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Effects of habitat quality and access management on the density of a recovering grizzly bear population

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Abstract

1. Human activities have dramatic effects on the distribution and abundance of wildlife. Increased road densities and human presence in wilderness areas have elevated human-caused mortality of grizzly bears and reduced bears' use. Management agencies frequently attempt to reduce human-caused mortality by managing road density and thus human access, but the effectiveness of these actions is rarely assessed.
2. We combined systematic, DNA-based mark–recapture techniques with spatially explicit capture–recapture models to estimate population size of a threatened grizzly bear population (Kettle–Granby), following management actions to recover this population. We tested the effects of habitat and road density on grizzly bear population density. We tested both a linear and threshold-based road density metric and investigated the effect of current access management (closing roads to the public).
3. We documented an *c.* 50% increase in bear density since 1997 suggesting increased landscape and species conservation from management agencies played a significant role in that increase. However, bear density was lower where road densities exceeded 0.6 km/km^2 and higher where motorised vehicle access had been restricted. The highest bear densities were in areas with large tracts of few or no roads and high habitat quality. Access management bolstered bear density in small areas by 27%.
4. *Synthesis and applications*. Our spatially explicit capture–recapture analysis demonstrates that population recovery is possible in a multi-use landscape when management actions target priority areas. We suggest that road density is a useful surrogate for the negative effects of human land use on grizzly bear populations, but spatial configuration of roads must still be considered. Reducing roads will increase grizzly bear density, but restricting vehicle access can also achieve this goal. We demonstrate that a policy target of reducing human access by managing road density below 0.6 km/km^2, while ensuring areas of high habitat quality have no roads, is a reasonable compromise between the need for road access and population recovery goals. Targeting closures to areas of highest habitat quality would benefit grizzly bear population recovery the most.

KEYWORDS
access management, connectivity, environmental change, grizzly bear, human-impacted systems, large carnivore, mortality, recolonisation, road density, spatially explicit capture-recapture

1 | INTRODUCTION

The world is becoming increasingly roaded, providing humans access to previously inaccessible areas (Ibisch et al., 2016). Wilderness across the globe is being lost (Watson, Shanahan, Marco, Sanderson, & Mackey, 2016) with wildlife incurring a high demographic cost (Benítez-lópez, Alkemade, & Verweij, 2010; Fahrig & Rytwinski, 2009). Increasing human–carnivore overlap as humans gain access into the remaining wilderness is elevating the cumulative pressures on carnivore populations (Ceia-Hasse, Borda-de-Agua, Grilo, & Pereira, 2017); however, large-scale carnivore recolonisation and human–carnivore coexistence are possible in human-dominated landscapes when targeted conservation efforts relieve human pressures on carnivores (Chapron, Kaczensky, & Linnell, 2014). A landscape of global human–carnivore coexistence will require an understanding of the factors limiting carnivore populations and robust management actions to mitigate these factors.

Grizzly (brown) bears (*Ursus arctos*) have experienced drastic range contractions across the globe due to habitat loss and direct persecution (McLellan, Proctor, Huber, & Michel, 2016; Ripple et al., 2014). Globally, grizzly bear survival decreases in areas where humans and bears overlap, especially near roads (Falcucci, Ciucci, Maiorano, Gentile, & Boitani, 2009; Schwartz, Haroldson, & White, 2010), even in unhunted populations (Boulanger & Stenhouse, 2014; Nielsen, Herrero, et al., 2004). Conservation of grizzly bears under increasing densities of humans and roads will require management of human access into bear habitat; this can be accomplished by either (1) reducing road densities, or (2) limiting public access to roads. Both of these management tools are currently used in North America, yet there is little empirical evidence to support their utility (but see Boulanger & Stenhouse, 2014; Schwartz et al., 2010) and none testing the effect of these management actions on bear density.

Our study focused on a provincially threatened grizzly bear population, the Kettle–Granby Grizzly Bear Population Unit (GBPU; Figure 1), at the species' southern range margin in south-central British Columbia (BC). This population was designated as provincially threatened based on a 1997 population inventory [38 bears (95% CI: 23–53), Boulanger, 2000; Boulanger et al., 2002] that estimated the population to be less than half the habitat-based carrying capacity (Gyug & Hamilton, 2007). Both prior to and following the 1997 population inventory, land and wildlife managers in the area undertook management actions to recover grizzly bears and maintain wilderness in an increasingly industrialised landscape. As is typical in many management scenarios, multiple management actions were enacted. Grizzly bear hunting was closed in the Kettle–Granby GBPU in 1995 because the bear population was thought to be declining. Between 1985 and 2001, as road densities continued to increase due to forestry, three provincial parks (covering 14% of land area in the GBPU) and two access management areas (5% of the GBPU land area) were created. Provincial parks do not allow industrial activities and thus serve as a potential refuge from roads and associated human access. Access management areas were put in place to eliminate motorised vehicle access by the public into sensitive grizzly bear habitat that had been roaded. In spite of these efforts, active road densities (mean = 1.64 km of road per km^2 of area) currently exceed the long-term target of 0.6 km/km^2 outlined in the Government Action Regulation for grizzly bears for the Kettle–Granby GBPU (BC Regulation 582/2004; General Wildlife Measures #8-373), stimulating scrutiny of provincial management of road densities for grizzly bear conservation (Forest Practices Board 2017; Ng & Dhaliwal, 2016).

In 2015, we conducted a DNA-based mark–recapture inventory of grizzly bears (Woods et al., 1999) in the Kettle–Granby GBPU to estimate the number of bears present following 20 years of management actions, and to investigate the ecological and anthropogenic factors that are currently influencing density. To accomplish this, we used spatially explicit capture–recapture (SECR) methods that incorporate covariates to examine the combined effects of road density, road closures, protected areas and habitat quality on population density. Land and wildlife managers often have greater control over road densities and access restrictions than they do habitat quality, thus our primary goal was to test the effect of road density on grizzly bear density and to then examine the efficacy of mitigation strategies: road closures (access management) and road density thresholds. Second, we compared the 2015 and 1997 population estimates to assess population trend in response to the management actions implemented in the interim. Third, we crafted recommendations for land managers based on our data and presented these here and in a condensed report tailored to local managers (Mowat, Lamb, Smit, & Reid, 2017). Finally, we used the density–landscape relationships from the Kettle–Granby GBPU to assess the potential for bears to recolonise adjacent extirpated areas. The approach outlined here provides a general framework and method for using mark–recapture information from any species to investigate potential limiting factors to population density and the effectiveness of management actions. Integration of spatial covariates with SECR methods provides a substantial step forward in the testing of hypotheses pertaining to the management of wildlife populations.

2 | MATERIALS AND METHODS

2.1 | Study area

In BC, Grizzly Bear Population Units (GBPUs) are used to group grizzly bears into jurisdictional units for management purposes (Figure 1). In southern BC, GBPU boundaries often follow natural and man-made

