

Complementary food resources of carnivory and frugivory affect local abundance of an omnivorous carnivore

Scott E. Nielsen, Terrence A. Larsen, Gordon B. Stenhouse and Sean C. P. Coogan

S. E. Nielsen (scottn@ualberta.ca) and S. C. P. Coogan, Dept of Renewable Resources, Univ. of Alberta, 751 General Services Building, Edmonton, AB, T6G 2H1, Canada. SCPC also at: School of Life and Environmental Sciences and the Charles Perkins Centre, Univ. of Sydney, Sydney, NSW, Australia. – T. A. Larsen and G. B. Stenhouse, JRI, Hinton, AB, Canada.

A major unresolved question for omnivorous carnivores, like most species of bears, is to what degree are populations influenced by bottom–up (food supply) or top–down (human-caused mortality) processes. Most previous work on bear populations has focused on factors that limit survival (top–down) assuming little effect of food resource supply. When food resources are considered, most often they consider only the availability/supply of a single resource, particularly marine-subsidized or terrestrial sources of protein (carnivory) or alternately hard or soft mast (frugivory). Little has been done to compare the importance of each of these factors for omnivorous bears or test whether complementary resources better explain individual animal and population measures such as density, vital rates, and body size. We compared landscape patterns of digestible energy (kcal) for buffaloberry (a key source of carbohydrate) and ungulate matter (a key source of protein and lipid) to local measures in grizzly bear *Ursus arctos* abundance at DNA hair snag sites in west-central Alberta, Canada. We tested support for bottom–up hypotheses in either single (carnivory [meat] versus frugivory [fruit]) or complementary (additive or multiplicative) food resources, while accounting for a well-known top–down limiting factor affecting bear survival (road density). We found support for both top–down and bottom–up factors with complementary resources (co-limitation) supported over single resource supplies of either meat or fruit. Our study suggests that the availability of food resources that provide complementary nutrients is more important in predicting local bear abundance than single foods or nutrients (e.g. protein) or simply energy per se. This suggests a nutritionally multidimensional bottom–up limitation for a low density interior population of grizzly bears.

Ecologists have long debated how the abundance and distribution of organisms are regulated and limited (Hairston et al. 1960, Power 1992, Terborgh et al. 2001). Since ecosystems are structured by the amount of energy and nutrients transferred from primary producers through the food chain, many have focused on trophic interactions as primary regulators of ecosystem processes and population dynamics. One school of thought holds that food resources are the primary regulatory control (bottom–up regulation) via competition whereas others consider predation (top–down limitations) to be more important. Perhaps more realistic is that ecosystems may be simultaneously regulated by both bottom–up and top–down factors which differ in their relative strengths among ecosystems and state conditions (Oksanen et al. 1981, Leibold 1989, Hunter and Price 1992).

Large apex predators were not historically thought of being controlled by top–down processes given their high trophic position. However, humans are now the global super-predator affecting the distribution and abundance of apex predators across freshwater, marine and terrestrial ecosystems (Estes et al. 2011). In North America, the grizzly (brown) bear *Ursus arctos* is an omnivorous apex-predator

(carnivore) that has been extirpated from much of its historical range due to persecution and habitat loss (Mattson and Merrill 2002). Human-caused mortality (top–down) is often considered the most important factor regulating grizzly bear populations (Boyce et al. 2001). However, bottom–up factors should not be overlooked given that they are known to influence grizzly bear vital rates (Mattson et al. 1992, Pease and Mattson 1999), population density (Hilderbrand et al. 1999, Pease and Mattson 1999, McLellan 2011), geographic distribution (Mattson and Merrill 2002, Bojarska and Selva 2012), habitat use (Nielsen et al. 2003, 2010), and fitness proxies of body size (McLellan 2011, Nielsen et al. 2013, Erlenbach et al. 2014) and body fat percentage (Robbins et al. 2012). Top–down and bottom–up factors may also be interactive supporting the suggestion that both factors can be simultaneously important. For instance, human-caused mortality in bears increases when food availability is low (especially during the hyperphagic period) as bears may seek anthropogenic food sources (Mattson et al. 1992, Pease and Mattson 1999, Gunther et al. 2004), or when bears forage in areas associated with humans, such as attractive sinks (sensu Nielsen et al. 2006, Northrup et al. 2012). A productive and nutritious natural supply of food can thereby mitigate the

effects of human-caused mortality in bears. This may be why grizzly bears in some populations experiencing high levels of human-caused mortality still maintain high local population density (Mowat et al. 2005, McLellan 2011).

When bottom-up resources are considered for bears, often the focus is limited to individual resources such as meat (Hilderbrand et al. 1999) or fruit (McLellan 2011). Although meat availability is commonly considered a major factor affecting local population size in bears (Hilderbrand et al. 1999), McLellan (2011) demonstrated that much of the positive relationship observed between bear density and the amount of meat in a diet was due to the presence of salmon (marine subsidized resources). In fact, when populations with access to salmon were removed, the relationship between bear density and amount of meat in the diet is negative (McLellan 2011), not positive as what it is typically assumed. This suggests that other resources, such as fruit, may be important determinants of interior populations of grizzly bears (McLellan 2011).

However, simply focusing on one resource or nutritional parameter (e.g. meat) may not be sufficient to resolve these complexities, especially for species like bears with omnivorous diets. There is a growing recognition of the multidimensional nature of animal nutrition, particularly for nutrient interactions since there is evidence that animals require a balanced intake of nutrients from foods in order to optimize their performance (Simpson and Raubenheimer 2012). Indeed, the macronutrients (proteins, carbohydrates, and lipids) required for energy provisioning, as well as other purposes (e.g. lipids for cell membranes, and protein for lean mass), are a driving force behind food selection and foraging behaviour in wild animals (Rothman et al. 2011), likely also including strict predators (reviewed by Kohl et al. 2015).

Studies of macronutrient self-selection in captive bears demonstrate that animals choose diets varying in protein to non-protein (lipid and carbohydrate) energy in proportions that optimize their energy intake and maximize mass gain (Erlenbach et al. 2014). In the wild, macronutrients available to bears are often found in variable environments among a diverse range of potentially complementary foods that vary in availability and nutrient content across both time and space (Nielsen et al. 2010, Mowat et al. 2013, Coogan et al. 2014). Bears must therefore forage across “complimentary landscapes” (Dunning et al. 1992) to obtain high quality food resources. Two foods can be considered complementary when they provide an animal with a blend of nutrients not found in either food alone, and that allow the animal to consume an optimal level of nutrients. Bears in captive trials preferred high lipid intake over carbohydrate when mixing their diets; however, in the absence of lipids bears consumed carbohydrates to reach the same preferred ratio of protein to non-protein energy (Erlenbach et al. 2014). Given the variable nature of environmental conditions and spatial patterns of resources available to grizzly bears, wild bears may be limited in their ability to consume complementary resources reaching optimal diets (Coogan et al. 2014) thereby limiting individual fitness and population abundance.

The purpose of this paper is to test whether local patterns in the abundance of an ‘interior’ grizzly bear populations (i.e. without access to marine resources) is co-limited by the distribution and abundance of two food resources

– fruit and ungulates – which are commonly examined independently, while accounting for a recognized top-down factor affecting survival in bears. Both fruit and ungulate matter are documented as a major component of the seasonal diets of interior grizzly bear populations in the Rocky Mountains of western North America (McLellan and Hovey 1995, Munro et al. 2006, McLellan 2011, López-Alfaro et al. 2015). Importantly, they also provide complementary macronutrients (i.e. carbohydrate from fruit and protein and lipid from ungulates) that may allow bears to optimize their diet and fitness when co-occurring (Coogan et al. 2014, Erlenbach et al. 2014). These contrasting nutritional characteristics (fruit versus meat) allow us to explicitly estimate food abundance and at the same time implicitly account for macronutrient composition. Our co-limitation hypothesis predicts that local abundance in bears should be higher in landscapes having simultaneously higher ungulate and fruit resource supply. We compared this co-limitation hypothesis against traditional single resource hypotheses that suggests resource supply in either meat (Hilderbrand et al. 1999) or fruits (McLellan 2011) alone affect local population density of bears. We test these hypotheses for a population of grizzly bears in west-central Alberta where we have information on local variation in bear abundance and mapped (modelled) abundance of ungulate and fruit resources in units (kcal) that are biologically relevant to measuring population responses.

Methods

Study area

Our study was located in west-central Alberta, Canada (approximate location 53°15′N, 118°30′W) and based around 176 square grid cells that were 7 × 7 km in size (8624 km²; Fig. 1). The study area is mainly public lands managed by the province and zoned for multiple uses with forestry and development from the energy sector (oil, gas and coal mining). The landscape is characterized as the eastern-slopes of the Rocky Mountains with the western border of the study area being mountainous and foothills to the east. Climate is continental with the mountains being colder and having higher average annual precipitation than the foothills. Forests dominate the landscape with lodgepole pine *Pinus contorta* being the most common tree species. Wet sites at moderate to low elevations have stands of black spruce *Picea mariana* and tamarack *Larix laricina*, whereas aspen *Populus tremuloides* and white spruce *Picea glauca* occur in more mesic upland sites at lower elevations. Finally, Engelmann spruce *Picea engelmannii* and subalpine fir *Abies lasiocarpa* forests occur at the highest elevations near treeline. Average grizzly bear density in the area was estimated during the time of study to be 4.79 bears per 1000 km².

Top-down models

Grizzly bear survival in the area is strongly associated with the proximity of roads (Boulanger and Stenhouse 2015). As such, road density is frequently used as a proxy for human-caused mortality since road access increases human–bear interactions leading to higher mortality rates (Benn and

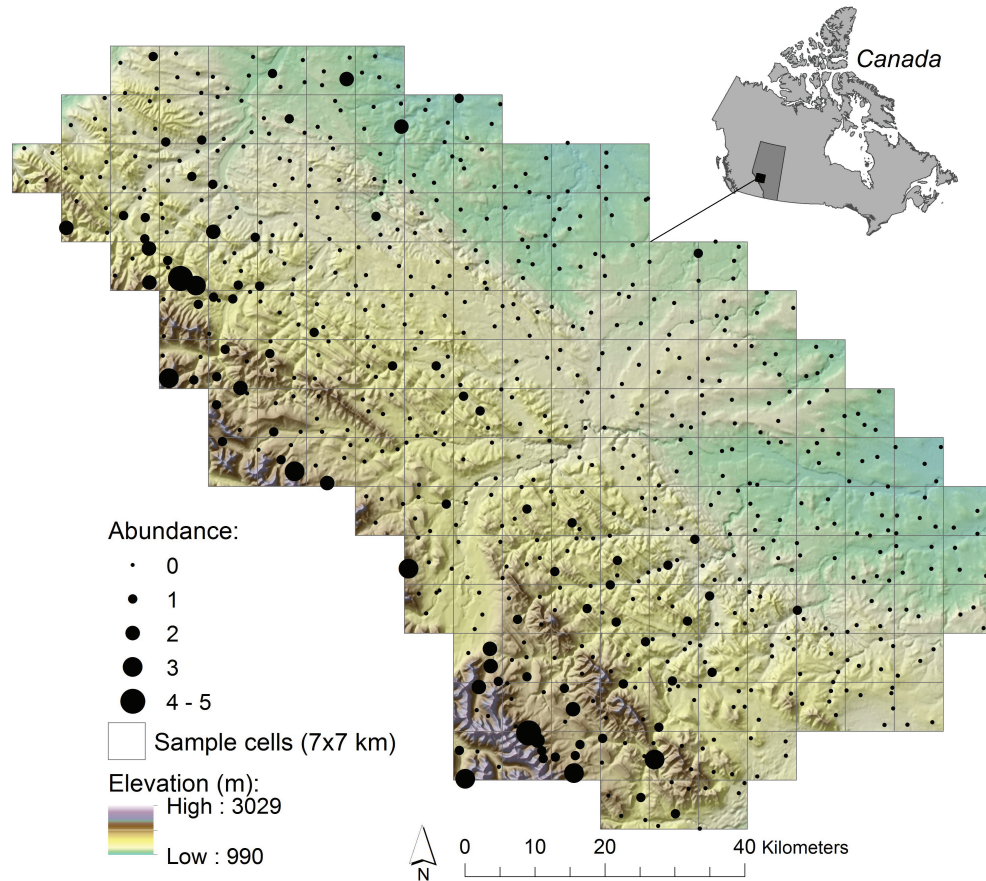


Figure 1. Location and terrain (elevation) of the Yellowhead grizzly bear study area in west-central Alberta, Canada illustrating DNA hair-snag sampling design (7 × 7 km grid), location of hair-snag sites and number of unique grizzly bears detected at a site (size of points) in 2004. Inset map shows location of study area within the Province of Alberta.

Herrero 2002, Johnson et al. 2004, Nielsen et al. 2004a). For example, in west-central Alberta demographic models suggest that stable grizzly bear populations occur in watersheds where road densities are at 0.75 km km⁻² or lower (Boulanger and Stenhouse 2015). For this study we estimated road density at a 7.44-km radius moving window scale representing the average daily movement of female and sub-adult grizzly bears during hyperphagia (Boulanger et al. 2013). Road densities in the area were generally higher in the east than in the west (Fig. 2).

