Grizzly bear ungulate consumption and the relevance of prey size to caching and meat sharing

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Prey consumption forms a large part of prey-handling time, and knowledge of where prey is ingested can inform management of predator—prey systems. Safeguarding habitats that promote prey consumption could enhance populations of facultative or obligate carnivores of conservation concern. We investigated habitat characteristics at 124 sites where radiocollared adult grizzly bears, *Ursus arctos* ($N = 9$) consumed ungulates, and we contrasted these sites with paired random sites. We developed a priori models incorporating the potential effects of ungulate and plant food distribution as well as risks of detection by humans and other carnivores on consumption site choice, and evaluated which factors best explain grizzly bear food-caching behaviour. Ungulates were consumed in forested areas, close to edges, and where horizontal cover was high, whereby vegetation impeded visibility of the ungulate carcass. Distance to roads had no effect on the distribution of prey consumption sites, but carcasses were further from trails than expected. Models incorporating presence/absence of key non-ungulate bear foods had little weight of evidence ($w_i \leq 0.01$). Food-caching behaviour did not appear to be related to variation in resource availability or risk of food spoilage but was significantly influenced by prey size. Although bears chose sites that minimized detection risk, spent more time at larger carcasses and cached 75.9% of ungulates, 50% of consumption sites had other carnivore sign, which was more likely to be present at large carcasses.
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To avoid food shortage and store food securely, some animals have developed caching as an evolutionary strategy integral to foraging behaviour (Smith & Reichman, 1984). In mammals, caching has been documented for various species, such as Arctic fox, *Vulpes lagopus* (Careau, Giroux, & Berteaux, 2007; Careau et al., 2008), badger, *Taxidea taxus* (Michener, 2000), otter, *Lutra lutra* (Lanszki, Molnar, & Molnar, 2006) and wolverine, *Gulo gulo* (Wright & Ernst, 2004). In theory, caching should preserve food for later use while minimizing detection by competitors. In the case of food caching by predators, scavenging by other carnivores probably diminishes the future reward of food caching, and other aspects could also affect the benefits of caching.

One explanation for the occurrence of caching behaviour relates to food consumption time, stating that caching is more likely for resources that take a long time to consume (Careau et al., 2007). Alternative explanations consider caching to be a strategy used for securing food during resource pulses (Careau et al., 2008) or during

harsh environmental conditions associated with food shortage (Lanszki et al., 2006). On the other hand, animals may cache food to avoid food spoilage, which is more likely when ambient temperatures and humidity are high, such as at low elevations and on moist sites (Bischoff-Mattson & Mattson 2009). Investigations on determinants of caching as well as caching effectiveness have seldom been performed, particularly for large carnivores in forested environments where direct observations are difficult. Moreover, basic knowledge about the choice of habitat where meat is consumed and the duration of prey consumption is also scarce for large carnivores because of their wide-ranging patterns, and because of monitoring and safety challenges.

Because human activities have the potential to alter animal behaviour profoundly (Caro & Sherman, 2012), researchers working at the interface of behaviour and conservation often want to know if and how wildlife behaviour is affected by humans (Blumstein & Fernández-Juricic, 2004). When large carnivores are among the wildlife potentially affected, understanding their behaviour is necessary to mitigate risk of conflict with humans. For example, if prey consumption by carnivores is lengthy and occurs in areas with human access, it could lead to conflict with people, which is more likely for carnivores that defend carcasses such as African lions,

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Panthera leo (Kissui, 2008) or grizzly bears, *Ursus arctos* (Quigley & Herrero, 2005). Although carnivores can adjust behaviourally to reduce risk of encounters with humans (Valeix, Hemson, Loveridge, Mills, & Macdonald, 2012), longer consumption times for solitary predators such as cougars, *Puma concolor* (Knopff, Knopff, Warren, & Boyce, 2009) may set these animals/individuals more at risk of conflict at the consumption site than group-living carnivores that have shorter consumption times (Webb, Hebblewhite, & Merrill, 2008). Improved knowledge of habitats where carnivores consume prey along with prey consumption times can be used proactively to prevent dangerous encounters, such as by implementing restrictions on human access.

Being an essential component of predator–prey relationships, prey consumption time (kill handling time/time spent at kill) is also important theoretically (Holling, 1959; Merrill et al., 2010), allowing parameterization of optimal foraging and patch residency models for carnivores. Technological advancements enable straightforward estimation of consumption time from GPS radiotelemetry (Merrill et al., 2010). Studies that employ this technology can decrease the bias associated with documenting prey consumption time by direct observations in open environments or during daytime only (Knopff et al., 2009; Webb et al., 2008).

Because of wide-ranging movements, seasonal habitat requirements, low reproductive rates and risk of conflict with people (Mattson & Merrill, 2002; Weaver, Paquet, & Ruggiero, 1996), the grizzly bear has declined throughout much of its range. In west-central Alberta, grizzly bears are designated as threatened and persist at low densities at the interface between largely pristine mountainous areas and heavily developed foothills. Similar to other interior populations of grizzly bears (Jacoby et al., 1999; Mowat & Heard, 2006; Zager & Beecham, 2006), ungulates form an important part of the diet of Alberta bears in late spring and early summer, during ungulate calving and fawning (Munro, Nielsen, Price, Stenhouse, & Boyce, 2006), with ungulate consumption occurring throughout the active season (outside denning) (Mattson, 1997; Wilmers, Crabtree, Smith, Murphy, & Getz, 2003).

Despite their importance to the demography of ungulate populations (Middleton et al., 2013), we know very little about the behaviour of brown bears at kill sites, particularly in forested environments. Records of caching by grizzly bears and their Eurasian conspecifics have been opportunistic and sparse. For example, Elgmork (1982) identified 16 meat caching sites by brown bears in Scandinavia, where the bears dug the ground and dragged litter, moss and debris on top of prey. Barker and Derocher (2009) observed two caches of broad whitefish, *Coregonus nasus*, made by grizzly bears in barren habitat in Canada.

