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Landscape estimates of carrying capacity for grizzly bears using nutritional energy supply for management and conservation planning

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ABSTRACT

Successful recovery and management of threatened and endangered species requires an understanding of the capacity of the available habitat to support the species. Measuring habitat supply, or specific elements of that habitat, has been a key objective and challenge in wildlife management, especially for wide-ranging omnivorous species. In this study, we provide a framework for estimating the carrying capacity of a threatened grizzly bear population in Alberta, Canada. Specifically, we compare current patterns in abundance from recent population inventories to potential abundance from our habitat-based estimates of carrying capacity to determine where conservation actions would be most effective in recovery. To estimate carrying capacity, we used field data from 2001 to 2016 to measure abundance of vegetation, insects (ants), and ungulates. We predicted spatial patterns in abundance and biomass from these field data using generalized linear models and combined these into one of five categories used by bears: roots, fruits, herbs, ants, and ungulates. Models were then converted to digestible energy (kilocalorie content) and summarized for individual watersheds. We then used a protected population of grizzly bears (i.e., a reference area) to calculate kilocalorie relationships per bear, and from that potential carrying capacities for watersheds using two methods. First, we considered the 'full resource' approach using kilocalories of all key food items. Second, we simplified it to only fruit and meat resources, for which data are more widely available and known to correlate locally with grizzly bear density. Despite differences between the two approaches, density (bears per 1000 km^2) estimates for carrying capacity were similar across most of the region for the two scenarios suggesting one can may be able to just use fruit and meat resources and thus other food items may not limit bear populations. Finally, we identified watersheds where differences between current bear densities and carrying capacity was large and road densities high (risk of bear mortality), and thus where management efforts are most needed. This study provides a comprehensive framework for estimating carrying capacity and demonstrates how these findings can be applied to support grizzly bear management and population recovery efforts.

1. Introduction

Wildlife populations are limited and regulated by a number of factors related to survival and productivity. Two elements influencing these factors are the availability and quality of food resources (Gordon, Hester, & Festa-Bianchet, 2004; Nijland, Nielsen, Coops, Wulder, & Stenhouse, 2014). Food resources and the nutrition they provide influence population performance and provide insight into the number of individuals a landscape can sustain (Chapman & Byron, 2018). This, in turn, has implications to wildlife managers for establishing population goals for management or, in the case of a threatened species, population recovery.

Carrying capacity is the theoretical maximum number of individuals of a species that can be sustained within a region given its environment (Verhulst, 1838; Whittaker, 1975). This measure can be used to determine the overall condition of an ecosystem (White & Gregovich, 2017),

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determine population thresholds to set goals and recommendations for management (Punt et al., 2020), measure the impact of anthropogenic disturbance (Punt et al., 2020, White & Gregovich, 2017), determine the length of time needed for population recovery (Russ & Alcala, 2004), and establish wildlife reintroduction thresholds (Doan & Guo, 2019). For threatened species, or those with small population sizes, knowledge of potential carrying capacity can be used to define and recommend recovery objectives (Lyons et al., 2018; Thapa & Kelly, 2017; Watari et al., 2013; Zerbini et al., 2019). While the International Union for Conservation of Nature (IUCN) has numerous criteria for determining whether a species is classified as threatened, such as whether a population has less than 1000 mature individuals (IUCN, 2012), these criteria are not species-specific (Hutchings & Kuparinen, 2014). For far-ranging, large-bodied mammals, population criteria are difficult and expensive to monitor (Proctor et al., 2010; Steenweg et al., 2016). Given this challenge, some have focused instead on "bottom-up" regulation of populations to acknowledge the linkage to habitat which ultimately can be managed (Nielsen, McDermid, Stenhouse, & Boyce, 2010, 2015; Nielsen, Larsen, Stenhouse, & Coogan, 2017). To help guide management actions, a more species-specific approach to determining carrying capacity involves estimating nutritional resources available to an animal's energetic requirements.

Although carrying capacity can be determined in a number of ways and is inherently dynamic, a widely used approach for monitoring wildlife is to compare the total available digestible energy within an area to an individual animal's energy requirement (Chapman & Byron, 2018;