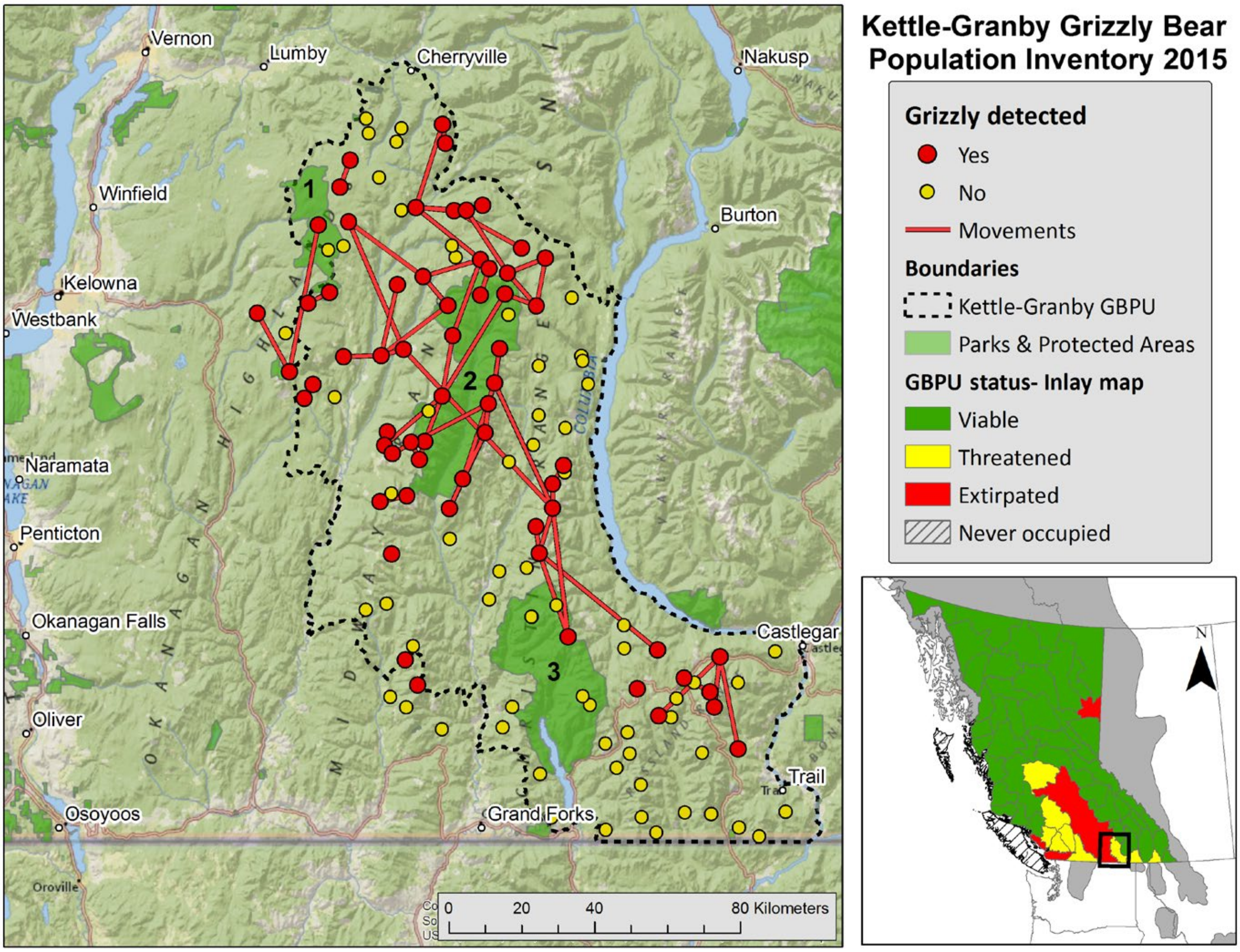

FIGURE 1 Study area for the 2015 grizzly bear population inventory of the threatened Kettle–Granby Grizzly Bear Population Unit (GBPU) in British Columbia, Canada. Grizzly bear sampling locations, detections and between-site movements within the Kettle–Granby are shown on the left. Provincial Parks (>100 km^2) within the unit include (1) Graystokes, (2) Granby and (3) Gladstone. Provincial status of GBPUs is shown on the bottom right, with the southern distribution of grizzly bears outside British Columbia shown in grey (portion of Yellowstone population omitted along the bottom right)

barriers that bears infrequently cross or, less often, boundaries between genetically distinct populations (Proctor et al., 2012). The Kettle–Granby GBPU (6,581 km^2) extends from the United States–Canada international border, north to Highway 6, and is bounded by the Kettle River to the west and Lower Arrow Lake to the east. Grizzly bear hunting was closed in the Kettle–Granby GBPU in 1995 (Stent, 2011). Logging occurs throughout the GBPU, except in provincial parks, and is the main motivation for backcountry road construction. Current road density in the Kettle–Granby GBPU is 1.64 km/km^2, and roads are used by industry to access cut blocks and by the public for recreation. Access management areas near Granby Provincial Park permit industry use but exclude the public, which nearly eliminates motorised traffic.

Terrain is variable throughout the Kettle–Granby GBPU; high plateaus and rolling hills are common in the southern portion of the area, while the northern half is more mountainous. Subalpine parkland is common at high elevations, but alpine meadows and avalanche chutes are rare. Areas of lower elevation are usually heavily forested; however, dry, south-facing hillsides dominated by shrubs and grasses are common in the southern portion of the GBPU.

2.2 | Inventory design

We followed study design suggestions from Efford and Boulanger (2015) who conducted a simulation exercise specific to the Kettle–Granby population to evaluate various sampling designs based on the goal of maximising both cost efficiency and the precision of population estimates. This involved using 7 × 7 km cells to distribute trap effort and checking 125 scent-lured hair snag sites across four successive sessions to achieve the target precision of <20% relative standard error. Efford and Boulanger (2015) found that moving sites between simulated sampling sessions did not improve precision and that small deviations from systematic site coverage did not cause bias or reduce precision.

2.3 | Field and genetic methods

Between June 15 and August 19, 2015, we set scent-lured hair snag sites throughout the Kettle–Granby GBPU and checked them for hair samples four times at roughly 2-week intervals. A total of 124 sites (96 ground and 28 helicopter access) were monitored throughout the summer (Figure 1). We used 3–4 litres of rotten cow blood and ½ litre of putrefied fish oil as a scent-lure at the sites. We used standard methods for site construction and sample collection (Kendall et al., 2008; Woods et al., 1999); further information can be found in Lamb, Walsh, and Mowat (2016) and Mowat and Lamb (2016).

Genetic analysis was done at Wildlife Genetics International (Nelson, BC, Canada). We analysed eight microsatellite loci and gender to assign individual identity with high confidence. Genotyping methods and subsampling procedures followed standard practices as detailed in Paetkau (2003), Mowat, Heard, Seip, and Poole (2005) and Lamb et al. (2016).

2.4 | Statistical analysis

We used SECR models (Borchers, 2012) to estimate the density and abundance of grizzly bears in the Kettle–Granby GBPU. We used the "secr" package (Efford, 2016), a likelihood-based approach accessed in program R (R Development Core Team, 2016), to conduct our population analysis. A "secr" model consists of two nested models, a detection model and a state model, which are fit to grizzly bear detection data. The detection model relates to the spatial detection of individuals, where the detection probability of a trap is related to the trap's proximity to an individual's home range centre, such that traps far from an individual's home range centre have reduced detection probability. The state model uses a latent Poisson point process to describe the distribution and density of home range centres within the region of analysis.

We fit SECR models to the detection data using a hazard half-normal detection function, which is described by the detection model and controlled by the parameters λ (lambda) and δ (sigma). Lambda describes the per capita detection probability per unit effort. Sigma describes the spatial extent of an individual's use of the landscape, such that animals with large home ranges have large sigma values. The state model (hereafter, density model) allows a null, homogenous density surface (D) to be fit to the region of interest, or permits the user to input spatial covariates (Figure 2) to create a heterogeneous density surface that potentially distributes home range centres in a more ecologically meaningful way.

We used three groups of spatial covariates (Figure 2) to refine density estimates and further investigate the factors that affect demography in the region:

1. Habitat (A): Maps of grizzly bear habitat suitability were created using Broad Ecosystem Units (*c.* 1,800 ha) from the provincial classification system (Resources Information Standards Committee, 2006). Each unit was subjectively rated (from 1 to 6) by bear habitat experts based on descriptions of ecological factors (climate, geology, terrain, physiography and vegetation), local grizzly bear research and inventory results, and local, experiential knowledge. The highest seasonal value for a unit was used for the annual map in order to best depict the habitat quality as perceived by a wide-ranging animal that can move between habitats seasonally. The suitability maps represent vegetation food only and do not include salmon, ungulates, insects, or human foods and garbage.

