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Berries and bullets: influence of food and mortality risk on grizzly bears in British Columbia

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Abstract

The influence of bottom-up food resources and top-down mortality risk underlies the demographic trajectory of wildlife populations. For species of conservation concern, understanding the factors driving population dynamics is crucial to effective management and, ultimately, conservation. In southeastern British Columbia, Canada, populations of the mostly omnivorous grizzly bear (*Ursus arctos*) are fragmented into a mosaic of small isolated or larger partially connected sub-populations. They obtain most of their energy from vegetative resources that are also influenced by human activities. Roads and associated motorized human access shape availability of food resources but also displace bears and facilitate human-caused mortality. Effective grizzly bear management requires an understanding of the relationship between habitat quality and mortality risk. We integrated analyses of bottom-up and top-down demographic parameters to understand and inform a comprehensive and efficient management paradigm across the region. Black huckleberry (*Vaccinium membranaceum*) is the key high-energy food for grizzly bears in much of southeastern British Columbia. Little is known about where and why huckleberries grow into patches that are useful for grizzly bears (i.e., densely clustered fruiting shrubs that provide efficient access to high energy food) and how

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forage supply and mortality risk influence population vital rates. By following 43 grizzly bears tracked with global positioning system (GPS) collars (57 bear years) in a 14,236-km^2 focal area spanning the Selkirk and Purcell mountain ranges, we developed a model to identify huckleberry patches from grizzly bear use data. Over 2 years we visited 512 sites used by bears, identifying more than 300 huckleberry patches. We used boosted regression tree modeling associating geophysical, ecological, soil, climate, and topographical variables with huckleberry patches. We integrated this modeled food layer depicting an important pre-hibernation resource, into broader bottom-up and top-down analyses. In addition to berries, we examined bottom-up variables indexing vegetative productivity that were previously found to be predictive of bear use (e.g., alpine, canopy cover, greenness, riparian). We also examined top-down variables including road presence, road density, distance-to-road, secure habitat (defined as 500 m away from a road open to vehicular access), highways, human development, and terrain ruggedness. We evaluated the relationship of these variables to female habitat selection, fitness, and population density, testing the predictability and interrelatedness of covariates relative to bottom-up and top-down influences. We estimated resource selection functions with 20,293 GPS telemetry locations collected over 10 years from 20 female grizzly bears. We modeled fitness using logistic regression of spatially explicit reproductive data derived from genetically identified family pedigrees consisting of a mother, father, and offspring. Data included 33 mothers and 72 offspring (1–8 offspring per female). We estimated density through spatial capture-recapture analysis of 126 grizzly bears detected with hair-sampled DNA 287 times between 1998 and 2005. In all 3 analyses (habitat selection, fitness, and density), huckleberry patches were the most influential bottom-up factor and secure habitat was the most consistent top-down variable (road density was similarly predictive). All of the best supported models contained bottom-up and top-down variables except the male density model, which only contained a top-down variable (secure habitat). These results suggest that both bottom-up and top-down forces drive several population processes of grizzly bears in the region, especially for females. We found that 38% of huckleberry patches (235 km^2) predicted by the top model were in non-secure habitat and that these patches were associated with lower fitness and density relative to those in secure habitat. Grizzly bear density was 2.6 times higher in habitat with road densities <0.6 km/km^2, supporting the use of this road density target for management. The models predict that applying motorized access controls to backcountry areas with huckleberry patches would increase grizzly bear abundance by 23% on average across the region and 125% in the lowest density portion of the study area (Yahk). Managing both bottom-up and top-down influences is necessary to best mitigate the expanding human footprint, which is affecting many carnivore species worldwide. We provide evidence that bottom-up forces were more influential for female habitat selection, fitness, and density than top-down effects. We also uncovered a critical pattern in the magnitude of top-down and bottom-up influences on behavioral (habitat selection) and demographic (population density and fitness) responses. We show that the relative influence of top-down influences on habitat selection and fitness are relatively weak compared to bottom-up influences, whereas top-down pressures exert much stronger limiting forces on population density. Forming conservation decisions around behavioral responses alone may misdirect actions and have limited benefits to populations. This insight can facilitate more effective decision-making for grizzly bear conservation. Our findings highlight the importance of considering both bottom-up and top-down influences, suggesting cautious interpretation of habitat selection models for any species. A comprehensive examination with population-level metrics such as density, vital rates, and fitness may be needed for effective management.

KEYWORDS

bottom-up, density, fitness, grizzly bear, habitat selection, huckleberry, SECR, top-down, *Ursus arctos*

Bayas y balas: influencia de la alimentación y el riesgo de mortalidad en los osos grizzly en la Columbia Británica

Resumen

La influencia de los recursos alimentarios y el riesgo de mortalidad subyace en la trayectoria demográfica de las poblaciones de vida silvestre; el primero mediante procesos de abajo hacia arriba y el segundo de arriba hacia abajo. Para especies de interés para la conservación, comprender los factores que impulsan la dinámica poblacional es crucial para una gestión eficaz y, en última instancia, para la conservación. En el sureste de la Columbia Británica, Canadá, las poblaciones del oso pardo (*Ursus arctos*), principalmente omnívoros, están fragmentadas en un mosaico de pequeñas subpoblaciones aisladas con otras de mayor tamaño parcialmente conectadas. Obtienen la mayor parte de su energía de recursos vegetales cuya disponibilidad está influenciada por las actividades humanas. Las carreteras y el acceso humano motorizado asociado dan forma a la disponibilidad de recursos alimentarios, pero también desplazan a los osos y facilitan la mortalidad causada por humanos. La gestión efectiva del oso pardo requiere comprender la relación entre la calidad del hábitat y el riesgo de mortalidad. Integramos análisis de parámetros demográficos de proceso abajo-arriba y arriba-abajo para comprender e informar un paradigma de gestión integral y eficiente en toda la región. El arándano negro (*Vaccinium membranaceum*) es el alimento clave de alta energía para los osos pardos en gran parte del sureste de Columbia Británica. Se sabe poco sobre dónde y por qué crecen los arándanos en parches que son útiles para los osos pardos (es decir, arbustos frutales densamente agrupados que proporcionan un acceso eficiente a alimentos de alta energía) y cómo el suministro de forraje y el riesgo de mortalidad influyen en las tasas vitales de la población. Siguiendo a 43 osos pardos rastreados con collares de sistema de posicionamiento global (GPS) (57 años-oso) en un área focal de 14,236 km^2 que abarca las cadenas montañosas Selkirk y Purcell, desarrollamos un modelo para identificar parches de arándanos a partir de datos de uso de osos pardos. Durante 2 años, visitamos 512 sitios utilizados por osos, identificando más de 300 parches de arándanos. Utilizamos modelos de árboles de regresión aumentada (boosted regression tree modeling en inglés) asociando variables geofísicas, ecológicas, del suelo, climáticas y topográficas con los parches de arándanos. Integramos esta capa de alimento modelada (que representa un recurso importante en la prehibernación) en análisis más amplios incluyendo controls abajo-arriba y arriba-abajo. Además de las bayas, examinamos variables de procesos abajo-arriba relacionadas con la productividad vegetal y que son predictores de uso de recursos por parte de osos (por ejemplo, vegetación alpina, cobertura vegetal, verdor, ribera). También examinamos variables de procesos arriba-abajo, incluida la presencia de carreteras, densidad de carreteras, distancia a la carretera, hábitat seguro (definido como 500 m de distancia de una carretera abierta al tránsito rodado), autopistas, desarrollo humano y rugosidad del terreno. Evaluamos la relación de estas variables con la selección de hábitat de hembras, la aptitud física y la densidad de la población, testando la predictibilidad e interrelación de covariables en relación con los procesos de abajo hacia arriba y de arriba hacia abajo. Estimamos funciones de selección de recursos (resource selection functions en inglés) con 20,293 ubicaciones de telemetría GPS recolectadas durante 10 años de 20 osas. Modelamos la aptitud física utilizando regresión logística de datos reproductivos espacialmente explícitos derivados de pedigríes familiares identificados genéticamente que consisten en una madre, un padre y su descendencia. Los datos incluyeron 33 madres y 72 descendientes (1-8 descendientes por hembra). Estimamos la densidad mediante análisis de captura-recaptura espacial de 126 osos pardos detectados en muestras de ADN de pelo 287 veces entre 1998 y 2005. En los 3 análisis (selección de hábitat, aptitud física y densidad), los parches de arándanos fueron el factor más influyente de los procesos de abajo hacia arriba y el hábitat seguro fue la variable más consistente de arriba hacia abajo (la densidad de carreteras fue igualmente predictiva). Todos los modelos mejor respaldados contenían variables de procesos de abajo hacia arriba y de arriba hacia abajo, excepto el modelo de densidad de machos, que solo contenía una variable de control de arriba hacia abajo (hábitat seguro). Estos resultados sugieren que las interacciones de abajo hacia arriba y de arriba hacia abajo impulsan varios procesos poblacionales de osos pardos en la región, especialmente para las hembras. Encontramos que el 38% de los parches de arándanos (235 km^2) predichos por el mejor modelo estaban en hábitat no seguro y que estos parches estaban asociados con una aptitud física y densidad poblacional más bajas en comparación con aquellos en hábitat seguro. La densidad del oso pardo fue 2.6 veces mayor en hábitat con densidades de carreteras <0.6 km/km^2, lo que respalda el uso de este umbral de densidad de carreteras para la gestión. Los modelos predicen que aplicar controles de acceso motorizado a áreas remotas con parches de arándanos aumentaría la abundancia de osos pardos en un 23% en promedio en toda la región y un 125% en la porción de menor densidad del área de estudio (Yahk). Es necesario gestionar los procesos de abajo-arriba y de arriba-abajo para mitigar mejor la expansión de la huella humana, que está afectando a muchas especies de carnívoros en todo el mundo. Proporcionamos evidencia de que los procesos de abajo hacia arriba fueron más influyentes para la selección de hábitat, la aptitud física y la densidad de las hembras que los efectos de arriba hacia abajo. También descubrimos un patrón crítico en la magnitud en que los procesos de arriba hacia abajo y de abajo hacia arriba influencian las respuestas conductuales (selección de hábitat) y demográficas (densidad de población y aptitud física). Mostramos que la influencia relativa de los procesos de control de arriba hacia abajo en la selección de hábitat y aptitud física es relativamente débil en comparación con las influencias de abajo hacia arriba, mientras que las presiones de arriba hacia abajo ejercen fuerzas limitantes mucho más fuertes en la densidad de población. Formar decisiones de conservación basadas únicamente en respuestas conductuales puede desviar acciones y tener beneficios limitados para las poblaciones. Esta perspectiva puede facilitar una toma de decisiones más efectiva para la conservación del oso pardo. Nuestros hallazgos resaltan la importancia de considerar tanto los procesos de abajo hacia arriba como los de arriba hacia abajo, lo que sugiere una interpretación cautelosa de los modelos de selección de hábitat para cualquier especie. En consecuencia, parece necesario un examen exhaustivo con métricas a nivel de población, como la densidad, tasas vitales y aptitud física, para conseguir una gestión efectiva.

Des baies et des balles : influence de l'alimentation et risques de mortalité chez les ours grizzlys de la Colombie-Britannique

Résumé

L'influence des ressources alimentaires (processus ascendants) et des risques de mortalité (processus descendants) sous-tend la trajectoire démographique des populations fauniques. En ce qui concerne les espèces menacées, il est crucial de comprendre les facteurs qui déterminent la dynamique des populations afin de les gérer efficacement et de les conserver. Dans le sud-est de la Colombie-Britannique au Canada, les populations d'ours grizzly (*Ursus arctos)*, principalement omnivores, sont fragmentées dans une mosaïque de petites sous populations isolées ou de plus grandes partiellement connectées. Ils obtiennent la majorité de leur énergie de ressources végétales incluant celles influencées par les activités humaines. Les chemins et accès motorisés associés déterminent la disponibilité des ressources alimentaires, mais déplacent les ours et facilitent la mortalité causée par les humains. La gestion efficace des ours grizzlys requiert une compréhension de la relation entre la qualité de leur habitat et les risques de mortalité. Nous avons intégré les analyses des paramètres démographiques ascendants et descendants afin de comprendre et d'informer un modèle de gestion efficace dans la région. Les airelles à feuilles membraneuses (*Vaccinium membranaceum*) constituent la nourriture à haute teneur énergétique clé pour les ours grizzlys dans la majorité sud-est de la Colombie-Britannique. On en sait peu sur les endroits ou sur les raisons pourquoi les airelles poussent en talles utiles au grizzly (c.-à-d. des arbustes fruitiers densément groupés fournissant un accès efficace à de la nourriture à haute teneur énergétique) ainsi que sur le rapport entre la disponibilité des aliments, les risques de mortalité et leur influence sur les taux démographiques. En suivant 43 ours grizzlys traqués à l'aide de colliers munis d'un système de géolocalisation (GPS) (57 années-ours) dans une zone d'intervention de 14,236 km^2 recouvrant les chaînes de montagnes Selkirk et Purcell, nous avons développé un modèle pour identifier les talles d'airelles à partir de données portant sur le terrain recouru par les ours grizzlys. Pendant 2 ans nous avons visité 512 sites visités par les ours, identifiant plus de 300 talles d'airelles. Nous avons utilisé un modèle amélioré d'arbre de régression associant des variables géophysiques, écologiques, topographiques, du sol et du climat, avec les talles d'airelles. Nous avons intégré ce modèle de couche alimentaire illustrant une ressource importante précédant l'hibernation, à des analyses plus considérables ascendantes et descendantes. En plus des baies, nous avons examiné les variables ascendantes en répertoriant la productivité végétative auparavant estimée prédictive de l'utilisation par les ours (p. ex. : pays alpin, couvert forestier, verdure, rives). Nous avons également examiné les variables descendantes telles que la présence de routes, leur densité, distance à la route, habitat tranquille (défini par une distance de 500 m d'une route active à la circulation véhiculaire), les autoroutes, le développement humain et le terrain accidenté. Nous avons évalué la relation entre ces variables et les choix d'habitats des ourses, leur santé ainsi que la densité des populations, en testant la prédictibilité et l'interdépendance des covariantes en relation aux influences ascendantes et descendantes. Nous avons estimé les fonctions de sélection de ressources à l'aide de 20,293 points télémétriques GPS recueillis en suivant 20 ourses grizzlys sur une période de 10 ans. Nous avons réalisé un modèle d'aptitude physique à partir de données de régression logistique sur la reproduction explicitement spatiale dérivées de pédigrés familiaux identifiés génétiquement consistant d'un père, d'une mère et de leur progéniture. Les données incluaient 33 mères et 72 petits (d'un à huit par femelle). Nous avons estimé la densité au moyen d'analyses de capture-recapture spatiale de 126 grizzlys détectés par l'ADN de leurs échantillons de poils 287 fois entre 1998 et 2005. Dans les trois analyses (sélection d'habitat, forme physique et densité de population), les talles d'airelles représentaient le facteur ascendant le plus marquant et un habitat sûr la plus consistante variable descendante (la densité routière était également prédictive). Tous les modèles les mieux supportés contenaient des variables ascendantes et descendantes sauf le modèle de densité de mâles qui démontrait uniquement une variable descendante (habitat sûr). Ces résultats suggèrent que les forces ascendantes et descendantes influencent toutes deux plusieurs processus de population des ours grizzlys dans la région, surtout des femelles. Nous avons observé que 38% des talles d'airelles (235 km^2) démontrées par le meilleur modèle se trouvaient en milieu peu sûr et que ces talles étaient associées avec une forme physique et une densité de population inférieure à celles des habitats sûrs. La densité de population des ours grizzlys est de 2,6 fois plus élevée dans les habitats avec une densité de réseau routier inférieure à 0,6 km/km^2, ce qui renforce l'inclusion de cet objectif de densité routière en lien avec la gestion. Les modèles prédisent que l'imposition de contrôle d'accès motorisé dans les régions reculées avec talles d'airelles augmenterait les populations d'ours de 23% en moyenne dans la région, et de 125% dans les zones de basse densité de la région étudiée (Yahk). La gestion des deux influences ascendante et descendante est nécessaire afin d'atténuer l'empreinte humaine qui affecte nombre d'espèces carnivores dans le monde entier. Nous présentons la preuve que les processus ascendants sont plus influents sur la sélection d'habitats, la forme physique et la densité pour les femelles que les effets descendants. Nous avons également découvert un modèle critique sur l'ampleur des influences ascendantes et descendantes sur les réponses comportementales (sélection d'habitat) et démographiques (densité de population et forme physique). Nous montrons que l'influence relative des processus descendants sur la sélection d'habitat et sur la forme physique est relativement faible comparée aux influences ascendantes, tandis que les pressions descendantes exercent des contraintes limitantes bien plus importantes sur la densité de population. La prise de décisions affectant la conservation faites à partir de réponses comportementales seules pourrait détourner les actions et résulter en bénéfices réduits pour les populations. Cette perspective peut faciliter une prise de décisions plus efficace quant à la conservation des ours grizzlys. Nos constatations soulignent l'importance de considérer les deux influences ascendantes et descendantes, suggérant une interprétation prudente des modèles de sélection d'habitats pour n'importe quelle espèce. En conclusion, il peut être nécessaire d'effectuer un examen exhaustif des statistiques au niveau des populations telles que de la densité, des taux démographiques et de la forme physique afin d'obtenir une gestion efficace.

Contents

INTRODUCTION

Effective wildlife management and conservation requires an understanding of the main forces driving population processes, notably food resources and mortality risk (Hunter and Price 1992, Power 1992, Oriol-Cotterill et al. 2015). Both of these factors are shaped by our increasingly human-dominated landscape (Johnson et al. 2006*b*, Barber-Mayer et al. 2012, Muhly et al. 2013) with our footprint affecting all trophic levels (Carbone et al. 2011, Ripple et al. 2014, Venter et al. 2016, Wolf and Ripple 2016, World Wildlife Foundation 2018). There is wide variability across taxa in behavioral and demographic responses to bottom-up (food) versus top-down (mortality) influences (Dyer and Letourneau 1999, Grange and Duncan 2006, Field et al. 2006, Greenville et al. 2014. Legagneux et al. 2012). For some large carnivores, food has been identified as the key driver of density (Fuller 1989, Carbone and Gittleman 2002, Sinclair and Krebs 2002, Karanth et al. 2004, McLellan 2015), while for others, mortality is the main influence on population dynamics (Kissui and Packer 2004, Lamb et al. 2020). Consideration of both influences may be necessary for effective conservation. For example, successful increase in tiger (*Panthera tigris*) densities occurred when management strategies extended beyond hunting and poaching (Kenney et al. 1995) to include prey abundance (Karanth et al. 2004, 2011; Chapron et al. 2008; Hebblewhite et al. 2014). Furthermore, within species, top-down versus bottom-up influences can vary dynamically over time and space (Krebs et al. 1995, Meserve et al. 2003, Grange and Duncan 2006, Pierce et al. 2012, Boulanger et al. 2018), necessitating comprehensive examination of forces on a population to achieve an effective conservation strategy.

High trophic levels (e.g., large carnivores), exerting top-down pressure on lower levels (Sinclair et al. 2003), shape ecosystems and community composition often in complex ways rather than a simple hierarchy (Berger et al. 2001, Beschta and Ripple 2009, Newsome and Ripple 2015, Winnie and Creel 2016). For example, several bear species, while being amongst the largest animals in the order Carnivora, are omnivores that can directly consume from multiple trophic levels ranging from vegetation and insects through to salmon and large ungulates (McLellan and Reiner 1994, Nielsen et al. 2016). Humans have been a source of mortality for carnivores for millennia (Woodroffe 2000, Ripple et al. 2014, Venter et al. 2016) and thus, despite being high in the trophic hierarchy with few natural predators, bear densities have and continue to be shaped by top-down influences. Human activities also affect the species on which bears feed. Carnivore populations suffer from human-induced prey depletion and habitat loss (Treves and Karanth 2003, Wolf and Ripple 2016, Theobald et al. 2020) and omnivores are additionally affected by altered habitats and access to natural plant foods (Nielsen et al 2004*b*, McLellan 2015).

Grizzly bears (*Ursus arctos*) are a significant predator in some areas (Boertje et al. 1988, Gasaway et al. 1992, Mattson 1997, Young and McCabe 1997, Brockman et al. 2017), but in others they rely heavily on a plant-based diet (McLellan 2011). The proportion of animal-based foods in their diets, including salmon, varies from 0 to 88% across western North America (Hilderbrand et al. 1999, 2018; Mowat and Heard 2006; Mowat et al. 2013). Body condition is important for North American grizzly bears that must hibernate up to 5 or 6 months, a period of winter dormancy inside a den (Watts and Jonkel 1988, Farley and Robbins 1995, Hilderbrand et al. 2000, Robbins et al. 2012). Females in particular, depend on extensive fat stores during winter when they give birth and nurse young. Where available, animal prey are usually preferred over plant foods, yielding bigger bears and a higher recruitment of young (Hilderbrand et al. 1999, 2018, 2019). In populations with little available meat, such as in southern British Columbia, Canada, bears tend to be smaller overall, but abundant berry crops in fall promote fat gain, facilitating successful reproduction and hibernation (McLellan 2011). In some systems, combinations of fruit and meat (i.e., carbohydrates and protein; Nielsen et al. 2016) have been associated with higher bear densities, which is thought to be from improved nutrition.

In much of southern British Columbia, grizzly bears consume large quantities of berries during August and September (McLellan and Hovey 1995). This hyperphagia facilitates fat deposition, important for hibernation (McLellan and Hovey 1995, McLellan 2011). McLellan (2015) determined that abundance of black huckleberry (*Vaccinium membranaceum*; hereafter huckleberry) was positively associated with greater cub production, and that inter-annual variation in huckleberry abundance aligned with decadal fluctuations in grizzly bear density.

Abundance of plant foods for bears can be influenced by human activities. For example, forest canopies can be opened through timber harvest, increasing spring herbs, forbs, and sometimes summer berries (Nielsen et al. 2004*a*, *b*), whereas tree planting ultimately closes canopies, inhibiting berry production (Nielsen et al. 2004*b*). Forest canopies may remain open longer in high-elevation logging cut blocks where tree growth is slow (Nielsen et al. 2004*b*). Decades of fire suppression have led to canopy closure and reduced bear foods that would otherwise proliferate after fires (Minore 1975, Minore et al. 1979, Hamer and Herrero 1987, McLellan 2015).

In addition to bottom-up influences, the southern periphery of current grizzly bear range reflects top-down forces from a century of overlap with humans (McLellan 1998, Mattson and Merrill 2002). While this declining population pattern has been halted, and in some populations reversed (United States Fish and Wildlife Service 2021), bear densities continue to be limited in some areas where they share the landscape with humans. In southern British Columbia, western Alberta, and areas of the United States within remaining grizzly bear distribution, bears often exist within a mosaic of anthropogenic mortality risk factors, predominantly roads and human settlements (McLellan et al. 1999, Nielsen et al. 2004*b*, Schwartz et al. 2010). Decades of forest harvest and other resource-based industries (e.g., mining) have left a network of roads over much of western North America in areas away from human settlements and highways (backcountry). People accessing this backcountry create a top-down pressure on grizzly bears (Mace et al. 1996, Nielsen et al. 2004*c*, Boulanger and Stenhouse 2014, Lamb et al. 2017, Proctor et al. 2019), both through direct mortality and displacement from productive habitats (Schwartz et al. 2010, Boulanger and Stenhouse 2014). While vehicle collisions are rare on backcountry resource roads, conflicts can result in direct mortalities associated with wildlife hunting; unsecured attractants, self-defense, mistaken identity, or illegal killings including poaching or malicious kills all contribute to top-down pressures on grizzly bear populations (McLellan et al. 1999, Benn and Herrero 2002, Schwartz et al. 2010). Public reporting of mortalities is typically considered a portion of total bear mortality.

In British Columbia, over past decades, a legal bear hunt occurred in larger populations that could sustain harvest, though it was closed in at-risk populations (McLellan 1998, Hamilton and Austin 2004). That hunt was halted in 2017 on ethical grounds (McLellan et al. 2017*a*). The vast majority of bears killed by legal grizzly bear hunting and non-hunt causes were shot within 500 m of an open backcountry road (open to vehicular causes; see review in Proctor et al. 2019) and some studies report mortality concentrated within 120 m of roads (McLellan 2015). These mortality patterns were observed in multiple-use landscapes that had legal bear and ungulate hunts (McLellan et al. 1999, Boulanger and Stenhouse 2014) but also in areas with no bear hunting such as national parks (Benn and Herrero 2002, Schwartz et al. 2010). Unreported human-caused grizzly bear mortality can contribute to high and potentially unsustainable mortality levels, as was suggested in an area of southeast British Columbia far from human settlements (McLellan et al. 2018). Extensive resource road networks may lead to unsustainable levels of total mortality in some areas despite a low level of publicly reported grizzly bear mortalities (McLellan et al. 2018).

The closure of a portion of backcountry road networks, motorized access management, has been a cornerstone of successful recovery of grizzly bear populations in the United States (Mace 2004, Interagency Grizzly Bear Committee 2016). In Canada, the unpopularity of backcountry vehicular restrictions has resulted in low political uptake, even in areas of at-risk grizzly bear populations (DeWolf 2016). British Columbia currently has >600,000 km of resource roads, and an additional 10,000 km are built annually, with no incentive provided for decommission (Auditor General of British Columbia 2017). Access management remains a controversial issue for grizzly bear conservation in British Columbia (Ciarniello et al. 2007, Lamb et al. 2018, Proctor et al. 2019, Morgan et al. 2020).

In western North America, grizzly bear research and management has historically focused on anthropogenic mortality as the driving force of population viability (McLellan et al. 1999). This focus arose from telemetry studies that estimated population trends from radio-tracking females and following the fates of individuals to directly estimate population-level birth rates and age-specific survival. These studies identified adult female survival as the most sensitive vital rate of a population (Knight and Eberhardt 1985, McLellan 1989*a*, Eberhardt et al. 1994, Garshelis et al. 2005, Mace et al. 2012). Additional studies have identified the negative effect of backcountry human-caused female mortality mediated through road networks (McLellan and Shackleton 1988, Mace et al. 1996, Nielsen et al. 2004*c*, Schwartz et al. 2006, Schwartz et al. 2010).

Some studies, in addition to focusing on top-down mortality, have examined bottom-up habitat quality and food resources as forces driving population viability. But these models have relied on surrogate indicators of bear foods such as riparian, canopy cover and greenness (Mace et al. 1999, McLellan and Hovey 2001, Nielsen et al. 2002, Ciarniello et al. 2007, Milakovic et al. 2012) instead of directly measuring these resources. In addition to not using direct predictors of population processes (Garshelis 2000, Beyer et al. 2010, Ayers et al. 2013), habitat selection analyses have been criticized for being disconnected from measures of population vitality and may thus miss the mark on understanding how to manage populations. For example, high-use habitats can be population sinks when they are associated with excessive mortality (Nielsen et al. 2006, 2009; Lamb et al. 2017, 2020; Boulanger et al. 2018), necessitating consideration of factors beyond habitat use.

The complex interaction of top-down and bottom-up forces shape grizzly bear densities, especially along the periphery of their range contraction. Low food supply, reduced access to foraging areas due to human disturbance, excessive human-caused mortality, and lack of inter-population connectivity can all contribute to low population viabilities for bears in human-dominated landscapes. Yet populations vary in viability, and thus the degree of conservation concern and management required necessarily also varies (Morgan et al. 2020). The complex interactions of top-down and bottom-up influences that underpin this variation are not well understood. More comprehensive models that integrate both bottom-up (habitat and foods) and top-down (mortality) variables (Nielsen et al. 2010, Lamb et al. 2018) better identify the drivers of grizzly bear populations (Nielsen et al. 2010, 2016; Braid and Nielsen 2015). For example, in Alberta, Nielsen et al. (2010) found that while food resources drove grizzly bear habitat selection, integrating mortality into their models was required to understand population processes. Not all models to date have been spatially explicit, despite this being an important component for land management (e.g., McLellan 2015).