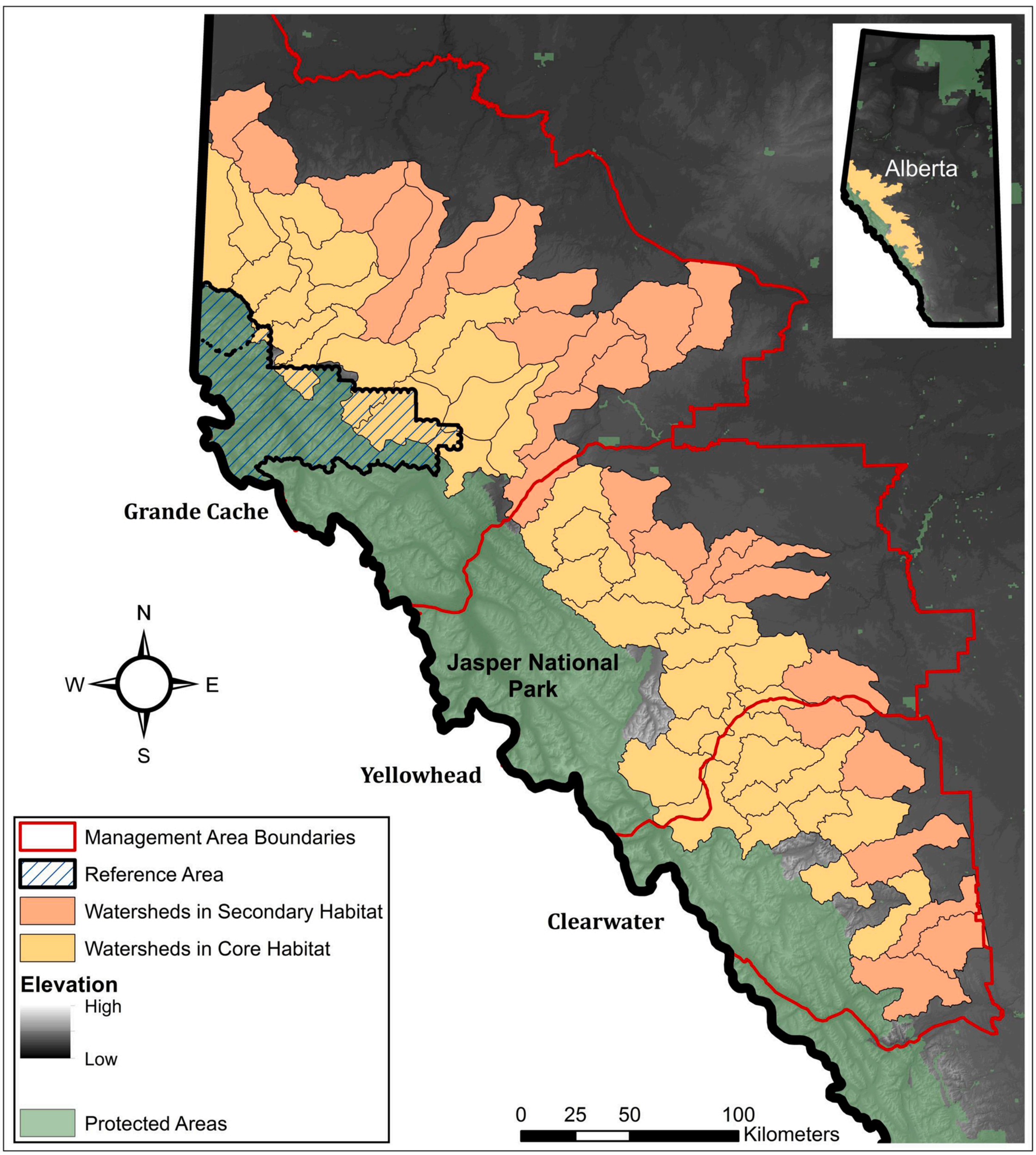

Fig. 1. Study area represented by watersheds in core (low road density) and secondary (low to moderate road density) grizzly bear habitats within Grande Cache, Yellowhead, and Clearwater management areas in west-central Alberta, Canada.

Lyons et al., 2018). Monitoring and measuring digestible energy has been employed in both marine and terrestrial ecosystems using field-based and remote sensing methods (Guyondet et al., 2015; Iijima & Ueno, 2016; Lyons et al., 2018; Perry & Schweigert, 2008). With rapid advances in remote sensing technologies and data, it is possible to estimate carrying capacity at increasingly fine spatial scales and over larger regions (Lyons et al., 2018). These fine-scale carrying capacity estimates can identify key areas where management or recovery efforts would be most likely to succeed (i.e., areas with high carrying capacity and low population size), and thus allow managers to focus conservation efforts and resources more efficiently.

Our goal in this study was to calculate and evaluate the carrying capacity of grizzly bears (*Ursus arctos*) for three management areas in Alberta, Canada, and to understand how two different analytic approaches (from complex to simple) influence carrying capacity estimates. We hypothesized that current landscape conditions in each management area would support a higher population of bears than already present, suggesting that top-down factors (mortality rates) limit local populations, but setting recovery targets requires knowing carrying capacity (habitat and food supply). We demonstrate the utility of our approach in a management context. Specifically, as higher road density has been associated with greater mortality risk among grizzly bears (Boulanger & Stenhouse, 2014), we compared the difference between carrying capacity estimates and observed population estimates to areas with high road densities to highlight places where conservation efforts may be the most effectively applied. Through this research, we demonstrate how carrying capacity can be used to support and guide management actions for the recovery of this provincially threatened species.

2. Methods

2.1. Study area

The study area is a 42,633 km^2 region of west-central Alberta, Canada (Fig. 1) that encompasses core and secondary grizzly bear habitat based on road densities, secure habitat, and grizzly bear use as defined by Nielsen, Cranston, and Stenhouse (2009). The area is subdivided into watershed units approximately 500 km^2 in size and covers three management areas managed as provincial, multiple use "crown" lands. These uses encompass industrial resource extraction activities, including forestry, oil, gas, and mining, as well as recreational activities including hiking, hunting, fishing, and off-highway vehicle use. The vegetation and climate are characteristic of the Rocky Mountain, Foothills, and Boreal Natural Regions (Natural Regions Committee, 2006), which are topographically rugged with a strong elevational gradient from west (mountains) to east (foothills). The high-elevation alpine environment, comprised of non-vegetated areas of rock and ice interspersed with herbaceous and shrub meadows, transitions to mainly forests of pure and mixed stands of evergreen and deciduous tree species. Conifers, including lodgepole pine (*Pinus contorta*) and spruce species (*Picea* spp.), are more common at intermediate- and high-elevation sites, whereas broadleaf species (*Populus* spp.) dominate south-facing slopes and moderate to low elevations. In low-lying wet and boggy areas at lower elevations, black spruce (*Picea mariana*) and tamarack (*Larix laricina*) occur. The area is also home to several ungulate species, including mountain goat (*Oreamnos americanus*), sheep *(Ovis canadensis)*, moose *(Alces alces)*, elk *(Cervus canadensis)*, mule and white-tailed deer (*Odocoileus hemionus* and *Odocoileus virginianus*, respectively), and woodland caribou (*Rangifer tarandus*).

2.2. Data

2.2.1. Field measures of vegetation and ants

Based on previous knowledge of seasonal foods used by grizzly bears in the area (Munro, Nielsen, Price, Stenhouse, & Boyce, 2006; Nielsen et al., 2010), we modelled the distribution of different species of vegetation and ants from a dataset consisting of 4663 plots obtained from five complementary studies across seven management areas within grizzly bear range in Alberta. Each management area was surveyed at least once over a 16-year period (2001–2016). At field plots, researchers recorded information on the distribution (i.e., presence/absence) and abundance (i.e., percent cover or count) of 19 food items (Table 1, Appendix S1). Although sampling protocols varied slightly among studies, we reconciled differences in plot size by standardizing to area-based measures. Abundance of herbs and shrubs was quantified by visually estimating percent ground cover. For fruit, ant colonies in mounds, or coarse woody debris, density was estimated by taking the raw plot-level count divided by the total ground area sampled and rounded up to the nearest integer.

2.2.2. Field measures of ungulates

Ungulate counts (9202 observations) were obtained from aerial ($n = 43$) and ground-based ($n = 1$) surveys that overlapped with the study area. Surveys were conducted by Alberta Environment and Parks (AEP), Alberta Conservation Association (ACA), Bighorn Wildlife Technologies Limited (BWT), and Teck Resources Limited (TR), and consisted of both stratified random block surveys and transect surveys. Most surveys were undertaken to estimate and monitor population sizes of multiple ungulate species within specific Wildlife Management Units. The remaining surveys were designed to quantify and monitor ungulate abundance associated with two open-pit coal mines south of Hinton, Alberta, Canada. While we recognize that deer and caribou represent a part of grizzly bear diets, survey data are less available; therefore, this study focused on moose, elk, and sheep, which represent the dominant source of ungulate protein for bears (Munro et al., 2006).

2.2.3. Environmental variables

We used climate, terrain, and land cover variables extracted at field plots and ungulate survey locations to estimate distribution and abundance of species. Variables included forest structure, forest composition, land cover (including natural openings such as grass and shrub lands and anthropogenic disturbances such as agricultural lands, roads, and coal mines), terrain, soil composition/moisture, wildfire and forest harvest history, and climate variables (such as temperature, precipitation, and frost-free days). For further details on environmental variables used, refer to Appendix S1 and S2.

