ROCKY MOUNTAIN CARNIVORE PROJECT

FINAL REPORT

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EXECUTIVE SUMMARY

World Wildlife Fund's Carnivore Conservation Strategy is founded on ecological science and emphasizes partnerships with government and the private sector for the purpose of achieving carnivore conservation goals. In 1997 WWF Canada contracted with us to strengthen the scientific foundation for carnivore conservation in the Rocky Mountains. The goal of this project was to develop the biological information necessary to conserve a broad suite of carnivore species over the long term. We sought to synthesize available knowledge into a series of predictive habitat and population models, which would allow us to map the relative suitability of areas for carnivores across the region, forecast how populations might respond to alternative future scenarios, and make recommendations for protection and management of specific areas to conserve carnivore species.

In the past, proposals for regional reserve designs and specific conservation areas generally made little use of spatially-explicit models and instead relied on expert opinion. Using both static habitat suitability models and dynamic population models, we evaluated potential core areas, buffer zones, and corridors for carnivores more rigorously than with conventional approaches, and with a broad consideration of landscape context. We examined the connection between habitat and population viability for a group of carnivore species across a large portion of the Rocky Mountain region from the Yukon/British Columbia border to the Greater Yellowstone Ecosystem and central Idaho (Fig. E1). Our objective was to develop scientifically-defensible regional-scale land management proposals as well as general guidelines for carnivore conservation and reserve design.

In Phase I of this project, completed in December 1999, we developed static habitat suitability models for ten carnivore species: wolf, coyote, grizzly bear, black bear, cougar, lynx,

bobcat, wolverine, fisher, and marten. The study region for Phase I extended from Jasper National Park to Yellowstone National Park, but difficulties obtaining data left some gaps, especially in the northern edge of the region. In the work reported here (Phase II), we extended the study region over 60 km eastward and northward to the Yukon border. We developed dynamic, individual-based population viability analyses, using a program called PATCH, for five of the focal species (all but the coyote, cougar, bobcat, black bear, and marten). We also used a site-selection algorithm, SITES, to select a subset of the study region that would most efficiently (i.e., in the least area) capture the best habitat for all six species. The SITES model goes through millions of iterations in an attempt to find the lowest-cost solution to the problem of identifying the best habitat areas for carnivores.

As expected, the wild northern portion of the study region generally shows higher habitat quality for carnivores than areas further south. Because our goals included maintaining well-distributed and connected populations across the region, we had to compensate for the fact that SITES selected intact priority areas chiefly in northern B.C. and fewer and more fragmented areas in the south. We did this by setting both regional and subregional goals for the SITES model, such that a certain percentage of high-quality carnivore habitat was selected across the region, but also a minimum amount of high-quality habitat was selected within each subregion. Identification of planning units that were selected in a number of runs of the SITES model, though not necessarily appearing in the "best" (i.e., lowest-cost) solution, provides flexibility to decision making and illuminates potential habitat linkages among core areas. In several cases we also identified restoration actions required for areas to contribute effectively to conservation goals. The overall design developed from the SITES model shows high-priority conservation areas and surrounding areas that may serve as buffer zones or linkages (Fig. E2).

We used the PATCH population viability model to build on the static models of habitat suitability developed in Phase I of this study. PATCH links carnivore survival and fecundity to GIS data on mortality risk and habitat productivity, then tracks populations through time as individuals are born, disperse, and die. The PATCH model allowed us to discriminate potential population source areas, where reproduction is expected to exceed mortality in an average year, from sink areas, where mortality is predicted to exceed reproduction. We found PATCH very useful for predicting the effects of landscape changes, such as degradation by development or restoration by road closures, on the viability of carnivore species. We assessed the effects of restoring corridors, for example in the Crowsnest Pass area, and found complex responses that varied with species. For example, the corridor became more valuable with time for grizzly bear but not necessarily for other species.

Our dynamic model predictions were highly correlated with independently-collected validation data from grizzly bear DNA-based surveys in three regions of B.C., lending confidence to conservation strategies built from these models. As expected, results from independent studies of carnivores in our study region conform best to our model predictions at a regional scale, but not as well at a local scale, where higher-resolution data on habitat conditions would improve predictability. Also, our models for the large carnivores species generally proved to have greater prediction accuracy than models for mesocarnivores such as lynx.

The PATCH model also allowed us to assess the vulnerability of potential core, buffer, and linkage areas to degradation, expressed in terms of reductions in expected population growth rates of carnivore species over the next 25 years as development proceeds. An average of about

15% regional decline in carrying capacity for carnivores was predicted within this time period if no additions to protected areas occur (Fig E3 a,b,c). In contrast, increasing the proportion of reserves in the region from the current 17.2% to 36.4% would result in a 1-4% increase over current carrying capacity. As protected area increases, the potential future carrying capacity increases (Fig. E4). The PATCH results highlighted as critically important several areas in northern B.C., for example between the Muskwa-Kechika area and Jasper National Park, as well as better-known areas such as the Crown of the Continent, and identified several potential linkage areas that were not chosen by the SITES model but whose protection would promote population viability (Fig. E2). Moreover, PATCH identified areas that are likely to have both high value as source habitat and a high level of threat if current trends continue (Fig. E5).

An important question in conservation planning is whether areas selected to serve one set of goals, such as conserving carnivores, will also serve other goals, such as capturing locations of rare species or representing a broad range of habitat types in the region of interest. We compared the priority areas selected by SITES for carnivores with those selected for other conservation targets (i.e., ecosystem representation and protection of rare species and other special elements). For this task, we coordinated our work with that of The Nature Conservancy and Nature Conservancy of Canada's Canadian Rockies ecoregional planning team, whose study region encompasses the central portion of our study area. A SITES design based on non-carnivore conservation goals coincidentally captured a large amount of carnivore habitat, but missed some critical areas for carnivore viability, for example north-central Idaho and between Wells Gray and Jasper Parks in British Columbia and Alberta (Fig. E6). On the other hand, areas selected to capture the best 35% of habitat for carnivores across the region met representation goals for 76%

of ecosystem types but failed to protect many of the documented and localized occurrences of rare species (for example, only 19% of non-vascular plants and 26% of vascular plants). Although a suite of carnivores provides much better coverage than any single carnivore species, carnivores are an imperfect umbrella for biodiversity. However, in regions such as the Rocky Mountains, where intensive biodiversity surveys have not been conducted but where relatively few endemic species exist, the focal species approach is particularly useful to define conservation priorities.

The tools we develop and apply here may be new and unfamiliar to many planners. As with the results of any complex model, they must be subject to sensitivity analysis, and should be seen as map-based hypotheses to be used and tested in adaptive management context. Nevertheless, our modeling results will help conservation planners identify areas of the Rocky Mountains that are irreplaceable with respect to carnivore conservation—that is, those areas that must be protected if conservation goals are to be attained. The combination of data on the irreplaceability and vulnerability of areas will allow planners to develop a scientifically rigorous and defensible strategy linking immediate conservation needs with longer-term goals.

In summary, our conclusions and recommendations from this study for conserving viable populations of native carnivores in the Rocky Mountains are these:

- Both static and dynamic models provided useful information for carnivore conservation, and management implications from the two types of model were similar. In addition, comparison of model predictions with new survey data suggests that both models were quite robust for large carnivores, but somewhat less so for mesocarnivores.
- Nevertheless, dynamic, spatially explicit population models (e.g., PATCH) provide many advantages over static models, particularly with respect to insights regarding population

processes such as source-sink dynamics and the effects of landscape context and alternative future scenarios on population viability. Reserve designs based on static models alone may be poor at conserving species that are more vulnerable than expected due to unique aspects of their demography or social structure (e.g., the wolf, with its large pack territories).

- Carnivores are excellent focal species for regional-scale conservation planning. They are particularly useful in regions where the potential for maintaining or restoring large core areas and broad-scale connectivity is high.
- The umbrella function of carnivores (i.e., where protection of adequate habitat area for carnivore species incidentally protects many other species or ecosystems) is fairly high but incomplete. Coverage of localized rare species or communities is poor. Hence, carnivores may be superior umbrella species in regions, such as the northern Rocky Mountains, with relatively low endemism and habitat heterogeneity.
- A suite of carnivore species provides a better umbrella function than any single species, because the range of habitats covered is greater.
- A contrast in habitat associations exists between carnivore species that use rugged terrain (grizzly bear and wolverine) vs. those that avoid such areas (wolf), and between forest species that are relatively tolerant of human activities (lynx, fisher, black bear) vs. habitat generalists that are less tolerant of human activity (grizzly bear, wolverine, wolf).
- Private lands are less valuable for most carnivore species than their proportion in the region would suggest, but have disproportionately high value for wolf, fisher, and black bear. Hence, current protected areas, which are concentrated in the most rugged portions

of the study region (e.g., the central Canadian Rockies), should be augmented by new protected areas in regions of lower topographic relief and higher biological productivity.

- Continuation of recent trends in development on both private and public lands will lead to the loss and fragmentation of carnivore habitat over the next several decades, making some local populations of carnivores more vulnerable to extinction.
- Given no change in the amount or configuration of protected area in the region, populations of most carnivore species can be expected to decline over time as habitat surrounding reserves becomes less suitable and as populations within reserves become more isolated. Substantial conservation commitments will be needed to prevent the northward retreat of carnivore populations in the region and sustain small transboundary populations.
- Thresholds are apparent in the effect of increased habitat protection on population viability, with increasing network size having the greatest effect on population viability up to approximately 37% of the study region.
- Tradeoffs must be addressed between allocating scarce conservation resources toward protecting strong population source areas, stemming the degradation of lands surrounding reserves, or restoring linkages that are already degraded to some degree, but which might contribute to long-term persistence of metapopulations.
- A useful way to resolve tradeoffs and prioritize conservation actions is to plot the irreplaceability of sites (i.e., the relative extent to which they contribute to conservation goals) vs. their vulnerability (i.e., their risk of being degraded in the near future). In the context of species conservation, irreplaceability can be approximated as the predicted rate

of population growth (i.e., the value of a site as source habitat), and vulnerability can be measured by the predicted decline in growth rate over a defined period of time, given particular trends in habitat conditions.

- Probably the two highest-priority areas for habitat conservation to enhance populations of carnivores in the study region are 1) the area between the Muskwa Kechika conservation areas and Jasper National Park in northern British Columbia and Alberta, and 2) north-central Idaho. Both of these regions combine high biological productivity and relatively low human influence, yet both are threatened by ongoing development and resource extraction. New protected areas and linkages are needed to connect the Muskwa-Kechika area to Jasper National Park and to connect protected areas in central Idaho northeastward to the Northern Continental Divide Ecosystem and eastward to the Greater Yellowstone Ecosystem.
- A third priority area for conservation is the transboundary region, from the Northern Continental Divide Ecosystem (e.g., the North Fork of the Flathead River, adjacent to Waterton Lakes and Glacier National Parks) north across Hwy. 3 (in the vicinity of Crowsnest Pass) to Banff National Park. This area is already a strong filter, if not absolute barrier, to several carnivore species, and will significantly isolate carnivore populations to the north and south unless conservation actions are implemented quickly. Our results suggest that adding reserves in the transboundary region would prevent the loss of connectivity between the Northern Continental Divide Ecosystem and the Canadian Rocky Mountain parks and sustain smaller grizzly bear populations in southeastern British Columbia and the northern U.S.

- The level of uncertainty that propagates through the models used in this study suggests that they are most informative for identifying generalized areas of conservation emphasis rather than exact reserve or management boundaries. Hence, our study provides a regional-scale picture of conservation priorities, which must be supplemented by site-level analysis and planning.

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INTRODUCTION

In 1995 World Wildlife Fund (Canada and United States) published a report, "Large carnivore conservation in the Rocky Mountains: A long-term strategy for maintaining free-ranging and self-sustaining populations of carnivores." Authored by Dr. Paul Paquet, a leading carnivore researcher in Canada, and Arlin Hackman, then director of the Endangered Spaces Campaign and now Vice President of WWF Canada, the report presented the backbone of a plan to ensure the survival of native carnivore species in the Rocky Mountains from northeastern British Columbia south to central Idaho and western Wyoming. At the core of WWF's Carnivore Conservation Strategy is a foundation in ecological science and a reliance on partnerships with government and the private sector for the purpose of achieving carnivore conservation goals. It was recognized in the report that the existing network of protected areas in the Rockies must be rigorously evaluated and expanded, along with surrounding compatible-use zones and linkages, to improve the prospects for carnivore viability. The report concluded that "improved basic knowledge of each species and its habitat needs will be a prerequisite to identifying these habitat areas and creating successful management strategies."

In 1997 WWF Canada contracted with the three of us to strengthen the scientific foundation for carnivore conservation in the Rocky Mountains. The goal of this project was to develop the biological information necessary to conserve a broad suite of carnivore species and to contribute to World Wildlife Fund's Carnivore Conservation Strategy. Recognizing that considerable research on the habitat requirements of carnivores and their sensitivities to human impacts has been conducted in the region, and continues at a rapid pace, we sought to synthesize available knowledge into a series of predictive habitat and population models. These models would allow us to map the relative suitability of areas for carnivores across the region and to forecast how populations might respond to alternative future scenarios.

APPROACH

Conservation resources are usually too scarce to allow us to evaluate in detail the conservation needs of the majority of species in an ecosystem. Therefore, the last decade has seen a shift from species-based to ecosystem-based conservation planning. Focal species analysis, however, can add an important component to ecosystem-level plans. Mammalian carnivores are often proposed as potential focal species because, due to their low population density and dispersal requirements, their populations may respond most rapidly to the landscape fragmentation expected eventually to affect a larger suite of species.

Most existing modeling approaches for carnivores in the Rocky Mountains have evolved out of a single-species or site-level planning paradigm. Moreover, suggestions for regional reserve designs and specific conservation areas often made little use of spatially-explicit models and instead relied on expert opinion and verbal models. In this study, we used both static habitat models and dynamic population models to evaluate potential core areas, buffer zones, and corridors for carnivores more rigorously than with conventional approaches, and with a broad consideration of landscape context. We examined the connection between habitat conditions and population viability for a group of carnivore species across a large portion of the Rocky Mountain region from the Yukon/British Columbia border to the Greater Yellowstone Ecosystem and central Idaho (Figure 1). Our objective was to develop scientifically-defensible regional-scale land management proposals as well as more general guidelines for carnivore conservation and reserve design.

In Phase I of this project, initiated in October 1997 and completed in December 1999, we developed static habitat suitability models for ten carnivore species: wolf, coyote, grizzly bear, black bear, cougar, lynx, bobcat, wolverine, fisher, and marten. The study region for Phase I extended from Jasper National Park to Yellowstone National Park, but difficulties obtaining data left some gaps, especially in the northern edge of the region. In the work reported here (Phase II), initiated in February 2000, we extended the study region over 60 km eastward and northward to the Yukon border. We developed dynamic, individual-based population viability analyses, using a program called PATCH, for five of the focal species (all but the coyote, cougar, bobcat, black bear, and marten). We also used a site-selection algorithm (SITES) developed by The Nature Conservancy to select a subset of the study region that would most efficiently (i.e., in the least area) capture the best habitat for all six species.

ASSESSING THE EFFECTS OF LANDSCAPE CHANGE

The habitat suitability models that we developed in Phase I of the Rocky Mountain Carnivore (RMC) project (Carroll et al. 2000) are examples of static models, which combine data on different components of habitat quality in a geographic information system (GIS) to provide a snapshot of habitat quality and potential population distribution. In contrast, dynamic models such as PATCH (Schumaker 1998) combine information on habitat characteristics with demographic data to evaluate area and connectivity factors that influence the probability that a patch of suitable habitat will remain occupied by a species over time. Because linking spatial data on the distribution of habitat resources to a species' demographic processes is difficult, most population viability analyses (PVA) provide a composite evaluation of viability across a region. However, PVA predictions linked to specific land-management options can provide a powerful tool for conservation planners. We used the PATCH model to assess what conservation actions could best assure the maintenance of landscape connectivity and the viability of carnivore populations over long-term time frames of one hundred years or more.

FROM SINGLE-SPECIES TO MULTI-SPECIES CONSERVATION

Early conservation assessments and reserve designs used manual mapping to delineate sites and simple scoring procedures to compare and rank sites. The larger number of conservation targets in this study demanded the use of a more systematic and efficient site selection procedure. We used the SITES software (Andelman et al. 1999) to select a subset of the regional landscape that would most efficiently capture the best areas for all conservation targets. SITES considers millions of possible alternatives to find solutions to a set of quantitative goals and develops a portfolio of sites that fulfills the selected goals as efficiently as possible. An efficient reserve design meets conservation objectives with a minimal investment of area by building a portfolio from complementary sites. A design is complementary when new conservation actions complement, rather than duplicate, prior actions. For example, if the first reserve selected by the algorithm protects high-quality habitat for fisher, lynx, and black bear, the next reserve selected might protect high-quality habitat for grizzly bear, wolverine, and wolf.

PLACING CARNIVORE CONSERVATION WITHIN A LARGER CONTEXT

Our research, which emphasizes the use of particular focal species in developing a regional conservation plan (Carroll et al. 2001a), complements two other major tracks of conservation planning; special elements and ecosystem representation. The special elements approach concentrates on occurrences of imperiled species, plant communities, and other rare natural features, as are found in Natural Heritage program (conservation data center) databases (Groves et al. 2000). The representation approach seeks to represent examples of all geoclimatic or vegetation types in protected areas. We compared, for the central portion of our study region (Figure 2), conservation portfolios designed around the needs of carnivore focal species with those developed from data on special elements and representation conservation targets to assess how a regional conservation plan can best integrate carnivore conservation goals with protection of other aspects of biodiversity. This comparison allows us to address, in part, how well carnivores serve as "umbrella species" for other species and communities. This work is presented in the Appendix.

The tools we develop and apply here may be new and unfamiliar to many planners. As with the results of any complex model, they must be subject to sensitivity analysis, and should be seen as map-based hypotheses to be used and tested in adaptive management context (Murphy and Noon 1992). We believe that in this context they can help make regional conservation planning for carnivores in the Rocky Mountain region more efficient and biologically-realistic, and ultimately more successful.

METHODS

STATIC MODELS

In Phase I of the Rocky Mountain Carnivore (RMC) project we developed habitat models for ten carnivore species - grizzly bear (*Ursus arctos*), black bear (*Ursus americanus*), gray wolf (*Canis lupus*), coyote (*Canis latrans*), mountain lion (*Puma concolor*), bobcat (*Lynx rufus*), lynx (*Lynx canadensis*), wolverine (*Gulo gulo*), fisher (*Martes pennanti*), and American marten (*Martes americana*). In Phase II, we extended these models to the east and north to encompass an enlarged study area stretching from the B.C./Yukon border to the Greater Yellowstone Ecosystem (Figure 1). Exceptions were made for two species, the bobcat and coyote. The coyote is a uniquely resilient habitat generalist, and in this region likely does not merit the same level of conservation concern as do the other carnivore species. The bobcat's range does not extend into the northern sections of the study region. Although its habitat needs were treated in the Phase I study, they contrasted strongly with the habitat associations of the other carnivores (Carroll et al. 2000). Therefore addressing their habitat needs separately for those portions of the region where their viability is of concern is probably most efficient.

Of the remaining eight species, habitat models for six species - grizzly bear, black bear , wolf, lynx, wolverine, and fisher - were of a much higher level of accuracy and rigor due to availability of better data on species distribution for use in model development and validation. Conceptual models for mountain lion and marten were also available. The four conceptual models - for grizzly bear, wolf, mountain lion, and marten - were identical in structure to those described in Phase I (Carroll et al. 2000)(Table 1). The empirical models for fisher, lynx, and wolverine, while similar to those described in Carroll et al. (2000), differed in the source of the satellite imagery used. Whereas in Phase I we relied on Landsat Thematic Mapper imagery, in Phase II we derived similar metrics from MODIS imagery. MODIS imagery, which was not yet available during the Phase I study, is more appropriate for regional-scale modeling because seamless coverage is available for any date throughout the year (Huete et al. 1997). We recomputed the regression models for fisher, lynx, and wolverine using the MODIS data. We also took advantage of new survey data for black bear (described below) to create an empirical model for that species.

DYNAMIC MODELS

After developing the static models, we performed population viability analyses using the program PATCH (Schumaker 1998). PATCH is a spatially-explicit population model that links the survival and fecundity of individual animals to the GIS data on mortality risk and habitat productivity measured at the location of the individual or pack territory. The model tracks the demographics of the population through time as individuals are born, disperse and die, predicting population size, time to extinction, and migration and recolonization rates. PATCH allows modeling of environmental stochasticity - that is, the year-to-year variation in vital rates - that can strongly affect species viability. The PATCH simulation results we report here are equilibrium predictions, in that “current” predictions depict the current capacity for an area to support a carnivore species over the long-term (200 years), which may be lower (e.g., grizzly bears in southeastern B.C.) or higher (grizzly bears in central Idaho) than the number of animals currently inhabiting an area. Although PATCH can be used to predict transient population dynamics, such as how many years it will take for currently resident animals to be extirpated, those predictions are generally less accurate.

The model also allows the landscape to change through time. This permits the user to quantify the consequences of landscape change for population viability, examine changes in vital rates and occupancy patterns that might result from habitat loss or fragmentation, and identify source and sink habitats (Pulliam 1988) within a landscape. The landscape change scenarios used here estimated potential change in human-associated impact factors (e.g., roads and human population) by proportionately increasing road density (except within protected areas) and increasing human population based on current trends derived from a time series of human census data. Census data were available for the period 1990-2000 (U.S.) or 1990-1996 (Canada). We predicted human population growth from 2000 to 2025 based on growth rates from 1990 to 1996/2000, but adjusted the predicted 2025 population to match state- and subprovince-level predictions based on more complex socioeconomic models. Road density was predicted to grow at 1% per year. The one study we area aware of that documents change in road density in a similar Rocky Mountain landscape in Colorado (Theobald et al. 1996) found increases of about 2% per year.

Lynx population dynamics in boreal habitats have been closely linked to cyclic change in habitat quality as it relates to snowshoe hare density and other factors such as climate (Mowat et al. 2000). We incorporated several cyclic habitat change scenarios into the lynx model by scaling the static-model-based habitat quality values to lynx demographic performance at different points in the cycle. Similarly, we evaluated the response of fisher populations to differing levels of mortality risk (e.g., trapping intensity) to evaluate how the area and isolation of habitat patches affected their ability to sustain viable populations. In all, we developed dynamic models for the five species - grizzly bear, wolf, wolverine, lynx, and fisher - for which we possessed reasonably accurate habitat models and demography data.

IRREPLACEABILITY AND VULNERABILITY ANALYSIS

A key concept in conservation planning is irreplaceability (Pressey et al. 1993, Margules and Pressey 2000, Pressey and Cowling 2001). Irreplaceability provides a quantitative measure of the relative contribution different areas make to reaching conservation goals, thus helping planners choose among alternative sites in a portfolio. As noted by Pressey (1998), irreplaceability can be defined in two ways: 1) the likelihood that a particular area is needed to achieve an explicit conservation goal; or 2) the extent to which the options for achieving and explicit conservation goal are narrowed if an area is not conserved.

Another key consideration in conservation planning is threat or vulnerability (Margules and Pressey 2000). An approach that sets priority areas for conservation action based on both their irreplaceability and vulnerability is practical in that it acknowledges that a completed reserve network will not be achieved immediately. Therefore, we must minimize the loss to conservation during an interim period where new reserves are being achieved in some areas while habitat loss is occurring elsewhere (Pressey and Taffs 2001). We define irreplaceability in this context as the relative value of an area as source habitat (lambda, or population growth rate, from the PATCH model). Vulnerability is measured here as the predicted decline in demographic value (lambda) over the next 25 years. Values were plotted on a graph of irreplaceability (y-axis) versus vulnerability (x-axis) and the graph divided into four quadrants, following the procedure of Margules and Pressey (2000). The upper right quadrant, which includes areas with high irreplaceability and high vulnerability, comprises the highest priority sites for conservation. This top tier is followed by the upper left and lower right quadrants, not necessarily in that order. The upper left quadrant holds areas that are important but relatively secure source habitat. Areas in the lower right quadrant might include sink habitat the protection of which would greatly enhance population viability by reducing mortality rates of animals dispersing from adjacent high-quality habitat. Finally, the lower left quadrant comprises areas that are relatively replaceable (low source value) and face less severe threats.

GAP ANALYSIS

To assess the contributions of various land management categories to carnivore conservation in the region, we overlaid data on management and ownership on predictions from the static and dynamic models. Whereas the static model comparisons allow us to compare gap analysis results for a large suite of species, the dynamic model gap analysis allows us to assess how the role of the different land management categories will change given current development trends.

MODEL VALIDATION

A primary weakness of most habitat suitability models is that they are rarely subject to rigorous validation, that is, comparison with new field data to assess how well they actually predict species distribution and abundance. When they are tested, many regional-scale habitat models tend to overpredict species occurrence (Bolger et al. 1997). One barrier to validating regional-scale models is the difficulty in gathering species occurrence data over such a broad area. While the RMC project did not have the resources to conduct field surveys of carnivore habitat use at this scale, we were able to collaborate with other researchers and make use of field data they had collected through broad-scale surveys involving snow tracking, radio telemetry, and DNA analysis of hair collected at bait stations (Gibeau 2000, Mowat and Strobeck 2000, Mowat and Paetkau 2001, Mowat and Stanley 2001, Poole et al. 2001, D. Smith, unpublished data) (Figure 1). We are grateful to Garth Mowat and colleagues of Aurora Wildlife Research, Mike Gibeau of the Eastern Slopes Grizzly Bear Project (ESGBP), and Douglas Smith of Yellowstone National Park for allowing the use of their data for model validation.

Carnivores are notoriously difficult to census or survey because they exist at low densities, often inhabit forest ecosystems, and avoid humans. DNA hair snag surveys and similar methods are among the first tools that allow accurate estimates of carnivore distribution and abundance at broad scales. However, even though the area of a DNA hair snag survey (e.g., the 8500 km^2 Prophet River study area) is much larger than most telemetry study areas, it is still small compared with the extent of our analysis area (750,000 km^2). Therefore any comparison of the predictions of our regional-scale models with validation data must be qualified by the fact that factors that are not incorporated into our models may become important at the scale of a single smaller study area. Our regional-scale models may be strongest at predicting differences in habitat quality between several widely-separated small study areas. We are fortunate to have several grizzly DNA survey data sets with the same survey protocol, which allows us to make these larger-scale comparisons. We compared validation data with predictions from both the static habitat suitability models (Carroll et al. 2000) and the dynamic viability models (the PATCH model [Schumaker 1998]).

GRIZZLY BEAR - BRITISH COLUMBIA HAIR SNARE DATA

Our static and dynamic model predictions were compared with independently-collected validation data from DNA-based grizzly bear surveys in 3 regions of B.C. (Mowat and Strobeck 2000, Poole et al. 2001). The survey design first divides the study area into square cells of eight to nine kilometers on a side, to approximate a small home range of a female grizzly bear in the region. Three or more bait stations are placed within each cell. Bears attracted to the bait leave hairs on barbed wire surrounding the bait. The DNA within these hairs is then analyzed to determine the animal's species, sex and individual identity (Mowat and Strobeck 2000). Only the species identification data was used in this validation.

GRIZZLY BEAR - ESGBP TELEMETRY DATA

We also compared regional-scale model predictions with telemetry data from a long-term study of grizzly bears in Banff National Park and adjacent areas. To avoid bias towards easily-accessible areas, we used only the telemetry locations gathered by air. Locations from all seasons were compared with random points from within either a 95% adaptive kernel (ADK) boundary or a minimum convex polygon (MCP) built from the telemetry points. The MCP boundary causes the comparison set to include much more area outside the parks (Figure 1).

WOLF - YELLOWSTONE TELEMETRY DATA

We compared the static wolf habitat suitability model predictions and the PATCH model predicted occupancy rates with wolf distribution in the Greater Yellowstone Ecosystem (D. Smith, unpublished data). Habitat within pack territory boundaries (as determined by the minimum convex polygon method, 2000 data) was compared to habitat in the GYE but outside current pack territories. This comparison may be conservative in that wolves, which were reintroduced to the GYE in 1995, may not yet have occupied all suitable habitat there.

BLACK BEAR - BRITISH COLUMBIA HAIR SNARE DATA

The conceptual model of black bear habitat suitability was developed in RMC Project Phase I by combining values for tasseled-cap greenness, predicted tree canopy closure, and habitat effectiveness (lack of human use) (Carroll et al. 2000). Predicted habitat suitability was compared with black bear presence/absence data from DNA-based bear surveys in the Alberta and Selkirk DNA study areas (Mowat and Strobeck 2000). Because no black bear occurrence data had been available for use in development of the Phase I model, we also created a new empirical black bear model based on the DNA data sets.

LYNX - BRITISH COLUMBIA SNOWTRACKING DATA

We compared the predicted habitat suitability for lynx as derived from the RSF model with snow tracking data from a study area in southeastern B.C. (Mowat and Stanley 2001).

MARTEN - BRITISH COLUMBIA HAIR SNARE AND SNOWTRACKING DATA

Marten survey data was available from Garth Mowat (Aurora Wildlife Research) for two areas in southeastern B.C. in the Slocan and Spillimacheen River drainages (Figure 1) (Mowat and Paetkau 2001, Mowat and Stanley 2001). Both areas were surveyed by snagging hair from martens attracted to bait stations, and then analyzing the sample’s DNA to determine species positively (for methodology see Foran et al. 1997, Mowat and Paetkau 2001). The Spillimacheen area also was surveyed by snowtracking. Covariates that potentially influenced the probability that a resident marten would successfully be detected at a station were the duration that a station was in place, the average temperature during that period, the total precipitation in that period, and whether the area was also trapped commercially for marten. We tested the ability of the habitat suitability model developed in RMC Phase I to predict marten occurrence, after accounting for these covariates. The Phase I marten model is a conceptual model that predicts occurrence based on factors reported in the literature as important limiting factors for the species. Marten are associated with high levels of tree canopy closure at the landscape scale in many regions, including the Rocky Mountains (Bissonette et al. 1997). In the Rocky Mountain region marten are associated with mesic conifer vegetation types with high annual snowfall (Buskirk and Ruggiero 1994). This may be due to lessened competition with other carnivores in areas of high snowfall (Krohn et al. 1997) or association with forest structure or specific prey communities. The conceptual model therefore predicted marten habitat suitability by multiplying scaled values for snowfall by those for tree canopy closure.