Ungulate models

To represent carnivory resources of ungulate matter, local abundance (population density) of five ungulate species were modelled: moose *Alces alces*, elk *Cervus canadensis*, bighorn sheep *Ovis canadensis*, white-tailed deer *Odocoileus virginianus* and mule deer *Odocoileus hemionus*. Abundance data (counts) were obtained from aerial surveys conducted by Alberta Environment and Sustainable Resource Development (AESRD) for a sample of survey blocks measuring 5' longitude by 5' latitude. Local density of ungulates were estimated for the study area using generalized linear models (GLMs) fit to observed abundances of individual ungulate species using a set of environmental predictors (land cover, land use and terrain; see Supplementary material Appendix 1

for details). Conversions to total biomass were estimated for each species, including neonates, based on average body sizes by sex for each species using a literature review (Supplementary material Appendix 1). Digestible energy (Dig E; kcal kg⁻¹) estimates for ungulates were based on ungulate biomass (kg) estimates. Ungulate biomass estimates were corrected for water and indigestible components using body composition estimates; however, since estimates were not available for some species and age classes, body composition estimates of whole ungulates were modelled using the average percent body composition of moose *Alces alces* minus hide and ingesta (ingesta-free body mass [IFB mass]; Hundertmark et al. 1997). We then applied a digestible energy (kcal kg⁻¹) conversion for meat (Pritchard and Robbins 1990) to estimate ungulate digestible energy using the following equation:

$$\begin{aligned} & \text{whole ungulate biomass (kg)} \times \% \text{ IFB mass} \\ & \quad \times \% \text{ dry matter IFB} \times \% \text{ ash-free} \\ & \text{IFB} \times \text{digestible energy (kcal kg}^{-1}\text{)} \end{aligned} \quad (1)$$

Specifically, percent IFB mass was 88.1, percent dry matter of IFB mass was 34.8, percent ash-free content IFB was 94.9 (100–5.1% ash), and digestible energy was taken as 6920 kcal kg⁻¹. Model predictions of ungulate digestible energy were mapped for each 30 m pixel, but averaged across the landscape in 7.44-km radius moving windows matching daily movement rates of bears in the study area. Given the

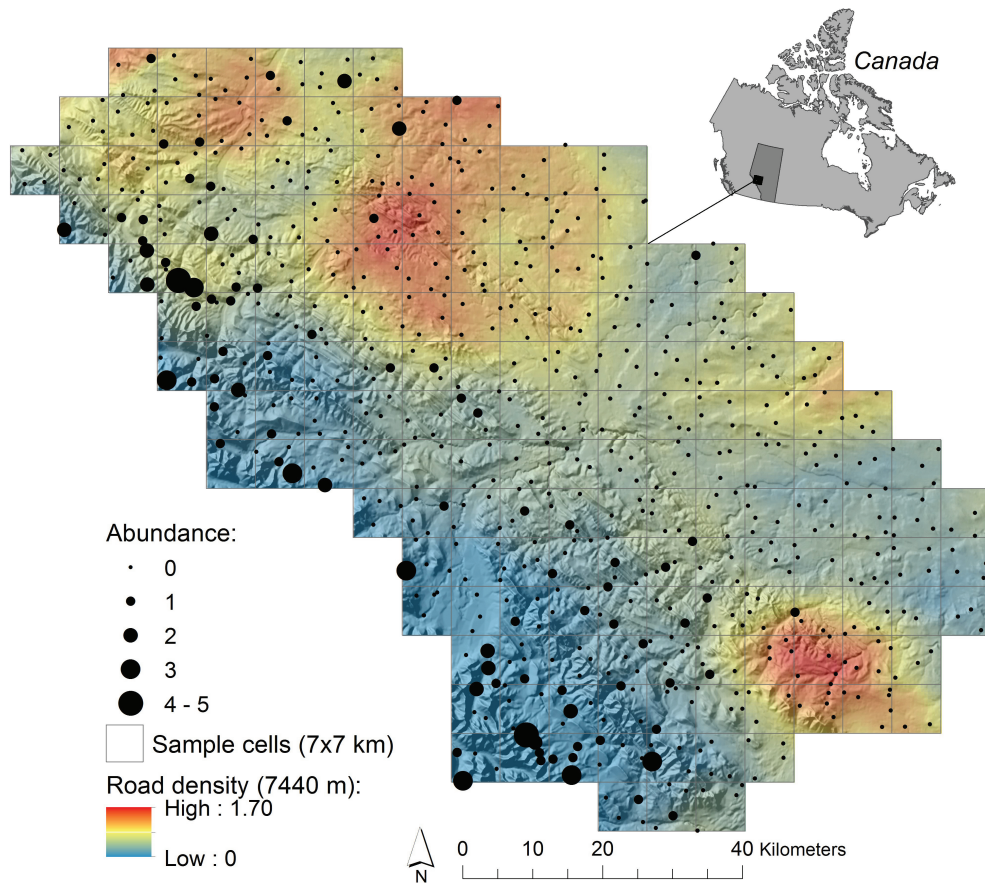


Figure 2. Road density (7.44-km radius moving window) patterns within the Yellowhead study area in west-central Alberta, Canada. Note higher road densities in the north and southeast. Number of unique bears detected at DNA hair snag sites indicated by increasing size of points.

scale at which ungulate resource supply is summarized and the type of data used for assessing local abundance of bears (unique bears at DNA hair snag sites), this approach avoids focus on localized habitat selection behaviours that were associated with use of individual resources patches. Behavioural selection of resources was not the focus of this paper, but rather explaining variation in abundance of bears in an area.

Fruit models

We chose Canada buffaloberry *Shepherdia canadensis* as a representative species to estimate fruit abundance since it is the most common fruit in the region (Nielsen et al. 2010) and consumed most by bears in the study area (Munro et al. 2006). A multi-stage modeling approach was used to estimate the nutritional landscape in digestible energy (kcal) for Canada buffaloberry. Specifically, three sets of model responses representing different measures of buffaloberry were fit using GLMs this included: 1) the distribution (presence/absence) of buffaloberry at a site; 2) shrub abundance (density) conditional on being present; and 3) fruit abundance conditional on being present. Field plot data on buffaloberry presence, shrub abundance and fruit density were used to predict landscape variation in the availability of buffaloberry fruit using environmental spatial predictors. Environmental variables included land cover, climate, ter-

rain, soils, and forest stand measures previously found in the area to be important landscape predictors of buffaloberry distribution (Nielsen et al. 2003, 2010, Roberts et al. 2014). See Supplementary material Appendix 1 for more details on modelling. Following model development, model predictions (distribution, shrub density, and fruit abundance) were mapped at a 30-m resolution in a Geographic Information System (GIS), but averaged across the landscape at a 1.69-km radius (larger radius of 7.44 km was marginally less supported; see Supplementary material Appendix 1) matching the scale of detectability of bears at lured hair-s snag sites (Boulanger et al. 2004). Fruit abundance therefore represents an average landscape-scale resource supply surrounding grizzly bear DNA hair-s snag sites, not localized use of the site itself. Number of fruit per pixel (900 m²) was predicted for the study area during a typical fruiting year of 2001. Fruit abundance was then converted to dry biomass using the dry weight of buffaloberry fruit (Coogan et al. 2014) and further converted to maps of available digestible energy (Dig E; kcal kg⁻¹) using biomass to digestible energy conversion of:

$$\text{Gross energy} \times \% \text{ Digestible energy} \quad (2)$$

Gross energy of buffaloberry fruit was estimated as 4310 kcal kg⁻¹, while percent digestible energy was estimated as 64.5% (Coogan et al. 2014) thereby resulting in 2780 kcal Dig E kg⁻¹ or on a per gram basis of 2.8 kcal Dig E g⁻¹.

We note that bears in the study area consume several different plant foods throughout the active period (e.g. the roots of *Hedysarum* spp. and herbaceous plants) which would provide macronutrients in ratios that may contribute towards a balanced diet (Munro et al. 2006, Coogan et al. 2014). The focus of this study, however, was to test the co-limitation hypothesis of fruit and meat on local patterns in bear abundance based on a priori evidence. Furthermore, both fruit and meat may provide a fundamentally different balance of macronutrients than other plant material, and are likely to be less available to bears in general than are herbaceous plants that are more ubiquitous in availability and thus unlikely to be limiting. Furthermore, patterns of vegetation productivity as measured by maximum values of the natural difference vegetation index (NDVI) demonstrated neutral to negative correlations with ungulate and buffaloberry food supply indicating that our measures of food resource were not simply surrogates for areas of higher vegetation productivity (Supplementary material Appendix 1). Indeed, relationships between NDVI and local bear abundance were negative suggesting that herbaceous resources were not limiting bear density (Supplementary material Appendix 1).

Local patterns in grizzly bear abundance

In 2004, the minimum count of grizzly bears was estimated at each of the 1138 lured hair-slug sites (Fig. 1) with an overall population estimate in 2004 at 36 bears (C.I. 28.6–45.3) (Stenhouse et al. 2015). Each site consisted of a single strand of barb wire set in a ‘corral’ fashion (~100 m² in size) at a 0.5 m height with a cow blood lure placed on a pile of brush in the middle of the corral to attract bears to the site. Barb wire height generally precludes cubs-of-the-year from being sampled thus targeting yearling to adult bears. Bear hair was collected non-invasively on the barb wire as animals entered and/or left the corral. Each hair-slug sample represented a two week session where hair was collected at the end of the session with sampling lasting from 25 May to 17 July 2004 and up to four possible sessions and sites per 49 km² (7 × 7 km) grid cell. Hair samples were genosequenced by Wildlife Genetics International to identify the number of unique grizzly bears detected at each hair-slug site (see Paetkau 2003 and Proctor et al. 2010 for more details on DNA lab techniques). We used the number of unique bears at each sample site to represent local abundance in bears,

which was subsequently related to the surrounding average road density (top–down) and landscape food resource supply measured in kcal (bottom–up). Maximum number of bears detected at a site was five individuals (a second site also recorded four bears). More typical were sites with singletons (n = 75), two bears (n = 15), or three bears (n = 7).

Single versus complementary resource hypotheses

To evaluate support for the single versus complementary resource hypotheses (bottom–up hypotheses) we tested six a priori models predicting patterns in local grizzly bear abundance (Table 1). Models tested included a null model where local abundance was assumed to be constant across the landscape (mean abundance), a null landscape model (base model) where we accounted for sampling session (time) and the expected effect of top–down factors influencing survival of bears as measured by surrounding road density (Boulanger and Stenhouse 2015; see Supplementary material Appendix 1 for details on model selection for the null landscape model), and finally different combinations of food resource models. The combinations of food resource models differentiated the importance of carnivory (ungulate sources of meat at 7.44-km radius) versus frugivory (buffaloberry fruit at a 1.69-km radius), thus, testing single and complementary resource hypotheses when combined either as an additive or multiplicative effect. Models were also fit for buffaloberry food resource supply summarized at a 7.44 km scale. However, the 1.69-km radius scale was more supported than the 7.44-km radius ($\Delta AIC = 4.08$; evidence ratio of 7.7) with no differences observed in the ranking of hypotheses (Supplementary material Appendix 1) so we only report here models where buffaloberry resource supply was summarized within 1.69 km of hair-slug sites. Note that for the complementary resource hypothesis we considered both an additive (meat + fruit) and a multiplicative (meat + fruit + meat × fruit) model to evaluate whether local abundance of bears increased more than expected in the presence of complementary foods (i.e. multiplicative model).

To evaluate these hypotheses, we used ordered logistic regression predicting the probability of an increased count of bears (0, 1, 2, ≥ 3) at a sample site/session. We used the different landscape and sampling covariates as predictors for the different hypotheses. An ordinal model was used rather than a zero-inflated or negative binomial count model since

Table 1. Set of hypotheses tested, model structure, and descriptions as it relates to testing top–down (mortality) and bottom–up (food resource supply) control in local patterns of grizzly bear abundance.

Hypothesis	Model structure	Description
Null	Null	No landscape pattern in bear abundance (mean count across study area)
Top–down	Null landscape (session + road density)	Bear abundance affected by session + local patterns in mortality risk/survival (top–down regulation)
Top–down + Bottom–up (single resource – fruit)	Null landscape + Fruit	Bear abundance affected by bottom–up regulation due to local variation in fruit abundance + top–down effects
Top–down + Bottom–up (single resource – meat)	Null landscape + Meat	Bear abundance affected by bottom–up regulation due to local variation in meat (ungulate) abundance + top–down effects
Top–down + Bottom–up (complementary additive)	Null landscape + Fruit + Meat	Bear abundance affected by the combined effect of fruit and meat (additive effect) + top–down effects
Top–down + Bottom–up (complementary interactive)	Null landscape + Fruit + Meat + Fruit × Meat	Bear abundance affected by the combined effect of fruit and meat (multiplicative effect) + top–down effects

the number of unique counts of bears at DNA hair-snag sites was low and the parallel assumption for ordered logistic regression was satisfied (Brant test of parallel regression assumption, $\chi^2 = 5.29$, $p = 0.726$, $DF = 8$). To account for potential correlation among local hair-snag sites, the variance (standard errors) of parameters in the ordered logistic models was estimated using the 'clustered sandwich' approach that accounts for intergroup correlation (Williams 2000). Clusters were identified as the individual 7×7 km DNA sampling cells used to allocate DNA hair snag sites across the study region. We evaluated support for each hypothesis based on the principle of parsimony using Akaike's information criteria (AIC) and associated Akaike weights (Burnham and Anderson 2002). For the most supported model, we present odds ratios as an effect size reflecting the change in probability of bear abundance for a one unit change in the model variables (e^{β}). We also report the odds ratio standardized to a one unit change in the standard deviation of that variable ($e^{\beta \text{StdX}}$) to allow direct comparisons of effect size among variables.

