidae (ants) and Coleoptera (beetles).

Similarly to the procedure for GPS cluster data, we summarized total number of broad food items sampled from scat analysis (Table 1), and calculated frequency of occurrence of each item relative to total items but also to total number of scats respectively. Detailed items were classified to species, genus or family level depending on our ability to identify subitems. We also calculated frequency of occurrence for each taxonomically identifiable subitem relative to total number of subitems.

To estimate biomass ingested based on scat analysis we used published correction factors from captive bear feeding trials (Hewitt and Robbins, 1996). Scat biomass estimates for ungulates are sensitive to proportion of hair ingested by bears which affects correction factor values. Rather than using the approach of Paralikidis et al. (2010) who assumed a maximum correction factor and likely overestimated ungulate biomass in bear diet, we followed the method of Dahle et al. (1998) and modified the Hewitt and Robbins (1996) correction factors based on field observations of hair ingestion and kill/scavenging data from GPS clusters (Table S.1).

2.5. Food availability

To assess food availability for foothills, mountains and reclaimed mines we estimated percentage cover of major grizzly bear plant foods (herbaceous, roots, berries) and performed ungulate pellet counts in 20×20 -m field plots ($n_{\text{foothills}} = 494$; $n_{\text{mountains}} = 225$; $n_{\text{reclaimed mines}} = 166$). These plots included a 50:50 ratio of field-visited sites used by radiocollared bears during our study and random sites 300 m away from used sites. All of the landscape, except steep rock and water bodies, is available to bears and used and random sites were included to characterize bear foods by land designation. The presence of bear plant foods was assessed in five 0.7×0.7 -m quadrants equally spaced on a north–south transect through the center of each plot. If this direction followed a stream or trail, the transect was shifted to east–west to minimize spatial autocorrelation in species composition between quadrants. With the exception of graminoids, herbaceous foods were identified to species

level and categorized into native or non-native. In addition, we carried out a complete inventory of herbaceous species in the same quadrants to estimate species richness by land designation. To avoid misrepresentation of availability based on phenology and detection error, we converted all cover estimates and counts to presence/absence of food items in the plots. Were we to use percentage cover data instead of presence/absence of bear plant foods, we would have artificially inflated availability estimates for plots sampled in summer, when plant cover of forbs and graminoids in particular are greater than during growth (spring) or fall (senescence). Presence of ungulates was primarily recorded based on occurrence of fecal pellets, and in 16.7% of cases when snow covered >25% of the plot, with the aid of foot tracks in the snow. We considered deer and bighorn sheep together because we were not able to reliably distinguish the pellets of these two species.

2.6. Statistical analyses

For both diet estimation methods, we used contingency table chi-square analyses to assess differences in food composition between foothills, mountains and reclaimed mines. In the case of the GPS method we did not include berries, small mammals and insects in statistical analyses because of small sample sizes. Birds were omitted from all analyses also because of low sample sizes.

We used generalized linear models (GLMs) to investigate differences in proportion occurrence of each food item in scat between land designations, with location (land designation) as predictor variable. Separate models were run for the GPS and scat methods and for berries, graminoids, native forbs, non-native forbs, *Hedysarum* spp. roots, deer and bighorn, elk, moose, small mammals, and insects (Frequency of occurrence: $n = 10$ models [GPS]; $n = 10$ models [Scat]). We set location on reclaimed mines as the base of comparison with foothill and mountain areas. Proportion of occurrence of a specific food type as dependent variable was rescaled to 0 and 1 to enable fitting of a logistic model in STATA, which was followed by back-transformation of the model-predicted scores to proportion (<http://www.ats.ucla.edu/stat/stata/faq/proportion.htm>). We used a similar approach to assess differences in proportion ingested biomass by land designation, performing separate GLMs for the GPS and scat methods and for each food item listed above (Biomass: $n = 10$ models [GPS]; $n = 10$ models [Scat]). Robust standard errors were calculated in STATA to account for potential misspecification of the probability distribution family. We assessed model fit by inspecting deviance residuals to identify potential outliers or influential observations. In addition, we computed predicted values from the model output and calculated the correlation with observed values of the dependent variable. High correlations were considered indicative of good predictive power (Zheng and Agresti, 2000).

To assess food availability, we used logistic regression with robust standard errors to estimate whether certain food items as quantified with our 0.7×0.7 -m quadrant and 20×20 -m plot data were more likely to be present on the landscape on specific land designations. We used Wald chi-square tests to test the null hypothesis that at least one of the predictor's parameter estimate from a given regression model equaled zero. Link tests were computed to check for specification error with regard to location being a relevant predictor. Pregibon leverage values were calculated and plotted against predicted probabilities of occurrence to detect potential influential observations. Differences in herbaceous species richness between land designations were assessed using two-sample Wilcoxon rank-sum tests.