MULTI-SPECIES PRIORITIZATION FOR THE ENTIRE RMC STUDY REGION

PORTFOLIO SELECTION PROCESS

SITES uses a “simulated annealing” algorithm to efficiently select representative sets of sites (Possingham et al. 2000). The algorithm attempts to minimize portfolio “cost” while maximizing attainment of conservation goals in a compact set of sites. The function SITES seeks to minimize is Cost + Species Penalty + Boundary Length, where Cost is the total monetary or area cost of all planning units selected for the portfolio, Species Penalty is a cost imposed for failing to meet target goals, and Boundary Length is a cost determined by the total boundary length of the portfolio (Andelman et al. 1999). Hence, SITES attempts to select the smallest overall area needed to meet target goals and select clustered rather than dispersed planning units.

SITES performed 1,000,000 iterative attempts to find the minimum cost solution per run and performed 100 such runs for each alternative conservation scenario we explored. SITES does not guarantee an optimal solution, which is prohibitive in computer time for large, complex data sets. However, performing such a large number of iterations provides a solution that is near optimal. Besides identifying this near-optimal “best run”, SITES also rates areas by how often they were selected in the 100 alternate runs. An area that scored highly in this “summed runs” output might not be included in the best solution, but could be considered a good alternative site.

Goals for the carnivore focal species were expressed as a percentage of the total habitat “value” in the region. This is more realistic than the common approach of classifying areas into just two classes of unsuitable and suitable habitat. Habitat value was measured by the output of the resource selection function (RSF) model (Carroll et al. 2001a). Because RSF value is proportional to the number of animals that could be supported in an area (Boyce and McDonald 1999), conserving 30% of the RSF value might be expected to conserve 30% of the potential regional population, if we ignore factors such as connectivity that may cause isolated habitat to remain unoccupied. However, because the habitat models for grizzly bear and wolf were conceptual models rather than RSFs (Carroll et al. 2001a), conserving 30% of modeled habitat “value” will protect more than 30% of their populations. Some additional percentage of the population will also be present on non-reserve lands.

Ecoregions are commonly considered an appropriate scale to plan biodiversity conservation (Dinerstein et al. 1995, Groves et al. 2000). However, a large ecoregion may encompass a wide range of ecosystems and levels of human impact and our study area spans several such ecoregions. Not surprisingly, the northern portion of the study region tends to show higher carnivore habitat quality for most species than do areas in the U.S. northern Rockies. SITES may find it can most efficiently achieve goals such as carnivore habitat protection by locating reserves entirely in the northern end of the region. However, this solution would be poor at preserving well-distributed populations. Because our goals included maintaining well-distributed and connected populations, we stratified goals by subdividing the study area into 88 sections. These sections were derived from subregional ecosection classifications (e.g., Demarchi and Lea 1992) which we modified to produce a system of sections of similar size across the study region. This improves the distribution of reserves but also causes some problematic side effects in that it works against the creation of large reserves. For example, a section containing a large protected area would be less likely to contain additional portfolio sites even if excellent habitat was also present outside the reserve, because the goals for that section would have already been met within the protected area. To balance the need for a well-distributed reserve network with the need for efficiency, we set an overall regional goal that was higher than the local section-level goal. For example, with a 40% regional/30% local goal, SITES sought to capture 30% of the habitat value in each section, and added another 10% of habitat value wherever in the region this could be captured at the least cost.

SITES requires an estimate of the cost of including each new site in the conservation network. This can be the monetary cost of the land if this is known. However this information is rarely available at the ecoregional scale, especially where most of the land base is in public ownership. A starting cost estimate could be the area of the site. We used the area of a site as a measure of cost in all SITES runs, as alternate cost structures, such as were used in the CanRock analysis (see appendix), tended to bias the reserve selection too heavily toward the northern portion of the study region. In addition, such cost structures potentially confounds interpretation of results, because human impacts (habitat effectiveness) are incorporated into the analysis both in the resource selection functions for certain focal species and in the cost equation.

Initial SITES runs were made using the static habitat suitability models for the eight species. Our portfolio design built upon the existing protected area network. This decision is made by locking existing protected areas into the SITES solution, so that the program only adds targets that are missing from the current park system. Locking in protected areas recognizes that it would be unreasonable to degazette existing parks and that it is easier to achieve conservation goals in protected areas than in currently ungazetted areas. Although this seems a reasonable assumption, there was concern that such a "locked-in" solution did not provide information on where biodiversity was actually distributed on the landscape irrespective of political boundaries. While the SITES scenarios that lock in protected areas are the most informative for land use planning, the "not locked in" SITES solutions are useful to gauge, for example, the overlap of priority areas for different types of conservation targets. Therefore we performed analyses for both options.

The SITES program attempts to discover the most efficient solution that balances the costs of not meeting conservation goals with the costs of protecting new areas. However, when many options are available for reserve placement that have similar costs and benefits, SITES may identify several reserve designs that have close to identical optimality. This rarely occurs in regions that have abundant information on exact locations of rare species or in which much of the land base has already been developed. However, it does occur in areas where most information on the distribution of biodiversity is based on models rather than point locations and where much of the land base is still relatively pristine. This situation occurs in the northern portion of our study region. Planners in these areas should supplement maps of the "best" SITES portfolio with information on "near-optimal" reserve locations.

USING PATCH OUTPUT AS NEW TARGETS IN SITES

In the second stage of the SITES modeling, we added goals derived from the PATCH models for grizzly bear, wolf, and wolverine. This allows us to prioritize protection of those areas with high irreplaceability and vulnerability, which are not identical to the areas with the highest habitat suitability. We used two PATCH-based goals per species. One goal targeted areas with both high value as source habitats and high threat. A second goal targeted highest value source habitats. By capturing both types of habitat, we could help stem short-term range contraction by protecting the most vulnerable sources while still protecting enough secure sources to build a reserve network that could maintain viability over the long term.

USING PATCH TO EVALUATE ALTERNATIVE SITES PORTFOLIOS

Because there is little information about what constitutes a threshold amount of habitat for insuring viable populations, and because we want to address factors such as connectivity that are ignored by SITES, we used the PATCH model to evaluate the gain from adding portfolio sites selected in the SITES modeling. These results differ from adding PATCH-based data to the SITES model itself, because now we evaluate how the potential new reserves function as a network to conserve viable populations as the landscape changes over time. We performed this evaluation for the two carnivore species, the grizzly bear and wolf, for which we had the most developed and accurate PATCH models.

INTEGRATING THE SITES AND PATCH RESULTS INTO CONSERVATION PLANNING

Models such as SITES are important tools for reserve selection, that is the process of answering the question “where is the best habitat?” We used the results of the SITES analysis to identify high-priority core areas and potential linkage and buffer areas. To move from reserve selection to reserve design required integration of both the SITES and PATCH models. The PATCH evaluation of alternate SITES portfolios helped us to assess “how much habitat is enough” to insure carnivore population viability. The more general results from the PATCH modeling suggested how reserve design rules might differ between the species regarding connectivity and patterns of threat. The overall conservation design builds on the “best run” solutions from SITES by adding optimal corridor areas between core areas using the “summed runs” results from SITES along with information on regional population structure from the PATCH models. This method uses the model results, not as a black box that can identify a single best reserve network, but as complementary sources of information in a decision-support system.

RESULTS

STATIC MODELS

Extension of the static models to the larger study area resulted in the predicted habitat suitability levels shown in Figures 3 to 10. Our static model results for the larger study area emphasize the two axes of habitat association developed in Carroll et al. (2000). The eight carnivore species can be grouped along an axis of topographic tolerance (use or avoidance of rugged terrain) and an axis ranging from human–impact-sensitive habitat generalists to human-tolerant forest specialists. This conceptual framework identifies several contrasting patterns of habitat suitability that have geographic implications for designing an effective multi-species reserve network:

1) Contrasts between the wolf and two other large carnivores, the grizzly bear and wolverine. The three species are similar in their association with areas of low human impact, but contrast in their use (grizzly bear, wolverine) or avoidance (wolf) of rugged terrain.

2) Contrasts between large carnivores and the lynx. The lynx is similar to the large carnivores in that it is also abundant in boreal/subboreal zone, and like the wolf is at low densities in the rugged central Canadian Rockies. However, it is tolerant enough of human impact to inhabit the more-developed transboundary region.

3) Contrasts within the “forest carnivores”, between the lynx and species such as the fisher, black bear, and mountain lion. Whereas all these species are at relatively low densities in the rugged central Canadian Rockies, their larger-scale patterns of abundance contrast. The lynx becomes less abundant from north-to-south, and the mountain lion from south-to-north, whereas the fisher and black bear show a more complex pattern.

These patterns imply that the current distribution of protected areas, concentrated in the most rugged portions of the study area (the central Canadian Rockies), should be augmented with new conservation areas in regions of lower topographic relief and higher biological productivity that still have low enough human impacts also to support the large carnivores. In addition to northcentral Idaho (Carroll et al. 2001a), portions of the northern Canadian Rockies between Jasper Park and the Muskwa region meet these criteria.

DYNAMIC MODELS

The results of the dynamic models for grizzly bear, wolf, wolverine, lynx, and fisher support many conclusions from the static habitat suitability models but also add information in three areas, two of which are summarized here:

1) The response of population to future landscape change, including areas of highest vulnerability to population decline or extirpation.

2) The locations of population source areas, which may differ from the areas of highest predicted habitat suitability or abundance.

A third area, the response of carnivore populations to potential conservation strategies, will be summarized later.

The results of the dynamic models are shown as maps of 1) predicted reduction in occupancy due to landscape change (Figures 11-13) and 2) distribution of source and sink habitat (Figures 14-16). PATCH is a stochastic model, and results are given as probabilities. Areas with long-term occupancy probability of less than 50% are not shown on the following maps. However, these areas may be occasionally occupied and provide some level of connectivity between otherwise disjunct populations.

CHANGES IN DISTRIBUTION

Grizzly bear

Results of the PATCH model for grizzly bear (Figure 11) show that, over the coming decades, refugia in the northern U.S. may be threatened on their margins by habitat loss. An even greater potential for range contraction and fragmentation exists in southern Canada. Low viability is predicted for small populations in the transboundary region, such as the Cabinet-Yaak and Selkirks, if habitat restoration or management changes do not occur. Range loss is likely to occur in the Highway 3 corridor, isolating the Northern Continental Divide (NCDE) population from the Canadian Mountain Parks. Other range contractions may occur east of Jasper National Park and between the mid-Fraser River valley and Wells-Gray Park.

Wolf

For the wolf (Figure 12), the results suggest that current potential exists for recolonizing animals to expand into much of the U.S. Northern Rockies. However, these areas are also threatened over the long-term with the prospect of becoming population sinks. Substantial range loss occurs in southeastern B.C. and southwestern Alberta, but greater loss may occur further to the south, e.g. between the central Idaho and GYE populations.

Wolverine

The pattern of range contraction (Figure 13) for the wolverine is similar to that for the grizzly bear. However, northern B.C. shows higher levels of threat for this species than for the bear. The wolverine's greater dispersal ability allows the NCDE population to remain connected to more northerly populations. Other U.S. populations, however, may be isolated.

DISTRIBUTION OF SOURCE HABITAT

Grizzly bear

The pattern of predicted demographic value for the grizzly bear (Figures 14a and 14b) under current and future conditions suggests that the northward range contraction described above will be accompanied by an increase in sink habitat in the northern portions of the study region. That is, even where the species persists, we will see the early stages of extirpation, in which previously continuous habitat becomes fragmented by development along road corridors and river valleys such as the Columbia Trench, Upper Fraser River, and Peace Lowlands.

Wolf

The pattern of demographic value for the wolf (Figures 15a and 15b) is similar to that for the grizzly bear. However, reduction in demographic potential is less evident in Canada than in the U.S. northern Rockies. The higher vagility and fecundity of the wolf causes greater interdependence between adjacent portions of its range. This means that the degradation or isolation of core source habitat may cause dramatic range contraction as is seen between the GYE and central Idaho (Figure 15).

Wolverine

The pattern of demographic value for the wolverine (Figure 16) is similar to that of the grizzly bear and wolf in southeastern B.C.. However, it differs in that isolated populations in the U.S. northern Rockies suffer less degradation than seen in the other two species. Conversely, degradation and fragmentation of habitat in the Canadian portion of the study region is generally more extreme than seen in the cases of the wolf and grizzly bear, especially in the Canadian mountain parks (e.g., the Transcanada Highway corridor) and the Peace River lowlands.

IRREPLACEABILITY AND VULNERABILITY

The irreplaceability/vulnerability graphs for the three species show broad similarities (Figure 17 a,b,c, key to sections shown in Figure 18). For example, the graphs highlight as critically endangered several areas in northern B.C. such as the McGregor Plateau (11), Bowron Valley (19) and Upper Fraser Trench (15), as well as better-known areas such as the Crown of the Continent (61). The irreplaceability and vulnerability values are also mapped (Figure 19) using a color scheme in which areas in red suffer higher loss of demographic potential than those in green, and brighter shades of red or green indicate higher irreplaceability (occupancy-weighted lambda). We can see that the bright red areas, which comprise the upper right quadrant in the irreplaceability/vulnerability graphs, occur primarily in the north, but the Crown of the Continent is uniquely vulnerable due to its small size and isolation, and the GYE area is also highly vulnerable (Figure 19 a,b,c). The grizzly bear shows a pattern of higher elevation core areas (bright green) fragmented by localized strong sinks (bright red), and fringed on the southern edge by a retreating range margin of more extensive sink habitat (pale red) (Figure 19a). Sink habitat for the wolf is more concentrated in productive lowland habitat in the Fraser valley and Peace lowlands and less in rugged southeastern B.C.(Figure 19b). Wolverine shows areas of vulnerability (bright red) even in the core of their range in this region (Figure 19c).

MESOCARNIVORE PATCH MODELS

Lynx

The more fragmented distribution and lower productivity of lynx habitat in the central and southern Canadian Rockies, when compared with boreal regions, results in PATCH predictions that only a small portion of the habitat that could theoretically function as a population source is actually occupied by lynx in these areas (Figure 20). This is due to the negative effect of population cycling as modeled in our simulations (Figure 21). Lynx populations from Jasper southward appear sensitive to extirpation given small changes in the assumptions concerning the intensity of population cycling (Figure 21).

Fisher

The fisher's optimal habitat, low to mid-elevation forest, is naturally fragmented by topography in many parts of the study region. This fact, when combined with aspects of the fisher's demography and dispersal characteristics, appears to result in a high level of vulnerability to increased mortality risk. Increased mortality could be due to either incidental trapping or increased predation by other carnivores due to loss of forest canopy cover and structure. The effects of increased mortality risk are felt disproportionately in smaller patches and near the edges of large patches (Figure 22). Under high mortality scenarios, smaller or more isolated areas of suitable habitat do not function as population sources in the PATCH simulations (compare Figure 23a and 23b). This causes a collapse of the range until it includes only the largest habitat aggregations, such as occur in northcentral Idaho (Figure 23).

GAP ANALYSIS

Comparison of management categories with predictions of habitat suitability (Table 2) from the static model suggest that parks in this region hold a higher than expected amount of habitat for the wolverine, a lower than expected amount for the lynx and fisher, and an amount similar to their proportion of the region (10.2%) for the other species. Non-park protected areas (primarily US Forest Service wilderness areas in Idaho) are more important than expected by their area (7.0% of region) for mountain lion, wolverine, and marten, and extremely so for fisher and black bear. General public lands, which make up 58.2% of the region, are generally more important than expected based on area, but especially so for lynx and marten, and also for wolf, wolverine, and mountain lion. Private lands hold less habitat than expected by their proportion of the region (24.6%). Private lands have the most value for wolf, fisher, and black bear. Grizzly bear habitat in the Rocky Mountain foothills north of Banff in Alberta causes private lands to show substantial habitat value for this species. Due to habitat data gaps for the other seven species, this area could only be mapped for the grizzly bear. This area is actually a mixture of leased provincial crown land and private lands. However, we lacked the detailed ownership data necessary to separate these management categories in this area.

Comparison of management categories with results from the PATCH models for grizzly bear, wolf, and wolverine (Tables 3 and 4) allows us to compare the current and future potential of the various management types. All three species show a gradual shift toward increased importance of protected areas and decreased occurrence on private lands, as might be expected due to increasing development of the landscape matrix (Table 3). Both the grizzly bear and wolverine are more strongly associated with protected areas than is the wolf. However, protected areas increase in their proportional value more dramatically under future landscapes for the grizzly bear than for the wolverine. The average lambda value shown by the various management categories does not change substantially between current and future landscapes. This is because the species' are gradually being extirpated from peripheral sink habitat at the same time that former source habitat is being degraded to form sink habitat.

A more informative measure of demographic change is the share of strong sources or sinks contained in a management category (Table 4). Grizzly bear source habitat is more strongly associated with parks, while source habitat for wolverine, and especially for wolf, is more widely distributed (Figure 24, Table 4). Because of the wolf's broader overall distribution, most of the loss in lambda for this species will be on general public land. However, parks do hold more strong sink habitat for wolves than they do for the other two species, due the wolf's vulnerability in rugged areas. Wolverine suffer more overall loss in lambda inside the parks than do the other two species.

MODEL VALIDATION

GRIZZLY BEAR - BRITISH COLUMBIA HAIR SNARE DATA

For a combined data set of survey sites from southwest Alberta, the Selkirk Mountains (B.C.), and the Prophet River (B.C.) (Figure 1), both the static (habitat suitability) and the dynamic (PATCH) model predictions were highly correlated with DNA survey results using the Wilcox rank sum test ($p < .001$, static $R_s = 0.109$, dynamic $R_s = 0.122$) (Table 5). The models performed more poorly at predicting whether a particular site within a single study area would be visited by bears. This is somewhat expected given the regional-scale nature of the models. At the within-study-area scale, the PATCH model overpredicted occupancy in the Prophet River study area. Because surrogates for human use such as road density are at such low levels in this boreal region, quantifying human impacts may require detailed data on locations of settlements, trails, and outfitter use that we lacked. Both the static and dynamic models performed better in the Selkirk study area (southeast B.C.) than in southwest Alberta. In contrast to the Selkirk results, grizzly bears in the Alberta study area were most often detected at the interface between predicted suitable and unsuitable habitat (the wildland-developed interface) than in the interior of core areas. We can only speculate as to possible causes for this contrast, e.g. effects of historical mortality or behavioral differences between wary and habituated populations as they relate to the bait-station protocol. In these comparisons, as in all the validation tests, even highly significant correlations show low R values, that is, they explain a low percentage of the variation in detection rate. This will be true with almost all such models, since habitat quality is only one of several factors that contribute to a survey station being visited by an animal. Other factors may include year-to-year variation in territory occupancy, weather, and variation in individual behavior.

GRIZZLY BEAR - ESGBP TELEMETRY DATA

Both the static habitat suitability model and the PATCH model were significant predictors at both ADK and MCP "scales". The two models were similar in predictive power at the ADK scale, with both showing significant correlations with the telemetry data ($p < .0001$), but the rank correlation being greater with the static model predictions ($R_s = .151$ vs .101). Both models were again significant predictors at the MCP scale ($p < .0001$), but here the PATCH model greatly outperformed the static model ($R_s = .239$ vs .077). Among the model input variables, tasseled-cap greenness was the more significant predictor of grizzly bear distribution for the ADK comparison ($p < .0001$, $R_s = .187$ vs $p = .0004$, $R_s = .041$ for habitat effectiveness). In the MCP comparison, bear telemetry points were slightly inversely correlated with greenness ($R_s = -0.06$), whereas habitat effectiveness (human impact factors) remained a significant predictor ($p < .0001$, $R_s = .104$). Although both static and dynamic models include both human impacts and greenness, how and at what scale the two factors are integrated differs between the two models. Although there are problems associated with defining the comparison between used and unused habitat (i.e. what is “available” habitat) using a crude measure such as a home-range estimator, the results suggest that where bears are within the Rocky Mountain parks is more influenced by fine-scale features such as greenness, but that where bears are located in the larger region is more influenced by human impacts.

WOLF - YELLOWSTONE TELEMETRY DATA

Both the static and dynamic model predictions are significantly correlated with wolf distribution in the GYE ($p < 0.001$). The dynamic model performs somewhat better, with a rank correlation (R_s) of predicted versus observed distribution of 0.35 versus the static model’s 0.19. Habitat effectiveness alone has a rank correlation with observed wolf distribution of 0.17. For comparison, a new static model developed from the GYE pack data achieves a rank correlation of

0.37, suggesting that the dynamic model achieves a predictive power near the maximum possible from a regional-scale model. Figure 25 shows the contrast in predicted occupancy values between pack territories and non-pack areas.

BLACK BEAR - BRITISH COLUMBIA HAIR SNARE DATA

Predicted habitat suitability, which was available for the Alberta and Selkirk (southeastern B.C.) DNA study areas, was significantly correlated with black bear presence ($p < 0.001$, df=680, $R_s = 0.13$). At the within-study area scale, the correlation was significant for Alberta (df=316, $R_s = 0.15$, $p < 0.01$) but not for the Selkirk area (df=362, $R_s = 0.08$, $p > .10$).

The new empirical black bear model based on the DNA data sets incorporated the following habitat variables: the MODIS tasseled-cap variables for brightness, greenness, and wetness, slope, and elevation. There is some indication of a positive association with protected areas and areas of low road density, but this may be an artifact of other unmeasured differences among the three DNA survey study areas.

LYNX - BRITISH COLUMBIA SNOWTRACKING DATA

When we compared the predicted habitat suitability for lynx as derived from the RSF model with snow tracking data (Figure 26), we found that the presence of lynx tracks within a survey cell is not correlated with predicted habitat suitability ($p > .10$). In the figure, cells with lynx tracks are shown in red, whereas cells without tracks are outlined in black. The predicted habitat suitability ranges from white (low) to dark green (high). It can be seen that the areas that we predicted to be low lynx suitability are not surveyed because they are extremely rugged.

Among the surveyed cells, lynx occur in the smaller montane valleys but are present only on the margins of the larger valley of the Columbia River on the eastern side of the study area. Because we generally predict valley bottoms to have high suitability, this accounts for the low predictive power of the model here. The western side of the Columbia River valley here is characterized by more open forests with lower snowfall, as well as increased human impacts due to private land ownership. The low predictive power of our RSF model here may be due to lack of variables such as forest type and snowfall that were unavailable for much of our study area and have proved important where available (Carroll et al. 2001a). However, if the mountainous sections of the study area had been included in the comparison, model predictive power would likely have increased. While concluding that highly rugged cells are not likely to contain lynx may seem trivial at this scale, this aspect of suitability is informative when comparing habitat across larger scales (e.g., between the US and Canadian Rocky Mountains [Carroll et al. 2001a]).

MARTEN - BRITISH COLUMBIA HAIR SNARE AND SNOWTRACKING DATA

For the Spillimacheen marten survey data, the significant covariates were average temperature ($p < 0.01$, positive effect) and commercial trapping ($p = 0.02$, negative effect). The marten suitability model predictions were highly significant ($p < 0.01$, positive effect). However, in the Slocan study area, all potential covariates are non-significant ($p > .10$), and the marten suitability model was negatively correlated with the observed marten occurrences. This is likely due in part to the fact that the Slocan data set was collected with a different sampling design that makes it less suitable for use in habitat modeling without further data screening (G. Mowat, pers. comm.). Survey sites in the Spillimacheen study area were randomly located within survey cells, whereas in the Slocan study area survey sites were placed in the best habitat within each cell. In cells with only small amounts of marten habitat, this meant that all survey sites were at or near the same location. This bias, while useful for the inventory purposes for which the data was originally collected, obscures habitat selection at finer scales.

MULTI-SPECIES PRIORITIZATION FOR THE RMC STUDY REGION

We performed static model-based SITES runs where protected areas were not locked into portfolio. The results for goals of 40% regional/30% local (Figure 27) reinforce the conclusions (described above) we drew from examining the static model output. The area between Jasper Park and the Muskwa-Kechika, as well as northcentral Idaho, are among the areas most frequently selected in the SITES runs.

USING PATCH OUTPUT AS NEW TARGETS IN SITES

In the second stage of the SITES modeling, we added two PATCH-based goals per species. Figure 28 shows an example of habitat meeting the two goals for grizzly bear. Areas shown in red lie in Quadrant 1 (upper right) of the irreplaceability/vulnerability graph for grizzly bear. They are areas with both high value as source habitats and high threat. Areas shown in green are the highest value source habitats, that is, the upper portions of quadrants 1 and 2 (upper left) of the irreplaceability/vulnerability graph for grizzly bear.

To illustrate the contrasts between using static and dynamic model-based goals, we compared SITES solutions for the three carnivores species (grizzly bear, wolf, and wolverine) alone (Figure 29). Areas in orange in Figure 29 were only selected in the static model-based

SITES runs (goals 35% regional/15% local), whereas areas in green were only selected in the PATCH model-based SITES runs (goals 50% regional/30% local), and areas in red were common to both scenarios. The static model-based portfolio sites are more concentrated at the edges of existing parks and in core areas in northern B.C., whereas the PATCH-based sites are found in vulnerable areas in the southern portion of the study region and in buffer zones in northern B.C. SITES solutions for the three species using the PATCH-based goals are slightly more efficient than those based on the three static models. For example, a portfolio based on PATCH goals requires 27% of the region to achieve the same level of potential grizzly bear population size shown by a static model-based portfolio covering 31% of the region.

Because portfolios based on both the eight static models and the PATCH results appear more efficient than those using the static models alone (Table 6), we use the former approach for all of our final SITES runs. The “best” portfolio for the lowest set of goals (30% regional/20% local) encompasses 27% of the region, that is, existing protected areas (17%) plus an additional 10% of the region. For the 40%/30% and 50%/30% goals, portfolio size increase to 36% and 45% of the region, respectively. About 10% of all the portfolios lies on private land. Therefore, the proportion of portfolios that lie on general public lands grows in size from 34% to 52% as goals increase (Table 6).

USING PATCH TO EVALUATE ALTERNATIVE SITES PORTFOLIOS

We found that a landscape with no further protected area additions would lose 13.8% (wolf) to 14.4% (grizzly bear) and 15.8% (wolverine) of its long-term carrying capacity within 25 years (Table 7). Losses in scenarios where only private lands were developed were 7.3% for the wolf and 6.1% for the grizzly bear. However, range loss is very unevenly distributed through this large study region. Recall that because current carnivore populations have not yet equilibrated to recent habitat loss, declines in carnivore populations over that 25 year period may be greater than suggested by the model results. Protecting portfolio sites identified using a 30% regional/20% local goal would reduce the expected loss due to landscape change to 4.6% (grizzly bear) and 2.6% (wolf) from current carrying capacity. Protecting portfolio sites identified using a 40% regional/30% local goal would result in a 1.3% (grizzly bear) to 3.7% (wolf) gain over current carrying capacity (Table 7).

Portfolios of increasing size capture a linearly increasing proportion of static habitat value, and this relationship is similar for the three species (Table 7). These results offer no surprises. However, if we project current development trends to 2025, and use the PATCH model to assess how the alternate portfolios function as a network in an increasingly developed matrix, we find results that cannot be predicted based on the static model results. The results suggest the existence of thresholds in the effect of increased habitat protection on population viability (Figure 30, Table 7). This contrasts with the lack of observed thresholds in the smaller CanRock analysis area (see Appendix). Another contrast to the CanRock results is that there is more similarity between the responses of grizzly bear and wolf over the larger region. Increasing portfolio size has the greatest effects on population viability up to approximately 37% of the study region (Figure 30).

When we contrast the future distribution of grizzly bear and wolf under current levels of protected areas to that under the 40% regional/30% local SITES portfolio (Figure 31), we find that, as seen in the CanRock analysis, the addition of sites in the transboundary region, as well as the addition of the SRMCA corridor (Highway 3 region), prevent the loss of connectivity between the NCDE and the Rocky Mountain Parks and sustains smaller grizzly bear subpopulations in southeastern B.C. and the northern U.S.. Larger portfolios also may restore connectivity between the GYE and central Idaho for grizzly bear. The wolf shows similar, but more broadly distributed increases in distribution (Figure 31b). While portfolio sites in the northern portion of the study area would help increase population abundance there, much of the increase in wolf distribution would be in the U.S. northern Rockies, especially between the GYE and central Idaho (Figure 31b).

INTEGRATING THE SITES AND PATCH RESULTS INTO CONSERVATION PLANNING

A landscape prioritization that locks in existing protected areas and uses both static models for the eight species and PATCH-based goals for three species is shown in Figure 32. It suggests priorities for one or more new protected areas in northcentral B.C. between Jasper National Park and the Muskwa-Kechika area (e.g., in the upper Parsnip River), a possible eastern addition to the Muskwa-Kechika protected area itself, and new protected areas in northcentral Idaho. Comparison of final SITES portfolios with high (40%/30%) and moderate (30%/20%) goals (Figure 32) show that much of the increased reserve area in the larger portfolio also lies in these three areas. The portfolio built from moderate goals includes the areas shown in dark green in Figure 32, while the portfolio built from high goals also includes the areas in light green. Priority areas identified in the 40%/30% SITES runs could serve as buffer and linkage areas surrounding core sites identified in the less extensive 30%/20% solution. Potential buffer/corridor areas are also identified in the “summed runs” solution for the 40%/30% goals (Figure 33).

Important buffer areas, whose management designation might vary with the landscape context, are suggested between Jasper and Wells-Gray Parks, and to the east of Tweedsmuir Park in the Fraser Plateau area. In southeastern B.C. and the larger transboundary region, linkages are suggested between existing parks. In the NCDE, an area with the north fork of the Flathead at its core is suggested as a priority site. In the U.S. portion of the Rocky Mountain Front, areas are identified to the east and south of the NCDE in the Lewis Range and Big Belt Mountains. In the GYE, areas to the northwest of Yellowstone Park (Gravelly/Snowcrest, Centennials, and Henry's Fork) are highlighted, as well as the Greybull River area in the southwest GYE.

Our results for areas outside the Rocky Mountain parks in Alberta are tentative, because, for foothills areas to the north of Banff, we could only map habitat suitability for grizzly bear and not for the other species due to missing data. In Alberta, preliminary Rocky Mountain Front priority sites included the Bighorn Country (Sheep Creek area), the Castle-Crown area, the Porcupine Hills, the Clearwater/Red Deer area along the eastern boundary of Banff National Park, and the Kakwa River valley.