We investigated both bottom-up and top-down influences affecting grizzly bears in southeastern British Columbia (Figure 1). In this region, the grizzly bear population is fragmented into a mosaic of sub-populations: some are small and isolated, others are larger and partially connected (Proctor et al. 2005, 2012). Several isolated populations span the Canada–United States border and are designated as threatened in the United States and by the International Union for Conservation of Nature (U.S. Fish and Wildlife Service 1993, McLellan et al. 2017*b*). Improved mortality management in both countries has resulted in some populations recovering from historical excessive human-caused mortality and habitat loss, alteration, and degradation (McLellan 1998; McLellan et al. 1999, 2017*b*; Mattson and Merrill 2002). Degree of recovery is variable in this region, and many threats continue today (Proctor et al. 2012, 2018). We selected 3 of these sub-populations within the Selkirk and Purcell mountain ranges (Figure 1) to assess the relationship between food and mortality risk influencing grizzly bears in this region. We developed several functional metrics for bottom-up and top-down variables and tested their relative predictive power in various models. First, we developed a model to predict location and size of patches of the most important grizzly bear food in the study area, black huckleberry (McLellan and Hovey 1995; McLellan 2011, 2015). We used the outcome of this huckleberry model as a bottom-up variable, combined with additional habitat variables and measures of mortality risk to explain female habitat selection, density, and realized reproductive success, (hereafter referred to as fitness). We had 3 predictions:

1. Huckleberry patches located through grizzly bear location data can be used predictively to model habitat selection and population characteristics better than previously used habitat models developed from surrogate bottom-up variables.
2. Habitat selection will be most influenced by bottom-up variables (e.g., huckleberry patches), whereas fitness and density will be influenced to a greater degree by top-down mortality risk variables (e.g., secure habitat, road density).

FIGURE 1 The focal and regional study areas in southeast British Columbia, Canada, within the North American grizzly bear distribution. Dashed lines of the focal region are Grizzly Bear Population Unit (GBPU) boundaries of the British Columbia Government (Morgan et al. 2020). The focal area was where we identified huckleberry patches through site visits. Visits were to clustered locations of global positioning system (GPS)-collared grizzly bears accumulated during 2004–2015. It was also the data-collection area underpinning the huckleberry patch, female habitat selection, fitness, and density models. The solid yellow line is the boundary of the regional study area where we modeled huckleberry occurrence.

3. The contribution of huckleberry patches to grizzly bear fitness and population density will diminish as the amount of secure habitat decreases.

STUDY AREA

Our study occurred at 2 geographic scales. We collected global positioning system (GPS) telemetry (2004–2017) and genetic data (1997–2017) in the primary 14,236-km^2 focal study area in the south Selkirk and Purcell mountains of southeastern British Columbia. We visited sites of clustered GPS locations to identify huckleberry patches associated with bear use (2014–2017; Figure 1). This area consists of 4 population units used for management by the British Columbia provincial government: South Purcell, Central Purcell, South Selkirk (threatened), and Yahk (threatened; McLellan et al. 2017*b*; Figure 1). This focal area was used for the population process modeling (i.e., habitat selection, fitness, and density). The secondary scale covered the broader region of 82,338 km^2, within which the primary study area was located. We modeled and predicted huckleberry plant occurrence from site visits assessing species presence to inform the huckleberry patch modeling. The geophysical, biological, and human environments of the focal and regional study areas are similar (Meidinger and Pojar 1991).

The regional study area is mountainous and predominantly covered by conifer forests with patches of deciduous forest throughout. It consists of mountain valleys, typically at 500–600 m asl, and upland forest, avalanche, riparian, and alpine ecosystems on the slopes of peaks that reach 3,000–3,500 m asl. The region is relatively wet with much of the annual precipitation received as snow in winter, especially at elevations above 1,000 m asl. Summers (mid-June through August) can be somewhat dry (<20 mm of rain/month) and hot (mean daily highs of 23°C), particularly at lower elevations. The predominant ecosystem types are Interior Eastern Red Cedar–Western Hemlock (*Thuja plicata*–*Tsuga heterophylla*) forests at lower elevations (400–1,500 m asl), Engemann Spruce–Sub-alpine fir (*Picea engelmannii*–*Abies lasiocarpa*) forests at higher elevations (1,500–2,200 m asl), and Interior Douglas-fir (*Pseudotsuga menziesii*) forests in drier eastern portions (900–1,500 m asl; Meidinger and Pojar 1991). The understory has some consistent representative site associations of mixed shrub and herb species depending on forest age, canopy closure, and microclimate. Shrubs include falsebox (*Pachistima myrsinites*), black huckleberry, Devil's club (*Oplopanax horridus*), and thimbleberry (*Rubus parviflorus*). Herbs include bunchberry (*Cornus canadensis*), oak fern (*Gymnocarpium dryopteris*), and five-leaved bramble (*Rubus pedatus*).

There are 4 national parks encompassing 4,328 km^2 or 5% of the region and 13 larger provincial protected areas of various sizes (50–2,000 km^2) covering 7% of the region. The timber-extraction industry and sporadic mining operate throughout this region except for several protected areas. Extraction activities have left an extensive network of backcountry roads in many areas. Mountain ranges are typically separated by valleys containing major highways and railways that connect urban centers. These valleys often support a linear assemblage of rural landowners or communities along portions of their length. Human settlement along highways varies from stretches with continuous rural settlement to stretches with very little development (Proctor et al. 2012). There are 21 towns with a population >500 in the mountain valleys across the region (~100,000 people in total) with approximately another 50,000 in rural areas, also in the valley bottoms. Less than 2% of the area is in agriculture (1,270 km^2).

Ocean-run spawning Pacific salmon, which were an important food source for grizzly bears in parts of the study area (Hilderbrand et al. 1996, 1999), were eliminated by dams on the lower Columbia River constructed in the mid-1900s (Gayton 2001). Naturally occurring land-locked sockeye salmon (kokanee; *Oncorhynchus nerka*) have also declined substantially (Ashley et al. 1997). Grizzly bears continue to use several localized remnant spawning kokanee runs; most are supported by hatcheries and enhanced spawning channels. Limited use by grizzly bears of spawning cutthroat trout (*Oncorhynchus clarki*), rainbow trout (*Oncorhynchus mykiss*), and bull trout (*Salvelinus confluentus*) occur sporadically in the region (Mowat et al. 2013).

Without access to Pacific or landlocked salmon, grizzly bear diets in the study area are approximately 85% vegetation-based (McLellan and Hovey 1995, McLellan 2011). Berries, primarily black huckleberry and secondarily buffaloberry (*Shepherdia canadensis*), are the dominant energy-storing foods (McLellan and Hovey 1995, McLellan 2011). They are supplemented by a wide variety of forbs including cow parsnip (*Heracleum lanatum*), horsetail (*Equisetum arvense*), and graminoids (McLellan and Hovey 1995). This diet is augmented by predation or scavenging of local ungulates (elk [*Cervus canadensis*], moose [*Alces alces*], black-tailed deer [*Odocoileus hemionus*], white-tailed deer [*Odocoileus virginianus*]), livestock (sheep, goat, pig, chicken), and ants (carpenter ants [*Camponotus* spp.]; McLellan and Hovey 1995, McLellan 2011).

Geographic distribution and year-to-year fluctuations in fruit crops, or the absence of huckleberry in some areas, make the quality of these diets variable across the regional study area (McLellan and Hovey 1995, Munro et al. 2006). Further, timber harvest and fire suppression have affected the mosaic of bear foods across the region. Berry crops are abundant in some areas that burned 30–70 years ago (Hamer and Herrero 1987; McLellan and Hovey 1995; Hamer 1996, 1999). More broadly, fire suppression (Klenner et al. 2008) has interrupted natural fire cycles causing forest canopies to remain closed and thus diminishing the abundance of productive fire-induced berry patches (Hamer and Herrero 1987, McLellan and Hovey 1995, McLellan 2015). Ongoing timber harvest has altered forest structure in ways that have both positive and negative impacts on bear foods (Nielsen et al. 2004*a*, *b*). In some areas, timber harvest results in bear foods in the early stages of forest regeneration, but this stage can be followed by forest canopy closure yielding minimal bear foods in the understory (Hamer and Herrero 1987; McLellan and Hovey 1995, 2001; Nielsen et al. 2004*b*).

METHODS

Study design

The study design involved 5 modeling analyses detailed below, with methods varied to suit questions, data, and model evaluation techniques (Table 1; Figure 2). Thus, this methods' section has been structured by modeling exercise. We first developed a bottom-up food resource huckleberry model that required creating a huckleberry plant occurrence model and then a huckleberry patch model. To develop the patch model, we used GPS telemetry data from grizzly bears and the occurrence layer. Second, we used the huckleberry patch model and other variables to explore the relationship of various bottom-up and top-down influences for 3 population processes or characteristics: female habitat selection, female fitness, and both sex density (Table 2; Figure 2). We included male density to contrast one process with females. We used these modeling analyses to evaluate which variables were the most predictive, and then to assess the relative influence of significant variables and the direction of their effect. We did this to include independent data (from the fitness and density data) while simultaneously evaluating the ability of the huckleberry patch model to predict female habitat selection, fitness, and density.

Huckleberry occurrence and patch modeling

We modeled huckleberry patches in 2 steps. First, we created a predictive model of huckleberry occurrence (or distribution, hereafter occurrence model) across the study region (Figure 1) developed from plant presence-absence data (yes vs. no; Table 1). Using that occurrence model as available huckleberry habitat, we then modeled huckleberry patch selection by grizzly bears in the focal area from use of these patches determined through the GPS telemetry data (hereafter patch model). This was a use versus availability analysis (Table 1). The occurrence

TABLE 1 Summary of the 5 modeling exercises including model type, input data, and evaluation method for grizzly bears in British Columbia, Canada (1998–2015).

Analysis	Model	Input data	Evaluation
Huckleberry occurrence	Boosted regression tree (BRT)	Presence vs. absence	AUC ROC score[a]
Huckleberry patch	Boosted regression tree (BRT)	Use vs. availability	Habitat selection, fitness, and density models
Female habitat selection	Resource selection function (RSF)	Use vs. availability	*k*-fold
Female fitness	Resource selection function (RSF)	Presence vs. absence	AUC ROC score
Sex-specific density	Spatially explicit capture-recapture (SECR)	Presence vs. undetected	95% confidence intervals

[a] Area under the curve of the receiver operating characteristic.

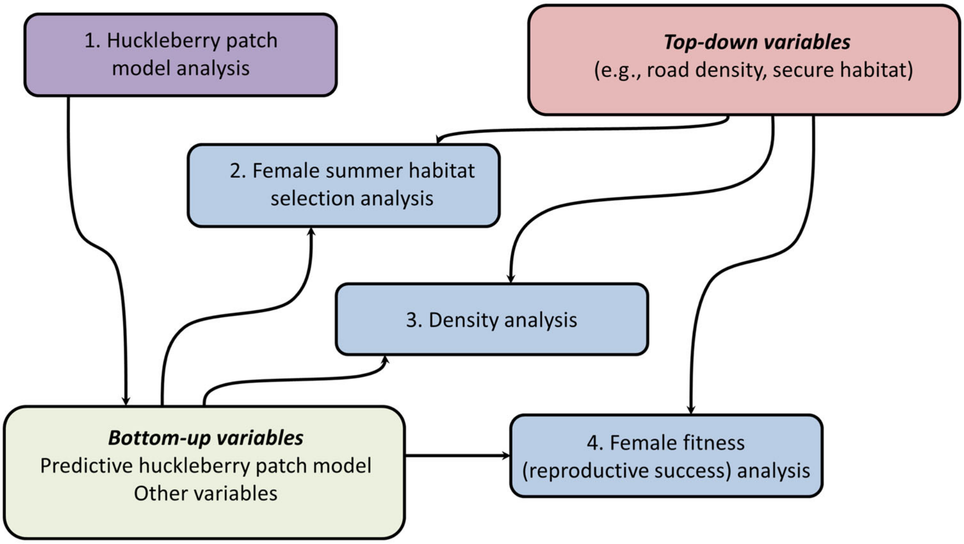

FIGURE 2 The analytic structure and the order of the modeling process. We first developed a huckleberry patch mode. This became the primary grizzly bear food variable for 3 subsequent modeling analyses (female summer habitat selection, density, and female fitness [reproductive success]). We used these analyses to evaluate the huckleberry patch model predictability using independent data and ecological processes. Following this, we assessed the relative influence of a suite of bottom-up and top-down covariates on these 3 grizzly bear population processes in British Columbia, Canada, between 2004–2015.

model represented where huckleberry plants occurred and constrained the patch model, which represented huckleberry patches that were selected by (and potentially important to) grizzly bears.

Huckleberry occurrence and patch data

For the occurrence model, we obtained huckleberry plant presence data (frequency and percent cover) from extensive and consistent vegetation plots surveyed by British Columbia government ecologists between 1981 and 2013 for the provincial Biogeoclimatic Ecosystem Classification (BEC) program (Meidinger and Pojar 1991). They stratified field sampling by BEC units, soil moisture, and nutrient regimes and sampled ≥5 sites for each combination of these criteria. They selected sites for homogeneity of these characteristics and used slope position, indicator plant species, relative tree growth, soil texture and seepage, and solid parent material to determine moisture and nutrient regimes for site selection (https://www.for.gov.bc.ca/hre/becweb/system/methods/index.html). Plot methods are described in British Columbia Ministries of Forests and Range and Environment (2010). The sampling strategy ensured good coverage of ecosystem variability across the study region. On average, they sampled 8 sites per 1 km^2 (Figure 3A). Experienced ecologists surveyed plots and documented the occurrence and percent ground cover of all vegetation species. We only used the presence and absence of huckleberry plants at each site. Huckleberry plants were detected at 4,297 of 10,125 20 × 20-m vegetation plots across the regional study area (British Columbia Ministries of Forests and Range and Environment 2010; Figure 3A).

To develop the patch model, we visited sites (described below) and identified locations with huckleberry that were used by radio-collared grizzly bears during the berry season, 15 July–15 September, across the focal study area. We used 30,254 GPS telemetry locations from 43 bears (21 female, 22 male) over 10 years (2004–2013;

TABLE 2 Predictive variable data ranges used to develop a multi-variable resource selection function model of summer female grizzly bear habitat selection, fitness, and density in the south Selkirk and Purcell mountains in British Columbia, Canada, between 1998–2015. For the fitness and density analyses, which were derived from DNA survey data, these variables were scaled at a 3-km and 8-km grain. Variables were tested within models for optimum proportions of secure habitat in fitness and density analyses.

Variable category	Variable	Units	Data range	Analysis 1, 2, or 3[a]
Bottom-up				
Forest cover	Canopy cover	Percent	0–100	1, 2, 3
	Recently logged	Categorical	0 or 1	1, 2
	Lodgepole pine	Categorical	0 or 1	1, 2
	Douglas fir	Categorical	0 or 1	1, 2
	Spruce-fir	Categorical	0 or 1	1, 2
	Deciduous	Categorical	0 or 1	1, 2
Forest age class	0–20 years	Categorical	0 or 1	1, 2
	20–60 years	Categorical	0 or 1	1, 2
	60–80 years	Categorical	0 or 1	1, 2
	80–100 years	Categorical	0 or 1	1, 2
	100–250 years	Categorical	0 or 1	1, 2
Land cover	Alpine	Categorical	0 or 1	1, 2, 3
	Avalanche	Categorical	0 or 1	1, 2, 3
	Riparian	Categorical	0 or 1	1, 2, 3
Ecological	Greenness	Continuous	0.002–0.997	1, 2, 3
	Wetness (CTI[b])	Index	3.4–27.2	1, 2, 3
	Solar radiation	kj/m^2	218–29,494	1, 2, 3
Food resources	Huckleberry patch	Categorical	0 or 1	1, 2, 3
	Huckleberry patch >5 ha	Categorical	0 or 1	1, 2, 3
	Huckleberry patch >10 ha	Categorical	0 or 1	1, 2, 3
	Distance to patch	km	0–12	1, 2, 3
	Distance to patch >5 ha	km	0–12	1, 2, 3
	Distance to patch >10 ha	km	0–12	1, 2, 3
	Huckleberry plant occur	Categorical	0 or 1	1, 2, 3
Top-down				
Human	Highway	Categorical	0 or 1	1, 2, 3
	Human development	Categorical	0 or 1	1, 2, 3
	Forest roads	Categorical	0 or 1	1, 2, 3
	Distance to road	km	0–25	1, 2, 3
	Road density	km/km^2	0–5	1, 2, 3
	Human access	Index of remoteness	0–32,000	1, 2, 3

TABLE 2 (Continued)

Variable category	Variable	Units	Data range	Analysis 1, 2, or 3[a]
	Secure habitat[c]	Categorical	0 or 1	1, 2, 3
	Secure habitat 5 km^2 min size	Categorical	0 or 1	1, 2, 3
	Secure habitat 10 km^2 min size	Categorical	0 or 1	1, 2, 3
	Secure habitat scaled to 3 km	Categorical	0 or 1	3
	Secure habitat scaled to 8 km	Categorical	0 or 1	3
Geography	Terrain ruggedness	Unitless	0–1,008	1, 2, 3

[a] 1 is habitat use, 2, is fitness, 3 is density.

[b] compound topographic index.

[c] >500 m from road.

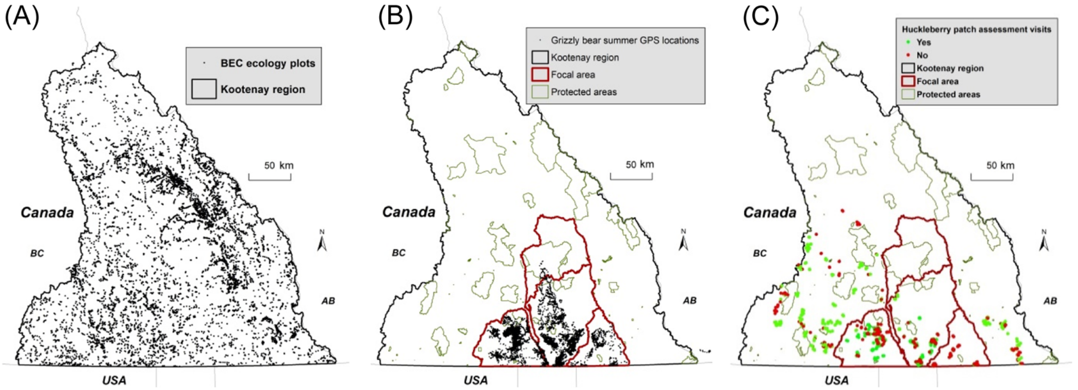

FIGURE 3 A) British Columbia Biogeoclimatic Ecosystem Classification (BEC) system vegetation plots (1981–2013) across the regional study area used to model huckleberry plant occurrence, B) global positioning system (GPS) locations (50,171) of 22 male and 21 female grizzly bears between 2004–2013, and C) sites visited to assess huckleberry patch presence in the south Selkirk and Purcell mountains of southeast British Columbia, Canada. We collected grizzly bear locations during the berry season (15 July–15 September) and used them to find huckleberry patches in 2014–2015. Yes indicates sites determined to be huckleberry patches, and no sites were not patches. We used sites visited to the east and west of the focal study area to assess the efficacy of the patch model for extrapolation to these areas. We visited sites outside of the focal area where ecological conditions were very similar to develop a model that would be applicable across a broader region.

Figure 3B). All radio-collared bears were independent of one another. The age range of collared bears spanned 3 to >20 years old (2–5 yr: 38%, 6–10 yr: 30%, 11–15 yr: 35%, and >16 yr: 7%). We captured bears with Aldrich foot snares (38) and occasionally with barrel traps (5). Bear handling procedures were in accordance with the Canada Council on Animal Care Standards. We used Telonics (Mesa, AZ, USA) Spread Spectrum radio-collars (and occasionally store-on-board collars) and remotely downloaded bear locations periodically.

We radio-collared most bears in May or June and monitored them for 1–3 years, usually spanning at least 2 non-denning periods (i.e., spring, summer, fall). To maximize spatial coverage of bear locations, we balanced collaring effort between areas with high bear use and thus high likelihood of capture, with areas where low densities constrained success. Bears have large multi-annual home ranges (females: 80–700 km^2, males: 900–3,000 km^2), which helped us attain broader spatial coverage of available habitat conditions. Because the focal area was partitioned into 4 population units by human-settled valleys and major highways (Figure 1; Proctor et al. 2005, 2012), the home range of a male bear almost covered any one population unit. Female bears covered less area, but with 43 radio-collared bears, spatial coverage was good (Figure 3B). Collars were programmed to collect locations every 1–4 hours depending on battery size. Smaller bears carried lighter collars with less battery life. Subadult bears carried collars designed to drop off earlier to not interfere with neck growth. We took care when fitting collars to allow for increases in bear size from foraging in preparation for hibernation.

We used only 2-dimensional (2D) and 3-dimensional (3D) fixes and overall fix success (the proportion of 2D and 3D fixes relative to fix attempts) was 84%. Mean positional dilution of precision (PDOP) indicates spacing of satellites and reflects location accuracy, with lower values being more accurate (D'Eon, Delparte 2005). We filtered location data for PDOP values <10, a value shown to minimize location inaccuracy (Lewis et al. 2006). Mean PDOP value was 3.9 (SE = 0.018) for all 2D (<50-m accuracy) and 3D (<12-m accuracy) locations. The final dataset had an average of 8.4 locations per day per bear across the non-denning period (April–October). We also assessed potential location bias for canopy cover, which was the variable with the most potential for low fix success rate (Frair et al. 2004). We placed 13 GPS radio-collars at ground level in conifer forest with canopy cover from 0 to 75% canopy and found no relationship between fix rate and canopy cover ($R^2 = 0.07$; regression significance, $P = 0.64$; Figure A1, Appendix I).

We pooled GPS location data and ran an ArcGIS (Esri, Redlands, CA, USA) tool that calculated the density of points across a 200-m moving window at a 30-m cell size. We converted areas with density values >50 into polygons and calculated their area. Polygons >1 ha became target field patches that we visited in person to assess if bears had likely used them to feed on huckleberry fruit (Figure 3C). Our goal was to determine if sites visited were a huckleberry patch worthy of a grizzly bears foraging time. We picked field plot centers to be in the middle of a habitat patch with huckleberry within a cluster of grizzly bear locations. If there were no huckleberry plants, the plot center became where there was evident bear sign (e.g., root digs, bear bed). We measured all metrics as per established ecosystem protocols (British Columbia Ministries of Forests and Range and Environment 2010). We focused on presence and the percent cover of huckleberry plants, presence of fruit, and type of bear sign. We visually estimated huckleberry cover from the center of a 400-m^2 plot. For all locations sampled, we used the British Columbia Government standard 20 × 20-m plot (British Columbia Ministries of Forests and Range and Environment 2010). Further details on field protocols are available in Table A1, Appendix I, Huckleberry Modeling Methods.

In areas where we did not have GPS telemetry coverage, we used a preliminary huckleberry patch model to help us locate potential huckleberry patches. We developed the model from the first 2 years of site visits where we did have telemetry locations (Figure 3B). We found that a combination of huckleberry plant canopy cover (>20%), percent fruiting (>10% fruiting; British Columbia Ministries of Forests and Range and Environment 2010), and forest canopy cover (<30% forest cover) were reliable predictors of huckleberry patches (Figure A2, Appendix I). We applied the same field methods and metrics that we used in the GPS clusters described above.

We chose the above methods because our goal was to identify huckleberry patches that were on average used by grizzly bears across years, not to relate bear use to any particular year's berry production. The benefit of using multiple-year GPS telemetry data is that it allowed us to overcome the inter-annual variation in berry crop production and identify these patches' influence on bear behavior (habitat selection), density, and fitness. In the use versus availability huckleberry patch selection analyses, we used confirmed huckleberry patches as use data, and extracted 10 random points as available data from within the huckleberry occurrence model for every used patch point (Figure 4).

Environmental variables thought to limit the occurrence of huckleberry include soil pH (Barney 1999, Barney et al. 2006), soil texture (Barney et al. 2006), climate (Holden et al. 2012), forest fires (Nielsen and Nielsen 2010), canopy cover (Minore 1984), and topography (Roberts et al. 2014). We calculated 32 variables within these categories (Table A2, Appendix I) from various data sources. For each variable we constructed spatial representations in 30-m resolution (geographic information system [GIS] raster layers with 30-m pixels). We removed areas of rock, ice, human settlement, lakes, and rivers and areas where data were missing.

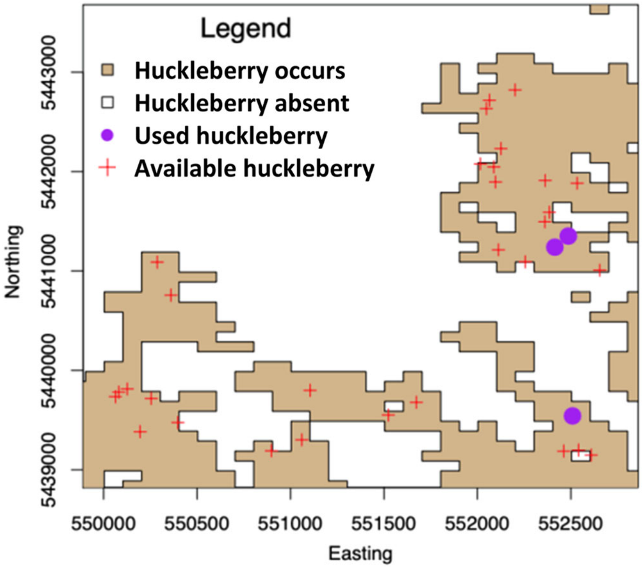

FIGURE 4 Example of the huckleberry patch selection modeling approach. We compared huckleberry patches (purple dots) determined to be used by grizzly bears to surrounding available huckleberry plant occurrence sites (red + signs) within the occurrence distribution (beige). We determined huckleberry occurrence habitat by modeling sites identified from Biogeoclimatic Ecosystem Classification field surveys. Work occurred in southeast British Columbia, Canada, between 2004–2013. White areas indicated huckleberry absence.

Huckleberry occurrence and patch modeling

For both occurrence and patch modeling, we used boosted logistic regression trees (BRT; Elith et al. 2008) and functional environmental response variables (Table A2, Appendix I) to predict the presence of huckleberry plants and patches; BRTs are an advanced form of a generalized linear model (GLM; Elith et al. 2008). Generalized linear models estimate coefficients for each variable in a model, whereas BRTs build regression trees (models that relate a response to their predictors by recursive binary splits) that estimate coefficients for each tree in a GLM framework. In a BRT, many trees are fit to the data. An initial tree is fit to the data such that it correctly classifies as many observations as possible and subsequent trees focus on classifying those observations poorly predicted by previous trees (Shirley et al. 2013).

The BRT method was suited to this application because it can handle the nonlinear and interactive relationships we expected to find, and provide greater predictive performance than GLMs (Elith et al. 2008). In addition, BRTs do not face the same issues as GLMs when fitting models with multicollinearity between predictors because trees are fit with recursive partitioning algorithms instead of matrix inversions (Shirley et al. 2013). Another advantage of BRTs is that *a priori* model definitions are not required. Instead, BRTs fit the meaningful ecological variables identified to be included in the data, and those variables that predict poorly will not affect results because these variables contribute very little to model predictions. These variables that contribute little to model predictions can be iteratively removed from the model using a *k*-fold cross-validation until an optimum is achieved (Elith et al. 2008).