3. Results

3.1. Overall patterns

We found differences in diet estimation between the GPS and scat methods ($\chi^2 = 149.58$, $df = 5$, $P < 0.05$). These differences were chiefly caused by high presence of ungulate items at clusters (42%) compared to scat samples (11%) and increased occurrence of non-ungulate items in scat (small mammals 9%; insects 5%; berries 7%) compared to clusters (small mammals 3%; insects 2%; berries 2%). However, both the GPS cluster visitation and the scat methods showed that ungulate and herbaceous material are primary components of grizzly bear diet in west-central Alberta (Fig. 2). Both methods also showed that grizzly bear diet composition differed between foothills and mountains (Scat $\chi^2 = 32.43$, $df = 5$, $P < 0.05$; GPS $\chi^2 = 42.04$, $df = 5$, $P < 0.05$), foothills and reclaimed mines (Scat $\chi^2 = 36.72$, $df = 5$, $P < 0.05$; GPS $\chi^2 = 84.97$, $df = 5$, $P < 0.05$) and mountains and reclaimed mines (Scat $\chi^2 = 45.88$, $df = 5$, $P < 0.05$; GPS $\chi^2 = 81.45$, $df = 5$, $P < 0.05$).

Deviance residuals for GLMs plotted against unique id-s of sites visited during GPS cluster sampling/scat collection generally did not reveal any major outliers or influential observations. However, berry, small mammal and insect models had higher deviances compared to herbaceous, root and ungulate models, suggesting better fits for the latter three food items. Correlations between predicted and observed values of the dependent variable also showed that herbaceous, root and ungulate models had best fit and results for these food items are detailed in the following two sections of the Results. This pattern held for both diet analysis methods (Table 2). Interpretations for berry, small mammals and insect foods must therefore be treated with caution due to lower model fit. These latter items accounted for much smaller amounts in the biomass ingested by bears. Small mammals (mostly ground squirrels [Sciuridae]) and berries (mainly *Shepherdia canadensis*, *Empetrum nigrum* and *Vaccinium scoparium*) were more likely to occur in bear scat samples outside mines than on mines. Insects in scat were almost exclusively Formicidae, and birds (Tetraoninae) were detected at two GPS location clusters but were absent in scat.