DISCUSSION

Conservation planning and reserve design for endangered species often involves expert assessment of potential habitat and delineation of linear linkage zones to insure connectivity. We take a different approach here by using multi-species optimization and dynamic models to assess the location and role of critical core and linkage areas. By linking demography to mapped habitat characteristics, the dynamic models help reveal how each of these areas may influence the overall viability of the region's carnivore species under current and future conditions. An understanding of the regional mechanisms driving population viability is a necessary foundation for reserve design, because without an accurate understanding of the regional context we cannot evaluate the relative demographic effect or likelihood of use of a potential core or corridor. The dynamic model results allowed us to rank potential core, buffer and corridor areas by their vulnerability as well as their role as sources or sinks in the regional population dynamics of the different species, highlighting areas that may not face the highest absolute level of threat but have a critical location adjacent to large source populations.

The results of extending the static models over the broader region reinforces the conclusions we drew in Phase I (Carroll et al. 2001a) as to the two major axes defining carnivore habitat associations in the region. Species range along an axis of topographic tolerance (use or avoidance of rugged terrain) and an axis ranging from human impact-sensitive habitat generalists to human-tolerant forest specialists. When considered as a whole, the static model results identify at least two priority areas for enhancing conservation of the carnivore community as a whole: northcentral Idaho (Carroll et al. 2001a) and the area between the Kakwa and Muskwa-Kechika protected areas in British Columbia. Many conclusions of the static model comparison agree with the results of the more complex dynamic models, lending added confidence to decisions based on these results. The area northwest of Kakwa Park has also been identified in field studies as supporting high densities of several carnivore species including grizzly bears (Mowat et al. 2001).

DYNAMIC MODELS

Comparison of the viability analysis results among the different carnivore species highlights several commonalities. Among those carnivores most sensitive to direct human impacts (grizzly bear, wolf, and wolverine), the overriding importance of factors influencing adult female survival is evident. Elasticity analyses of population matrices for long-lived vertebrates commonly identify female survival as the key demographic parameter (Doak 1995; Caswell 2000). This results in some overlap in core areas and critical linkages among these three species. The interplay of habitat productivity and mortality risk, however, is mediated by the species' differing ecological resilience, as expressed in their demographic and social structure (Weaver et al. 1996). This results in greater contrasts in the distribution patterns and conservation priorities among the species than would be expected based on habitat associations alone. For example, although the grizzly bear and wolverine showed broad overlap in high quality habitat in the static model (Carroll et al. 2001a), wolverine appear more vulnerable to range contraction in areas that are undergoing rapid landscape change. This may be due to the lower fecundity of wolverines versus grizzly bears. Due to its greater vagility, the wolverine, unlike the grizzly bear, appears to maintain connectivity between the Northern Continental Divide Ecosystem (NCDE) and more northerly populations. Other U.S. populations, however, may be isolated, a prediction supported by genetic data (Kyle and Strobeck 2001).

The dynamic modeling results predict that current trends in land use and human population growth will strongly affect the distribution of carnivores in the Rocky Mountain region. The predicted loss in long-term carrying capacity ranges from 13-16% for the grizzly bear, wolf, and wolverine. This reduction is due about equally to development on private lands and to degradation of habitat on public lands. However, range loss is very unevenly distributed through this large study region. The contrast between the types of predictions provided by non-spatial population viability analyses (PVAs) (e.g., overall extinction probability) and spatial PVAs such as PATCH is striking. Rather than simply preventing regional extinction, spatial PVAs help suggest methods to preserve and enhance well-distributed carnivore populations.

Although the presence of large existing core areas such as the Canadian Rocky Mountain Parks buffers populations from extirpation, changing landscape conditions produce substantial northward range contraction in the grizzly bear, wolf , and wolverine. However, areas of highest threat differ between these three species, with the wolf having its greatest potential range loss further to the south due to its avoidance of rugged terrain and greater tolerance of human impacts.

Because of the legacy of past predator control and the rapid rate of current landscape change, carnivore distribution in the region differs from the “equilibrium” distribution of the species, i.e. where they might persist given current habitat. For the larger carnivores, some areas such as central Idaho lack species that they could support under current conditions. Conversely, areas of southeastern British Columbia and western Alberta show a large range contraction from current distribution in the PATCH simulations. Peninsular populations such as those in the transboundary region appear most vulnerable. We can see these as “non-equilibrium” metapopulations (Harrison 1994) that may not persist unless habitat restoration occurs. This "extinction debt" is a hidden but foreseeable consequence of current landscape condition. Future habitat loss would accelerate this process.

A critical point differentiates focal species planning based on dynamic models from that based purely on habitat suitability. The most threatened areas in the irreplaceability/vulnerability graphs, such as the Crown of the Continent, do not face the highest level of development threat, but qualify due to their critical locations adjacent to large source populations. This makes habitat degradation in these areas a major demographic threat to regional carnivore populations. Improving conditions in strong sinks can be as important to regional viability as is protecting strong source habitat.

Coordinated management strategies addressing habitat and connectivity across national, state, and provincial boundaries are critical to the survival of carnivores in the Rocky Mountain region. Tradeoffs must be addressed between allocating scarce conservation resources towards protecting relatively secure core areas, stemming the degradation of threatened buffer zones, or restoring corridor areas that are already degraded but might contribute to long-term connectivity. The combination of data on irreplaceability and vulnerability allows us to develop a defensible incremental strategy linking immediate conservation needs with longer-term goals for a comprehensive conservation network.

The status of mesocarnivores such as the lynx and fisher, although not as clearly linked to development threats, shows vulnerability related to the interaction between habitat fragmentation and mortality risk. Although our mesocarnivore analyses are more exploratory, we feel they reveal qualitative insights on population viability that would not be possible without the linkage between demography and habitat maps. For example, the demographic vulnerability of some smaller protected areas containing fisher habitat, such as in southeastern British Columbia, reflects earlier predictions of a threshold response to trapping mortality from a non-spatial model (Powell 1979), but adds the synergistic effects of habitat area and isolation. This interaction between mortality risk and patch area may arise from aspects of fisher demography not shared by the larger carnivores: it has more limited dispersal abilities than all but the grizzly bear and yet has relatively higher mortality and fecundity rates. Therefore, territory recolonization must occur more frequently than in larger carnivores, increasing the demographic vulnerability of small or isolated populations. Fishers may occupy a vulnerable middle ground between the more abundant smaller carnivores (e.g., marten) and the more vagile and long-lived large carnivores. This is supported by genetic evidence showing higher levels of genetic differentiation in fisher than in marten or wolverine (Kyle et al. in press). High-quality fisher habitat is also found primarily outside protected areas and thus is vulnerable to increased mortality under the scenario used here. These results suggest that these areas may help enhance regional viability but could cease to function as effective refugia if isolated from adjacent subpopulations.

Lynx populations, especially those in the southern portions of the study region, also appear to show non-linear responses to habitat area and connectivity. Whereas the boreal zone is occupied consistently due to its high habitat value—and the most southerly areas are vacant for the opposite reason—areas in between along the southern periphery of the range are occupied because of a complex combination of site habitat value and proximity to sources of dispersers. In some areas, if a lynx population is extirpated during a cyclic low, an insufficient number of dispersers are available from regional source habitats alone to ensure that the area will be recolonized during a cyclic increase. Hence, the observed lynx distribution is aggregated to a greater degree than expected by the distribution of suitable habitat alone. Recent research on lynx genetics supports the conclusion that southern populations may be dependent on maintenance of connectivity with boreal populations (Schwartz et al. 2002).

For the fisher and lynx, our results suggest that proportionately small changes in habitat area and connectivity may result in threshold effects with major consequences for species viability. Whether this is a hopeful or cautionary message depends on the efficacy of conservation efforts, but it underscores the necessity of coordinating planning for these wide-ranging species across many jurisdictions and ownerships. The ability of existing protected areas to serve as refugia varies between the species, but even the largest parks are unlikely to retain their full complement of species if isolated. Population viability depends on a combination of a refugium's area, lack of isolation and habitat quality. Because of desires to reduce loss of resources for human use, parks tend to be created in areas of low biological productivity. This effect grows in importance with increasing latitude and elevation as productive habitat forms proportionally less of the landscape. Refugia that still retain carnivores at their southern range limits (e.g. Yellowstone and central Idaho) are large and fairly productive. Newly-created protected areas in the increasingly fragmented subboreal regions may need to have greater area and connectivity than those to the south. For example, viability of large carnivore populations in the large Canadian mountain parks complex is strengthened by their current connectivity to populations to the north and west. If further isolated by landscape change, however, the mountain parks may suffer from their relative scarcity of productive source habitat. The region from Highway 3 to the NCDE, which lacks the large habitat area of the Idaho and GYE refugias and the connectivity of the Rocky mountain parks complex to its north, is most vulnerable to loss of large carnivores. The importance of regional connectivity is also evident in the low viability of lynx populations when isolated from larger boreal populations. Whereas such forest mesocarnivores as the fisher and lynx are less dependent on large protected refugia, they do seem vulnerable if habitat loss occurs in key areas of southeastern British Columbia and northern Idaho. These conclusions are reinforced by the results of the gap analysis, which suggests that the current system of protected areas is skewed towards higher elevations and poorly captures habitat for many carnivore species.

MODEL VALIDATION

The results of the comparisons between our model predictions and validation suggest that the predictive power of our regional-scale models differs between large carnivores and forest carnivores. The models were more successful at predicting distribution of species such as the grizzly bear and wolf which are more closely associated with areas of low human impact than with a particular vegetation type. The models were less successful with species such as the lynx which are more closely associated with particular habitat types than with areas of low human impact. The black bear, although a large carnivore, could also be placed in the latter category.

The relatively high predictive power of the static and dynamic models when compared with grizzly bear hair snag and telemetry data and wolf pack boundaries lends confidence to regional-scale conservation strategies built from these models. Both the static and dynamic models seem useful at predicting relative suitability at the larger scales, but need more refinement before being used at the scale similar to that of the DNA study areas (~5000 km^2). Although the dynamic models appear slightly superior to the static models overall, it appears that relatively simple static models can perform well at predicting large carnivore occurrence in many areas. The dynamic models are superior in areas where connectivity and minimum area factors predominate over local habitat quality. This would be most evident along the margins of the species distribution, for example in southeastern British Columbia. However, this improvement may only be evident in regional-scale comparisons rather than within a particular validation study area, as the PATCH model results tend to be dominated by regional-scale factors.

The static models do tend to show more fine-scale detail in habitat quality that is swamped by regional trends in the PATCH model. In addition the static models are less complex and thus available even for species for which demographic data is limited. If the simpler models perform as well as complex models, they may be preferable for conservation planning in some cases. However, models are useful for both prediction and interpretation. Even with similar predictive power, the dynamic model is superior to the static model in its ability to help us interpret the biological mechanisms that produce observed patterns of carnivore distribution. This allows us to compare the effects of alternate scenarios of future development or restoration.

The results of the validation comparison for lynx suggest that although readily-available information such as topographic data can produce regional-scale predictive models with value for initial conservation planning, development of models suitable for detailed planning will require data on vegetation type and forest structure that is less readily available at regional scales. The relatively successful validation results for marten suggest that these stringent data requirements may not hold for some mesocarnivore species whose habitat associations can be mapped using satellite imagery. However, overall, we should be cautious in our use of mesocarnivores as regional-scale focal species or indicators of biological integrity until we can further improve both habitat data and our understanding of their more complex habitat associations. In contrast, it appears that we currently have enough understanding of limiting factors for large carnivores, and the data to map such factors, to develop detailed map-based conservation strategies to ensure their future distribution and viability.

ASSESSING MODEL UNCERTAINTY

We have somewhat ambitiously attempted to develop models for a range of both well- and poorly known carnivore species. In order for our results to successfully support conservation decision-making, we must assess the relative level of uncertainty in the models for the different species. For four species, the fisher, lynx, wolverine, and black bear, we could build empirical models based on survey or sightings data. Model fit varied with the complexity of the species' habitat associations, ranging from good for the fisher to poor for wolverine. For the grizzly bear and wolf, we have an extensive body of literature from which to build well-supported conceptual models. For the two remaining species, marten and mountain lion, we lacked much information on regional-scale habitat associations and could build more preliminary conceptual models.

Although attempting to map habitat suitability over such a large study area is useful, even for the poorly known species, we must be aware of the increased uncertainty of our predictions the farther we extrapolate the models from the region for which they were originally developed. For the fisher, lynx, and wolverine, the sightings data used in model creation came exclusively from the U.S. northern Rockies. Any continental scale (north-south) gradient in abundance would be difficult to estimate from sightings data limited to small part of study region. Similarly, the northern range limit for mountain lion lies near the northern limit of our study region. The conceptual habitat model does not accurately capture the decrease in habitat suitability near the range limit. The models may also be weakened if species use contrasting habitat types in different portions of their range. For example, the marten conceptual habitat model may not accurately estimate habitat suitability in more coastal marten habitat (western Fraser Plateau). Boreal plains habitat appears to support low densities of grizzly bears (Mowat et al. 2001, Poole et al. 2001) but shows moderate habitat productivity in our model, which was based on non-boreal habitat associations. Similarly, the mixed hardwood/conifer forest of the central Fraser Plateau, which is distinct from Rocky Mountain forest types, supports higher fisher abundance than predicted in our model. The models may also be weakened where available habitat data is of poorer resolution. Human-impact (census) data was only available to us at coarse resolution for Canada, which affected the accuracy of the wolverine model in which this is a dominant variable. Because the wolverine RSF did not include a factor for protected status, we are probably overestimating the level of threat caused by development within national parks (e.g., Jasper National Park).

There are also varying levels of uncertainty in the dynamic models for the different species. The dynamic model has proven surprisingly robust to variation in poorly-known parameters such as dispersal distance. Of greatest importance in our analysis are the demographic parameters and how they are assigned to habitat classes. Although published demographic data may guide this step for the grizzly bear and wolf, little such data exists for the mesocarnivores. Although new reserves are a necessary component in a credible carnivore conservation strategy, we know less about how the different management of reserves versus non-reserved lands affect habitat suitability for species such as the lynx and fisher, which are not as limited by human impacts as are the large carnivores. Therefore, we use the mesocarnivore PATCH models to identify areas of conservation focus and draw general management guidelines rather than to compare specific portfolios of reserves.

INTEGRATING CARNIVORE AND OTHER CONSERVATION GOALS

The Canadian Rockies ecoregion is an appropriate area for testing methods that integrate the needs of wide-ranging species such as carnivores with other conservation planning tracks such as rare species and ecosystem representation. Carnivore viability is the premier conservation issue in the region, but this goal must increasingly be integrated with the larger mandate of biodiversity conservation. Our results (see Appendix) show that there are no easy shortcuts to conserving biodiversity. We cannot assume that even an intelligently-selected group of potential umbrella species will coincidentally conserve rare species or other special elements. A suite of carnivore species performs fairly well in this region in representing ecosystem-level diversity. However, we would not expect this to be true in ecoregions, unlike the Canadian Rockies, where much of the land base showed levels of human settlement that preclude use by many carnivore species. In those more-developed ecoregions, many ecosystem types would exist only as remnants. Conversely, a representation-based portfolio in such regions, if it ignored development data, would be a poor fit for conserving carnivores. In the Canadian Rockies and other reasonably pristine ecoregions, the overlap between the goals of wide-ranging species and ecosystem representation may simplify reserve design. However, neither approach will compensate for a lack of data on locally-distributed rare species. Lack of such information will be a greater problem in lower-latitude regions with higher rates of endemism than present in the Rocky Mountains.

LANDSCAPE PRIORITIZATION FOR MULTIPLE SPECIES

The reserve design approach used here integrates population viability analysis tools such as PATCH with reserve selection tools such as the SITES program to build more flexible and biologically-realistic conservation strategies. Decisions concerning whether to protect the most vulnerable areas or more secure critical habitat can be made based in part on the strategic timeline and policy focus of a particular organization. The completed reserve designs target areas identified in the SITES runs that use both static model and PATCH-based goals, and add additional linkage areas that appear to affect population distribution in PATCH and also score highly in the SITES "sum runs" results.

FROM RESERVE SELECTION TO RESERVE DESIGN: ASSESSING CONNECTIVITY IN THE PORTFOLIO

This study provides an example of the design of conservation networks in regions where 1) much of the landscape has not yet been developed and thus is in a sense "available" for conservation, and 2) due to this lack of development, intensive biodiversity surveys (e.g., of rare species locations) have not been conducted throughout the region. This example will be increasingly relevant as agencies and NGOs attempt to apply reserve design techniques to other relatively intact regions in western Canada, Alaska, and other continents. If complex reserve selection algorithms such as SITES are to become useful tools for conservation planners, they must be treated as decision-support tools, rather than as a "black box" that can identify a single best portfolio. As with any complex model, the SITES results must be subjected to a sensitivity analysis before they can be confidently used to help make real-world decisions. In regions where data on rare species occurrences is scarce, we can expect high variability in which areas SITES identifies as conservation priorities. Rather than being a wholly negative result, this variability, if it is documented through the sensitivity analysis, can provide flexibility for conservation planners.

When we use the PATCH model to compare SITES portfolios of different size across the study region as a whole, thresholds are evident that help us answer the question "how much is enough?" to ensure carnivore population viability. The answer differs depending on whether one considers the study region as a whole or its various subregions individually. For example, the thresholds evident in the overall analysis (Figure 30) are not seen in the smaller CanRock analysis area (see Appendix). If we divide the study area into three large subregions (the Canadian Rockies north of Kakwa Park, the central Canadian Rockies, and the region south of Highway 3), we might expect to see three distinct responses to increasing portfolio size (Figure 34). In the northernmost region, a relatively small investment in new protected areas would be required to protect populations of large carnivores against landscape change over the next 25 years. In the central Canadian Rockies, which is at the shrinking margins of carnivore distribution, each increase in protected areas results in a corresponding increase in carnivore viability. Therefore no clear thresholds are evident there. In the region from Highway 3 to Yellowstone, a larger investment in new protected areas is necessary before carnivore populations respond with increased distribution. Of course, the response of each species will differ somewhat from these broad generalizations.

If our goal is to prevent the northward retreat of carnivore populations in the region, our results suggest that substantial conservation commitments will be necessary to sustain small transborder populations such as in the Selkirks, Cabinet-Yaak, and Granby areas, and to maintain functional connections between the Northern Continental Divide and more northerly populations. Areas such as the North Fork of the Flathead (British Columbia), which are within linkage zones and predicted as future sinks for some species, are obvious conservation priorities. Our results suggest that protection of the Southern Rocky Mountains Conservation Area (western Highway 3 corridor) will be critical to preserving connectivity in the transboundary region. New research on levels of gene flow in grizzly bear populations in southeastern B.C. (Proctor 2001) demonstrates that functional connectivity may have already been lost between grizzly bear populations in some areas of the transboundary region such as the southern Selkirk Mountains. While the Northern Continental Divide (NCDE) bear population is large enough to be primarily threatened by incremental habitat degradation, the smaller subpopulations to the west are also threatened by the additional demographic risks suffered by small isolated populations in a non-equilibrium metapopulation.

Species presence or absence is often a poor indicator of the importance of an area for maintaining population viability (Tyre et al. 2001). Our PATCH results suggest that reserve design based only on static habitat suitability models may be poor at conserving species that are more vulnerable than expected due to unique aspects of their demography or social structure. In the CanRock region, new portfolio sites capture similar amounts of habitat for both the wolf and grizzly bear, but wolf populations respond more dramatically. This contrast is not evident for the study region as a whole, which is less dominated by rugged terrain. The wolf is more able to use, and, in fact, may depend on, semi-developed, mid-to-low elevation landscapes (Carroll et al. 2001b). The large territory size of the wolf as a social animal may make it particularly sensitive to mortality risk near the boundaries of reserves and other apparently secure areas in fragmented landscapes (Woodruffe and Ginsberg 1998), including those that are naturally fragmented by rugged terrain. These results highlight the fact that in extremely rugged terrain such as the central Canadian Rockies, it may be more challenging to conserve wolves than grizzly bears, the opposite situation as occurs in much of the U.S. Rocky Mountains. The results of the comparison of PATCH scenarios with and without environmental stochasticity suggest that the wolf is also most vulnerable to this factor, as might be predicted by its large home range size (Woodruffe and Ginsberg 1998). Environmental stochasticity does not affect all portions of wolf distribution equally, but instead disproportionately affects the viability potential of more fragmented portions of the distribution, such as corridor areas. This is an example of an "extinction vortex", in that these already vulnerable areas are further impacted by stochastic factors (Gilpin and Soulé 1986).

Our approach allows conservation planners to move beyond such simple design rules as "bigger is better" and "connected is better than disconnected," to rigorous and defensible design prescriptions. It allows planners to address the perennial question – how much is enough? – empirically. Given an agreed-on set of conservation goals, we can derive portfolios of sites that meet these goals. Sometimes several alternative portfolios will meet a set of goals almost equally well, which lends flexibility to the decision-making process.

Our results suggest that although the habitat needs of wide-ranging species overlap with other aspects of biodiversity, they bring a unique component into the conservation planning process by requiring us to consider population viability and habitat configuration in judging the effectiveness of alternative reserve networks. A representation-based reserve network that captures a significant amount of carnivore habitat may be insufficient if the collection of individual sites do not form a functionally connected network. Although carnivore focal species appear to require a larger commitment of the land base than do other conservation goals such as ecosystem representation (assuming that representation goals are typically modest), this may be only because we know more about the biology of individual carnivore species. Meeting the needs of wide-ranging species may help forestall the still poorly-known effects of loss of connectivity on other species and ecosystems by creating a reserve system that is a whole greater than the sum of its parts. Given the contrasts between species, building a conservation strategy that combines priority areas for the entire carnivore guild is challenging. The results of these analyses can help provide a foundation to guide the detailed planning and negotiation necessary to achieve on-the-ground results that will insure the survival of native carnivore populations in the Rocky Mountain region.

CONCLUSIONS AND RECOMMENDATIONS

In summary, our conclusions and recommendations from this study for conserving viable populations of native carnivores in the Rocky Mountains are these:

- Both static and dynamic models provided useful information for carnivore conservation, and management implications from the two types of model were similar. In addition, comparison of model predictions with new survey data suggests that both models were quite robust for large carnivores, but somewhat less so for mesocarnivores.
- Nevertheless, dynamic, spatially explicit population models (e.g., PATCH) provide many advantages over static models, particularly with respect to insights regarding population processes such as source-sink dynamics and the effects of landscape context and alternative future scenarios on population viability. Reserve designs based on static models alone may be poor at conserving species that are more vulnerable than expected due to unique aspects of their demography or social structure (e.g., the wolf, with its large pack territories).
- Carnivores are excellent focal species for regional-scale conservation planning. They are particularly useful in regions where the potential for maintaining or restoring large core areas and broad-scale connectivity is high.
- The umbrella function of carnivores (i.e., where protection of adequate habitat area for carnivore species incidentally protects many other species or ecosystems) is fairly high but incomplete. Coverage of localized rare species or communities is poor. Hence, carnivores may be superior umbrella species in regions, such as the northern Rocky Mountains, with relatively low endemism and habitat heterogeneity.

- A suite of carnivore species provides a better umbrella function than any single species, because the range of habitats covered is greater.
- A contrast in habitat associations exists between carnivore species that use rugged terrain (grizzly bear and wolverine) vs. those that avoid such areas (wolf), and between forest species that are relatively tolerant of human activities (lynx, fisher, black bear) vs. habitat generalists that are less tolerant of human activity (grizzly bear, wolverine, wolf).
- Private lands are less valuable for most carnivore species than their proportion in the region would suggest, but have disproportionately high value for wolf, fisher, and black bear. Hence, current protected areas, which are concentrated in the most rugged portions of the study region (e.g., the central Canadian Rockies), should be augmented by new protected areas in regions of lower topographic relief and higher biological productivity.
- Continuation of recent trends in development on both private and public lands will lead to the loss and fragmentation of carnivore habitat over the next several decades, making some local populations of carnivores more vulnerable to extinction.
- Given no change in the amount or configuration of protected area in the region, populations of most carnivore species can be expected to decline over time as habitat surrounding reserves becomes less suitable and as populations within reserves become more isolated. Substantial conservation commitments will be needed to prevent the northward retreat of carnivore populations in the region and sustain small transboundary populations.
- Thresholds are apparent in the effect of increased habitat protection on population viability, with increasing network size having the greatest effect on population viability up

to approximately 37% of the study region.

- Tradeoffs must be addressed between allocating scarce conservation resources toward protecting strong population source areas, stemming the degradation of lands surrounding reserves, or restoring linkages that are already degraded to some degree, but which might contribute to long-term persistence of metapopulations.
- A useful way to resolve tradeoffs and prioritize conservation actions is to plot the irreplaceability of sites (i.e., the relative extent to which they contribute to conservation goals) vs. their vulnerability (i.e., their risk of being degraded in the near future). In the context of species conservation, irreplaceability can be approximated as the predicted rate of population growth (i.e., the value of a site as source habitat), and vulnerability can be measured by the predicted decline in growth rate over a defined period of time, given particular trends in habitat conditions.
- Probably the two highest-priority areas for habitat conservation to enhance populations of carnivores in the study region are 1) the area between the Muskwa Kechika conservation areas and Jasper National Park in northern British Columbia and Alberta, and 2) north-central Idaho. Both of these regions combine high biological productivity and relatively low human influence, yet both are threatened by ongoing development and resource extraction. New protected areas and linkages are needed to connect the Muskwa-Kechika area to Jasper National Park and to connect protected areas in central Idaho northeastward to the Northern Continental Divide Ecosystem and eastward to the Greater Yellowstone Ecosystem.
- A third priority area for conservation is the transboundary region, from the Northern

Continental Divide Ecosystem (e.g., the North Fork of the Flathead River, adjacent to Waterton Lakes and Glacier National Parks) north across Hwy. 3 (in the vicinity of Crowsnest Pass) to Banff National Park. This area is already a strong filter, if not absolute barrier, to several carnivore species, and will significantly isolate carnivore populations to the north and south unless conservation actions are implemented quickly. Our results suggest that adding reserves in the transboundary region would prevent the loss of connectivity between the Northern Continental Divide Ecosystem and the Canadian Rocky Mountain parks and sustain smaller grizzly bear populations in southeastern British Columbia and the northern U.S.

- The level of uncertainty that propagates through the models used in this study suggests that they are most informative for identifying generalized areas of conservation emphasis rather than exact reserve or management boundaries. Hence, our study provides a regional-scale picture of conservation priorities, which must be supplemented by site-level analysis and planning.

APPENDIX I - INTEGRATING CARNIVORE AND OTHER CONSERVATION GOALS IN THE CANADIAN ROCKIES ECOREGION

METHODS

For this task, we coordinated our work with The Nature Conservancy (TNC) and Nature Conservancy of Canada's (NCC) Canadian Rockies (CanRock) ecoregional planning team, whose study region encompasses the central portion of the RMC study area (Figure 2). The goal of the TNC ecoregional planning process is to identify a conservation network or portfolio of areas that, taken together, will conserve all aspects of biodiversity in perpetuity (Groves et al. 2000). While earlier ecoregional plans primarily emphasized the special elements and representation approaches, the CanRock plan, through its coordination with the RMC project, is one of the first to integrate the focal species approach into portfolio design. It thus can provide a model for balancing the needs of these three facets of biodiversity in other regions. We thank the members of the CanRock planning team, especially Bart Butterfield, for their help in making this aspect of the analysis possible.

CONSERVATION TARGETS

Carnivores

Five of the carnivore species studied in the larger RMC analysis - grizzly bear, wolf, lynx, wolverine, and fisher - were identified as conservation targets for the CanRock region by the TNC/NCC planning team. We used the values from the static habitat suitability models as targets in the SITES analysis as described below.

Special elements

Following guidelines established by The Nature Conservancy (Groves et al. 2000), we identified special element targets by considering species with Heritage ranks of G1 (critically imperiled globally) to G3 (vulnerable globally), and then added other species of special concern due to factors including declining population trends or status as an endemic, disjunct, or vulnerable population. We generally omitted G3 taxa that are peripheral or widespread and whose occurrences in the ecoregion have low contribution to species' viability. Element occurrence data were assembled for several types of conservation targets:

1) Rare plant community occurrences

2) Expert-nominated best examples of more widespread plant communities

3) Rare vascular and non-vascular plant species

4) Terrestrial animals that are either rare (6 gastropods) or declining (4 amphibians, 1 butterfly, Townsend's big-eared bat (*Corynorhinus townsendii*) and Merriam's shrew (*Sorex merriami*))

5) Breeding sites for several bird species that are declining or of special concern: Common Loon, Trumpeter Swan, Harlequin Duck, Bald Eagle, White-tailed Ptarmigan, Short-eared Owl, Black Swift, and Black Rosy-Finch.

The special element goals for the SITES runs sought to capture within the portfolio a set proportion of the known occurrences of each species or community type. All occurrences of the rarest elements were targeted. For more common species, the goal was the proportion of the known occurrences thought to be sufficient to insure viability of the population.

<u>Representation</u>

Ecosystem-based conservation strategies include the goal of representing all major environmental gradients. This approach aids in conserving ecological processes and species habitats within their natural range of variability, which provides a buffer against climate change and other environmental changes. This “coarse filter”is also hypothesized to capture occurrences of species about which little is known (and therefore would not be captured by the special elements or focal species approaches) (Noss 1987, Groves et al. 2000). Although Natural Heritage programs have been reasonably successful at tracking locations of rare species, only a few programs have tracked rare plant communities, and fewer still track common plant communities. In the absence of good maps of how plant communities are distributed in response to environmental gradients, we built our representation goals around Ecological Land Units (ELUs). A variety of factors, including aspect, temperature, soil moisture, and plant-available nutrients, can be considered driving abiotic variables influencing vegetation pattern across the earth’s surface. Indirect measures of these variables may be combined with a vegetation map to characterize and assess biophysical variation captured by the set of conservation sites (Noss et al. 1999, in press). These measures include elevation, landform, slope, aspect, hydrologic regime, and surficial geology. Landform character (e.g., Ridge Top, Steep Slope, Toe Slope) is primarily a function of slope angle - from flat topography to steep cliff faces, and landscape position - from lowest to highest, relative to adjacent areas. A Surface Flow Index was used to differentiates land that is very wet, merely moist to very dry based on their surrounding catchment area. Each landform was further modified by its surficial geology class. Finally, all landforms were nested within elevation zones. The coarse-scale map of potential vegetation type or biogeoclimatic zone

(DeMarchi and Lea 1992) was then overlaid on the ELUs across the entire ecoregion. Representation targets were set at 10% of each ELU/vegetation type combination, and at least 30% of each overall vegetation type.