2.3. Modelling approach

Here we provide a brief overview of the modelling procedures used (also see Fig. 2). For more detailed methods, see Appendices S1 and S2.

For vegetation and ants, we used plot-level data and logistic regression to model their distribution (occurrence), following methods from Nielsen et al. (2010). For each individual plant model, we implemented a purposeful variable selection approach which saw the least-significant explanatory variables successively removed from candidate models until only those with significance levels below a certain threshold ($p = 0.1$) remained (Hosmer & Lemeshow, 2005). To model plant abundance at the plot level, which was conditional on plant presence, we used linear regression applied to logit-transformed percent cover data (bound between 0 and 1). We then modelled non-transformed fruit and ant density with negative binomial regression. For fruit models, we included percent cover of the shrubs as a fixed explanatory variable since abundance of the plant should scale with potential abundance of fruit, and we restricted inclusion of our fruit data per species according to the first and last Julian date of fruit detections across all vegetation plots. We assigned zeros to plots in which plants had been observed, but no fruit was counted during that fruiting period. To evaluate the performance of models, we used 10-fold cross-validation repeated ten times to evaluate the area under the curve (AUC), root mean squared error (RMSE), and Efron's R^2 (see Appendix S1 for more details).

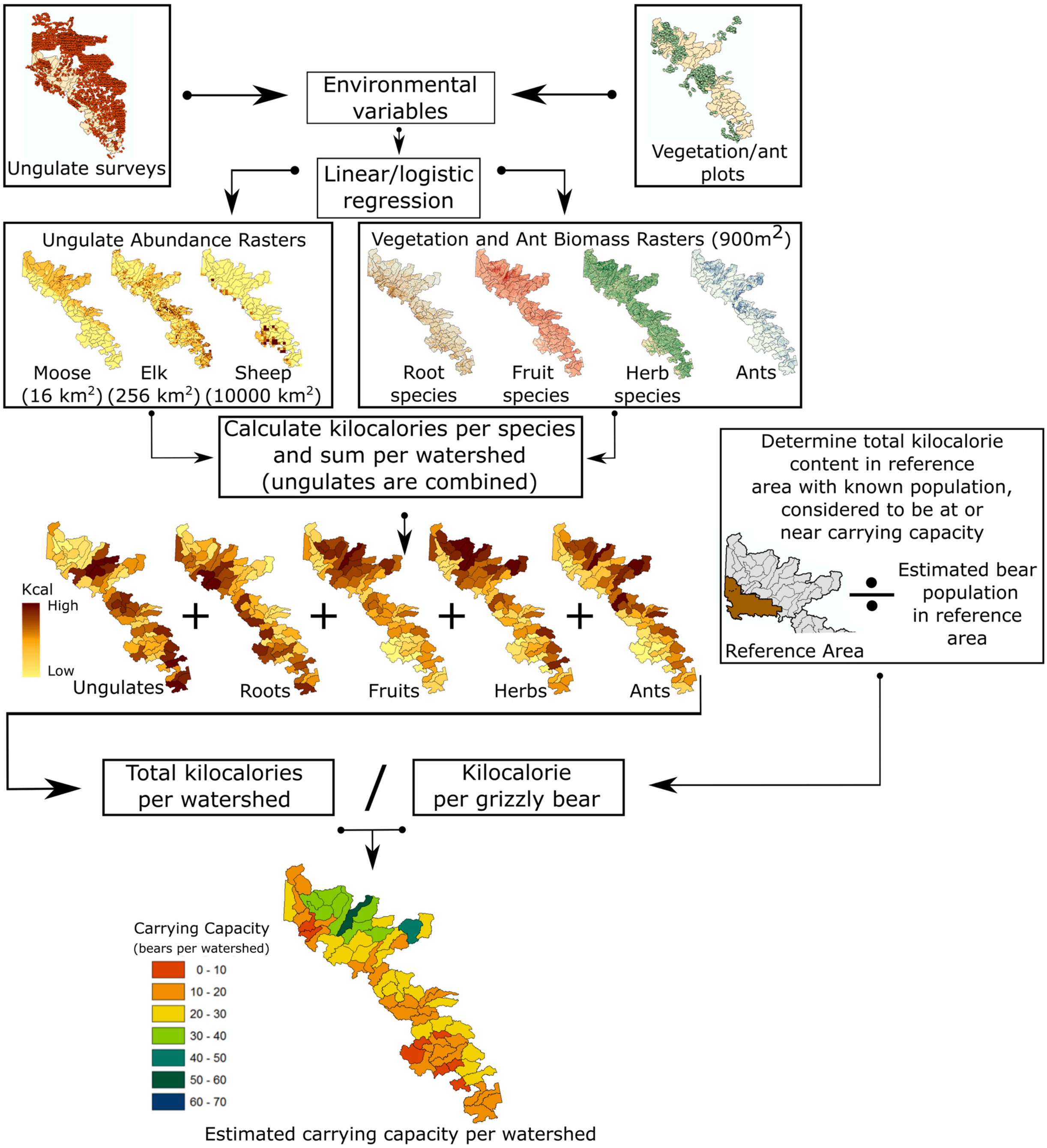

Fig. 2. Flow diagram illustrating the methods used to estimate carrying capacity for watersheds in west-central Alberta, Canada, using a reference population assumed to be at carrying capacity.

Models of ungulate distribution and abundance were developed using methods outlined in Nielsen et al. (2017). Briefly, the best-fitting logistic and count models for each species was estimated using a purposeful model selection approach (Bursac, Gauss, Williams, & Hosmer, 2008; Hosmer & Lemeshow, 2000). Primarily, we fit univariate models for each form (binary and continuous) of a specific explanatory variable, then we fit univariate models that incorporated only the best-fitting form of each explanatory variable from stage one. Only variables with a p-value of 0.25 or less were included as candidates in multivariable regression models. We then fit and re-fit regression models until all significant ($p = 0.1$) variables and confounders were present (Zuur, Ieno, & Elphick, 2010). We also considered non-linear effects by adding a squared term where appropriate. Finally, we determined whether an interaction between latitude and elevation would account for any unexplained geographic patterns and improve model fit. To evaluate the predictive performance of logistic and count models, we used 10-fold cross-validation repeated ten times and calculated the mean and standard deviation of the AUC, RSME, and Efron's R^2. For count models, we also used Pearson's correlation coefficient, Spearman's rank correlation coefficient, and model calibration (Potts & Elith, 2006).