We used the gbm package (Ridgeway 2015) in Program R (R Core Team 2016) to fit the BRT. A BRT is fit to data using 3 main parameters. First, the learning rate is the contribution of each tree to the model. Smaller learning rates force each tree to contribute a relatively small amount to the predictions, resulting in more trees being required to fit the model. In general, a lower learning rate is preferred because fitted values in the final model are the sum of all trees multiplied by the learning rate. Thus results from models with more trees (lower learning rate) are more stable because they are generated from many different trees (Elith et al. 2008). The second parameter, tree complexity, is the number of nodes or splits allowed in each tree, where more reflect increased complexity. The last parameter is the bag fraction, which is the percent of the data used to build the model (train) and data used to test predictions that were not involved in model creation (test) for each iteration (new tree).

We tested several learning rates (0.0005, 0.001, 0.01) and tree complexities (2, 4, 6, 8) and selected the top model that minimized deviance of huckleberry occurrence predictions based on sites withheld from the model (Elith et al. 2008). Occasionally, in the field we sampled several sites in a cluster to produce an accurate representation of huckleberry patches. To accommodate this, we weighted observations inversely to their number in these clusters, such that those with many samples were not over-represented in the data. We simplified the model using *k*-fold cross validation to remove uninformative parameters. We calculated the relative influence of each predictor associated with huckleberry patches, and the marginal effect (predictive response from one variable at a time while other variables are held constant) across its range.

Huckleberry model spatial projections

Because BRT modeling provides a continuous occurrence probability between 0 and 1, we generated a cut-off value where we considered predicted values larger than the cut off to be huckleberry presence and smaller values an absence. We calculated this cut-point for both huckleberry models by determining the value where the product of sensitivity and specificity are maximized, which is also analogous to minimizing the distance between the receiver operating characteristic (ROC) curve and point 0, 1 on plot.

In addition, as huckleberry plant occurrence does not necessarily translate to berry presence, or bear food, we applied a canopy cover rule. We considered occurrence sites with <50% forest canopy cover to have fruit-producing shrubs (Nielsen et al. 2004*b*) and occurrence sites above that threshold to be absent of fruit, or have fruit densities below what would be biologically meaningful to bears. We therefore constrained the model to areas where canopy cover was <50%. This refinement allowed us to test the patch model against the clustered GPS locations we visited and rated as huckleberry patches used by bears. We generated an occurrence surface for potential fruit-producing huckleberry using a raster within Program R (Hijmans 2023).

Model evaluation

To avoid overfitting the models and ensure predictions represented the trends in the data, we partitioned the data into training (bag fraction = 60%) and testing data (40%) for each iteration (new tree). We used the testing data and model predictions to calculate predictive accuracy using the ROC area under the curve (AUC), which represents the probability of correct classification (in this case as either an available or used point). Area under the curve values of 0.5 represent the same discrimination as a random guess, values >0.7 and <0.9 represent good model accuracy, and >0.9 represent high model accuracy (Nielsen et al. 2005). To calculate AUC, we substituted testing data (those data not used to build the model) into the model and evaluated the model predictions by comparing the predicted and true values for each presence-absence. We acknowledge that the AUC values are biased low in the patch (use-available) model because some presence points were sampled as available. This created a situation where some presence and available points are incorrectly scored in the AUC calculation (Boyce et al. 2002). However, this metric still served to give us insight into relative and minimum model predictability on test data.

We constructed marginal effects plots for the top 12 variables in the huckleberry occurrence and patch models to demonstrate the direction, magnitude, and shape of responses. Variables beyond these top 12 have a diminishing small influence on our top model. We also calculated estimates of relative influence of each variable, which are based on the number of times a variable improves model fit when adding a split averaged over all trees (Friedman 2001, Elith et al. 2008).

We used the final huckleberry patch model within a portion of the focal area (Nature Conservancy Canada [NCC] lands) where there were consistent spatial and temporal forestry data to explore the relationship between disturbance regimes and huckleberry patches. This included descriptive statistics relative to the type of disturbance prior to huckleberry patch identification: time since disturbance (e.g., years since logged, wildfire), and post-harvest treatments (e.g., slash burn, trees planted or not). We determined historical wildfire evidence from site visits.

Habitat selection, fitness, and density modeling variables

Bottom-up food and habitat variables

We used the huckleberry occurrence and patch models to represent direct food resources that grizzly bears use regionally. We tested for the influence of huckleberry patch size by developing 3 patch categories: all patch sizes, >5 ha, and >10 ha. We also included variables of distance to huckleberry patches in these 3 size categories.

We also included a suite of potential predictor variables used by Proctor et al. (2015) for the habitat selection, fitness, and density analyses (Table 2). We obtained baseline thematic mapping land-cover (recently logged, alpine, avalanche, and riparian), and vegetation resource inventory variables (dominant tree species, forest cover types, canopy cover) from the British Columbia Government Data Warehouse (https://www2.gov.bc.ca/gov/content/data/bc-data-catalogue). Alpine, avalanche, burned, and riparian areas contain a variety of grizzly bear foods including berries (e.g., blueberries and huckleberries [*Vaccinium* spp.], Saskatoon serviceberry [*Amelanchier alnifolia*]), herbs, forbs, and roots (e.g., glacier lily [*Erythronium grandiflorum*], cow parsnip; McLellan and Hovey 1995, 2001; Mace et al. 1996). We used forest variables because they have been found to influence grizzly bear habitat selection by providing cover and as a component of edge habitat, adjacent to a food source (Zager et al. 1983, Waller and Mace 1997, Apps et al. 2004, Nielsen et al. 2004*a*). Greenness, an index of leafy green productivity, correlates with a diverse set of bear foods, and is often found to be a good predictor of habitat use (Mace et al. 1999, Nielsen et al. 2002, Stevens 2002). Foods found in areas with high greenness values such as avalanche paths include graminoids (grasses and sedges), forbs such as angelica (*Angelica arguta*), stinging nettle (*Urtica dioica*), twisted stalk (*Streptopus* spp.), and Saskatoon serviceberries (Ramcharita 2000). We derived greenness from 2005 Landsat imagery using a tassled cap transformation that estimates where high values indicate areas of high plant reflectance, an index of deciduous leaf surfaces (Crist and Ciccone 1984, Manley et al. 1992). We derived terrain variables of compound topographic index (CTI), solar radiation, and terrain ruggedness from a digital elevation model (DEM) in ArcGIS. The CTI is an index of soil wetness estimated from a DEM using the script from Rho (2002) and may reflect forb or grass presence (Nielsen et al. 2004*b*). We estimated solar radiation for the summer solstice (day 172), using a DEM, and the ARC macro language (AML) called shortwavc.aml from Kumar et al. (1997) that was modified by Zimmerman (2000). We estimated terrain ruggedness from the DEM based on methods from Riley et al. (1999) and scripted as an ArcInfo AML called TRI.aml (terrain ruggedness index) by Evans (2004). Ruggedness is associated with bears avoidance of people (Apps et al. 2004, Nielsen et al. 2004*c*).

Top-down human disturbance variables

We used human-use and disturbance variables for the population processes analyses that previously have been associated with habitat selection (Table 2; Mace et al. 1996, 1999; Nielsen et al. 2002; Apps et al. 2004). We obtained the provincial road layer from the British Columbia Government Data Warehouse and used backcountry road presence-absence, distance to, and road density as human disturbance variables. It is possible that some trails used solely by all-terrain vehicles are not included in the Provincial road layer. We derived road density within a GIS using a 1-km^2 moving window and recorded it in km/km^2. For human developments we digitized all buildings on 1:50,000 topographic maps and ortho-photos. We buffered highways, human developments, and backcountry roads by 500 m on either side to reflect their influence on grizzly bear habitat use (Mace et al. 1996, Proctor et al. 2019). We also included a human access variable developed by Apps et al. (2004) and improved by Apps et al. (2016). This variable assigned a value for each pixel in the study area using a decay function over the travel distance from human population centers. We weighted values by size (the number of residents) over the open road network, including both front and backcountry routes (Apps et al. 2016). This variable represents how easy it is for people to get into the backcountry and potentially kill bears for the reasons listed above. Front country routes are major highways and paved roads near human settlements.

We also added the quantity of secure habitat (>500 m from an open road) within the study areas as a human disturbance variable (Figure 5). Secure habitat has been shown to be important for reducing human-caused mortality of grizzly bears in the backcountry (Mace et al. 1996, Schwartz et al. 2010, Proctor et al. 2019). We buffered all open roads by 500 m and classified all remaining patches that were a minimum of either 5 km^2 or 10 km^2 as secure habitat (Gibeau et al. 2001). Other researchers have found that patches larger than 9 km^2 were required to provide security within an average daily movement radius (Gibeau et al. 2001); however, we suspected that the smaller 5-km^2 patches were more relevant in the study area, as our average home range sizes are smaller than those of Gibeau et al. (2001). Although road density and secure habitat are related, we included both variables because the arrangement of roads can produce areas of relatively low road density where the resulting secure habitat patches may be too small to be effective for bears (Figure A3, Appendix I; Gibeau et al. 2001, Jaeger et al. 2006, Schwartz et al. 2010, Proctor et al. 2019).

Habitat selection, fitness, and density modeling

We first fit univariable models for assessing the relationship of predictor variables with habitat selection, fitness, and density. Second, we tested these relationships for each population process within multi-variable models. We then tested for the relative importance of all variables within the best multi-variable models in each of the

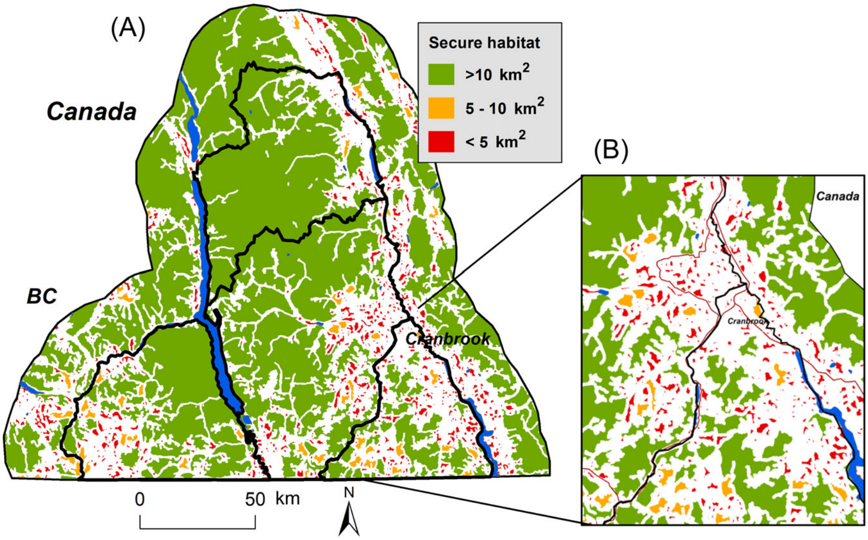

FIGURE 5 A) Secure habitat (>500 m from an open road) in the focal study area of the south Selkirk and Purcell mountains of southeastern British Columbia, Canada, and B) a close up highlighting an area with fragmented secure habitat. We used secure habitat as a variable to examine grizzly bear habitat selection, density, and fitness in southeastern British Columbia between 2004–2015.

3 analyses. To determine the relative importance of each variable, we removed each variable, iteratively, and reran the model to determine the change in predictability (as per Schwartz et al. 2010). We used log likelihood as the metric because it underpins Akaike's Information Criterion (AIC) model selection methods. We plotted relative selection strength for top habitat selection and fitness models to compare the relative magnitude and direction of selection (Avgar et al. 2017).

Female summer habitat selection modeling

The importance of female demographic parameters to grizzly bear population vitality (Eberhardt et al. 1994, McLellan 1989*a*, Garshelis et al. 2005. Mace et al. 2012) led us to focus on female berry-season habitat selection. The berry season (15 July–15 September) in the study area is the peak foraging and fat deposition period, which is important for reproduction and hibernation (McLellan 2011, 2015; Robbins et al. 2012). We developed resource selection function (RSF) models to determine, explain, and spatialize female habitat selection across the focal study area (Boyce and McDonald 1999, Nielsen et al. 2002, Johnson et al. 2006*a*) and to assess the relative importance of a range of top-down and bottom-up variables on habitat selection (Table 2).

Grizzly bear GPS location data

We radiocollared female grizzly bears between 2004 and 2015 (Figure 3B; see the Huckleberry occurrence and patch data sub-section above for details on the live-capture methods and selection of location data). We used 20,293 locations from 20 female grizzly bears. Number of locations ranged from 100–2,800 locations per bear. Eight bears had 100–500 locations, 2 had 501–1,000, 4 had 1,001–1,500, 4 had 1,501–2,000 and 2 had >2,000 locations.

Habitat selection modeling

We used a matched case-control RSF design where we paired each individual bear's used locations (GPS locations) with a set of available (random) locations generated within a minimum convex polygon for that bear's home range at a density of 5 points/km^2 (Nielsen et al. 2004*a*). We extracted covariate values across all used and available locations. We used conditional logistic regression (Manly et al. 2007) within Program R's survival package (Thurneau 2023) to estimate selection coefficients of the exponential RSF. We estimated robust standard errors treating each bear as a separate cluster to account for repeated samples by individuals. This avoids non-independent locations that can otherwise lead to underestimates of biased variance around coefficient standard errors and overestimated significance of model parameters (White 1980; Nielsen et al. 2002, 2004*c*; Prima et al. 2017). We mapped predictions by multiplying the RSF selection coefficients for each variable by its value in a raster stack with a 100-m pixel size in ArcGIS. We classified spatial predictions into 10 equal-area bins, where bin 1 had the lowest RSF score and bin 10 had the highest (Morris et al. 2016).

Prior to fitting RSFs, we tested all predictor variables for pairwise correlations (Chatterjee et al. 2000). Only terrain ruggedness and compound topographic index were highly correlated ($r > 0.7$) and therefore not used in the same model (Hosmer and Lemeshow 1989, Nielsen et al. 2002). We developed a suite of candidate models built with the huckleberry patch model and other variables shown to influence female habitat selection during previous research in the same study area (Table 2; Proctor et al. 2015). We used sample-size adjusted AIC (AIC$_c$) selection methods to determine which model was best supported by the data (Burnham and Anderson 1998). We plotted the relative selection strength for each continuous variable in the top model by setting all other continuous variables to their mean values and categorical variables to 0, and then predicted the response across the full range of values for the variable of interest. To predict responses for binary variables, we repeated the process above but set the binary variable of interest at 1.

To evaluate our top RSF model, we used a *k*-fold cross-validation approach (Boyce et al. 2002), randomly partitioning our dataset into 5 folds using an 80%:20% training:test ratio and iteratively training our model using 4 of the 5 folds. Within each fold, we mapped the predictions from models fit to the training data, and binned the predictions into 10 equal-area bins ranked from lowest (bin 1) to highest (bin 10). We then tallied the number of used locations in the withheld test dataset that fell within each bin (Morris et al. 2016). Finally, we calculated the Spearman's rank correlation between the RSF map bin (1–10) and the frequency of locations in each bin for each fold.

Density modeling

To explore the relationship between bottom-up and top-down variables, we reanalyzed the results from 6 previous and adjacent DNA-based abundance surveys using spatially explicit capture-recapture (SECR) analyses (Efford 2004, 2011; Efford et al. 2004, 2013). A previous project conducted DNA-based surveys from 15 June and 15 August between 1998 and 2005 across the South Selkirk, South Purcell, Central Purcell, and Yahk grizzly bear population units within the focal study area (Figure 6A). Correspondingly, the density estimates reflect that time period; however, our main goal was to assess the influence of bottom-up and top-down variables and yield baseline estimates for future comparisons. Proctor et al. (2007) provide a meta-analysis of these projects (Table 3) and any differences in density estimates reflect change in methodology, especially improved handling of closure violation and the use of spatially explicit estimation methods (SECR; Efford 2011). These data were also published within a larger region-wide analysis in Apps et al. (2016). Both previous analyses were focused on abundance estimation, not assessing correlations in the current context of bottom-up versus top-down influences.

Field methods were similar across years and consisted of 4, 2-week hair collection sessions at sampling sites (Woods et al. 1999, Proctor et al. 2010). Each study area had a grid of cells to partition sampling with

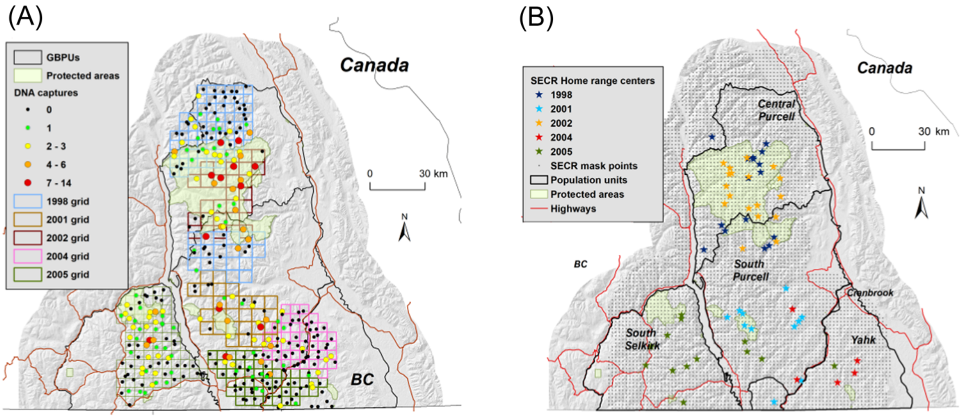

FIGURE 6 A) Grizzly bear DNA-based population surveys carried out for various research goals in the South Selkirk, South Purcell, Central Purcell, and Yahk Grizzly Bear Population Units (GBPU). Units are in southeast British Columbia, Canada, and surveys occurred between 1998 and 2005. We used these data in the grizzly bear density analyses. We present categories of the number of individual bears sampled at a site (DNA captures). B) Spatially explicit capture-recapture (SECR) home range centers of sampled grizzly bears with the 23-km buffer surrounding the mask (area with dots 2 km apart) used in the density analysis.

TABLE 3 Sampling grids used for hair-capture and DNA surveys of grizzly bears in the south Selkirk and Purcell mountains of southeast British Columbia, Canada. All surveys were conducted over 8 weeks between approximately 10 June–10 August from 1998 to 2005. Cell size differences reflect the proportion of unsuitable cover types in different areas (e.g., rock and ice).

Study area	Year	Area	Cell size (km^2)	Cells	Sessions	Grizzly bears identified
Jumbo	1998	1,650	25	66	4	28
South Purcells	2001	1,500	64	24	4	29
Purcell Wilderness	2002	1,300	49	26	4	36
Highway 3 east	2004	1,125	25	45	4	12
Highway 3 west	2005	1,375	25	55	4	20
South Selkirk	2005	1,950	25	77	4	30

1 site every 25–50 km^2 (Figure 6A). Sampling sites consisted of a barbed-wire corral that snagged a bear hair as it investigated a scent lure. Hair follicles were a source of DNA used to genetically identify individuals. Capture histories of bears across sampling sessions informed a mark-recapture abundance estimate. Cell sizes were larger in the South Purcell and Purcell Wilderness for several reasons, mainly because higher elevation rock and ice is not grizzly bear habitat. Also, it has been shown that cell sizes within the range of this study do not bias density results (Humm et al. 2017, Clark 2019, Efford and Boulanger 2019).

Genetic analysis

Hair samples were analyzed at Wildlife Genetics International (WGI) in Nelson, British Columbia. We extracted DNA using DNeasy columns (Qiagen, Mississauga, Ontario, Canada). We distinguished grizzly bear from black bear samples using a species-specific microsatellite marker (G10J; Paetkau 2003) and determined sex according to protocols detailed by Ennis and Gallagher (1994). We initially identified individuals with 6 or 7 microsatellite loci (Paetkau et al. 1998, Woods et al. 1999) but subsequently genotyped all individuals to 21 loci to increase power for the female fitness analyses. We used the following markers: G1A, G10B, G10C, G1D, G10H, G10J, G10L, G10M, G10P, G10U, G10X, MU23, MU50, MU51, MU59, CXX20, CXX110, MSUT-2, CHP9, REN145P07, and REN144A06 (Ostrander et al. 1993; Taberlet et al. 1997; Paetkau et al. 1998; Proctor et al. 2002, 2018). We determined genotypes on Applied Biosystems 320 and 3130 automated sequencers, and scored updated genotypes with the help of Genotyper software (Applied Biosystems, Foster City, CA, USA). Genotyping was standardized between projects, but to eliminate genotyping error (Gagneux et al. 1997, Goossens et al. 1998, Taberlet et al. 1999, Paetkau 2003), we scrutinized all 21-locus genotypes for close mismatches. We reran all pairs of samples that matched at all except 1, 2, or 3 loci to confirm the genotype or resolve errors (Paetkau 2003; Figure A4). Kendall et al. (2009) used testing with blind samples and other methods to show that these protocols prevent the identification of spurious individuals and relatives through genotyping error.

Density surface variables

We used a similar suite of bottom-up and top-down variables as in the habitat selection and fitness analyses (Table 2). For the density and fitness analyses, we scaled variables to a grain relative to values in surrounding cells within ArcGIS (Apps et al. 2004, 2016). We derived variable data at a 3-km radius to reflect a grain approximating the average daily movement of a female bear in our study area. We also derived variables with an 8-km-radius circle

(201 km^2 area) to represent a female annual home range. Therefore, any influence we detect from variables reflects the daily movement or home range scale (Apps et al. 2004, 2016).

To explore an optimum proportion of secure habitat for the density and fitness analyses, we used derivations of the secure habitat as competing variables in the modeling analysis as follows. We scaled the secure habitat layer to 3-km and 8-km grains as described above. This procedure resulted in a layer with values for each pixel between 0 and 1. We then classified all pixels below and above various thresholds of secure habitat (0.2, 0.4, 0.6, and 0.8; Figure A5A, Appendix I). For example, the secure habitat layer scaled to the 3-km grain was reclassified above and below values of 0.2 such that a 0 value was assigned to pixels with scores <0.2 and a 1 value was assigned to pixels with scores >0.2. This process was repeated for scores of 0.4, 0.6, and 0.8. Each of the resulting layers consisted of a polygon with different proportions of secure habitat that we used to examine how bear density was related to these proportional categories. Each of these layers was then associated with a polygon with a different proportion of unscaled secure habitat. At the 3-km scale, the percentages of secure habitat at threshold values of 0.2, 0.4, 0.6, and 0.8 were 67%, 79%, 89%, and 98%, respectively. At the 8-km scale the percentages of secure habitat at threshold values of 0.2, 0.4, 0.6, and 0.8 were 62%, 73%, 83%, and 94%, respectively. For example, the proportion of secure habitat within the layer scaled to an 8-km grain and set to values above and below 0.4, resulted in a polygon with 73% secure habitat (Figure A5B, Appendix I). The lower the threshold value, the more roads would be tolerated in a polygon coded as secure habitat.

Spatially explicit capture-recapture analyses

We organized yearly data sets into sampling sessions (Table 3). Unlike closed mark-recapture models that pool data from multiple DNA sites within each occasion for each bear, the SECR method uses multiple detections of bears at unique DNA sampling sites within a session. This is used to model a parameter that estimates the decline in bear detections as a function of distance from home range center. We estimated the detection probabilities of grizzly bears at their home range center (g_0), spatial scale of grizzly bear movements (σ) around home range centers, and bear density. An assumption of this method is that a grizzly bear home range can be approximated by a circular symmetrical distribution of use (Efford 2004); however, SECR methods are relatively robust to violations of this assumption (Efford 2019). We used the shape and configuration of the sampling grid to estimate bear detection probabilities and scale of movement. This accounted for the effect of study-area size and influence on the degree of closure violation and subsequent density estimates.

The SECR methods, as implemented in the secr R package, use a mask that is a set of systematic points that cover the sampling grid and surrounding areas. The mask represents the area of integration (Borchers and Efford 2008, Efford 2022) that encompasses locations of home range centers (average of detected locations) of bears that were detected on the grid. In Bayesian SECR, the mask area is described as the state space; however, this approach does require the use of a defined mask. We constructed a mask that encompassed all the yearly data sets (Figure 6B). We determined a spacing of 2 km between mask points by assessing the sensitivity of density estimates to mask spacing. We estimated the extent of the SECR mask based upon analyses of the single year data set to reflect potential bear movements within a survey period (not between years). The mask included a buffer of 23 km (Figure 6B). The buffer distance is the estimated maximum distance in which a bear home range center would occur if it were detected in hair snag sites in the sampling area (Efford 2022). We analyzed sexes separately for base model and density surface analyses.

We then estimated density for each mask point. Density surface models test the association of each SECR mask point with covariates, therefore allowing inference on factors associated with density in both sampled and surrounding areas (Royle et al. 2013, Efford 2014, Boulanger et al. 2018, Lamb et al. 2018). We considered large lakes as non-habitat and did not include them as mask points or buffer.

We conducted preliminary model runs to determine the optimal base detection models. Of particular interest was whether it was possible to assume similar detection parameters across yearly sessions or whether session-specific parameters were required. In addition, we considered trap-specific response (bk) models based upon the result of other grizzly bear SECR studies (Lamb et al. 2018). These models allowed the detection (g_0) or movement of bears (σ) to change after initial detection at a given site. Previous research (Boulanger et al. 2018) also suggested that canopy cover and terrain ruggedness could affect the detection of bears at DNA sites. Therefore, we considered canopy cover and terrain ruggedness, at 3-km and 8-km grains, as site covariates for g_0 and σ. We used the 3-km grain for g_0 under the assumption that smaller grain factors might influence detection at sites and used the 8-km grain for σ under the assumption that larger grain factors would influence movements in the vicinity of sites.

Density surface model methods

We fit surface models that constrained density for each SECR mask point to be a function of bottom-up and top-down variables. For this analysis, we extracted values for all variables (Table 2) for each mask point. We used the corrplot package (Wei and Simko 2016) in R to identify potential confounding of variables. We initially ran univariable analyses to determine which variables had the highest predictive power. We evaluated models using AIC_c scores. From those results, we selected a suite of variables for further consideration (Table 2). We considered geographic variables primarily as null models given that several top-down and bottom-up predictors are correlated with elevation and terrain ruggedness. For example, road density was negatively correlated with elevation and to a lesser degree with ruggedness. We expected that the more specific variables would have better explanatory power than the geographic ones.

We then considered the best bottom-up and top-down variables together. We plotted predictions for the most supported models to assess their overall differences and explored the relationships between variables graphically. We conducted all analyses using the secr (Efford 2014) package in R (R Core Team 2016) with additional explorations using plot3d (Soetaert 2014) and ggplot2 (Wickham 2009). We conducted GIS analyses in program R and QGIS (QGIS Foundation 2015).

Carrying capacity - potential increased abundance

To assess the relative influence of roads and secure habitat on grizzly bear density, we conducted 2 additional analyses. First, we estimated the change in bear density and abundance by simulating the effect of removing roads in the top models. To do this we set the proportion of secure habitat in the top female and male models to 1, which estimates the effect of the removal of roads in each population unit within the focal study area. This analysis yields a point estimate of maximum carrying capacity relative to the current crop of bear foods including huckleberry patches. We also simulated a road density of 0.6 km/km^2 to estimate the potential increase in bear abundance given the current food conditions if this target was implemented.