Our goals were to (1) evaluate competing hypotheses for explaining the motivation behind caching behaviour, (2) identify habitats conducive to ungulate consumption by grizzly bears, (3) investigate consumption times by grizzly bears and (4) describe inter- and intraspecific ungulate carcass sharing by grizzly bears and other carnivores. We made the following predictions. Bears should (1) be more likely to cache large prey, because a large carcass contains sufficient meat to warrant storage and later consumption (prey size hypothesis), (2) be more likely to cache during the seasonal resource pulse of ungulate calving, because calves are available during a limited period and their storage would enable feeding at later times (resource pulse hypothesis), (3) be less likely to cache at lower elevations, under low vertical cover and on wet sites to avoid spoilage of meat (resource spoilage hypothesis), and (4) preferentially consume ungulates in areas with high probability of presence of ungulates and other bears foods (in high forage areas) but consume carcasses away from roads, trails and habitat edges, and where horizontal cover is high, to minimize detectability by other predators. We also predicted that (5) consumption

time would be longer for larger-bodied ungulates, because more meat intake is generally available from larger carcasses, and (6) cached ungulates would be less likely to be visited by predators other than bears compared to ungulates that were not cached, because caches are presumably difficult to locate; however, larger carcasses should be more likely to be visited by nonbear carnivores, because large prey is difficult to conceal entirely through caching.

METHODS

Study Area

The 3200 km^2 study area was located in west-central Alberta, Canada at the interface between the eastern slopes of the Rocky Mountains and foothills (Fig. 1). Elevation and ruggedness are greater in the western section, which is mountainous, whereas the eastern section is characterized by rolling hills. The predominant natural land cover is coniferous forest composed of white (*Picea glauca*), black (*Picea mariana*) and Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*), balsam (*Abies balsamea*) and subalpine fir (*Abies lasiocarpa*). Mixed and deciduous forests also occur in the study area, primarily at lower elevations and on sunny south facing slopes, and include trembling aspen (*Populus tremuloides*) and balsam polar (*Populus balsamifera*).

Grizzly bear foods in the study area are diverse (Nielsen, McDermid, Stenhouse, & Boyce, 2010), with the primary foods being sweetvetch roots (*Hedysarum* spp.), a variety of herbaceous plants and berries as well as ungulates, including elk, *Cervus elaphus*, moose, *Alces alces*, white-tailed deer, *Odocoileus virginianus*, mule deer, *O. hemionus*, and bighorn sheep, *Ovis canadensis* (Munro et al., 2006). Grizzly bears coexist with wolves, cougars and American black bears, *Ursus americanus*, as well as mesocarnivores such as coyotes, *Canis latrans*, Canada lynx, *Lynx canadensis*, and red fox, *Vulpes vulpes*.

The eastern side of the study area is primarily Crown (public) land with human activities including extensive recreation (All Terrain Vehicles, hunting, horseback riding, mountain biking, hiking and camping), as well as open-pit coal mining, forest harvesting, oil and gas development. The western side is primarily protected provincially (Whitehorse Wildland Park) and federally (Jasper National Park), with a small amount of Crown lands, two reclaimed coal mines, one operational mine and a cement quarry with employees commuting daily. Only one permanent human settlement (Cadomin) with a population of 60 is present in the study area. Although no data were available on levels of human use, density of linear access features is high (Nielsen, Boyce, Stenhouse, & Munro, 2002), the area receives recreational users from nearby urban centres, and off-highway vehicle use is perceived as unsustainable (McFarlane, Stumpf-Allen, & Watson, 2007). The area is bordered to the north by a major highway, and the Crown lands have a complex network of roads and trails used by recreationists, oil, gas and forestry companies.

Data Collection

During spring/early summer and autumn 2008–2010 we captured and deployed remotely downloadable GPS radiocollars (Telus UHF; Followit, Lindesberg, Sweden) on adult grizzly bears. With assistance from the Foothills Research Institute Grizzly Bear Program (Hinton, Alberta), we used baited culvert traps, aerial darting from a helicopter and limited leg-hold snaring (Cattet et al., 2008) and attempted to capture bears on reclaimed mines, protected areas (Whitehorse Wildland Park) and Crown lands to reduce bias in sampling bears that might have used only one land designation. All bears were captured and handled according to
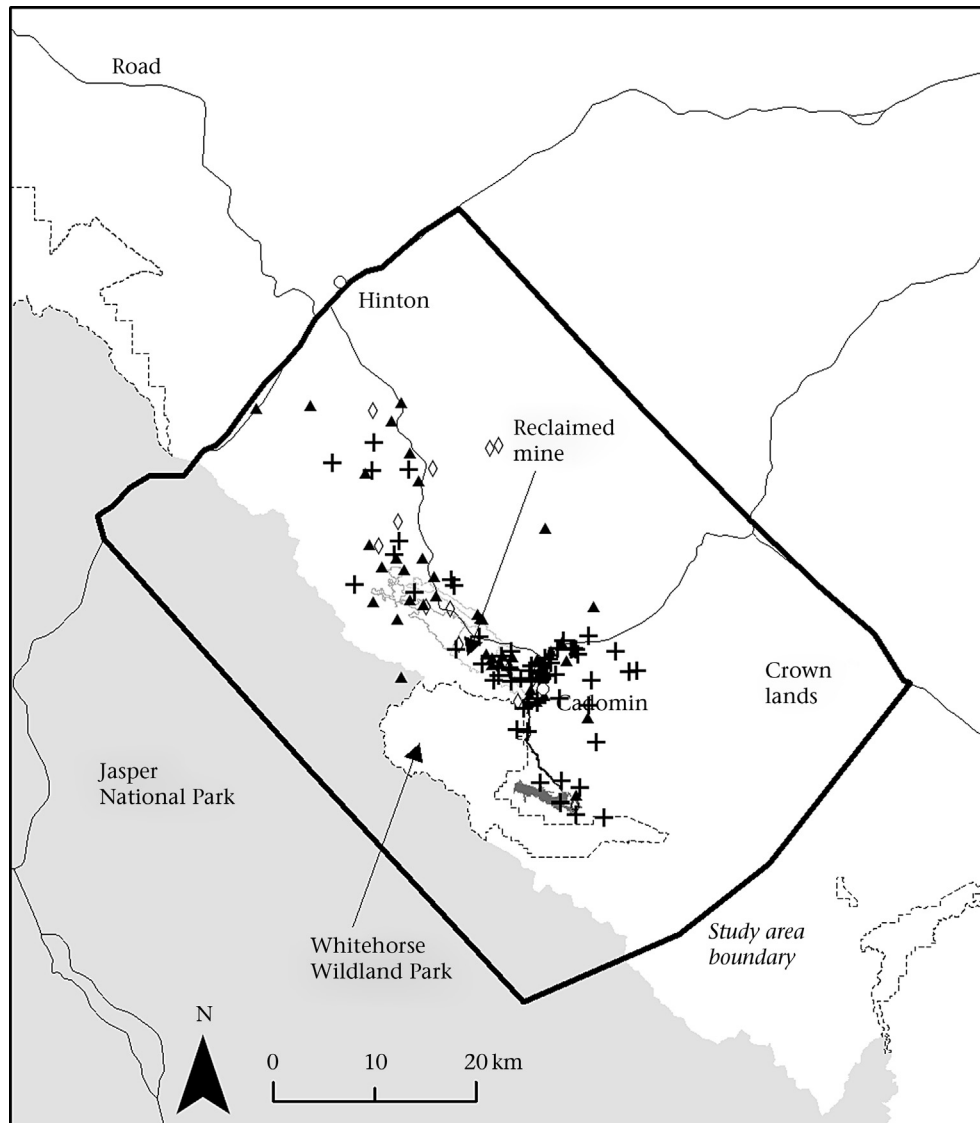
Figure 1. Study area for grizzly bear ungulate consumption in west-central Alberta, Canada, with colour-coded land designations: Crown lands (white shading), protected areas (National and Wildland parks, light grey shading), reclaimed mines (light grey boundary and white shading) and active mine (dark grey shading). Confirmed sites where radio-collared grizzly bears consumed ungulates during 2009–2010 are illustrated by black crosses (N = 124).