COMPLEMENTARITY AND SENSITIVITY ANALYSES

The alternative scenarios that we explored by varying the inputs to the SITES function fall into two categories: complementarity of carnivore and non-carnivore goals and general sensitivity analysis. To evaluate the ability of carnivore focal species to acts as umbrellas for special element and representation targets, we ran SITES portfolios with only carnivore targets and measured the amount of non-carnivore biodiversity coincidentally captured by the carnivore portfolio. We also performed a similar analysis of the ability of non-carnivore targets to coincidentally protect carnivores. We also varied the target level used for the carnivore goals from 0% to 50% of the total habitat "value" in the region.

In our sensitivity analysis, we varied how current protected areas were treated by either locking or not locking them into the SITES solutions. We also varied to what extent the conservation portfolio was well distributed across the region by either stratifying or not stratifying the goals by subregions (ecosections) (Figure 2). We also altered how the "cost" of land varied across the landscape. For a few SITES runs, we used an area-based cost estimate identical to that used in the overall RMC analysis. For most CanRock SITES runs, however, we multiplied the site area by an index (habitat effectiveness - Merrill et al. 1999) that measured the level of development (human population and roads) under the assumption that land would be more expensive in more developed areas. The formula took the form Cost = [Area * (1 - Habitat

Effectiveness)] + 300. This cost structure was chosen based on a decision by the CanRock TNC/NCC planning team. We discovered that SITES solutions are very sensitive to seemingly trivial variation in the details of the cost equation. We chose a base cost of 300 units, which gives a tenfold range in cost between the least and most expensive areas, after evaluating several other cost equations.

RESULTS

COMPARING PORTFOLIOS BASED ON CARNIVORE GOALS WITH THOSE BASED ON SPECIAL ELEMENTS AND REPRESENTATION GOALS

As stated above, we report SITES scenarios that "lock in" protected areas as the most informative for land use planning, but also report results from the "not locked in" SITES solutions to assess the distribution of biodiversity across the landscape without regard to political boundaries. We compared two contrasting non-locked-in portfolios based on either carnivore goals or non-carnivore goals. For the purposes of this comparison, we set carnivore goals at a level - 35% - that produced a reserve network of the same size as the non-carnivore portfolio, about 31% of the region (Table 8). About half (55%) of each portfolio was shared, that is, selected in both the carnivore and non-carnivore reserve networks (Figure 35). Because only a 31% overlap would be expected between two randomly-located portfolios of this extent, this indicates a moderate degree of overlap between carnivores and other facets of biodiversity. Using another measure, the "sum runs" outputs for the two portfolios are highly correlated ($R = 0.59$, $p < 0.001$). Areas of overlap (shown in blue in Figure 35) tend to be located in those regions with both high biological productivity and low human impacts, including the Clearwater drainage

(Idaho), the Purcell Wilderness, Wells-Gray and Kootenay Parks (B.C.), and portions of the Rocky Mountain Front. These areas are, of course, relatively rare (Carroll et al. 2001a), because settlement and human impacts have tended to occur first in lower elevation, productive sites. Areas selected only in the carnivore portfolio (shown in green in Figure 35) tend to lie in the northern, less-developed portions of the ecoregion. Areas selected only in the non-carnivore portfolio (shown in orange) are scattered throughout the region, due to the more fragmented distribution of non-carnivore targets such as rare species occurrences. Though the specific level of overlap will vary, these general patterns are likely to be applicable in other ecoregions.

WHAT CARNIVORE SPECIES DID NON-CARNIVORE GOALS PROTECT?

A SITES solution without carnivore goals, and without locking in existing parks, encompasses 31.9% of the ecoregion. The solution captures 30-34% of the total habitat value for the different carnivore species. Value captured is slightly lower for lynx (30.4%) and fisher (30.7%), and higher for grizzly bear (33.3%), wolverine (33.7%), and wolf (34.0%). We saw above that a carnivore-based portfolio captured 35% of total habitat value in a similar-sized portfolio. The non-carnivore-based portfolio captures only slightly more carnivore habitat than that captured in a random portfolio, but at least is not biased against representation of certain species. This bias is a problem with current protected areas, which are disproportionately in higher-elevation areas. Protected areas, which comprise approximately 22.6% of the region, capture disproportionately large amounts of habitat value for wolverine (31.6%), grizzly bear (25.5%) and wolf (23.5%), but perform poorly at capturing habitat value for lynx (17.7%) and especially fisher (9.9%) (see also Carroll et al. 2001a). In summary, a reserve network based on representation and special element goals gives more balanced protection to focal species than do current protected areas, but does not do this in the most efficient manner.

WHAT TYPES OF NON-CARNIVORE GOALS DID CARNIVORE GOALS CAPTURE AND MISS?

A SITES solution developed from carnivore goals only (35% level) was evaluated for its success in capturing non-carnivore goals. Although the use of a diverse set of carnivore species produced a better “umbrella” effect than would the use of a single species, we found that coverage varied widely depending on the type of non-carnivore goal (Table 9). Overall, coverage of special elements was poorer than coverage of representation targets. However, this may be partially an artifact of the lack of survey effort for rare species in the northern portions of the ecoregion. Very few special elements are recorded in British Columbia as compared the United States (Figure 2). Because British Columbia also contains the best carnivore habitat, this “white hole” in the special elements data leads to artificially poor congruence between carnivore and special elements targets. In this ecoregion, coverage of representation (ELU) targets may give a more accurate assessment of the ability of carnivores to serve as umbrella species. Whereas the proportion of targets covered by carnivores ranged from 19% (non-vascular plants) to 50% (birds) for special elements, carnivores covered 76% of the representation targets (Table 9).

COMPARISON OF SITES SOLUTIONS WITH DIFFERING CARNIVORE TARGET LEVELS

We compared non-locked SITES solutions which included both non-carnivore goals and differing target levels of carnivore habitat goals (Figure 36). As noted above, a SITES solution based on special elements and terrestrial representation goals alone (shown in dark red in Figure 36) coincidentally captured about 30% of carnivore habitat value for all five species. Therefore, adding a carnivore goal of 30% adds areas of only minor extent (shown in light red). As carnivore targets are increased to 40% (shown in orange) and then to 50% (shown in yellow), the portfolio adds areas in northcentral Idaho and between Wells-Gray and Jasper Parks, as well as smaller areas in the Cabinet-Yaak (MT) and Monashee Mountains (B.C.). Total size of the portfolio is close to 31% of the region for the 0% and 30% goals (Table 8). Portfolio size increases to 38% and then 47% of the region for the 40% and 50% carnivore goals, respectively. Largely, the solutions with differing target levels are nested within each other, such that the larger portfolios include most of the sites contained in the smaller ones.

PROTECTED AREAS IN THE NON-LOCKED PORTFOLIOS: WHAT PORTIONS OF THE PARKS ARE MOST IMPORTANT FOR BIODIVERSITY?

Even when protected areas are not "locked in" to the SITES solution, they tend to be included more often than do non-protected areas. This is somewhat more pronounced when carnivore goals are present (Table 8). However, even non-carnivore-based portfolios assume that "cost" of land is lower within less-developed areas. Thus they tend to favor inclusion of park lands if they contain significant amounts of the conservation targets. Protected areas also often tend to have more complete data on occurrences of rare species, which would bias them towards inclusion in the portfolio. However, portions of the Rocky Mountain Parks (Alberta and B.C.) that are primarily "rock and ice" are generally not included in either the non-carnivore or carnivore-based portfolios (Figure 35).

THE “LOCKED-IN” SITES SOLUTIONS

The previous examples help show where carnivore and other biodiversity are distributed in the region and what factors can influence the SITES solutions. We can now use the portfolios that start from the existing protected area network to help inform a practical strategy for biodiversity conservation. Figure 37 shows existing protected areas in purple. A locked-in portfolio with 0% carnivore goals adds the areas shown in dark red. A 30% goal adds the areas in bright red, which, as we saw with the non-locked-in examples, are of minor extent. A 40% goal adds the areas in orange, and a 50% goal adds the areas in yellow. In general, all the locked-in portfolios choose to add new sites in the relatively unprotected transboundary region and northcentral Idaho, as well as adding areas to the periphery of the Canadian parks. Although SITES cannot explicitly target functional connectivity as a goal, when boundary length is a significant component of cost it will generally seek to build larger reserves from several small reserves, as in southeastern B.C. Raising the carnivore goals to greater than 30% adds additional areas in northcentral Idaho and near Wells-Gray and Jasper Parks in Canada, as well as smaller areas in the Monashee Mountains (B.C.). It is somewhat surprising that including current protected areas in the portfolio, although it changes the location of new priority sites, does not reduce the size of the final conservation network (measured as the area of existing parks plus new portfolio sites) (Table 8). In other words, even if SITES already credits all biodiversity values within the parks as part of the solution, it still must add the same amount of non-park area as it would when starting from a blank slate. This may be because many targets are associated with low-elevation productive sites that are poorly represented in current protected areas.

HOW WELL DO THE SITES SOLUTIONS FUNCTION AS CONSERVATION NETWORKS?: RESULTS FROM THE PATCH MODEL

As the SITES carnivore goals were increased and the resulting portfolios grew in size, the portfolios captured an increasing proportion of the current carrying capacity of the region for that species (Table 10). This increase was linear and similar for both the grizzly bear and wolf, although the wolf benefitted slightly more from new portfolio sites in the transboundary region. Both the locked and non-locked portfolios based on special elements and representation (carnivore goal 0%) capture similar amounts of habitat value. However, because a portfolio that builds on current parks results in larger core areas, this locked portfolio is better able to maintain carnivore populations in the face of landscape change (Table 10, last column). In another example, contrasting a “no-action” scenario with the “carnivore 40% locked” SITES solution (Table 10), we find that the latter portfolio adds the same amount of habitat value for grizzly bear and wolf. However, wolf population responds 56% more strongly to this increased protection than do grizzly bear populations (Figure 38 and Table 10, last column).

When we contrast the future distribution of grizzly bear and wolf under the “no-action” scenario to that under the “carnivore 40% locked” SITES solution (Figure 39), we find that the portfolio’s addition of sites in the transboundary region, as well as the addition of a corridor in the form of the Southern Rocky Mountains Conservation Area (Highway 3 region), prevents the loss of connectivity between the NCDE and the Rocky Mountain Parks and sustains smaller subpopulations in southeastern B.C. and the northern U.S.. Grizzly bear populations in the

Selkirks and Granby show increased viability (Figure 39a). The wolf shows similar, but more broadly distributed increases in distribution (Figure 39b).

SENSITIVITY ANALYSIS

Uncertainty and flexibility in the SITES solutions

In Figure 40, the best portfolio out of 100 alternate SITES runs (40% carnivore goals plus non-carnivore goals, not locked) is shown in blue hatching. The percentage of times an area was included in one of those 100 runs is shown in red with darker areas selected more often. Areas in the U.S. and transboundary region show little flexibility, as most red areas are overlain by the blue final portfolio. In contrast, in the northern portion of the portion, many red areas, or alternate sites, lie outside of the final portfolio. Some of these areas could become potential corridor areas in the final conservation design.

Effect of cost structure and stratification decisions

Complex models are less useful when they are highly sensitive to a parameter that is difficult to measure accurately. Although estimating land costs on an ecoregional scale is difficult, SITES appears fairly sensitive to this parameter. The alternate portfolios shown in Figure 41 were created using the same conservation goals (40% carnivore goals plus non-carnivore goals, not locked) but with cost measured either by the area of a site or by our more complex cost formula that includes information on human impacts. Areas in orange in the figure were chosen only in the area-based cost example, while areas in green were chosen only in the “normal” cost example. Areas in blue are common to both scenarios. The scenarios are of similar size (38% of the region), but only two-thirds of each scenario is common to both solutions. Using development data in the cost calculations moves more of the portfolio into the less-settled northern portions of the region.

The portfolio results are less sensitive to the decision about whether carnivore habitat should be well-distributed (i.e., stratified by ecosection). Between 72 and 74% of the portfolio is shared by both the stratified and non-stratified runs (shown in blue in Figure 42). Areas in green in Figure 42 are chosen only in the stratified runs and areas in orange are chosen only in the unstratified runs. Because the narrow ecosections used as strata run north to south (Figure 2), stratification tends to move sites away from the large parks on the eastern edge of the region.

APPENDIX II: EFFECTS OF LANDSCAPE CHANGE AND CONSERVATION OPTIONS ON LARGE CARNIVORES: CASE STUDY - THE CANADA/U.S. TRANSBOUNDARY REGION, INCLUDING THE HIGHWAY 3 CORRIDOR

We summarize here results of a case study using carnivore habitat and viability models to address conservation options in the Canada/U.S. transboundary region. The simulation results we report here are equilibrium predictions, in that "current" predictions depict the current capacity for an area to support a carnivore species over the long-term (200 years), which may be lower (e.g., grizzly bears in southeastern B.C.) or higher (grizzly bears in central Idaho) than the number of animals currently inhabiting an area. The simulation model used (PATCH) is most informative at scales that encompass many home ranges of the species of interest. For large carnivores with home range sizes of 100-1000 km^2 this would mean at the regional scale (e.g., the northern Rocky Mountains). For this case study, we apply PATCH to the sub-regional scale (e.g., the transboundary region) in order to assess its utility in informing more detailed land use decisions. However, it would be inappropriate to use the model to address land use questions at fine scales within a home range. The accuracy of results from a complex model such as PATCH is contingent on the parameters used in the simulations. The demographic parameters and habitat models used here meet the test of plausibility and results have been validated against new field data. However, even in well-studied carnivore species, much uncertainty inevitably remains as to the relationship between habitat, fecundity, and mortality. Therefore, we present model predictions as model-based hypotheses subject to further testing. We focus on the transboundary region because this area lies near the southern margin of continuous distribution for several large carnivores, and because it is an area of human settlement separating large parks and undeveloped areas to north from more isolated southern refugia ranging in size from Glacier/Waterton in the Northern Continental Divide Ecosystem (NCDE) to smaller areas such as the Idaho Selkirks, the Cabinet/Yaak (Montana), and Granby areas (Figure 43). The species considered here are the grizzly bear (*Ursus arctos*), gray wolf (*Canis lupus*), and wolverine (*Gulo gulo*). Other mesocarnivores such as lynx (*Lynx canadensis*) and fisher (*Martes pennanti*) are treated in the larger report but not in this case study because of their more complex response to human-associated development and protected area designation. However, the transboundary region may also be of conservation concern for these species due to lack of continuously-distributed suitable habitat that could facilitate regional connectivity.

The land use scenarios considered here include:

1) current carrying capacity

2) current trends to 2025, assuming development on both public and private lands

3) current trends to 2025, assuming no further road construction on public lands

4) creation of an absolute barrier or zone of inhospitable habitat along the Highway 3 corridor

5) proposed Waterton Park expansion enlarging the park to encompass areas primarily in the North Fork of Flathead (B.C.)(Figure 43)

6) proposed Southern Rocky Mountains Conservation Area (SRMCA) connecting the NCDE to the Rocky Mountains parks across the Highway 3 corridor in the area of Fernie, B.C. (Figure 43) We assume here that the SRMCA would be managed under a mandate similar to that in Waterton.

Finally, we contrast these results with the effects of scenarios 1-3 in northeastern B.C. (Peace River lowlands/Muskwa Plateau).

RESULTS

Grizzly bear

Under current conditions without restoration, there is little long-term probability of maintaining a continuous population across the Highway 3 corridor. Connectivity is defined in this case as continuous distribution, rather than occasional dispersal events by transient individuals. The highest probability of connectivity is within areas identified as linkage zones by Clayton Apps and others north of the town of Fernie (B.C.)(Figure 44). The area south of Fernie is also a possible but less likely linkage. The Alberta portion of the Highway 3 area is less likely to facilitate connectivity, but merits conservation focus due to potential range loss to the north and south of the highway. Predicted landscape change to 2025 makes the above connection even more tenuous due to the retreat of grizzly bear range to the south and north (Figure 44). The remaining potential for viability in the Idaho Selkirks is lost by 2025 unless additional conservation steps besides those considered here are taken in southeastern B.C. There is a noticeable negative ripple effect of habitat loss in other parts of southeastern B.C. on grizzly bear distribution to the north of Highway 3, making it more difficult to maintain connectivity there. Loss in demographic potential (lambda) is greatest along the Rocky Mountain Front and in the Columbia Trench (Figures 45 and 46). Assuming no further road construction on public lands greatly reduces range loss, but it is still extensive in the Rocky Mountain Front, the immediate Highway 3 corridor, and the Columbia Trench (Figure 47). The effect of an absolute barrier or hostile habitat in the Highway 3 corridor is noticeable under current conditions, but minor under 2025 conditions, as development will have already effectively excluded bears from the highway zone. The Waterton expansion is effective at counteracting the effects of landscape change to the south of the highway, but the SRMCA is most effective at retaining a level of connectivity at or higher than the current condition, despite increasing development in other parts of transboundary region (Figure 48). The ripple effect for both the Waterton expansion and the SRMCA is most pronounced to the west of Flathead, but is also extensive beyond boundaries of the proposed park areas in both Alberta and B.C.

Wolf

Current carrying capacity supports a continuous distribution across Highway 3 throughout the area (Figure 49a). Connectivity is most pronounced on the Alberta side of border south of the Bob Creek Wildland. By 2025, under current trends, long-term connectivity is effectively lost (Figure 49b). Loss in carrying capacity is more widespread throughout the region than was seen for the grizzly bear because the wolf is more tolerant of human impacts and hence currently uses more of the landscape matrix (Figure 50). Loss in demographic potential for wolves is greatest along Rocky Mountain Front. The SRMCA would preserve connectivity both within its boundaries and through a ripple effect in the Alberta Highway 3 area (Figure 51). Greater dispersal ability and hence interlinkage of populations in the wolf versus the grizzly bear makes the effect of the Highway 3 absolute barrier more noticeable, but still of little impact by 2025 as development trends alone approximate a barrier there. The positive ripple effect of the SRMCA is similar though not as strong as for the grizzly bear. The effect of Waterton expansion is less pronounced than for the bear (Figure 51).

Wolverine

The largest range loss due to development from 2000 to 2025 occurs in southeastern B.C. to the northwest of Highway 3, in the Idaho Selkirks, and in the southern Rocky Mountain Parks. The NCDE populations remain continuous with the Rocky Mountain parks due to the species' high dispersal abilities when compared with the grizzly bear.

Northeastern British Columbia

Currently the large carnivore species are well-distributed throughout this area, which is close to strong source populations. Because the area is in an earlier stage of the process leading to extirpation, landscape change there results in changes in the demographic role of a site from source to sink rather than actual range contraction. Reduction in carrying capacity in the next 25 years is largely confined to the area near and to the north of Fort St. John for grizzly bear (Figure 52a) and wolf, but is more extensive for the wolverine. Reduction in demographic potential (lambda) is however extensive along the eastern portion of Muskwa Plateau, northward along the Alaska Highway, and eastward along Hart Highway (Chetwynd)(Figure 52b). The latter may forecast the early stages of fragmentation between the Muskwa and Rocky Mountain Parks.

It is evident that these modeling techniques can provide information at the subregional scale on the efficacy of alternative restoration options and contrasts between species in their response to landscape change. One conclusion, which reinforces earlier work by other researchers, is that restoration is already necessary in the transboundary region and that current trends, if left unchecked, may create an effective barrier to connectivity there within the next few decades.

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Figure 50. Reduction in potential wolf carrying capacity in the Canada/U.S. transboundary region from 2000-2025 as predicted by the PATCH model, assuming road development on both private and public lands (a), or assuming road development on private lands only (b). Areas in dark red show greatest reduction in potential occupancy due to expected human population growth and landscape change.

Figure 51. Increase in potential wolf carrying capacity in the Canada/U.S. transboundary region under future landscape conditions (2025), assuming road development on both private and public lands, given park expansion within the proposed Waterton expansion area (a), or SRMCA area (b).

Figure 52. Reduction in potential grizzly bear carrying capacity (a) or demographic potential (b) in northeastern British Columbia from 2000-2025 as predicted by the PATCH model, assuming road development on both private and public lands.

Table 1. Summary of static habitat suitability models by species, showing type of model and input variables.

MODEL TYPE	CONCEPTUAL				EMPIRICAL (RSF)			
SPECIES	GRIZZLY BEAR	WOLF	MOUNTAIN LION	MARTEN	WOLVERINE	LYNX	FISHER	BLACK BEAR
VARIABLE								
Brightness						X	X	X
Greenness	X	X	X			X	X	X
Wetness							X	X
Precipiatation							X	
Snowfall				X	X			
Road density	X	X	X					X
Human population	X	X	X		X			
Topography		X	X		X	X	X	X
Tree Closure				X				
Protected status								X
Elevation/Latitude						X	X	X

Table 2. Summary of GAP analysis of static model results for the RMC study region.

MANAGEMENT CLASS	% OF REGION	PERCENT OF HABITAT VALUE							
		Grizzly bear	Wolf	Wolverine	Lynx	Fisher	Black bear	Mountain lion	Marten
PRIVATE	24.6	19.2	13.3	8.6	10.4	14.9	11.0	9.7	6.8
GENERAL PUBLIC	58.2	61.6	67.0	67.8	74.7	63.7	59.4	68.4	72.0
PROTECTED NON-PARK	7.0	7.7	7.9	9.7	5.7	15.1	19.5	10.1	9.9
PARK	10.2	11.5	11.9	13.9	9.2	6.3	10.2	11.8	11.3

Table 3. Summary of GAP analysis of PATCH model results for the RMC study region, part 1.

MANAGEMENT CLASS	% OF REGION	PERCENT OF POTENTIAL CARRYING CAPACITY						MEAN DEMOGRAPHIC POTENTIAL (LAMBDA)					
		Grizzly bear		Wolf		Wolverine		Grizzly bear		Wolf		Wolverine	
		2000	2025	2000	2025	2000	2025	2000	2025	2000	2025	2000	2025
PRIVATE	24.6	14.0	11.8	13.1	10.0	8.0	6.0	.96	.96	.96	.97	.97	.98
GENERAL PUBLIC	58.2	63.0	62.7	67.9	69.1	66.8	67.5	1.02	1.02	1.03	1.02	1.02	1.01
PROTECTED NON-PARK	7.0	8.5	9.1	8.2	8.6	9.9	10.9	1.08	1.07	1.06	1.05	1.05	1.04
PARK	10.2	14.4	16.4	10.9	12.2	15.3	15.6	1.12	1.12	1.06	1.06	1.05	1.02

Table 4. Summary of GAP analysis of PATCH model results for the RMC study region, part 2.

MANAGEMENT CLASS	% OF REGION	PERCENT LOSS IN DEMOGRAPHIC POTENTIAL (LAMBDA)			PERCENT SHARE OF STRONG SOURCE HABITAT (2000)			PERCENT SHARE OF STRONG SINK HABITAT (2000)		
		Grizzly bear	Wolf	Wolverine	Grizzly bear	Wolf	Wolverine	Grizzly bear	Wolf	Wolverine
PRIVATE	24.6	20.8	16.0	8.2	4.0	3.8	3.8	36.2	33.8	26.6
GENERAL PUBLIC	58.2	68.1	70.4	58.0	56.7	63.7	61.0	59.4	57.1	63.7
PROTECTED NON-PARK	7.0	6.2	6.8	8.1	13.5	14.9	15.2	2.9	2.3	4.7
PARK	10.2	4.9	6.8	25.7	25.8	17.6	20.0	1.5	6.8	5.0

Table 5. Results of comparison of grizzly bear hair snag data with regional-scale model predictions.

STUDY AREA	ALBERTA	PROPHET	SELKIRK	OVERALL
% SITES W/ GRIZZLY BEAR	17.6	20.9	22.9	20.6
% HABITAT SUITABILITY	61.7	80.6	64.2	71.0
% OCCUPANCY - PATCH MODEL	72.2	100	98.9	91.9
OBSERVED VS HAB. SUIT.	ns	##	####	####
OBSERVED VS PATCH	ns	n/a *	####	####

* Prophet area PATCH predictions were 100% occupancy for all sites

Degrees of freedom =
Alberta - 321
Prophet - 485
Selkirk - 378
Overall - 1188

Significance levels for wilcox rank sum test:

$p < .001$
$p < .01$
$p < .05$
ns $P > .05$

Table 6. Summary of SITES portfolios for the RMC study region

PORTFOLIO GOALS		TOTAL% OF REGION	PERCENT IN MANAGEMENT CATEGORY			
Regional (%)	Local (%)		PARK	PROTECTED NON-PARK	GENERAL PUBLIC	PRIVATE
30 RSF	20 RSF	27.2	34.2	22.5	34.1	9.2
30 RSF/PATCH	20 RSF/PATCH	27.3	34.0	22.4	34.5	9.2
40 RSF	30 RSF	36.4	26.7	17.5	44.6	11.2
40 RSF/PATCH	30 RSF/PATCH	36.4	26.2	17.5	44.2	12.1
50 RSF/PATCH	30 RSF/PATCH	44.6	22.3	14.6	51.9	11.2

Table 7. Evaluation of SITES solutions for the RMC region using the PATCH model.

PORTFOLIO GOALS		TOTAL% OF REGION	PERCENT OF RSF HABITAT VALUE			SHARE OF CURRENT CARRYING CAPACITY (PATCH MODEL)			TOTAL REGIONAL CARRYING CAPACITY 2025 (AS % OF 2000 CAPACITY)	
Regional (%)	Local (%)		GRIZZLY	WOLF	WOLV-ERINE	GRIZZLY	WOLF	WOLV-ERINE	GRIZZLY	WOLF
30 RSF	20 RSF	27.2	30.1	30.9	34.8	33.1	29.9	35.6	95.1	--
30 RSF/PATCH	20 RSF/PATCH	27.3	30.1	31.0	34.8	33.2	29.9	35.4	95.4	97.4
40 RSF	30 RSF	36.4	40.0	41.0	45.0	43.0	39.8	45.3	100.8	--
40 RSF/PATCH	30 RSF/PATCH	36.4	40.1	41.1	44.6	43.2	39.9	45.2	101.3	103.7
50 RSF/PATCH	30 RSF/PATCH	44.6	50.1	52.1	57.0	54.8	50.9	58.0	104.3	105.9
CURRENT PROTECTED AREAS		17.2	19.2	19.8	23.6	22.9	19.1	25.2	85.6	86.2

Table 8. Summary of SITES portfolios for the Canadian Rockies ecoregion

PORTFOLIO	% OUTSIDE PARKS	% INSIDE PARKS	TOTAL% OF REGION	TOTAL PLUS PARKS
NOT LOCKED				
CARNIVORE 0%	60.1	39.9	31.3	41.4
CARNIVORE 30%	61.4	38.6	31.6	42.0
CARNIVORE 40%	63.2	36.8	38.3	46.8
CARNIVORE 50%	63.0	37.0	46.8	52.1
CARNIVORE 50% ONLY	61.5	38.5	46.0	50.9
LOCKED				
CARNIVORE 0%	46.6	53.4	42.3	42.3
CARNIVORE 30%	47.2	52.8	42.8	42.8
CARNIVORE 40%	51.7	48.3	46.8	46.8
CARNIVORE 50%	56.7	43.3	52.2	52.2
CARNIVORE 50% ONLY	55.2	44.8	50.5	50.5
CURRENT	0	100	22.6	22.6

Table 9. Capture of non-carnivore targets by CanRock carnivore (35% target, non-locked) portfolio

CLASS OF TARGET	NUMBER OF TARGETS	NUMBER MET	PROPORTION MET	AVERAGE SHORTFALL
Vascular plants	215	56	26%	89%
Non-vascular plants	57	11	19%	94%
Birds	36	18	50%	89%
Gastropods	12	1	8%	94%
Amphibians	14	6	43%	94%
Rare mammals	11	3	27%	90%
Carnivores	55	55	100%	N/A
Butterflies	5	2	40%	90%
Rare plant communities	105	40	38%	95%
ELU/Vegetation types	3052	2327	76%	74%
Matrix plant communities	75	26	35%	64%
Riparian communities	34	17	50%	46%
Patch plant communities	170	86	51%	74%
Wetlands	11	7	64%	58%
TOTAL (excluding carnivores)	3796	2600	68%	78%

Table 10. Evaluation of CanRock SITES solutions using the PATCH model

SITES SOLUTION	PERCENT OF REGION (PARKS INCLUDED)	PERCENT OF RSF HABITAT VALUE (INCLUDING PARKS)		SHARE OF CURRENT CARRYING CAPACITY (PATCH MODEL)		TOTAL REGIONAL CARRYING CAPACITY 2025 (AS % OF 2000 CAPACITY)	
		GRIZZLY	WOLF	GRIZZLY	WOLF	GRIZZLY	WOLF
no action (parks alone)	22.6	25.5	23.5*	32.9	27.9	92.9	92.7
carnivore goal 0%, parks not locked	41.4	44.5	43.4	49.1	46.2	102.2	107.1
carnivore goal 0%, parks locked in	42.3	44.5	43.7	49.0	46.4	106.7	116.8
carnivore goal 30%, parks locked in	42.8	45.2	44.5	49.8	47.3	106.7	114.0
carnivore goal 40%, parks locked in	46.8	49.8	49.5	53.9	52.3	109.2	118.8
carnivore goal 50%, parks locked in	52.2	55.6	56.0	58.8	58.3	112.8	125.6

*approximate due to areas of missing data

Figure E1. Map of study area in the Rocky Mountains of Canada and the United States. Protected area complexes and the proposed Southern Rocky Mountains Conservation Area are shown. The subregion used for comparison of carnivore and non-carnivore reserve designs is shown by cross-hatching.