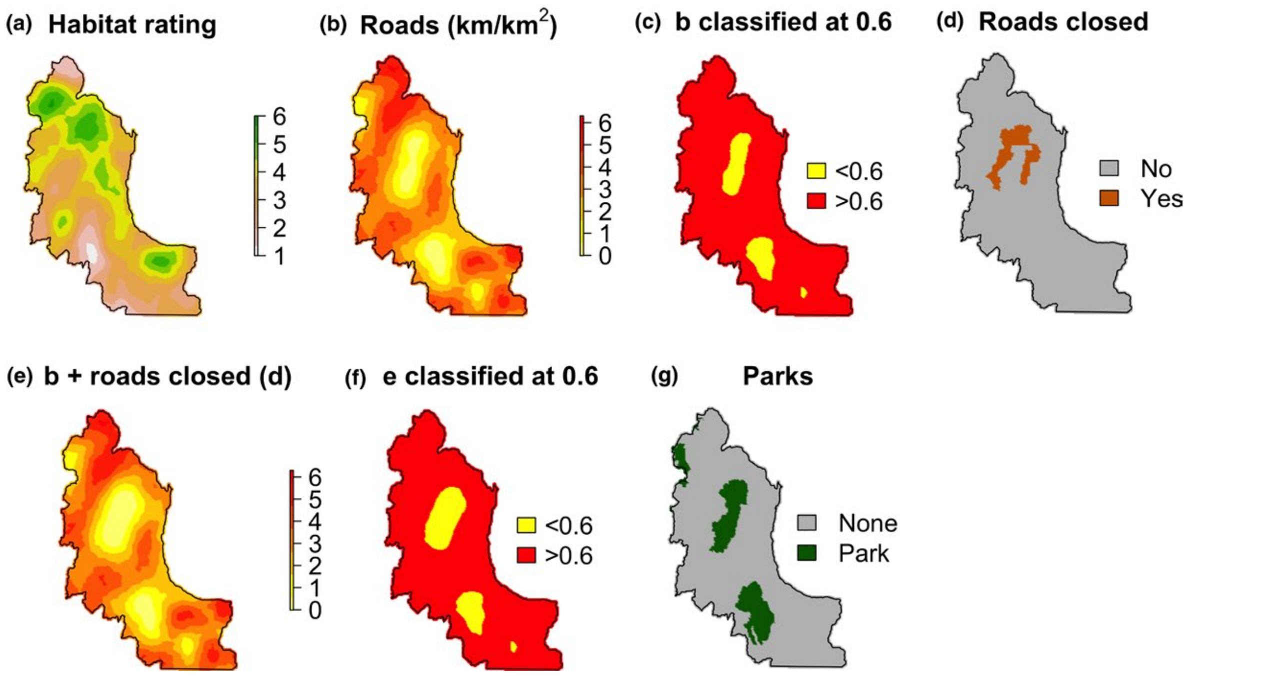

FIGURE 2 Spatial depiction of covariates hypothesised to influence grizzly bear density in the Kettle–Granby GBPU of south-central British Columbia in 2015

2. Road density (B-F): We used a provincial road lines product from 2015 (Provincial Grizzly Bear Technical Working Group, 2016), which is the most accurate and up-to-date provincial road layer available. We tested both road density (B, Road Dens) and a threshold road density covariate classified at 0.6 km/km^2 (C, Road Dens 0.6) based on proposed provincial road density standards (Provincial Grizzly Bear Technical Working Group, 2016) and research suggesting grizzly bear females select home ranges with road densities below this threshold (Mace, Waller, Manley, Lyon, & Zuuring, 1996), or face survival consequences (Boulanger & Stenhouse, 2014). Due to the potential negative effects of roads, managers in some jurisdictions close roads to motor vehicle traffic (D, Road Closures) to reduce human presence (some permitted industrial use is allowed) in grizzly bear habitat. We tested the effects of roads and road closures simultaneously by creating a road density variable that was based only on roads open to motor vehicles and compared models. We again tested a continuous measure of roads open to motor vehicles (E, Open Road Dens) and a threshold variable classified at 0.6 km/km^2 (F, Open Road Dens 0.6).
3. Protected areas (G, Parks): Protected areas can be sanctuaries for wildlife as these areas receive increased protection from development.

We summarised habitat and road density using an 8-km radius moving window analysis carried out in ArcGIS 10.3 (ESRI). We chose to use a moving window because the relationship between an individual's home range centre and the surrounding habitat extends beyond the habitat characteristics directly adjacent to the home range centre, especially for wide-ranging animals. Annual home ranges for grizzly bears range between 200 and 1,250 km^2 (8–20 km radii) depending on sex, age and habitat quality (Graham & Stenhouse, 2014; McLellan, 2015; M. Proctor, unpubl. data), thus we used an 8-km radius (200 km^2) as an approximation of the area used by bears during our period of investigation (*c*. 2.5 months, or just under half of the non-denning season).

The area of density integration in our "secr" model was constrained to a 20-km buffer around all traps, which represents the extreme edge of detection for the individuals in the sample. We bounded the area of integration using a polygon of non-habitat (see Figure S1), which we defined using expert opinion and landscape features such as large lakes, habitat suitability and large valleys settled by people. Using an area of integration that is too small can positively bias "secr" density estimates, while too large an area does not, as density estimates asymptote with buffer width (Figure S2).

We created a priori hypotheses pertaining to both the detection and density models and compared the fit of these models using Akaike's information criterion (Table 1; Akaike, 1974; Burnham & Anderson, 2002). Fitting complex "secr" models can be computationally intensive, thus we first fit a series of detection models to the data using a homogenous density surface and used the top detection model in our subsequent runs of the density model. Covariates hypothesised to influence λ included session-specific detection (*t*, time) and behavioural response (bk, site-learned response). We fit only one model for δ, a null model where home range index was static through time and space because differences in home range size between the sexes have been shown to be compensatory with λ in other study areas (Efford & Mowat, 2014). Following the identification of a top detection model, we fit this model to each sex separately to estimate sex-specific detection parameters (λ and δ), and to test whether the sum of our sex-specific abundances was similar to the model with both sexes included.

We also explored the road density threshold of 0.6 km/km^2 proposed by the province of BC (Provincial Grizzly Bear Technical Working Group 2016) and other jurisdictions (such as Alberta, Canada; Alberta Grizzly Bear Recovery Plan 2008–2013, 2008 and the United States; Mace et al., 1996) as a road density target above which grizzly bear conservation is a concern. We classified the open road density (Figure 2e) using breakpoints between 0.1 and 3 km/km^2, fit "secr" models while implicitly controlling for habitat quality by including the Habitat variable in our models, and finally computed log likelihoods and weights for each model. In this comparison, each model had the same number of parameters (*k*) and only differed in the breakpoint used to classify road density variables. Thus, we directly compared models with log likelihood, where the model with the maximum log likelihood characterised the optimal break point. In addition, we calculated cumulative model weights to identify the range of breakpoints with competing fit to the data.

Finally, we used the habitat-density relationships from the top "secr" model to create a density surface within the Kettle–Granby GBPU and extrapolated these relationships into the west where grizzly bears are currently absent. Producing a density surface

TABLE 1 Model selection table for spatially explicit capture–recapture model implemented in "secr." Detection model for all models below: lambda ~ t + bk, sigma ~ 1. See Section 2 text for variable definitions. *k* = number of parameters in model

Model	*k*	AIC_c	$dAIC_c$	AIC_c weight
D ~ Habitat + Open Road Dens 0.6	9	1,246.599	0	0.455
D ~ Habitat + Road Dens 0.6	9	1,247.225	0.626	0.333
D ~ Habitat + Open Road Dens	9	1,249.745	3.146	0.094
D ~ Habitat + Park	9	1,250.777	4.178	0.056
D ~ Habitat + Road Dens	9	1,250.841	4.242	0.054
D ~ Habitat	8	1,255.376	8.777	0.005
D ~ Open Road Dens 0.6+ Park	9	1,266.298	19.699	0
D ~ 1	7	1,272.986	26.387	0

within the Kettle–Granby also allowed us to produce region-specific abundance estimates, such as estimates for protected areas, which are far too small to conduct a stand-alone mark–recapture study. We constrained density extrapolations to a 50-km area west of our sampling grid.