Second, we estimated the effect of management scenarios by decreasing and increasing the mean values of both bottom-up and top-down variables for each population characteristic by 10%. We assessed the respective changes in bear response in habitat selection, fitness, and density by applying those adjusted values into the top models. We did this to estimate how changing available management levers by realistic amounts might alter bear population characteristics.

Finally, we used the above analysis to produce a synthetic map of source-like and sink-like habitats across the focal study area as has been done by various authors (Nielsen et al. 2006, Aldridge and Boyce 2007, Kirol et al. 2015, Boulanger et al. 2018). We characterized source-like habitat where the fitness habitat was associated with reproductive success. We characterized sink-like habitats where road densities were >0.6 km/km^2, a value above which we found that huckleberry patches were no longer associated with fitness or density. We also report on an opportunistic internal experiment where a private owner (NCC Darkwoods property) of 650 km^2 of backcountry land used for timber harvest for the past 4 decades has applied an access management program since the purchase in 2008. We assessed bear density on the NCC Darkwoods property relative to bottom-up and top-down influences compared to the surrounding provincial land with no access management.

Female fitness modeling

To assess the variables associated with female fitness (Table 2), we used logistic regression to compare habitat characteristics at DNA sampling sites where we detected females that we could assign reproductive events (72 mother-offspring events from 33 mothers) to sites where we did not sample such individuals. Output consisted of an RSF score that we used as an index to relative habitat quality that supported fitness. We obtained DNA sample data from the abundance surveys (described in the Spatially explicit capture-recapture density section above) and through live capture for radio collaring. We identified mother-offspring events using 21-locus microsatellite genotypes. We used only mother-offspring relationships that were confirmed by identification of a complete triad family group: mother-father-offspring. Complete family triads occurred where the offspring complementarily shared an allele with each parent. We limited the search to complete triads in part because the modest genetic variability in these subpopulations reduced the power to correctly identify individual parents. Many pairs (when detected by mother-offspring only) were clearly false based on data such as age (of captured females), sharing alleles at all loci, and having a >0.95 probability of being assigned an offspring to its mother by the software. At the same time, it was clear that sampling intensity was high enough that few relationships were missed by limiting parentage searches to triads. Thus, using pairs instead of triads would add more false relationships than correct relationships. This balance would have been different had genetic variability been higher, and sampling intensity lower, in the study area (Proctor et al. 2012). These family pedigrees provide a signal of lifetime fitness as some offspring may have been separated from their mother for years when they were sampled. We identified family triads using program PARENTE (Cercueil et al. 2002). To identify and eliminate genotyping errors, which will occasionally cause parent and offspring appear to not share an allele at a given locus, we reanalyzed the mismatching markers in triads where genotypes matched at all but 1 or 2 loci and that PARENTE assigned a probability >0.5 of being assigned an offspring to its mother by the software. This is the concept or targeted reanalysis that is used to prevent erroneous identification of an individuals based on a genotyping error (Paetkau 2003) but adapted to ensuring that matches between parent and offspring are not overlooked. Fitness modeling was limited to 13,686 km^2 within the south Selkirk and Purcell mountains, as this was the area where DNA sampling intensity was high enough that both parents of any new offspring were likely to have been genotyped. In that regard, 33 mothers representing 72 mother-offspring events came from a population of 139 bears where approximately 25% (~35) are adult females (McLellan 1989*b*).

As described in the density section above, we derived variable data at a 3-km radius to reflect a grain approximating the average daily movement of a female bear in the study area. We also developed a grain of an 8-km-radius circle (201 km^2 area) to represent a female annual home range. We developed a suite of competing models that we compared using AIC model selection methods (Burnham and Anderson 1998). We evaluated models using ROC AUC scores and considered scores >0.7 as predictive.

We examined the most supported multi-variable model for the relative influence of each contributing variable by removing one variable at a time and comparing the resulting log likelihoods, as per Schwartz et al. (2010). We also present relative selection strength plots for all variables in the most supported model. We represented the most supported models using raster calculator within ArcGIS.

RESULTS

Huckleberry occurrence and patch modeling

Huckleberry occurrence

Predictive success was high for the huckleberry occurrence model, with AUC = 0.88 (95% CI = 0.88–0.90; Figure 7A and B). The top 5 predictors, in decreasing order of importance, were 1) precipitation as snow in winter, 2) mean annual precipitation, 3) canopy cover, 4) maximum summer temperature, and 5) elevation (Figure 7C). Overall, huckleberry plants were most likely to occur in areas of high snow loads, moderate to high annual precipitation, moderate to high canopy cover, cooler maximum temperature, and elevations between 1,200–2,000 m (Figure 8).

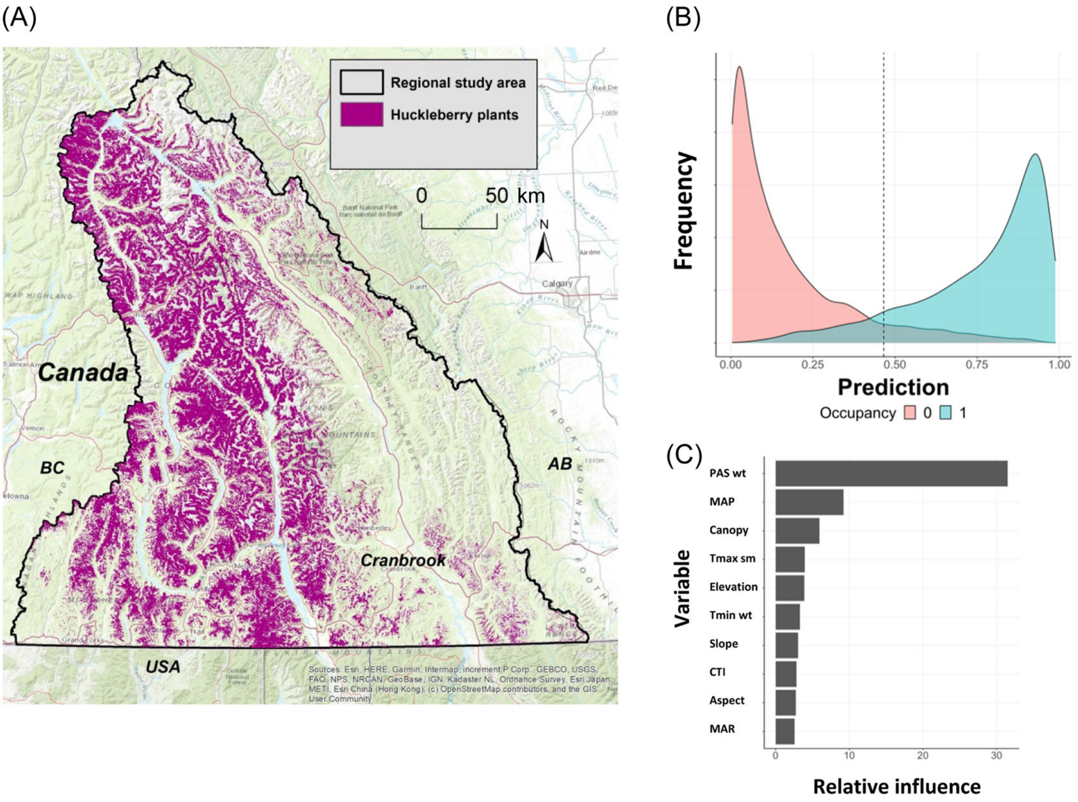

FIGURE 7 A) Predicted huckleberry occurrence (plants) across the regional study area in southeastern British Columbia, Canada (1981–2013), and B) discrimination plot to assess how well the top model predicted field determination of whether a site was a huckleberry patch (1) or not (0). The *x*-axis represents predictions from the top huckleberry occurrence model and the *y*-axis represents the frequency of these predictions (patch = 0, 1). The vertical dashed line depicts the cut point (0.46) where sensitivity and specificity are maximized. Good discriminatory power results from little overlap between the distributions of presence and absence points, as can be seen here. C) Relative influence of the top 10 predictor variables in the occurrence model. We calculated relative influence as the number of times each variable is included in a boosted regression tree, scaled such that the influence of all variables sum to 100%. Variables included precipitation as snow in winter (PAS wt), mean annual precipitation (MAP), canopy cover (canopy), maximum temperature in summer (Tmax sm), minimum temperature in winter (Tmin wt), mean annual solar radiation (MAR), and a wetness index (CTI).

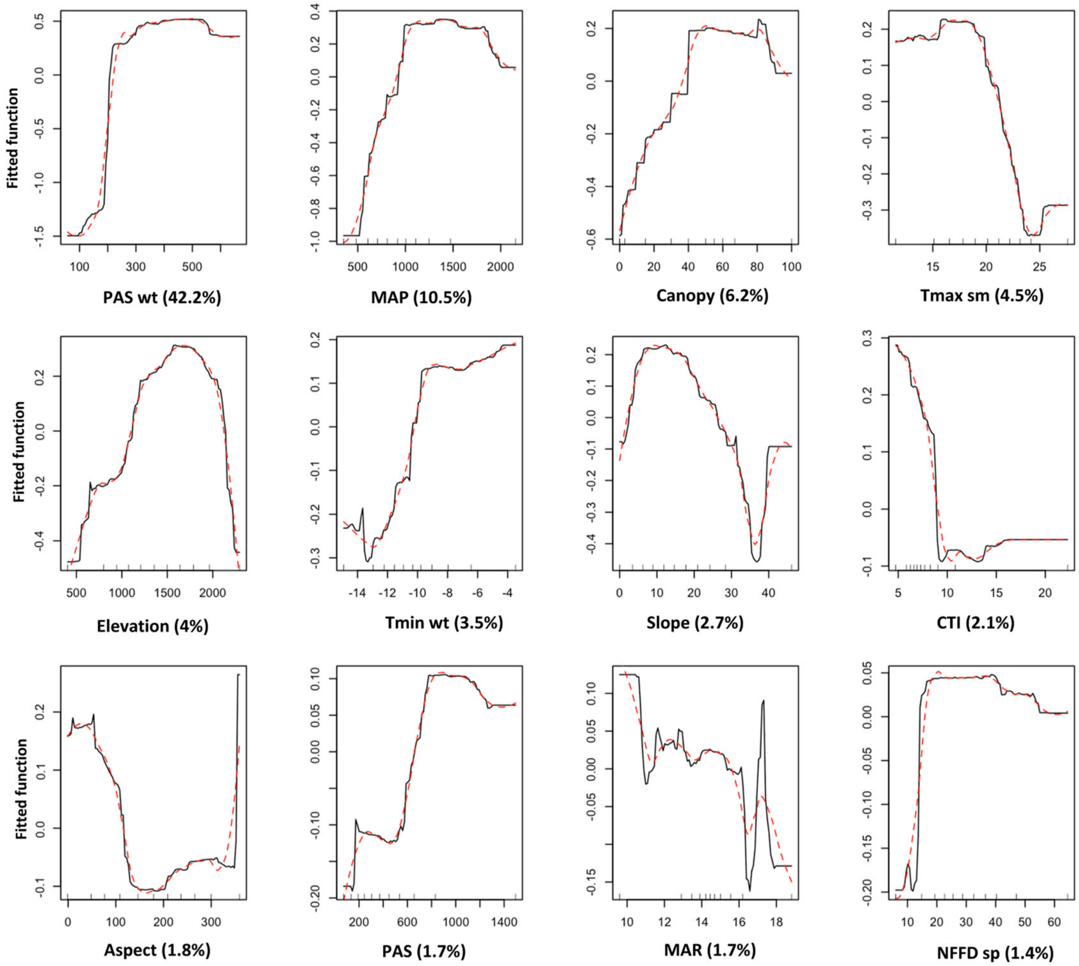

FIGURE 8 Marginal effect plots for the top 12 variables in the huckleberry occurrence model based on data from southeastern British Columbia, Canada (1981–2013). Numerical values in parentheses are the relative influence of each variable in the top model (Elith et al. 2008). Fitted function refers to the marginal effect on huckleberry occurrence. The dashes on the inside of the *x*-axis signify where we have data in the model. The solid line represents the prediction from the top boosted regression tree model and the red dashed line is a smoothed representation of those predictions. Variables included precipitation as snow in winter (PAS wt), mean annual precipitation (MAP), canopy cover (canopy), maximum temperature in summer (Tmax sm), minimum temperature in winter (Tmin wt), a wetness index (CTI), precipitation as snow (PAS), mean annual solar radiation (MAR), and number of frost free days (NFFD sp).

Huckleberry patch model

Predictive success also was high for the huckleberry patch model, with AUC = 0.86 (95% CI = 0.83–0.89; Figure 9A and B). This analysis was use versus availability, rather than a yes versus no analysis. In a use versus availability analysis, some available points (considered no sites) can also be use sites (considered yes sites). Therefore, this ROC score was likely an underestimate of the accuracy of the model (Boyce et al. 2002). The top 5 predictors in decreasing importance were 1) canopy cover, 2) coarse fragments in soil, 3) slope, 4) precipitation as snow, and 5) annual average radiation (Figure 9C). Overall, we found that compared to the distribution of huckleberry plants, those with fruit that grizzly bears used (the patch model) were in areas of low canopy cover, low angle slope, lower

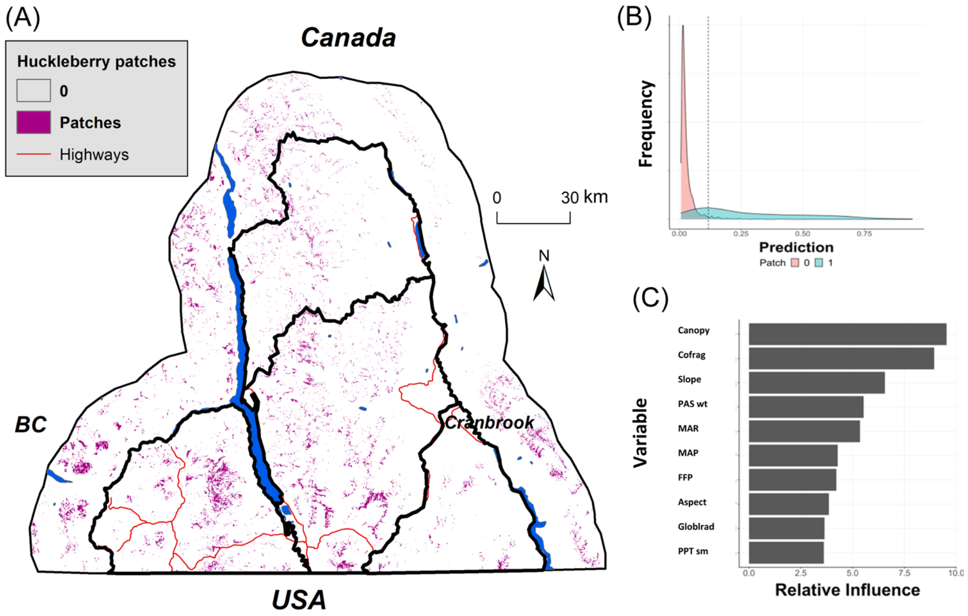

FIGURE 9 A) Huckleberry patch model area across the south Selkirk and Purcell mountains focal study area in southeastern British Columbia, Canada (2004–2013). Huckleberry patches cover approximately 28% of the occurrence distribution model. B) Top model discrimination plot to assess how well the model predicted the field determination of whether a site was a huckleberry patch (1) or not (0). The *x*-axis represents predictions from the top huckleberry patch model and the *y*-axis represents the frequency of these predictions (patch= 0, 1). The dashed vertical line depicts the cut point (0.11) where sensitivity and specificity are maximized. Good discriminatory power results from little overlap between the distributions of used and available points, as can be seen here. C) Relative influence of the top 10 predictor variables in the patch model. We calculated relative influence as the relative number of times each variable is included in a boosted regression tree, scaled such that the relative influence of all variables sum to 100%. Variables include canopy cover (canopy), coarse fragments in soil (cofrag utm), precipitation as snow in winter (PAS wt), mean annual solar radiation (MAR), mean annual precipitation (MAP), frost free period (FFP), global radiation (globrad), and precipitation in summer (PPT sm).

amounts of coarse fragments in soil, high precipitation as snow, and high solar radiation (Figure 10). The response to canopy cover was the opposite of that in the huckleberry occurrence model where there was a positive relationship to canopy cover (Figures 8 and 10). Outside of the focal area where we had GPS telemetry, 89% of the sites that were considered huckleberry patches (determined from site visits) were predicted by the patch model. We therefore ran the model across a portion of southeastern British Columbia in those areas of the regional study area with similar ecology to the focal study area (Figure 11).

The mean percent forest canopy cover of huckleberry patches visited in the field was 11%. Canopy cover <30% was the most predictive variable for huckleberry patches, but there was no difference between mean canopy cover levels (*t*-test, $P = 0.30$) in timber harvest cut blocks with or without huckleberry patches. The mean ground cover of huckleberry plants within patches was 36% (range = 10–75%). The mean elevation of visited huckleberry patches was 1,790 m (range = 1,084–2,246 m). Seventy percent were in the mid-slope position (between the upper generally convex and lower concave portions of a mountain slope; British Columbia Ministries of Forests and Range and Environment 2010), while 19% were in the upper slope position. The aspect for huckleberry patches was 55% west (225–315 degrees), 19% south (135–225 degrees), 17% east (35–135 degrees), and 8% to the north (315–45 degrees).

In the portion of the focal study area where there were detailed timber harvest records (i.e., the NCC Darkwoods conservation property in the south Selkirk Mountains), we found that fire and logging were the most common disturbances preceding establishment of a huckleberry patch. The mean number of years post-logging of huckleberry patches was 39 ($n = 942$, $SE = 0.83$) with patches appearing increasingly after 10 years. Huckleberry

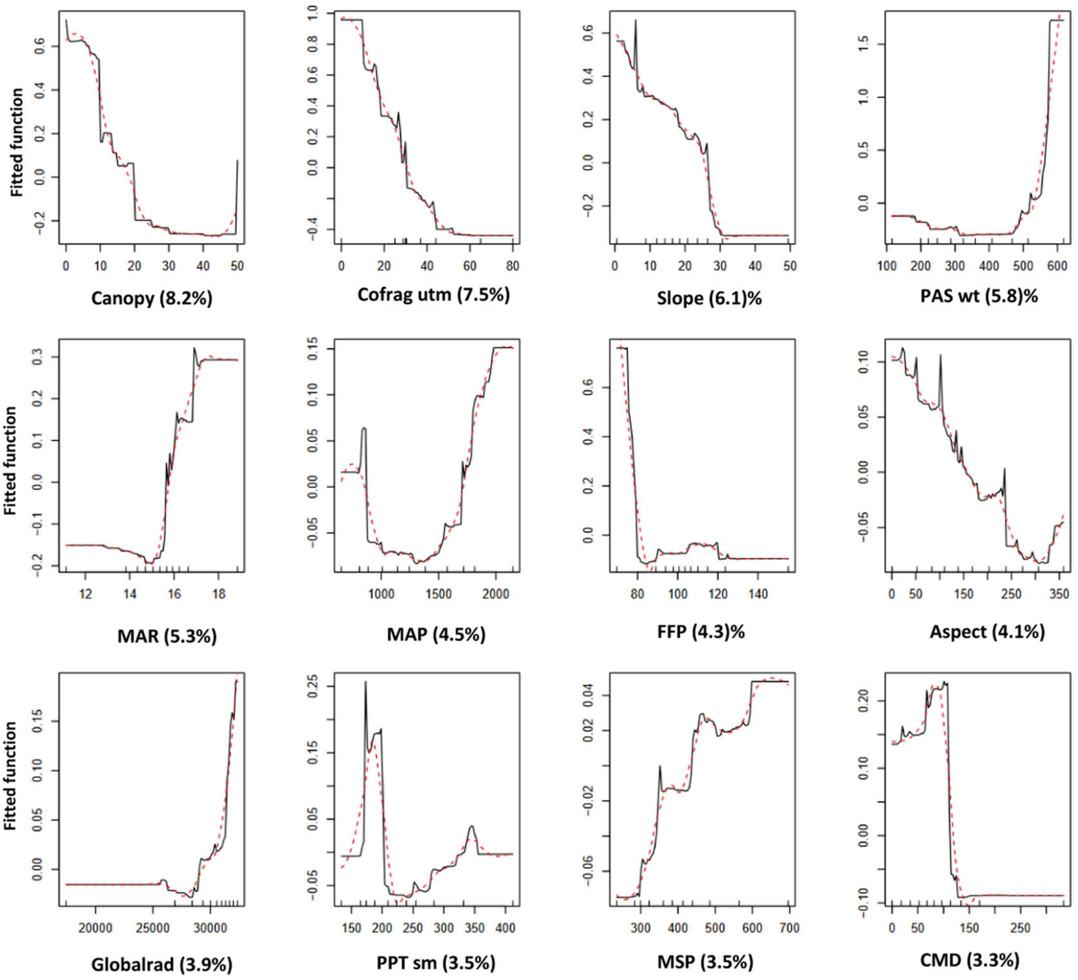

FIGURE 10 Marginal effect plots for the top 12 variables in the huckleberry patch model from southeastern British Columbia, Canada (2004–2013). Numerical values in parentheses are the relative influence of each variable in the top model (Elith et al. 2008). Fitted function refers to the marginal effect on huckleberry occurrence. The dashes on the inside of the *x*-axis signify where we have data in the model. The solid line represents the prediction from the top boosted regression tree model and the red dashed line is a smoothed representation of those predictions. Variables include canopy cover (canopy), coarse fragments in soil (cofrag utm), precipitation as snow in winter (PAS wt), mean annual solar radiation (MAR), mean annual precipitation (MAP), frost free period (FFP), global radiation (globalrad), precipitation in summer (PPT sm), mean annual summer precipitation (MSP), and Hargreaves climate moisture deficit (CMD).

patches were almost 3 times more likely to occur in sites with evidence of past wildfire compared to sites without wildfire ($\chi_1^2 = 28.6$, $P \leq 0.001$). Slash burning post timber harvest did not appear to influence whether or not a cut block contained a huckleberry patch ($\chi_1^2 = 0.77$, $P = 0.38$). Of cut blocks found to contain huckleberry patches (761 of 1,123), 96% (731) had not received post-harvest planting treatment.

Female summer habitat selection modeling

The most supported bottom-up variable for female summer habitat selection in univariable analyses was the distance to huckleberry patches (Table 4). Female grizzly bears generally stayed within 1 km of huckleberry patches

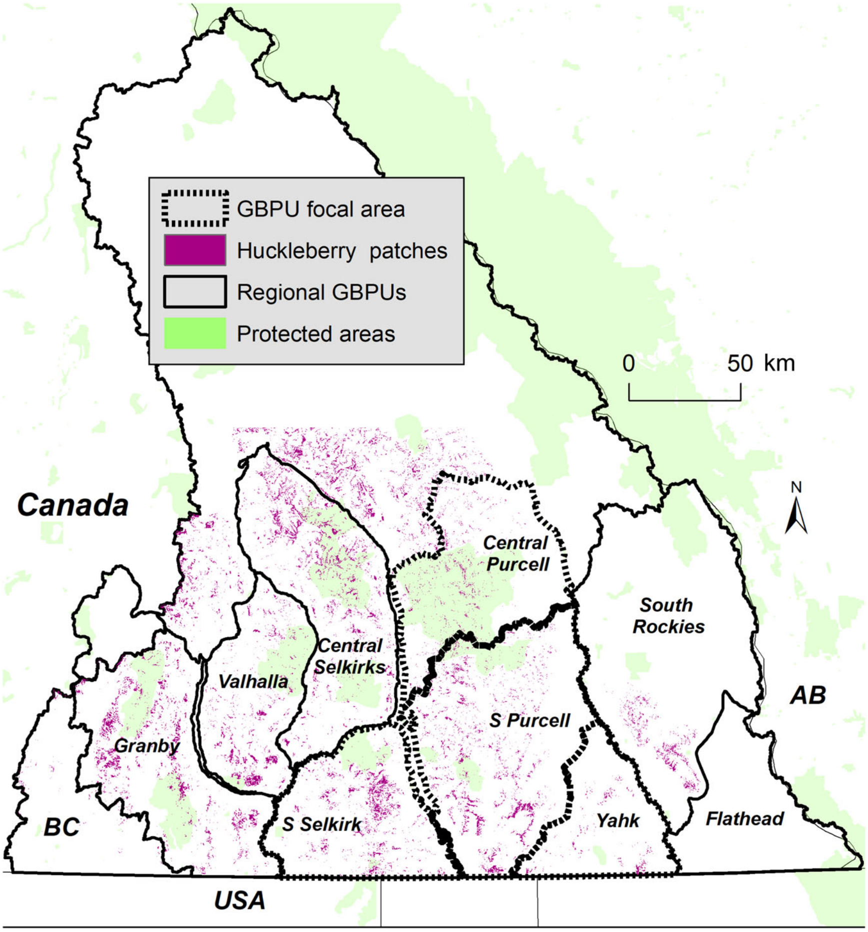

FIGURE 11 The most supported huckleberry patch model extrapolated across the southern portion of the regional study area in southeast British Columbia, Canada (2004–2013). Grizzly bear population units (GBPUs) include the Central Selkrik, Valhalla, and Granby to the west of the focal study area and the Flathead and South Rocky units to the east.

throughout the summer foraging period (Figure 12A). Less predictive, but also significant, bottom-up variables were those often used as indirect measures when direct food resource layers are not available. For example, canopy cover and greenness have been previously shown to predict female habitat selection (Proctor et al. 2015).

The most supported top-down variable in univariable analyses was secure habitat >10 km^2 (Table 4). Several other variables had only slightly lower log likelihood values, including secure habitat patches >5 km^2, all patches, roads, and road density. The selection threshold for road density, above which female grizzly bears avoided areas, was 0.9 km/km^2 (Figure 12B).

The most supported multi-variable model contained, in decreasing order of influence, distance to huckleberry patches, greenness, alpine, solar radiation, and secure habitat >10 km^2 (Tables 4 and 5; Figure 13). The 95% confidence intervals of coefficients for all variables did not overlap zero. Plots of relative selection strength indicate that huckleberry patches and greenness were more influential than alpine, solar radiation, and, in particular, secure habitat. Female bears selected for areas closer to huckleberry patches, areas with higher greenness, and higher solar radiation. They also selected for alpine area and secure habitat (Figure 14). In all models, secure habitat >10 km^2 was more supported than road density, but models with road density substituted for secure habitat were similarly

TABLE 4 Consolidated and abbreviated uni- and multi-variable model selection related to influence on summer female grizzly bear habitat selection. We included the best bottom-up, top-down, and composite models for the south Selkirk and Purcell mountains in southeast British Columbia, Canada, between 2005–2015. Model 13 was similar to the best model from Proctor et al. (2015) prior to development of the huckleberry patch model. We present log-likelihood (LL), sample-size adjusted Akaike's Information Criterion (AIC_c), difference in AIC_c between most supported and given model (ΔAIC_c), and the number of parameters (K).