Data accessibility

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.771t4>> (Nielsen et al. 2016). Data on sample locations of bears is not provided due to the sensitive nature of locality data for a provincially threatened species.

Results

Nutritional landscape models and local patterns in grizzly bear abundance

High concentrations of digestible energy from ungulate matter were predicted within the mountainous western region of the study area (Fig. 3a). However, some of the highest concentrations of ungulate resources occurred around specific locales such as the reclaimed Greg River/Luscar coal mine where ungulate species such as elk and sheep are high. Available digestible ungulate matter (kcal) was generally lower in the eastern foothills where elk and sheep were absent (sheep) or less abundant (elk), although moose tended to be more common in the eastern foothills. DNA hair-snag sites recorded areas of high local bear abundance (≥ 3 bears) in areas predicted to have relatively high amounts of digestible energy from ungulates (Fig. 3a).

Spatial patterns in the digestible energy of buffaloberry fruit were more variable than that of ungulates. This reflects the more localized scale at which buffaloberry resources were measured around DNA hair snag sites (1.69-km radius) and local variation in forest structure. Areas of high buffaloberry resources were predicted for both the mountains and foothills regions with the greatest abundance of fruit often following valley bottoms (Fig. 3b). DNA hair-snag sites measuring local grizzly bear abundance were generally related to areas with higher buffaloberry fruit (Fig. 3b), although the relationship was less apparent in the east where road density was higher (Fig. 2).

Single versus complementary resource hypotheses

Models comparing local patterns in grizzly bear abundance supported the additive complementary resource model of ungulates and buffaloberry with an Akaike weight of 0.720 (Table 2). The second most supported models was the bottom-up complementary interactive model with a ΔAIC of 1.95 and an Akaike weight of 0.272. In comparison, the null landscape model representing the top-down hypothesis (road density and sampling session covariate) was much less supported at a ΔAIC of 49.63, thereby illustrating the strong effect of adding bottom-up factors measuring local resource supply to traditional top-down models that assume abundance is related only to top-down mechanisms (see Supplementary material Appendix 1 for further separation of bottom-up and top-down models, but notably no changes in inferences). When considering only the single resource hypotheses, carnivory (ungulate matter) was more supported than frugivory (buffaloberry fruit) with a ΔAIC from the top complementary model being 8.92 and 35.71 respectively. Indeed, buffaloberry fruit alone was poorly correlated to patterns in bear abundance illustrating that buffaloberry is additive over that of carnivory and does not alone support variations in bear abundance.

Model parameters for the most supported model confirmed the expected inverse relationship between road density and observed local abundance in grizzly bears. Specifically, each one unit increase in road density resulted in a 62.3% decrease (odds ratio [e^{β}] = 0.516) in local abundance of bears (Table 3). Road density was highest in the north and east regions of the Yellowhead population unit, with an additional area of high density found in the southeast (Fig. 2). In contrast, areas of low road density were located in the central and western regions of the study area adjacent to the Rocky Mountains. An inverse relationship was also found between session number (seasonality) and bear abundance with a 35.6% decrease in odds (Odds ratio [e^{β}] = 0.695) in local abundance of bears at a site across each session period (Table 3).

Relationships between food supply and local abundance of bears predicted that for each 10-fold increase in buffaloberry food supply (\log_{10} [kcal of fruit] at 1.69-km radius around hair-snag sites), local abundance of bears increased by a factor of more than 2 (odds ratio [e^{β}] = 2.125). On the other hand, each 10-fold increase in ungulate food supply (\log_{10} [kcal of ungulate meat] at 7.44-km radius around hair-snag sites) increased local abundance of bears by a factor of 59 (odds ratio [e^{β}] = 59) demonstrating the importance per unit increase in ungulate matter on local patterns in bear abundance. However, standardized coefficients ($e^{\beta \text{StdX}}$) demonstrated that when considering a one unit standard deviation change in ungulate and fruit resources, both ungulate and buffaloberry food supply were similar in their effect on local grizzly bear abundance with standardized coefficients for both being 2.0 (i.e. two-fold increase in local bear abundance per standard deviation change in resource supply) (Table 3). On a per digestible kcal basis, ungulates were therefore 29.5 times more important in affecting local abundance of bears, although these differences were similar

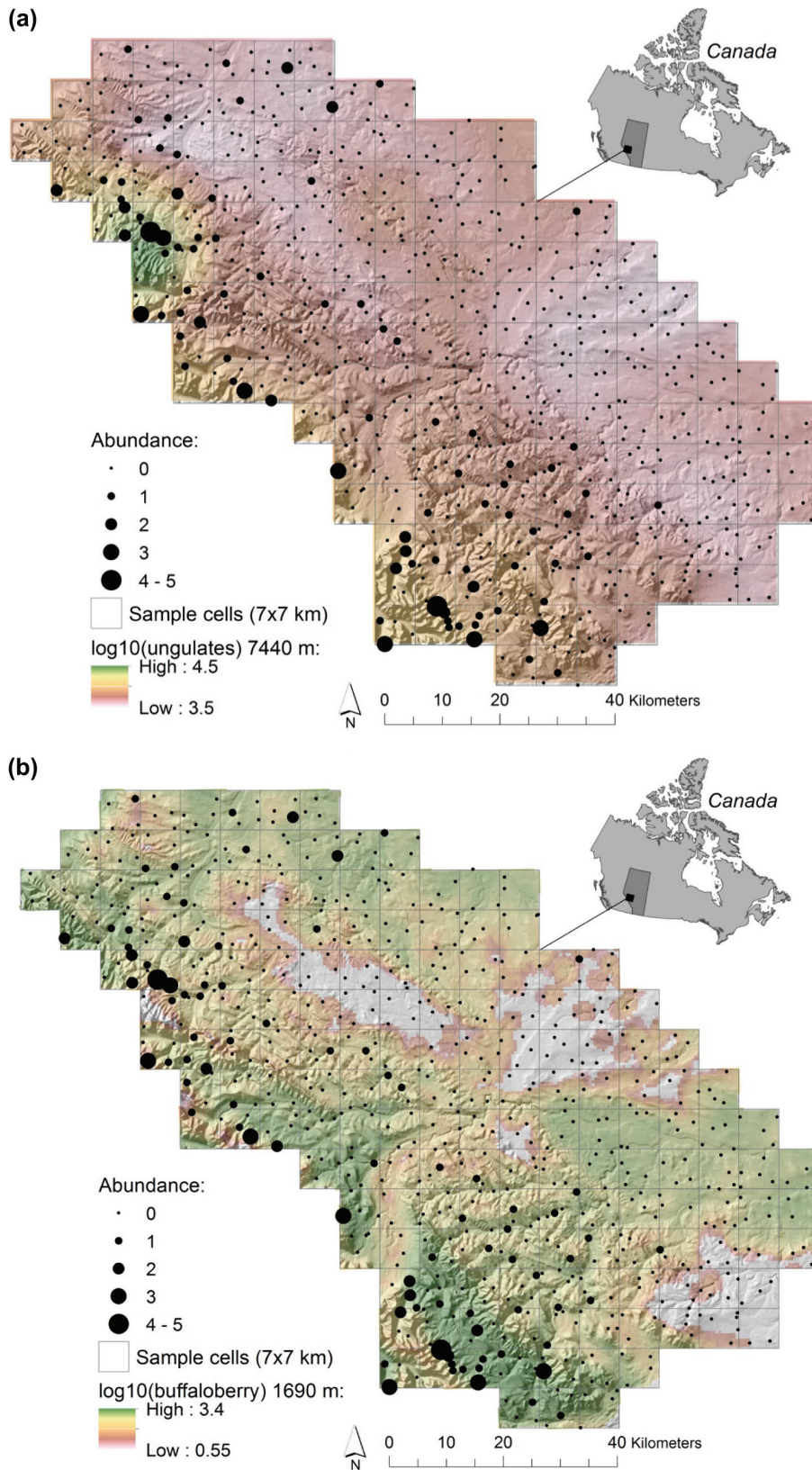


Figure 3. Patterns of grizzly bear abundance and predicted digestible energy for the two most dominant food resources: (a) ungulates at a 7.44-km radius moving window (above) and (b) Canada buffaloberry fruit at a 1.69-km radius moving window (below) for the Yellowhead ecosystem, Alberta, Canada.

Table 2. Comparison of candidate models explaining local abundance of grizzly bears. Model selection results listing model log likelihoods (LL), model complexity (K), Akaike's information criteria (AIC), change in AIC (Δ AIC) and overall support (weights) of the models given data and models tested (w_i AIC). Models are rank ordered from most to least supported. Bottom-up complementary additive refers to Meat + Fruit, while bottom-up complementary interactive refers to Meat + Fruit + Meat \times Fruit.

Hypothesis (model)	Model LL	K	AIC	Δ AIC	w_i AIC
Top-down + Bottom-up (complementary additive)	-350.03	7	714.05	0.00	0.720
Top-down + Bottom-up (complementary interactive)	-350.00	8	716.00	1.95	0.272
Top-down + Bottom-up (single resource of meat)	-355.49	6	722.97	8.92	0.008
Top-down + Bottom-up (single resource of fruit)	-368.88	6	749.77	35.71	0.000
Top-down	-376.84	5	763.68	49.63	0.000
Null model (mean count of bears at all sites)	-407.02	3	820.04	105.99	0.000

when considering standardized changes in available resource supply.

Differences in the interpretation of the importance of individual resources are due in part to greater landscape variation in local fruit supply compared with that of the supply of ungulate meat measured at broader spatial scales (Fig. 4). Regardless, both factors were found to contribute to the observed patterns in local abundance of bears with model support of the complementary effect being 90 times more supported than the most supported single resource model of ungulate meat (ratio of Akaike weights; Table 2). Figure 4 illustrates graphically this additive complementary effect with the probability of observing no bears (Fig. 4a) or the largest count (≥ 3) of bears (Fig. 4b) at a site. Only in situations where both ungulate and buffaloberry resource supply were abundant were the counts of bears predicted to be highest, although variation in buffaloberry food supply made little difference in high counts of bears unless moderate or high levels of ungulate resource supply were first available.

Discussion

We demonstrate here that local patterns in grizzly bear abundance were associated with both top-down and bottom-up factors, and specifically that areas high in energy from complementary resources (ungulates and fruit in an additive manner) were more important in predicting patterns in local abundance of bears than either food source alone. This supports the complementary resource hypothesis where the availability of complementary foods, and therefore diet quality at the landscape level, is positively associated with local population density by enabling individual bears

to better optimize their diet thereby increasing their fitness (Coogan et al. 2014, Erlenbach et al 2014). Importantly, the availability of complementary foods was more essential in explaining bear abundance than energy or protein intake per se. For example, if energy or protein were most important, then bear density would have been strongly associated with high-ungulate areas regardless of fruit abundance; however, there are several areas within the study having high ungulate and low fruit abundance with low bear abundance. Our work, therefore, further supports the supposition that purely energy-or single nutrient-based foraging studies may be insufficient to accurately predict or understand animal foraging behavior, particularly for omnivores (Illius et al. 2002, Simpson et al. 2004, Robbins et al. 2007, Erlenbach et al 2014).

Although the co-limitation hypothesis of ungulate matter (meat) and fruit was most supported, our study suggested that ungulate matter was more important than fruit in predicting local abundance of grizzly bears. This is consistent with the observation that captive grizzly bears restricted to fruit-only diets are constrained in their ability to gain weight (Welch et al. 1997). One reason may be the resource size and efficiency between kcals of different food items. For example, 1 kcal of ungulate meat is more likely to be associated with several other kcals of ungulate meat (e.g. a whole carcass), than is 1 kcal of fruit which is packed in a far smaller and less energy dense 'package'. Meat also provides both protein and lipid to bears, thereby offering a source of two macronutrients (importantly protein and a non-protein macronutrient) in an easily digestible form – adequate protein intake is important for bears in order to support lean mass growth and lactation costs (López-Alfaro et al. 2013). Another explanation is that the availability of fruit energy in the area is not enough to dilute the protein intake of grizzly bears to optimal levels (perhaps especially for highly carnivorous bears), such that bears are more likely to consume a high ungulate diet despite not being optimally balanced – bears should have a high tolerance to dietary imbalances similar to that observed in other omnivores (Raubenheimer and Simpson 1997). It may also be that the diet of grizzly bears is within a 'nutrient space' (sensu Simpson and Raubenheimer 2012) that requires relatively little fruit to reach their optimal intake of non-protein energy (Coogan et al. 2014). Carbohydrates are likely to be important in this ecosystem, because it may be the only means for bears to optimize their nutrient intake given the absence of high-lipid food items. Another factor may be that bears can potentially consume ungulates throughout the active season, as opposed to fruit which has a limited window of availability. Yet,

Table 3. Model parameters (β and SE) predicting local counts in grizzly bears as a function of sampling time (session), local mortality risk (road density within a 7.44 km moving window), buffaloberry fruit food supply (log₁₀ digestible energy, kcal; 1.69 km radius), and ungulate (meat) food supply (log₁₀ digestible energy, kcal; 7.44 km radius). Odds ratio change in probability of count for a one unit change in variable (e^{β}) and a one standard deviation change in that variable ($e^{\beta \text{StdX}}$) are presented. Standard errors (SE) are based on cluster sandwich estimates using DNA cell as the cluster.