3 | RESULTS

3.1 | Hair collection

We identified 74 individual grizzly bears (38 males and 36 females) from 177 detection events (unique individual and session). We captured 36 of the 74 individuals, or approximately half of the total bears detected, during the first sampling occasion (Figure S3).

3.2 | Population estimate and density

Detection models fit the data best when λ varied by session and allowed different capture probabilities for bears caught the first time at a site compared to subsequent detections at that site (trap-specific behaviour variation). Our 20-km buffer was sufficient to encompass home range centres of all bears detected in our sample (Figures S1 and S2).

Grizzly bear density across the Kettle–Granby GBPU was estimated as 13.2 (95% CI: 10.3–16.7) grizzly bears/1,000 km^2, with error below the 20% relative standard error threshold (RSE = 12.3%), suggesting a reasonably precise estimate. Sex-specific abundances (Table 2) were 41 females (95% CI: 29–57) and 46 males (95% CI: 32–64). Summing sex-specific abundances [Table 2, Female: 41 (95% CI: 29.3–57.4), Male: 45.7 (95% CI: 32.4–64.4)] resulted in an identical abundance (87 individuals, 95% CI: 66–108) as the combined-sex model. Detection parameters (Table 2, lambda and sigma) were compensatory, as suggested by Efford and Mowat (2014), with males occupying a larger spatial extent than females, but having a lower per capita detection probability than females, due to their larger range. Sex ratios for the Kettle–Granby were nearly equal, at 0.90 females to every male.

Our top "secr" model included a positive effect of habitat quality and a negative effect of road densities >0.6 km/km^2 on grizzly bear density (Table 1 and Figure 3). Results suggest a second competing model because the top two models (differing only by the inclusion/exclusion of closed roads from the road density surface) have comparable support (AIC$_c$ weight = 0.455 and 0.333). The spatial difference between the Road Dens 0.6 and Open Road Dens 0.6 variables (Figure 2c,f) is minimal, and results from removing roads from the relatively small access management area (*c*. 400 km^2; 6% of study area); however, we felt that the slight increase in model likelihood for Open Road Dens 0.6 represented a biologically meaningful signal, and we expect the gains in likelihood would be even greater had the access management area represented a larger portion of the study area. To investigate the biological effect of road closures, we estimated grizzly bear abundance inside the *c*. 400 km^2 of road closures in the Kettle–Granby GBPU and contrasted this to abundance had the roads not been closed (by adding roads inside the road closures back into the surface). Results suggest 27% fewer grizzly bears (*c*. 4 individuals) in the *c*. 400 km^2 of road closures had the roads not been closed [without access management: 11 (95% CI: 7.6–15.9), with access management: 15.1 (95% CI: 9.9–23.1) grizzly bears/1,000 km^2]. Thus, we selected (D ~ Habitat + Open Road Dens 0.6) as the most supported model.

Grizzly bear density was heterogeneous across the landscape and structured towards areas of high habitat quality and low road densities (Figures 3 and 4). Protected areas were characterised by generally low road densities, moderate to high habitat quality and higher grizzly bear densities compared to non-protected areas (Table 3).

We tested for an optimal breakpoint in road density that best predicts the pattern of grizzly bear density observed in the Kettle–Granby GBPU. Results generally support the threshold of *c*. 0.6 km of road per km^2 of area that is currently proposed or used in many jurisdictions (Figure 5). Our analyses demonstrated that 0.5 km/km^2 was the optimal threshold for the Kettle–Granby, with 0.6 a very close second. Values between 0.2 and 0.7 accounted for >80% of cumulative model weight, suggesting that although 0.5 was the most likely breakpoint, a range of values (*c*. ±0.2) on either side of 0.5 are also likely. We chose to keep 0.6 km/km^2 as our breakpoint to maintain consistency with the provincial cumulative effects analysis and proposed policy guidelines. Values higher than 0.6 quickly produced poorer model fit.

Although the Okanagan Valley to the west of our study area is characterised by high road densities and generally poor grizzly bear habitat, our model predicted local nodes of low to medium grizzly bear densities in the area, although these nodes were all in relatively close proximity to large human populations and several were isolated by wide expanses of low grizzly bear density (Figure 6).

4 | DISCUSSION

We used recently developed SECR methods that allow the inclusion of covariates to investigate factors correlated with the local density of a provincially threatened grizzly bear population. Grizzly

TABLE 2 Parameter estimates from top "secr" model. 95% confidence intervals shown in parentheses. Grizzly bear density is bears/1,000 km^2 and sigma is in metres

Sex	Abundance	Density	Lambda	Sigma
Total	86.6 (68.1–110.1)	13.2 (10.3–16.7)	0.149 (0.1–0.221)	5,959.5 (5,306.4–6,692.9)
F	41 (29.3–57.4)	6.2 (4.5–8.7)	0.235 (0.137–0.402)	5,121.6 (4,383.5–5,984.1)
M	45.7 (32.4–64.4)	6.9 (4.9–9.8)	0.097 (0.054–0.174)	6,842.7 (5,749.1–8,144.5)

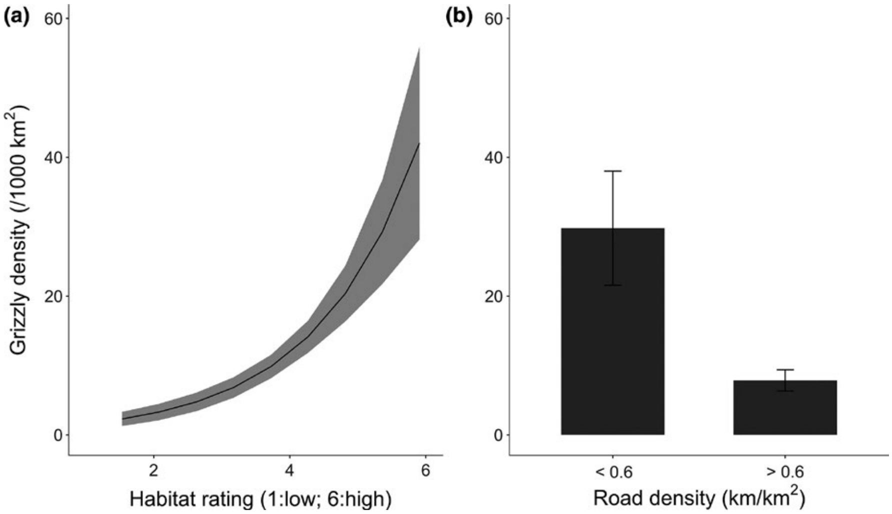

FIGURE 3 (a) Predicted responses of the most supported model illustrating the positive relationship between habitat quality and grizzly bear density (with Road Density fixed to >0.6 km/km^2, reflecting most of the landscape). (b) Effect of road density threshold on grizzly bear density. Areas with road densities below 0.6 km/km^2 had much higher grizzly bear densities than areas with road densities above 0.6 km/km^2 (with Habitat Rating fixed at 3, which was median habitat quality)