2.4. Digestible energy (kilocalorie) conversions

To simplify food models, we combined associated food items into five broader categories of fruit, herbs, roots, ants, and meat. We determined fruit and ant biomass per 900 m^2 (30-m cell resolution) across the study area using ArcMap version 10.3.1 (ESRI 2015) based on model coefficients using all fruit items and ant density predictions in conjunction with dry weights from field sampling and the literature (Table 1, Appendix S4; Coogan, Raubenheimer, Stenhouse, & Nielsen, 2014). For all herbaceous food items, except *Taraxacum officinale*, we developed generalized linear mixed-effects models with a random effect for sample plot. For *Taraxacum officinale*, we developed an allometric generalized linear model. These models related percent cover to dry weight (Table 1, Appendix S1), which was measured from vegetation clippings collected in the field at a sub-sample of sites. We then applied model coefficients to estimate biomass across the study area based on predicted cover. For the roots of *Hedysarum alpinum*, percent cover values were first converted to root density using coefficients from a linear mixed-effects model, with a random effect for study area, prior to estimating biomass using root dry weight. Digestible energy was then estimated using biomass predictions and kilocalorie (kcal) values per food type obtained from López-Alfaro, Coogan, Robbins, Fortin, and Nielsen, 2015; Table 1, Appendix S4), similar to the approach of Nielsen et al. (2017).

For ungulate (meat) abundance, we estimated biomass of moose, elk, and sheep at spatial scales of 4, 16, and 100 km^2, respectively (Table 8, Appendix S2), using spatially predicted abundance and body mass values from the literature averaged across gender and age classes for each species (Table 9, Appendix S2). To adjust live-weight biomass for each species, we removed water and indigestible components based on average percent body composition estimates for moose without hide and ingesta (ingesta-free body mass [IFB mass]; Hundertmark, Schwartz, & Stephenson, 1997), as values for elk and sheep were not available. We then calculated digestible energy using conversion factors for meat (Pritchard & Robbins, 1990) and Equation 1, in which IFB mass was taken to be 88.1 %, dry matter of IFB mass was 34.8 %, ash-free content IFB was 94.9 % (Hundertmark et al., 1997), and digestible energy was 4800 kcal/kg (López-Alfaro et al., 2015; Table 1, Appendix S4).

$$\text{Whole ungulate biomass (kg)} \times \%\ \text{IFB mass} \times \%\ \text{dry matter IFB} \times \%\ \text{ash-free IFB} \times \text{digestible energy (kcal/kg)} \quad (1)$$

2.5. Estimating kilocalorie requirements per bear

To estimate the kilocalorie requirement of a grizzly bear, we used a reference population assumed to be at carrying capacity (see Reference Area, Fig. 1). The reference area consisted of the Willmore Wilderness Park and Kakwa Wildland Provincial Park in the northwest portion of the study area that is part of the Grande Cache management area. We chose this area and population as it is protected and recent population densities estimates have shown that this area has among the highest bear densities in the province and densities are substantially higher than any other area within the region (Alberta Grizzly Bear Inventory Team 2008, 2009Alberta Grizzly Bear Inventory Team 2008, 2009). Furthermore, the protected status of the reference area meant that habitat alteration caused by active resource developments were absent, and that human-caused mortality of bears was low due to the prohibition of sport hunting in the province since 2006. Given these conditions, we feel it is appropriate to assume our reference area, and the population within is at or near carrying capacity. To calculate total kilocalories per bear in the reference area, we summed the digestible energy for all modelled food resources and divided this by the population estimate of the reference area of 124.4 bears (Alberta Grizzly Bear Inventory Team 2008, 2009Alberta Grizzly Bear Inventory Team 2008, 2009).

2.6. Carrying capacity scenarios

Based on our understanding of the local grizzly bear foraging ecology and diet in this region (Munro et al., 2006), we used two approaches to determine how different combinations of fruit, herbs, roots, ants, and meat affected habitat-based carrying capacity estimates. The first approach was more complex and considered all major food resources (fruit, herbs, roots, ants, and meat) in the diet of bears (Munro et al., 2006) and is hereafter referred to as the “full resource” approach. The second approach, called the “fruit and meat” approach, simplified items to just fruit and meat, which is considered to be a limiting factor when related to local patterns in bear density (Nielsen et al., 2017). The value of this simple approach is that it would be easier to implement elsewhere and over time as ungulate data are generally collected and updated by government agencies and thus readily available, and fruit data can be obtained more cost-effectively than the full spectrum of vegetation consumed by bears which is quite diverse. In comparing these two approaches, we assess in relative terms how sensitive estimates of carrying capacity are to different combinations of food items.

2.7. Calculating watershed-scale estimates of carrying capacity

For each approach, we calculated total digestible energy for each watershed across the three bear management areas by summing mapped estimates of kilocalories among food items. Watershed boundaries were defined by subdividing major watershed units along terrain and watercourse boundaries into the approximate home range size of an adult female grizzly bear (~ 500 km^2; Boulanger & Stenhouse, 2014). To better compare the kilocalorie content between watersheds, we divided total kilocalories in the watershed by the area of the watershed to get kilocalories per km^2. The carrying capacity of each watershed was then estimated using both approaches by dividing the total kilocalories per watershed by the kilocalorie per bear derived from the reference population. These were then standardized to densities for each watershed as bears per 1000 km^2, allowing comparison among different sized watersheds and to the literature, where bear densities are reported at this scale.

We assume grizzly bear population size scales with total available food energy within the reference area, since carrying capacity estimates from consumption rates (e.g., Hobbs & Swift, 1985) is largely lacking for grizzly bears. Whether bears were allotted a portion of or all available food, dividing total digestible energy by the kilocalories per bear would yield identical results and further, is capable of addressing the use of food resources by competitors. Therefore, our methods adjust for potential over- or under-estimation of predicted grizzly bear food supply.

2.8. Management example

We provide a management example by comparing carrying capacity density estimates (bears per 1000 km^2) among watersheds to the most current grizzly population inventory estimates of bear density. Population estimates were conducted in 2008 (Grande Cache; Alberta Grizzly Bear Inventory Team 2008, 2009Alberta Grizzly Bear Inventory Team 2008, 2009), 2014 (Yellowhead; Stenhouse et al., 2015) and 2018 (Clearwater; Stenhouse, Boulanger, Phoebus, Graham, & Sorensen, 2020). Densities per watershed were derived from grizzly bear density surface models from Boulanger, Nielsen, and Stenhouse (2018) by averaging surface (cell) values within each watershed unit. We then calculated the difference between carrying capacity and population density to identify watersheds in which the largest difference in bears per 1000 km^2 occur and to determine how these differences relate to road density within watersheds. Thus, we identify where management of road access would be predicted to be most effective and therefore should be prioritized for conservation recovery of the species. In particular, watersheds with road densities between 0.65 and 0.75 km per km^2 or over 0.75 km per km^2 were highlighted because road densities above a 0.75 km threshold have been shown to negatively affect grizzly bear populations (Boulanger & Stenhouse, 2014).