University of Alberta and University of Saskatchewan protocols for Animal Care and Use.

We programmed radiocollars to acquire a location every hour, 24 h/day, during 15 March to 1 December when the bears were mostly outside their winter dens. Every month of the monitoring period we radiolocated individual bears from the ground or from fixed-wing aircraft or helicopter. To acquire GPS locations remotely from the radiocollars, once per month we approached each bear within a safe distance that minimized disturbance to the animal, triangulating its position if on foot (>200 m). To identify clusters from monthly GPS data sets, we used a cluster algorithm developed by Knopff et al. (2009), which we modified for 1 h location inputs and 50 m distance between the two initial points in a cluster. We used a minimum cutoff of 3 h for cluster duration, and we field visited the four clusters with the largest number of locations from each bear each month (May–November), along with randomly selected clusters other than the four largest. We uploaded cluster geometric centroids to hand-held GPS units to access cluster locations by truck, ATV, helicopter, and on foot. We visited clusters

41 ± 15 days after the first fix in the cluster because of safety concerns (bears defending or returning to carcasses) and to avoid disturbing the animals, and because of logistical limitations. This is comparable to field visits within 45 days of cluster occurrence in the Webb et al. (2008) wolf study and lower than 201 days from cluster occurrence in the Anderson and Lindzey (2003) cougar study.

At each cluster site we recorded whether a cache was present and the carcass information, habitat characteristics and occurrence of other carnivores and ungulates (see Supplementary material). We replicated the search for a carcass and the habitat-sampling protocol described in the Supplementary material at one (available) location 300 m away on one of four cardinal directions from the consumption site, with subsequent directions being chosen clockwise (north, east, south and west, respectively). We chose 300 m based on movement rates of adult bears (annual mean step length 269 m/h outside winter denning; range 175–367, based on 11 adult bears monitored in the area before this study).

Caching of Ungulates

We used logistic regression to test hypotheses on factors that could influence the occurrence of caching behaviour (caching = 1; no caching = 0). Caching behaviour hypotheses tested included the resource pulse hypothesis, prey size hypothesis, meat spoilage hypothesis, and combinations thereof. For the resource pulse hypothesis, we generated a categorical variable for peak of neonate ungulate consumption by bears (peak = 1; outside peak = 0). The 'peak' was identified visually as the highest bar in a frequency histogram of biweekly young-of-year ungulate consumption by collared bears. In the case of the prey size hypothesis, we calculated prey biomass for each carcass (prey size variable detailed in the Supplementary material). For the meat spoilage hypothesis we used a combination of vertical cover, site severity index (SSI) and elevation also described therein, assuming that spoilage would be more substantial at shaded sites (high vertical cover) with high humidity and greater temperature (indexed by lower elevation). We were unable to test another classical hypothesis (kleptoparasitism risk) because we did not have an estimate of the distribution of predators/scavengers in the region before a kill was made, nor did we know which predator had made the kill.

To eliminate uncertainty over assigning ungulate cause of death to predation or scavenging, we used all data with associated prey biomass information to model cache occurrence ($N = 112$), pooling data for males and females to achieve model convergence. Because bears probably scavenged larger prey, but ungulate biomass available would have generally been lower at scavenging than at predation sites, thereby potentially affecting a bear's motivation to cache, we included a squared term for prey size in all models that incorporated the prey size hypothesis. We screened variables for correlations, assessed collinearity and used robust clustering to control for heteroscedasticity). We excluded variables that were highly correlated (Pearson $|r| > 0.6$) from the same model and examined potential collinearity between linear predictor variables by using variance inflation factors (VIF) diagnostics. When VIF scores of individual variables were greater than 10 or when the mean of all VIF scores was considerably larger than 1, the respective variables were classified as collinear and were not used in the same model structure (Chatterjee & Hadi, 2006). We used robust clustering estimation of standard errors to account for unequal sample sizes (sites with caches present) between different bears (Nielsen et al., 2002). This technique calculates the variance using the Huber–White sandwich estimator (Huber, 1967; White, 1982) allowing independence between bears (clusters) but not necessarily within clusters, resulting in parameter estimates and significance levels unbiased by individual variation.

We used Akaike's Information Criterion corrected for small sample size (ΔAIC_c) and Akaike weights (w_i) to select the best models (Anderson, Burnham, & Thompson, 2000; Burnham & Anderson, 1998) from the set of candidate models. We evaluated model accuracy using the receiver operating characteristic (ROC) area under the curve (AUC) recommended by Boyce, Vernier, Nielsen, & Schmiegelow (2002) for used–unused designs, where values of 0.9 and higher indicate high model accuracy, values of 0.7–0.9 indicate good model accuracy and values of 0.5–0.7 indicate low model accuracy (Manel, Williams, & Ormerod, 2001; Swets, 1988). We used the absolute minimum of the difference between sensitivity and specificity values to estimate the optimal probability cutoff for classifying presence/absence of a cache at a consumption site (Liu, Berry, Dawson, & Pearson, 2005).

Modelling Habitat Where Grizzly Bears Consume Ungulates

We used discrete choice models (Cooper & Millspaugh, 1999) estimated using conditional logistic regression to assess the factors (covariates) that influenced bear choice of sites for ungulate consumption. The matched design with one random site associated with each ungulate consumption site was a trade-off between sampling availability and maximizing field visits of clusters that were potential ungulate consumption sites. In conditional logistic regression, the contrast in the binary response variable is constrained by values of 1, and in this instance, the available location (0) was conditioned to occur 300 m away from the location selected for site consumption (1). Our data fit an used–unused sampling design with 0% contamination (sensu Keating & Cherry, 2004), as we found no evidence of consumption of ungulates at any of the paired random locations. Similar to the caching occurrence analyses, we pooled ungulate consumption data across males and females because of sample size limitations. To avoid potential uncertainty in distinguishing between predation and scavenging events, we used all data, irrespective of ungulate cause of death ($N = 124$).