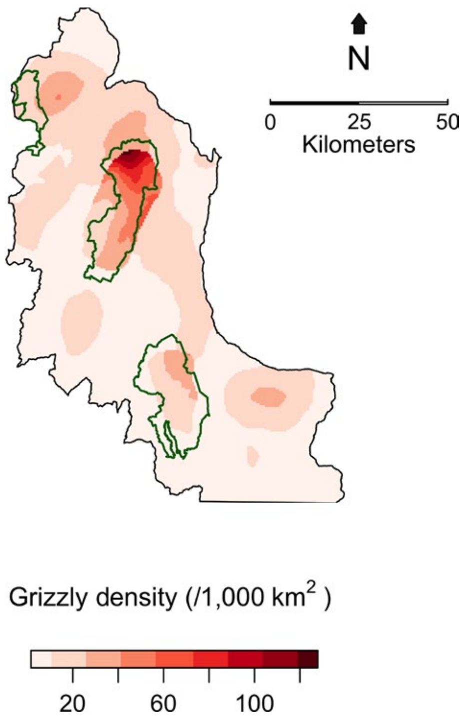

FIGURE 4 Grizzly bear densities (bears/1,000 km^2) within the Kettle–Granby GBPU in 2015 as estimated by the best-fit spatial capture–recapture model. Provincial parks are outlined in green (top: Graystokes, middle: Granby, bottom: Gladstone)

bear density was highest in areas of high habitat quality and low road density. Increased human access into the backcountry, most often through resource extraction roads, increases human–bear conflict and thus increases bear mortality in both hunted and unhunted populations (Falcucci et al., 2009; McLellan, 2015; McLellan & Shackleton, 1988; Nielsen, Herrero, et al., 2004). In addition to direct mortality near roads, perceived risks by bears may decrease foraging efficiency (Hertel et al., 2016), and alter activity patterns (Martin, Basille, Moorter, Kindberg, & Swenson, 2010; McLellan & Shackleton, 1989; Northrup et al., 2012) and movements (Bischof, Steyaert, & Kindberg, 2017; Roever, Boyce, & Stenhouse, 2010), thus potentially reducing habitat effectiveness. Our work builds on these mechanisms and links the effects of roads to reduced grizzly bear density.

Although roads produce myriad consequences to wildlife (Fahrig & Rytwinski, 2009; Ibisch et al., 2016), management agencies have the ability to mitigate these negative effects by restricting access or limiting the creation of new roads. However, the efficacy of these methods to safeguard grizzly bear density has yet to be tested, which has hindered uptake by practitioners. A lack of empirical evidence linking road closures to reduced mortality or increased population density also exists for other large mammals (Rowland, Wisdom, Johnson, & Penninger, 2004). Here, we tested the generality of the 0.6 km/km^2 (0.6 km of road per km^2 of area) threshold—proposed by the Alberta Grizzly Bear Recovery Team (Alberta Grizzly Bear Recovery Plan 2008–2013, 2008) and applied in the US Grizzly Bear Recovery Areas—in a small population of grizzly bears in southern BC. We found grizzly bear densities to be much higher in areas below the 0.6 threshold, even after controlling for habitat quality, and this threshold version of road density fit the data better than continuous road density. Furthermore, we assessed the sensitivity of this threshold by varying it from 0.1 to 3 and found greatest support for a threshold between 0.5 and 0.6, above which grizzly bear density was much lower. It should be noted that there was decreasing but comparable model fit for threshold values on either side of the maximum (0.2–0.7; Figure 5). Our results generally corroborate the 0.6 km/km^2 threshold and we suggest that managers, unless they have local empirical data on grizzly bear response to roads, use this as a target where grizzly bear conservation is a priority. Further investigation into the modifying effects of region-specific habitat productivity, grizzly bear population density and traffic volume may uncover mechanisms that allow more locally relevant thresholds. For example, McLellan (2015) documented grizzly bear densities four times greater than found here, yet, McLellan's study area had 0.74 km/km^2 of two-wheel drive roads plus another 0.9 km/km^2 of smaller, more ephemeral roads. However, McLellan's study area was >75 km from the nearest human settlement and had much higher habitat quality, including large huckleberry fields, avalanche chutes and riparian areas, which likely buffered some of the negative impacts of roads. McLellan (2015) suggested little impact of increasing road density in

TABLE 3 Region-specific abundance and density estimates, ranked from lowest to highest density, within the Kettle–Granby GBPU. 95% confidence intervals shown in parentheses

Name	Area (km^2)	Density	Abundance
Outside Protected Area	5,674	10.7 (8.1–14.1)	60.8 (46.1–80.1)
Gladstone Park	394.8	14.2 (8.4–23.6)	5.6 (3.3–9.3)
Graystokes Park	119.6	15.9 (11.7–22.6)	1.9 (1.4–2.7)
Granby Park	411.5	44.2 (27.9–70.2)	18.2 (11.5–28.9)

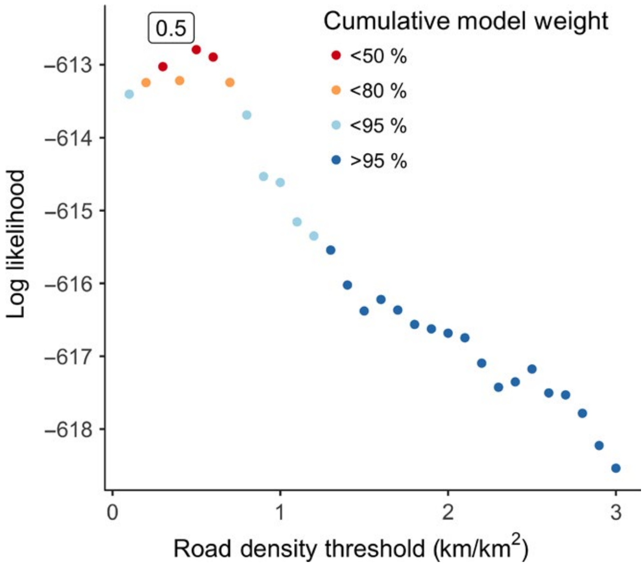

FIGURE 5 Distribution of log likelihood values and cumulative model weights used to find an optimal road density breakpoint for grizzly bear density in the Kettle–Granby GBPU of south-central British Columbia in 2015

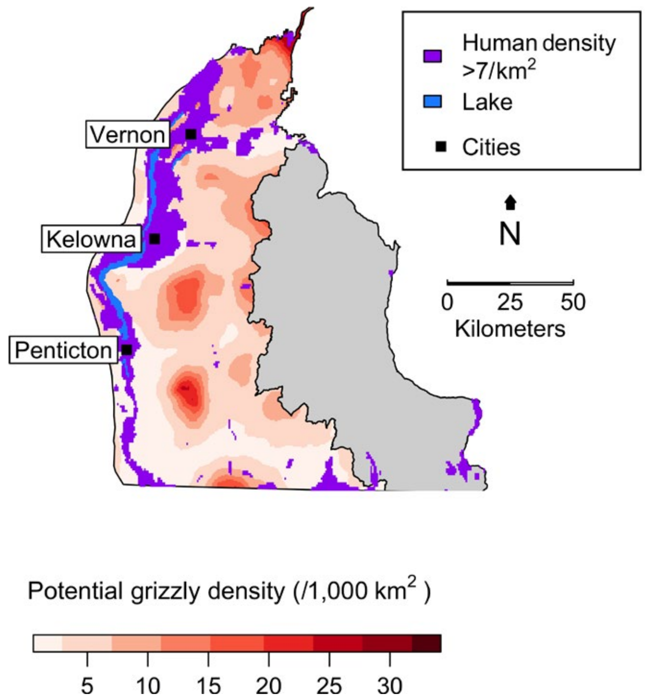

FIGURE 6 Predicted grizzly bear densities (bears/1,000 km^2) in the southeast Okanagan region where grizzly bears are currently extirpated. Kettle–Granby GBPU shown in grey

portions of that area because the number of people using the road network may not increase with more roads.

Although the 0.6 km/km^2 threshold is a useful road density target, this measure does not account for the spatial distribution of roads. In theory, a landscape with 0.6 km/km^2 of road could have 600 m of road in every km^2 of habitat, offering little sanctuary for wildlife. Schwartz et al. (2010) found that the proportion of land >500 m from open roads was important for grizzly bear conservation. Our results are consistent with this finding; many bears were captured, and had home range centres, in the largest tract of unroaded area: Granby Provincial Park (Figures 1, 2b and 4). Consequently, in addition to keeping landscape-level road densities below 0.6 km/km^2, practitioners should strive to manage the areas of highest habitat quality for no open roads (i.e. secure habitat >500 m from open roads) and reduce road densities in areas of intermediate habitat quality. Allowing higher road densities in low-quality bear habitat and outside of movement corridors should have the least impact. In Mowat et al. (2017), we suggested a number of priority areas where reducing road densities would facilitate increased population connectivity and security.