Number	Model	Type	LL	K	AIC_c	ΔAIC_c
1	Bottom-up (huckleberry patches, greenness, alpine, solar) + top-down (secure habitat 10 km^2)	Composite	−119,787	5	239,584	0
2	Bottom-up (huckleberry patches, greenness, alpine, solar) + top-down (secure habitat 5 km^2)	Composite	−119,804	5	239,617	34
3	Bottom-up (huckleberry patches, greenness, alpine, solar) + top-down (road density)	Composite	−119,838	5	239,686	102
4	Bottom-up (huckleberry patches, greenness, alpine, solar)	Bottom-up	−119,881	4	239,769	186
5	Bottom-up (huckleberry patches, greenness, alpine) + top-down (secure habitat 10 km^2)	Composite	−119,894	4	239,797	213
6	Bottom-up (huckleberry patches, greenness, solar) + top-down (secure habitat 10 km^2)	Composite	−119,964	4	239,935	352
7	Bottom-up (huckleberry patches, greenness, alpine)	Bottom-up	−119,998	3	240,002	419
8	Bottom-up (huckleberry patches, greenness) + top-down (secure habitat 10 km^2)	Composite	−120,057	3	240,120	536
9	Bottom-up (huckleberry patches, alpine, solar) + top-down (secure habitat 10 km^2)	Composite	−120,110	4	240,228	644
10	Bottom-up (huckleberry patches, greenness)	Bottom-up	−120,197	2	240,399	815
11	Bottom-up (huckleberry patches 5 ha)	Bottom-up	−120,362	1	240,726	1,143
12	Bottom-up (huckleberry patches 10 ha)	Bottom-up	−120,414	1	240,830	1,246
13	Bottom-up (canopy cover, greenness, alpine, solar) + top-down (secure habitat 10 km^2)	Composite	−120,503	5	241,015	1,432
14	Bottom-up (greenness, alpine, solar) + top-down (secure habitat 10 km^2)	Composite	−120,732	4	241,472	1,889
15	Bottom-up (huckleberry patches all sizes)	Bottom-up	−121,124	1	242,251	2,667
16	Bottom-up (canopy cover)	Bottom-up	−121,241	1	242,484	2,900
17	Bottom-up (greenness)	Bottom-up	−121,315	1	242,632	3,049
18	Bottom-up (huckleberry occurrence)	Bottom-up	−121,491	1	242,984	3,400
19	Top-down (secure habitat 10 km^2)	Top-down	−121,525	1	243,052	3,469
20	Top-down (secure habitat 5 km^2)	Top-down	−121,546	1	243,094	3,511
21	Top-down (open roads)	Top-down	−121,561	1	243,125	3,541
22	Top-down (open road density)	Top-down	−121,577	1	243,156	3,573
23	Top-down (distance to open roads)	Top-down	−121,623	1	243,247	3,664

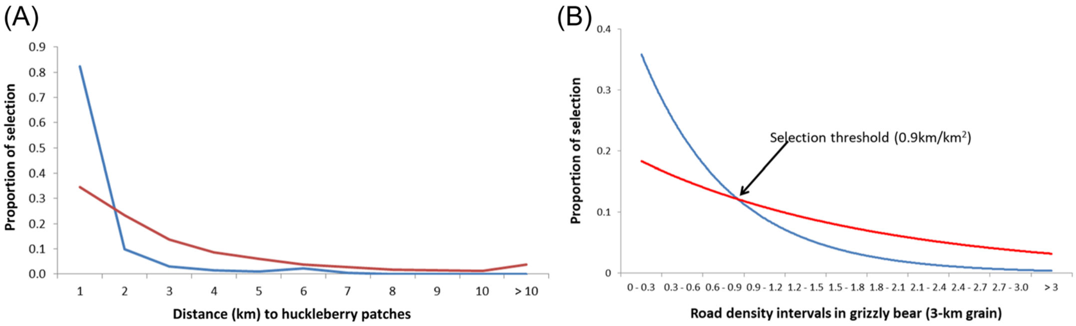

FIGURE 12 A) Response curves for distance to huckleberry patches show that proximity to patches >10 ha was an important draw for female grizzly bear habitat selection. Data were collected in the south Selkirk and Purcell mountains of southeast British Columbia, Canada (2004–2015). The red curve is available habitat and the blue curve is use. B) Response curves for habitat selection in summer (15 July–15 September) associated with road density show that grizzly bears can tolerate road densities between 0.6 and 0.9 km/km^2 but prefer habitats (and likely have increased survival) with road density <0.6 km/km^2.

TABLE 5 Coefficients from the most parsimonious bottom-up and top-down multi-variable female grizzly bear summer habitat selection model for populations in the south Selkirk and Purcell mountains in southeast British Columbia, Canada, between 2005–2015. We present standardized coefficients, robust standard error (SE), probability of z (P(z)), robust probability, and the upper and lower 95% confidence intervals.

					95% CI	
Model	**Coefficient**	**Robust SE**	**P(z)**	**Robust probability**	**Lower**	**Upper**
Distance to huckleberry	−0.547	0.180	−3.039	0.002	−0.899	−0.194
Greenness	0.218	0.036	6.093	<0.001	0.148	0.288
Alpine	0.460	0.058	7.858	<0.001	0.345	0.574
Solar	0.115	0.039	2.972	0.003	0.039	0.191
Secure habitat	0.261	0.093	2.799	0.005	0.078	0.444

predictive. The top model with only bottom-up variables (huckleberry patch + greenness + alpine + solar) had a ΔAIC score of 186 (model 4 in Table 4), which suggests that top-down variables were an improvement in explaining female habitat selection.

Our top model with distance to huckleberry was substantially more supported than a similar model where huckleberry was replaced by canopy cover (model 13 in Table 4). A similar model with the surrogate variable canopy cover was in the top model in Proctor et al. (2015) for a similar area. Models fit using all 5 sets of training data in the cross-validation procedure had very similar selection coefficients to those from the full top model (Table A3, Appendix I). The average Spearman's rank correlation between the ranked equal-area RSF bin (1–10) frequencies of RSF scores within these bins across all 5 withheld test datasets was $r_s = 0.99$ (SE = 0.002; Figure A6, Appendix I).

Density modeling

Female density

We sampled 155 individual grizzly bears from 6 different DNA surveys that were used for SECR-derived density estimates (Table 3). There was one pair of genotypes that mismatched at <3 markers, indicating that the set of 7

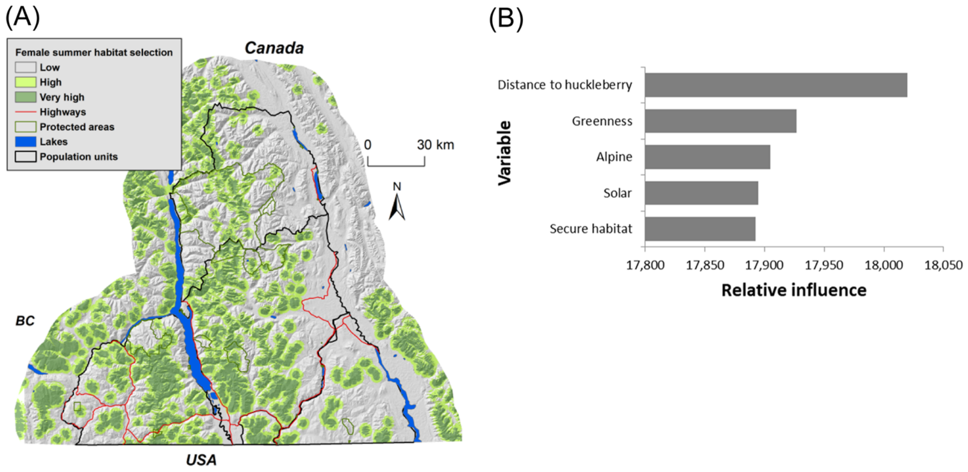

FIGURE 13 A) Female grizzly bear summer habitat selection (green) in the south Selkirk and Purcell mountains of southeast British Columbia, Canada. The map was developed from our most supported model partitioned into 10 bins of resource selection function scores using the same equal-area method we used in our *k*-fold evaluation (Morris et al. 2016). We have collapsed the bins into 3 categories. Low is bins 1–6, high is bins 7–8, and very high is bins 9–10). Data represent selection between 15 July and 15 September from 2004 to 2015. B) The relative influence of variables within the best supported female grizzly bear habitat selection model depicted in panel A. We determined influence by calculating the magnitude of decrease in predictability as measured by the change in log likelihood after removing each variable from the top model.

markers used to identify individuals was able to generate a unique genotype for every individual sampled (Figure A4, Appendix I). The mismatching data points in these pairs were replicated to confirm that each genotype represented a different bear (Figure A4, Appendix I).

The primary density analyses focused on female grizzly bears ($n = 94$) sampled from 1998–2005 (Figure 6). Base detection model selection results suggested study-area-specific detection (session/year sampled) for home range centers (g_0) and movement (σ) with a trap-specific behavioral response (Table 6). No other detection models were supported (all other models had $\Delta\text{AIC} > 2$). A plot of detection functions from the top model (Table 6) indicated differences in detection and scale of movement between study area or years sampled, justifying the use of the more complex detection model with additional variables (Figure A7, Appendix I).

Home range centers of detected bears provided an estimate that was based on trap layout and estimated movements as detected through resampling of bears with DNA. The distribution of bears was clustered centrally within several survey grids with some estimated home range centers occurring on the edges of the grids (Figure 6B). We found a subset of variables that were correlated (Figure A8, Appendix I) and therefore we did not include them in the same models.

Univariable models suggested that the variable with the most influence on female density was huckleberry patches at a 3-km grain followed closely by patches at the 8-km grain (Table 7). A plot of the distribution of huckleberry patches summarized at a 3-km grain relative to detections suggests an association with some exceptions in the Yahk (low huckleberry patches; Figure 15A). While bottom-up variables were more supported than top-down in univariable analyses, secure habitat (at 73% at the 8-km grains and 89% at the 3-km grain), and road presence at the 3-km grain were close in support (Table 7). A plot of the distribution of secure habitat summarized at an 8-km grain versus detections also suggests an association (with some exceptions; Figure 15B). Therefore, we considered huckleberry and secure habitat for multi-variable bottom-up and top-down models.

For multi-variable models, a model with huckleberry patches represented at the 3-km grain (female daily movement) and secure habitat at 8 km (annual female home range) was most supported as composite predictors of female density

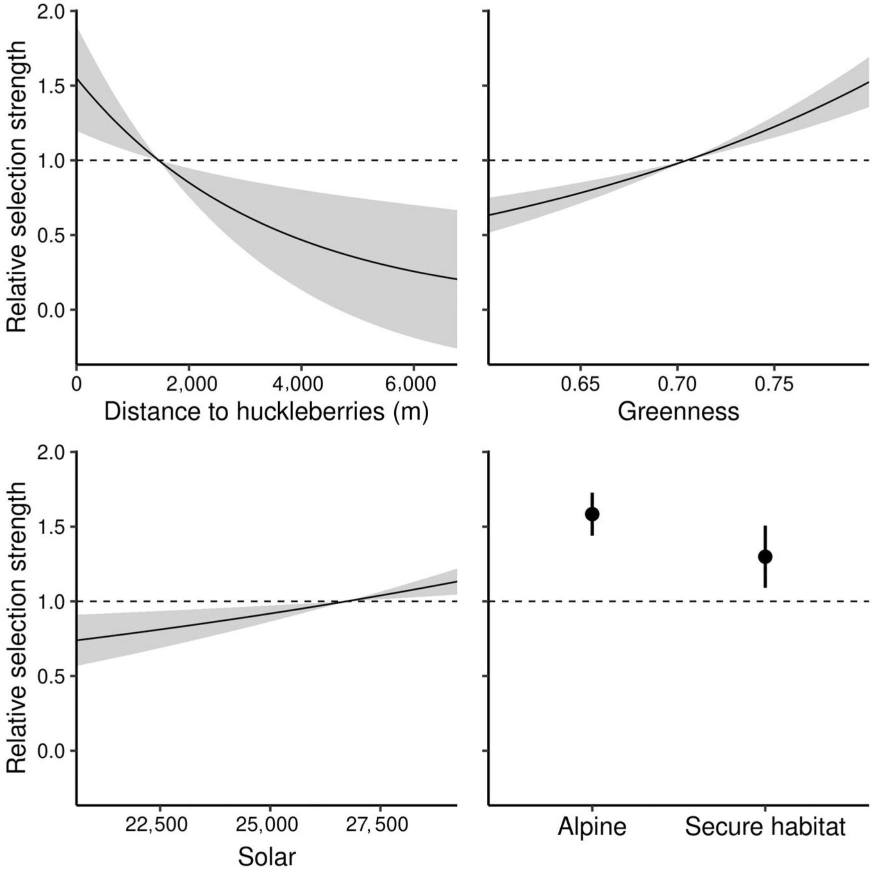

FIGURE 14 Relative selection strength plots with 95% confidence intervals for variables in the top female grizzly bear habitat selection model. Alpine and secure habitat were binary variables. The model was derived from global positioning system telemetry data collected between 2004 and 2015 in the south Selkirk and Purcell mountains of southeastern British Columbia, Canada. All continuous variables not featured in a plot were set to their mean value (pooled across all observations in the dataset), while binary variables were set to 0. Continuous variable ranges on the *x*-axis include the middle 95% of values available to bears in resource selection function models (excluding values below and above the 2.5% and 97.5% quantiles, respectively). The horizontal dashed line indicates where predicted selection is proportional to availability.

(Table 7; Figure 16A). Presence of huckleberry patches within 3 km (β = 7.28, SE = 1.23, 95% CI = 4.87–9.70) and presence of secure habitat within 8 km (β = 3.15, SE = 2.16, 95% CI = −1.08–7.37) were positively related to female density. Of the competing configurations of secure habitat, the polygon representing secure habitat >0.4 when scaled at the 8-km grain was the most supported. This secure habitat polygon had on average 73% of habitat that was >500 m from an open road. Areas predicted to have higher bear density closely followed the secure habitat univariable model (Figures 15B and A5B, Appendix I) with hotspots predicted by the univariable huckleberry patch model (Figure 15A). Eight other composite models were more supported than the stand-alone bottom-up model with huckleberry patches and greenness (model 9 in Table 7), suggesting that both top-down and bottom-up variables influenced the density of bears. The analysis to compare the relative influence of variables in the most supported female density model (removing one variable at a time and comparing the decrease in log likelihood scores) found that huckleberry patches were more influential than secure habitat (comparing model 13 with secure habitat removed [ΔAIC = 14.7] to model 14 with huckleberry patches removed [ΔAIC = 18.2]; Table 7).

TABLE 6 Base female grizzly bear density detection model selection results in southeast British Columbia, Canada, between 1998–2005. We present log-likelihood (logLik), sample-size adjusted Akaike's Information Criterion (AIC_c), difference in AIC_c between most supported and given model (ΔAIC_c), and the number of parameters (*K*). Variables include study area (area), chance a site will be visited a second time (bk), canopy cover (cc), and ruggedness (tri) with numbers indicating a 3-km or 8-km radius for deriving variables.

Number	Density	Detection (g_0)	Scale (σ)	logLik	*K*	AIC_c	ΔAIC_c
1	constant	area+bk	area	−686.1	12	1,399.91	0.00
2	constant	area+cc3	area	−687.5	12	1,402.77	2.85
3	constant	area	area+tri8	−688.0	12	1,403.89	3.97
4	area	area+bk	area	−685.2	16	1,409.34	9.42
5	area	area+bk	area	−685.2	16	1,409.34	9.42
6	constant	area+tri3	area	−690.9	12	1,409.60	9.69
7	constant	area	tri8	−696.4	8	1,410.46	10.54
8	constant	area	area+cc8	−691.8	12	1,411.46	11.54
9	area	area	constant	−691.9	12	1,411.62	11.70
10	area	area	area	−688.5	16	1,415.97	16.05
11	constant	area	cc8	−700.4	8	1,418.52	18.61
12	area	area	area	−692.5	15	1,421.04	21.13
13	constant	cc3	area	−702.5	8	1,422.63	22.72
14	area	area	constant	−701.2	11	1,427.64	27.72
15	area	area	constant	−701.2	11	1,427.64	27.72
16	constant	tri3	area	−705.0	8	1,427.77	27.85
17	area	constant	area	−704.2	11	1,433.64	33.72
18	area	constant	constant	−710.2	7	1,435.65	35.73

Male density

The most supported univariable bottom-up variables for male grizzly bear density were alpine cover at the 3-km grain, and canopy cover scaled to the 3-km grain (Table 8). These were followed by distance to, and 3-km grain, huckleberry patch variables (Table 8). Top-down variables (secure habitat and roads) were more influential than bottom-up for male grizzly bears in univariable analyses (Table 8). The highest ranking composite model for males (distance to huckleberry + secure habitat 8 km) was essentially tied with the top model ($\Delta AIC = 0.1$), but the addition of a second variable (distance to huckleberry) did not improve it enough to be more supported and 95% confidence intervals for the distance to huckleberry coefficient overlapped 0 ($\beta = -0.13$, SE = 0.11, 95% CI = −0.34–0.08; Table 8; Figure 16B). Presence of secure habitat at the 8-km grain had a positive relationship with male habitat selection ($\beta = 1.48$, SE = 0.32, 95% CI = 0.85–2.11).

Density of both sexes

We derived average female and male density from the top models for each sex (Figure 16C). The average 2005 both-sex density in the entire South Selkirk population unit was 13.1 grizzly bears/1,000 km^2. In contrast, within the privately owned NCC Darkwoods property in the same population unit, the density was 33/1,000 km^2.

TABLE 7 Consolidated and abbreviated uni- and multi-variable model selection relative to influence on female grizzly bear density models. We include the best bottom-up, top-down, and composite models (having both bottom-up and top-down variables) for the south Selkirk and Purcell mountains of southeast British Columbia, Canada (1998–2005). We present log-likelihood (LL), sample-size adjusted Akaike's Information Criterion (AIC_c), difference in AIC_c between most supported and given model (ΔAIC_c), and the number of parameters (K).

Number	Model	Type	LL	K	AIC_c	ΔAIC_c
1	Bottom-up (huckleberry patches 3 km) + top-down (secure habitat 73% 8 km)	Composite	−667.5	14	1,368.2	0.0
2	Bottom-up (huckleberry patches 3 km) + top-down (secure habitat 73% 8 km) + interactive (secure habitat 73% × road density)	Composite	−666.8	15	1,369.6	1.4
3	Bottom-up (huckleberry patches 3 km) + top-down (secure habitat 73% 8 km, road density 3 km)	Composite	−666.9	15	1,370.0	1.8
4	Bottom-up (huckleberry patches 3 km) × top-down (secure habitat 73% 8 km)	Composite	−667.4	14	1,370.9	2.7
5	Bottom-up (huckleberry patches 3 km) + top-down (road density 3 km)	Composite	−668.9	15	1,371.0	2.8
6	Bottom-up (huckleberry patches 3 km) + top-down (road density 3 km)	Composite	−668.9	14	1,371.0	2.8
7	Bottom-up (huckleberry patches 3 km) + top-down (secure habitat 73% 8 km, road density 3 km) + interactive (secure habitat 73% × road density)	Composite	−666.6	17	1,372.1	3.9
8	Bottom-up (huckleberry patches 3 km) + top-down (road density 8 km)	Composite	−669.9	14	1,373.2	5.0
9	Bottom-up (huckleberry patches 3 km + greenness 3 km)	Bottom-up	−671.7	14	1,376.6	8.4
10	Bottom-up (huckleberry patches 3 km)	Bottom-up	−673.5	13	1,377.5	9.3
11	Bottom-up (huckleberry patches 8 km)	Bottom-up	−673.6	13	1,377.8	9.6
12	Top-down (secure habitat 73% 8 km, roads 3 km, highways 8 km)	Composite	−673.2	15	1,382.5	14.3
13	Bottom-up (distance to huckleberry 3 km)	Bottom-up	−676.2	13	1,382.9	14.7
14	Top-down (secure habitat 89% 3 km)	Top-down	−678.0	13	1,386.4	18.2
15	Top-down (secure habitat 73% 8 km)	Top-down	−678.6	13	1,387.6	19.4
16	Top-down (road presence 3 km)	Top-down	−678.6	13	1,387.7	19.5
17	Bottom-up (canopy cover 3 km)	Bottom-up	−681.4	13	1,393.4	25.2

Female fitness modeling

We identified 33 individual mothers with 72 offspring in the family pedigree analysis. Distance to huckleberry patches >10 ha was the most influential bottom-up covariate in univariable models followed by distance to huckleberries >5 ha (and all patches) and alpine both at the 3 km grain (Table 9). The most supported top-down variable was riparian at the 8-km grain followed by secure habitat (Table 9).

The top multi-variable female fitness model had an AUC ROC score of 0.84 (Table 9; Figure 17A). In the multi-variable context, greenness was the most influential variable, followed by riparian, secure habitat, distance to

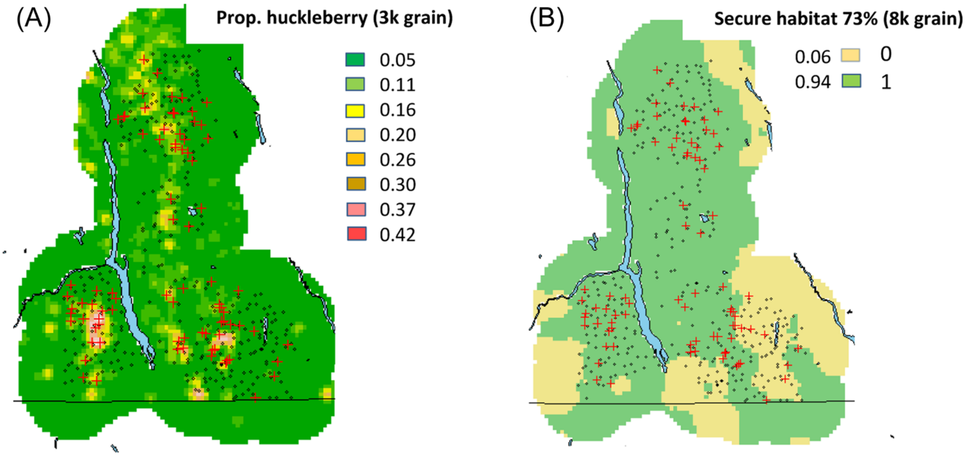

FIGURE 15 A) The proportion (prop.) of huckleberry patches at the 3-km grain (the top bottom-up variable in the most supported female density model) relative to grizzly bear detections. Grizzly bear data were collected in the focal study area of southeastern British Columbia, Canada, between 1998–2005. B) Secure habitat at the 8-km grain and representing 73% of the area (the most influential top-down variable in the most supported female density model) relative to grizzly bear detections in the focal study area. Ninety-four percent is the proportion of grizzly bear home range centers within secure habitat. Six percent were in non-secure habitat. Pluses (+) are sites with grizzly bear detections and dots are sites with no detections.

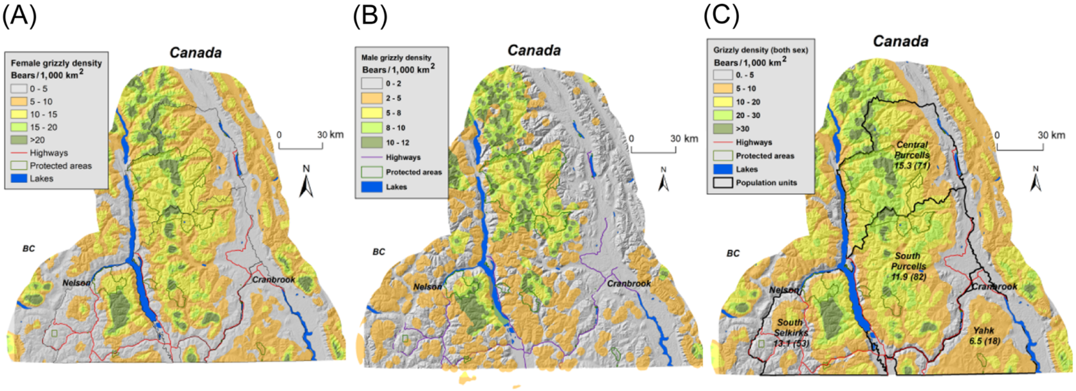

FIGURE 16 A) Predicted female grizzly bear density from the most supported bottom-up and top-down model. It included huckleberry patches at the 3-km grain and secure habitat at 73% at the 8-km grain. Data were collected across the south Selkirk and Purcell mountains of southeast British Columbia, Canada, between 1998 and 2005. B) Predicted density from the most supported bottom-up and top-down male density model, and C) average predicted density (bears/1,000 km^2) from the most supported composite female and male models for each Grizzly Bear Population Unit in the focal study area. Abundance is shown in parentheses. Note the difference in densities by color across the 3 panels.

huckleberry patches, and alpine (Figure 17B). All coefficient 95% confidence intervals in the top fitness model did not overlap zero (Table 10). Plots of selective strength (Figure 18) also support the conclusion that greenness was the most influential variable and that secure habitat had a smaller influence (but wide variation across bears) than bottom-up variables (Figure 18). Coefficients indicate that greenness, secure habitat, alpine, and huckleberry patches had a positive influence (the influence of huckleberry patches diminished with distance) on fitness, whereas

TABLE 8 Consolidated and abbreviated uni- and multi-variable model selection relative to influence on male grizzly bear density models. We include the best bottom-up, top-down, and composite models for the south Selkirk and Purcell mountains of southeast British Columbia, Canada (1998–2005). We present log-likelihood (LL), sample-size adjusted Akaike's Information Criterion (AIC$_c$), difference in AIC$_c$ between most supported and given model (ΔAIC$_c$), and the number of parameters (*K*).

Number	Model	Type	LL	*K*	AIC$_c$	ΔAIC$_c$
1	Top-down (secure habitat 94% 8 km)	Top-down	−682.0	10	1,384.0	0.0
2	Bottom-up (distance to huckleberry) + top-down (secure habitat 94% 8 km)	Composite	−681.0	11	1,384.1	0.1
3	Top-down (secure habitat 98% 3 km)	Top-down	−682.1	10	1,384.2	0.2
4	Bottom-up (distance to huckleberry) × top-down (secure habitat 94% 8 km)	Composite	−680.2	12	1,384.3	0.3
5	Top-down (roads 8 km)	Top-down	−682.7	10	1,385.4	1.4
6	Bottom-up (huckleberry 8 km) + top-down (secure habitat 94% 8 km)	Composite	−682.0	11	1,386.0	2.0
7	Bottom-up (alpine 8 km) + top-down (secure habitat 94% 8 km)	Composite	−682.0	11	1,386.0	2.0
8	Bottom-up (canopy cover 3 km) + top-down (secure habitat 94% 8 km)	Composite	−683.5	11	1,389.0	5.0
9	Bottom-up (canopy cover 3 km) + top-down (secure habitat 98% 3 km)	Composite	−683.5	11	1,389.0	5.0
10	Top-down (secure habitat 89% 3 km)	Top-down	−685.5	10	1,391.0	7.0
11	Bottom-up (alpine areas 3 km)	Bottom-up	−687.1	10	1,394.2	10.2
12	Top-down (secure habitat 98% 3 km, distance to road 3 km)	Top-down	−687.4	11	1,396.8	12.8
13	Top-down (secure habitat 79% 3 km)	Top-down	−690.1	10	1,400.2	16.2
14	Bottom-up (canopy cover 3 km)	Bottom-up	−690.6	10	1,401.2	17.2
15	Top-down (road density 3 km)	Top-down	−691.9	10	1,403.8	19.8
16	Bottom-up (canopy cover 8 km)	Bottom-up	−692.1	10	1,404.2	20.2
17	Bottom-up (distance to huckleberry)	Bottom-up	−692.4	10	1,404.8	20.8
18	Top-down (secure habitat 98% 3 km, road density 3 km)	Top-down	−691.9	11	1,405.8	21.8
19	Bottom-up (huckleberry 3 km)	Bottom-up	−693.8	10	1,407.6	23.6

riparian had a negative effect (Table 10). Roads often follow riparian habitat in the valley bottoms, likely influencing the negative influence on fitness.