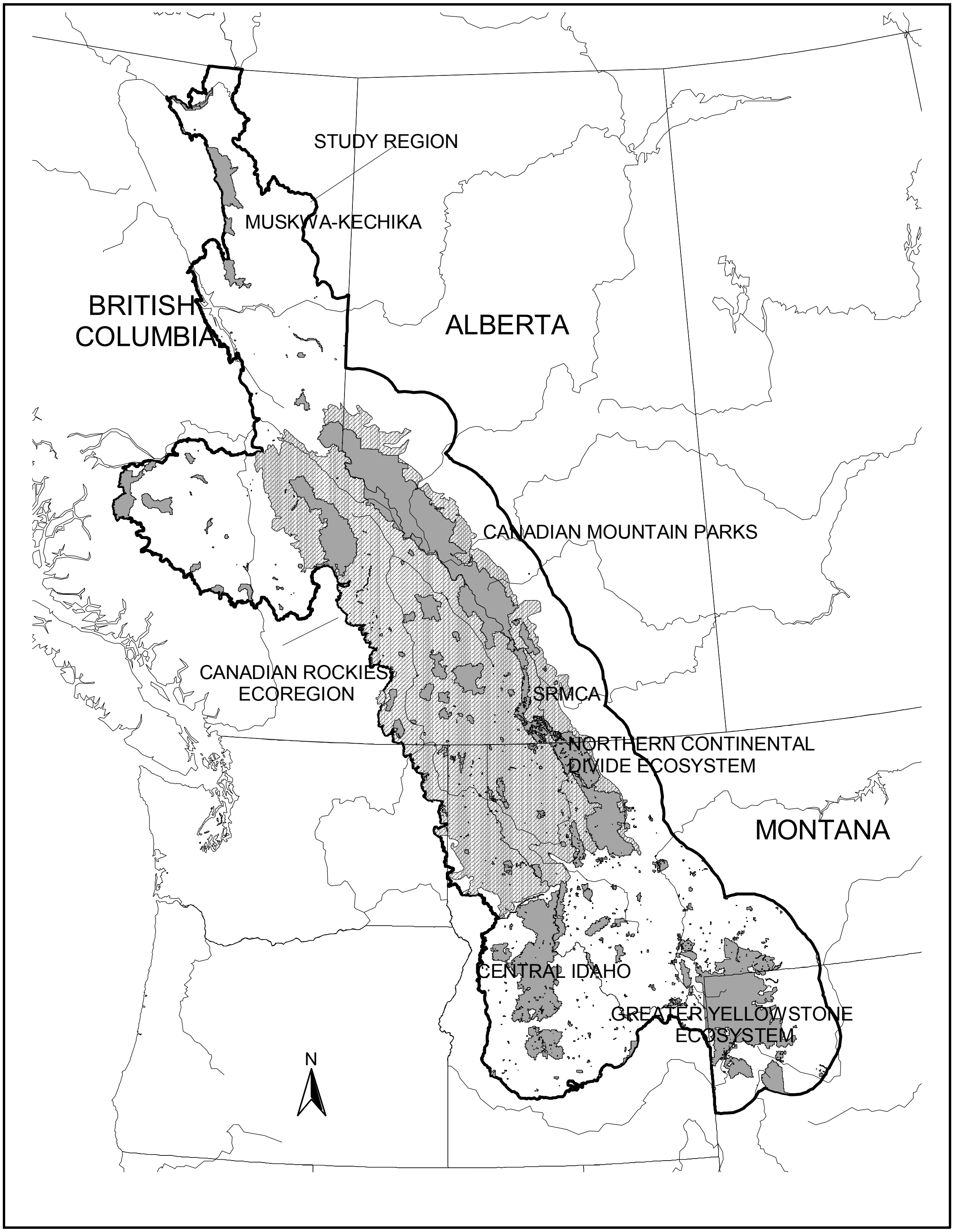


Figure E2. A composite network, selected by the SITES algorithm, incorporating current protected areas (green) and priority areas from the 40% regional/30%local goals SITES best run (purple). Red areas were included in one or more of 100 replicate SITES solutions, with darker red indicating inclusion in a larger proportion of the 100 solutions.

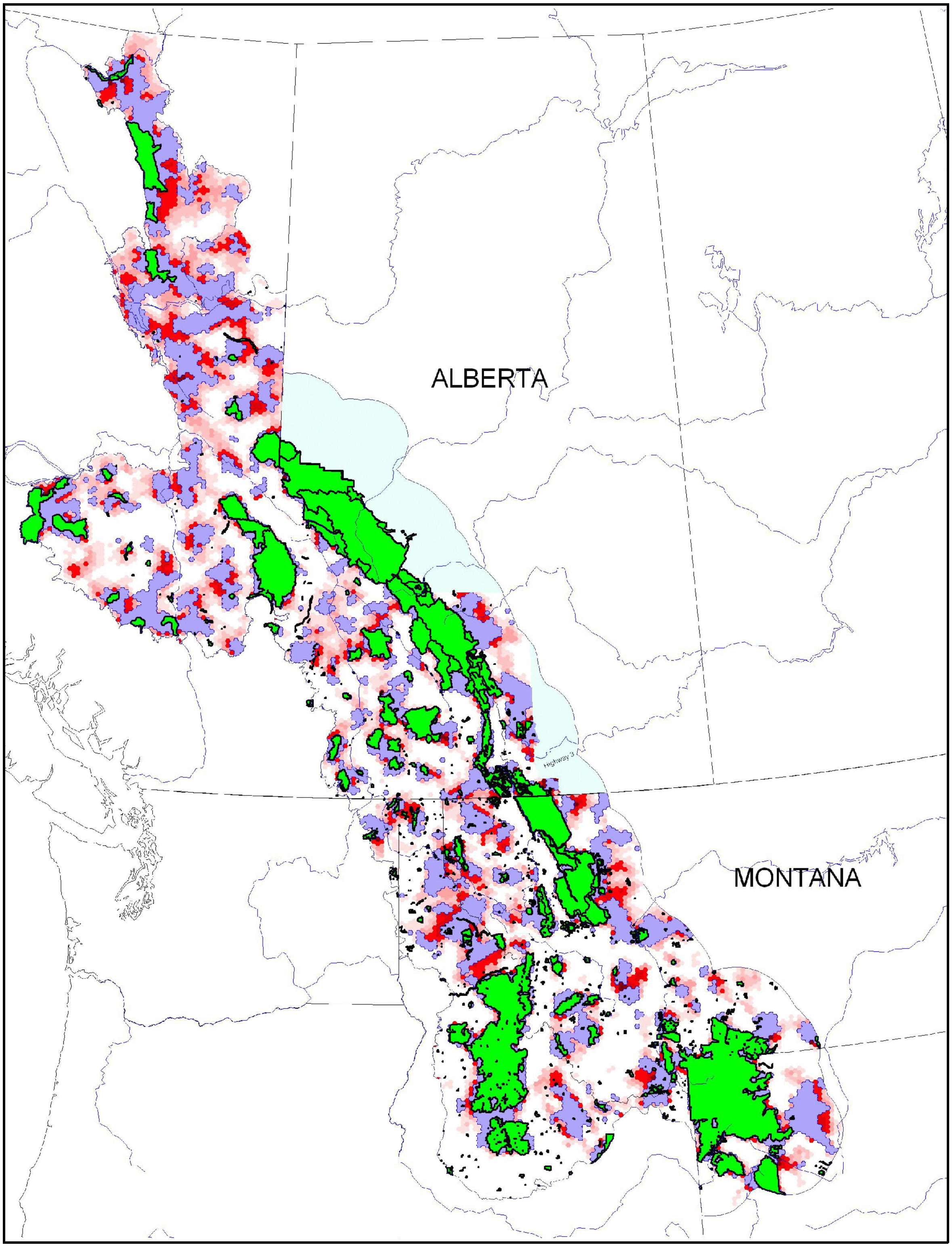


Figure E3A. Reduction in potential carrying capacity from 2000-2025 for grizzly bear, as predicted by the PATCH dynamic model. Areas in dark red show greatest reduction in potential occupancy due to expected human population growth and landscape change.

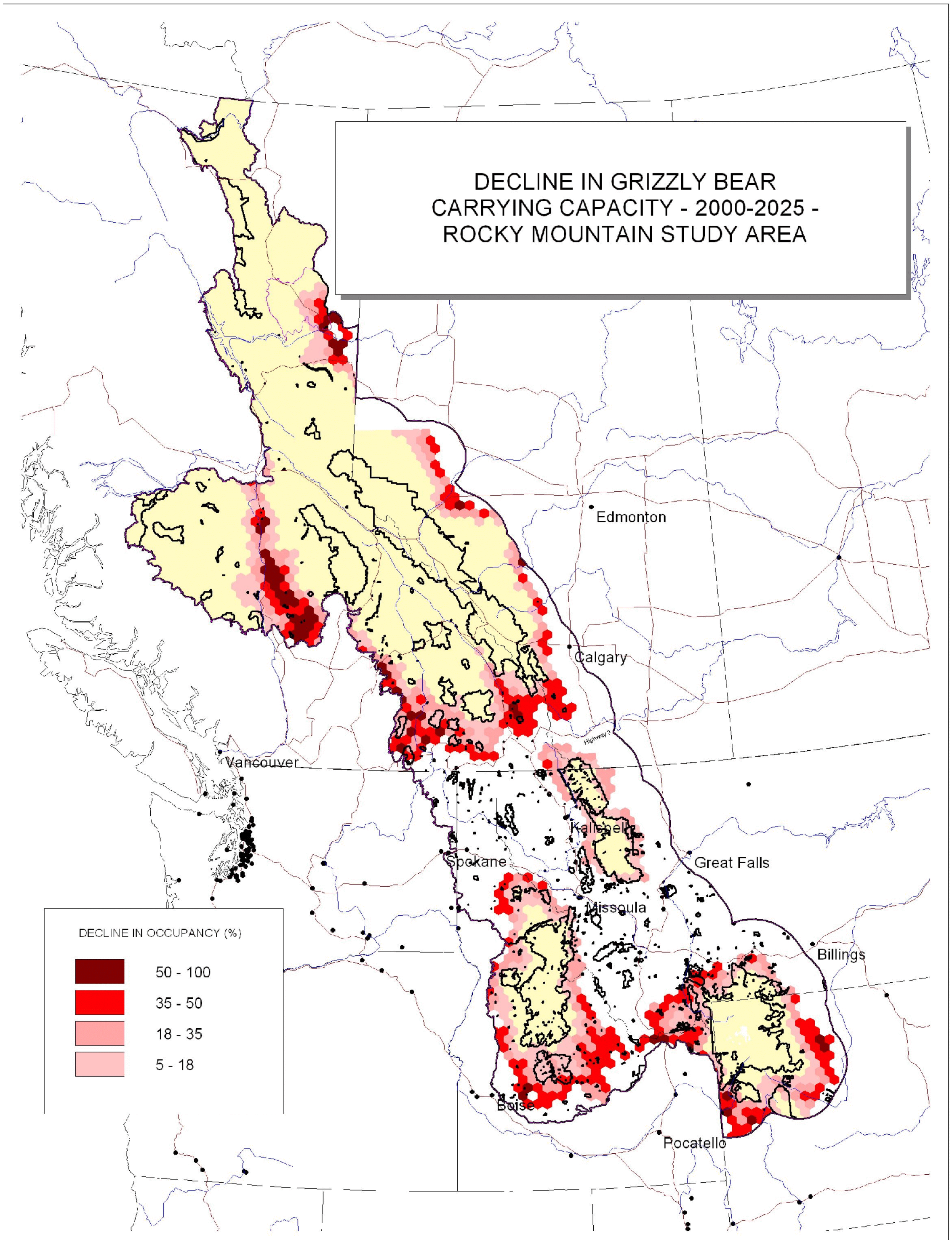


Figure E3B. Reduction in potential carrying capacity from 2000-2025 for wolf, as predicted by the PATCH dynamic model. Areas in dark red show greatest reduction in potential occupancy due to expected human population growth and landscape change.

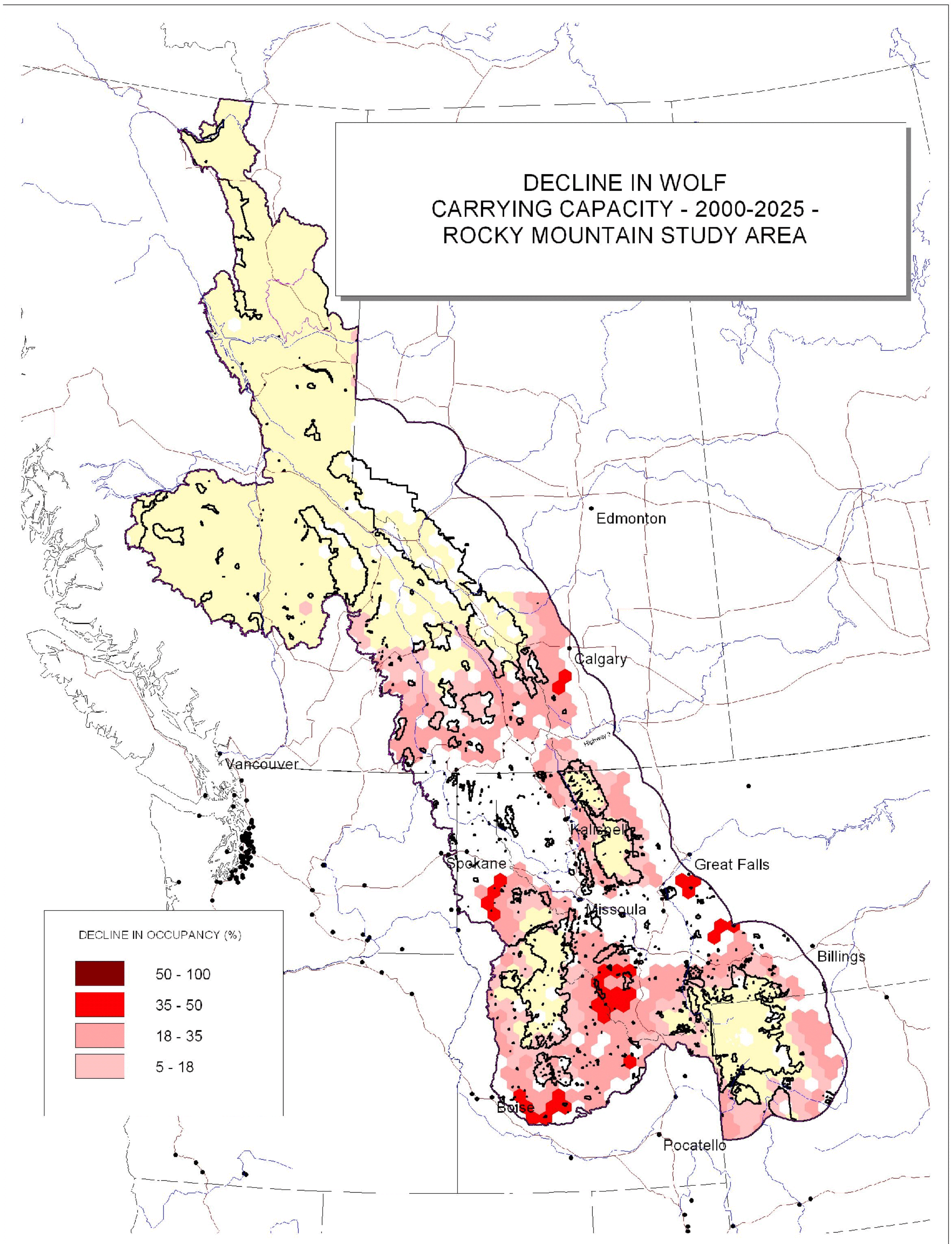


Figure E3C. Reduction in potential carrying capacity from 2000-2025 for wolverine, as predicted by the PATCH dynamic model. Areas in dark red show greatest reduction in potential occupancy due to expected human population growth and landscape change.

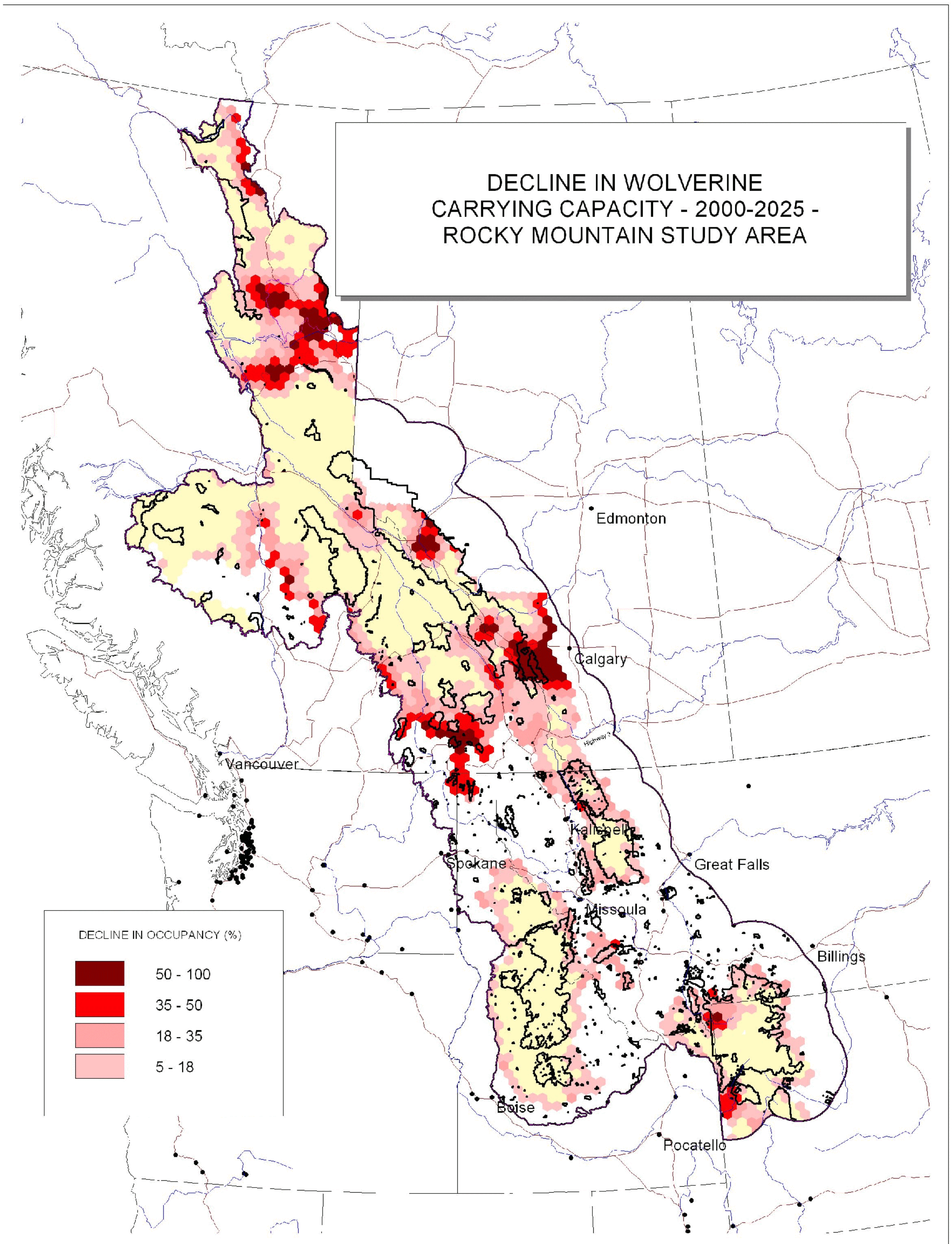
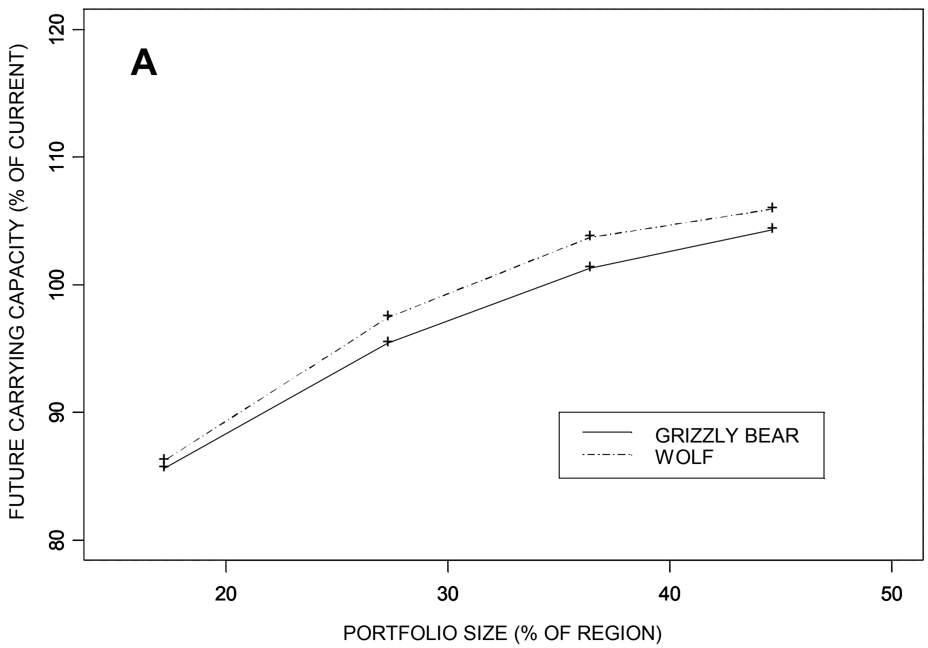


Figure E4. Response of grizzly bear and wolf populations, as predicted by the PATCH model, to reserve networks of varying size in (A) the study region as a whole, and (B) the Canadian Rockies ecoregion.



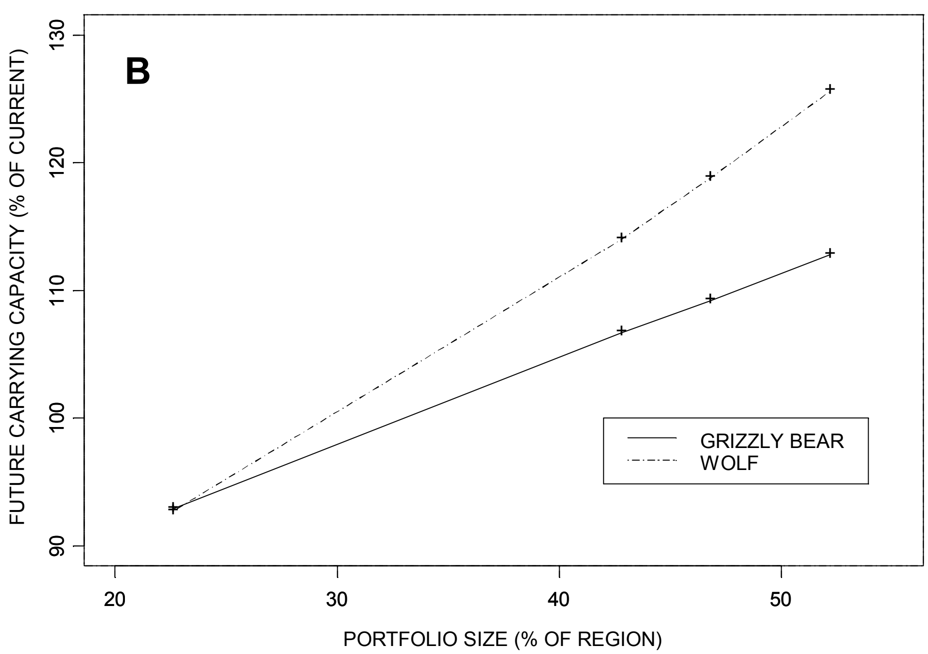


Figure E5. Example of how population goals based on the dynamic PATCH model were used in reserve selection (SITES) runs. Areas shown in red lie in quadrant 1 (top right) of the irreplaceability/vulnerability graph for grizzly bear. These areas have both high value as source habitat and high threat. Areas shown in green are the highest value source habitats, that is, the upper portions of quadrants 1 and 2 (top left) of the irreplaceability/vulnerability graph for grizzly bear.

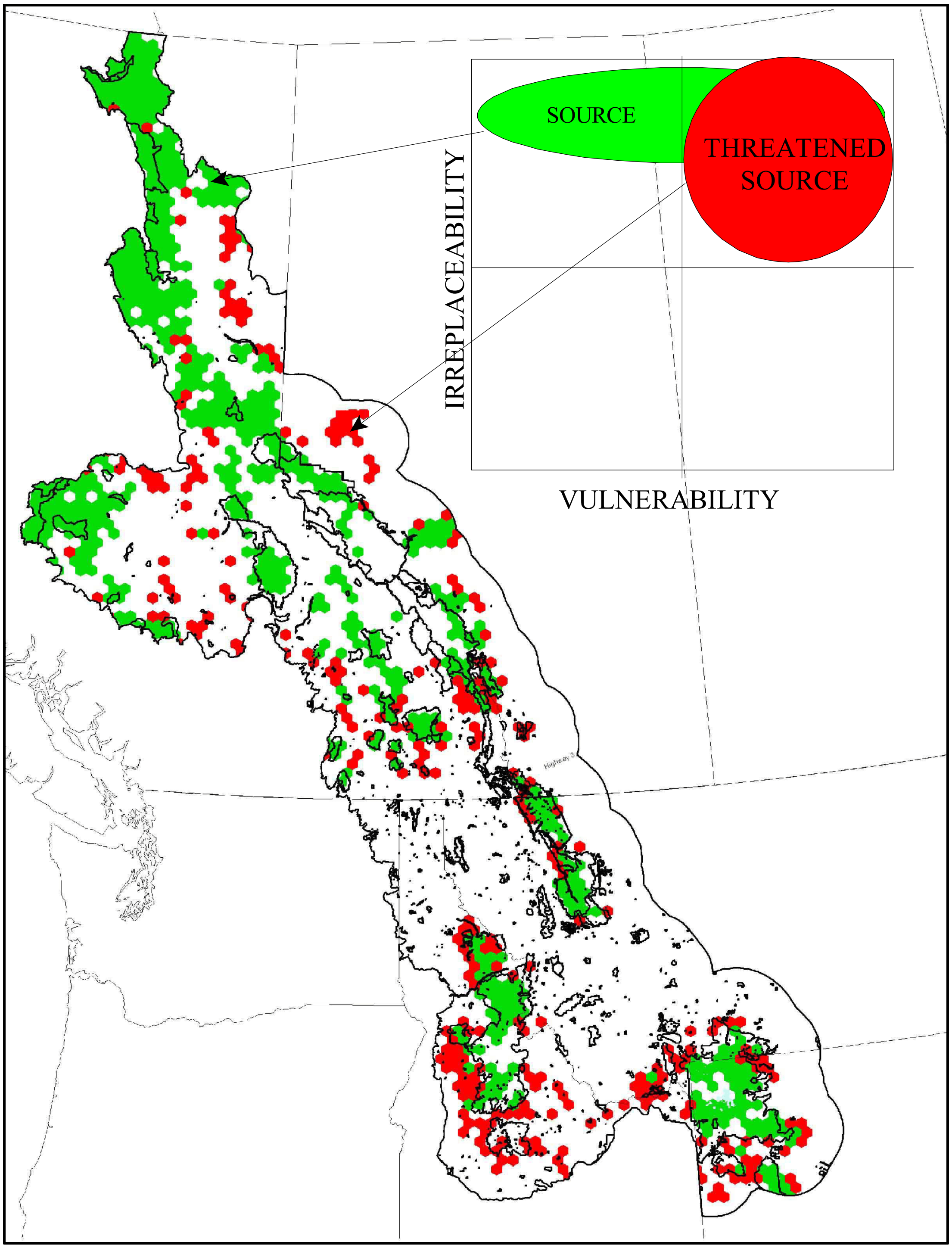
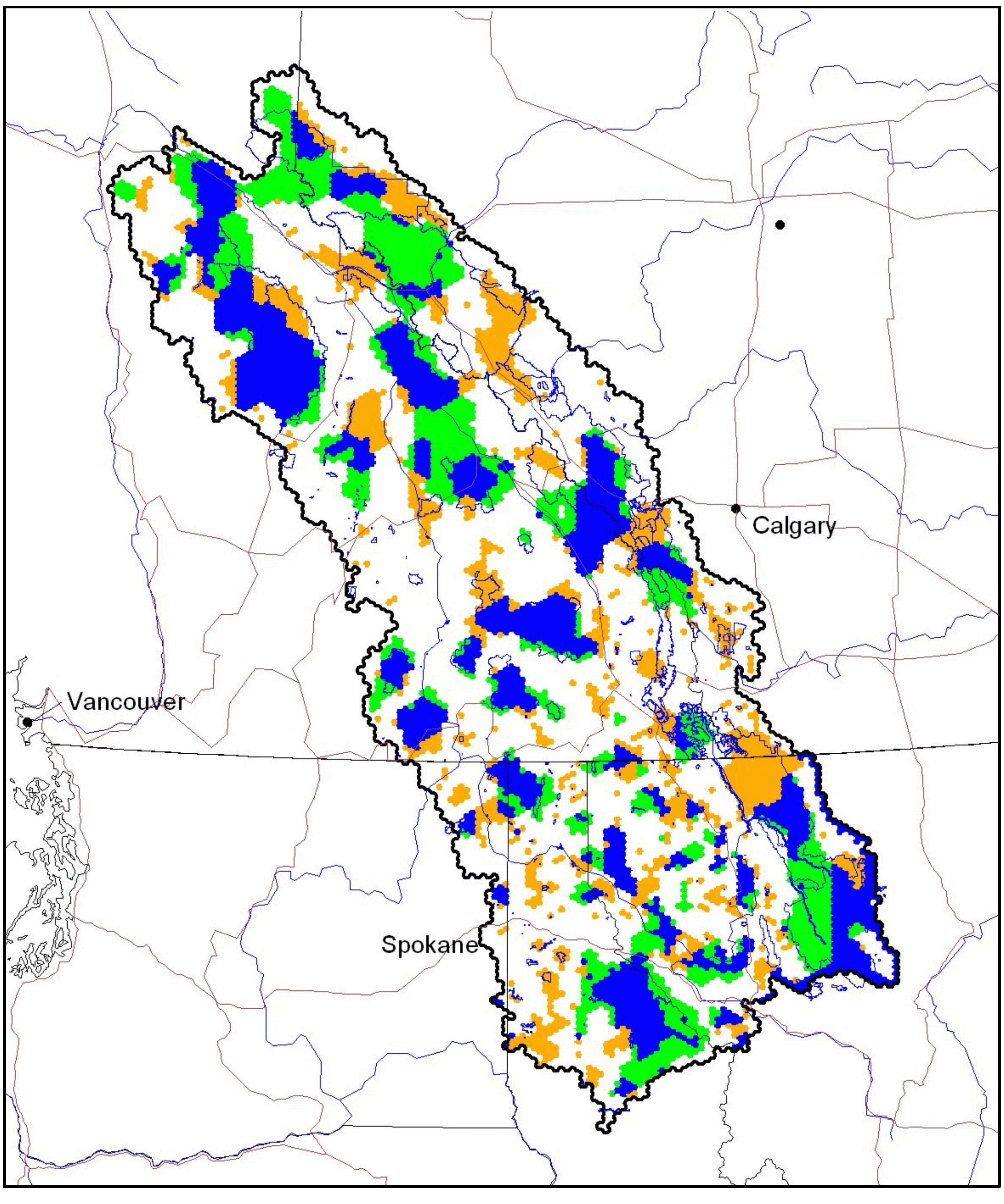


Figure E6. Contrasts between SITES portfolios based on carnivore goals and special elements and representation goals in the Canadian Rockies ecoregion. Areas in green were selected only in the carnivore-based portfolio, areas in orange only in the special elements/representation portfolio, and areas in blue in both portfolios.