There are many cases where grizzly bear conservation is a concern and the 0.6 km/km^2 road density threshold has already been exceeded; leaving practitioners little choice but to actively remove roads or restrict human access on roads to address grizzly bear conservation needs. In 1985, road closures were enacted in the Kettle–Granby to protect alpine environments, and in 1997, road closures specifically designed to support grizzly bear recovery were established on both sides of Granby Provincial Park, where road densities (0.9 km/km^2) were higher than proposed targets (0.6 km/km^2) and roads overlapped productive habitat. Our results suggest grizzly bear density would be 27% lower within these areas if access management had not been enacted. While the Kettle–Granby grizzly bear densities are concentrated and at relatively high levels in protected areas and adjacent areas with access controls (Table 3), our results suggest the potential exists to increase bear densities outside the protected areas and further recover this population through future access controls (Braid & Nielsen, 2015; Mowat et al., 2017).

We show that the provincially threatened grizzly bear population in the Kettle–Granby GBPU has increased since the previous estimate in 1997. Population estimates from the 1997 mark–recapture data have been generated using numerous approaches and consistent estimates of 7.8–8.5 grizzly bears/1,000 km^2 were obtained (Apps, McLellan, Proctor, Stenhouse, & Servheen, 2016; Boulanger et al., 2002; Efford & Boulanger, 2015). In 2015, we detected 74 individuals in our sampling and estimated the Kettle–Granby grizzly population at 87 individuals or a density of 13.2 grizzly bears/1,000 km^2; an *c*. 55%–69% increase in density from 1997. Although comparing two point estimates is a relatively weak measure of population trend, the 2015 data suggest the population density is higher than it was in 1997. If the population continues to increase, more bears may be forced to use more heavily roaded portions of our study area, and the 0.6 km/km^2 road density threshold proposed here may change.

It may be surprising that the grizzly bear population has increased in the Kettle–Granby GBPU given that logging and associated road construction have continually expanded into wilderness (unroaded) areas in the Kettle–Granby. However, parks and access management areas were created in the 1990s, human access into areas of high-quality habitat was restricted, and hunting was stopped in 1995 which reduced human-caused mortality. Combined, these measures likely contributed to grizzly bear population recovery. Furthermore, increased early seral habitat from logging can also improve grizzly bear habitat (Nielsen, Munro, Bainbridge, Stenhouse, & Boyce, 2004). Protected areas cover less than 20% of the GBPU, and they are all relatively small (Table 3), yet these areas of elevated protection and low road densities harboured the highest densities of grizzly bears; nearly as many individuals currently occupy these small areas as occupied the entire area in 1997. Small, but connected, protected areas may thus serve as effective conservation options for umbrella species, especially in multi-use landscapes where large protected areas may be unrealistic.

Grizzly bears were legally hunted in the Kettle–Granby GBPU until 1995. Hunting plus other forms of human-caused mortality likely reduced bear numbers within our study area in the past. Like many populations monitored in greater detail over the past several decades (Garshelis, Gibeau, & Herrero, 2005; Mace et al., 2012; McLellan, 2015; Schwartz et al., 2006), the Kettle–Granby population is likely expanding due, at least in part, to reduced human-caused mortality. Stopping the legal kill may have been a factor supporting recovery, but because more female bears appear to be killed for non-hunting causes in other areas (McLellan, 2015; Mowat & Lamb, 2016), limiting access to important habitat likely reduced the kill of female bears by people accessing high-quality habitat for other reasons (e.g. ungulate hunting, motorised recreation, etc.). In contrast to hunting mortalities, which are regulated, non-hunting mortalities are difficult to quantify and control (Lamb, Mowat, McLellan, Nielsen, & Boutin, 2017). Since the cessation of the hunt in 1995, only 13 human-caused grizzly bear mortalities have been recorded in the Kettle–Granby GBPU (1995–2015), largely due to human–bear conflicts (61%) and poaching (31%). Unfortunately, the number of unreported mortalities is unknown, although they are often equal to or greater than the number of reported mortalities (McLellan et al., 1999).

The Kettle–Granby population is at the southwestern edge of the southern interior grizzly bear distribution in North America. Stent (2011) summarised the distribution of grizzly bears within and around the Kettle–Granby GBPU between 1980 and 2009 and noted an erosion of the western edge of the distribution, which effectively increased the size of the extirpated area in the Okanagan Valley. Our results suggest the population is now expanding westward, and there is potential for recolonisation of at least part of the extirpated zone. Indeed, grizzly bear sightings and mortalities have been recorded in the extirpated zone since the Stent (2011) review, and our results suggest this area has the potential to support a low-density grizzly bear population in areas removed from human settlements. However, recolonisation is contingent on demographic rescue (immigration) from the Kettle–Granby population, which will require both sufficient connectivity between habitat patches and public acceptance of grizzly bears in these areas which are close to dense human populations.

Human use of natural areas for economic reasons is ubiquitous around the globe. Biodiversity loss and species extinctions are occurring through generally small, but successive disturbances (Laurance et al., 2014). The negative impacts of activities that disturb landscapes and ecosystems for economic prosperity can often be mitigated post-use for the benefit of biodiversity and ecological processes. We show here that road density is negatively related to grizzly bear density, but this undesirable effect can be ameliorated when access controls or road removal are implemented to limit human presence. Utilisation of natural resources and the disturbance associated with their extraction is currently non-negotiable; however, having protocols in place to reduce the negative impacts of resource extraction (i.e. limiting new road development or closing roads when work is finished) is an encouraged approach. We believe there is opportunity in research focused on understanding the key industry-related factors limiting biodiversity and suggest policymakers strive for a no-net increase, or reduction, in these factors where possible.

5 | CONCLUSIONS

Our density model allowed us to compare grizzly bear density, habitat quality, and road density to identify locales that could generate the greatest response in bear density with the lowest mitigation cost (Mowat et al., 2017). Efforts to reduce or eliminate road density in areas of high habitat quality should generate the greatest increase in grizzly bear abundance. The population we studied was grouped in four partially isolated areas in summer, which suggested that greater connectivity of ranges would further reduce conservation risk. Our data demonstrated that bears moved among these locales during summer, which likely put those individuals at higher mortality risk as they crossed through heavily roaded valleys. With this in mind, we recommend reducing road densities in three areas of moderate road density to improve population connectivity at a modest overall cost (Mowat et al., 2017). The spatial nature of the population model used here allowed the formulation of management options that went well beyond what was possible with non-spatial capture–recapture models.

Our analysis firmly links the negative effects of roads on grizzly bear density and suggests that access management is a viable mitigation strategy. Secondly, our results corroborate the 0.6 km/km^2 road density threshold currently in use by many management agencies. However, we do note that much of the work recommending this threshold (including our own) comes from recovering bear populations in medium quality habitat, and the degree to which population status, habitat quality and ranging behaviour influences optimal road density thresholds remains unknown. Where possible, investigators should test and publish their thresholds to allow for an effective meta-analysis. If defensible, area-specific road density thresholds were available, generalised relationships could be extrapolated to areas where bear conservation is a priority but local research efforts are limited or non-existent. Finally, it bears repeating that a road density threshold does not incorporate the distribution of roads across the landscape, thus prudent management will also maintain a portion of the landscape >500 m from roads (Mace et al., 1996 suggests 56%, preferably in high-quality habitat; Schwartz et al., 2010), as was done in our study area where large protected areas were roadless.