Model variable	β	SE	e^{β}	$e^{\beta \text{StdX}}$
Sampling session number (season)	-0.364	0.111	0.695	0.688
Mortality risk (road density)	-0.662	0.420	0.516	0.761
Buffaloberry food supply	0.754	0.273	2.125	1.994
Ungulate (meat) food supply	4.080	0.520	59.12	1.998

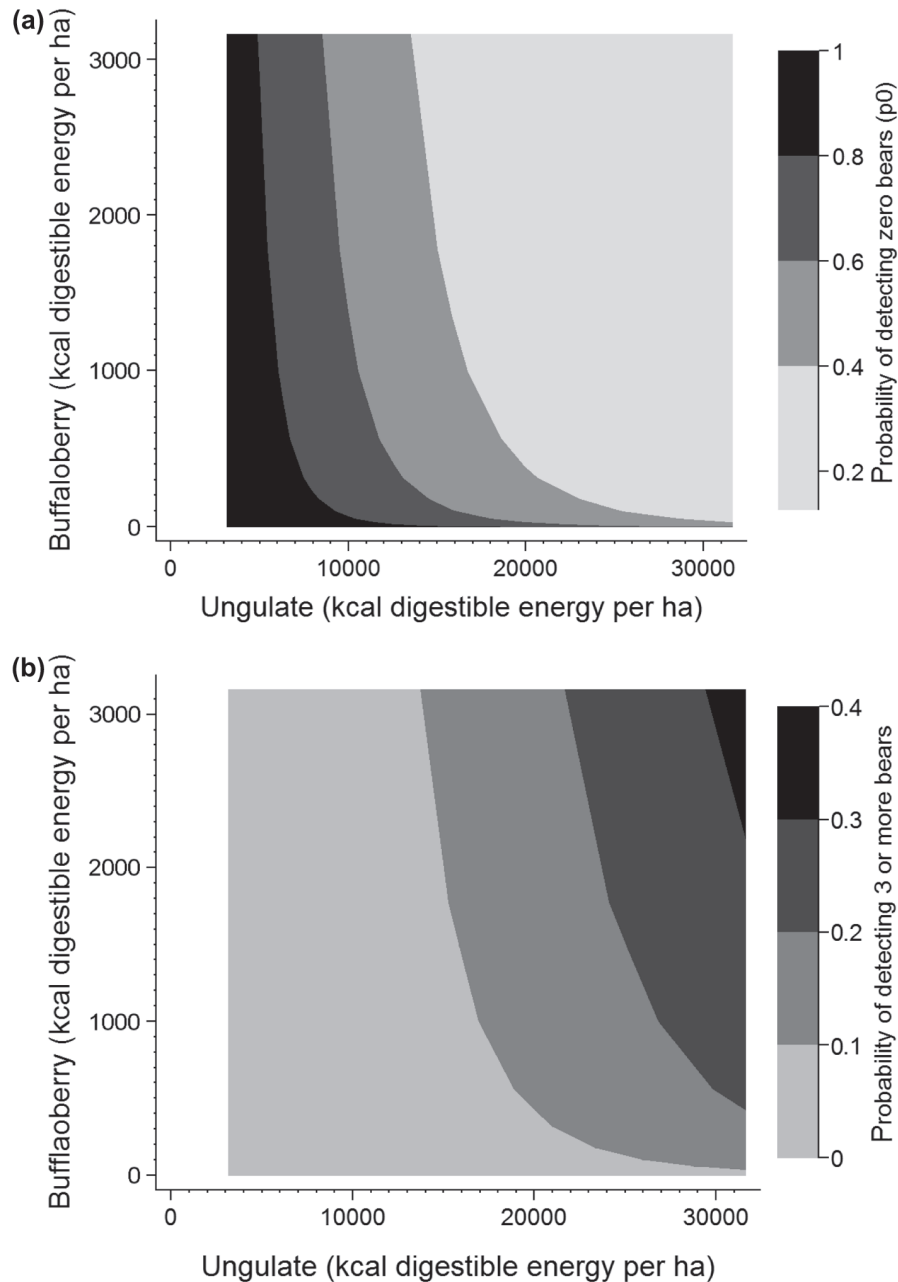


Figure 4. Predicted local abundance of grizzly bears as a function of tradeoffs in available digestible energy (per ha) in ungulate and buffaloberry fruit resources. Model assumes no local roads (road density = 0) and the time of sampling being the first sampling session. Probability that a site has no grizzly bears (a) and a count of ≥ 3 bears (b) is illustrated as filled contours.

despite the relative importance of one food over the other, both fruit and ungulates were better at predicting local bear abundance than either food resource in isolation and only when both were available at high levels were counts of bears high. Higher bear abundance in areas offering both meat and fruit supports our co-limitation hypothesis. Although the most supported model did not include an interactive (multiplicative) effect between fruit and ungulate calories, there was secondary support for the multiplicative effect given that $\Delta AIC < 2$ (Burnham and Anderson 2002), although Arnold (2010) points out that this is a case of an 'uninformative parameter' since complexity increased with little gain in fit. We therefore support the additive response. Although the

interactive effects of food resources have been shown to exist at the individual level, they may not directly translate with patterns in local abundance.

Although our focus is on local patterns in grizzly bear abundance, higher number of grizzly bears at hair snag sites may be due in part to females with offspring. Cub-of-the-year are unlikely to be captured by barb wire corrals since hair snag heights are high (0.5 m) relative to their size. Furthermore, a low birth rate and population size may further reduce the likelihood of capturing cub-of-the-year bears (Garshelis et al. 2005). However, if dependent offspring are being captured in barb wire corrals, then the relationship between increased local bear abundance and the availability

of fruit and ungulate matter may suggest that availability of complementary resources increases reproductive success and litter size and thus indicates areas of greater population performance. Female reproductive success of bears is influenced by their capacity to store both fat and lean mass before hibernation (Robbins et al. 2012, López-Alfaro et al. 2013), as well as the availability of food resources during the post-denning lactation (spring) period, especially food resources high in protein which have been found to be important for bears (Noyce and Garshelis 1998). Fruit consumption during summer and early fall is an important source of energy that allows grizzly bears to accumulate fat mass prior to denning (McLellan 2011), as well as optimize their macronutrient intake and mass gain when combined with complementary resources (Coogan et al. 2014, Erlenbach et al. 2014). These complementary resources may therefore be critical to reproductive rates in bears, which are known locally to be among the lowest recorded for the species in the least productive high elevation environments where mean age of first reproduction was 6.7 years and mean age of first surviving litter was 8.4 years (Garshelis et al. 2005). These same high elevation habitats are also associated with smaller body sizes (Nielsen et al. 2013). Together this suggests strong bottom-up limitations in the population.

Our results support the hypothesis that bottom-up factors were offset partly by top-down factors related to human-caused mortality of grizzly bears with an inverse relationship between road density and local abundance of bears. This supports existing recovery efforts of limiting road access since roads are associated with increases in the number of human-caused mortalities in bears in this and other study areas (McLellan and Shackleton 1988, Benn and Herrero 2002, Nielsen et al. 2004a, Boulanger and Stenhouse 2015). This is especially important since grizzly bears can be attracted to roadside habitats where food sources are concentrated (Nielsen et al. 2004b, Roeber et al. 2008, Graham et al. 2010) resulting in an attractive sink conditions (Nielsen et al. 2006, Northrup et al. 2012). It would be informative if future work examined this from a nutritionally-explicit perspective.

Our results suggest that conservation and management should consider the non-substitutability of habitats on which bears rely on to balance their nutritional intake. When comparing the difference in support between bottom-up factors and top-down factors, bottom-up factors were more important (AIC values and standardized coefficients) in explaining local patterns in abundance of bears. Indeed, regional differences in bear density are largely explained by ecosystem productivity, not human-caused mortality (Hilderbrand et al. 1999, Mowat et al. 2013). This suggests that greater recognition of bottom-up limitations in bear populations is needed, especially when considering the number of bears that can be supported and thus the degree to which population recovery targets can be set. To hasten population recovery and increase population sizes, forest harvesting and prescribed fire may be effective management tools that can maintain and increase simultaneously complementary resources of ungulates and fruit (Nielsen et al. 2004c) if access management strategies are utilized. Reducing the harvest of the key protein source (ungulates) by human hunters may be a strategy that could

benefit bears (Levi et al. 2012) if ungulate populations are low.

Traditionally, resource co-limitation studies have often been applied to autotrophic and herbivorous consumers, where individual growth responses to specific nutrient-limitation scenarios have been examined (Elser et al. 2007, Simpson and Raubenheimer 2012, Sperfeld et al. 2012). Our results suggest that the concept of nutrient co-limitation is also relevant to larger scale population measures. For example, under the more traditional resource limitation model of Liebig's law of the minimum, growth is strictly limited by the most limiting nutrient. The co-limitation hypothesis suggests instead that growth can be simultaneously limited by > 1 nutrient (Sperfeld et al. 2012). The association between bear density and both fruit and ungulates (Fig. 4) is similar to co-limitation patterns in interactive essential resources (see Fig. 1b in Sperfeld et al. 2012), where areas of rounded probability isoclines indicate a smooth transition of limitation by fruit to ungulates and a range of resource availabilities where both resources are simultaneously limiting. Similarly, while macronutrient self-selection studies necessarily tend to focus on the behavioral and physiological responses of individual animals, our results suggests that fitness benefits of a mixed-diet can influence spatial patterns of population density across an ecosystem. We demonstrate both the importance of bottom-up regulation using grizzly bears and that a multidimensional approach to modeling bottom-up regulation is more informative than simply investigating food availability, energy per se, or single nutrients. Fundamentally, a bottom-up approach to ecology, management, and conservation relies on understanding the relationships between an animal, their habitats, and the food resources providing the necessary nutrients and energy. Yet, lack of knowledge of the nutritional requirements of wild animals, and the nutrient content of foods they consume, often limits such an approach. Better integration of nutritional parameters within studies is therefore needed. Our study demonstrates the importance of bridging this gap, in order to further develop an interactive and nutrient-specific approach to understanding the nutritional ecology of animals in the wild.

Acknowledgements – The Alberta Environment and Sustainable Resource Development provided data from ungulate surveys and supported the DNA hair-snag work. We thank C. López-Alfaro for commenting on an early manuscript and C. Nielsen for assistance with GIS and remote sensing data.

Funding – This work was supported by an Alberta Innovates-BioSolution grant, the fRI Research, the University of Alberta, and Natural Sciences and Engineering Council (NSERC) of Canada Discovery grant for SEN.

Conflict of interest – No authors have a conflict of interest.

References

- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's information criteria. – *J. Wildl. Manage.* 74: 1175–1178.
- Benn, B. and Herrero, S. 2002. Grizzly bear mortality and human access in Banff and Yoho National Parks, 1971–1998. – *Ursus* 13: 213–221.