We created a priori models for ungulate consumption site choice based on ecological relevance of various factors that might influence where consumption sites occur. Habitat models tested multiple hypotheses and combinations thereof, which considered ungulate occurrence, risk of carcass detection by bears and other carnivores as well as human risk. Ungulate occurrence was recorded directly based on presence of pellet groups, as well as indexed by vertical cover and distances to edge and stream. Risk of carcass detection by bears was assumed to be higher if other bear foods (herbaceous material, roots and berries) also were present at the site. More broadly, risk of detection by carnivores was considered based on confirmed presence of carnivore scat, as well as assumed to be influenced by visibility (indexed by horizontal cover) and proximity to linear access features used by carnivores (distances to road and trail). Human risk was assumed to be greater in areas with high visibility (low vertical and horizontal cover) and closer to human access routes (distances to road and trail).

We screened variables for correlations, assessed collinearity and used robust clustering to control for heteroscedasticity. In the case of highly correlated variables, we estimated models with each of the correlated variables one at a time and kept the variable that best improved fit. These rules resulted in dropping stand basal area and forest age as they were highly correlated with each other and with vertical cover. We also excluded the habitat classification according to the seven classes assigned during field visits (see Supplementary material), because of high correlations with vertical cover, and we ran a separate conditional logistic regression model to estimate selection coefficients for different habitat classes using a categorical variable for habitat as the predictor variable. Pooled barren land and herbaceous class was chosen as the reference category in contrasting habitat classes.

We tested the effects of quadratic terms on model performance and included squared terms for distance to nearest road, nearest trail, nearest edge and nearest stream to account for nonlinearities in the predictor variables. We ranked candidate models using ΔAIC_c and Akaike weights, used ROC to evaluate model accuracy and estimated optimal probability cutoff to classify presence/absence of an ungulate carcass.

Grizzly Bear Ungulate Consumption Time and Carcass Size

To estimate the number of hours that bears spent within 50 m of a carcass, we applied the cluster algorithm parameterized as

described under Data Collection, recognizing that the calculation has up to 2 h of error corresponding to the uncertainty around the first and last locations in a cluster. The data set for this analysis included 112 consumption sites representing pooled predation and scavenging events with known prey biomass, given that for 12 sites biomass was unknown. We used linear regression to investigate whether larger prey resulted in overall longer consumption time by bears, with log ungulate biomass as predictor and log time at carcass as dependent variables. Because the analysis was univariate we were able to fit separate regression models for each bear sex, but needed to pool data for single females and females with cubs because of sample size limitations.

Intra- and Interspecific Meat Sharing

To investigate whether radiocollared bears shared ungulate carcasses, for all consumption sites ($N = 124$) we plotted the data in ArcMap and used Spatial Statistics tools to identify whether GPS locations of two or more individuals occurred within a 50 m buffer around a carcass. We used carnivore presence based on scat to assess carcass sharing by grizzly bears with predators in the study area, pooled as 'other carnivores' (wolf, cougar and coyote). We performed logistic regression with cache presence as the predictor variable and presence of other carnivores (scat present = 1, scat absent = 0) as the dependent variable to assess whether cached ungulates were less likely to be visited by carnivores. To investigate the relationship between carcass size and carnivore presence, we used logistic regression again, with ungulate biomass as the predictor variable and presence of other carnivores as the dependent variable. Only sites with available ungulate carcass biomass estimates ($N = 112$) were included in the latter two analyses.

RESULTS

Grizzly Bear Data Set

We captured and deployed GPS radiocollars on 12 adult grizzly bears. Two males removed their collars within 1 month of capture and nine of the 10 remaining bears consumed ungulates during the monitoring period. The nine bears included in statistical analyses comprised females ($N = 6$) and males ($N = 3$) that were monitored for 383 bear-days during hypophagia (mean 7.1 bears), 629 bear-days in early hyperphagia (mean 11.6 bears) and 618 bear-days in late hyperphagia (mean 7.5 bears), with seasonal delineation following Nielsen, Boyce, and Stenhouse (2004). The sample size ($N = 9$ adult bears) represents a substantial proportion of the grizzly bear population in the 3200 km^2 study area, which has a population density of 4.79 bears/1000 km^2 (Boulanger et al., 2005).

During May−November 2009 and 2010 we located a total of 128 sites where radiocollared bears had consumed animal matter. Four sites at which bears had consumed birds ($N = 2$), a hare and a mustelid were excluded from analyses because of insufficient sample size for small prey kill sites and because our focus was on sites where bears had consumed ungulates ($N = 124$). Of the 124 ungulate consumption sites that represented our sample size, pooled across years and seasons (mean ± SE = 14 ± 4 sites/bear, range 2−43), the majority of sites had one ungulate carcass, but 3.2% had two carcasses. When two carcasses were present, prey biomass calculation included the summed biomasses for both carcasses.

Caching of Ungulates

Caches were present at the majority (75.9%) of bear consumption sites under analyses, with the rest (24.1%) not having caches.

We did not locate multiple caches, and in the rare ($N = 4$) cases where two ungulate carcasses were present at a site, they had both been hidden in the same cache.

The bear that made the kill or first scavenged at the site revisited the carcass the majority of the time (76.8%). Carcasses were revisited regardless of whether they had been cached or not (logistic regression: Wald $\chi_1^2 = 0.57$, $P = 0.45$), but larger prey were more likely to be revisited (logistic regression: Wald $\chi_1^2 = 4.01$, $P < 0.05$). Bears were not more likely to cache during the peak of ungulate resource use (calving/fawning/lambing season), which fails to support the resource pulse hypothesis (Table 1). Also, bears were not more likely to cache to minimize meat spoilage, refuting the resource spoilage hypothesis (Table 1). However, bears were more likely to cache medium-sized ungulates (logistic regression: Wald $\chi_2^2 = 14.35$, $P < 0.001$), thereby partially supporting the resource size hypothesis for caching. The predicted relative probability of caching fitted an inverse quadratic function (Fig. 2).

Only the prey size and a combination of prey size and resource pulse models received support (Table 1). However, the confidence interval of the peak neonates parameter estimate overlapped zero in the model combining prey size and resource pulse, strengthening the finding that prey size is a key predictor of caching behaviour. The prey size model received good weight of evidence ($w_i = 0.60$) whereas the prey size and resource pulse model received modest weight ($w_i = 0.27$), with all other models having lower weight of evidence compared with the null model ($w_i = 0.04$) (Table 1). The prey size model had good fit ($P < 0.001$), explained 7.9% of the deviance, had moderate predictive power (AUC = 0.68) and an optimal probability cutoff at 77%. A linear term and a squared term for prey size were the only variables in the top model, whereas most other models were more complex.