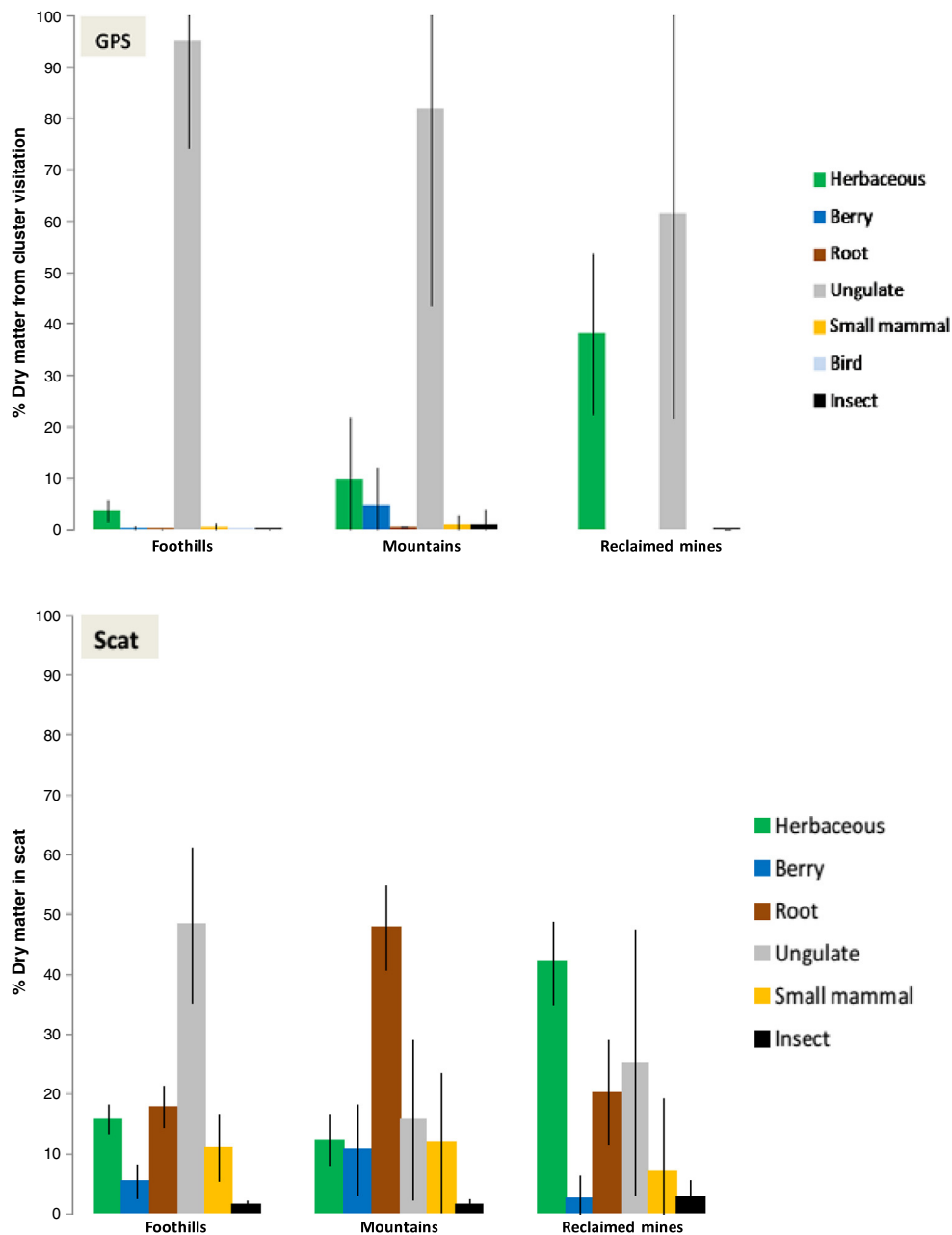


Fig. 2. Diet of grizzly bears in west-central Alberta by land designation, using 2 methods: scat analysis and GPS location cluster visitation. Error bars are means \pm 95% CI. Confidence intervals for the GPS cluster method are truncated at 100%.

The full results across land designations and the two diet estimation methods are available in [Table 1](#) (summary of diet item occurrence), [Table 2](#) (outputs of testing differences in frequency of occurrence between land designations) and [Table 3](#) (outputs of testing differences in biomass between land designations). The supporting information provides detailed taxonomic listing of food item occurrences (Table S.2) and total and relative food item biomasses (Table S.3), the latter including a correction for land designation as described in the caption for Table S.3.

3.2. Diet estimation through GPS cluster visitation

Grizzly bears foraged on all land designations, including reclaimed mines ([Fig. 2](#)). Of the 445 location clusters visited in the field, we found evidence of bear feeding at 234 clusters (52.6%). The majority of clusters (91.5%) had only one type of bear feeding activity, with some clusters having two types of feeding (8.5%). This method resulted in 23 plant and animal

Table 2

Variation in frequency of occurrence of food items ingested by grizzly bears in west-central Alberta, Canada, April–October 2009 and 2010. Diet was assessed by estimating species-specific frequency of occurrence of foods available to bears from feeding sign at GPS location clusters and scat analyses. Reclaimed mines were withheld as the reference category in all models run.

Food category	GPS						Scat					
	Fth		Mt		Model fit ^b		Fth		Mt		Model fit ^b	
	β_i^a	Robust SE	β_i^a	Robust SE	Correlation coefficient	P_{corr}	β_i^a	Robust SE	β_i^a	Robust SE	Correlation coefficient	P_{corr}
Plant												
Berry	14.83**	0.61	15.70**	0.62	0.11	0.11	1.02**	0.50	1.28**	0.53	0.11	<0.05
Graminoid	-2.08**	0.59	-3.19**	1.07	0.31	<0.05	-0.73**	0.17	-1.24**	0.25	0.29	<0.05
Native forb	0.53	0.63	-0.51	0.86	0.11	0.11	-0.88**	0.36	-1.03**	0.46	0.16	<0.05
Non-native forb	-4.01**	0.68	-3.86**	1.05	0.62	<0.05	-1.11**	0.19	-1.54**	0.29	0.36	<0.05
Root	15.59**	0.24	17.40**	0.28	0.48	<0.05	0.51**	0.30	1.62**	0.32	0.35	<0.05
Animal												
Deer & Bighorn	-0.51	0.40	-1.51**	0.58	0.18	<0.05	0.33	0.50	-0.25	0.58	0.08	0.15
Elk	1.93**	0.61	1.47**	0.69	0.18	<0.05	2.13**	0.61	-0.03	0.82	0.25	<0.05
Moose	16.92**	0.12	13.50**	0.99	0.32	<0.05	16.32**	0.45	NA ^c	NA ^c	0.11	<0.05
Small mammal	14.91**	0.46	15.26**	0.61	0.10	0.14	1.14**	0.50	0.97**	0.55	0.12	<0.05
Insect	-1.18	1.43	0.39	1.19	0.10	0.14	0.46	0.46	0.88	0.54	0.07	0.20

^a Coefficient estimated from GLM.

^b Model fit assessed based on correlation between predicted values fitted via GLM and observed dependent variable values. Models with best fit ($\alpha = 0.05$) are in bold.

^c Moose was not detected in scat samples collected in the mountains and on reclaimed mines.

* $\alpha = 0.05$.