We expect the benefit of access management to cascade beyond grizzly bears to other wildlife negatively affected by roads (Benítez-lópez et al., 2010; Ceia-Hasse et al., 2017; Fahrig & Rytwinski, 2009). Many species are negatively affected by roads (Fahrig & Rytwinski, 2009); African lions (*Panthera leo*), wild dogs (*Lycaon pictus*), cats (*Felidae* sp.) and apes (*Gorilla* and *Pan* sp.) are among the charismatic megafauna faced with increased roads and resulting demographic consequences (Ceia-Hasse et al., 2017; Walsh et al., 2003). Even for these species, despite their charismatic status and high conservation risk, dedicated habitat restoration and mortality reduction is required for long-term persistence (Stephens, 2015). Mitigating the negative effect of roads on such species may require species-specific road density thresholds (Ceia-Hasse et al., 2017), which will vary by life history and susceptibility to road mortality and disturbance. Nevertheless, we expect the reduction of road densities and human access in high-quality habitat to have positive results for wildlife.

We demonstrate how spatial capture–recapture methods can be used to investigate factors that correlate spatially with animal density, and these methods have applications for many species that are surveyed using techniques that identify individuals. Many species are inventoried for immediate management needs such as assessing population status, investigating causes of decline or managing harvest. Analyses similar to ours could be a value-added component to many inventories around the world because the link between top-down and bottom-up influences on animal density is a key ecological question (Nielsen, Larsen, Stenhouse, & Coogan, 2017), with many immediate applications.

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AUTHORS' CONTRIBUTIONS

C.L. wrote the manuscript and conducted the analyses with help from all co-authors; C.L., L.S., A.R., G.M. and B.M. conducted the field work. All co-authors gave final approval for publication of the manuscript.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.bk0rd (Lamb, Mowat, Reid, et al., 2017).

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REFERENCES

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, *19*, 716–723. https://doi.org/10.1109/TAC.1974.1100705

Alberta Grizzly Bear Recovery Plan 2008–2013. (2008). *Alberta Sustainable Resource Development, Fish and Wildlife Division, Alberta Species at Risk Recovery Plan No. 15*. Edmonton, Alberta.

Apps, C. D., McLellan, B. N., Proctor, M. F., Stenhouse, G. B., & Servheen, C. (2016). Predicting spatial variation in grizzly bear abundance to inform conservation. *The Journal of Wildlife Management*, *80*, 396–413. https://doi.org/10.1002/jwmg.1037

Benítez-lópez, A., Alkemade, R., & Verweij, P. A. (2010). The impacts of roads and other infrastructure on mammal and bird populations: A meta-analysis. *Biological Conservation*, *143*, 1307–1316. https://doi.org/10.1016/j.biocon.2010.02.009

Bischof, R., Steyaert, S. M. J. G., & Kindberg, J. (2017). Caught in the mesh: Roads and their network-scale impediment to animal movement. *Ecography*, 1–12. https://doi.org/10.1111/ecog.02801

Borchers, D. (2012). A non-technical overview of spatially explicit capture-recapture models. *Journal of Ornithology*, *152*, 435–444. https://doi.org/10.1007/s10336-010-0583-z

Boulanger, J. (2000). *Granby-Kettle/Boundary Forest District 1997 Grizzly Bear DNA Mark-Recapture Inventory Project: Statistical Analysis and Population Estimates*. Nelson, BC.

Boulanger, J., Mclellan, B. N., Woods, J., Proctor, M. F., Himmer, S., & White, G. C. (2002). A meta-analysis of grizzly bear DNA mark-recapture projects in British Columbia, Canada. *Ursus*, *13*, 137–152.

Boulanger, J., & Stenhouse, G. B. (2014). The impact of roads on the demography of grizzly bears in Alberta. *PLoS ONE*, *9*, e115535. https://doi.org/10.1371/journal.pone.0115535

Braid, A. C. R., & Nielsen, S. E. (2015). Prioritizing sites for protection and restoration for grizzly bears (*Ursus arctos*) in southwestern Alberta, Canada. *PLoS ONE*, *10*, 1–15.

Burnham, K., & Anderson, D. (2002). *Model selection and multi-model inference*. New York, NY: Springer-Verlag.

Ceia-Hasse, A., Borda-de-Agua, L., Grilo, C., & Pereira, H. M. (2017). Global exposure of carnivores to roads. *Global Ecology and Biogeography*, *26*, 592–600. https://doi.org/10.1111/geb.12564

Chapron, G., Kaczensky, P., & Linnell, J. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, *346*, 1517–1520. https://doi.org/10.1126/science.1257553

Efford, M. G. (2016). secr: Spatially explicit capture-recapture models. R package version 3.0.1. Retrieved from https://CRAN.R-project.org/package=secr

Efford, M., & Boulanger, J. B. (2015). *Evaluation of sampling strategies for grizzly bears in the Granby-Kettle Bear Management Unit*. Nelson, BC.

Efford, M. G., & Mowat, G. (2014). Compensatory heterogeneity in spatially explicit capture-recapture data. *Ecology*, *95*, 1341–1348. https://doi.org/10.1890/13-1497.1

Fahrig, L., & Rytwinski, T. (2009). Effects of roads on animal abundance: An empirical review and synthesis. *Ecology & Society*, *14*, 1–20.

Falcucci, A., Ciucci, P., Maiorano, L., Gentile, L., & Boitani, L. (2009). Assessing habitat quality for conservation using an integrated occurrence-mortality model. *Journal of Applied Ecology*, *46*, 600–609. https://doi.org/10.1111/j.1365-2664.2009.01634.x

Forest Practices Board (2017). *Forest roads and grizzly bear management in the Kettle-Granby area*. Victoria, BC: Forest Practices Board.

Garshelis, D. L., Gibeau, M. L., & Herrero, S. (2005). Grizzly bear demographics in and around Banff National Park and Kananaskis Country, Alberta. *The Journal of Wildlife Management*, *69*, 277–297. https://doi.org/10.2193/0022-541X(2005) 069<0277:GBDIAA>2.0.CO;2

Graham, K., & Stenhouse, G. (2014). Home range, movements, and denning chronology of the grizzly bear (*Ursus arctos*) in West-Central Alberta. *The Canadian Field-Naturalist*, *128*, 223–234. https://doi.org/10.22621/cfn.v128i3.1600

Gyug, L., & Hamilton, D. (2007). *Kettle-Granby Grizzly Bear Population Unit : Habitat Analyses 2006*. Victoria, BC: Province of British Columbia.

Hertel, A. G., Zedrosser, A., Mysterud, A., Støen, O.-G., Steyaert, S. M. J. G., & Swenson, J. E. (2016). Temporal effects of hunting on foraging behavior of an apex predator: Do bears forego foraging when risk is high? *Oecologia*, *182*, 1019–1029. https://doi.org/10.1007/s00442-016-3729-8

Ibisch, P. L., Hoffmann, M. T., Kreft, S., Pe'er, G., Kati, V., Biber-Freudenberger, L., … Selva, N. (2016). A global map of roadless areas and their conservation status. *Science (New York, NY)*, *354*, 1423–1427. https://doi.org/10.1126/science.aaf7166

Kendall, K. C., Stetz, J. B., Roon, D. A., Waits, L. P., Boulanger, J., & Paetkau, D. (2008). Grizzly bear density in Glacier National Park, Montana. *The Journal of Wildlife Management*, *72*, 1693–1705. https://doi.org/10.2193/2008-007

Lamb, C. T., Mowat, G., McLellan, B., Nielsen, S., & Boutin, S. (2017). Forbidden Fruit: Human settlement and abundant fruit create an ecological trap for grizzly bears. *Journal of Animal Ecology*, *86*, 55–65. https://doi.org/10.1111/1365-2656.12589

Lamb, C. T., Mowat, G., Reid, A., Smit, L., Proctor, M. F., McLellan, B. N., … Boutin, S. (2017). Data from: Effects of habitat quality and access management on the density of a recovering grizzly bear population. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.bk0rd

Lamb, C. T., Walsh, D., & Mowat, G. (2016). Factors influencing detection of grizzly bears at genetic sampling sites. *Ursus*, *27*, 31–44. https://doi.org/10.2192/URSUS-D-15-00025.1