- Bojarska, K. and Selva, N. 2012. Spatial patterns in brown bear *Ursus arctos* diet: the role of geographic and environmental factors. – *Mammal Rev.* 42: 120–143.
- Boulanger, J. et al. 2004. Sources of heterogeneity bias when DNA mark–recapture sampling methods are applied to grizzly bear (*Ursus arctos*) populations. – *J. Mammal.* 85: 618–624.
- Boulanger, J. et al. 2013. Use of multi-state models to explore relationships between changes in body condition, habitat and survival of grizzly bears *Ursus arctos horribilis*. – *Wildlife Biol.* 19: 274–288.
- Boulanger, J. and Stenhouse, G.B. 2015. The impacts of roads on the demography of grizzly bears in Alberta. – *PLoS ONE* 9: e115535.
- Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. – Springer.
- Boyce, M. S. et al. 2001. Population viability for grizzly bears: a critical review. – *Int. Ass. for Bear Res. Manage. Monogr. Ser.* 4: 1–45.
- Coogan, S. C. P. et al. 2014. Macronutrient optimization and seasonal diet mixing in a large omnivore, the grizzly bear: a geometric analysis. – *PLoS ONE* 9: e105719.
- Dunning, J. B. et al. 1992. Ecological processes that affect populations in complex landscapes. – *Oikos* 65: 169–175.
- Elser, J. J. et al. 2007. Global analysis of nitrogen and phosphorous limitation of primary producers in freshwater, marine and terrestrial ecosystems. – *Ecol. Lett.* 10: 1135–1142.
- Erlenbach, J. A. et al. 2014. Macronutrients optimization and energy maximization determines diet of brown bears. – *J. Mammal.* 95: 160–168.
- Estes, J. A. et al. 2011. Trophic downgrading of planet earth. – *Science* 15: 301–306.
- Garshelis, D. L. et al. 2005. Grizzly bear demographics in and around Banff National Park and Kananaskis Country, Alberta. – *J. Wildl. Manage.* 69: 277–297.
- Graham, K. et al. 2010. Spatial and temporal use of roads by grizzly bears in west-central Alberta. – *Ursus* 21: 43–56.
- Gunther, K. A. et al. 2004. Grizzly bear-human conflicts in the Greater Yellowstone ecosystem, 1992–2000. – *Ursus* 15: 10–22.
- Hairston, N. G. et al. 1960. Community structure, population control and competition. – *Am. Nat.* 94: 421–424.
- Hilderbrand, G. V. et al. 1999. The importance of meat, particularly salmon, to body size, population productivity and conservation of North American brown bears. – *Can. J. Zool.* 77: 132–138.
- Hundertmark, K. J. et al. 1997. Estimation of body composition in moose. – Alaska Dept of Fish and Game, Juneau, AK, USA.
- Hunter, M. D. and Price, P. W. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom–up and top–down forces in natural communities. – *Ecology* 73: 724–732.
- Illius, A. W. et al. 2002. The evolution of the control of food intake. – *Proc. Nutr. Soc.* 61: 465–472.
- Johnson, C. J. et al. 2004. Modelling survival: application of the Anderson–Gill model to Yellowstone grizzly bear. – *J. Wildl. Manage.* 68: 966–978.
- Kohl, K. D. et al. 2015. Do wild carnivores forage for prey or nutrients? – *BioEssays* 37: 701–709.
- Leibold, M. A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. – *Am. Nat.* 134: 922–949.
- Levi, T. et al. 2012. Using grizzly bears to assess harvest–ecosystem tradeoffs in salmon fisheries. – *PLoS Biol.* 10: e1001303
- López-Alfaro, C. et al. 2013. Energetics of hibernation and reproductive tradeoffs in brown bears. – *Ecol. Model.* 270: 1–10.
- López-Alfaro, C. et al. 2015. Assessing nutritional parameters of brown bear diets among ecosystems gives insight into differences among populations. – *PLoS ONE* 10: e0128088.
- Mattson, D. J. and Merrill, T. 2002. Extirpations of grizzly bears in the contiguous United States, 1850–2000. – *Conserv. Biol.* 16: 1123–1136.
- Mattson, D. J. et al. 1992. Yellowstone grizzly bear mortality, human habitation and whitebark pine seed crops. – *J. Wildl. Manage.* 56: 432–442.
- McLellan, B. N. 2011. Implications of a high-energy and low protein diet on the body composition, fitness, and competitive abilities of black (*Ursus americanus*) and grizzly (*Ursus arctos*) bears. – *Can. J. Zool.* 89: 546–558.
- McLellan, B. N. and Hovey, F. W. 1995. The diet of grizzly bears in the Flathead River drainage of southeastern British Columbia. – *Can. J. Zool.* 73: 704–712.
- McLellan, B. N. and Shackleton, D. M. 1988. Grizzly bears and resource-extraction industries: effects of roads on behaviour, habitat use and demography. – *J. Appl. Ecol.* 25: 451–460.
- Mowat, G. et al. 2013. Predicting grizzly bear density in western North America. – *PLoS ONE* 8: e82757.
- Mowat, G. et al. 2005. Grizzly *Ursus arctos* and black bear *U. americanus* densities in the interior mountains of North America. – *Wildl. Biol.* 11: 31–48.
- Munro, R. H. M. et al. 2006. Seasonal and diel patterns of grizzly bear diet and activity in west-central Alberta. – *J. Mammal.* 87: 1112–1121.
- Nielsen, S. E. et al. 2003. Development and testing of phenologically driven grizzly bear habitat models. – *Ecoscience* 10: 1–10.
- Nielsen, S. E. et al. 2004a. Modelling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies ecosystem of Canada. – *Biol. Conserv.* 120: 101–113.
- Nielsen, S. E. et al. 2004b. Grizzly bears and forestry I: selection of clearcuts by grizzly bears in west-central Alberta, Canada. – *For. Ecol. Manag.* 199: 51–65.
- Nielsen, S. E. et al. 2004c. Grizzly bears and forestry II: distribution of grizzly bear foods in clearcuts of west-central Alberta, Canada. – *For. Ecol. Manag.* 199: 67–82.
- Nielsen, S. E. et al. 2006. A habitat-based framework for grizzly bear conservation in Alberta. – *Biol. Conserv.* 130: 217–229.
- Nielsen, S. E. et al. 2010. Dynamic wildlife habitat models: seasonal foods and mortality risk predict occupancy–abundance and habitat selection in grizzly bears. – *Biol. Conserv.* 143: 1623–1634.
- Nielsen, S. E. et al. 2013. Environmental, biological and anthropogenic effects on grizzly bear body size: temporal and spatial considerations. – *BMC Ecol.* 13: 31.
- Nielsen, S. E. et al. 2016. Data from: Complementary food resources of carnivory and frugivory affect local abundance of an omnivorous carnivore. – Dryad Digital Repository, <<http://dx.doi.org/10.5061/dryad.771t4>>.
- Northrup, J. M. et al. 2012. Agricultural lands as ecological traps for grizzly bears. – *Anim. Conserv.* 15: 369–377.
- Noyce, K. V. and Garshelis, D. L. 1998. Spring weight changes in black bears in northcentral Minnesota: the negative foraging period revisited. – *Ursus* 10: 521–531.
- Oksanen, L. et al. 1981. Exploitation ecosystems in gradients of primary productivity. – *Am. Nat.* 118: 240–260.
- Paetkau, D. 2003. An empirical exploration of data quality in DNA-based population inventories. – *Mol. Ecol.* 12: 1375–1387.
- Pease, C. M. and Mattson, D. J. 1999. Demography of Yellowstone grizzly bears. – *Ecology* 80: 957–975.

- Power, M. E. 1992. Top-down and bottom-up forces in food webs: do plants have primacy. – *Ecology* 73: 733–746.
- Pritchard, G. T. and Robbins, C. T. 1990. Digestive and metabolic efficiencies of grizzly and black bears. – *Can. J. Zool.* 68: 1645–1651.
- Proctor, M. et al. 2010. Ecological investigations of grizzly bears in Canada using DNA from hair, 1995–2005: a review of methods and progress. – *Ursus* 21: 169–188.
- Raubenheimer, D. and Simpson, S. J. 1997. Integrative models of nutrient balancing: application to insects and vertebrates. – *Nutr. Res. Rev.* 10: 151–179.
- Roberts, D. R. et al. 2014. Idiosyncratic responses of grizzly bear habitat to climate change based on projected changes in their food resources. – *Ecol. Appl.* 24: 1144–1154.
- Robbins, C. T. et al. 2007. Optimizing protein intake as a foraging strategy to maximize mass gain in an omnivore. – *Oikos* 116: 1675–1682.
- Robbins, C. T. et al. 2012. Maternal condition determines birth date and growth of newborn cubs. – *J. Mammal.* 93: 540–546.
- Roever, C. L. et al. 2008. Grizzly bears and forestry. I. Road vegetation and placement as an attractant to grizzly bears. – *For. Ecol. Manage.* 256: 1253–1261.
- Rothman, J. M. et al. 2011. Nutritional geometry: gorillas prioritize non-protein energy while consuming surplus protein. – *Biol. Lett.* 7: 847–849.
- Simpson, S. J. and Raubenheimer, D. 2012. The nature of nutrition: a unifying framework from animal adaptation to human obesity. – Princeton Univ. Press.
- Simpson, S. J. et al. 2004. Optimal foraging when regulating intake of multiple nutrients. – *Anim. Behav.* 68: 1299–1311.
- Sperfeld, E. et al. 2012. Multiple resource limitation theory applied to herbivorous consumers: Liebig's minimum rule vs interactive co-limitation. – *Ecol. Lett.* 15: 142–150.
- Stenhouse, G. B. et al. 2015. Estimates of grizzly bear population size and density for the 2014 Alberta Yellowhead Population Unit (BMA 3) and south Jasper National Park Inventory Project. – Weyerhaeuser Ltd., West Fraser Mills Ltd., Alberta Environment and Parks, and Jasper National Park.
- Terborgh, J. W. et al. 2001. Ecological meltdown in predator-free forest fragments. – *Science* 294: 1923–1926.
- Welch, C. A. et al. 1997. Constraints on frugivory by bears. – *Ecology* 78: 1105–1119.
- Williams, R. L. 2000. A note on robust variance estimation for clustered-correlated data. – *Biometrics* 56: 645–646.

Supplementary material (available online as Appendix oik-03144 at <www.oikosjournal.org/appendix/oik-03144>). Appendix 1.

Nielsen, S. E., Larsen, T. A., Stenhouse, G. B. and Coogan, S. C. P. 2016. Complementary food resources of carnivory and frugivory affect local abundance of an omnivorous carnivore. – Oikos doi: 10.1111/oik.03144

Appendix 1

Nutritional landscape modeling of ungulate (meat) supply

Ungulate observations

We obtained winter ungulate survey data from a portion of the Yellowhead bear management unit that included: 1) aerial moose *Alces alces* surveys collected by Alberta Environment and Sustainable Resource Development (AESRD); and 2) aerial and ground-based surveys of sheep (*Ovis canadensis*) conducted by AESRD, Teck Coal Ltd., and Bighorn Wildlife Technologies Ltd. Moose surveys were undertaken within WMUs 338 (February 2009), 339 (February 2011), and 340 (January 2010). Sheep surveys occurred (January/February 2011) within WMUs 436-446, excluding 445, and included the Gregg River, Luscar, Cheviot (December 2005), and Coal Valley (RobbTrend – December 2008; RobbWest – January 2011) mine sites.

Moose surveys followed a modified stratified random block (SRB) design using fixed and rotary winged aircraft (Gasaway et al. 1986). Sheep surveys were also completed using a rotary winged aircraft to conduct a comprehensive inventory of mountain complexes (winter range) where animals tend to concentrate as well as census portions of the Cheviot and Coal Valley mine sites by flying pre-determined transects (orientated NW–SE and at approximately 800 m apart). The 2011 comprehensive survey was complemented by a systematic ground survey of the Gregg River and Luscar mine sites by walking, driving, and viewing ungulates from strategic vantage points. For our purpose, we only considered the most recent survey by WMU because ungulate populations are dynamic and may fluctuate from year to year due to predation, disease, climate (snowfall, temperature), or hunting (Edwards 1956, Rolley and Keith 1980, Post and Stenseth 1998, Ferguson et al. 1999, DeCesare and Pletscher 2006, Hebblewhite et al. 2006, Dekker 2009, Boyce et al. 2012). Although surveys were focused on quantifying (counts) and classifying (gender, age class) moose or sheep, other ungulates were also documented in the process.

Analysis scale and environmental predictors of ungulate abundance models

We used survey grid size, 3' × 5' for WMU 339 and 5' × 5' for WMUs 338 and 340, to define the

analysis scale for moose survey data. In doing so, search effort could be accounted for explicitly in abundance models. For the other aerial and ground-based survey data that did not implement the SRB method, we extended the 5' × 5' survey grid since this size accounted for the majority of the SRB observations. We assume that search effort was adequately represented in each of the corresponding grids. Although our approach allows for the investigation of habitat relationships to ungulate abundance at a common scale and temporal period, we recognize the potential weakness of inference derived at a single scale and solely relying on winter surveys for several reasons. Ungulate species may respond to local environmental conditions at specific scales (Maier et al. 2005), ungulate densities may vary locally as animals alter their habitat use and movements to cope with reduced food availability and snow depth (Telfer 1978, Parker et al. 1984, Poole and Mowat 2005), and individual animals may migrate long distances from summer to winter ranges (Nicholson et al. 1997, Hebblewhite et al. 2006). While our approach to estimating density does not address the issue of ungulate migrations, we believe that the relatively large area (~38–63 km²) of the survey grids was appropriate given that changes in animal behavior associated with local habitat (mountain tops and valley bottoms) would be captured in a single survey grid.

Spatial environmental variables that mirrored those used in previous studies of ungulate distribution and abundance were used for modeling. Variable types created from raster (30 × 30 m pixel) and vector data sources were grouped into classes reflecting broad differences in habitat composition associated with vegetation (land cover), forest attributes (age, leading tree species, and canopy cover), topography, water (streams, lakes), and anthropogenic land use (Table A1). We distinguished vegetated from non-vegetated habitats using a land cover map (McDermid 2005). Anthropogenic features including well-sites, pipelines, powerlines, railways, and roads were buffered based on feature width visually estimated from a Landsat image (30 × 30 m pixel). We rasterized (30 × 30 m) anthropogenic features along with vector data identifying cutblocks and reclaimed mine footprint. We then created a final habitat layer by replacing land cover values that corresponded to each rasterized layer. In doing so, herb, shrub, and barren land cover classes would be associated with naturally occurring meadows and alpine vegetation. Attributes were retained to distinguish anthropogenic features from cutblocks and the Gregg River/Luscar and Coal Valley mines. We discriminated between the two mine sites because sheep were not found on the Coal Valley lease given its proximity to the Rocky Mountains. We created a binary raster layer to identify conifer (> 50% conifer) and deciduous forests by reclassifying a continuous leading species raster for conifer or deciduous trees. A digital elevation model was used to create slope and aspect grids. The aspect grid was scaled ($\pm 180^\circ$) so that positive values were westerly, negative values were easterly, and 0 was south (Keating et al. 2007). To identify escape terrain for sheep, we created two raster layers; one to identify slopes greater than 27° and the other to represent

contiguous patches of slopes greater than 27° and larger than 7000 m^2 (DeCesare and Pletscher 2006). We used a vector layer depicting rivers and grouped them by order as follows: 1) headwater streams that are relatively small in size and that may flow intermittently or permanently (orders 1 and 2); and 2) rivers relatively large in size and that are permanently flowing (orders 3-5). Waterbodies includes all types of naturally occurring standing water, such as wetlands or lakes (AltaLIS 2008).