** $\alpha = 0.10$.

Table 3

Variation in biomass ingested by grizzly bears in west-central Alberta, Canada, April–October 2009 and 2010. Diet was assessed by estimating species-specific biomass available to bears from feeding sign at GPS location clusters and scat analyses employing correction factors. Whenever possible, corrections incorporated season, age and sex of prey. Reclaimed mines were withheld as the reference category in all models run.

Food category	GPS						Scat					
	Fth		Mt		Model fit ^b		Fth		Mt		Model fit ^b	
	β_i^a	Robust SE	β_i^a	Robust SE	Correlation coefficient	P_{corr}	β_i^a	Robust SE	β_i^a	Robust SE	Correlation coefficient	P_{corr}
Plant												
Berry	15.38**	0.59	16.26**	0.60	0.11	0.10	1.18*	0.62	1.49**	0.66	0.10	0.06
Graminoid	-2.08**	0.62	-2.68**	1.07	0.29	<0.05	-0.53**	0.23	-1.06**	0.32	0.18	<0.05
Native forb	0.48	0.64	-0.19	0.84	0.08	0.25	-0.24	0.50	-0.27	0.68	0.03	0.64
Non-native forb	-3.85**	0.67	-3.91**	1.05	0.62	<0.05	-1.43**	0.26	-1.85**	0.38	0.36	<0.05
Root	15.65**	0.31	17.65**	0.31	0.47	<0.05	0.31	0.31	1.61**	0.34	0.34	<0.05
Animal												
Deer & Bighorn	-0.45	0.40	-1.40**	0.58	0.17	<0.05	0.21	0.48	-0.74	0.61	0.11	0.05
Elk	2.04**	0.61	1.47**	0.69	0.20	<0.05	2.00**	0.70	-0.12	0.90	0.24	<0.05
Moose	17.26**	0.57	14.50**	1.14	0.32	<0.05	15.66**	0.48	NA ^c	NA ^c	0.10	0.06
Small mammal	15.48**	0.27	15.89**	0.46	0.10	0.14	1.09	0.66	0.67	0.74	0.10	0.07
Insect	-1.18	1.43	0.01	1.28	0.07	0.28	-0.00	0.53	-0.28	0.62	0.03	0.56

^a Coefficient estimated from GLM.

^b Model fit assessed based on correlation between predicted values fitted via GLM and observed dependent variable values. Models with good fit ($\alpha = 0.05$) are in bold.

^c Moose was not detected in scat samples collected in the mountains and on reclaimed mines.

* $\alpha = 0.05$.

** $\alpha = 0.10$.

species/genera consumed by bears, including 5 berry, 12 herbaceous, 1 root, 5 ungulate, as well as 7 taxonomic groups encompassing 1 plant, 4 small mammals, 1 bird and 1 insect (Table S.2). Overall, the top three occurring food items consumed by bears and located via cluster visitation were *Hedysarum* spp. roots (22.2%), elk (11.3%) and deer (10.2%).

Based on GPS location cluster visitation, graminoids and non-native forbs (*Trifolium/Melilotus* spp. and *Medicago* spp.) were more likely to be used by bears (Table 2) and contribute biomass (Table 3) when clusters were on reclaimed mines compared to outside mines (Fig. 3). *Hedysarum* spp. roots were more likely to be excavated by bears (Table 2) and contribute biomass (Table 3) when clusters were outside mines than on mines.

Moose and elk were more likely to occur at clusters (Table 2) and contribute biomass to bear diet (Table 3) outside mines compared to reclaimed mines (Fig. 4). Deer and bighorn were more likely to be found at clusters (Table 2) and contribute biomass to diet (Table 3) on mines than in the mountains (Fig. 4).