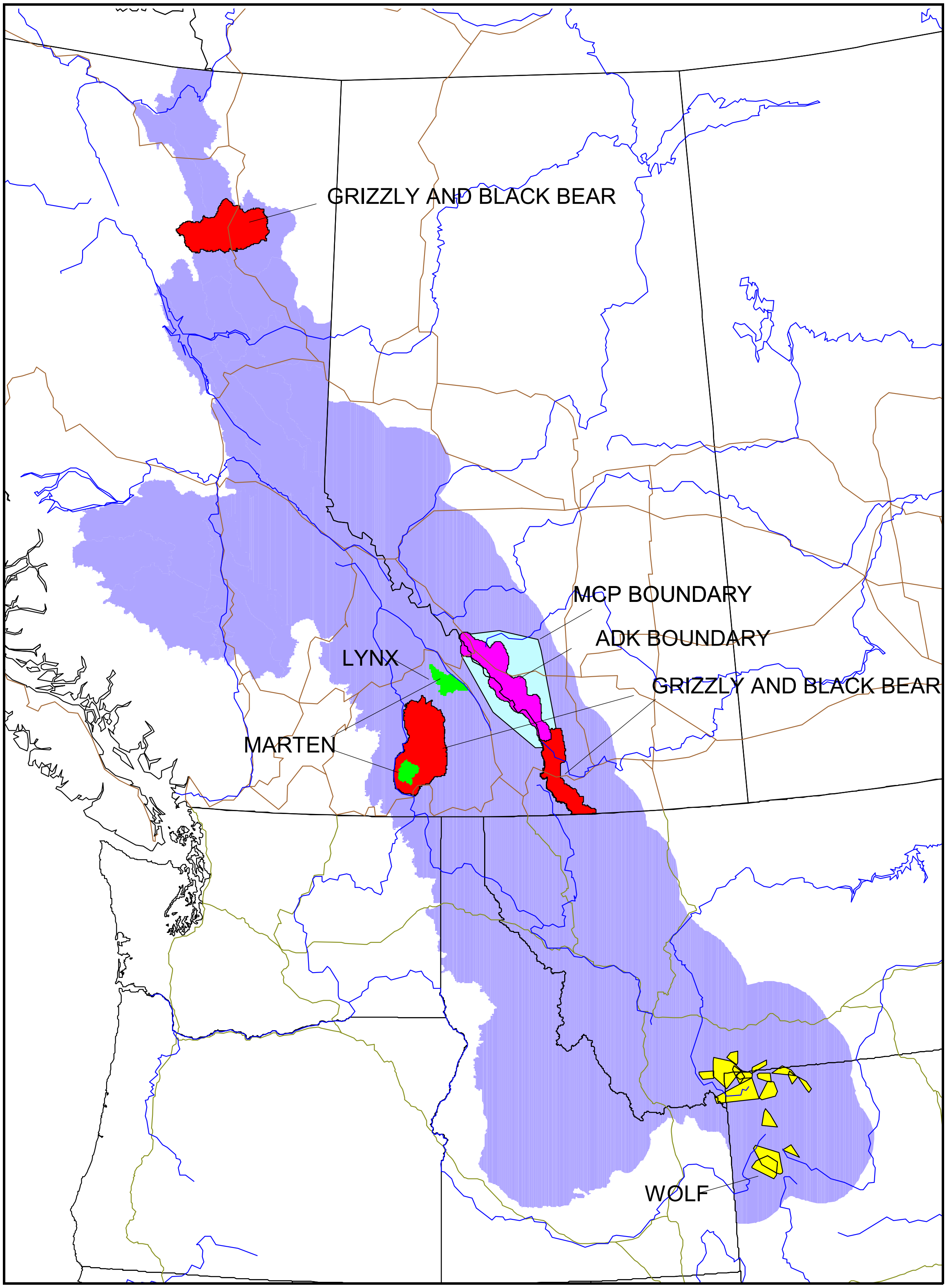


Figure 1. Map of study area and validation data sources.

Figure 2. Distribution of special element data within the Canadian Rockies ecoregion. Ecosections are outlined in red.

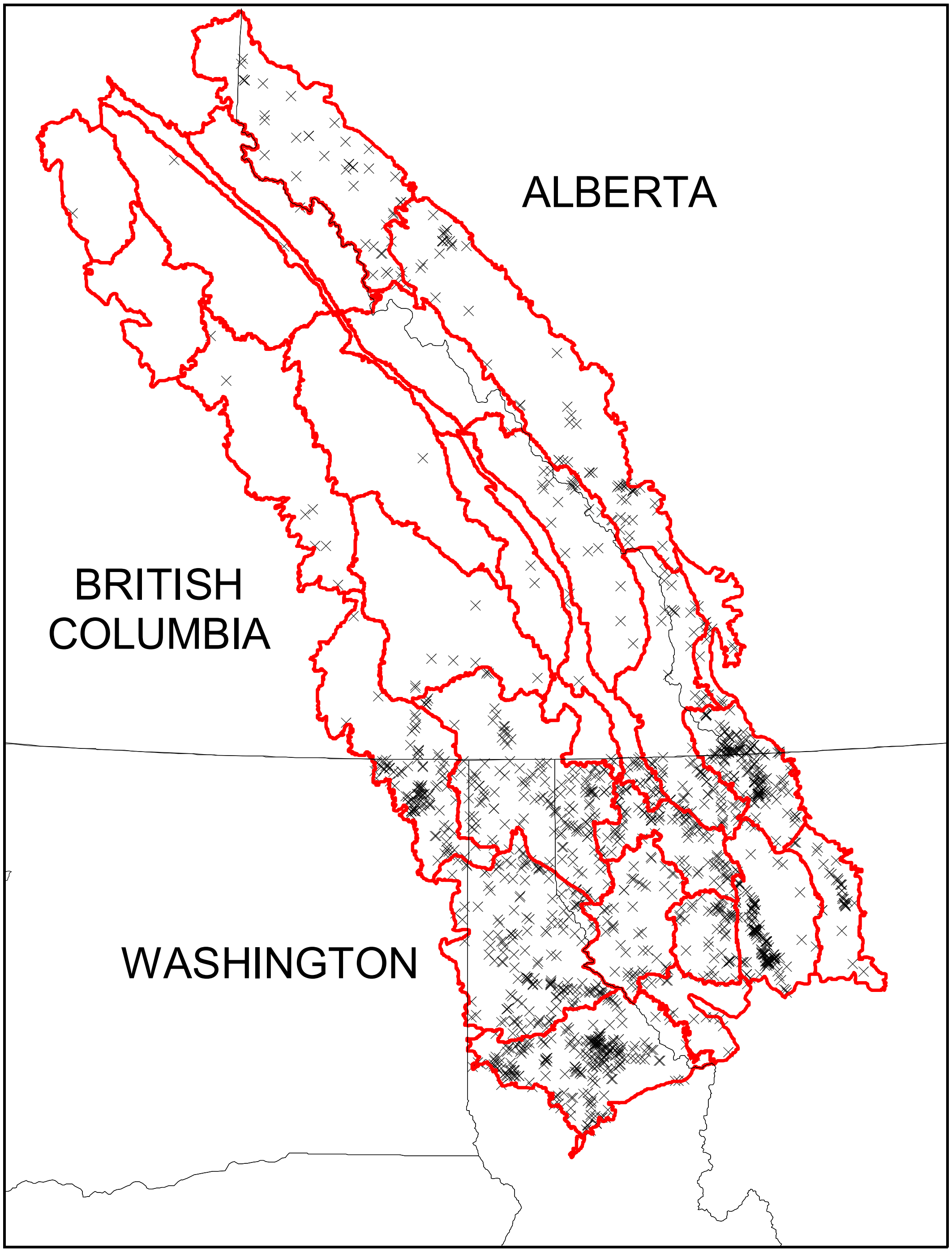


Figure 3. Distribution of grizzly bear habitat in the Rocky Mountains of the United States and Canada as predicted by a regional-scale conceptual habitat model adapted from Merrill et al. (1999) and Mace et al. (1999).

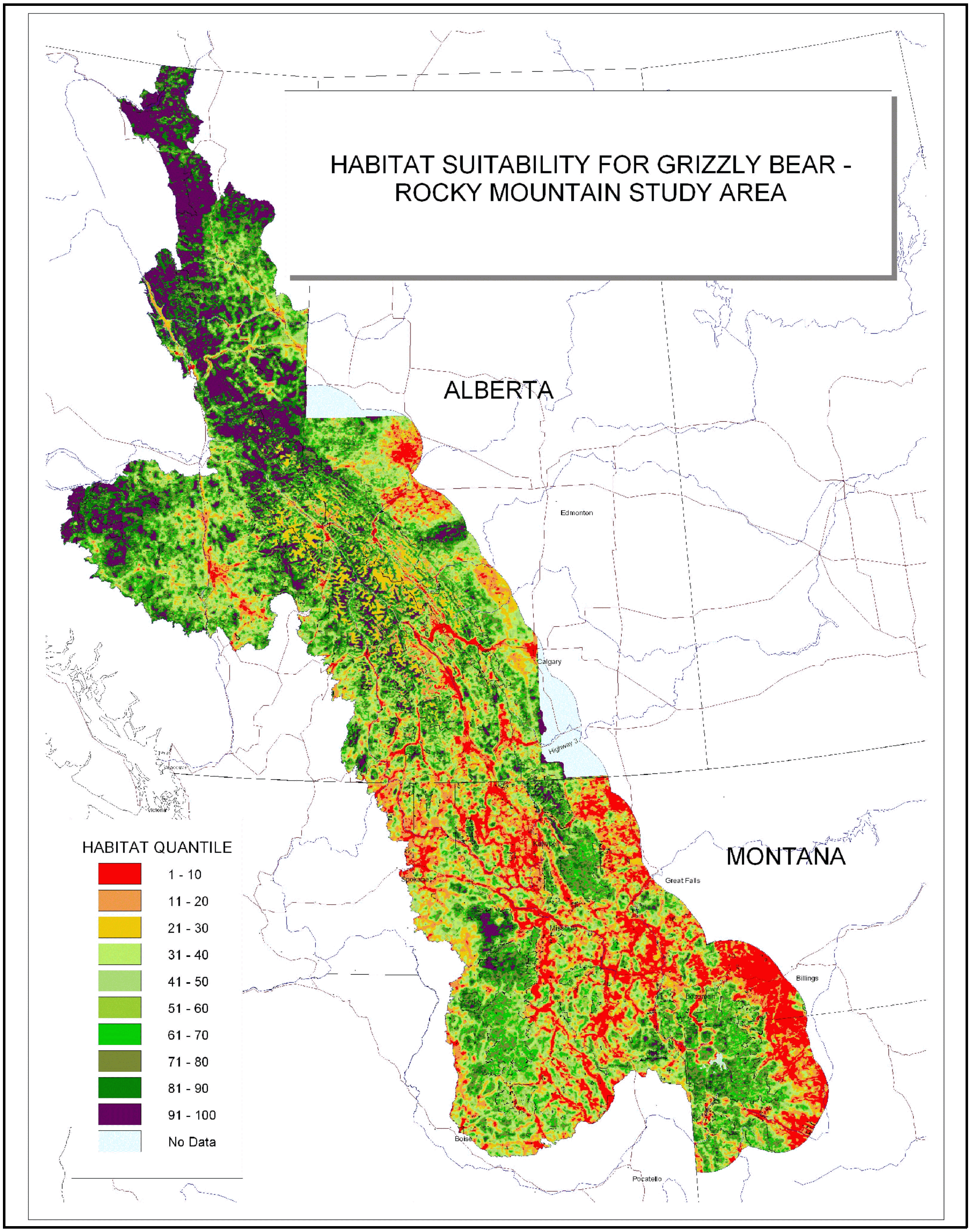


Figure 4. Distribution of gray wolf habitat in the Rocky Mountains of the United States and Canada as predicted by a regional-scale conceptual habitat model adapted from Paquet et al. (unpublished) and others.

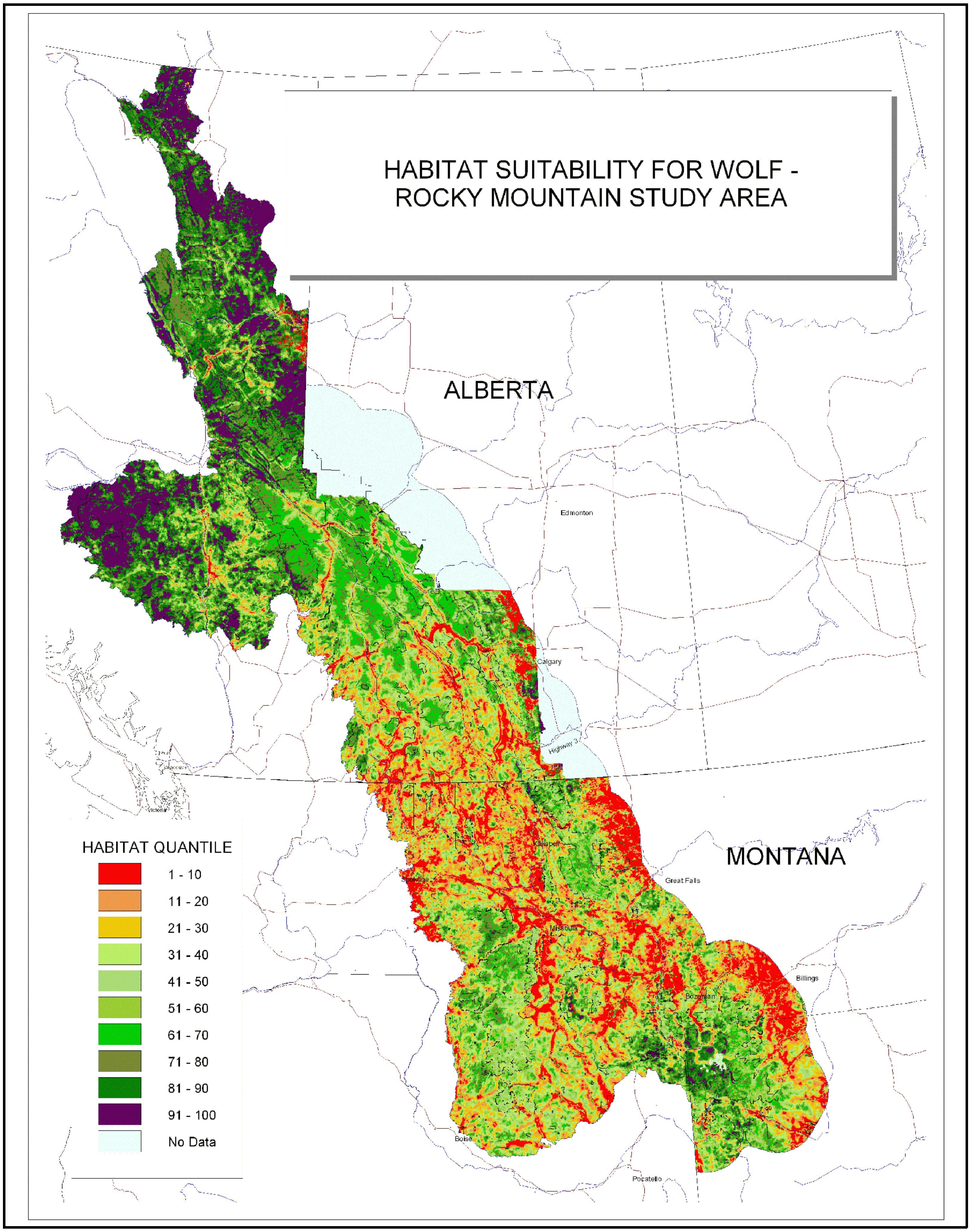


Figure 5. Distribution of wolverine habitat in the Rocky Mountains of the United States and Canada as predicted by the resource selection function (RSF) analysis.

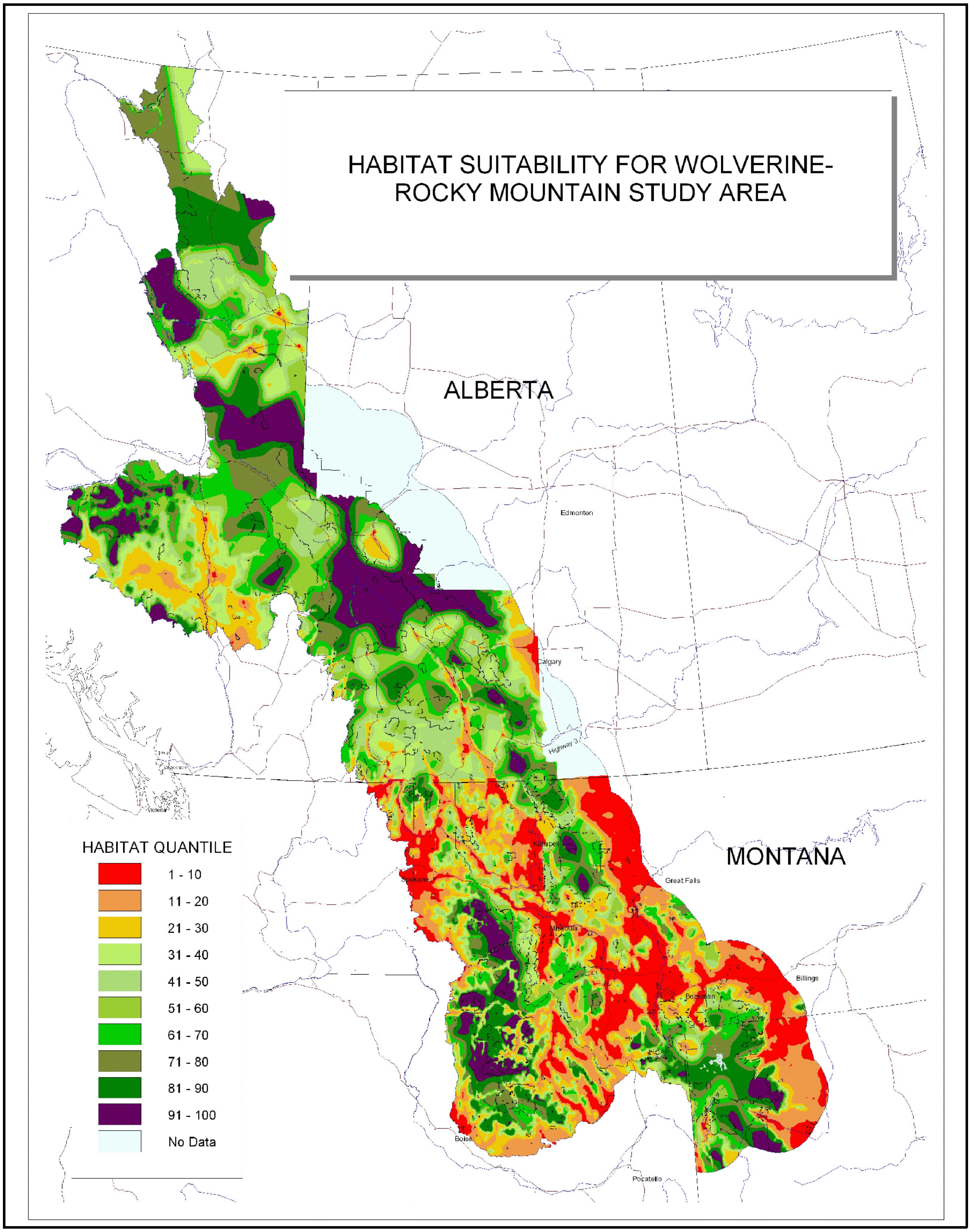


Figure 6. Distribution of lynx habitat in the Rocky Mountains of the United States and Canada as predicted by the resource selection function (RSF) analysis.

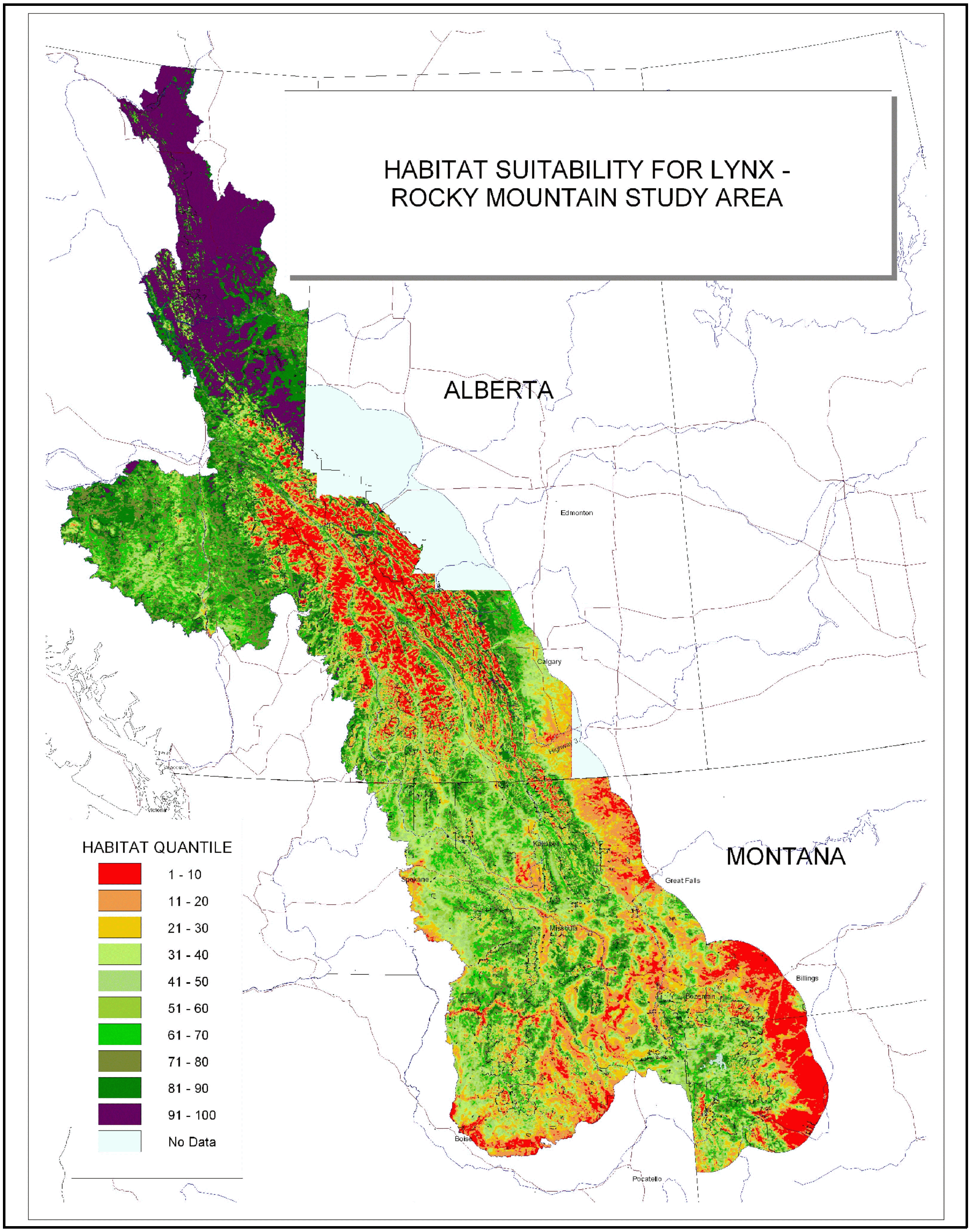


Figure 7. Distribution of fisher habitat in the Rocky Mountains of the United States and Canada as predicted by the resource selection function (RSF) analysis.

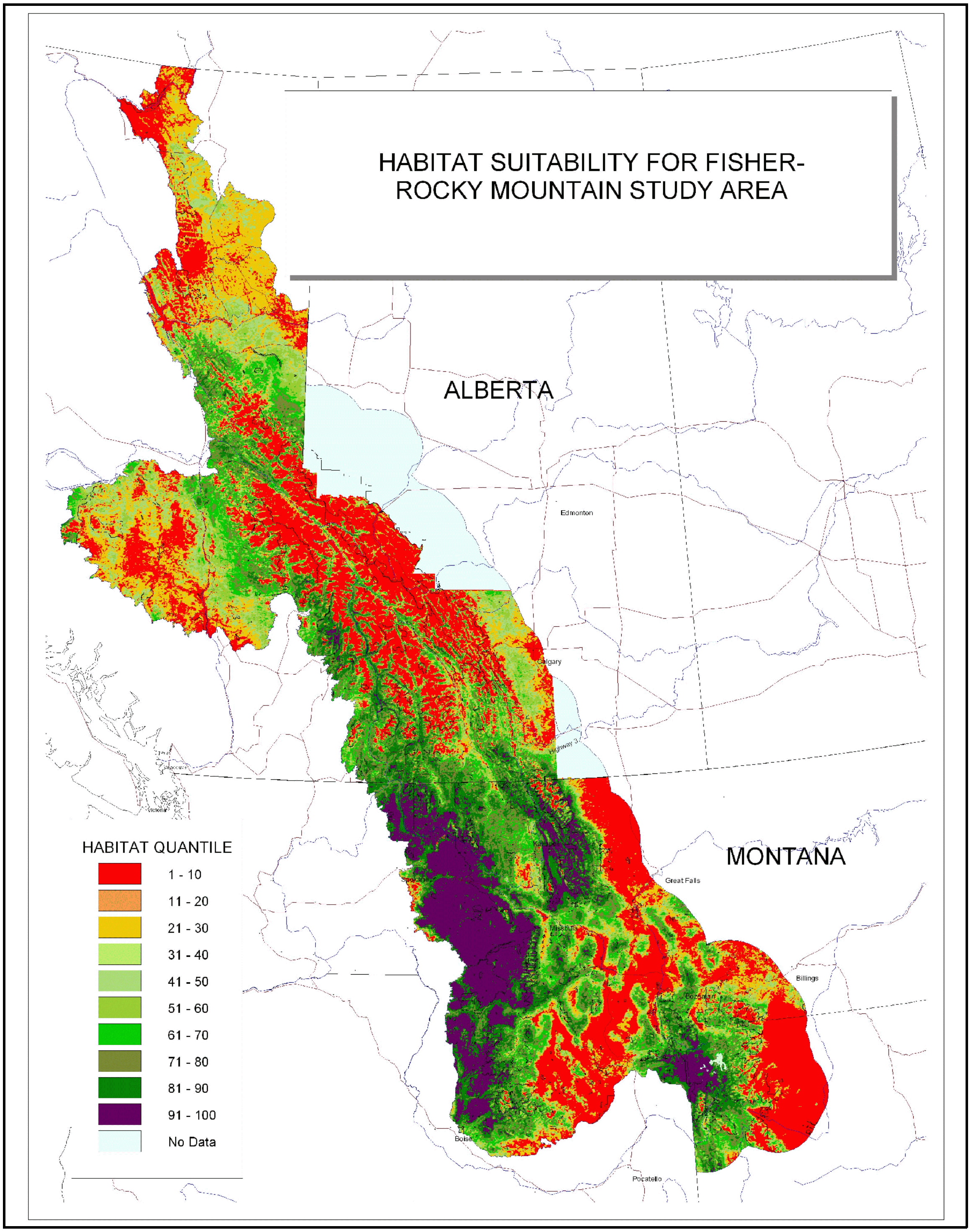


Figure 8. Distribution of black bear habitat in the Rocky Mountains of the United States and Canada as predicted by the resource selection function (RSF) analysis.

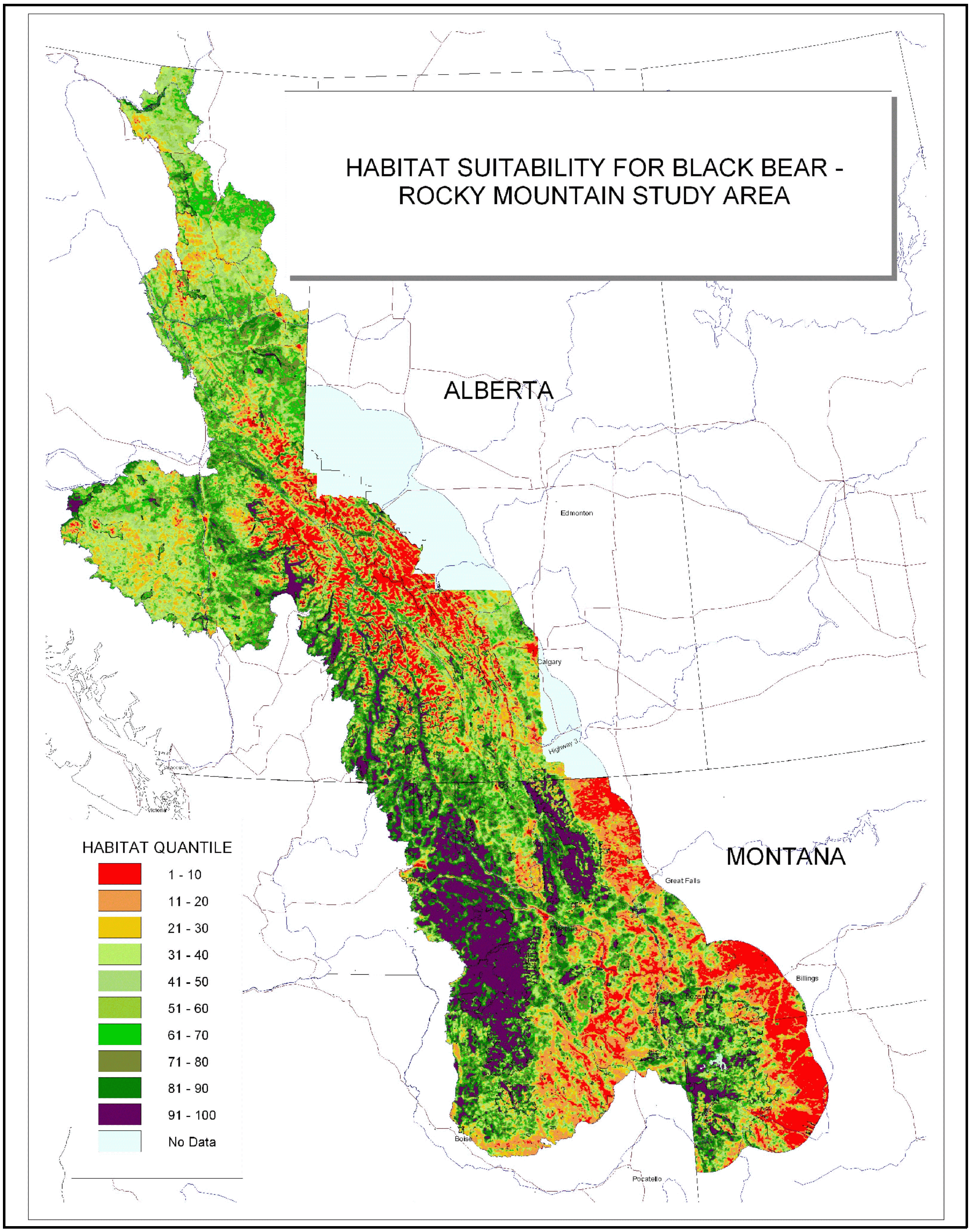


Figure 9. Distribution of mountain lion habitat in the Rocky Mountains of the United States and Canada as predicted by a regional-scale conceptual habitat model adapted from Jalkotzy et al. (1999) and others.