Ungulate Consumption Habitat

The majority of sites were located on Crown lands (84.7%), and the small proportion of sites on reclaimed mines (10.5%), in protected areas (3.2%) and on active mine leases (1.6%) precluded analyses by land designation. Consumption of ungulates was significantly higher in moderate and dense coniferous forests than in all other habitat classes (Table 2), but the model had low predictive power (AUC = 0.65). This overall pattern held for mined landscapes, with 11 out of 13 ungulate consumption sites on reclaimed mines in moderate and dense coniferous forest, and two carcasses on an active mining lease, also in dense coniferous forest.

Of the 12 candidate models tested, two of the top three included ungulate presence as well as detection by scavengers, and the third was an ungulate presence-only model (Table 3). All other models including those for detection by humans or other bears received very little ($7 \leq \Delta_i < 10$) or no support ($\Delta_i \geq 10$), with three models having larger Δ_i than the null model. The top three models received substantial weight of evidence (combined $w_i = 0.95$), with the best model having the largest weight ($w_i = 0.76$). The percentage deviance explained varied between the different models, with the largest amount of deviance explained by the best model (14.5%) (Table 3). The top three models had good predictive power and fit, with optimal probability cutoffs being 50% (Table 4).

The top models had intermediate complexity ($K_i = 6$, 5 and 7, respectively; Table 3). Consumption sites were more likely to occur in areas used by ungulates, and models in which we replaced the ungulate presence variable with a species-specific variable (e.g. moose presence rather than overall ungulate presence) had lower fit than generic ungulate presence models, hence final models included pooled ungulate data (Table 4). Models that included vertical cover had better fit than those in which vertical cover was replaced by stand basal area or forest age. Vertical cover and

Table 1
Model structure and deviance for candidate models describing multiple hypotheses for presence/absence of a cache at grizzly bear ungulate consumption sites in west-central Alberta, Canada

Hypotheses	Variables	K_i	$-2LL$	%Deviance	AIC_c	Δ_i	w_i
R_{size}	**Prey size+Prey size^2**	**3**	**114.0**	**7.9**	**120.6**	**0.0**	**0.60**
R_{size}+R_{pulse}	Prey size+Prey size^2+Peak neonates	4	113.1	8.6	122.2	1.6	0.27
Null		1	123.7	0.0	125.8	5.2	0.04
R_{size}+$R_{spoilage}$	Prey size+Prey size^2+V_{cover}+SSI+Elevation	6	111.6	9.8	126.0	5.4	0.04
R_{size}+R_{pulse}+$R_{spoilage}$	Prey size+Prey size^2+Peak neonates+V_{cover}+SSI+Elevation	7	110.3	10.8	127.7	7.1	0.02
R_{pulse}	Peak neonates	2	123.6	0.1	127.9	7.2	0.02
$R_{spoilage}$	V_{cover}+SSI+Elevation	4	120.9	2.3	130.0	9.4	0.01
R_{pulse}+$R_{spoilage}$	Peak neonates+V_{cover}+SSI+Elevation	5	120.9	2.3	132.6	12.0	0.00

R_{size}: resource (ungulate prey) size; R_{pulse}: resource pulse (peak in ungulate neonates); $R_{spoilage}$: resource spoilage; V_{cover}: vertical cover; SSI: site severity index; %Deviance: percentage of deviance explained. Model assessment was done by ranking Akaike's Information Criterion values, corrected for small sample size, AIC_c (Δ_i) and Akaike weights (w_i) describing model likelihood. Model complexity (number of parameters) is given by K_i. Models are presented in decreasing ranking order, with the top model given in bold. Models with Δ_i larger than the null model are at the bottom of the list.

distance to nearest habitat edge were important predictors in two of the top three models, and in both cases consumption sites were more likely to occur in areas with high cover and close to edge.

Horizontal cover was an important predictor covariate in the top two models, although only for the second model did the confidence interval for the coefficient estimate not overlap zero. Distance to nearest trail was important in one top model, with consumption sites being more likely to occur away from trails. Distance to nearest stream was included in the third-ranked model, but the confidence interval for its coefficient overlapped zero.

Grizzly Bear Ungulate Consumption Time and Carcass Size

Average consumption time at ungulate carcasses was at least 24 h for males (mean $\pm$ SE = 40.3 $\pm$ 8.7 h, range 3–249) as well as females (24.0 $\pm$ 2.7 h, range 3–125), with the latter having shorter time at carcasses. Time spent at carcasses increased with carcass size for both males ($r = 0.449$, residual $df = 28$, $P < 0.05$) and females ($r = 0.234$, residual $df = 80$, $P < 0.05$; Fig. 3), and males used larger ungulates (212.9 $\pm$ 31.6 kg) than females (106.8 $\pm$ 15.0 kg).

Intra- and Interspecific Meat Sharing

Based on the radiocollar data, we documented 16 instances of use of ungulate carcasses by multiple bears, representing 12.9% of our sample of carcass sites. In 15 of these instances, two bears used
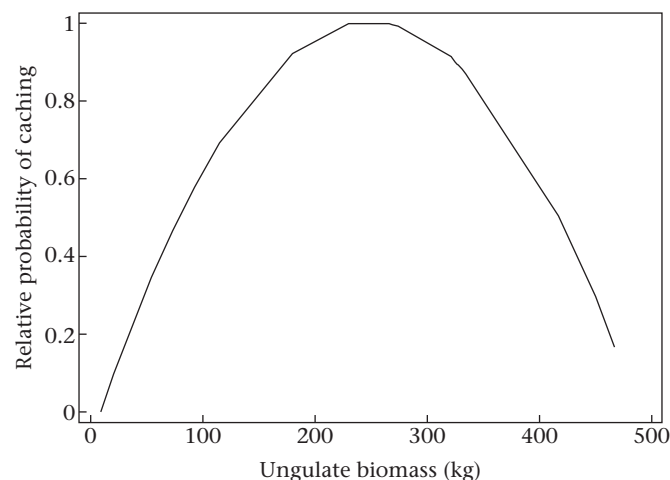
the carcass, whereas in one instance three different bears fed on an adult whitetail deer carcass. Of these instances, nine involved use of a carcass by a male and a female, six involved use of a carcass by two females and one involved one male and two females. Only in two cases did two bears use the carcass concurrently, feeding on it simultaneously for 2 h and 5 h, respectively, and both cases involved a male and a female. We did not document any use of the same carcass by two males or direct displacement of the first bear by the second bear. For consumption sites used by multiple bears, the second bear arrived at the carcass 210.8 $\pm$ 35.2 h (range 3–400 h) after the first bear.