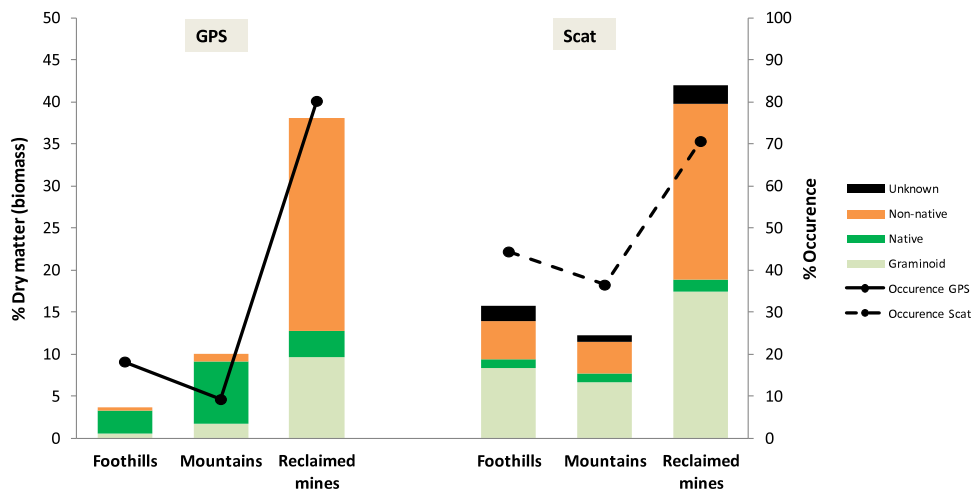


Fig. 3. Herbaceous diet of grizzly bears in west-central Alberta by land designation, using two methods. The primary vertical axis represents % biomass whereas the secondary vertical axis is % occurrence of herbaceous food items relative to total items in scat. Sample sizes (number of items/taxonomically identifiable subitems) were much larger for the scat method ($n_{\text{foothills}} = 223/1535$; $n_{\text{mountains}} = 73/559$; $n_{\text{reclaimed mine}} = 116/940$) compared to GPS field visitation ($n_{\text{foothills}} = 30/\text{NA}$; $n_{\text{mountains}} = 6/\text{NA}$; $n_{\text{reclaimed mines}} = 57/\text{NA}$).

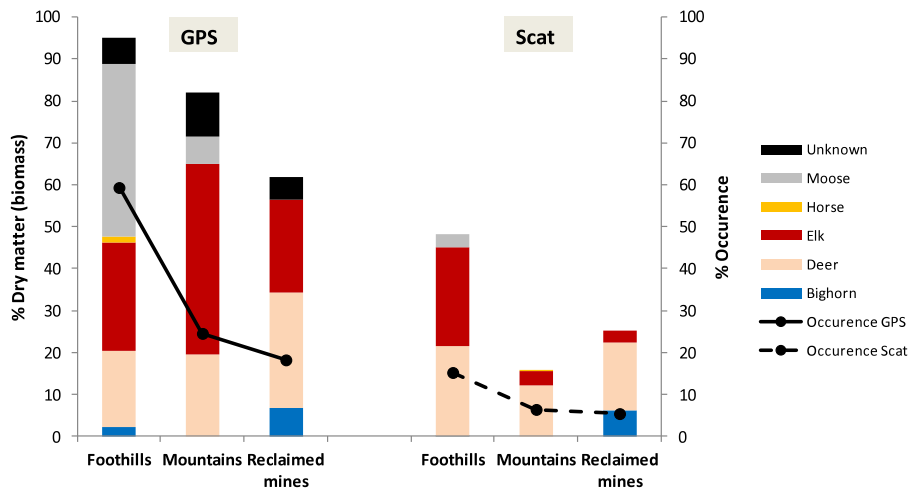


Fig. 4. Ungulate consumption by grizzly bears in west-central Alberta by land designation, using two methods. The primary vertical axis represents % biomass whereas the secondary vertical axis is % occurrence of ungulates relative to total items in scat. With the exception of subitems, sample sizes (number of items/taxonomically identifiable subitems) were comparable for scat analysis ($n_{\text{foothills}} = 77/1276$; $n_{\text{mountains}} = 13/208$; $n_{\text{reclaimed mine}} = 9/133$) and GPS field visitation ($n_{\text{foothills}} = 98/\text{NA}$; $n_{\text{mountains}} = 16/\text{NA}$; $n_{\text{reclaimed mines}} = 13/\text{NA}$).

3.3. Diet estimation through scat analysis

We collected and analyzed 331 scat samples, found 866 broad food items and selected 6877 subitems for taxonomical identification. Only 20.9% of scats had a single food item, with most scats (90.3%) having 1–4 items (331 scats; range 1–7). We identified 32 species or genera, including 14 berry, 6 herbaceous, 1 root, 5 ungulate, 6 small mammal, along with 5 taxonomic groups comprised of 1 plant, 2 small mammal and 2 insect (Table S.2). Similar to cluster data, the principal items occurring in bear scat was *Hedysarum* spp. roots (21.5%). However, the second and third most common items in scat were represented by plant, not animal matter: graminoids (19.4% of items; 25.1% of subitems) and clovers, *Trifolium/Melilotus* spp. (15.6% of items; 17.3% of subitems).

Similar to the patterns identified with GPS clusters, graminoids and non-native forbs were more likely to occur more frequently (Table 2) and contribute biomass (Table 3) to the scat samples collected on mines than outside mines (Fig. 3), whereas roots were more likely to occur more frequently in scat samples collected outside mines than on reclaimed mines (Table 2). Root biomass was more likely to be high in scat samples from the mountains than those from mines (Table 3). In addition, native forbs were more likely to occur in scat samples from mines than from outside mines (Table 2; Fig. 3), with the reverse pattern observed for berry occurrence (Table 2).