3. Results

3.1. Spatial distribution of digestible energy

Total fruit and herbaceous kilocalorie contents were generally higher in the eastern part of the study area (Fig. 3), along with the central and northern portions of the Grande Cache management area. Average kilocalorie content per km^2 for both fruit and herbs was highest in the Grande Cache management area and lowest in the Clearwater management area (Fig. 4a) that also corresponds to large-scale patterns in current population estimates. Total root kilocalorie content was higher in the mountainous regions to the west (Fig. 3), with the highest root kilocalories per km^2 occurring in the Clearwater management area and the lowest occurring in the Grande Cache management area (Fig. 4a). Total ant kilocalorie content was generally higher in the eastern section of the study area (Fig. 3), whereas ant kilocalories per km^2 were highest in the Yellowhead management area and lowest in the Clearwater management area (Fig. 4a). Total ungulate kilocalorie content was generally higher in the eastern part of the study area (Fig. 3), while ungulate kilocalories per km^2 were highest in the Yellowhead management area and lowest in the Grande Cache management area (Fig. 4a).

3.2. Distribution of digestible energy

Herb and fruit resources comprised the majority of the digestible energy in all management areas (Fig. 4b) and represented the greatest proportion of kilocalorie content in the Grande Cache management area. Roots, ants, and ungulates comprised the lowest percentages of digestible energy across all management areas, but their contribution to total digestible energy was greatest in the Clearwater management area.

3.3. Carrying capacity

3.3.1. Full resource approach

When considering the full resource approach, the Grande Cache management area was estimated to have the highest carrying capacity of the three management areas with a total of 756 bears, or 35 bears per 1000 km^2. Estimates ranged from 8 to 56 bears per watershed, which was the largest amount of variation observed across the three management areas, with the highest carrying capacity estimates found in the central part of the management area (Fig. 5). The Yellowhead management area was estimated to have a carrying capacity of 324 bears, or 28 per 1000 km^2, with estimates ranging from 5 to 29 bears per watershed. The highest carrying capacity estimates were in the northern and southern portions of this management area (Fig. 5). The Clearwater management area was estimated to have the lowest carrying capacity of the three management areas with 222 bears, or 23 per 1000 km^2 (Table 1). Watershed estimates within the Clearwater management area had the least variation of the three management areas examined, ranging from 5 to 24 bears, with the highest carrying capacity estimates in the east-central portion of the management area (Fig. 5).

3.3.2. Fruit and meat approach

When considering the simplified fruit and meat approach, the Clearwater management area continued to have the lowest carrying capacity estimate and the Grande Cache management area the highest, with estimates being reduced from 2 to 16 % in the Yellowhead and Clearwater management areas respectively, while increasing by 1 % in the Grande Cache management area. The Clearwater management area had a carrying capacity of 188 bears (reduced by 35 bears from the full resource approach) or 19 bears per 1000 km^2 (reduced by 4 bears per 1000 km^2; Table 1) and ranged from 4 to 20 bears per watershed. The Yellowhead management area had an estimated carrying capacity of 319 bears (reduced by 5 bears from the full resource approach) or 28 per

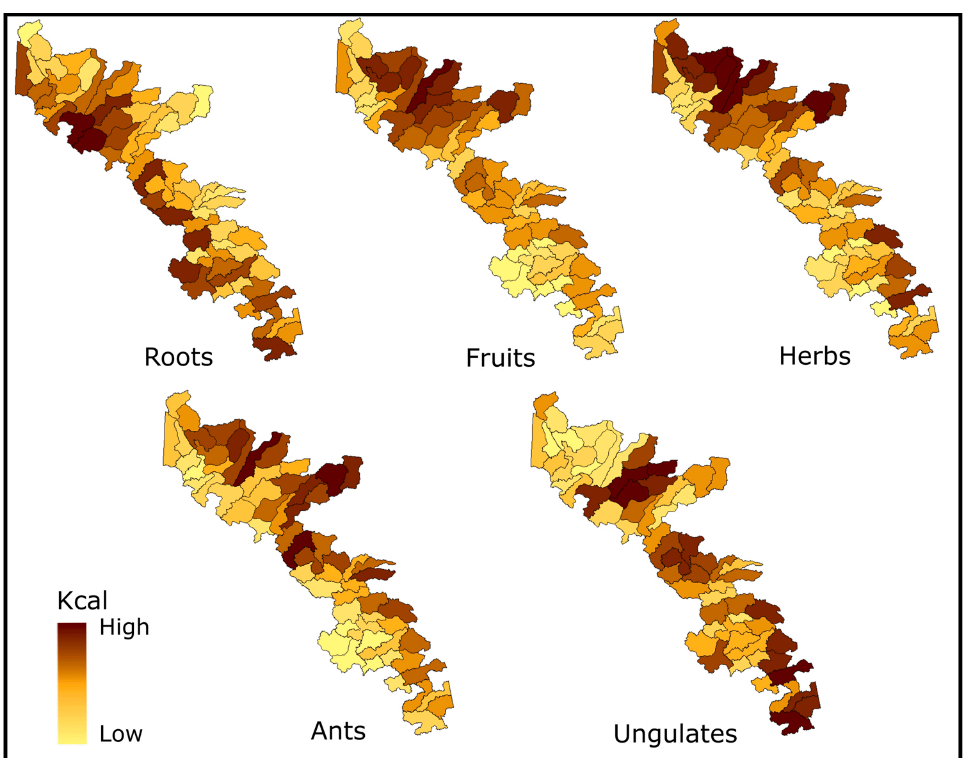

Fig. 3. Watershed kilocalorie distribution per food species in watershed units for core and secondary habitat throughout the Grande Cache, Yellowhead, and Clearwater Management areas of west-central Alberta, Canada.