For each survey grid, we calculated the proportion of each land cover class, anthropogenic footprint, conifer and deciduous forest, escape cover ($> 27^\circ$), escape cover greater than 7000 m^2 in size, and waterbodies. We also calculated the total length (m) of each stream order class, the average and standard deviations of forest age, canopy closure, slope, and aspect as well as the average distance (m) to escape cover and escape cover greater than 7000 m^2 in size. For canopy closure and forest age, average and standard deviations were calculated by re-coding other non-forested habitats as no data and as zeros. Standard deviations were used in addition to averaged values since habitat heterogeneity tends to be an important factor influencing animal distribution and health (Mysterud et al. 2001, Kie et al. 2002, Boyce et al. 2003). All GIS manipulations and calculations were performed using ArcGIS 10.1 and the spatial analyst extension (ESRI 2012).

Abundance models

Treating the survey grid as the sample unit, we summed ungulate counts by species, sex and age class (neonate, adult, and unclassified). We then associated the summed counts in each sample survey unit to the underlying habitat. A preliminary assessment suggested that due to a relatively small sample size (grid observations) and correlations amongst the count data, models could be developed for adult male ($n = 54$) and female ($n = 84$) moose, elk ($n = 26$), white-tailed ($n = 50$) and mule ($n = 21$) deer, and sheep ($n = 26$). Counts of male and female moose were not correlated, whereas counts of male and female sheep were highly correlated ($|r| = 0.91$). In addition to the binary and continuous variables described previously, we created additional continuous variable types by grouping herbs and shrubs, and rivers as well as introduce quadratic (squared) terms to investigate non-linear relationships. We also created binary variables to differentiate small from large survey blocks, the presence or absence of escape terrain, and reclaimed coal mine footprint. Large survey blocks were distinguished from small ones according to the smallest $5' \times 5'$ grid ($\sim 51 \text{ km}^2$). We transformed our response variables by taking the natural log of count observations and used a generalized linear model (GLM) with a gaussian distribution and identity link to estimate regression coefficients (McCullagh and Nelder 1989). Prior to model fitting, we identified potential outliers from plots of response vs. predictor variables and Cleveland dotplots (Zuur et al. 2009). We then used Pearson's correlation coefficients to identify predictor variables that were not correlated

($|r| \leq 0.55$) for each of the response variables. For those predictors that were not correlated, we considered all possible combinations (all-subset approach) of variables (additive effects) as biologically plausible candidate models. However, we excluded models with variance inflation factors above 3 to avoid issues of collinearity (Zuur et al. 2009). Diagnostic plots (residuals vs fitted, hat matrix, and Cook's distance) were used to confirm the absence of influential observations. We used Akaike's information criterion (AIC) adjusted for small sample size and Akaike weights (w_i) to evaluate candidate models. Squared terms for variables were included in the candidate model set if the AICc score was 2 units less than a model with a single term. Because no 'best' model could clearly be identified ($w_i \geq 0.9$), we used multi-model inference for model selection by calculating a weighted average of coefficients from the full set of candidate models (Burnham and Anderson 2002). Averaged model coefficients (Table A2) were applied to environmental predictors across the Yellowhead bear management unit. However, for sheep we limited our model predictions to those survey grids that overlapped with the Rocky Mountain Natural Region, and where elevation values were above a specific threshold ($ELEV_x \geq 1488$ and $ELEV_{sd} \geq 100$) to reflect the known limitation in the range of the species. Raw survey data revealed that below these thresholds and outside of mountainous areas, sheep were not present.

Estimates of biomass

We back transformed estimated counts by taking the exponent of each grid prediction. We then calculated biomass (kg km^{-2}) of adult males, adult females (including yearlings for sheep), and neonates for each species by multiplying abundance estimates in each grid by fall (October–December) live body mass (kg) per unit area (km^2). Because we did not have gender specific models, except for moose, we multiplied grid counts by the proportion of females as follows: elk (0.85), white-tailed (0.85) and mule (0.79) deer, and sheep (0.55). Proportions were derived from raw survey data where species were classified by gender. Based on literature values of reproductive success, we calculated the number of neonates per adult female (> 1 year old) moose (0.84; Schwartz 1992), elk (0.78; Hegel 2003), white-tailed (1.0; Alberta 1995) and mule deer (0.85; Alberta 1989), and sheep (0.91; Gaillard et al. 2002). Sheep were not considered adults until after two years of age (Jorgensen et al. 1993). Thus, we determined the proportion of grid counts that would have been adult females based on the proportion of female yearlings (0.07) observed on the Gregg River and Luscar mine sites. We also calculated the number of twins expected per female moose (0.15; Schwartz 1992), white-tailed (2.08; Alberta 1995) and mule (1.6; Alberta 1989) deer; elk rarely have twins and sheep, not at all. Body mass values (averaged or predicted) for moose (male = 442, female = 401, neonate = 184, and Lynch et al., 1995), elk (male = 327, female = 230, and neonate = 122; Bender et al. 2003), white-tailed deer (male and female averaged = 87, neonate

= 28; Kuzyk et al. 2009) and mule deer (male and female averaged = 110, neonate = 28; Renecker 1991), and sheep (male = 89, female = 67, and neonate = 32; Festa-Bianchet et al. 1996) were obtained from the literature to estimate typical live weight biomass.

Nutritional landscape model of buffaloberry *Shepherdia canadensis* fruit supply

Three models were used to estimate total kcal of buffaloberry fruit per 30 m landscape raster cell in the study area. First logistic regression models were used to estimate presence/absence of shrubs across the study area. Second, quantile regression was used to estimate shrub density (log transformed) at a site, given presence, using the 50th percentile. And third, quantile regression was used to estimate fruit abundance (log transformed), given presence of shrubs, again using the 50th percentile. Although zero-inflated count models could have been considered for modeling shrub and fruit density, substantial differences were evident in the factors affecting presence versus abundance of shrubs or fruit when present. The complexity of fitting functions as both zero-inflated and count processes simultaneously was seen as too complicated since processes affecting presence can fundamentally be different from those affecting abundance (see Nielsen et al. 2005 for supporting examples). Here we split up the process into separate models to improve clarity and possible independence among each process (e.g. presence, abundance and reproduction). Quantile regression was used rather than linear regression or generalized linear models since count data for shrub and fruit density (even without absences and transformed) were skewed. Final map predictions were determined by first estimating presence, followed by estimates of shrub and fruit abundance for only those sites where it was predicted to be present. In a sense, these models were hierarchical or multi-staged where abundance models depended on the occupancy model (zero-truncated) and the fruit density model depended on shrub abundance. Below are descriptions of each model.

Buffaloberry shrub presence (distribution)

Logistic regression models were used to predict the presence of buffaloberry shrubs from 1849 field plots from within and immediately surrounding the study area (see Nielsen et al. 2004 for field methods) using environmental predictor variables from five hypothesized main factors (themes). These factors included land cover, climate, soils, canopy (sunlight), and terrain (including one factor for sunlight) (Table S3). Terrain factors were split into either a full set of terrain variables that represented both solar radiation and terrain wetness (CTI), or for the 'sunlight' factor we included terrain-derived solar radiation together with canopy cover. No variables were used where there was a Pearson correlations of $r > |0.7|$ between them, thus high correlated variables like climate variables were first examined to find uncorrelated variables (one temperature variable and one precipitation variable). Support for different a priori combinations of hypothesized factors were

tested across 14 candidate models using Akaike's information criteria (AIC) (Burnham and Anderson 2002). These models included potential interaction terms where first hypothesized. The most supported model included land cover, climate, soil and 'sunlight' (canopy cover and terrain-derived solar radiation) (Table A4). Land cover variables included positive relationships with conifer forest, mixedwood forest, deciduous forest, shrub, and herb habitats, a negative relationship with treed wetland, and a positive relationship with forest canopy cover (Table A5). Climate variables included non-linear responses in mean annual temperature (MAT) and growing season precipitation (GSP), as well as a positive interaction between MAT and GSP (Table A5). Soil factors included a non-linear response to soil pH and a positive relationship with percent sand. Terrain effects were observed through a positive relationship with solar radiation (southern slopes), and a negative interaction between canopy cover and solar radiation (Table A5). Probabilities of occurrence for buffaloberry shrubs were predicted spatially to the study area using the most supported AIC model (coefficients from Table A5). Binary predictions of presence (1) / absence (0) in raster map cells were based on the optimal cut-off threshold probability determined by the probability where model sensitivity and specificity values were equalized (Liu et al. 2005). The threshold in the top supported model (Table A4) was 0.1865 (i.e. predicted to be absent (0) if probability of presence was <0.1865 ; predicted present (1) if probability of presence was ≥ 0.1865). Model predictive accuracy was assessed from ROC AUC statistics at 0.79.

Buffaloberry shrub density

Shrub density (stems per 20 m² strip plot) data were collected at 325 plots within the study area between 2001 and 2003 representing both random and animal use (telemetry) locations. Shrub densities were log transformed ($\log(\text{shrub density} + 1)$) with quantile regression (50th percentile or median) used to relate environmental data to variations in shrub density where shrubs were present. A Hosmer and Lemeshow (2000) model building approach was used for estimating environmental relationships to observed shrub density were present using environmental from Table A3. Sampling design covariates that included random vs. animal use location plot type (0 = random plot in study area, 1 = randomly selected bear telemetry location) and year of sample (2001 as reference year) were used as a 'base model' to account for potential biases associated with plots selected from animal telemetry locations. Of all the environmental variables assessed, one climatic variable – end of frost free period (EFP) – was the most supported environmental factor being negatively related to buffaloberry shrub density (Table A6). Bears selected for areas with higher buffaloberry shrubs based on the binary dummy variable of random vs. used plots, while shrub densities were lower in plots sampled in 2002 and 2003 perhaps generally reflecting poorer berry crops in those years (Table A6). Model parameters were used to predict shrub density in the study area by back

transforming to original density counts and scaling to 900 m² to reflect raster cell size. Reference variables for sampling design covariates (i.e. random plots and year of 2001) were used in all predictions of shrub abundance with predictions only made for raster cells where buffaloberry was predicted to be present and only within the range of values observed within plots (1 to 80 shrubs per 20 m²).

Buffaloberry fruit density

Fruit density data were collected within the same 325 plots where shrub densities were counted by counting fruit when present within the same 20 m² strip plot used to count shrub density. Because fruit were only available from mid to late summer (weeks 26 to 40), a subset of plots (n = 268) were used for modeling variation in Canada buffaloberry fruit density. Fruit density were log₁₀ transformed (log₁₀(fruit+1)) with quantile regression (50th percentile or median) used to relate environmental data, local shrub abundance (density), and sampling design covariates to variations in fruit density where shrubs were present during the fruiting season. A Hosmer and Lemeshow (2000) model building approach was again used based on environmental from Table A3. Sampling design covariates (plot type and year) were used in the base model to account for any biases associated with sampling methods. This included a plot type by year interaction since fruit abundance was variable among years and some plots were animal locations where we'd expected selection towards areas of higher fruit abundance. Because of the elevation gradient in the study area may result in later fruit availability, we also used week number (between 26 and 40 with a quadratic relationship tested) and an interaction between week number and mean annual temperature (which represents the elevation gradient) in the base model. As would be expected, fruit density was significant and positively related to shrub density (Table A7). Canopy cover was a significant predictor of fruit abundance (Table A7) with a quadratic relationship predicting that fruit density was highest between 35% and 40% forest canopy cover. Fruit density was also positively related to mean annual temperature (Table A7) predicting greater fruit abundance at lower elevations. The remaining variables in the model were associated with sampling design covariates (base model), although only week number and the interaction of week number and mean annual temperature (MAT) were substantially related to observed fruit abundance. Model parameters were used to predict fruit density in the study area by back transforming to fruit density and scaling up densities to 900 m² to reflect the raster cell size. Reference variables for sampling design covariates (i.e., random plots, 2001 base year, and week number assumed to be 32 which is around the start of ripening of buffaloberry fruit on ~ 1 August) were used in predictions of fruit density with predictions only made where buffaloberry was predicted to be present and only within the range of fruit density observations (0 to 6618 fruit per 20 m²). Note that the shrub density model above was

used as one of the predictors of fruit density so this model required both of the prior models for final map predictions.

Supporting analyses: null models, top–down vs bottom–up, scale and NDVI

Null models

Null models used in the main text included both a statistical null model with an intercept term and an ecological null model that included both road density and the ‘nuisance’ parameter of session number. The ecological null model therefore accounted for possible top–down effects on local abundance of grizzly bears via human activity associated with roads that reduce survival (Boulanger and Stenhouse 2015) and seasonal changes in detectability across sessions. Here we illustrate all combinations of null models in an AIC table demonstrating that the most supported model includes both road density (a priori top–down surrogate) and session number (Table A8). Note, however, that most of the support is with road density with the nuisance parameter of session being rather minor overall.