Table 4

Variation in grizzly bear food availability by land designation. Availability was assessed by sampling presence/absence of major bear foods in 20 × 20 m plots ($n_{\text{foothills}} = 494$; $n_{\text{mountains}} = 225$; $n_{\text{reclaimed mines}} = 166$). Reclaimed mines were withheld as the reference category in all models run.

Food category	Fth		Mt		Wald ^b		Link test ^b		
	β_i^a	Robust SE	β_i	Robust SE	χ^2	df	P_{Wald}	P_{hat}	P_{hatsq}
Plant									
Berry	3.79**	0.28	1.56**	0.22	188.35	2	<0.05	<0.05	1
Graminoid	0.81**	0.35	0.57	0.40	5.33	2	0.07	0.94	1
Native forb	1.44**	0.20	0.69**	0.23	62.49	2	<0.05	<0.05	1
Non-native forb	-1.48**	0.19	-2.75**	0.27	111.90	2	<0.05	<0.05	1
Root	1.06**	0.37	2.15**	0.37	51.11	2	<0.05	0.11	1
Animal									
Deer & Bighorn	-1.20**	0.19	-0.72**	0.21	41.39	2	<0.05	<0.05	1
Elk	-0.59**	0.019	-0.44**	0.21	10.04	2	<0.05	0.74	1
Moose	1.46**	0.41	0.80*	0.45	17.20	2	<0.05	0.70	1

^a Coefficient estimated from logistic regression.

^b Models with good fit ($\alpha = 0.05$) are in bold.

* $\alpha = 0.05$.

** $\alpha = 0.10$.

Moose and elk were more likely to occur more frequently in bear scat samples from the foothills compared to those from reclaimed mines (Table 2; Fig. 4). Scat samples from the foothills were more likely to contain higher biomass of elk compared to samples from mines (Table 3; Fig. 4).

3.4. Food availability

With the exception of marginal differences in graminoid occurrence between land designations, all models showed locational differences in bear food presence ($\alpha = 0.05$; Table 4). Location was a particularly relevant predictor for half of the food occurrence models ($P_{\text{hat}} < 0.05$), specifically berry, native forb, non-native forb and deer/bighorn models. Berries, native forbs, *Hedysarum* spp. roots and moose were least likely to be present on reclaimed mines. Conversely, non-native forbs, deer, bighorn and elk were most likely to be present on mines.

As anticipated, reclaimed mines had considerably lower herbaceous species richness (5.3 ± 3.8 species) than foothills (8.9 ± 4.8 species) and mountains (8.2 ± 4.1 species). Differences in richness were recorded for mines compared to foothills (Two-sample Wilcoxon rank-sum, $z = -8.65$, $df_1 = 166$, $df_2 = 494$, $P < 0.05$), mines compared to mountains (Two-sample Wilcoxon rank-sum, $z = -6.96$, $df_1 = 166$, $df_2 = 225$, $P < 0.05$) but not for foothills and mountains (Two-sample Wilcoxon rank-sum, $z = 1.31$, $df_1 = 494$, $df_2 = 225$, $P = 0.19$).

4. Discussion

Mine reclamation in the otherwise predominantly forested foothills and mountains in our study area resulted in habitat openness (Cristescu et al., 2011), dominance of non-native vegetation and low plant species richness. Reclaimed mines support large ungulate populations (BWT, 2010) particularly elk and bighorn sheep likely because of concentrated forage sown as part of reclamation. Mines also might serve as predator refugia because high visibility in open habitats allows early predator detection (Kie, 1999; Ripple and Beschta, 2004).

We demonstrated that grizzly bears on reclaimed mines consume large biomasses of non-native forbs and graminoids and to a much lower extent native plants. Munro et al. (2006) also found graminoids and the non-native *Trifolium* spp. to be an important part of bear diet in the region six years before our work, but did not detect a greater overall dominance of non-native herbaceous plants in bear diet compared to native forbs. Non-native herbaceous foods lose nutritional value in the fall (Morgantini and Hudson, 1989; Alldredge et al., 2002; Wagner and Peek, 2006), when bears move primarily outside mines (Cristescu et al., 2011). Bears use mines primarily during summer (Cristescu et al., 2012b), with mines making up to 43% of individual bear home ranges (Cristescu et al., 2011). By consuming herbaceous material on mines, bears have become an integral part of ecological processes and ecosystem succession for this particular type of industrial disturbance.

Hedysarum spp. roots are a key grizzly bear food in the Rocky Mountains (Zager and Jonkel, 1983; Weaver et al., 1996) and similarly to Munro et al. (2006), we found that roots were the primary bear food in the mountains, where they were most available. Unlike brown bear populations in Spain (Naves et al., 2006) and Greece (Paralikiidis et al., 2010), which rely on hard masts (acorns) in the fall, in many North American systems berries are an important energy source for grizzly bears in preparation for winter denning (Weaver et al., 1996; Welch et al., 1997) and least berry consumption in our study occurred on mines, a pattern reflective of berry availability.