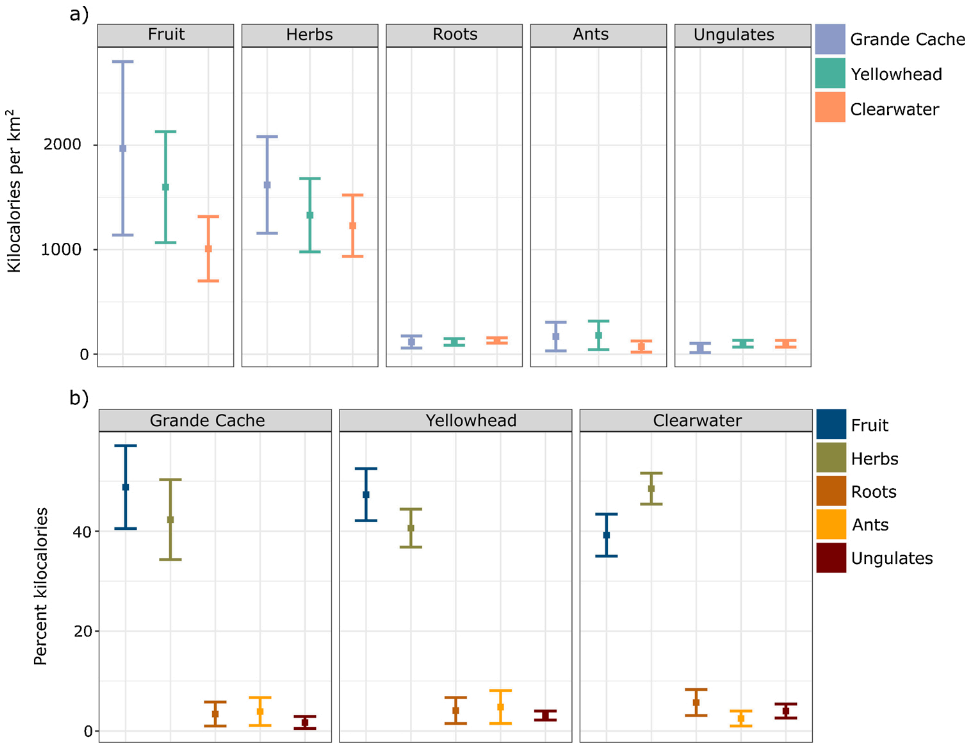

Fig. 4. a) Mean and standard deviation of kilocalories per km^2 (divided by 1000 for scale) of each food type (ungulates, fruit, herbs, roots, and ants) for watersheds in the Grande Cache (n = 30), Yellowhead (n = 19), and Clearwater (n = 16) Bear management areas in west-central Alberta. b) Percentage of total digestible energy (kilocalories) comprised of each food type (ungulates, fruit, herbs, roots, and ants) in watershed units, summarized over Grande Cache (n = 30), Yellowhead (n = 19), and Clearwater (n = 16) management areas in west-central Alberta.

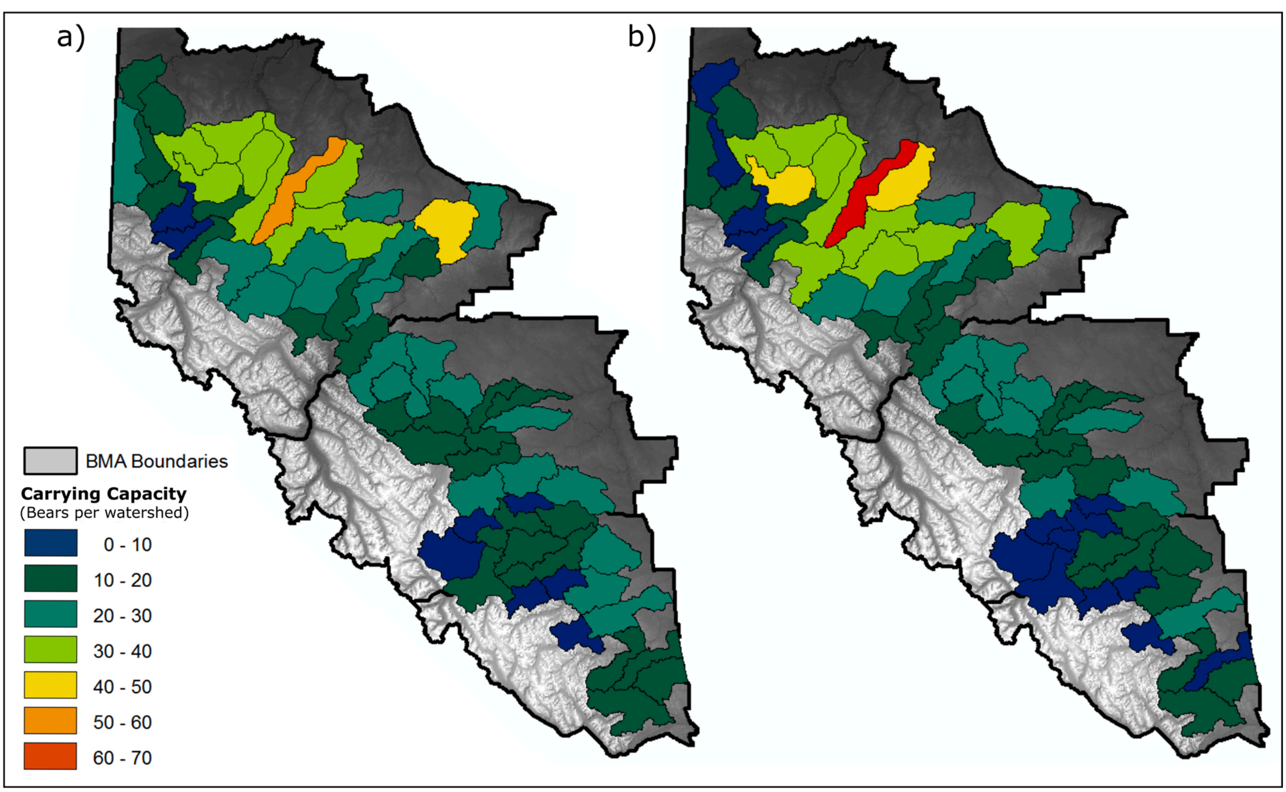

Fig. 5. Carrying capacity distribution (number of bears) for a) the full resource approach and b) the fruit and meat approach for core and secondary habitat in Grande Cache, Yellowhead, and Clearwater management areas.

1000 km^2 (reduced by 1 bear per 1000 km^2), with estimates ranging from 3 to 28 bears per watershed. The Grande Cache management area had an estimated carrying capacity of 766 bears (increased by 10 bears from the full resource approach) or 36 per 1000 km^2 (increased by 1 bear per 1000 km^2), with watershed estimates ranging from 8 to 66 bears.

Table 1
Total carrying capacity and bears per 1000 km^2 calculated for core and secondary grizzly bear habitat in the Grande Cache, Yellowhead, and Clearwater management areas.