Separating bottom–up and top–down hypotheses

The main question addressed in the text is whether complementary or single food resource items better correlate with local patterns of grizzly bear abundance. In the main text all of the non-null models were fit using the most supported ecological null model from Table A8 which included the nuisance parameter of session and road density as a top–down surrogate variable to account for the inverse relationship between road density and survival rates in the study area (Boulanger and Stenhouse 2015). Here we separate all the bottom–up (food resource) from top–down (road density) hypotheses (see Table A9 for model/hypothesis description), while accounting for the nuisance parameter of ‘session’ to demonstrate that the ranking of complementary versus single food resource items is the same whether adding the top–down factor of roads or not (Table A10). Inferences are therefore robust to inclusion or separation of top-down factors with a small improvement in support for a model that includes the top-down factor (road density). When isolating the bottom–up factors, the complementary additive hypothesis is the most supported hypothesis.

Buffaloberry food supply measured at larger spatial scales

In the manuscript, road density and ungulates food supply were measured within moving window sizes of 7.44 km radius matching the average daily movement rate of solitary female and sub-adult grizzly bears during hyperphagia (Boulanger et al. 2013), while buffaloberry was measured at a 1.69 km radius matching detection scales around bait sites (Boulanger et al. 2004). Here we analyze

local bear abundance using the same larger (7.44 km radius) spatial scale for all variables. Model results demonstrate that hypotheses were ranked the same between scales (Table 2 in text and Table A11 below). Moreover, the top-ranked model using the 1.69 km scale for buffaloberry had an AIC of 714.05 (Table 2), while the same model at a 7.44 km scale was ranked at 718.13 (Table A11) for a Δ AIC of 4.08. This translated into an Akaike weight for the 1.69 km scale of 0.885 and the Akaike weight of the 7.44 km scale of 0.115 with an evidence ratio supporting the 1.69 km scale over that of the 7.44 km scale of 7.7 times.

Vegetation productivity (NDVI) and local bear abundance

Although not a formal part of the hypotheses being tested in the main text, surrogates of vegetation productivity, such as NDVI (natural difference vegetation index) and greenness, have often used to assess grizzly bear habitat and population density (Mace et al. 1999, Nielsen et al. 2002, Mowat et al. 2013). To ensure no strong correlations between metrics of vegetation productivity and key hypothesized variables of ungulate and buffaloberry food supply, we correlated maximum NDVI values for a representative year (2006) from MODIS satellite data (US Geological Survey 2015) with ungulate and buffaloberry food supply. This included correlations at three scales for NDVI: 250 m pixel and mean NDVI at 1.69 km mean and 7.44 km radii matching the scale of summarized buffaloberry and ungulate food supply.

Overall, correlations between NDVI and modelled food supply were neutral ($\text{NDVI}_{1.69 \text{ km}}$ and $\text{Buffaloberry}_{1.69 \text{ km}}$ $r = 0.08$) to negative ($\text{NDVI}_{7.44 \text{ km}}$ and $\text{Ungulates}_{7.44 \text{ km}}$ $r = -0.55$) in association (Fig. A2). As scale the scale at which NDVI was measured increased to the 7.44 km radius scale, the correlation with buffaloberry and ungulates became more negative. This demonstrates the general inverse relationship between key food resources considered in the paper (ungulates and buffaloberry) and vegetation productivity.

Baseline ecological models (session and road density) fit with the most supported NDVI variable (7.44 km radius) demonstrated a negative correlation between NDVI and local bear abundance ($\beta = -0.00071$, $\text{SE} = 0.00017$; $e^{\beta \text{StdX}} = 0.639$), opposite to what would be expected if vegetation productivity was most correlated to local patterns in grizzly bear abundance. Likewise, model support from AIC comparisons was weak with an AIC of 740.49 and a Δ AIC of 26.44 units from the most supported model (AIC = 714.05) which ignored vegetation productivity, but used instead ungulate and buffaloberry food supply. This suggests that vegetation productivity – as measured by maximum NDVI – was a poor predictor of local patterns in grizzly bear abundance, despite its widespread use in the literature. Use of metrics like NDVI likely reflects the ease at which these data are available, not the direct measure of resources that influence grizzly bear populations (at least in this study region).

References

- AltaLIS 2008. 20K Base Features. – <www.altalis.com/index.html>.
- Boulanger, J. et al. 2004. Sources of heterogeneity bias when DNA mark–recapture sampling methods are applied to grizzly bear (*Ursus arctos*) populations. – *J. Mammal.* 85: 618–624.
- Boulanger, J. et al. 2013. Use of multi-state models to explore relationships between changes in body condition, habitat and survival of grizzly bears *Ursus arctos horribilis*. – *Wildlife Biol.* 19: 274–288.
- Boulanger, J. and Stenhouse, G.B. 2015. The impacts of roads on the demography of grizzly bears in Alberta. – *PLoS ONE* 9: e115535.
- Boyce, M. S. et al. 2012. Managing moose harvests by the seat of your pants. – *Theor. Popul. Biol.* 82: 340–347.
- Boyce, M. S. et al. (2003). Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. – *Ecoscience* 10: 421–431.
- Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. – Springer.
- DeCesare, N. J. and Pletscher, D. H. 2006. Movements, connectivity, and resource selection of Rocky Mountain bighorn sheep. – *J. Mammal.* 87: 531–538.
- Dekker, D. 2009. Declines of bighorn sheep, *Ovis canadensis*, on deteriorating winter range in Jasper National Park, Alberta, 1981–2010. – *Can. Field Nat.* 123: 157–164.
- DMTI 2003. Digital Elevation Model. Markham, Ontario: DMTI Spatial Inc. – <www.dmtispatial.com>.
- ESRI 2012. ArcGIS Desktop: Release 10.1 – Environmental Systems Research Institute.
- Edwards, R. Y. 1956. Snow depths and ungulate abundance in the mountains of western Canada. – *J. Wildl. Manage.* 20: 159–168.
- Ferguson, S. H. et al. 2000. The influences of density on growth and reproduction in moose *Alces alces*. – *Wildlife Biol.* 6: 31–39.
- Gasaway, W.C. et al. 1986. Estimating moose population parameters from aerial surveys. – *Biological Papers of the Univ. of Alaska* No. 22, Fairbanks, Alaska, USA.
- Hebblewhite, M. et al. 2006. Is the migratory behavior of montane elk herds in peril? The case of Alberta's Ya Ha Tinda elk herd. – *Wildl. Soc. Bull.* 34: 1280–1294.
- Hosmer, D. W. and Lemeshow, S. 2000. Applied logistic regression, 2nd edn. – Wiley.
- Kie, J. G. et al. 2002. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. – *Ecology* 83: 530–544.

- Liu, C. et al. 2005. Selecting thresholds of occurrence in the prediction of species distributions. – *Ecography* 28: 385–393.
- Mace, R. D. et al. 1999. Landscape evaluation of grizzly bear habitat in western Montana. – *Conserv. Biol.* 13: 367–377.
- Maier, J. A. K. et al. 2005. Distribution and density of moose in relation to landscape characteristics: effects of scale. – *Can. J. For. Res.* 35: 223–2243.
- Mowat, G. et al. 2005. Grizzly *Ursus arctos* and black bear *U. americanus* densities in the interior mountains of North America. – *Wildl. Biol.* 11: 31–48.
- McCullagh, P. and Nelder, J. A. 1989. Generalized linear models, 2nd edn. – Chapman and Hall.
- McDermid, G. J. 2005. Remote sensing for large-area, multi-jurisdictional habitat mapping. – PhD thesis. – Dept of Geography, Univ. of Waterloo, Waterloo, ON, Canada.
- Mysterud, A. 2001. Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. – *J. Anim. Ecol.* 70: 915–923.
- Nicholson, M. C. et al. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. – *J. Mammal.* 78: 483–504.
- Nielsen, S. E. et al. 2004. Grizzly bears and forestry II: distribution of grizzly bear foods in clearcuts of west-central Alberta, Canada. – *For. Ecol. Manage.* 199: 67–82.
- Parker, K. L. et al. 1984. Expenditures for locomotion by mule deer and elk. – *J. Wildl. Manage.* 48: 474–488.
- Poole, K. G. and Mowat, G. 2005. Winter habitat relationships of deer and elk in the temperate interior mountains of British Columbia. – *Wild. Soc. Bull.* 33: 1288–1302.
- Post, E. and Stenseth, N. C. 1998. Large-scale climatic fluctuation and population dynamics of moose and white-tailed deer. – *J. Anim. Ecol.* 67: 537–543.
- Rolley, R. E. and Keith, L. B. 1980. Moose population dynamics and winter habitat use at Rochester, Alberta, 1965–1979. – *Can. Field Nat.* 94: 9–18.
- Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. – *Trans. Am. Geophys. Union* 38: 913–920.
- Telfer, E. S. 1978. Cervid distribution, browse and snow cover in Alberta. – *J. Wildl. Manage.* 42: 352–361.
- US Geological Survey. 2015. MODIS Vegetation Indices 16-Day L3 Global 250m (MOD13Q1) [digital data]. – NASA EOSDIS Land Processes DAAC, USGS Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota.
<https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/mod13q1>.

Tables A1. Variables used to predict ungulate abundance within the Yellowhead bear management unit in west-central, Alberta, Canada.

Class	Type	Description	Code
Landcover			
	upland tree	>5% tree cover by crown closure; mesic/dry moisture regime	UT
	wetland tree	>5% tree cover by crown closure; wet/aquatic moisture regime	WT
	upland herb	>5% herbaceous cover; mesic/dry moisture regime	UH
	wetland herb	>5% herbaceous cover; wet/aquatic moisture regime	WH
	shrub	>5% shrub cover; any moisture regime	SHR
	herb/shrub	UH+WH+SHR	SHRHRB
	water	<5% vegetated; aquatic moisture regime	WAT
	barren	<5% vegetated; mesic or dry moisture regime	BAR
	agriculture	Agricultural areas	AGR
Anthropogenic			
	well-sites	Buffered by 70m	ANT
	pipelines	Buffered by 20m	
	powerlines	Buffered by 30m	
	roads	Buffered by 30m	
	railway	Buffered by 30m	
	cutblocks	Forestry cutblocks	BLK
	coal mine	Reclaimed Cardinal/Gregg River open pit coal mine	Cmine
		Reclaimed Coal Valley open pit coal mine	Rmine
		Presence/absence of Cmine	Cmine1
		Presence/absence of Rmine	Rmine1
Forest attribute			
	conifer	Conifer dominated (>50% conifer)	CON
	deciduous	Deciduous dominated (\leq 50% conifer)	DEC
	canopy closure	Average canopy closure (non-forested = nodata)	CCx
		Average canopy closure (non-forested = zero)	CCndx
		Standard deviations in canopy closure (non-forested = nodata)	CCsd
		Standard deviations in closure (non-forested = zero)	CCndsd
	stand age	Average stand age (non-forested = nodata)	AGEx
		Average stand age (non-forested = zero)	AGEndx
		Standard deviations in stand age (non-forested = nodata)	AGEsd
		Standard deviations in stand age (non-forested = zero)	AGEndsd
Topography			
	slope	Average slope	SLPx
		Standard deviation of slope	SLPsd
	escape terrain	Amount of slopes >27°; patch size >7000m ²	ESCP1
		Amount of slopes >27°	ESCP01
		Presence/absence of ESCP1	ESCP1_1
		Presence/absence of ESCP01	ESCP01_1
		Average distance to slopes >27°; patch size >7000m ²	ESCPx1
		Average distance to slopes >27°	ESCPx01
	aspect	Average aspect scaled (-180, +180)	ASPx

	elevation	Standard deviation of aspect Average elevation Standard deviation of elevation	ASPsd ELEVx ELEVsd
<hr/>			
Water			
	small rivers	Stream length (Strahler order 1 and 2)	ORD0
	large rivers	Stream length (Strahler order 3–5)	ORD1
	rivers	ORD0 + ORD01	ORD01
	waterbodies	Naturally occurring wetlands and lakes	WATB

Table A2. Model averaged regression coefficients explaining variation in ungulate abundance as function of predictor variables. Coefficients were obtained by fitting generalized linear models and weighting predictions by Akaike weights (w_i) across the full set of candidate models.

Variable	Moose - male	Moose - female	Elk	White-tailed deer	Mule deer	Sheep
AREAc	0.27		1.37			
WT		1.38				
CON		-0.34				
DEC	1.18	0.15		5.46		
AGEndx			0.03			
AGEsd		-0.02				
CCx	0.02					
CCndsd					0.06	
ELEVsd			0.47 ⁻⁴	0.02		
SLPsd	0.08					
ESCPx01	0.45 ⁻⁴	0.49 ⁻⁶				
ESCPx01 ²	-0.56 ⁻¹¹	-0.37 ⁻¹¹				
ORD01		-0.53 ⁻⁷				
BLK			-0.88	-0.92		
Cmine			1.65			11.61
Rmine				1.29	0.91	
Constant	-0.71	1.24	-0.69	0.44	0.39	2.74

Table A3. Hypothesized environmental factors (themes), variables, and variable abbreviations of univariate, quadratic (\wedge^2) and interaction terms used to statistically model occupancy, shrub density, and fruit density of Canada buffaloberry *Shepherdia canadensis* at sampling plots in west-central, Alberta, Canada.