The second most supported model (ΔAIC = 0.6) contained road density at the 3-km grain in place of secure habitat, indicating similar but slightly less support (Table 9). The highest ranked model with only bottom-up variables (distance to huckleberry + greenness + alpine) had substantially less support (ΔAIC = 14.9, model 12 in Table 9), indicating support for the addition of top-down covariates influencing female fitness. The quantity of habitat that was conducive to fitness varied among population units within the focal area with the Yahk area having a very low fitness RSF score (0.02) relative to the South Selkirk and South Purcell units with average scores of 0.16 each (Figure 17A).

TABLE 9 Consolidated and abbreviated uni- and multi-variable model selection related to influence on female grizzly bear fitness. We include the best bottom-up, top-down, and composite models for the south Selkirk and Purcell mountains of southeast British Columbia, Canada (1998–2015). We present sample-size adjusted Akaike's Information Criterion (AIC_c), difference in AIC_c between most supported and given model (ΔAIC_c), the number of parameters (K), and log likelihood (LL).

Number	Model	Type	LL	K	AIC_c	ΔAIC_c
1	Bottom-up (distance to huckleberry 10 ha, greenness 8 km, alpine areas 3 km) + top-down (secure habitat 79% 3 km, riparian 8 km)	Composite	−140.8	6	293.8	0.0
2	Bottom-up (distance to huckleberry 10 ha, greenness 8 km, spruce-fir forest 8 km) + top-down (road density 3 km, riparian 8 km)	Composite	−141.1	6	294.3	0.6
3	Bottom-up (distance to huckleberry 10 ha, greenness 8 km, alpine areas 3 km) + top-down (secure habitat 79%, riparian 8 km) + (distance to huckleberry × secure habitat)	Composite	−140.2	7	294.6	0.8
4	Bottom-up (distance to huckleberry 10 ha, greenness 8 km, alpine areas 3 km) + top-down (road density 3 km, riparian 8 km)	Composite	−142.2	6	296.5	2.8
5	Bottom-up (huckleberry patch 3 km, greenness 8 km, alpine areas 3 km) + top-down (secure habitat 79%, riparian 8 km)	Composite	−142.8	6	297.8	4.0
6	Bottom-up (distance to huckleberry 10 ha, greenness 8 km, spruce-fir forest 8 km) + top-down (secure habitat 79% 3 km, riparian 8 km)	Composite	−143.6	6	299.4	5.6
7	Bottom-up (distance to huckleberry 10 ha, greenness 8 km) + top-down (secure habitat 79% 3 km, riparian 8 km)	Composite	−143.8	5	297.7	3.9
8	Bottom-up (greenness 8 km, alpine areas 3 km) + top-down (secure habitat 79% 3 km, riparian 8 km)	Composite	−144.2	5	298.4	4.6
9	Bottom-up (distance to huckleberry 10 ha, greenness 8 km, alpine areas 3 km) + top-down (riparian 8 km)	Composite	−144.4	5	298.9	5.1
10	Bottom-up (distance to huckleberry 10 ha, greenness 8 km, alpine areas 3 km) + top-down (secure habitat 79% 3 km)	Composite	−144.9	5	300.0	6.2
11	Bottom-up (distance to huckleberry 10 ha, alpine areas 3 km) + top-down (secure habitat 79% 3 km, riparian 8 km)	Composite	−149.5	5	309.0	15.2
12	Bottom-up (distance to huckleberry 10 ha, greenness, alpine areas 3 km)	Bottom-up	−150.3	4	308.7	14.9
13	Top-down (secure habitat 79% 3 km, riparian 8 km)	Top-down	−158.8	3	323.7	29.9
14	Bottom-up (distance to huckleberry 10 ha)	Bottom-up	−161.8	2	327.7	33.9
15	Top-down (riparian areas 8 km)	Top-down	−165.4	2	334.8	41.0
16	Bottom-up (distance to huckleberry 5 ha)	Bottom-up	−169.0	2	342.1	48.3
17	Top-down (secure habitat 79% 3 km)	Top-down	−170.6	2	345.2	51.4
18	Bottom-up (huckleberry patches all 3 km)	Bottom-up	−170.6	2	345.3	51.5
19	Top-down (roads 3 km)	Top-down	−171.9	2	347.8	54.0
20	Top-down (road density 3 km)	Top-down	−172.6	2	349.3	55.5

TABLE 9 (Continued)

Number	Model	Type	LL	*K*	AIC$_c$	ΔAIC$_c$
21	Bottom-up (alpine 3 km)	Bottom-up	−174.2	2	352.5	58.7
22	Bottom-up (higher elevation open forest 8 km)	Bottom-up	−180.6	2	365.3	71.5
23	Bottom-up (greenness 8 km)	Bottom-up	−181.2	2	366.5	72.7
24	Bottom-up (canopy cover 3 km)	Bottom-up	−181.4	2	366.8	73.0

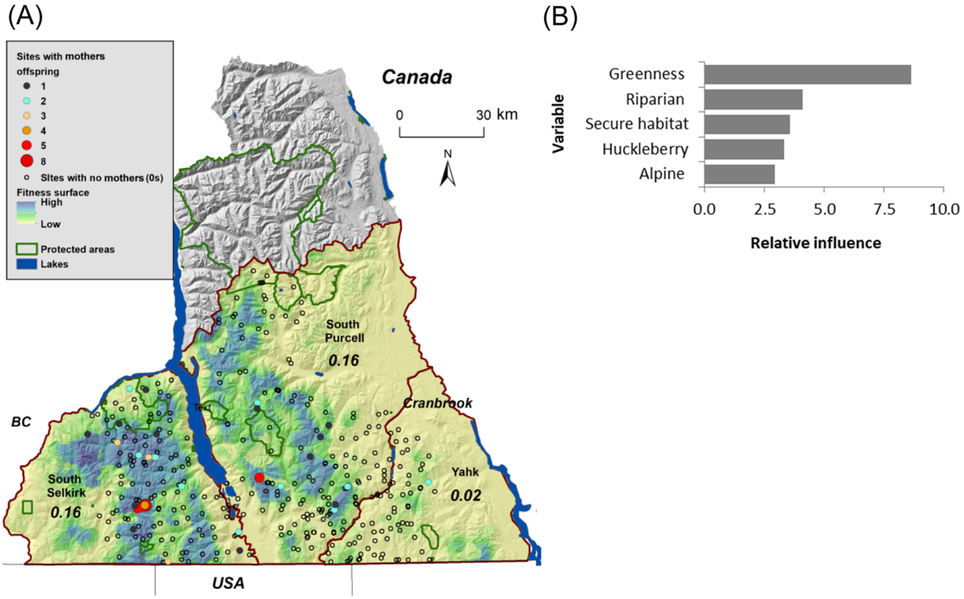

FIGURE 17 A) The composite multi-grain female grizzly bear fitness surface (female reproductive events) developed from 33 mothers with 72 offspring from a series of family pedigrees determined from samples collected in the south Selkirk and Purcell mountains of southeast British Columbia, Canada, between 1998 and 2015. B) The relative influence of variables within the best supported female grizzly bear fitness model depicted in panel A. We determined influence by calculating the magnitude of decrease in predictability as measured by the change in log likelihood after removing each variable from the top model.

Result synthesis

Compromised huckleberry patches

We found that approximately 38% (235 of 626 km^2) of huckleberry patches were in non-secure habitat (within 500 m of an open road; Figure 19A). When we explored the relationship between huckleberry patches, secure habitat, and female density using the top model (Table 7), we found that the positive effect of huckleberry patches on density mainly occurred in secure habitats. We applied the huckleberry coefficients from our top model to predict bear density in secure and non-secure habitats (Table A4, Appendix I) to graphically demonstrate this pattern (Figure 19B). There was minimal contribution to female density from huckleberry patches in non-secure habitat. The most supported model that included an interaction term between these 2 variables (model 4 in Table 7) had a ΔAIC value of 2.7, suggesting our data does not support a significant interaction. We suspect there was a

TABLE 10 Coefficients from the most parsimonious model for grizzly bear female fitness in the south Selkirk and Purcell mountains in southeast British Columbia, Canada, in 1998–2015. We present coefficients, robust standard error (SE), probability of z (P(z)), robust probability, and the upper and lower 95% confidence intervals.

					95% CI	
Variable	**Type**	**Coefficient**	**SE**	**P(z)**	**Lower**	**Upper**
Distance to huckleberry 10 ha	Bottom-up	−0.0003	0.0001	0.02	−0.0006	−5.56E−05
Greenness 8 km	Bottom-up	45.0	13.2	0	19.2	70.8
Alpine 3 km	Bottom-up	4.3	1.8	0.02	0.8	7.8
Secure habitat (79%)	Top-down	1.5	0.6	0.02	0.2	2.8
Riparian 8 km	Top-down	−42.9	16.8	0.01	−75.7	−10.0

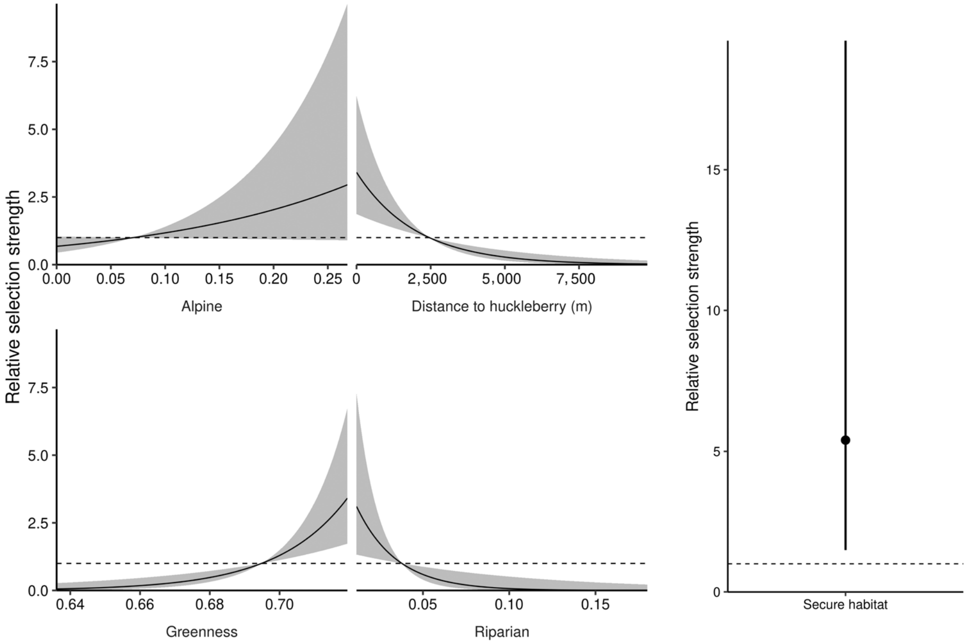

FIGURE 18 Relative selection strength plots with 95% confidence intervals for variables in the top female grizzly bear fitness model. The dotted line indicates the threshold between selection and avoidance. The model was derived from global positioning system telemetry data collected between 1998 and 2015 in the south Selkirk and Purcell mountains of southeastern British Columbia, Canada. Secure habitat was a binary variable. All continuous variables not featured in a plot were set to their mean value (pooled across all observations in the dataset), while binary variables were set to 0. Continuous variable ranges on the *x*-axis include the middle 95% of values available to bears in resource selection function models (excluding values below and above the 2.5% and 97.5% quantiles, respectively). The horizontal dashed line indicates where predicted selection is proportional to availability.

relatively low amount of non-secure huckleberry habitat and variation of huckleberry patches across the spectrum of secure habitat, minimizing our ability to detect an interaction (Table A4, Appendix I). When secure habitat was set at its mean value, an average positive relationship between huckleberry patches and female bear density was apparent (middle panel in Figure 19B).

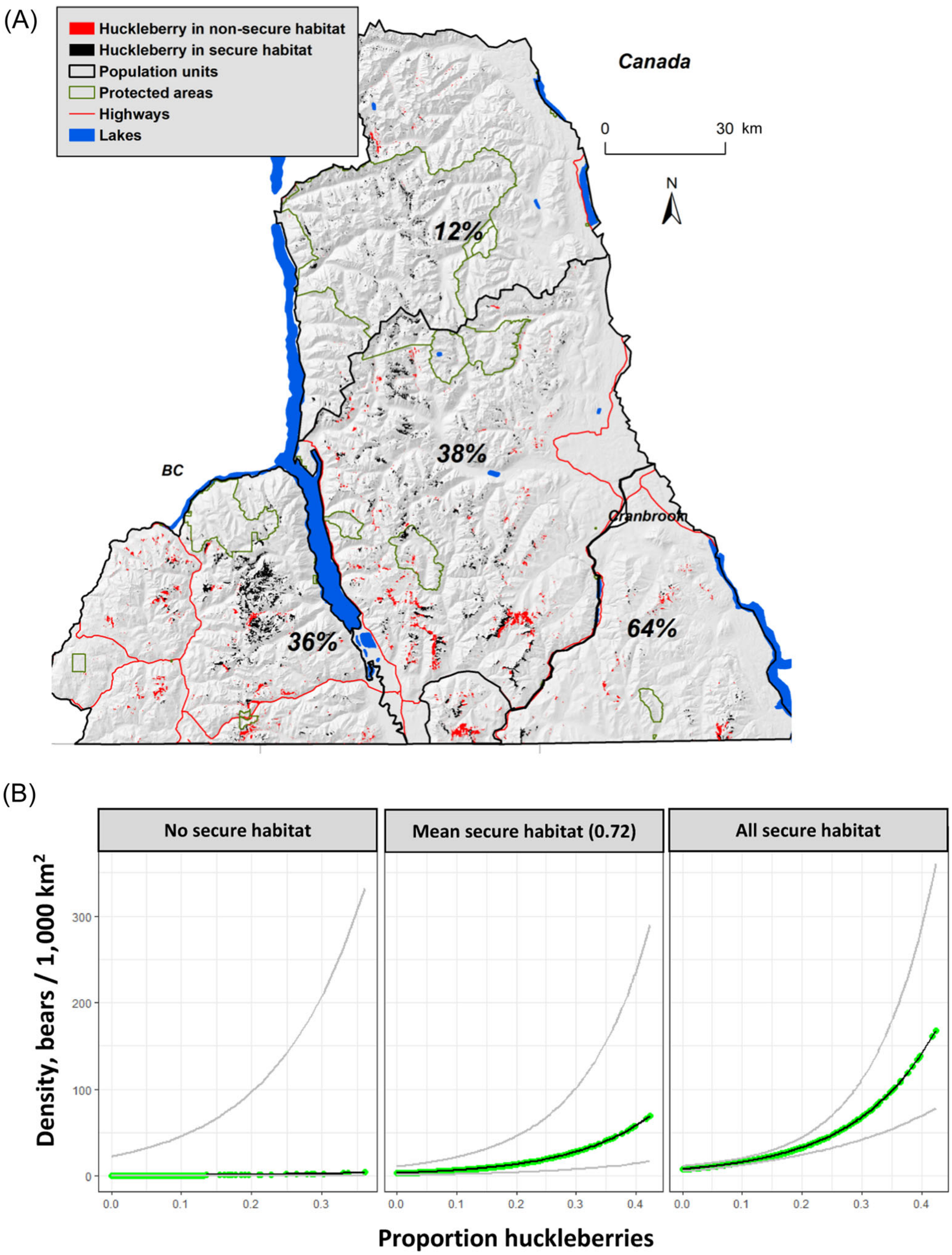

FIGURE 19 A) Huckleberry patches compromised by backcountry resource extraction roads (red – within non-secure habitat) to some degree across the south Selkirk and Purcell mountains in southeast British Columbia, Canada (2004–2013). Percentages are the proportion of huckleberry patches in non-secure habitat in each population unit. Black lines are population unit boundaries and green lines are protected areas. B) The predicted relationship between grizzly bear density (bears/1,000 km^2) and the proportion of huckleberry patches outside (left panel) and inside (right panel) and combined (center panel) of secure habitat from the most supported female density composite model.

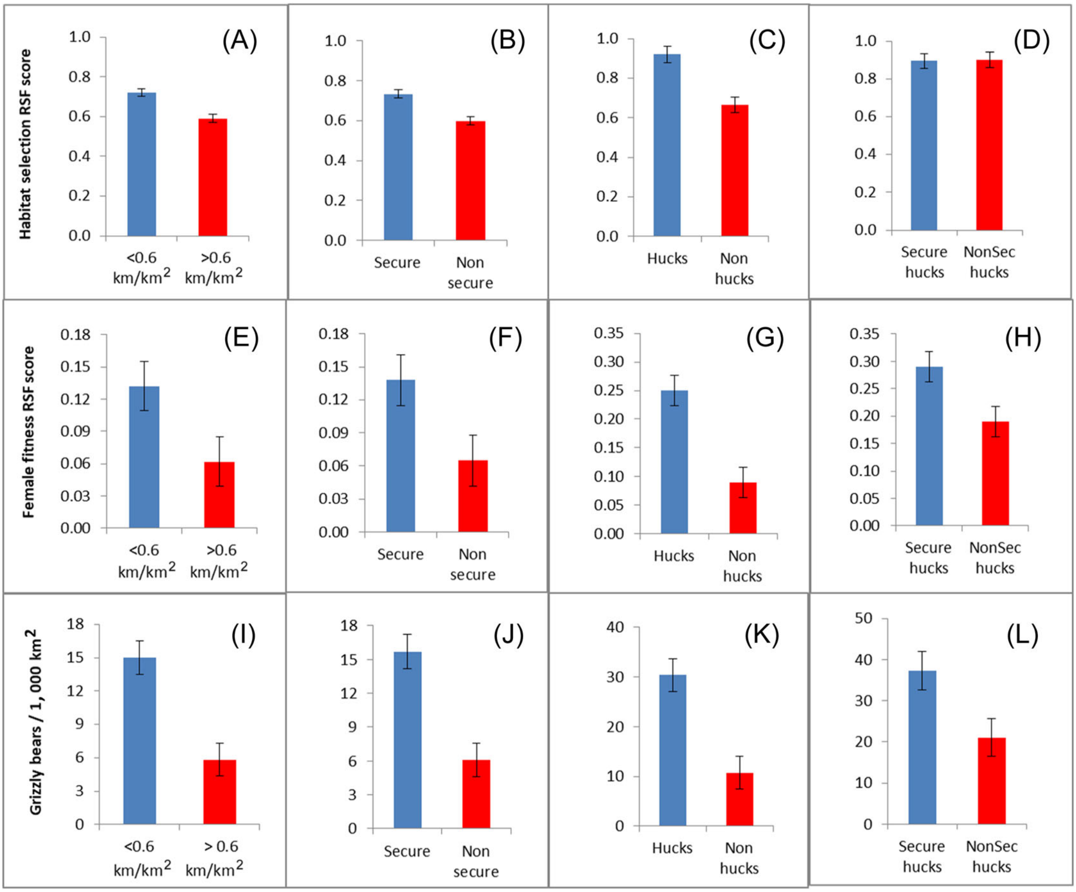

FIGURE 20 A–D) Female grizzly bear habitat selection based on resource selection function (RSF) methods, E–H) female fitness, and I–L) both-sex density in relation to road density (< or >0.6 km/km^2), secure or non-secure habitat, huckleberry patches (hucks) or not (non hucks), and secure or non-secure huckleberry patches (NonSec hucks). Analyses reflect bear population processes in southeastern British Columbia, Canada, between 1998–2015. Habitat with higher road density or less secure habitat has reduced selection, fitness, and density relative to more secure habitat. Note the difference in *y*-axis quantities between 2 left columns, road density and habitat security, and the 2 right columns, huckleberry and huckleberry security.

Generally, the road target (0.6 km/km^2), habitat security, and the presence of huckleberry patches influenced habitat selection (Figure 20A–D), female fitness (Figure 20E–H), and density of both sexes (Figure 20I–L). Selection of secure huckleberry patches increased fitness and density at the population level. Secure habitat and areas with open road density <0.6 km/km^2 were associated with double the rate of female fitness (Figure 20E and F). These patterns culminated in grizzly bear density being 2.6 times higher in habitats <0.6 km/km^2 than those greater than that threshold (Figure 20I) and in secure rather than non-secure habitat (Figure 20J).

Relative influence of variables

We found that huckleberry patches may be more important for female density than males. In at least one area (Yahk), low huckleberry patch density, low fitness habitat index, low proportion of secure habitat, and high road

TABLE 11 Habitat conditions during the study (2005) for secure habitat (>500 m from an open road), road density, huckleberry patch area proportion, and fitness habitat indices. Data describes 4 grizzly bear population units within the focal study area in the south Selkirk and Purcell mountains of southeast British Columbia, Canada. Fitness habitat index refers to the logistic regression output for the female fitness analysis that assigned a value to habitat based on the associated patterns of female fitness. The fitness data (family pedigrees) in the Central Purcell unit were not sufficient enough to yield rigorous pedigree results.

Population unit	Secure habitat (%)	Road density (km/km^2)	Huckleberry patch (%)	Fitness habitat index
South Selkirk	50	1.1	4.2	0.16
Yahk	24	1.6	1.7	0.02
South Purcell	53	1.0	3.7	0.16
Central Purcell	74	0.7	2.1	

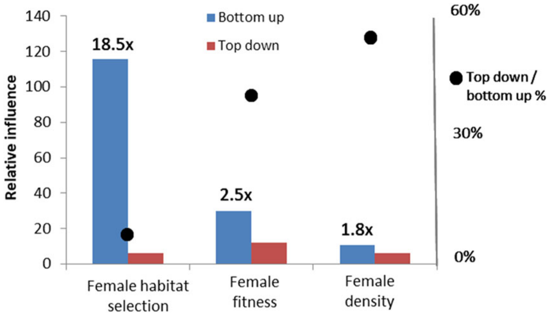

FIGURE 21 Relative influence of bottom-up and top-down factors on female habitat selection (2004–2015), fitness (1998–2015), and density (1998–2005) in the south Selkirk and Purcell mountains of southeast British Columbia, Canada. We determined values by removing either bottom-up or top-down variables from the top models within each analysis and calculating the reduction in the log likelihood scores. A large reduction indicates more influence. Bottom-up variables had a larger influence on all 3 population processes. Black dots represent the relative influence of top-down versus bottom-up variables in percent and are quantified by the right *y*-axis.

density likely all contributed to a relatively low grizzly bear density (Table 11; Figure 16). We also found that food resources were most influential for females across all 3 population processes examined. Bottom-up variables had an order of magnitude (18.5 times) more influence on female summer habitat selection than the top-down road density variable (Figure 21). While huckleberry patches were most influential overall, mortality risk associated with road density and lack of secure habitat had an increasingly higher proportional influence on female fitness and density (Figure 21). When we simulated an increase to bottom-up variables (huckleberry patches and habitats associated with foods) or decreased top-down risk through reducing road density and thus increasing secure habitat, we found that the behavioral habitat selection was more influenced by bottom-up food variables (Figure 22). Demographic fitness, however, responded almost equally to each realm, and density responded more to top-down variables (Figure 22).

Carrying capacity - potential increased abundance

We found that when the effect of roads was reduced (through simulation) to 0.6 km/km^2 in the top female and male density models, grizzly bear density rose 23%. When partitioned by population unit, the Yahk had the greatest

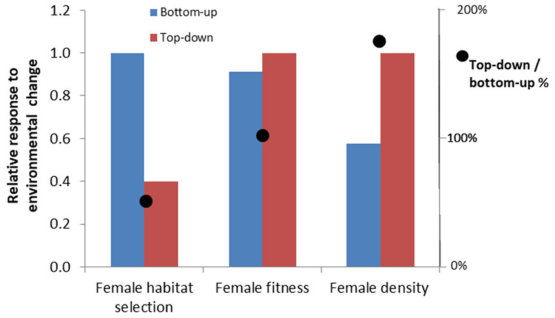

FIGURE 22 Relative response of grizzly bears to simulated environmental change. We increased and decreased bottom-up and top-down predictive input variables by 10% and then reapplied the top models for each analysis to estimate grizzly bear response in southeast British Columbia, Canada (1998–2015). Response has been standardized between 0 and 1 for relative comparison within each analysis. While selection, a behavioral characteristic, responded more to food resources, fitness and density, demographic characteristics, responded increasingly to top-down mortality risk in this simulation. The right *y*-axis is the ratio of top-down to bottom-up influence across the analyses. Density has the highest proportion of top-down influence relative to habitat selection and fitness.

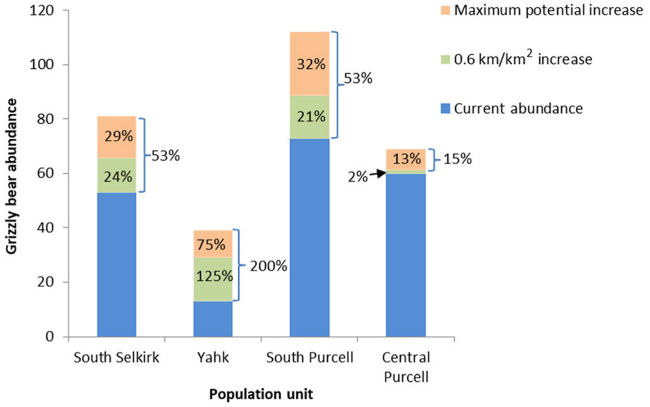

FIGURE 23 Potential increase in grizzly bear abundance (number of bears) within each of 4 population units across the focal study area in southeast British Columbia, Canada, between 1998 and 2005. We obtained estimates by hypothetically removing the effect of open roads. Blue bars were current abundance (2005), green bars represent estimated abundance with access control reducing open roads to 0.6 km/km^2 and with current huckleberry patches. Orange bars represent the maximum potential increase obtained by setting secure habitat to 1 (no roads, all habitat is secure) for the top female and male density models.

potential for increase through open road management (125% or 16 bears). The Central Purcell unit had the least potential for increase (2% or 1 bear) because road density for this unit was 0.7 km/km^2 (very close to 0.6 km/km^2). The South Selkirk and South Purcell units had potential for an increase of 24% or 13 bears and 21.4% or 16 grizzlies, respectively (Figure 23). Based on current huckleberry patch availability and removing the influence of all roads (setting secure habitat to 1), the maximum potential abundance estimate was 51% higher than the current numbers of bears in the focal study area. The greatest potential for increase was in the Yahk at 200% and the least potential in the Central Purcell at 15% (Figure 23).

Road density and secure habitat thresholds – optimum for female bear density

Models of female density illustrated that habitats with a road density <0.5 km/km^2 were preferred. Competing models with thresholds above or below this metric (0.3 to 1.2; Figure A9A, Appendix I) were close enough that 0.5 cannot be considered a fully supported optimal road density threshold. Therefore, while 0.5 km/km^2 was most supported by the data, thresholds on either side also showed some level of support.

We suspected that the influence of road density on grizzly bear density was related to the amount of available secure habitat. This suggested that areas with more secure habitat would have different relationships between road density and bear density. To explore this relationship, we reran the road threshold analysis with secure habitat in the model (Figure A9B, Appendix I) and found that a threshold of 0.3 km/km^2 was most supported by the data; however, the difference in likelihoods at different thresholds was minimal. This suggested that inclusion of secure habitat in the model accounted for much of the variation in bear density caused by roads.

Fitness and mortality risk dynamics

The negative association between roads and female fitness and density, even in the presence of huckleberry patches, led us to develop a map to represent habitats that related to population dynamics. Our goal was to identify habitats in the focal area that were conducive to higher (source-like) and lower (sink-like) fitness, density, and mortality risk. To do this, we contrasted fitness habitats (and higher female density in the northern Purcell Mountain portion of the focal study area) with mortality risk represented by higher road density and low habitat security to identify source-like and sink-like habitats (Figure 24).