Approach	Carrying Capacity	Grande Cache	Yellowhead	Clearwater
Full resource approach	*Total Bears*	756	324	223
	Bears per 1000 km^2	35	29	23
Fruit and meat approach	*Total Bears*	766	319	188
	Bears per 1000 km^2	36	28	19

3.4. Management example

While recent grizzly bear population inventory data illustrate that density estimates increase westward (Fig. 6a), carrying capacity (density) estimates demonstrate the opposite trend corresponding to a general gradient in ecosystem productivity (Fig. 6b). Therefore, when calculating the difference between the two, it is apparent that western watershed units are closer to carrying capacity or, in the case of five watersheds in the Yellowhead and Clearwater management areas, slightly exceeding our estimated carrying capacities (Fig. 6c). The watersheds in the eastern portion of our study area, however, have a much larger discrepancy in the number of bears. When road density (an indicator potential of mortality risk) is considered, it is evident that almost all watersheds with a road density of more than 0.75 km per km^2 are found in the eastern parts of our study area and largely coincide with watersheds that have a greater difference between population density and carrying capacity density estimates. There were 11 watershed units with a difference in bear numbers that was greater than 21 (shown in yellow, Fig. 6c) and a road density that was higher than 0.75 km per km^2 (Fig. 6d).

4. Discussion

We demonstrate a comprehensive method for estimating carrying capacity for a large-ranging omnivore using landscape predictions of digestible energy. We illustrate that even when considering just two key food resources results were similar to a more complex approach considering all major food items. Our management example highlights priority areas for implementation of management actions. Furthermore, the methods described here can be simplified and tailored to different management objectives for a variety of wildlife species, from carnivores to herbivores, to provide spatially explicit information regarding where conservation efforts would be of greatest value.

4.1. Comparing modelling approaches

Carrying capacity estimates were compared using two approaches: the more complex full resource approach, and a simplified approach focusing on fruit and meat resources (Table 1). When comparing general results for the three management areas, we found that the Clearwater management area had the lowest total carrying capacity for both approaches, which reflects its smaller size; it also had the lowest estimated carrying capacity density for each approach due to lower supplies of digestible energy. This may reflect the fact that the Clearwater management area as a whole is the most dissimilar to our reference area, and that our models do not account for the food resource supply associated with agricultural lands (e.g., livestock and grains), which may be an important contributor to the diets of bears along the eastern edge of the Clearwater management area, where agricultural lands are prevalent (Northrup, Stenhouse, & Boyce, 2012). In contrast, the Grande Cache management area had both the highest total carrying capacity, as well as the highest carrying capacity density for both approaches, with areas of high digestible energy well-distributed throughout the management area. These findings were expected given that the reference area is within the Grande Cache management area, and that the remainder of the management area contains similar environments with little or no agricultural influence.

When contrasting results from both approaches within individual management areas, we found that the difference in carrying capacity density between the complex and simplified approaches was negligible in both the Yellowhead and Grande Cache management areas. Here, the simpler fruit and meat approach differed from the more complex full resource approach by only 1 bear per 1000 km^2, suggesting that the simpler fruit and meat approach can be applied in both management areas with little loss in precision. Comparatively, in the Clearwater management area, differences in carrying capacity density were more pronounced with lower estimates when using the simplified fruit and meat approach, with a difference of 4 bears per 1000 km^2. This larger difference suggests that the more complex, full resource approach may better represent carrying capacity within the region. However, while the more complex approach may be more accurate, the simplified approach was still reasonably close and importantly identified the same watersheds where differences between observed population densities and estimated carrying capacity densities associated with high road densities were highest. Therefore, we suggest that the more cost-effective and simplified approach could be reasonably applied to all management areas.

4.2. Management application

We compared grizzly bear population densities from recent inventories with estimated densities of carrying capacity by watershed units to demonstrate the management application of our findings. We found that watersheds with low population densities and high levels of mortality risk (identified by high road densities; Boulanger & Stenhouse, 2014) do contain the food resources necessary to support higher grizzly bear numbers. Watersheds in the eastern portion of all three management areas were associated with the largest differences between observed populations and carrying capacity density estimates, with carrying capacity being noticeably higher than population densities in these watersheds. This is likely due to increasing levels of natural resource extraction and human activity (Boyce, Blanchard, Knight, & Servheen, 2001; Nielsen et al., 2010), which are accompanied by an increase in road densities (Boulanger & Stenhouse, 2014) and should be prioritized for the implementation of management actions.

As it may be economically unfeasible to manage all watersheds with differences in grizzly bear numbers, we suggest that managers focus on areas where management actions would be most effective. In our example, we highlighted 11 watersheds that have both a difference in 21 or more bears between observed population estimates and carrying capacity estimates and a road density higher than 0.75 km per km^2 (Fig. 6d) which is known to reduce bear survival (Boulanger & Stenhouse, 2014). We suggest that management actions within these watersheds be directed toward reducing road densities and motorized access to existing roads to most support grizzly bear recovery (Proctor et al., 2020). This may be accomplished by permanently decommissioning roads no longer in use or by implementing a gate system to reduce motorized vehicle traffic. We would expect these actions to increase the number of bears using these watersheds coupled with an increase in bear survival (Lamb et al., 2018). Our models further identified watersheds near carrying capacity; we suggest that these areas be managed with the goal of sustaining long-term food supplies and reducing mortality risk.

While our management example identified areas to focus management efforts, it also highlighted five watersheds in the south-western parts of our study area in the Yellowhead and Clearwater management areas where current densities marginally exceeded carrying capacity. As