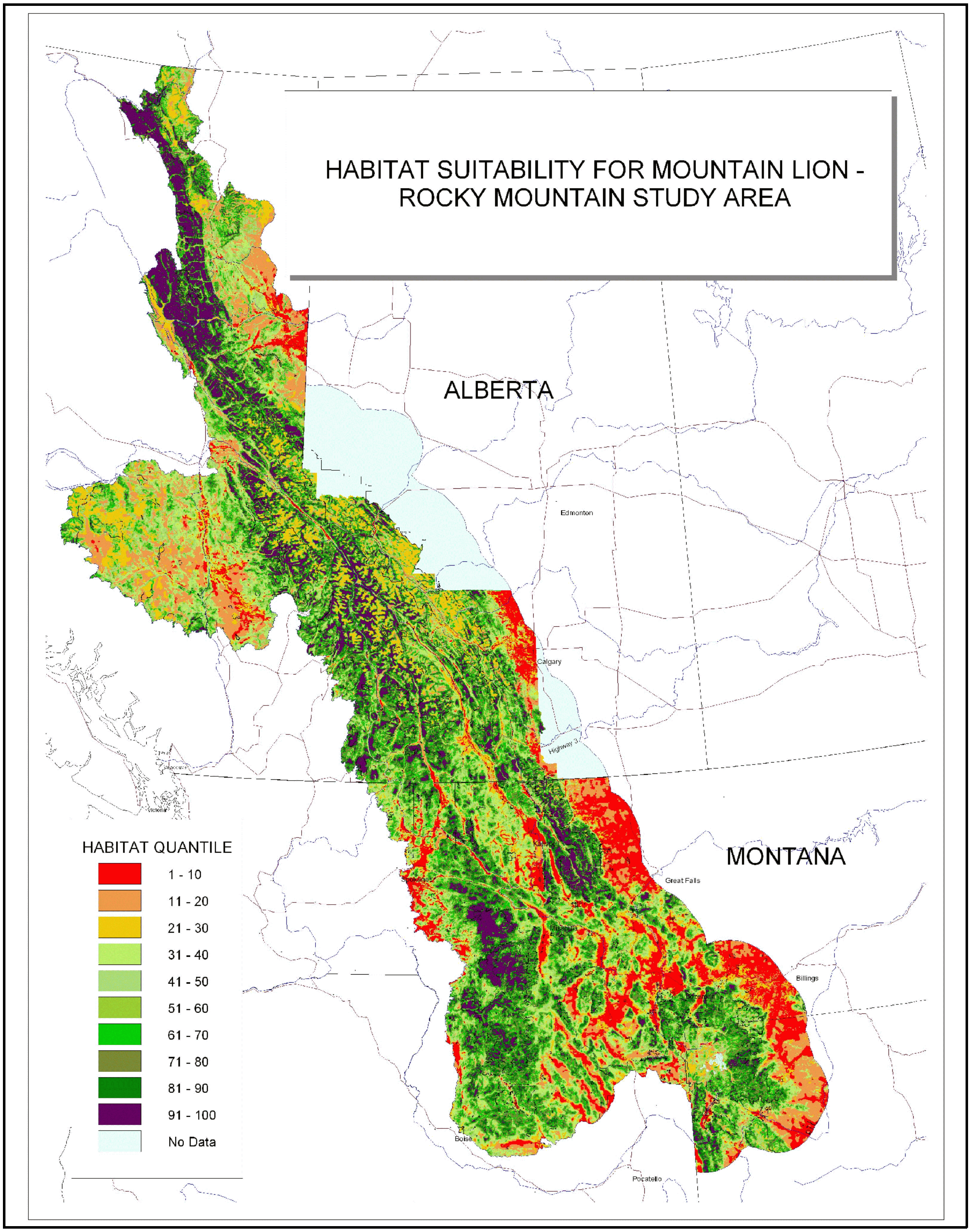


Figure 10. Distribution of American marten habitat in the Rocky Mountains of the United States and Canada as predicted by a regional-scale conceptual habitat model.

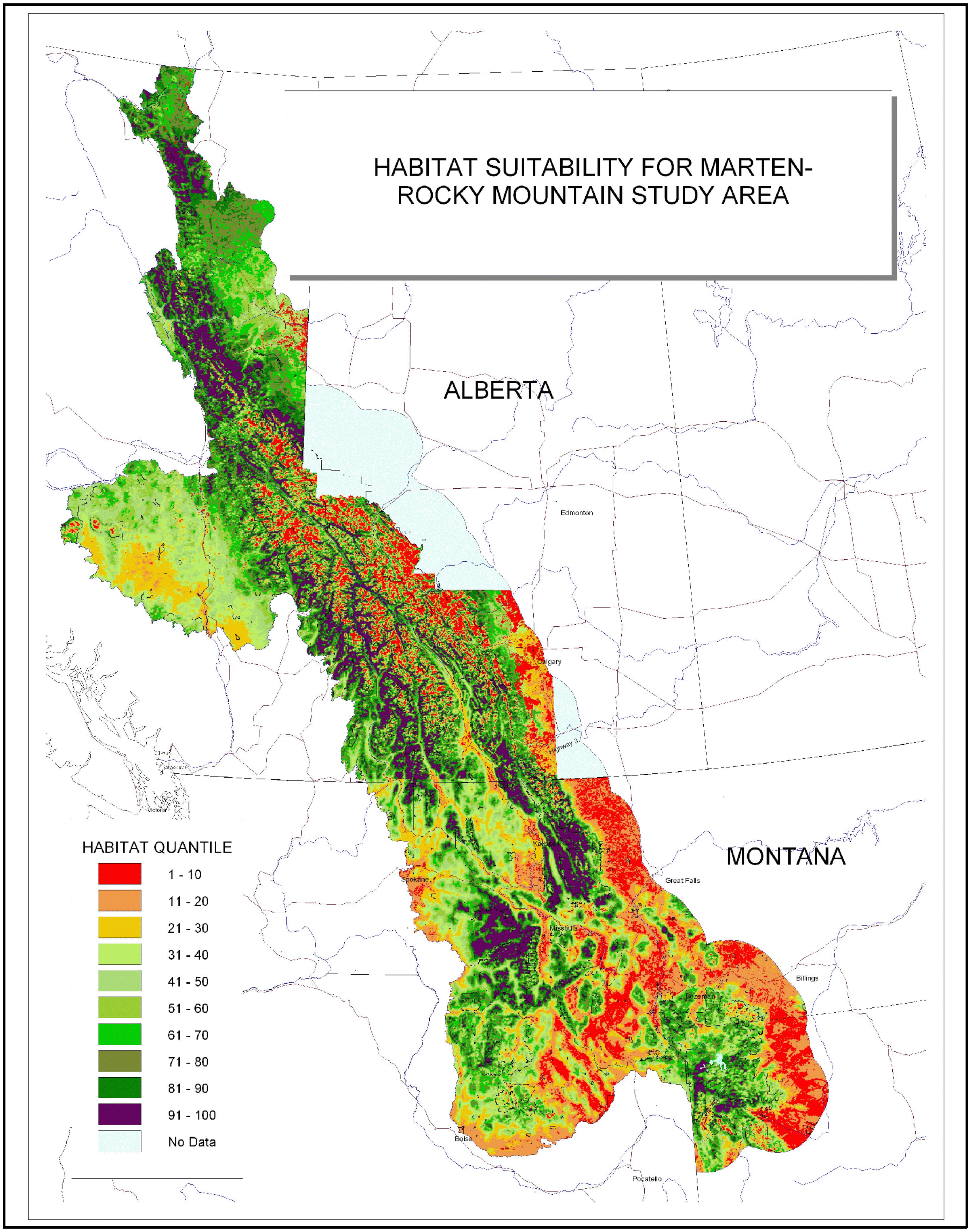


Figure 11. Reduction in potential grizzly bear carrying capacity from 2000-2025 as predicted by the PATCH dynamic model. Areas in dark red show greatest reduction in potential occupancy due to expected human population growth and landscape change.

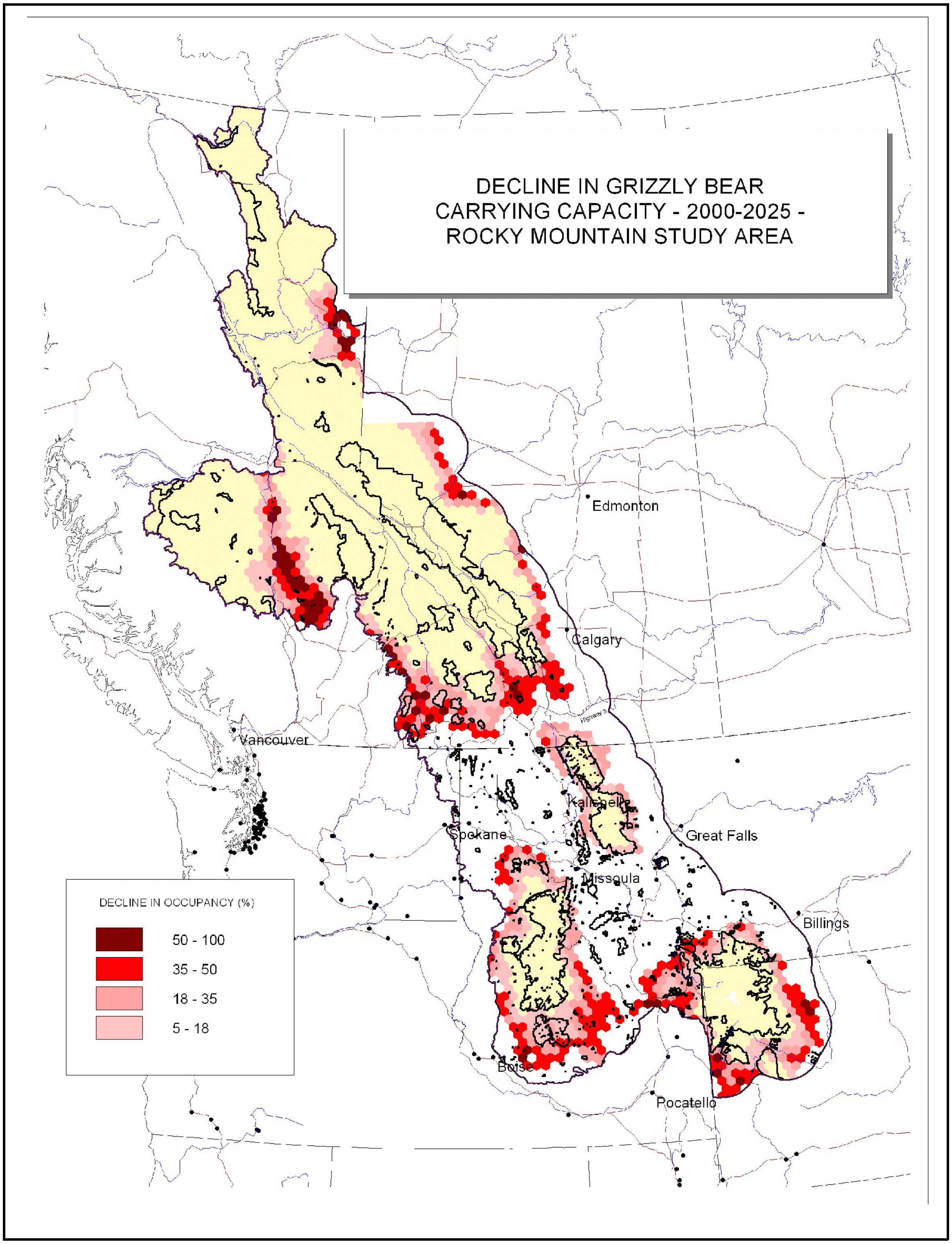


Figure 12. Reduction in potential wolf carrying capacity from 2000-2025 as predicted by the PATCH dynamic model. Areas in dark red show greatest reduction in potential occupancy due to expected human population growth and landscape change.

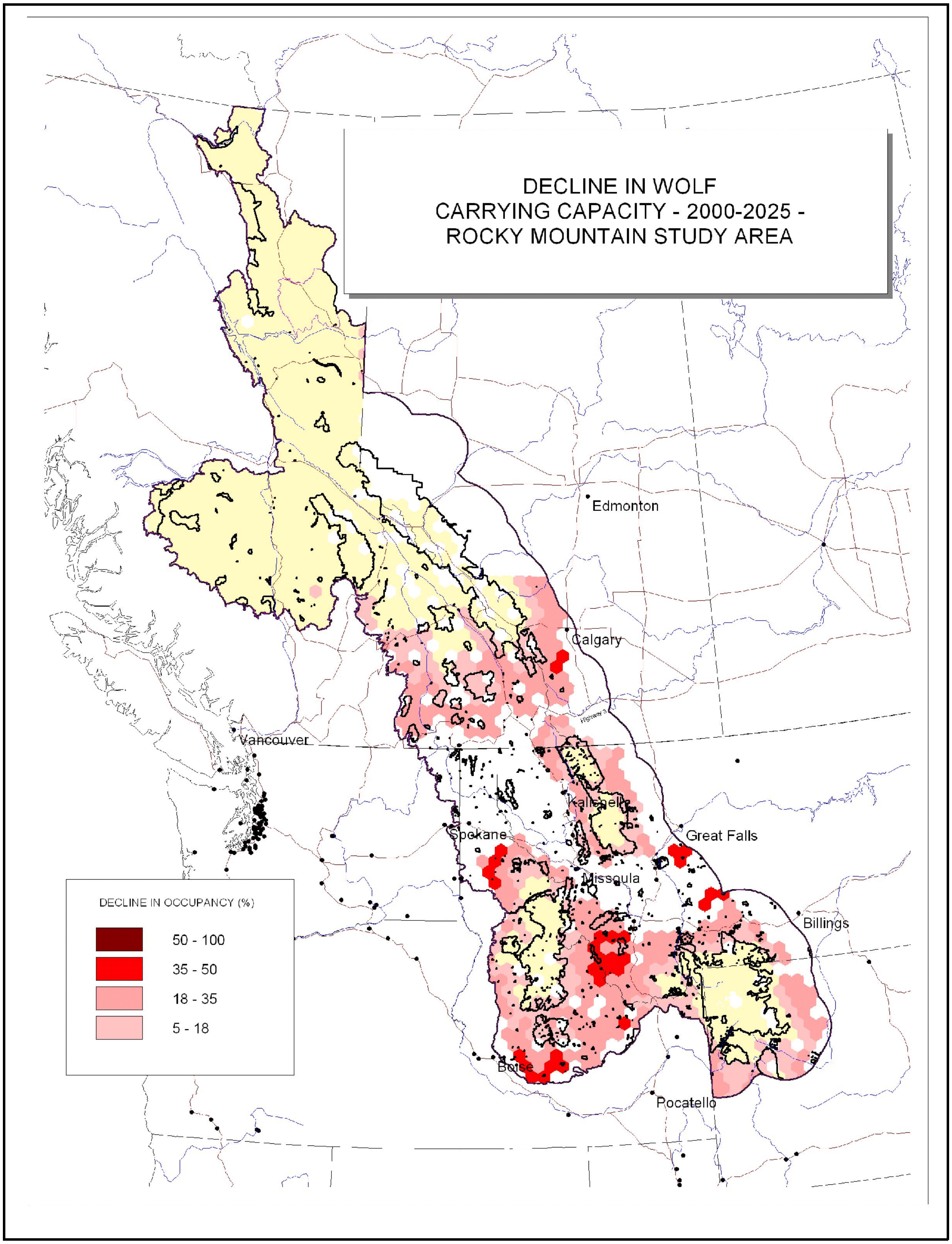


Figure 13. Reduction in potential wolverine carrying capacity from 2000-2025 as predicted by the PATCH dynamic model. Areas in dark red show greatest reduction in potential occupancy due to expected human population growth and landscape change.

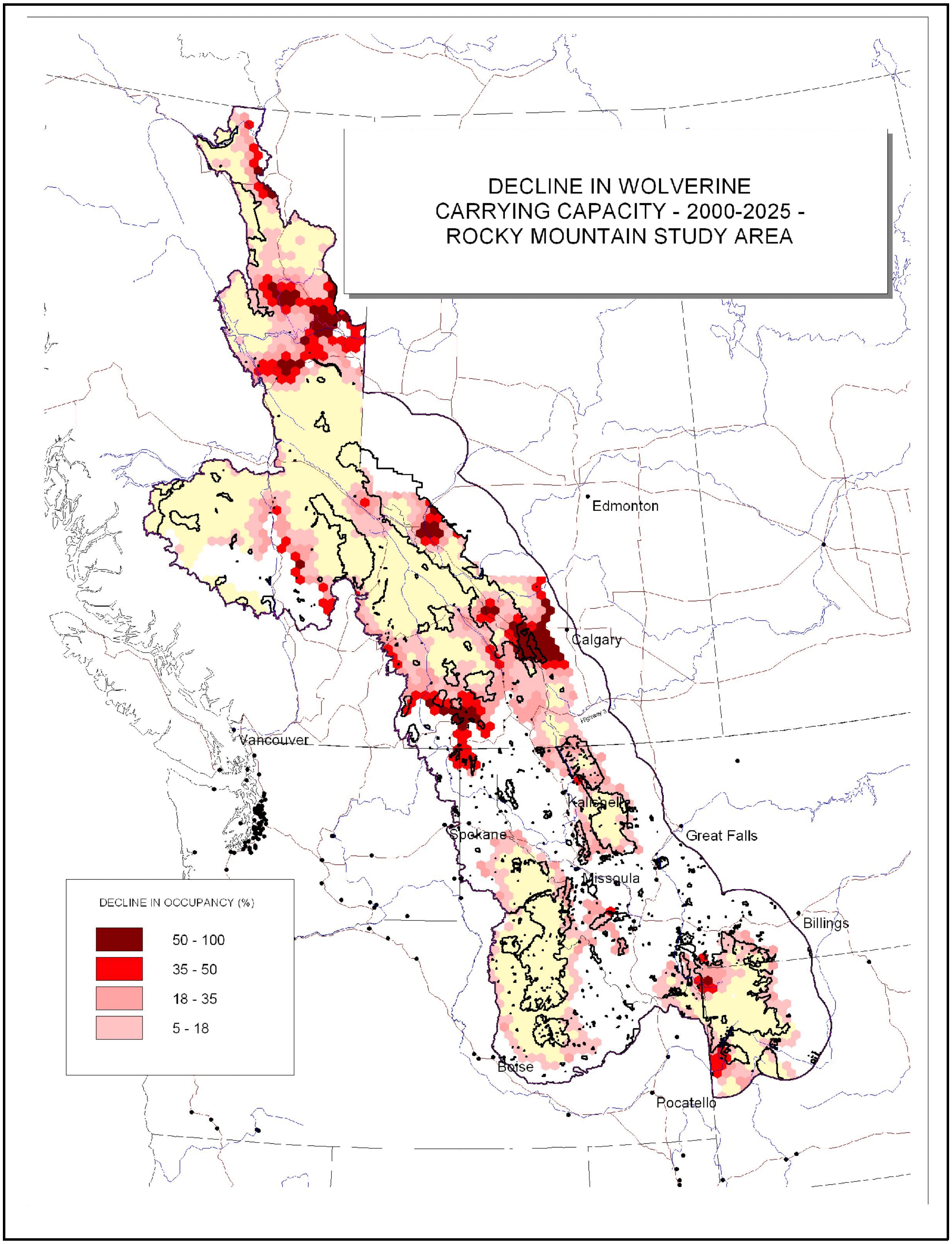


Figure 14. Demographic potential of grizzly bears under (a) current and (b) future landscape conditions (2025), assuming road development on both private and public lands. Legend shows population growth rate (lambda) values predicted by the PATCH model simulations. Only areas with greater than 50% probability of occupancy are shown.

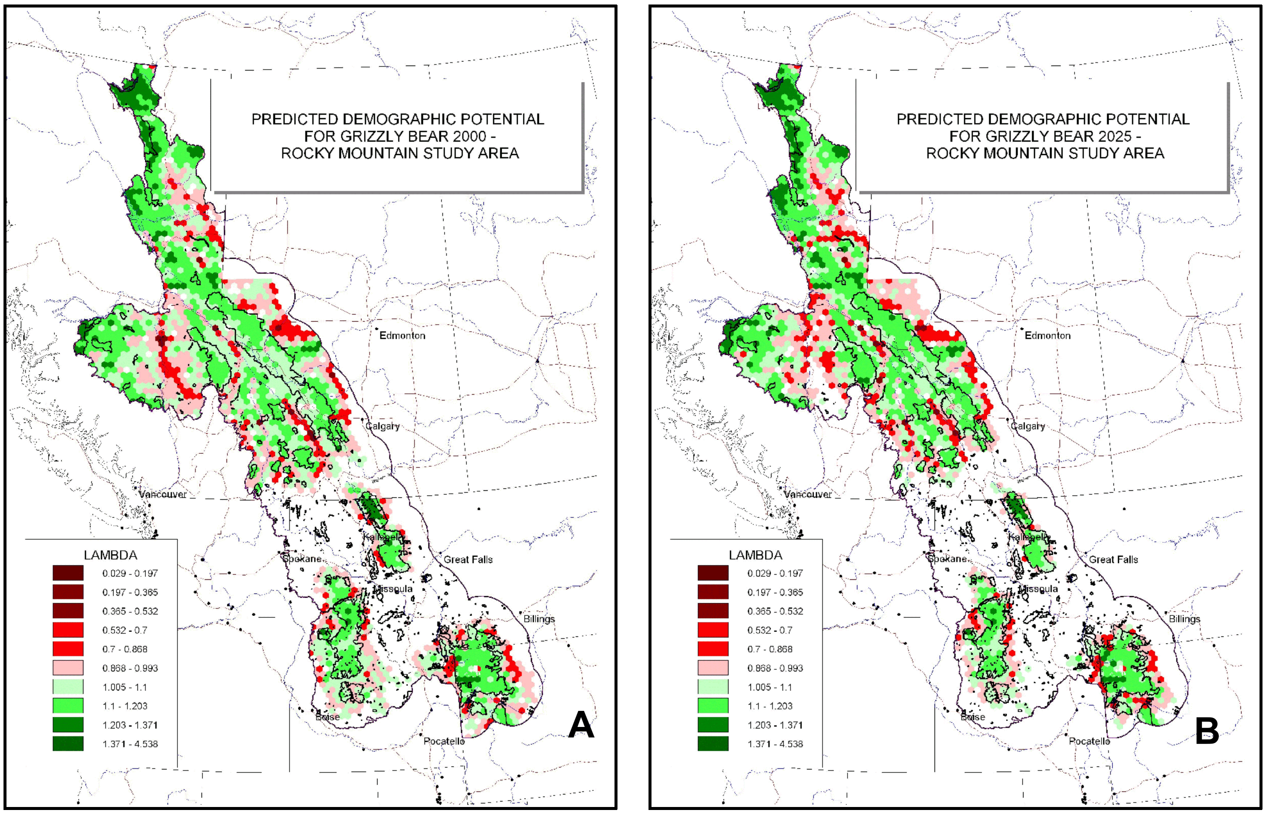


Figure 15. Demographic potential of wolves under (a) current and (b) future landscape conditions (2025), assuming road development on both private and public lands. Legend shows population growth rate (lambda) values predicted by the PATCH model simulations. Only areas with greater than 50% probability of occupancy are shown.

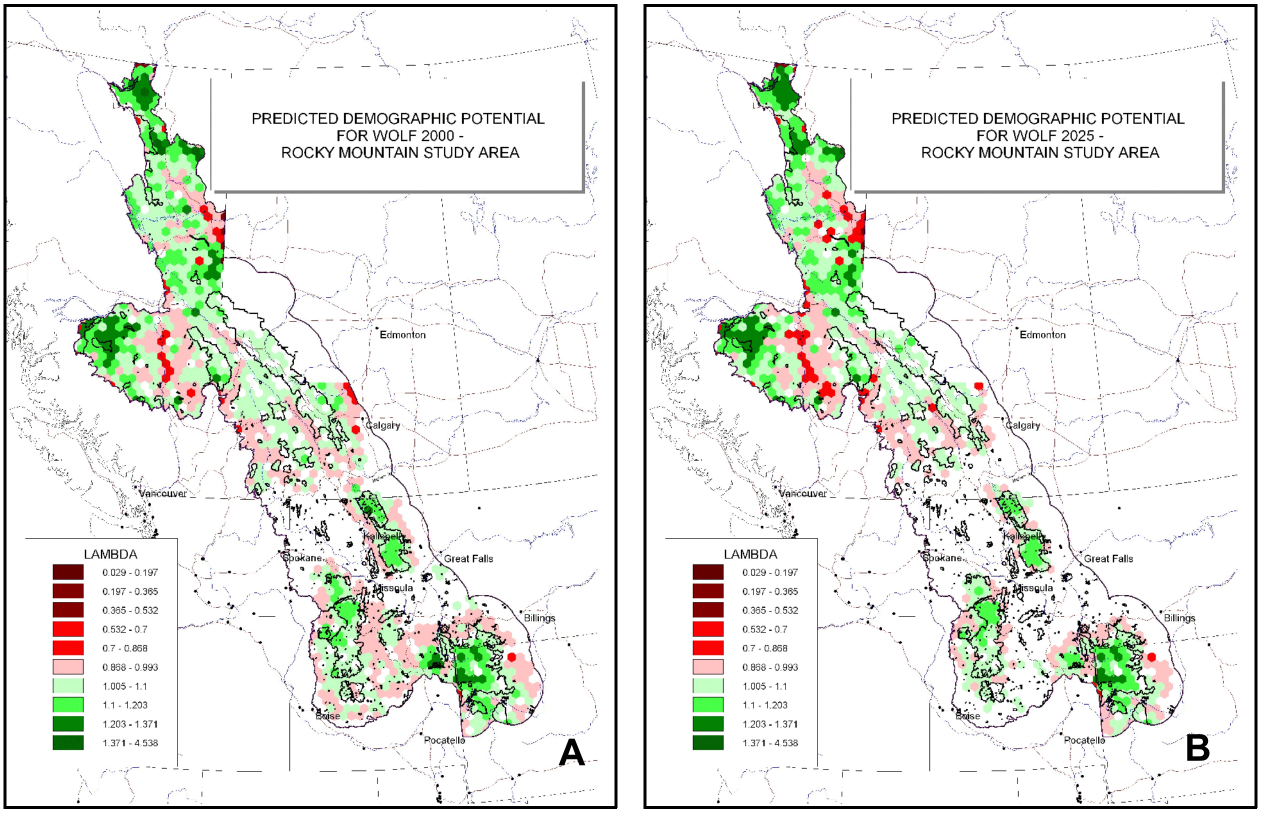


Figure 16. Demographic potential of wolverine under (a) current and (b) future landscape conditions (2025), assuming road development on both private and public lands. Legend shows population growth rate (lambda) values predicted by the PATCH model simulations. Only areas with greater than 50% probability of occupancy are shown.