A high proportion of meat in bear diet results in increased body mass (Hilderbrand et al., 1999) and is associated with increased reproductive success (Stringham, 1990; Bartareau et al., 2011). Unlike bear populations with access to salmon such as those on the North American West coast (Mowat and Heard, 2006) or Hokkaido Island in Japan (Matsubayashi et al.,

2014), bears in our study system fed exclusively on non-marine sources of protein including a variety of small mammals, primarily ground squirrels. However, the latter made a small contribution to total ingested biomass, especially as compared to bears in the Arctic (Gau et al., 2002). Ants also contributed little biomass to bear diet, unlike for brown bears in Scandinavia (Swenson et al., 1999), black bears (Noyce et al., 1997) or sloth bears (Joshi et al., 1997) which are more myrmecophagous. Bears acquired most animal protein from consuming ungulates, particularly in the foothills, a similar finding to Munro et al. (2006). In the latter study the authors identified moose as the main ungulate consumed by bears (83%), followed by deer (16%) and elk (1%), and did not distinguish mammalian species consumed by bears other than based on 54 field visited ungulate carcasses. Using data from 127 ungulate carcasses and 2357 unique hairs from scat identified in the lab, we found that on reclaimed mines bears consumed deer, elk and bighorn sheep, with the latter species not detected in the Munro et al. (2006) study. Deer and bighorn sheep are more likely to occur on mines, but our pellet data did not allow differentiation between these two species. Using direct visual counts, an independent survey found 74 mule deer and 480 bighorn sheep on the larger reclaimed mine in our study area (BWT, 2010). Because bears consumed more deer than bighorn sheep biomass but deer were present in lower numbers than bighorn sheep, we can conclude that bears selected for deer on mines. Bighorn sheep use of open habitats with high visibility combined with flocking behavior and presence of escape terrain (Risenhoover and Bailey, 1985) renders this species less vulnerable to predation on reclaimed mines than the more solitary deer which cannot access the artificial escape terrain custom designed for bighorns (MacCallum and Geist, 1992).

Perhaps the most noteworthy difference in 2009–2010 ungulate diet compared to 2001–2003 was the substantial increase in elk consumption by bears in the region. Although elk are most available on mines compared with outside mines, large group sizes, vigilance and ease of predator detection in open grasslands (Hebblewhite et al., 2005) characteristic of mines make elk difficult to capture and elk numbers on the largest reclaimed mine in the study area increased from 145 individuals in 2001 to 277 in 2009 (BWT, 2010). Outside mines and particularly in the foothills, bears are effective predators of elk calves, with kills located under the cover of forest (Cristescu et al., 2014). In Yellowstone National Park bears also effectively predate on elk calves, with predation success depending on time since calving (Gunther and Renkin, 1990). Based on field evidence at GPS location clusters visited in the field, scavenging on cougar and wolf kills is an important meat acquisition strategy by grizzly bears in our study area.

We propose that reclaimed mines function as a source of bighorn sheep, elk and possibly mule deer for the surrounding landscape. While reclaimed mines provide feeding opportunities for grizzly bears, ungulates were least consumed on mines as compared to foothills and mountains. Similar to Scandinavia (Swenson et al., 2007) and Alaska (Ballard et al., 1990) where moose are an important component of bear diet, in our study area moose dominated bear diet in the foothills. In contrast, reclaimed mines had the lowest moose availability likely due to rarity of moose browsing material, and we found no evidence of bears feeding on moose on mines.

In our study it is possible that scat analysis underestimated biomass of moose consumed by bears because of relatively low values of the scat correction factors for moose. These values were modified from Hewitt and Robbins (1996) following the approach of Dahle et al. (1998), based on our expectation that bears would ingest large amounts of hair at moose carcasses they scavenged because of depletion of meat before bear arrival at the site. In our study system, if bears were highly effective at detecting wolf- and cougar-killed moose, then they would be ingesting large quantities of meat and less hair.