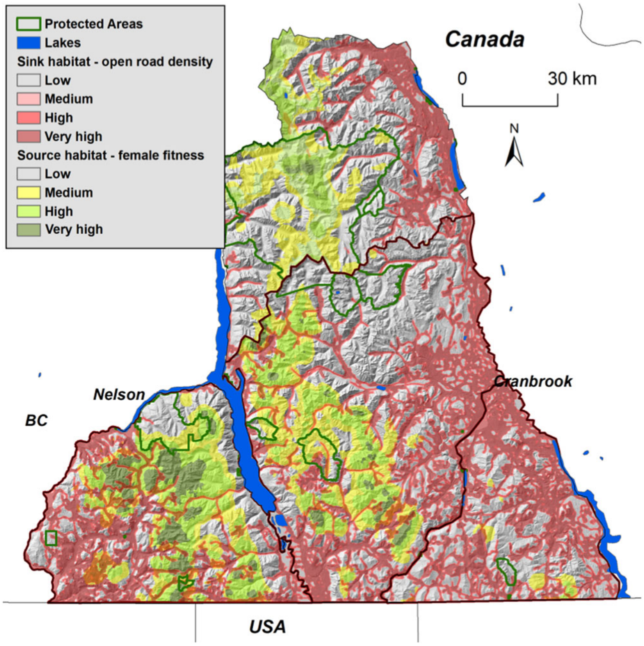

FIGURE 24 Spatial representation of the underlying mechanisms representing areas of higher female grizzly bear fitness (source-like habitat) and mortality risk (sink-like habitats) for the south Selkirk and Purcell mountains in southeastern British Columbia, Canada (1998–2015). Fitness habitat was derived from the female fitness model (and female density in the northern Purcell Mountains). Mortality risk habitat was derived from the open road density layer.

DISCUSSION

Our analyses demonstrated the value of modeling population processes, habitat selection, and populations density using a direct measure of an important food resource rather than with habitat surrogates only. The top habitat selection model using huckleberry patches was similar to, but significantly more predictive than, the top model describing the same study area in Proctor et al. (2015) that did not include huckleberry patches. The current model and the Proctor et al. (2015) habitat selection model are very similar except canopy cover was replaced with the output of the huckleberry patch model. In the Proctor et al. (2015) model, low canopy cover was contributing to a robust model likely because it influences the amount of sunlight affecting availability of plant-based bear foods.

Past habitat selection studies on grizzly bears in North America have generally used habitat surrogates for food resources, primarily because they were more available and specific food layers did not exist (Mace et al. 1999, McLellan and Hovey 2001, McLoughlin et al. 2002, Nielsen et al. 2002, Ciarniello et al. 2007, Milakovic et al. 2012). To develop our own food model, we identified huckleberry patches from habitat site visits informed by GPS telemetry locations. We focused on huckleberries because they have been shown to be the most important fat-producing food in the regional study area (McLellan and Hovey 1995, McLellan 2011, 2015). Abundance of huckleberry fruit from mid-July through mid-September is essential to grizzly bears for hibernation and reproduction (McLellan and Hovey 1995; McLellan 2011, 2015). For example, an abundant fall berry crop can delay den entrance dates, providing an opportunity for extra fat storage (Pigeon et al. 2016). In the fall, females are known to resorb their embryos prior to implantation if they do not store sufficient fat reserves (>~20–24% body fat) necessary for gestation, birth, and nursing of their young while in the den, and for some time after emergence (Robbins et al. 2012, McLellan 2015). As predicted, we determined that huckleberry patches were more influential than previously used bottom-up variables (prediction 1).

Integrating foraging resources into habitat selection efforts requires that researchers develop their own food layers. Most previous efforts to predict berry resources, such as huckleberry, have focused on plant occurrence (Roberts et al. 2014, Braid and Nielsen 2015, Lamb et al. 2017, but see Pigeon et al. 2016). Nielsen et al. (2004*c*, 2010) modeled habitat selection integrating various food items, identifying landscape characteristics to predict huckleberry occurrence with fruit production being related to low canopy cover. They considered food-based selection models an improvement over past efforts using only habitat-related variables. They argued that the use of habitat acting as surrogate for food variables does not reveal the mechanisms driving performance of population characteristics. Understanding these mechanisms that directly influence survival and reproduction allowed them to more accurately characterize their regional conservation needs and thus management direction. Our results are consistent with this conclusion, as we identified the mechanism of population vitality (fitness) and the habitats that confer higher fitness (also see Hertel et al. 2018) and density to direct conservation management.

We found that although huckleberry plants (occurrence) are relatively widespread in the region, patches significant to bears (found using telemetry data) were only a portion (~28%) of the occurrence distribution. The difference likely reflects the different response to canopy cover between the occurrence and patch models. Huckleberry plants occur across a wide range of forest cover, but only develop into a patch with productive fruit useful to a grizzly bear in areas of lower canopy cover. In the study area, these tended to be in higher elevations where slower forest regeneration may leave canopies open longer. Post-logging tree planting also likely hastens canopy cover, inhibiting huckleberry patch development. Nielsen et al. (2004*b*) found a similar pattern for 3 *Vaccinium* species, including black huckleberry. Plants occurred at a spectrum of canopy cover, but berry production was significantly greater when canopies were <50% closed.

The DNA survey period overlapped approximately half of the huckleberry season. Bears consume many other foods including other less abundant fruit, roots, herbaceous plants, ants, ungulate carrion, and more (McLellan and Hovey 1995, Nielsen et al. 2010). Some spring and late fall bear food occurs in similar habitats as huckleberry. While we do not have specific models that predict these other species, they often are found in habitats represented by greenness, a reasonably predictive surrogate food resource variable (Mace et al. 1999, Nielsen et al. 2002, Stevens 2002, Boyce and Waller 2003, Ciarniello et al. 2007). Buffaloberry, bearberry (*Arctostaphylos uva-usri*), Saskatoon serviceberry, and elderberry (*Sambucus* spp.) are well-known bear fruit foods regionally (McLellan and Hovey 1995). With a few exceptions, we did not find any of these other berry species to be as clustered and significantly visited by the collared bears as huckleberry patches.

Nielsen et al. (2016) found that when ungulate resources were present and considered in addition to the berry crop in western Alberta, grizzly bear abundance was on average higher. They argued that this pattern suggested a bottom-up limit to grizzly bear abundance after accounting for top-down impacts from road density. We suspect that this pattern was less important in our area because ungulate populations are likely lower in our wetter, more dense forests relative to the more open drier forests in Alberta (McLellan and Hovey 1995, Mowat and Heard 2006). McLellan (2011) found bears in a mountain valley adjacent to our study area focused on berries because they were abundant enough to compensate for being lower in protein. These bears with a fruit-dominated diet, tended to be smaller and fatter than those with higher protein and meat diets (Hilderbrand et al. 1999, 2018) and were able to attain relatively higher densities than other populations with less berries but more non-salmon meat sources (McLellan 2011). The importance of huckleberry patches to most of the bears in the focal area suggests the pattern found by McLellan (2011) may be more applicable to our area than that found by Nielsen et al. (2016).

Many of the best variables associated with huckleberry patches were related to micro- and macro-climate conditions (precipitation as snow in winter, mean annual precipitation, precipitation in summer, frost free period, precipitation in summer). Ongoing climate change may alter the long-term patterns of several of these variables (Prevey et al. 2020). Roberts et al. (2014) modeled several critical grizzly bear food items in Alberta and predicted that huckleberry will maintain, or increase, current distribution with climate change. Prevey et al. (2020) predicts huckleberry range will shift to higher latitude and elevation with climate change across the Pacific Northwest and adjacent interior mountains. Therefore, development of a more dynamic huckleberry patch model may be necessary for our results to be more spatially relevant into the future.

We used the output of the huckleberry patch model as a bottom-up variable in the models to examine population processes. As predicted, both bottom-up and top-down variables were important to explain female habitat selection, fitness, and density. For all processes studied except male density, bottom-up and top-down variables were additive. Our results highlight the importance of considering both habitat characteristics and human-caused forces in developing conservation management strategies for grizzly bears in North America. Traditionally, focus has often been on reducing human-caused mortality rates stemming from studies showing sensitivity of population trajectory to female survival (McLellan 1989*a*, Garshelis et al. 2005, Mace et al. 2012). We surmise this top-down focus reflects the most readily available management tools (reductions to mortality risk) and the lack of studies incorporating effect of food abundance on population processes.

Recently, however, with a shift in grizzly bear research to understand bottom-up influences, habitat selection studies have become more prolific in North America. These studies have provided insight into the influence of food on bear densities across North America (Hilderbrand et al. 1999, Mowat and Heard 2006). Several studies have shown densities to be bottom-up driven across western North America. Mowat et al. (2013) found grizzly bear density to be loosely and variably associated with habitat-based surrogate food variables with the additive influence of anthropogenic influence. Coastal bear densities in areas with ocean-run salmon showed a strong relationship with the number of migrating fish (Mowat et al. 2013). McLellan (2015) found grizzly bear density to vary with undulant huckleberry productivity over 3 decades. Our results support this relationship between bear density and huckleberries but additionally illustrate the negative influence of top-down pressure that can reduce a population's ability to reach carrying capacity that food availability allows.

As with other studies examining bottom-up and top-down variables, we found a complex relationship between roads and habitat surrogates or actual food layers (Mace et al. 1999; McLoughlin et al. 2002; Nielsen et al. 2002, 2010; Ciarniello et al. 2007; Boulanger et al. 2018). Nielsen et al. (2010) integrated food layers and mortality risk to predict realized habitat use by grizzly bears and found that food layers predicted habitat selection, but it was necessary to add top-down processes to make population-level inferences. Braid and Nielsen (2015) developed and integrated food layers into their model-based assessment of grizzly bear habitat selection in relation to road density (mortality risk), facilitating identification of areas for protection (road closure to reduce mortality risk) or habitat restoration. We similarly found that benefits from food resources depend on the mortality risk associated with those resources. Beyond bears, Hebblewhite et al. (2014) similarly found both prey resources and anthropogenic mortality affected conservation of the Amur tiger (*Panthera tigris altaica*), an obligate carnivore threatened by human-caused mortality. They recommended limiting road density to reduce mortality of both tigers and their ungulate prey.

That bottom-up and top-down influences need to be considered together, rather than as independent factors, has been demonstrated by others, and is applicable beyond carnivores to other trophic levels. For example, it has been shown that a component of caribou (*Rangifer tarandus*) survival can be measured through habitat selection, but inclusion of predation risk vastly improves survival prediction (DeCesare et al. 2014). Similarly, Rowland et al. (2018) developed and integrated a nutrition-based (foods) model into a spatial habitat use model incorporating human disturbance (road density), improving elk management. Kortello et al. (2019) developed a habitat model for marmot (*Marmota caligata*), an important prey for wolverine (*Gulo gulo*). Marmot habitat and human disturbance (road density) were the most consistent predictors of wolverine occupancy. This informed management of critical food habitat, and reductions of mortality risk for conservation of wolverines (Mowat et al. 2020).

While bottom-up forces were more influential overall, as we predicted, their relative influence varied spatially. For example, we suspect that in at least one portion of the study area, the Yahk unit, mortality risk from both high road densities and a low proportion of secure habitat resulted in lower fitness habitat and bear density. This was supported by the carrying capacity simulation, which demonstrated that closing roads had the potential to more than double the number of bears in this threatened population (Figure 23). In contrast, the Central Purcell unit had the potential to increase abundance through road management by 2% (Figure 23).

Spatial variation in the relative influence of bottom-up and top-down influence on grizzly bears was similarly reported by Mowat et al. (2013). They found that populations experiencing overlap with humans were more influenced by top-down effects than more remote ones. Nielsen et al. (2006) integrated habitat and mortality risk variables to reveal a mosaic of source-like and sink-like habitats. Studying the same system, Boulanger et al. (2018) expanded on this idea identifying source-like and sink-like habitats where the relative influence of bottom-up and top-down variables on western Alberta bear density varied with the proportion of habitats characterized by higher mortality risk or productivity.

At a larger scale, Lamb et al. (2020) found the relative influence of bottom-up and top-down influences fueled a source-sink dynamic across British Columbia that facilitated coexistence between people and grizzly bears. Backcountry wilderness bears in productive habitat with lower mortality risk dispersed into front country human-dominated landscapes to backfill spaces left from the high mortality rates there. These dispersers experienced higher mortality rates while some adapted and survived by adopting nocturnal behaviors. In addition to this back- versus front-country pattern, our work revealed that within backcountry habitat, areas can be sink-like (highly roaded). This pattern highlights the importance of effectively managing productive (food-rich) backcountry habitats to facilitate source populations to mitigate the higher mortality risk occurring in human-settled areas.

The mosaic of habitats associated with higher fitness, density, or mortality risk led us to develop a map depicting areas of safe and productive source-like and risky sink-like habitats (Figure 24). Similar mapping has informed conservation management for greater sage-grouse (*Centrocercus urophasianus*). Aldridge and Boyce (2007), and Kirol et al. (2015) combined habitat selection modeling and a measure of fitness (reproduction and survival) to identify source-like and sink-link habitats for this at-risk prairie bird. They found that limited source habitats reduced survival and nest success and recommended conservation measures to mitigate these patterns. Laundre et al. (2014) used the spatial variability of relative influence between bottom-up and top-down habitats to describe a landscape of fear. He predicted areas with higher proportions of safe habitat (low mortality risk) should yield more animals. Conversely, assuming equal levels of bottom-up resources, areas with higher proportions of risky habitat would be top-down limited, resulting in lower abundance. We found this paradigm to be applicable to our study area. Habitats with higher road density were risky versus secure (no roads) habitat that was relatively safe. The interaction of road densities and huckleberry patches characterized a space as either sink-like or source-like habitat. Areas of abundant huckleberry patches and high security (low road density) were obvious source-like habitat.

We also found that the relative importance of top-down versus bottom-up influences was not constant across behavioral and demographic processes (prediction 2). Top-down influences had small effects on habitat selection and larger effects on fitness, with the greatest relative effect on population density. Given this pattern, researchers and managers should use caution when inferring population-level effects from habitat selection studies; the magnitude and direction of a behavioral response (habitat selection) may translate poorly to demographic effects (density). Using different analyses, a similar inference has been made elsewhere for grizzly bears (Nielsen et al. 2006, 2010; Boulanger et al. 2018) and across taxa (greater sage-grouse [Aldridge and Boyce 2007], caribou [DeCesare et al. 2014]), concluding that habitat selection alone was insufficient as a basis for population management, necessitating incorporation of survival, mortality risk, or fitness.

At the intersection of top-down and bottom-up influences, we found that areas of higher road density offset food resources even if abundant, preventing effective use of the resource (prediction 3). With the omnivorous grizzly bear, top-down influences in our study area were not only associated with mortality risk, but they limited contributions of food resources to fitness and density, in essence having a similar effect as habitat loss. This doubly negative effect likely contributes to the ubiquitous detriment that high road density confers to grizzly bear populations in western North America (Nielsen et al. 2004*c*, Schwartz et al. 2010, Boulanger and Stenhouse 2014, Lamb et al. 2018, Proctor et al. 2019). In an earlier study in the same ecosystem that did not explore fitness or density, Wielgus and Vernier (2003) found avoidance of otherwise selected habitats when they were associated with roads. In a review of the impacts on grizzly bears from recreation, Fortin et al. (2016) concluded that displacement may yield reductions in reproduction and survival through increased energetic costs and decreased nutritional intake. The double impact of increased mortality risk and reduced access to food resources that is caused by human disturbance is not uncommon (Chapron et al. 2008, Dussault et al. 2012, Hebblewhite et al. 2014, Rosenblatt et al. 2016). Elk have also been shown to avoid roads, forfeiting the benefit of abundant food resources when they are near roads; this lost use of habitat was positively associated with the degree of human disturbance (Rowland et al. 2018). Using multiple and cumulative measures, Stewart et al. (2016) determined that human disturbance could reduce use of otherwise productive habitats by wolverines. They confirmed habitat avoidance (Krebs et al. 2007), adding to existing conservation concerns of direct mortality through trapping (Krebs et al. 2004, Lofroth and Ott 2007), and climate change that decreases spring snow needed for denning when raising kits (Copeland et al. 2010).

Beyond inhibiting food use, human activities also directly influence grizzly bear food supply in our study area. Huckleberries are reduced by fire suppression that allows forest canopies to close (Minore 1975, Minore et al. 1979, Hamer and Herrero 1987, Klenner et al. 2008, McLellan 2015). Conversely, activities that open the forest canopy, including timber harvest (Nielsen et al. 2004*a*, *b*), thinning, prescribed burns, and unsuppressed wildfire, can increase bear forage (McLellan 2015, 2018). Nielsen et al. (2004*a*) proposed that forests with minimal natural openings might benefit from cut blocks that open the canopy but suggested motorized access control around any good food patches created to ensure habitat security. Our results support this prescription. We found that canopy opening activities (e.g., logging or burns) may yield productive huckleberry patches where the underlying soil, topography, and climate conditions are conducive to huckleberry patch genesis. Roads associated with timber harvest would likely offset any potential benefit to bears from huckleberry patch creation unless they were closed following logging.

We explored the data to attempt to identify thresholds for road densities and levels of secure habitat that might inform management. We developed competing variables with differing proportions of secure habitat to test whether or not bears had higher fitness or density associated with an optimal amount of security in their home ranges. We found that while bears had higher fitness and densities in more secure habitat, scale had to be considered: while some bears used habitats with only 40% security, this occurred within a larger area that averaged approximately twice that amount (79%). This result is consistent with Mace et al. (1996) who found that bears can survive and reproduce using habitat that is roaded to some degree, but that at the larger scale, they require a substantial amount of secure habitat

(>60%) to persist and thrive. Schwartz et al. (2010) found that road density and the amount of secure habitat were both significant predictors and additive when modeling female grizzly bear survival. They found that as the amount of secure habitat declined, average road densities also needed to decline to maintain a sustainable female survival rate. They concluded that appropriate conservation management required the amount of secure habitat to be balanced with road density targets. This would alleviate isolated patches of secure habitat being surrounded by a matrix of high road density where grizzly bear mortality risk was elevated (also see Proctor et al. 2019).

A maximum open road density target of 0.6 km/km^2 (Mace et al. 1996) has been used by several jurisdictions across western North America where grizzly bear conservation management is a priority because females reproduce and survive at sustainable levels below this (Wakkinen and Kasworm 1997). Population decline has been documented in habitats with open road densities >0.75 km/km^2 (Boulanger and Stenhouse 2014). The comparisons of habitat selection, fitness, and bear density using road densities above and below 0.6 km/km^2 support findings of Lamb et al. (2018). They concluded that road densities 0.4–0.6 km/km^2 were optimal for grizzly bears reporting bear densities 3–4 times higher in habitats with <0.6 km/km^2 road densities. But even a road density target of <0.6 km/km^2 does not guarantee mortality risk will be low enough to support recovery of a bear population; such was the case with the Stein-Nahatlatch population in southwestern British Columbia where a depressed food supply (or other non-human-caused mortality factors) may limit recovery (McLellan et al. 2019, Proctor et al. 2019) despite a low road density estimated at 0.2 km/km^2 (Proctor et al. 2019). This is in contrast to a long-term study in southeastern British Columbia where despite road densities of approximately 1.2 km/km^2, populations have not declined (McLellan 2015). This discrepancy is thought to highlight differences in mortality risk, resource abundance, and spatial distribution of foods. In southeastern British Columbia, the productive huckleberry patches within the Flathead management unit are farther from human population centers, reducing the risk of human-caused mortality despite a relatively high road density. Likely more important, the abundant huckleberry patches are separated from roads, diminishing the encounter rate with humans and thus mortality risk and displacement from foods (McLellan 2015). In our study area, the NCC Darkwoods property within the South Selkirk population unit presented a similar scenario. Access management has effectively separated the abundant huckleberry patches from high human use areas so that despite an extensive road network within the population unit (road density = 1.1 km/km^2), strategic closures in the NCC property (road density = 0.3 km/km^2) have resulted in grizzly bear densities 2.5 times higher than in the population unit as a whole.

We show that roads are a conservation concern for bears to some degree from displacement from good habitat, reducing fitness and density. This is on top of unreported human-caused grizzly bear mortality associated with backcountry road networks in some regions of southern British Columbia. While imperfectly understood (Morgan et al. 2020), extrapolation of results from recent work (McLellan et al. 2018) has shed light on this conservation issue across British Columbia. Some areas may be experiencing unsustainable human-caused mortality rates from people accessing backcountry roads (Morgan et al. 2020). Road closures will reduce unreported direct mortalities, and the management approach stemming from our results (see below) outlines how to strategically select roads for closure, for maximum benefit to bears.

Genetic pedigrees - fitness

Habitat selection and density studies using telemetry data are relatively common (Mace et al. 1996, Nielsen et al. 2002, Ciarniello et al. 2007, Proctor et al. 2015), but the use of genetic pedigrees to examine habitat drivers of fitness are less so. That said, the use of pedigrees from genetic sampling to quantify fitness is not new (Boudry et al. 2002, Blouin 2003, Pemberton 2008, Lemay and Boulding 2009, Ford et al. 2011). Recent advances in sampling efficiency and the use of many genetic markers has made it more affordable and accurate (Lamb et al. 2019). Genetic pedigrees have been used in mandrills (*Mandrillus sphinx*) to assess the impact of demographic and behavioral factors on reproductive success but with no consideration for habitat (Charpentier et al. 2005); in orca (*Orcinus orca*) pods off the coast of British Columbia to assess reproductive success (Ford et al. 2011), but again, without reference to habitat variables; and in Canadian lynx (*Lynx canadensis*) to study size and variability of litters in relation to habitat characteristics without consideration of top-down influence (Kosterman et al. 2018). Studying fitness in brown bears (grizzly) using genetic pedigrees to date has been restricted to describing reproductive success of males (Craighead et al. 1995).

Unlike other studies, we used genetic pedigrees to derive an index of female fitness to examine patterns of land use to underpin grizzly bear conservation management. The offspring in the pedigree spanned a range of ages, some still with their mother, but many long since dispersed. In that regard, this metric may be closer to a realized fitness measure than the surrogates used historically (Aldridge and Boyce 2007, DeCesare et al. 2014, Kirol et al. 2015). Our sampling spanned 2 decades of consistent effort, allowing for the influence of survival after the dispersal of offspring from their mothers. A key to the feasibility of our approach was the long duration of the study in a small population. Over the entire study period, we sampled mothers (33) and offspring from the focal study area where we estimated approximately 139 grizzly bears, about 25% (~35) of which would be females of reproductive age (McLellan 1989*b*). Kasworm et al. (2021) also successfully used pedigrees to confirm reproductive success of augmented bears in a thoroughly sampled small grizzly bear population in the Cabinet Mountains of northwest Montana. In that population all sampled bears fit into a family triad, confirming the power of this approach but emphasizing the importance of extensive sampling over time.

Because of the challenge of differentiating mothers from daughters, we limited pedigree assignments to only groups where we had perfect allele sharing patterns within triads (mother-father-offspring), where the offspring had an allele from each parent at all loci. Another issue was that young females may not have been alive long enough to accumulate surviving offspring. We think, however, that longer-term sampling with a large sample size, relative to the population size, reduced any potential bias; any particular area had a mix of young and older successful females.

Our work provides a link between theory and on-the-ground management by spatializing important food resources, secure habitat, road densities, and associated mortality risk to inform where landscape habitat management would be the most effective. Backcountry motorized access controls, even minimal controls, are unpopular among resource road users including hunters, firewood cutters, and recreational all-terrain vehicles users. This unpopularity argues for informed, targeted, and accurate management strategies (DeWolf 2016). Our results inform the ability to implement strategic motorized access controls over portions of the backcountry landscape. They also provide for the least disruption for motorized users but maximum benefit for grizzly bears. Our work supports Proctor et al. (2019) who recommend implementing habitat-structured motorized access management relative to the quality of the habitat and the presence of the most important late summer and fall hyperphagic food resources.

Limitations

We focused on covariates of density, rather than density per se, and realize several of the density estimates are out of date. The data that we used to generate density estimates were the same as those used by Proctor et al. (2007) so the estimates strictly reflect changes in methodology, especially improved handling of closure violation and the use of spatially explicit estimation methods (SECR; Efford 2011). Other SECR studies that have compared SECR models with closed models using empirical approaches (Boulanger et al. 2018) have found general agreement when radio-collar data is used to correct closed estimates (Ivan et al. 2013*a*). Simulation methods have also been used to assess the influence of how regional areas are defined (Efford and Fewster 2013), patchy distributions of animals (Efford 2014), and bear home range shape (Ivan et al. 2013*b*, Efford 2019). All of these applications have suggested that SECR is relatively robust to assumptions and likely scenarios if sampling methods are designed appropriately (Efford and Boulanger 2019). Also, SECR methods focus on home-range scale selection across the time period of sampling; therefore, smaller-scale spatial and temporal inference is limited by this analysis.

MANAGEMENT IMPLICATIONS

Understanding the mechanisms of population processes where critical food resources and mortality risk exist across a landscape provides justification and direction for strategic place-based management approaches. This is particularly important when those resources are spatially and temporally variable and may be affected by outside factors (e.g., anthropogenic disturbance and mortality risk). We found bottom-up and top-down influences to be additive across processes, and suggest that the management paradigm dominating western North America would benefit from consideration of both realms.

Our work provides the framework for on-the-ground management of grizzly bears, whether in North America or elsewhere, and may also provide insights into customized wildlife management plans for other species in human-disturbed landscapes. Management recommendations can be summarized as follows: spatialize important food or prey resources to inform where to reduce human access (and thus mortality risk) if required. The securing of important food resources like huckleberry patches to make them accessible to bears may require restriction of human access (i.e., road closure); one action without the other may be ineffective at recovering or conserving a population. Proctor et al. (2019) recommended implementing habitat-structured motorized access management relative to the quality of the habitat and the presence of the most important late summer and fall hyperphagic food resources. Our results support this management recommendation and provide a science-based foundation upon which to develop spatially strategic motorized access control over portions of the backcountry landscape. To achieve a balanced approach between human use and bear conservation, we recommend a place-based management plan developed by first identifying areas where bear foods are minimal versus abundant, allowing greater open road densities in poorer habitats, and reducing access to areas with high-quality food resources. Especially for bear populations where conservation management or recovery is a priority, we recommend backcountry road densities be maintained, on average, below approximately 0.6 km/km^2 and secure habitat of >60% (as per Proctor et al. 2019). We further recommend restricting motorized human access in areas of high-quality food resources, clustered to ensure sufficiently large areas for bears separated from motorized access areas. Larger patches of secure habitat are beneficial to avoid small habitat patches (<5–10 km^2) sometimes created by clustered or evenly spaced roads. We found benefit to bears from huckleberry patches larger than 5 ha. Industrial activities such as timber harvest and prescribed burning that open forest canopy may also increase huckleberry supply if other factors align (e.g., appropriate soil, slope, precipitation, solar incidence), but our results suggest that benefits of increased bear foods are not fully realized unless access to the associated roads is restricted. Specific to our focal area, targets for access management to optimize the amount of secure habitat include the Yahk, and portions of the South Selkirk, Central Purcell, and Central Selkirk population units where road densities are high and huckleberry patches are present.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

Bear handling procedures were in accordance with the Canada Council on Animal Care Standards and British Columbia Ministry of Environment, Fish and Wildlife Branch Animal Care Protocols. All live capture and DNA sampling work was done under the following permits, which required procedures equaling or exceeding the above animal handling standards: British Columbia Parks permit number 104738 and BC MoE Wildlife Act permits CB10-61709 and CB16-169998.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request. Some limitations apply for raw telemetry data of this sensitive species.

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APPENDIX I

METHODS

Huckleberry modeling methods

TABLE A1 Plot attributes recorded at field site visits for black huckleberry.