Laurance, W. F., Clements, G. R., Sloan, S., Connell, C. S. O., Mueller, N. D., Goosem, M., … Arrea, I. B. (2014). A global strategy for road building. *Nature*, *513*, 229–232. https://doi.org/10.1038/nature13717

Mace, R. D., Carney, D. W., Chilton-Radandt, T., Courville, S. A., Haroldson, M. A., Harris, R. B., … Wenum, E. (2012). Grizzly bear population vital rates and trend in the Northern Continental Divide Ecosystem, Montana. *The Journal of Wildlife Management*, *76*, 119–128. https://doi.org/10.1002/jwmg.250

Mace, R. D., Waller, J. S., Manley, T. L., Lyon, I. J., & Zuuring, H. (1996). Relationships among grizzly bears, roads and habitat in the Swan Mountains, Montana. *Journal of Applied Ecology*, *33*, 1395–1404. https://doi.org/10.2307/2404779

Martin, J., Basille, M., Moorter, B. Van., Kindberg, J., & Swenson, J. E. (2010). Coping with human disturbance: Spatial and temporal tactics of the brown bear (*Ursus arctos*). *Canadian Journal of Zoology*, *883*, 875–883. https://doi.org/10.1139/Z10-053

McLellan, B. N. (2015). Some mechanisms underlying variation in vital rates of grizzly bears on a multiple use landscape. *The Journal of Wildlife Management*, *79*, 749–765. https://doi.org/10.1002/jwmg.896

McLellan, B. N., Hovey, F. W., Mace, R. D., Woods, J. G., Carney, D. W., Gibeau, M. L., … Kasworm, W. F. (1999). Rates and causes of grizzly bear mortality in the interior mountains of British Columbia, Alberta, Montana, Washington, and Idaho. *The Journal of Wildlife Management*, *63*, 911–920. https://doi.org/10.2307/3802805

McLellan, B. N., Proctor, M. F., Huber, D., & Michel, S. (2016). 2016 IUCN RedList Assessment for Brown Bears.

McLellan, B., & Shackleton, D. (1988). Grizzly bears and resource-extraction industries: Effects of roads on behaviour, habitat use and demography. *Journal of Applied Ecology*, *25*, 451–460. https://doi.org/10.2307/2403836

McLellan, B. N., & Shackleton, D. M. (1989). Grizzly bears and resource-extraction industries: Habitat displacement in response to seismic exploration, timber harvesting and road maintenance. *Journal of Applied Ecology*, *26*, 371–380. https://doi.org/10.2307/2404067

Mowat, G., Heard, D., Seip, D., & Poole, K. (2005). Grizzly *Ursus arctos* and black bear *U. americanus* densities in the interior mountains of North America. *Wildlife Biology*, *11*, 31–48. https://doi.org/10.2981/0909-6396(2005)11[31:GUAABB]2.0.CO;2

Mowat, G., & Lamb, C. T. (2016). *Population Status of the South Rockies and Flathead Grizzly Bear Populations in British Columbia, 2006-2014*. Nelson, BC.

Mowat, G., Lamb, C. T., Smit, L., & Reid, A. (2017). *The relationships among road density, habitat quality, and grizzly bear population density in the Kettle-Granby area of British Columbia*. Victoria, BC.

Ng, H., & Dhaliwal, S. (2016). *Protecting Granby Valley Grizzly Bears*. Victoria, BC.

Nielsen, S., Herrero, S., Boyce, M. S., Mace, R. D., Benn, B., Gibeau, M. L., & Jevons, S. (2004). Modelling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies ecosystem of Canada. *Biological Conservation*, *120*, 101–113. https://doi.org/10.1016/j.biocon.2004.02.020

Nielsen, S. E., Larsen, T. A., Stenhouse, G. B., & Coogan, S. C. P. (2017). Complementary food resources of carnivory and frugivory affect local abundance of an omnivorous carnivore. *Oikos*, *126*, 369–380. https://doi.org/10.1111/oik.03144

Northrup, J. M., Pitt, J., Muhly, T. B., Stenhouse, G. B., Musiani, M., & Boyce, M. S. (2012). Vehicle traffic shapes grizzly bear behaviour on a multiple-use landscape. *Journal of Applied Ecology*, *49*, 1159–1167. https://doi.org/10.1111/j.1365-2664.2012.02180.x

Paetkau, D. (2003). An empirical exploration of data quality in DNA-based population inventories. *Molecular Ecology*, *12*, 1375–1387. https://doi.org/10.1046/j.1365-294X.2003.01820.x

Nielsen, S., Munro, R. H. M., Bainbridge, E. L., Stenhouse, G. B., & Boyce, M. S. (2004). Grizzly bears and forestry II. Distribution of grizzly bear foods in clearcuts of west-central Alberta, Canada. *Forest Ecology and Management*, *199*, 67–82. https://doi.org/10.1016/j.foreco.2004.04.015Proctor, M. F., Paetkau, D., Mclellan, B. N., Stenhouse, G. B., Kendall, K. C., Mace, R. D., … Strobeck, C. (2012). Population fragmentation and inter-ecosystem movements of grizzly bears in western Canada and the northern United States. *Wildlife Monographs*, *180*, 1–46. https://doi.org/10.1002/wmon.6

Provincial Grizzly Bear Technical Working Group. (2016). *Cumulative effects framework: Assessment protocol for grizzly bear in British Columbia*. Victoria, BC: Province of British Columbia.

R Development Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Resources Information Standards Committee. (2006). *Standard for mapping ecosystems at risk in British Columbia: An approach to mapping ecosystems at risk and other sensitive ecosystems*. Victoria, BC.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., … Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science (New York, NY)*, *343*, 1241484. https://doi.org/10.1126/science.1241484

Roever, C. L., Boyce, M. S., & Stenhouse, G. B. (2010). Grizzly bear movements relative to roads: Application of step selection functions. *Ecography*, *33*, 1113–1122. https://doi.org/10.1111/j.1600-0587.2010.06077.x
Rowland, M. M., Wisdom, M. J., Johnson, B. K., & Penninger, M. A. (2004). Effects of roads on elk: Implications for management in forested ecosystems. Transactions of the 69th North American Wildlife and Natural Resources Conference, pp. 491–508.
Schwartz, C. C., Haroldson, M. A., & White, G. C. (2010). Hazards affecting grizzly bear survival in the Greater Yellowstone Ecosystem. *The Journal of Wildlife Management*, *74*, 654–667. https://doi.org/10.2193/2009-206
Schwartz, C. C., Haroldson, M. A., White, G. C., Harris, R. B., Cherry, S., Keating, K. A., … Servheen, C. (2006). Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife Monographs*, *161*, 29941–30008.
Stent, P. (2011). *Kettle-Granby and Central Monashee grizzly bear population review*. Nelson, BC.
Stephens, P. A. (2015). Land sparing, land sharing, and the fate of Africa's lions. *Proceedings of the National Academy of Sciences of the United States of America*, *112*, 14753–14754. https://doi.org/10.1073/pnas.1520709112
Walsh, P. D., Abernethy, K. A., Bermejo, M., Beyers, R., De Wachter, P., Akou, M. E., … Wilkie, D. S. (2003). Catastrophic ape decline in western equatorial Africa. *Nature*, *422*, 611–614. https://doi.org/10.1038/nature01566
Watson, J. E. M., Shanahan, D. F., Marco, M. Di., Sanderson, E. W., & Mackey, B. (2016). Report catastrophic declines in wilderness areas undermine global environment targets. *Current Biology*, *26*, 2929–2934. https://doi.org/10.1016/j.cub.2016.08.049
Woods, J. G., Paetkau, D., Lewis, D., Mclellan, B. N., Proctor, M., & Strobeck, C. (1999). Genetic tagging of free-ranging black and brown bears. *Wildlife Society*, *27*, 616–627.

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