We found scat of other carnivores at 50% of sites used by bears for ungulate consumption. Cached prey was more likely to have carnivore scat in the vicinity (logistic regression: Wald $\chi^2_1 = 5.75$, $P < 0.05$), and carnivores other than grizzly bears were more likely to be present at ungulate carcasses used by bears if the carcasses were large (logistic regression: Wald $\chi^2_1 = 5.74$, $P < 0.05$).

DISCUSSION

In severe environments that have variable productivity and inconsistent availability of food, resource pulses can trigger caching behaviour (Careau et al., 2008). For grizzly bears inhabiting foothills and eastern slopes of the Rocky Mountains, the number of prey caches was unrelated to the period of highest ungulate availability (i.e. the period shortly after calving). Medium-sized ungulates were more likely to be cached than the smallest or largest ones, which only partially supports the prey size hypothesis. Although small

Figure 2. Relative probability of grizzly bear caching of ungulate carcasses in west-central Alberta, Canada as a function of carcass size ($N = 112$ ungulate consumption sites), based on the top model for caching occurrence.

Table 2
Estimated coefficients (β_i), robust SEs and 95% CIs for a categorical habitat model describing the probability of sites where grizzly bears consumed ungulates in west-central Alberta, Canada

Variable	β_i	Robust SE	95% CI	
			Lower	Upper
Habitat class				
Shrub	0.944	0.757	−0.539	2.428
Mixed forest	1.318	1.382	−1.390	4.026
Open conifer	0.930	0.608	−0.262	2.122
Moderate conifer	**1.671**	**0.691**	**0.317**	**3.026**
Dense conifer	**1.690**	**0.636**	**0.444**	**2.936**
Model evaluation	χ^2	df	P	
Wald test	24.33	5	<0.001	
ROC (AUC)	0.65			
Cutoff probability	0.50			

ROC: receiver operating characteristic; AUC: area under the curve. Estimates for which the confidence interval (CI) did not overlap zero are given in bold. Model fit, predictive power and cutoff probability also are reported. Pooled barren land and herbaceous habitat classes were withheld as a reference category.

Table 3
Model structure and deviance for candidate models (resource selection functions) describing habitat at sites where grizzly bears consume ungulates in west-central Alberta, Canada

Hypotheses	Variables	K_i	−2LL	%Deviance	AIC_c	Δ_i	w_i
Ungulate+Scavengers	**Ungulate+V$_{cover}$+H$_{cover}$+Edge+Edge^2**	**6**	**146.9**	**14.5**	**161.4**	**0.0**	**0.76**
Ungulate+Scavengers	Ungulate+H$_{cover}$+Trail+Trail^2	5	153.3	10.8	165.0	3.6	0.13
Ungulate	Ungulate+V$_{cover}$+Edge+Edge^2+Stream+Stream^2	7	149.0	13.3	166.4	5.0	0.06
Humans	V$_{cover}$+H$_{cover}$+Road+Road^2+Trail+Trail^2	7	151.9	11.6	169.3	7.9	0.01
Ungulate+Bears	Ungulate+Herb+Root+Berry	5	158.3	7.9	170.0	8.6	0.01
Ungulate+Scavengers	Ungulate+V$_{cover}$+H$_{cover}$+Edge+Edge^2+Trail+Trail^2	8	149.6	13.0	170.1	8.7	0.01
Ungulate	Ungulate	2	166.9	2.9	171.2	9.8	0.01
Ungulate	Ungulate+Edge+Edge^2	4	162.6	5.4	171.7	10.4	0.00
Ungulate+Scavengers	Ungulate+Edge+Edge^2+Trail+Trail^2	6	158.9	7.6	173.4	12.0	0.00
Null		1	171.9	0.0	174.0	12.6	0.00
Ungulate+Bears	Ungulate+Herb+Root+Berry+Edge+Edge^2+Stream+Stream^2	9	152.2	11.4	176.0	14.7	0.00
Ungulate+Bears	Ungulate+Herb+Root+Berry+Road+Road^2+Trail+Trail^2	9	154.3	10.3	178.1	16.7	0.00
Humans	Road+Road^2+Trail+Trail^2	5	167.6	2.5	179.3	18.0	0.00

Ungulate: ungulate presence; Scavengers: detection by scavengers, including bears and other predator species; Bears: detection by bears; Humans: detection by humans; V$_{cover}$: vertical cover; H$_{cover}$: horizontal cover. Distance to edge (Edge), trail (Trail), stream (Stream) and road (Road). Presence of herbaceous material (Herb), roots (Root) and berries (Berry). %Deviance: percentage of deviance explained. Model assessment was done by ranking Akaike's Information Criterion values, corrected for small sample size, AIC_c (Δ_i) and weights (w_i) describing model likelihood. Model complexity (number of parameters) is given by K_i. Models are presented in decreasing ranking order, with the top model given in bold. Models with Δ_i larger than the null model are at the bottom of the list.

ungulates were probably mostly consumed at one sitting, thereby eliminating the need for caching, young-of-the-year calves were not always entirely consumed by grizzlies, and other carnivores were sometimes present at carcasses despite being cached, unlike what Garneau, Post, Boudreau, Keech, and Valkenburg (2007) suggested. The largest ungulates would have been difficult to cache, or were scavenged, making their scattered remains too energetically costly to cache.

Caching is more common in temperate regions than in tropical regions, because food spoilage in the latter works against caching efficiency (Smith & Reichman, 1984). In temperate regions, cougars cache at low elevation where temperatures are higher (Bischoff-Mattson & Mattson, 2009). Caching may be influenced by site humidity, because moisture favours microbial activity but also might increase detection by olfactory predators (Conover, 2008; Smith & Reichman, 1984), given that scent travels better under moist conditions (Conover, 2008). However, we found no evidence for the resource spoilage hypothesis, possibly because of rapid consumption times (before food spoilage) or insensitivity to spoiled food.

In the context of caching, pilfering is the removal of cached food items by an individual that is not the cacher (Vander Wall & Jenkins, 2003). Meat subsidy to conspecifics through reciprocal pilferage (Vander Wall & Jenkins, 2003) plays a role in energetic loss and gain. Reciprocal pilfering may resemble cooperative behaviour but is in reality driven by individual selfishness (Grodzinski & Clayton, 2010). In our study, only 12.9% of carcasses were used by more than one bear and 75% of intraspecific pilferage occurred during the 2.5-month-long brown bear mating season (Steyaert, Endrestol, Hacklaender, Swenson, & Zedrosser, 2012). We did not document displacement of a bear by another bear at carcass sites, but because we did not radiocollar the entire population of grizzly bears, these observations should be interpreted with caution given that we found more than one adult bear bed at 35.8% of 67 ungulate consumption sites that had beds visible.