Yes/No – Was it a huckleberry patch or not (based on bear sign and expert opinion)?

Description – A general description of the vegetation community, major indicator plants, major bear foods, and why a bear likely used area, if it did.

Biogeoclimatic Ecosystem Classification (BEC) zone, subzone, variant, and site series – Zone, subzone, and variant were based on regional BEC mapping. Site series was based on vegetation composition and site characteristics, regional BEC field guides, and our field experience in 2014 (Meidinger and Pojar (1991)).

Elevation – At the center of the plot and read from a hand-held GPS in meters.

Slope – Percent slope gradient of the plot measured with a clinometer.

Aspect – Orientation of slope in degrees; 999 was recorded for level ground. Aspect was a fixed point measurement from the center of the plot.

Mesoslope position – As per British Columbia Ministries of Forests and Range and Environment (2010), Site Description section, page 25.

Structural stage – As per British Columbia Ministries of Forests and Range and Environment (2010), Site Description section, page 21.

Site disturbance – As per British Columbia Ministries of Forests and Range and Environment (2010), Site Description section, page 27.

Canopy cover – Estimate of the percent tree canopy cover.

Huckleberry fruit abundance – As per British Columbia Ministries of Forests and Range and Environment (2010), Vegetation, page 17.

Huckleberry patch quality – A subjective assessment value between 1 and 10, where 1 was lowest quality and 10 was highest quality.

Huckleberry modal height – Measured height in centimeters.

Huckleberry cover – Estimated percent cover of black huckleberry.

Huckleberry fruit phenology – Recorded as green; reddish hue, not quite ripe; generally ripe; overripe; or finished.

Bear sign - Old or recent bear sign within or in the vicinity of the plot.

Environmental predictors for huckleberry occurrence and patch modeling

We constructed ecologically informed derivations of all the hypothesized drivers for this species and produced spatial surfaces in 30-m resolutions across the study area for each predictor. We removed all areas of rock, ice, human settlement, lakes, and rivers and where we had missing data for any predictor variable. Environmental variables hypothesized to limit the occurrence of huckleberry (Table A2) include soil pH (Barney 1999, Barney et al. 2006), soil texture (Barney et al. 2006), climate (Holden et al. 2012), forest fires (Nielsen and Nielsen 2010), canopy cover (Minore 1984), and topography (Roberts et al. 2014).

We obtained soil data from the British Columbia government. These data are composed of a categorical classification of soil type across the province and approximately 5,000 soil pits used to evaluate and refine these classifications. The soil pits include empirical information on the pH, texture, and composition of soil within each categorical soil type. We used the soil pits dug across the province to produce a spatial representation of the soils across the Kootenay region, including the pH, percent sand, percent silt, percent clay, percent coarse fragments, and percent organic matter of the soil. We used only the top 40 cm of each soil pit to derive soil measures because we did not believe soils deeper than 40 cm would have a large effect on huckleberries, which are generally rooted quite shallow. In some cases, no soil pits were available for specific soil types so we lacked empirical measures for this soil, which we remedied by interpolating information from similar soils across the province. We first classified the province into regions that shared the same biogeoclimatic zone (BEC), soil development type, and geologic parent material. We then calculated the soil characteristics for each region using soil pits from across the province and filled holes in the soil surface of the Kootenays with these data.

We gathered climate variables using the Climate BC desktop application produced by the Centre for Forest Conservation Genetics at the University of British Columbia (http://cfcg.forestry.ubc.ca/projects/climate-data/climatebcwna/#ClimateBC). Climate variables included frost free period, mean annual temperature, mean winter temperature, mean annual precipitation, mean summer precipitation, and mean winter snowfall. We produced a grid of points spaced 300 m apart in ArcMAP 10.1 (Esri) and extracted the climatic information to these points using Climate BC, and then converted this information into a raster surface with a 300-m resolution. Other climate variables included Hargreaves climatic moisture deficit, degree-days below 5°C, mean annual solar radiation, mean coldest month temperature, mean warmest month temperature, precipitation as snow, summer heat-moisture index, maximum temperature – summer, minimum temperature – spring, and temperature minimum – winter (Table A2).

We acquired spatial information on forest fires from the Wildfire Management Branch of British Columbia (data from 1920–2014, https://apps.gov.bc.ca/pub/geometadata/metadataDetail.do?from=search&edit=true&showall=showall&recordSet=ISO19115&recordUID=57060) and used it to calculate time since last fire for each plot, and produce a time since last fire surface. We calculated time since last fire as the date the plot survey was conducted minus the date of the last fire that occurred prior to the survey. For our final map, we built a time since last fire surface across the region using 2015 as the current date and subtracting the date of the most recent fire from 2015. In many cases across the landscape a fire had not occurred (or not been recorded) in the last approximately 90 years, so we opted to bin the time since last fire variable into ecologically meaningful bins. We created 5 bins: 1) 0–20 years since last fire, 2) 20–50 years since last fire, 3) 50–80 years since last fire, 4) >80 years since last fire, and 5) never burned.

We gathered information on canopy cover from the Vegetation Resource Information data from the British Columbia government and filled missing data with cover information from industry partners. We calculated global radiation, compound topographic index (CTI), and aspect slope using a digital elevation model and ArcMap 10.1.

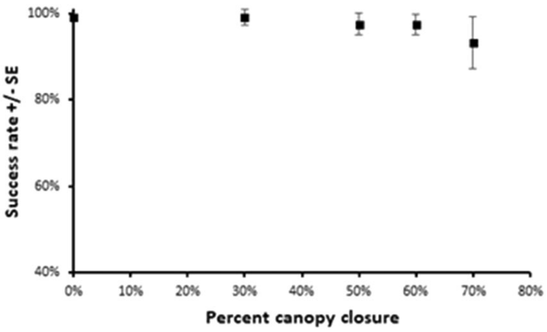

FIGURE A1 Global positioning system radio-collar fix success test in various levels of canopy cover. Result demonstrates that canopy cover did not significantly affect fix success of location data in the southeast British Columbia, Canada, study area (2004–2015).

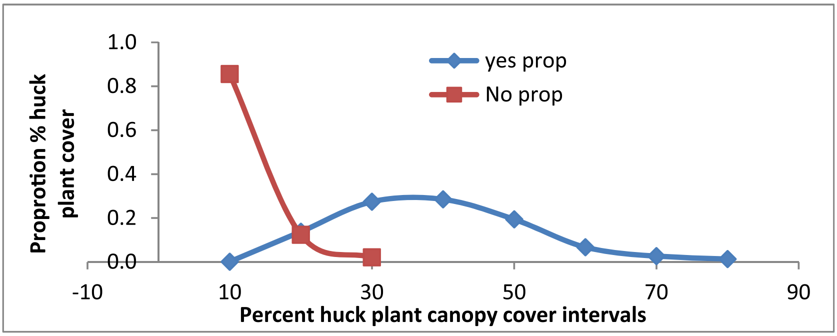

FIGURE A2 Proportion huckleberry (huck) plant cover in visited sites of potential huckleberry patches important for grizzly bears. Visits were between 2014–2015 across our study area in southeast British Columbia, Canada. In years 2017–2018 in areas without global positioning system (GPS) telemetry coverage, we determined sites were huckleberry patches when they had >20% huckleberry plant cover. For the few sites that were used by grizzly bears with huckleberry plant cover <20% (14% of sites determined to be huckleberry patches), we used >10% fruiting plants and <30% forest canopy cover to help discriminate huckleberry patches. This combination of metrics and thresholds allowed us to identify huckleberry patches in areas where we did not have GPS telemetry data.

TABLE A2 Environmental variables used to predict huckleberry occurrence and patches used by grizzly bears in southeast British Columbia, Canada (2004–2013).

Abbreviation	Name
Soil	
cofrag_utm	Coarse fragments in soils
orgcarp	Organic carbon % in soils
ph2	Soil pH, dissolved using water
phca_utm	pH of soils
tcaly_utm	% clay in soils?
tclay	Clay % in soils
tsand	Sand % in soil
Climate	
CMD	Hargreaves climatic moisture deficit (mm)
DD5	Degree-days below 5°C
FFP	Frost free period
MAP	Mean annual precipitation
MAR	Mean annual solar radiation (MJ m-2 d-1)
MAT	Mean annual temperature
MCMT	Mean coldest month temperature (°C)
MSP	Mean annual summer (May–Sep) precipitation (mm)
MWMT	Mean warmest month temperature (°C)
NFFD	Number of frost-free days
PAS	Precipitation as snow
PAS_wt	Precipitation as snow (winter)
PPT_sm	Precipitation in summer
SHM	Summer heat-moisture index
Tave_wt	Average temperature- winter
Tmax_sm	Maximum temperature – summer
Tmin_sp	Minimum temperature – spring
Tmin_wt	Temperature minimum – winter
Fire	
fire_cnt	Number of fires in a region since 1900
Last fire binned	Time since last fire binned into 5 categories
Canopy	
Canopy_cov	Canopy cover
Topography	
cti	Compound topographic index

(Continues)

TABLE A2 (Continued)

Abbreviation	Name
globlrad	Global radiation
slope	Slope
aspect	Aspect

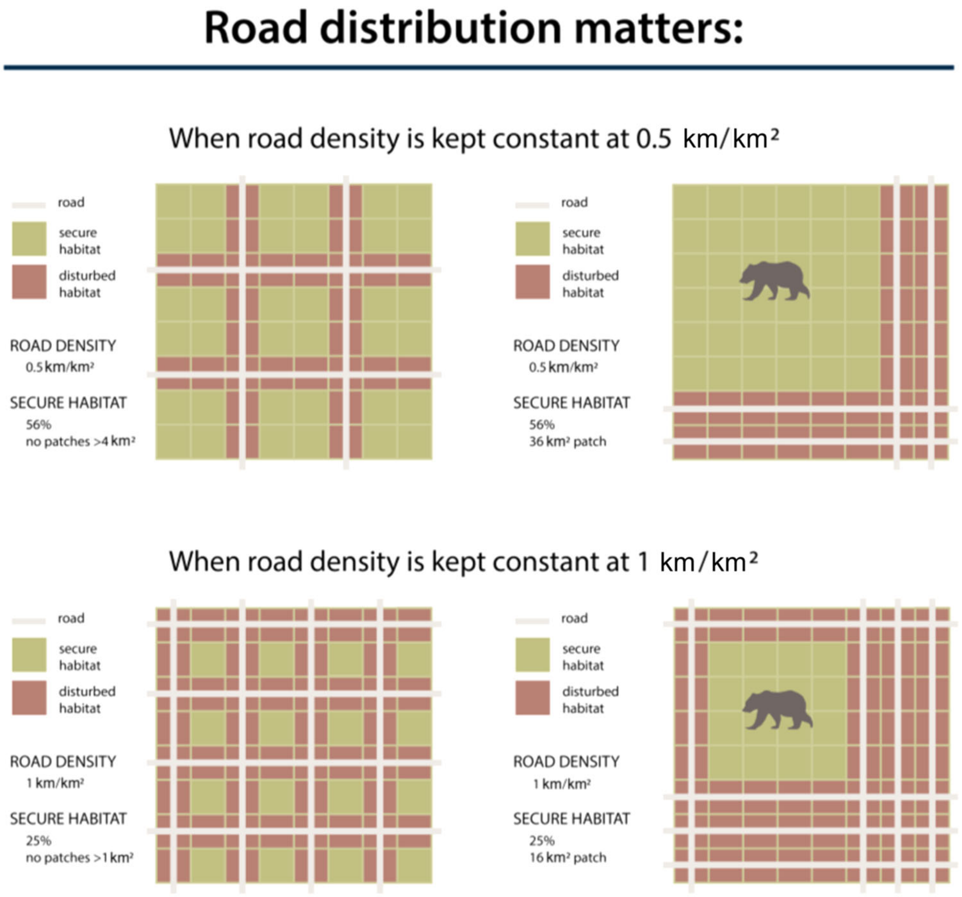

FIGURE A3 Schematic of the relationship between road density and the proportion of secure habitat. Evenly spaced roads across a unit can result in small patches of secure habitat (i.e., areas >500 m from an open road) that require female grizzly bears to cross roads often during a day (panels on left). Managing road distribution to yield larger patches of secure habitat (panels on right), even at similar road densities, should benefit females. Adapted from Proctor et al. (2019).

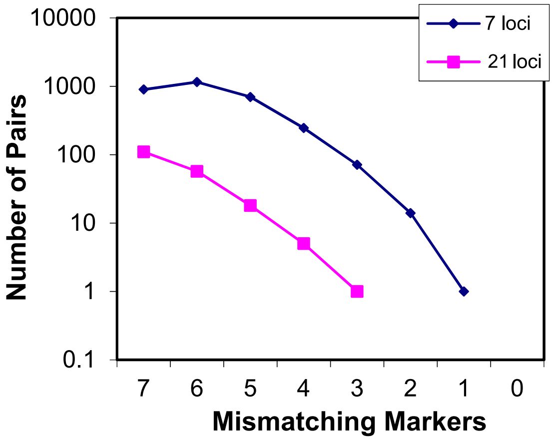

FIGURE A4 Distribution of similar genotypes for mismatching multi-locus grizzly bear genotypes from the Selkirk and Purcell Mountains of southeast British Columbia, Canada (1998–2005).

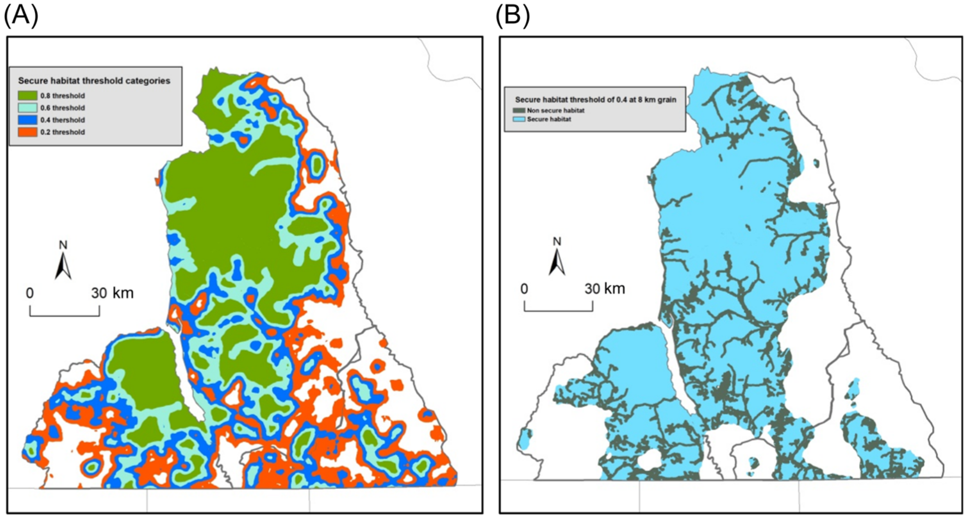

FIGURE A5 A) An example of polygons of various proportions of scaled secure habitat for grizzly bears to a 3-km grain in southeast British Columbia, Canada, 2005. Each color represents a different proportion of secure habitat above a threshold. Polygons are layered on top of each other to show how each one is smaller than the one underneath it such that the full extent of each different colored polygon is obscured by the layer on top of it. For example, the light blue polygon also includes the area within the green polygon. Similarly, the dark blue polygon includes the area included in the light blue and green polygon and so on. B) An example of one of the thresholds shown in panel A; the proportion of secure habitat in the scaled layer at 8-km grain centered on a 0.4 score. This layer was the most supported secure threshold layer in the top female density model. Bears within this polygon have higher fitness and the proportion of secure habitat within this polygon was 73%.

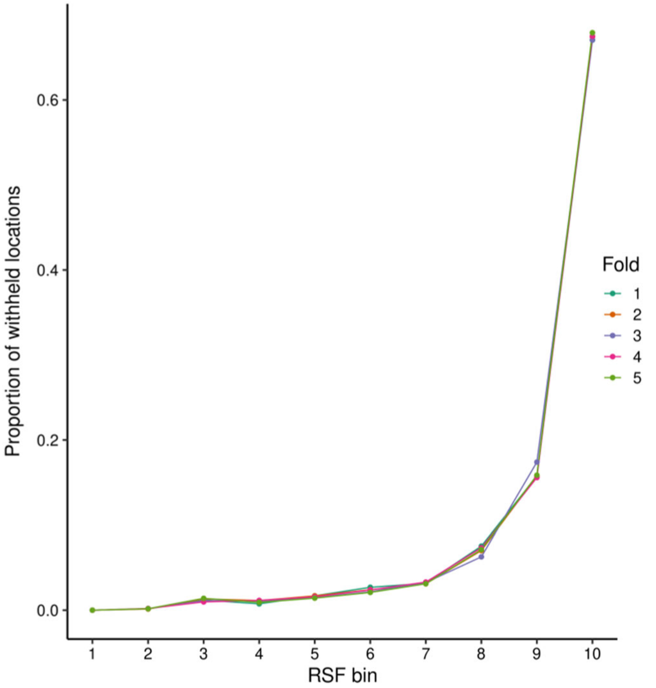

FIGURE A6 Area-adjusted evaluation of the resource selection function (RSF) of female grizzly bear summer habitat selection. Curves for each *k*-fold compare RSF scores in 10 bins from the building dataset (80% of locations) and model evaluation dataset (20% of locations) in southeast British Columbia, Canada (2004–2015). Similarity of curves suggests that the model building dataset predicted the evaluation data well.

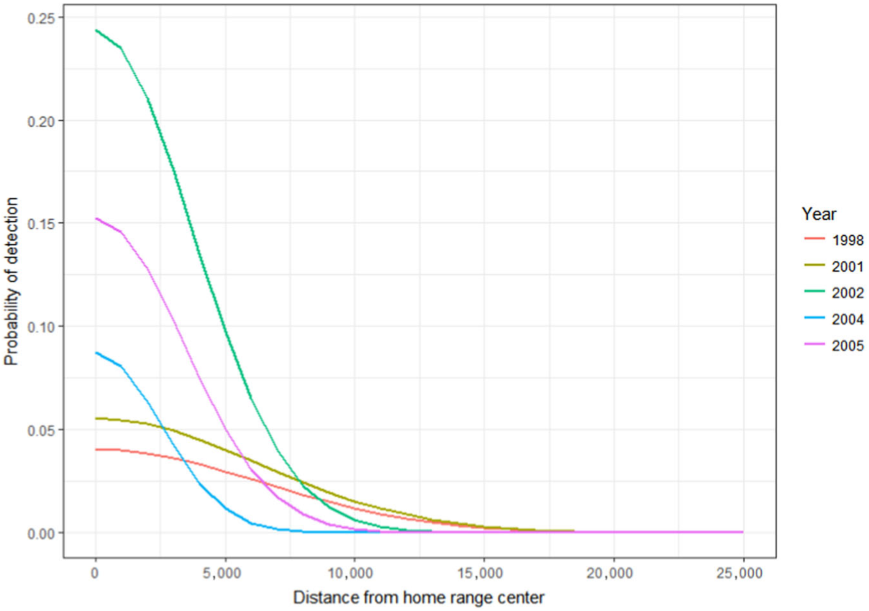

FIGURE A7 Initial detection probabilities in a spatially explicit capture recapture (SECR) analysis for female grizzly bear density as a function of study area-year for bears sampled across the South Selkirk and Purcell Mountains of southeast British Columbia, Canada, 1998–2005.

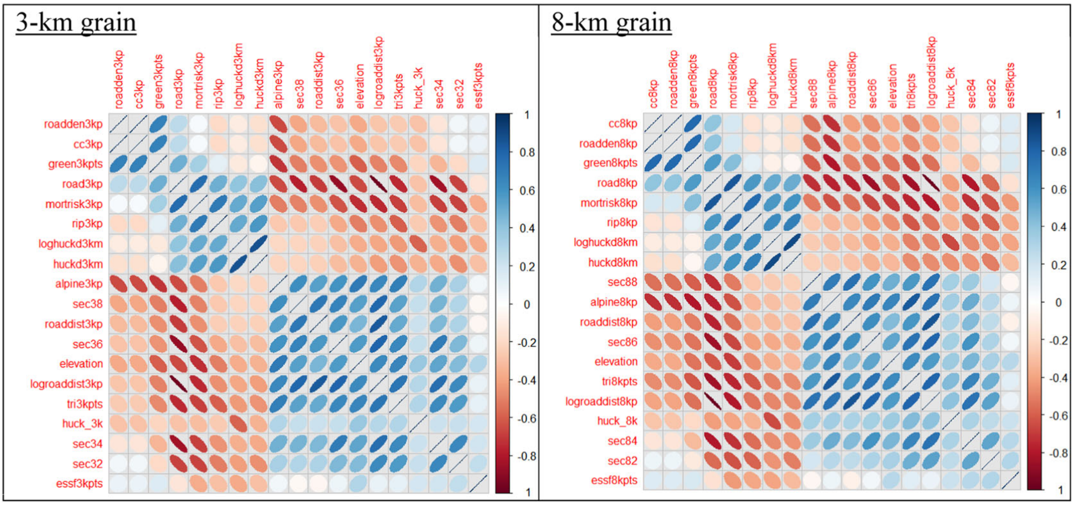

FIGURE A8 Correlation plot of variables grouped by grain summaries in southeast British Columbia, Canada (1998–2005). Variables are grouped in terms of similar correlations. The color and size of an ellipse indexes the strength of correlations. Roadden is road density, cc is canopy cover, green is greenness, road is road presence, mortrisk is mortality risk habitat, rip is riparian, loghuck is the log of the huckleberry patch model, huckd is distance to huckleberry patch, sec is habitat security, roaddist is distance to road, tri is terrain ruggedness, huck is huckleberry patch, and essf is Englemann spruce – sub-alpine fir forest.

RESULT

Density results

TABLE A3 Multi-variable female grizzly bear resource selection function (RSF) models in southeast British Columbia, Canada (2004–2015). We used an 80% random sample for model training, and withheld the remaining 20% of bear locations for model evaluation (Boyce et al. 2002, Nielsen et al. 2002). We used a *k*-fold cross evaluation method (Boyce et al. 2002). Within each fold, we mapped the predictions from models fit to the training data, and binned the predictions into 10 equal-area bins ranked from lowest (bin 1) to highest (bin 10). We then tallied the number of used locations in the withheld test dataset that fell within each bin (Morris et al. 2016). All 5 *k*-fold models were similar, with only minor variations in variable coefficients. Coefficients were standardized to occur between 0 and 1.

					95% confidence interval	
Model	Coefficient	Robust SE	Statistic	Robust probability	Lower	Upper
k = 1						
Distance to huckleberry	−0.548	0.180	−3.053	0.002	−0.901	−0.196
Greenness	0.224	0.034	6.688	<0.001	0.159	0.290
Alpine	0.461	0.063	7.365	<0.001	0.339	0.584
Solar	0.111	0.040	2.779	0.005	0.033	0.189
Secure habitat	0.274	0.100	2.733	0.006	0.077	0.470
k = 2						
Distance to huckleberry	−0.551	0.177	−3.114	0.002	−0.898	−0.204
Greenness	0.218	0.038	5.743	<0.001	0.144	0.292

(Continues)

TABLE A3 (Continued)

Model	Coefficient	Robust SE	Statistic	Robust probability	95% confidence interval	
					Lower	Upper
Alpine	0.449	0.056	7.975	<0.001	0.339	0.559
Solar	0.116	0.040	2.939	0.003	0.039	0.194
Secure habitat	0.262	0.093	2.799	0.005	0.078	0.445
$k = 3$						
Distance to huckleberry	−0.545	0.179	−3.047	0.002	−0.895	−0.194
Greenness	0.209	0.036	5.733	<0.001	0.137	0.280
Alpine	0.447	0.057	7.824	<0.001	0.335	0.559
Solar	0.115	0.041	2.815	0.005	0.035	0.195
Secure habitat	0.267	0.092	2.910	0.004	0.087	0.447
$k = 4$						
Distance to huckleberry	−0.538	0.185	−2.902	0.004	−0.902	−0.175
Greenness	0.217	0.035	6.179	<0.001	0.148	0.286
Alpine	0.471	0.058	8.142	<0.001	0.358	0.585
Solar	0.118	0.038	3.114	0.002	0.044	0.192
Secure habitat	0.250	0.096	2.594	0.009	0.061	0.438
$k = 5$						
Distance to huckleberry	−0.550	0.179	−3.074	0.002	−0.900	−0.199
Greenness	0.221	0.036	6.081	<0.001	0.150	0.293
Alpine	0.470	0.062	7.626	<0.001	0.349	0.591
Solar	0.116	0.037	3.157	0.002	0.044	0.189
Secure habitat	0.257	0.095	2.696	0.007	0.070	0.444

TABLE A4 Female grizzly bear density response in our top model from huckleberry patches in secure and non-secure habitat. We applied the huckleberry coefficients from our top model to predict bear density in secure and non-secure habitats. Data were collected in southeastern British Columbia, Canada, 2004–2013.

Secure habitat (79%) 8 km	Huckleberry 3 km	Coefficient	exp(coeff)	Bear density exp(coeff) × 100,000
0	0	−12.62	0.000003	0.331
0	0.05	−12.26	0.000005	0.476
0	0.1	−11.89	0.000007	0.685
0	0.15	−11.53	0.00001	0.986
0	0.2	−11.16	0.000014	1.419

TABLE A4 (Continued)

Secure habitat (79%) 8 km	Huckleberry 3 km	Coefficient	exp(coeff)	Bear density exp(coeff) × 100,000
0	0.25	−10.8	0.00002	2.042
0	0.3	−10.43	0.000029	2.939
0	0.35	−10.07	0.000042	4.231
0	0.4	−9.71	0.000061	6.090
1	0	−9.48	0.000077	7.673
1	0.05	−9.11	0.00011	11.044
1	0.1	−8.75	0.000159	15.897
1	0.15	−8.38	0.000229	22.881
1	0.2	−8.02	0.000329	32.935
1	0.25	−7.65	0.000474	47.406
1	0.3	−7.29	0.000682	68.234
1	0.35	−6.93	0.000982	98.215
1	0.4	−6.56	0.001414	141.368

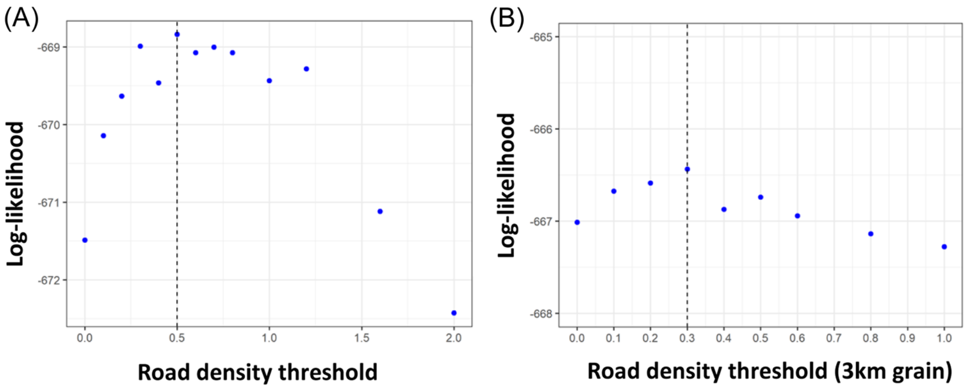

FIGURE A9 A) Log-likelihood scores of road density threshold models from a base (huckleberry 3 km + road density threshold) female grizzly bear density model in southeastern British Columbia, Canada (1998–2005) and B) log-likelihood scores of secure habitat and secure area threshold models from a base (huckleberry patches 3 km + secure habitat 8 km) model.