Another potential bias in estimating prey composition from scat comes from scat collection at preferential feeding sites. While sampling scat randomly avoids such bias, collection of scat encountered along transects, trails or roads produces lower sample sizes and does not allow inferences on habitat features associated with the actual feeding site. In addition, sampling along linear features may raise other biases, such as over-representation of herbaceous material grazed by bears on road right-of-ways, or under sampling from individuals that avoid trails or roads. Collection of scat at GPS location clusters allowed a direct comparison of the two diet estimation methods and gut retention time likely removed some of the potential bias in collection, with items in scat representing what the bear had ingested before cluster formation. However, gut retention might have affected our scat analysis by land designation, with some scats collected on mines possibly reflecting bear diet in the vicinity of mines. With median gut retention times ranging from approximately 6 h for berries to over 14 h for meat (Elfstrom et al., 2013), combined with the ability of bears to move large distances and a relatively small area of reclaimed mine landscape, we found it necessary to assess how reflective scat samples collected on reclaimed mines were of locations where the foraging occurred. We achieved this by tallying number of individual bear-specific GPS radiocollar hourly locations occurring in a 50-m radius around each scat sample collected on mines, provided they were within 15 h of the last location within this given radius. Based on these calculations we were able to estimate that bears spent on average 72% of time on reclaimed mines and 28% in the area neighboring mines within the 15-h temporal window (median time outside mines = 20%, 1st and 3rd quartiles time outside mines = 0% and 53%). Bears therefore spent a majority of time on mines within our specified spatio-temporal constraints, which supports our scat analyses by land designation. While gut retention time might still influence our results particularly for foods with high retention, the above-mentioned assessment was overall conservative because it utilized gut retention time for meat, which is higher than retention of vegetative matter.

For optimal description of composition and biomass of complex facultative carnivore diets we recommend scat analysis in conjunction with GPS cluster visitation, an approach that is also increasingly applied for diet estimation of wild canids (Morehouse and Boyce, 2011) and felids (Bacon et al., 2011; Tambling et al., 2012). Cluster visitation becomes particularly important in the case of diets with high proportion of meat, such as grizzly bears in our study system. Cluster investigations

can be used to refine scat analysis, such as through improved estimation of prey biomass by incorporating prey sex and age recorded during cluster visitation. This information is not available from microscopic analysis of hair in scat. In addition, cluster visitation allows estimation on percentage of hair ingested by the predator and thus informed choice of correction factors for meat consumption. Without field knowledge of amount of hair consumed, estimates of meat biomass ingested by grizzly bears can vary 15-fold (Hewitt and Robbins, 1996).

Because of low reproductive rates, grizzly bear populations are likely the least resilient of all Rocky Mountains large carnivores (Weaver et al., 1996), but our results suggest that this species may be more adaptable than previously thought. Despite this behavioral ability to adapt to change, persistence of bears is linked to availability of seasonal food sources and their presence on the landscape occurs in the context of large wilderness areas. Close proximity to protected areas with minimal human activity likely buffered the effects of mining on bears, as the animals were able to move outside mines to exploit certain foods unavailable on mines. The almost exclusive consumption of ungulates in forested areas (Cristescu et al., 2014) suggests that original tree cover should be maintained whenever possible during mining to enhance ungulate hunting opportunities for bears. Planting willows (*Salix* spp.) and dwarf birch (*Betula nana*) on reclaimed mines could accelerate ecological succession while encouraging use of these sites by moose, which would thereby become available to bears on mines. In addition, planting berries and *Hedysarum* spp. as part of reclamation may encourage use of mines in all seasons, but law enforcement would be recommendable to decrease the risk of illegal hunting on these predominantly open landscapes especially during ungulate hunting seasons, when firearms are a common occurrence. During our study the reclaimed mines had strictly regulated human access along designated trails, with land-use options once the mines have been fully reclaimed including maintenance of access restrictions, or allowing recreational activities more freely. Increased human recreational activity on reclaimed mines could result in bear avoidance, or continued use of reclaimed areas at the risk of enhanced possibility for bear–human encounters. Overall, substantial consumption of non-native plants and ungulates that we documented calls for incorporating these foods into planning schemes designed to minimize risk of bear–human conflict. These considerations along with potentially greater risk of bear–human conflict associated with concentrated food resources (Kavcic et al., 2015) highlight the need for land-use planning and access management that incorporate protection of reclaimed mines and wildlife using mines following mine closure.

While bears might in the short term be benefitting from feeding on mines, it would be useful to monitor long-term effects of food consumption on the fitness of adult bears and their offspring. In particular, plant species used for reclamation purposes are often chosen because of good capacity for bioaccumulation, and could therefore contribute toxic elements to bears and other wildlife ingesting them. If toxicity is a concern then temporary fencing could be considered to limit consumer access to the site. Fencing might also limit dispersal of non-native plant seeds by bears from within reclaimed mines to outside the mined area, but would come at the cost of limiting dispersal of native plants from wilderness areas to the mine sites.

Brown bears have evolved to easily adapt to naturally occurring changes in food resources, as illustrated by their broad diet patterns across geographic and environmental variability (Bojarska and Selva, 2011). We showed for an industrially reclaimed landscape that grizzly bears adjusted their feeding patterns in response to anthropogenic habitat change by shifting their diet to exploit novel availability of foods. While concerns over the consequences of industrial development are legitimate, much of the impact is associated with road development. Protected landscapes including reclaimed areas can provide resources to support grizzly bears, and access management to decrease direct mortality from shooting bears along human access features is key to bear population persistence.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.gecco.2015.06.007>.

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