Hypothesized factor (theme)	Variable	Variable abbreviation
Climate	mean annual temperature	MAT (\wedge^2)
Climate	growing season precipitation	GSP (\wedge^2)
Climate	end of frost free period*	EFFP*
Soils	soil ph	pHca (\wedge^2)
Soils	sand content	TSand
Canopy cover — sunlight	canopy cover	Canopy
Terrain — sunlight	solar radiation	Solar
Terrain wetness	compound topographic index	CTI (\wedge^2)
Land cover — forest habitat	conifer forest	Conifer
Land cover — forest habitat	mixedwood forest	Mixedwood
Land cover — forest habitat	deciduous forest	Deciduous
Land cover — forest habitat	bog/fen	Treed wetland
Land cover — non-forest habitat	shrub	Shrub
Land cover — non-forest habitat	herbaceous	Herb
Climate interaction	interaction	MAT:GSP
Canopy cover-terrain interaction	interaction	CTI:Canopy
Sunlight-terrain interaction	interaction	CTI:Solar
Canopy cover-sunlight interaction	interaction	Canopy:Solar

* EFFP considered as an alternate to MAT in shrub and fruit density models.

Table A4. Ranking of candidate models predicting Canada buffaloberry *Shepherdia canadensis* occupancy at field plots in west-central Alberta, Canada.

Model				
ID	Model structure	AIC	Δ AIC	Model rank
12	land cover + climate + soil + sunlight ¹	2244.1	0	1
13	land cover + climate + soil + terrain	2246.3	2.2	2
1	global	2249.3	5.2	3
9	land cover + climate + soil	2303.4	59.3	4
10	land cover + climate + sunlight	2322.5	78.4	5
11	land cover + climate + terrain	2322.7	78.6	6
14	land cover + climate + sunlight + terrain	2326	81.9	7
8	land cover + climate	2388	143.9	8
2	soils and terrain global	2389.4	145.3	9
3	climate global	2427.6	183.5	10
7	soils global	2434.6	190.5	11
4	sunlight global	2555.4	311.3	12
5	land cover global	2562.8	318.7	13
6	terrain global	2604.8	360.7	14

¹Note that the ‘sunlight’ factor includes both canopy cover and terrain-derived solar radiation. This differs from the ‘terrain’ factor in including all terrain variables (solar radiation and terrain wetness).

Table A5. Logistic regression coefficients predicting the occurrence of Canada buffaloberry *Shepherdia canadensis* in field plots in west-central Alberta, Canada.

Variables	Coefficient (β)
Intercept (constant)	-26.59
Landcover	
conifer	0.746
mixedwood	1.157
deciduous	0.811
treed wetland	-0.204
shrub	0.460
herb	0.062
Climate	
MAT	-4.518
MAT ²	0.328
GSP	0.169
GSP ²	-0.000229
Soils	
Soil pH	-4.192
Soil pH ²	0.388
Soil (% Sand)	0.0173
Forest stand condition	
Canopy	0.00914
Terrain	
Solar	6.79
Interactions	
MAT:GSP	0.0100
Canopy:Solar	-0.0112

Table A6. Quantile regression coefficients (β) used to predict Canada buffaloberry shrub density (log transformed) within 20 m² plots based on environmental factors and survey design covariates. Standard error (SE) and significance (p) of parameters provided.

Variable	β	SE	p
EFFP (end of frost free period)	-0.067	0.027	0.015
plot type (bear use site)	0.539	0.149	<0.001
Year 2002 (vs 2001)	-0.480	0.158	0.003
Year 2003 (vs 2001)	-0.547	0.183	0.003
Constant	18.860	6.795	0.006

Table A7. Quantile regression coefficients (β) used to predict Canada buffaloberry (SHCA) fruit density (\log_{10} transformed + 1) within 20 m² plots based on environmental factors, shrub density (SHCA), and survey design covariates. Standard error (SE) and significance (p) of parameters provided.

Variable	β	SE	p
log(SHCA density)	0.692	0.080	<0.001
Canopy	0.028	0.011	0.009
Canopy ²	-0.000361	0.000129	0.005
MAT	1.731	0.522	0.001
plot type (used)	0.670	0.330	0.043
Year 2002	0.345	0.299	0.251
Year 2003	-0.611	0.810	0.451
plot type (used) \times 2002	-0.928	0.368	0.012
plot type (used) \times 2003	-0.353	0.841	0.675
week number	1.393	0.289	<0.001
week number ²	-0.020	0.004	<0.001
week number \times MAT	-0.059	0.015	<0.001
Constant	-24.195	4.793	<0.001

Table A8. Comparison of null models predicting local abundance of grizzly bears in west-central Alberta, Canada. Model selection results listing model log likelihoods (LL), model complexity (K), Akaike's information criteria (AIC), change in AIC (Δ AIC) and overall support (weights) of the models given data and models tested (w_i AIC). Models are rank ordered from most to least supported. The top ecological null model and the statistical null model were used in the main text.

Null model	Model LL	K	AIC	Δ AIC	w_i AIC
Session + Roads	-376.84	5	763.68	0.00	0.979
Roads	-381.67	4	771.35	7.67	0.021
Session	-402.71	4	813.43	49.75	0.000
Intercept	-407.02	3	820.04	56.36	0.000

Table A9. Set of hypotheses tested, model structure, and descriptions as it relates to testing top–down (mortality) and bottom–up (food resource supply) control in local patterns of grizzly bear abundance.

Hypothesis	Model structure	Description
Null	Null	No landscape pattern in bear abundance (mean count across study area)
Top–down	Null landscape (session + road density)	Bear abundance affected by session + local patterns in mortality risk/survival (top–down regulation)
Bottom–up (single resource – fruit)	Session + Fruit	Bear abundance affected by session + bottom–up regulation due to variations in fruit abundance (1.69 km radius)
Bottom–up (single resource – meat)	Session + Meat	Bear abundance affected by session + bottom–up regulation due to variations in ungulate abundance (7.44 km radius)
Bottom–up (complementary additive resources)	Session + Meat + Fruit	Bear abundance affected by session + bottom–up regulation of the combined additive effects of ungulates and fruit
Bottom–up (complementary interactive resources)	Session + Meat + Fruit + Meat × Fruit	Bear abundance affected by session + bottom–up regulation of the combined interactive effects of ungulates and fruit
Top–down + Bottom–up (single resource – fruit)	Null landscape + Fruit	Bear abundance affected by bottom–up regulation due to local variation in fruit abundance + Top–down effects
Top–down + Bottom–up (single resource – meat)	Null landscape + Meat	Bear abundance affected by bottom–up regulation due to local variation in meat (ungulate) abundance + Top–down effects
Top–down + Bottom–up (complementary additive)	Null landscape + Fruit + Meat	Bear abundance affected by the combined effect of fruit and meat (additive effect) + Top–down effects
Top–down + Bottom–up (complementary interactive)	Null landscape + Fruit + Meat + Fruit × Meat	Bear abundance affected by the combined effect of fruit and meat (multiplicative effect) + Top–down effects

Table A10. Comparison of candidate models explaining local abundance of grizzly bears separating bottom-up and top-down (landscape-null model) factors. All models, except the null model, have session number as a ‘nuisance’ parameter. Model selection results listing model log likelihoods (LL), model complexity (K), Akaike’s information criteria (AIC), change in AIC (Δ AIC) and overall support (weights) of the models given data and models tested (w_i AIC). Models are rank ordered from most to least supported. Bottom-up complementary additive refers to Meat + Fruit, while bottom-up complementary interactive refers to Meat + Fruit + Meat \times Fruit. Note that ranking of top models for complementary versus single resource hypotheses are the same.

Hypothesis (model)	Model LL	K	AIC	Δ AIC	w_i AIC
Top-down + Bottom-up (complementary additive)	-350.03	7	714.05	0.00	0.474
Bottom-up (complementary additive)	-351.67	6	715.33	1.28	0.250
Top-down + Bottom-up (complementary interactive)	-350.00	8	716.00	1.95	0.179
Bottom-up (complementary interactive)	-351.67	7	717.33	3.28	0.092
Top-down + Bottom-up (single resource of meat)	-355.49	6	722.97	8.92	0.005
Bottom-up (single resource of meat)	-361.26	5	732.52	18.47	0.000
Top-down + Bottom-up (single resource of fruit)	-368.88	6	749.77	35.71	0.000
Top-down	-376.84	5	763.68	49.63	0.000
Bottom-up (single resource of fruit)	-380.97	5	771.93	57.88	0.000
Null model (mean count of bears at all sites)	-407.02	3	820.04	105.99	0.000

Table A11. AIC table for main hypotheses (matching Table 2 in text) but measuring buffaloberry food supply at 7.44 km radius. Note rank order of hypotheses does not change.

Hypothesis (model)	Model LL	K	AIC	Δ AIC	w_i AIC
Top-down + Bottom-up (complementary additive)	-352.066	7	718.13	0.00	0.551
Top-down + Bottom-up (complementary interactive)	-351.389	8	718.78	0.65	0.399
Top-down + Bottom-up (single resource of meat)	-355.49	6	722.97	4.84	0.049
Top-down + Bottom-up (single resource of fruit)	-370.942	6	753.88	35.75	0.000
Top-down	-376.84	5	763.68	45.55	0.000
Null model (mean count of bears at all sites)	-407.02	3	820.04	101.91	0.000

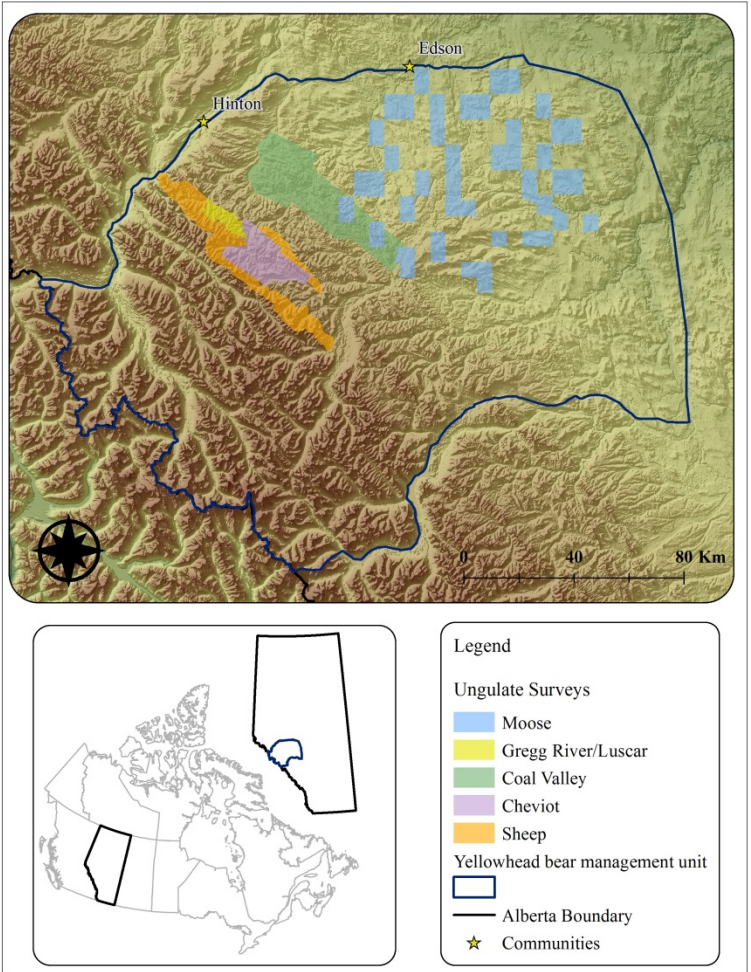


Figure A1. Map depicting ungulate survey areas in relation to the Yellowhead bear management unit study area boundary.

	NDVI-250 m (pixel)	NDVI-1.69 km	NDVI-7.44 km	Buffaloberry- 1.69 km	Buffaloberry- 7.44 km	Ungulates- 1.69 km	Ungulates- 7.44 km
NDVI-250 m (pixel)	1.00						
NDVI-1.69 km	0.39	1.00					
NDVI-7.44 km	0.14	0.69	1.00				
Buffaloberry-1.69 km	-0.01	0.08	-0.12	1.00			
Buffaloberry-7.44 km	-0.07	-0.05	-0.18	0.81	1.00		
Ungulates-1.69 km	-0.07	-0.28	-0.55	0.39	0.43	1.00	
Ungulates-7.44 km	-0.05	-0.28	-0.55	0.32	0.38	0.90	1.00

Figure A2. Pearson correlation matrix of vegetation productivity (maximum NDVI), buffaloberry food supply ($\log_{10}[\text{kcal}]$) and ungulate food supply ($\log_{10}[\text{kcal}]$). NDVI was measured at 3 scales: 250 m pixel, 1.69 km radius moving window, and 7.44 km radius moving window. Buffaloberry and ungulate food supply was measured only at the two larger scales. The yellow highlighted section illustrates neutral to moderately negative correlations between vegetation productivity and buffaloberry or ungulate food supply.