Table 4
Estimated coefficients (β_i), robust SEs and 95% CIs for the top three models describing the probability of occurrence for grizzly bear ungulate consumption sites in west-central Alberta, Canada, as assessed by Akaike's Information Criterion values, corrected for small sample size, AIC_c (Δ_i) and weights (w_i)

Variable	Model 1				Model 2				Model 3			
	β_i	Robust SE	95% CI		β_i	Robust SE	95% CI		β_i	Robust SE	95% CI	
			Lower	Upper			Lower	Upper			Lower	Upper
Ungulate												
Ungulate	**0.524**	**0.237**	**0.059**	**0.990**	**0.656**	**0.241**	**0.184**	**1.128**	**0.544**	**0.197**	**0.158**	**0.930**
V$_{cover}$	**0.014**	**0.005**	**0.004**	**0.025**					**0.018**	**0.006**	**0.006**	**0.030**
Edge	**−0.021**	**0.005**	**−0.031**	**−0.010**					**−0.022**	**0.005**	**−0.321**	**0.012**
Edge^2	**0.073***	**0.019***	**0.035***	**0.111***					**0.084***	**0.017***	**0.051***	**0.116***
Stream									−0.001	0.002	−0.004	0.002
Stream^2									0.216[†]	1.850[†]	−3.400[†]	3.840[†]
Scavengers												
H$_{cover}$	0.177	0.100	−0.018	0.372	**0.302**	**0.110**	**0.087**	**0.518**				
Trail					**0.005**	**0.001**	**0.003**	**0.008**				
Trail^2					−5.220[†]	3.010[†]	−11.100[†]	0.693[†]				
Model evaluation	χ^2	*df*	*P*		χ^2	*df*	*P*		χ^2	*df*	*P*	
Wald test	29.18	5	<0.001		24.09	4	<0.001		53.36	6	<0.001	
ROC (AUC)	0.74				0.72				0.73			
Cutoff probability	0.50				0.50				0.50			

Ungulate: ungulate presence; Scavengers: detection by scavengers, including bears and other predator species; V$_{cover}$: vertical cover; H$_{cover}$: horizontal cover. Distance to edge (Edge), stream (Stream) and trail (Trail). Models 1 and 2 are ungulate and detection models, whereas model 3 is an ungulate model. Estimates for which the confidence intervals (CI) did not overlap zero are given in bold. Model fit, predictive power and cutoff probability also are reported. ROC: receiver operating characteristic; AUC: area under the curve.

　* Parameter estimate reported at 10^3 times its actual value.

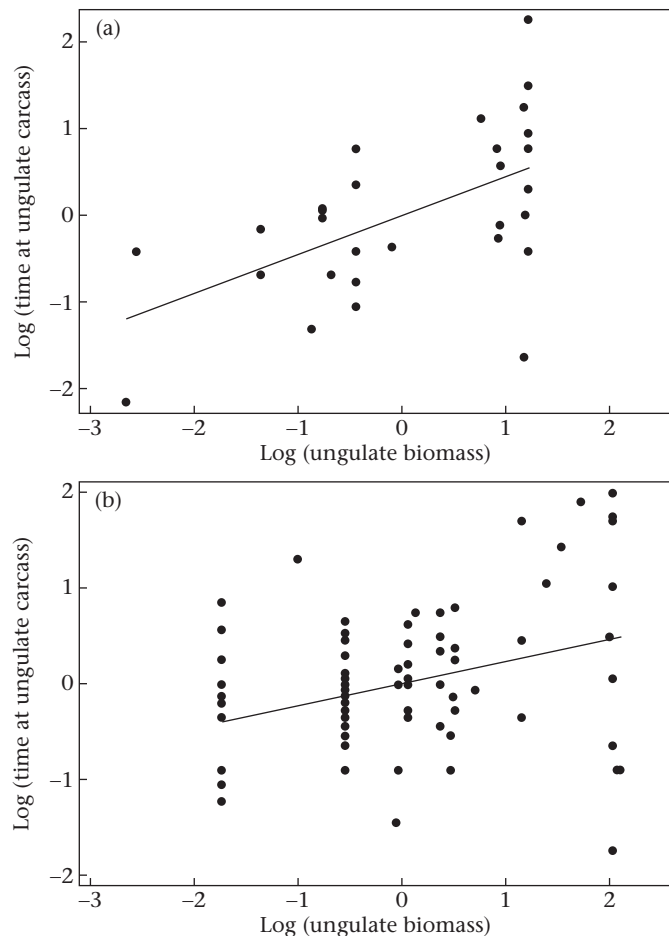　† Parameter estimate reported at 10^6 times its actual value.

Figure 3. Time spent by male (a) and female (b) grizzly bears in west-central Alberta, Canada (2009–2010) at a carcass as a function of carcass size (males: $N = 30$ ungulate consumption sites; females: $N = 82$ ungulate consumption sites).

Many animals have adaptations for caching (Smith & Reichman, 1984). In grizzly bears, it has been speculated that the long claws and large shoulder muscles are adaptations for digging roots, tubers and rodents (Herrero, 1978). Because digging is energetically costly (Vleck, 1979), bears possibly compensate behaviourally by digging when rewards are high (Mattson, 2004). Energetic cost–benefit calculations incorporating energy losses through carcass dragging to a concealed location, carcass caching and kleptoparasitism would be required to assess whether caching of ungulates is associated with a high reward.

In the presence of wind, the odour plume emitted by a carcass will disperse, thereby increasing the chance of a scavenger encountering it (Ruzicka & Conover, 2011). Bears consumed ungulates in areas with high horizontal cover, which decreases detection by visual and possibly olfactory scavengers too, if cover provides shelter from wind. Numerous studies on felids have identified horizontal cover to be a key habitat feature for prey consumption sites in cougars (Logan & Irwin, 1985), Eurasian lynx, *Lynx lynx* (Podgorski, Schmidt, Kowalczyk, & Gulczynska, 2008), tigers, *Panthera tigris*, and leopards, *Panthera pardus* (Karanth & Sunquist, 2000). Dense undergrowth may decrease the movement rates of scavengers, and consumption of carcasses in open areas increases kleptoparasitism (Gorini et al., 2011).