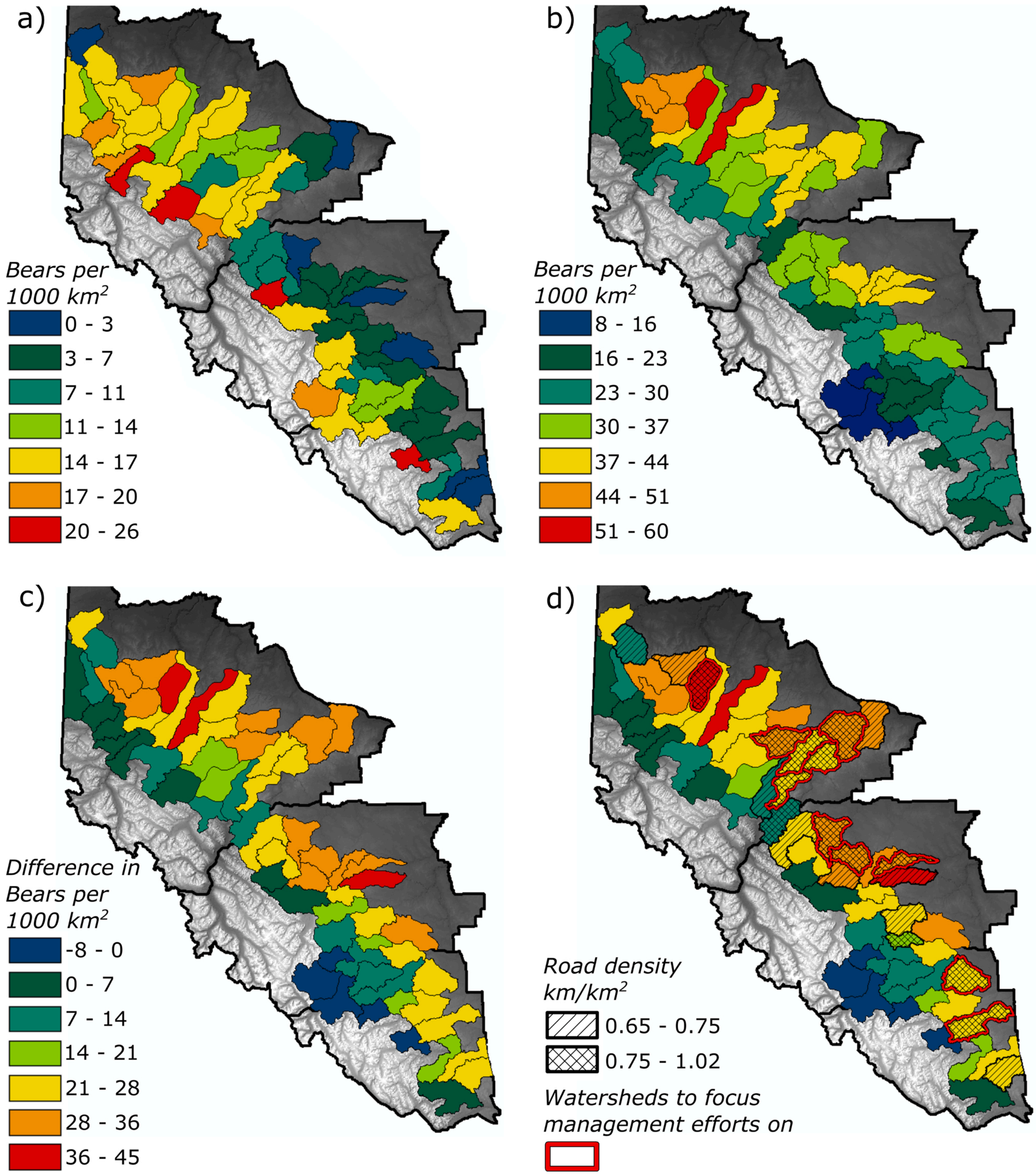

Fig. 6. a) Current observed grizzly bear densities by watershed, b) carrying capacity density estimates, c) difference between current and carrying capacity densities, and d) difference between current and carrying capacity densities overlaid with road density thresholds (0.65–0.75 km/km^2; moderate risk, 0.75–1.02 km/km^2; high risk), identifying 11 watersheds with a greater than 21 bears per 1000 km^2 difference in current to carrying capacity and higher than 0.75 km/km^2 road density, where management efforts should be focused.

there is no evidence for density-dependent effects such as grizzly bear die-off (Price, 1999), decreased populations of other wildlife species due to over-predation (Schoener & Spiller, 1996), or increased competition for resources (Vetter, 2005), it may point to inaccuracies in either the carrying capacity estimates or estimates of observed current densities. Our methods may be underestimating carrying capacity within these areas as a result of having similar environments to our reference area (mountainous regions), with a comparable ratio of access, digestible energy, and grizzly bear population. Second, our food models may under-predict digestible energy within mountainous environments due to the variable and heterogeneous nature of both terrain and climate or the seasonal distribution of ungulates in mountainous terrain.

4.3. Limitations and future work

While carrying capacity is useful from a management, conservation, and recovery perspective for setting possible recovery objectives or prioritizing areas for conservation action, there are some inherent limitations to basing estimates on digestible energy. First, it can be a challenge to locate a reference area with a population that is at carrying capacity. Here, we assumed our reference area to have a grizzly bear population at or near carrying capacity; though there is evidence to support this, the actual carrying capacity of this area is unknown due to the lack of comprehensive, long-term field data, which is difficult to obtain for grizzly bears. Therefore, we feel that the selection of a large protected area with little to no anthropogenic landscape change or human-caused bear mortality is a reasonable choice. Second, we did not specifically account for the distribution or energetic requirements of other wildlife, which could compete for resources and thus lower carrying capacity estimates for bears (Chadès, Curtis, & Martin, 2012). However, the approach of using a reference population addresses this concern as the calculated kilocalorie requirement per bear is related to total food supply and takes into account what is consumed by competitors. Moreover, our study area is fairly similar and geographically coincident meaning that competitors are similar between regions. We also did not account for prey catchability (e.g., a moose may be easier prey than a sheep), as incorporating those aspects would greatly increase methodological complexity and potentially introduce more error. Third, we did not examine the relationship between food supply and denning (non-active period). Future work could incorporate aspects of the wintering ecology of grizzly bears to inform management decisions (Pigeon, Stenhouse, & Côté, 2016). However, there is evidence that den site selection is positively related to autumn and spring food supply and therefore reflected in these models." Finally, we did not evaluate long-term temporal variation in carrying capacity estimates resulting from changes in land cover, industrial activities, and infrastructure development. Some areas may be more variable than others and exhibit variability in carrying capacity due to natural and anthropogenic disturbance dynamics (Souliere, Coogan, Stenhouse, & Nielsen, 2020). To better understand carrying capacity and its influences, we suggest using our methods at regular intervals to forecast changes in carrying capacity with changing land cover. This would provide resource and land managers with data to identify important practices for managing wildlife populations over time.

4.4. Conclusion

While this methodology and the carrying capacity estimates produced here can contribute to the establishment of population recovery targets for wildlife species, it is important to recognize that they approximate the maximum population based on biological potential. In the case of grizzly bears, these values may not align with social and economic preferences or be feasible from a local management perspective, particularly in areas with high rates of human-bear conflict, where proximity to humans may not favour increased bear densities (e.g., agricultural lands; Morehouse & Boyce, 2016; Northrup, Pitt et al., 2012; Northrup, Stenhouse et al., 2012). Managers must balance competing interests and determine where management strategies may be most effectively and efficiently implemented. This balance may vary geographically, with some carrying capacity values centred around biological potential, and others more constrained by low social acceptability (Pyare, Cain, Moody, Schwartz, & Berger, 2004). One possible framework could involve setting population recovery targets as a percentage of carrying capacity according to geographic location, social constraints, and implementation efficiency.

Our results contribute information that managers can use to guide decisions on land use activities and wildlife conservation efforts. With this methodology, we provide a basis for implementing large- (management area level) or fine-scale (watershed level) management or recovery goals for grizzly bears that can be transferred to other wildlife species. While the use of carrying capacity for managing wildlife populations has its limitations, these methods represent a comprehensive framework for understanding how the nutritional resources needed by a species are distributed on the landscape. When combined with an understanding of top-down regulatory factors that influence population dynamics, wildlife managers can gain greater insight into management decisions that will play a vital role in species recovery planning.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.jnc.2021.126018.

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