Ungulate carcasses were more likely to be located where ungulate occurrence was highest, close to streams and habitat edges. Distance to stream is an index of importance in riparian habitat (Bowyer, Kie, & Van Ballenberghe, 1998), and in our study area,

species richness of nonwoody plants decreases with increased distance to stream areas ($r_{888} = -0.200$, $P < 0.05$). Moose (Courtois, Dussault, Potvin, & Daigle, 2002) and deer (Laundre, 2010) favour edges because of foraging opportunities. Elk also use edges, trading off high diet quality in open areas for decreased wolf predation risk near edges (Hernandez & Laundre, 2005). Edges can provide hiding opportunities for bears (Nielsen, Boyce, et al., 2004), but they could also channel wind currents and enable faster ungulate carcass detection by other carnivores moving along edges.

The lack of support for models incorporating key bear plant foods suggests that carcass detection by other bears is probably not a major factor in site choice for this low density grizzly bear population. Interestingly, human access along roads did not appear to influence choice of consumption sites, and we recorded scavenging events on hunter kills in the vicinity of roads. Many bears in our study area readily move near to roads or cross roads (Graham, Boulanger, Duval, & Stenhouse, 2010; Roever, Boyce, & Stenhouse, 2010), and vegetative foods associated with some roads can be attractive to bears (Roever, Boyce, & Stenhouse, 2008). Although grizzly bears can benefit from moderate habitat disturbance (Nielsen, Boyce, et al., 2004), trails are a form of disturbance that can displace bears (Kasworm & Manley, 1990). Ungulate consumption sites were more likely to be located far from trails, a potential mechanism to avoid detection by humans or other predators. Facultative scavengers including coyotes and wolves use trails for movements (Latham, Latham, Boyce, & Boutin, 2011; McKenzie, Merrill, Spiteri, & Lewis, 2012; Thornton, Sunquist, & Main, 2004) because of fast displacement and decreased energetic cost along linear features.

Caching did not effectively protect carcasses from other carnivores, which were in fact more likely to be present at cached carcasses than at noncached ones, probably because caching usually involved large prey. Males spent more time at carcasses than females, possibly because of their ability to more effectively intimidate or protect the carcass against other carnivores, or simply because larger carcasses used by males took longer to consume. Consumption of larger ungulates by males suggests that males were capable of killing larger prey and/or of usurping prey killed by competitively inferior predators.

Although grizzly bears spent, on average, more than 24 h at ungulate carcasses, we are uncertain of the interactions occurring at carcass locations. Unlike bears, cougars kill coyotes while defending carcasses (Koehler & Hornocker, 1991). The absence of mesopredator kills at ungulate carcasses used by bears suggests that further research could test whether grizzlies lack effective lethal mechanisms to avoid interference competition at carcass sites. We probably underestimated interspecific carcass sharing because we used scat as an index of occurrence for other carnivores. We attempted to standardize scat detection by including only those sites with less than 25% snow cover and by searching all sites for carnivore scat, including using shovels to dig under snow when present.

Beyond providing insights into evolutionary adaptations and energetic trade-offs, understanding behaviour of grizzly bears at ungulate kill sites can facilitate prevention of conflict with humans. Moreover, identifying habitat characteristics at locations where predators consume prey is important for managing declining populations of predator(s) and/or prey. In Alberta, increases in early seral stage habitats connected to industrial footprints can result in increased forage biomass for ungulates and higher ungulate densities (James, Boutin, Hebert, & Rippin, 2004; Latham, Latham, McCutchen, & Boutin, 2011; Visscher & Merrill, 2009). In contrast, grizzly bears are adversely affected by human activity, which can result in habitat degradation and sinks (Nielsen, Herrero, et al., 2004; Nielsen, Stenhouse, & Boyce, 2006). Because ungulates

form an important part of grizzly bear diet in west-central Alberta (Munro et al., 2006), identification of habitats where bears consume ungulates can inform land use planning to provide opportunities of energy gain for bears while minimizing risky encounters with people. Models to predict ungulate consumption site distribution on the landscape (Nielsen et al., 2010) should strive to incorporate the distribution of important food sources such as elk, which has the highest proportion of occurrence in bear diet in our study area (Cristescu, Stenhouse, & Boyce, n.d.), and also deer (Munro et al., 2006) in addition to moose. For times of the year when consumption of ungulates is expected to be highest (e.g. calving season), restrictions on recreational access could be enforced selectively in habitats where bears are most likely to consume ungulates.

Studies that have attempted to quantify habitat where bears consume ungulates have done so at the coarse scale of categorical habitat (Munro et al., 2006) or by recording the percentage of forest cover (Mattson, 1997; Nielsen et al., 2010) without testing multiple hypotheses on drivers of consumption site choice. We found that forested environments were chosen for ungulate consumption, in accordance with Munro et al. (2006) and Nielsen et al. (2010). This finding highlights the importance of preserving forest patches when modifying landscapes such as through open-pit mining, because treed areas promote meat protein acquisition in grizzly bears. Although we were interested in assessing habitat choice for ungulate consumption on reclaimed mines, we located only 14 carcasses on reclaimed land, which precluded analyses by land designation. The small number of carcasses on mines is likely connected to the relatively small proportion overlap of bear home ranges with reclaimed mines (median <0.2 in all seasons, $N = 8$ bears) (Cristescu, Stenhouse, Symbaluk, & Boyce, 2011).

From a theoretical perspective, the study showed that bears choose sites for ungulate consumption to minimize risk of detection by potential competitors/pilferers. Multiple hypothesis testing showed that caching in grizzly bears is primarily determined by prey size, whereas empirical documentation of ungulate consumption times can parameterize theoretical foraging models. From an applied perspective, the study illustrates how information on animal behaviour can be used to inform management decisions. Knowledge of site characteristics conducive to ungulate consumption enabled suggestions for bear conservation such as maintenance of treed areas to encourage meat consumption (energetic gain), as well as enforcement of human access restrictions in habitats where bears are likely to consume ungulates (human–bear conflict prevention).

In birds it has been suggested that social species that cache are better at locating caches than are solitary species that cache or than noncaching social species (Grodzinski & Clayton, 2010). In carnivorous mammals, further understanding of the relation between predator sociobiology and fluctuation in need for caching through space use and territoriality (Smith & Reichman, 1984) will help improve estimates of prey partitioning and provide insights into how these factors affect consumption rates. In addition, future work could compare habitat choice, consumption times and caching at predation and scavenging sites, more accurately quantify meat sharing, and contrast habitat choice, caching and rates of pilferage of caches in simple systems with those in areas with multiple obligate and facultative scavengers, where subsidies to scavengers might be more complex.

Supplementary Material

Supplementary material for this article is available, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2014.03.020.

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