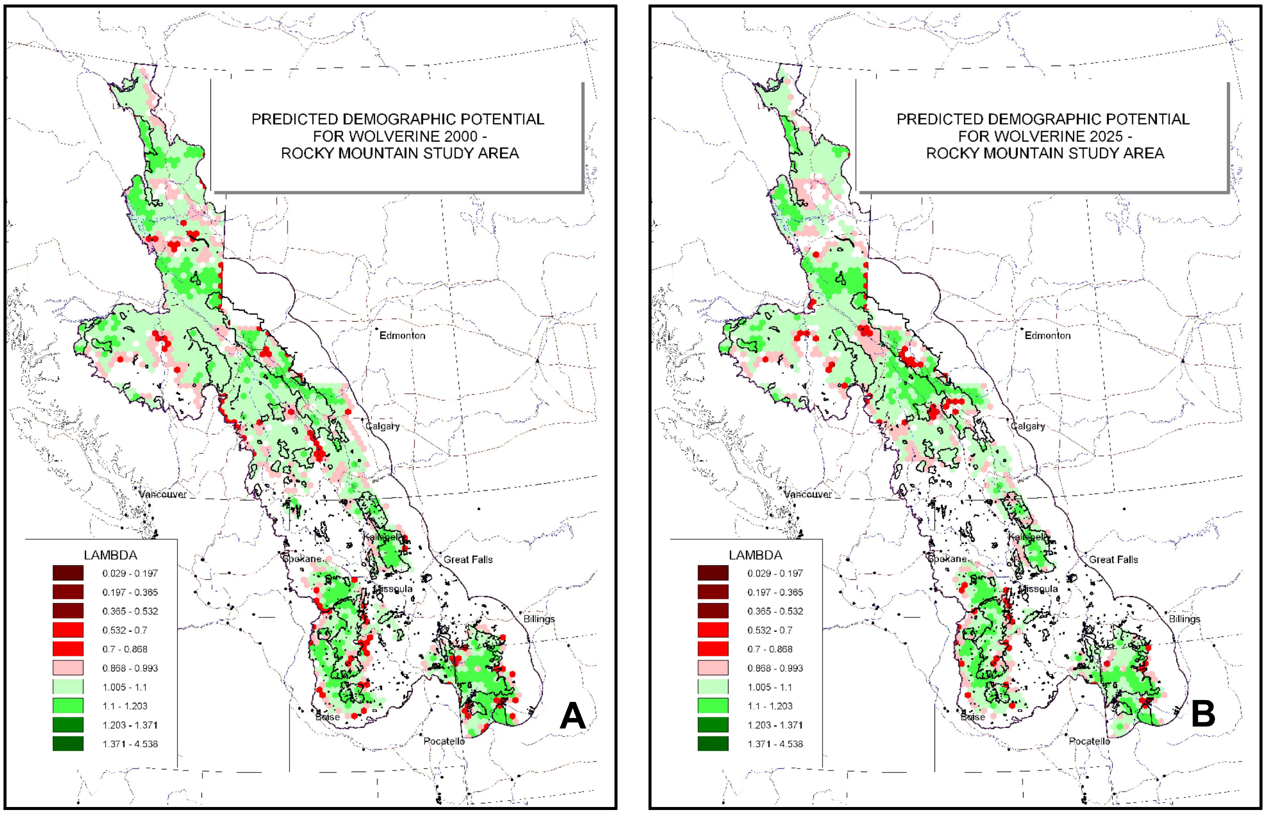
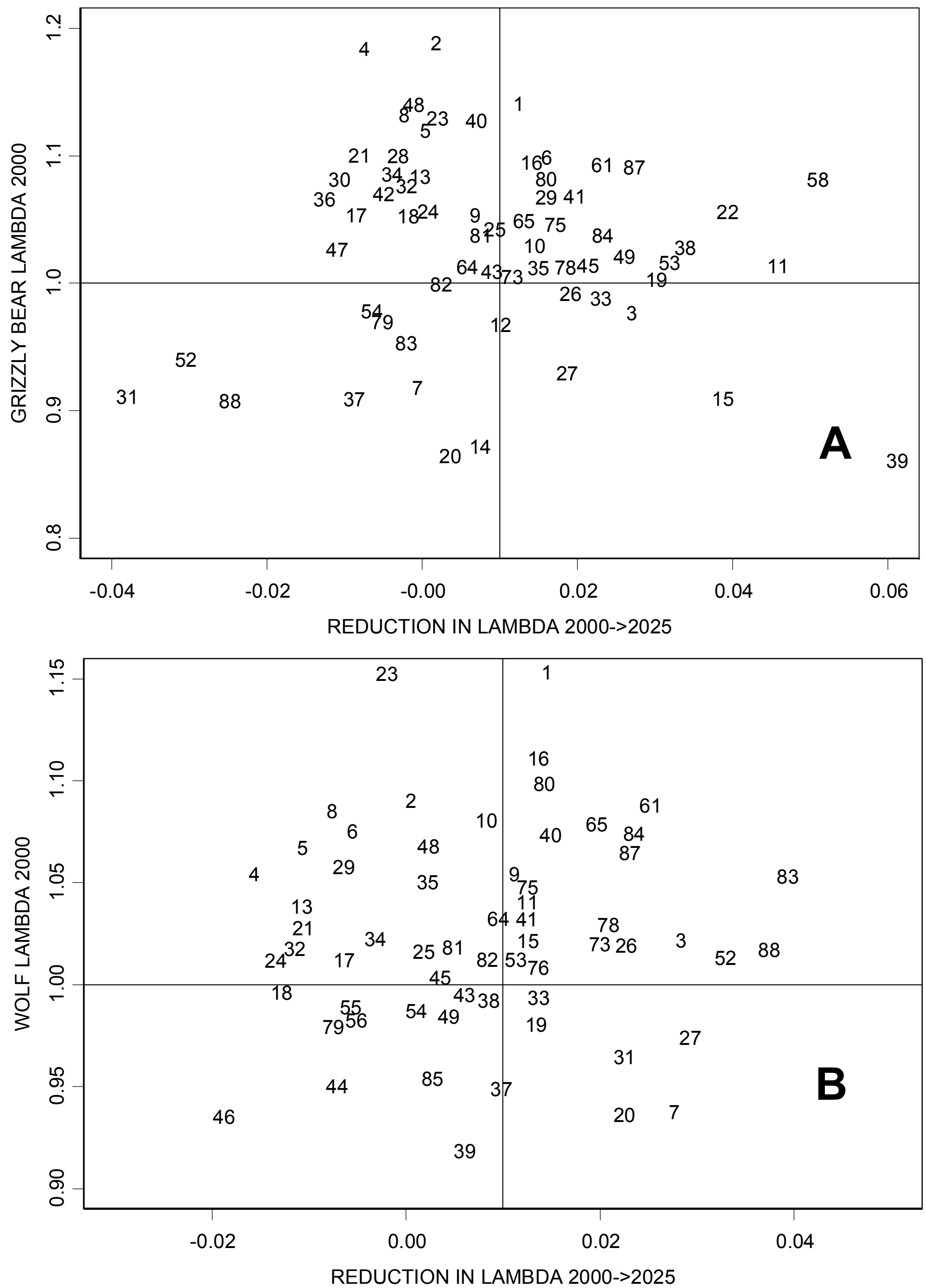
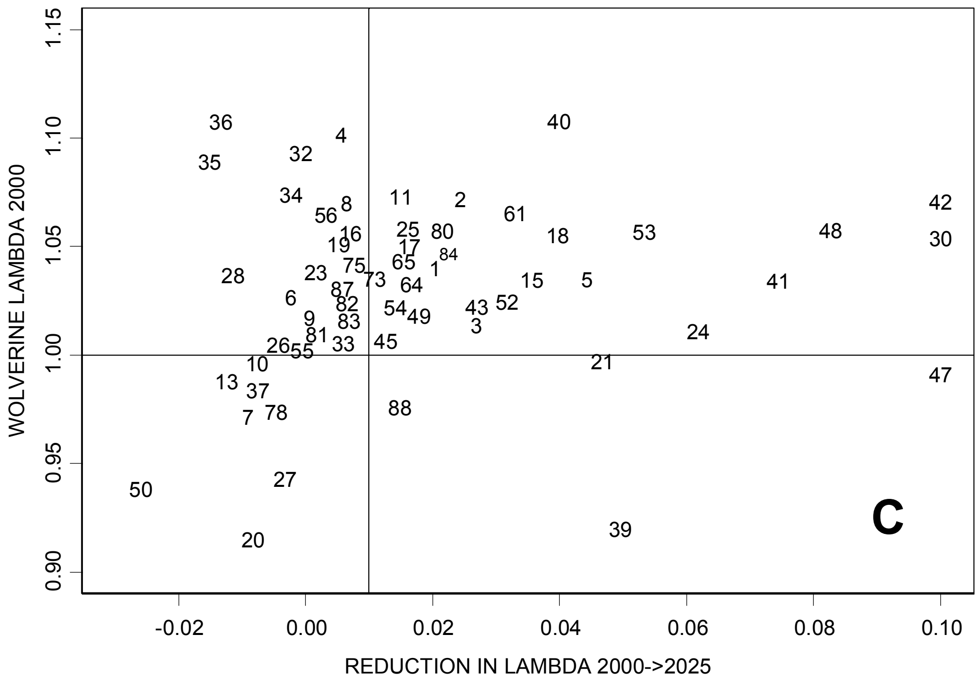


Figure 17. Irreplaceability and vulnerability by section for grizzly bear (A), wolf (B), and wolverine (C). Irreplaceability in this context is the value of an area as source habitat. Vulnerability is measured here as the predicted decline in demographic value (lambda) over the next 25 years. Only those sections with greater than 50% probability of occupancy by a species are shown.





WOLVERINE LAMBDA 2000
REDUCTION IN LAMBDA 2000->2025
C

Figure 18. Key to section numbering used in Figure 17.

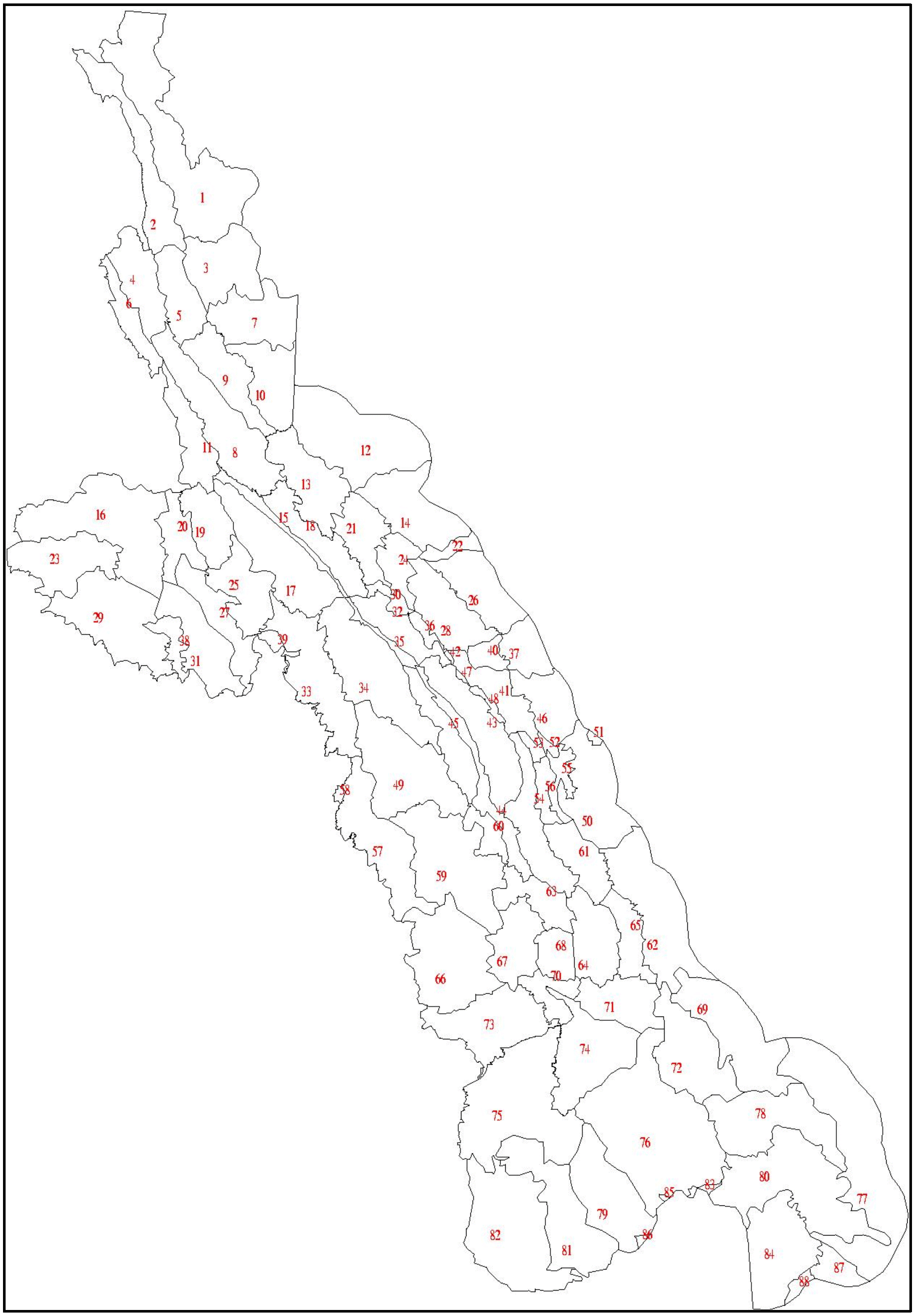


Figure 19. Map of predicted irreplaceability and vulnerability by ecosubsection for (A) grizzly bear, (B) wolf, and (C) wolverine. Areas in red suffer higher loss than those in green, with brighter shades of red or green indicating higher irreplaceability (occupancy-weighted lambda). Bright red areas represent threatened source habitat, bright green areas represent secure souces, and paler red areas represent threatened sinks.

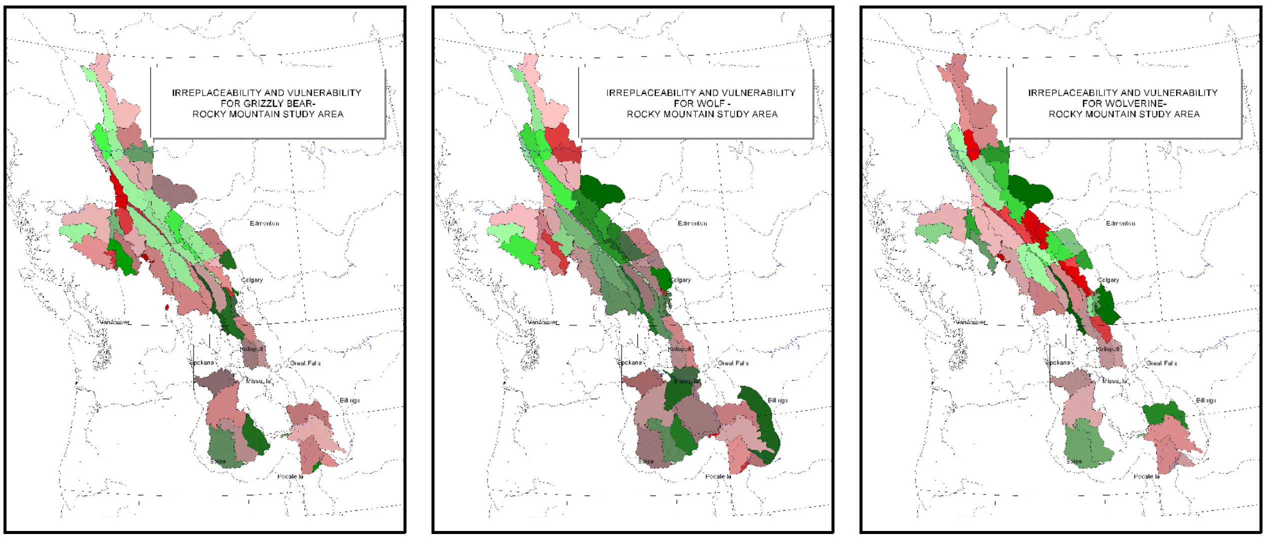


Figure 20. Comparison between static and dynamic models for lynx. Results of the static RSF model are shown with darker green areas representing higher RSF values. PATCH results in are overlaid in blue, with areas in blue having higher probability of occupancy by lynx in the PATCH simulations.

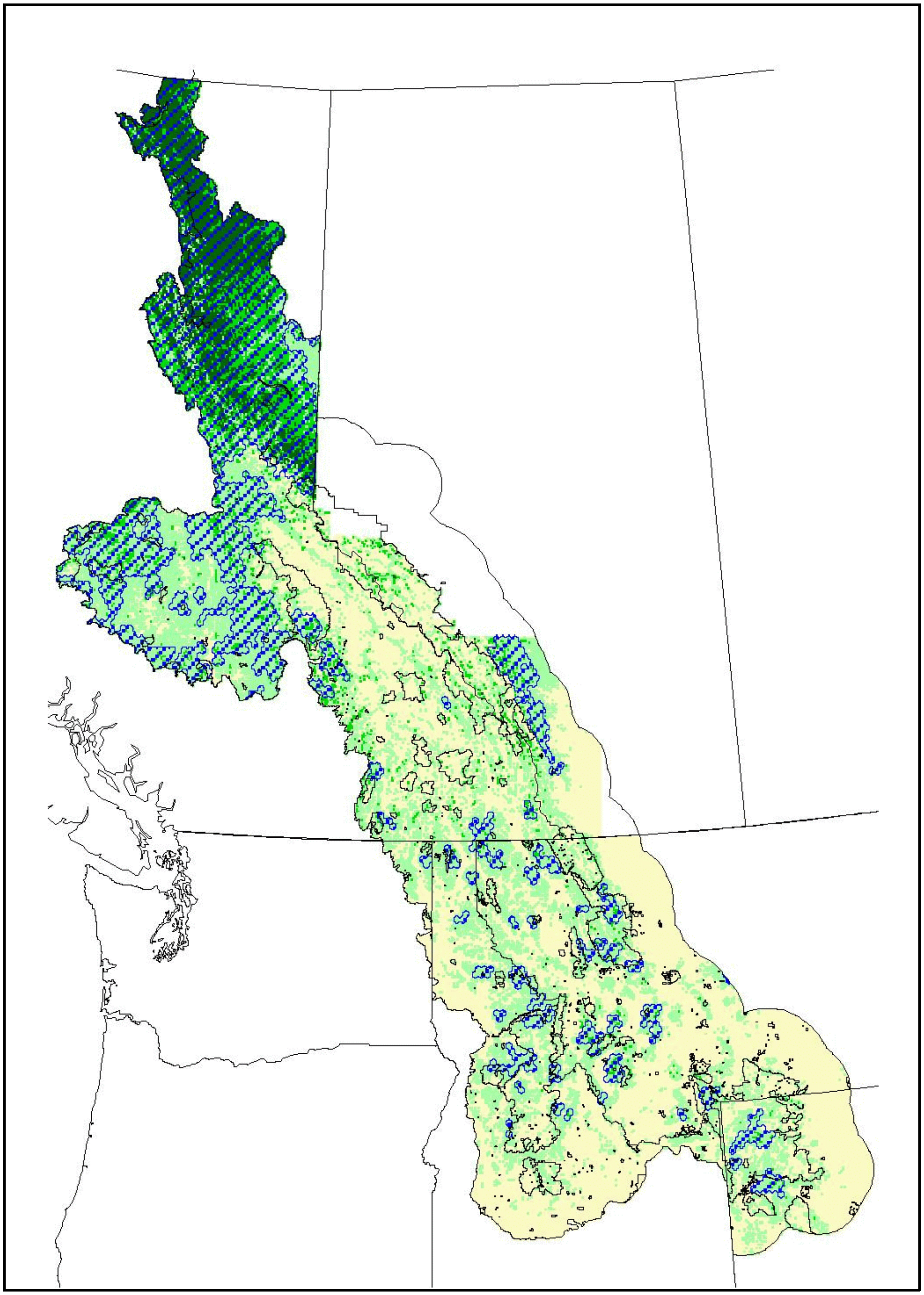


Figure 21. Total lynx population size over time in the southern half of the RMC study area, beginning from saturated habitat, as predicted under parameter sets with high (dotted lines) and low (solid lines) variance.

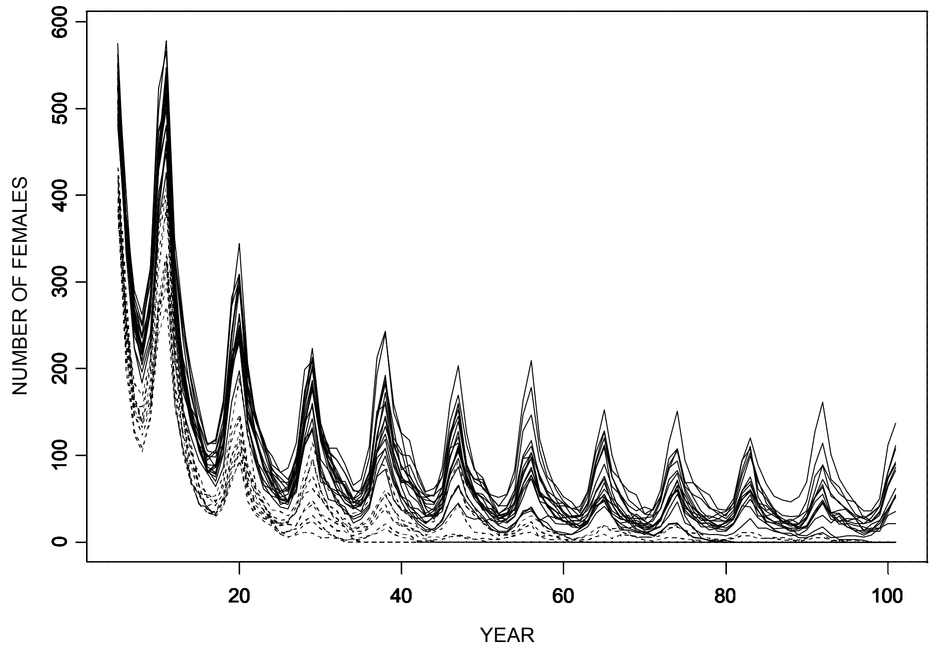


Figure 22. Occupancy probability of fisher source habitat versus distance from sink habitat as observed in the PATCH simulations under three mortality scenarios.

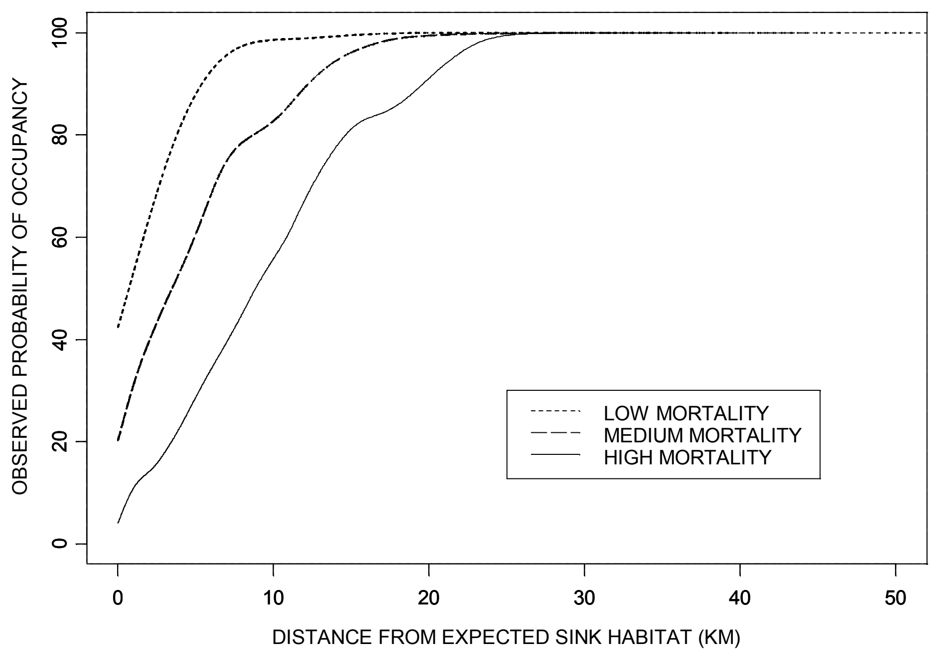
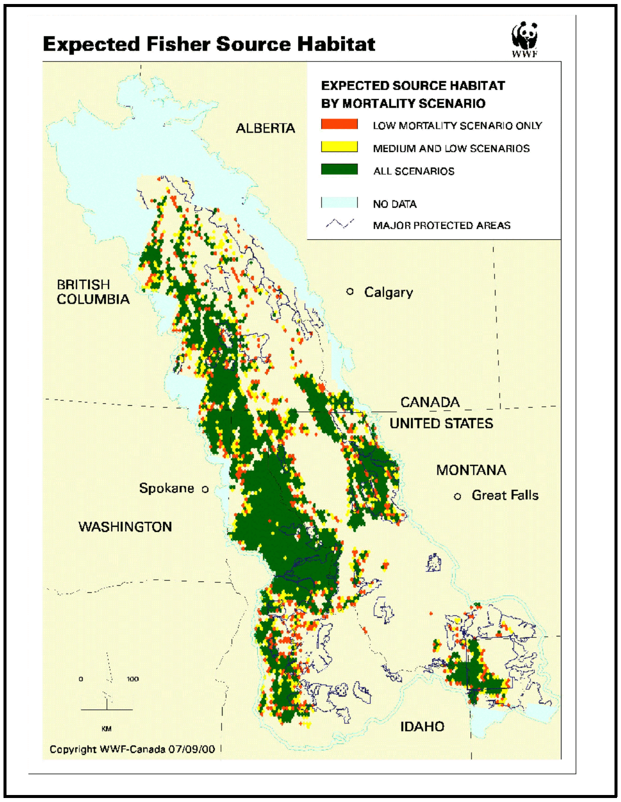


Figure 23. Regional distribution of demographic sources and sinks for the fisher under three mortality scenarios. Expected sources and sinks are based on demographic parameters scaled to habitat quality whereas observed sources and sinks are based on simulation results using these scaled parameters.



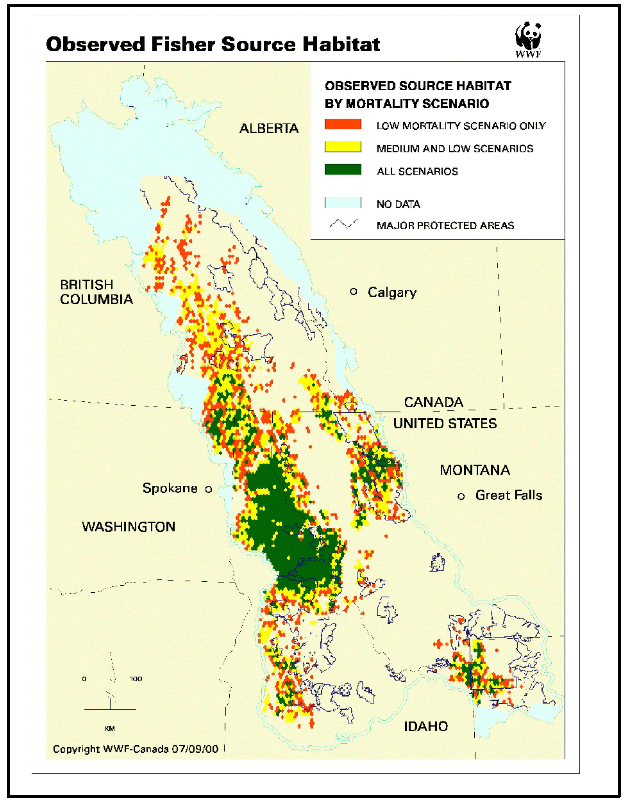


Figure 24. Relationship between management class and predicted lambda in the RMC study region for grizzly bear, wolf, and wolverine.

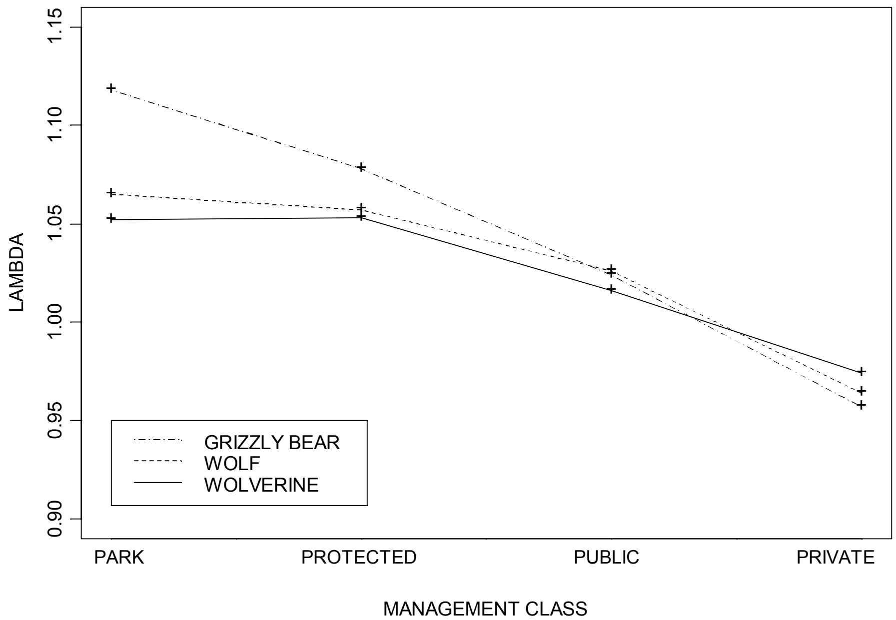


Figure 25. Contrast in predicted occupancy values from PATCH model between wolf pack territories and non-pack areas in the GYE.

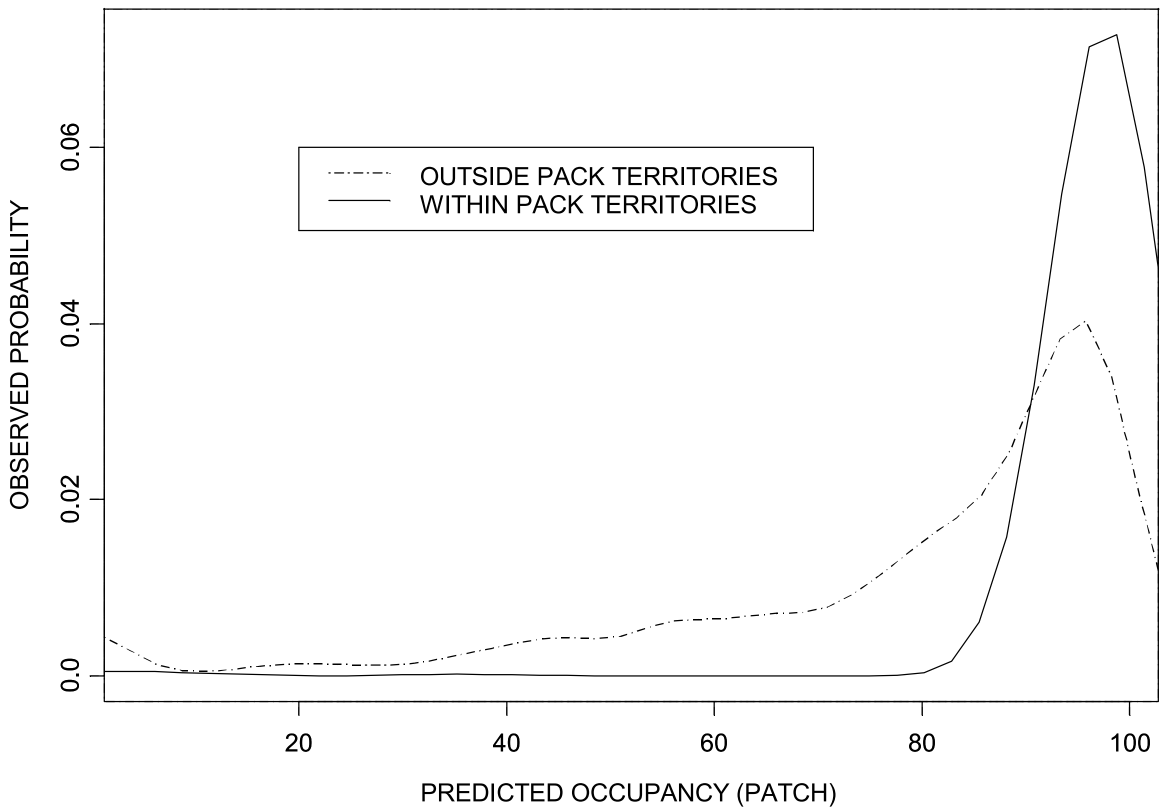


Figure 26. Lynx validation data, overlaid on predictions from the lynx RSF model. Cells with lynx tracks are shown in red, whereas cells without tracks are outlined in black. The predicted habitat suitability ranges from white (low) to dark green (high).

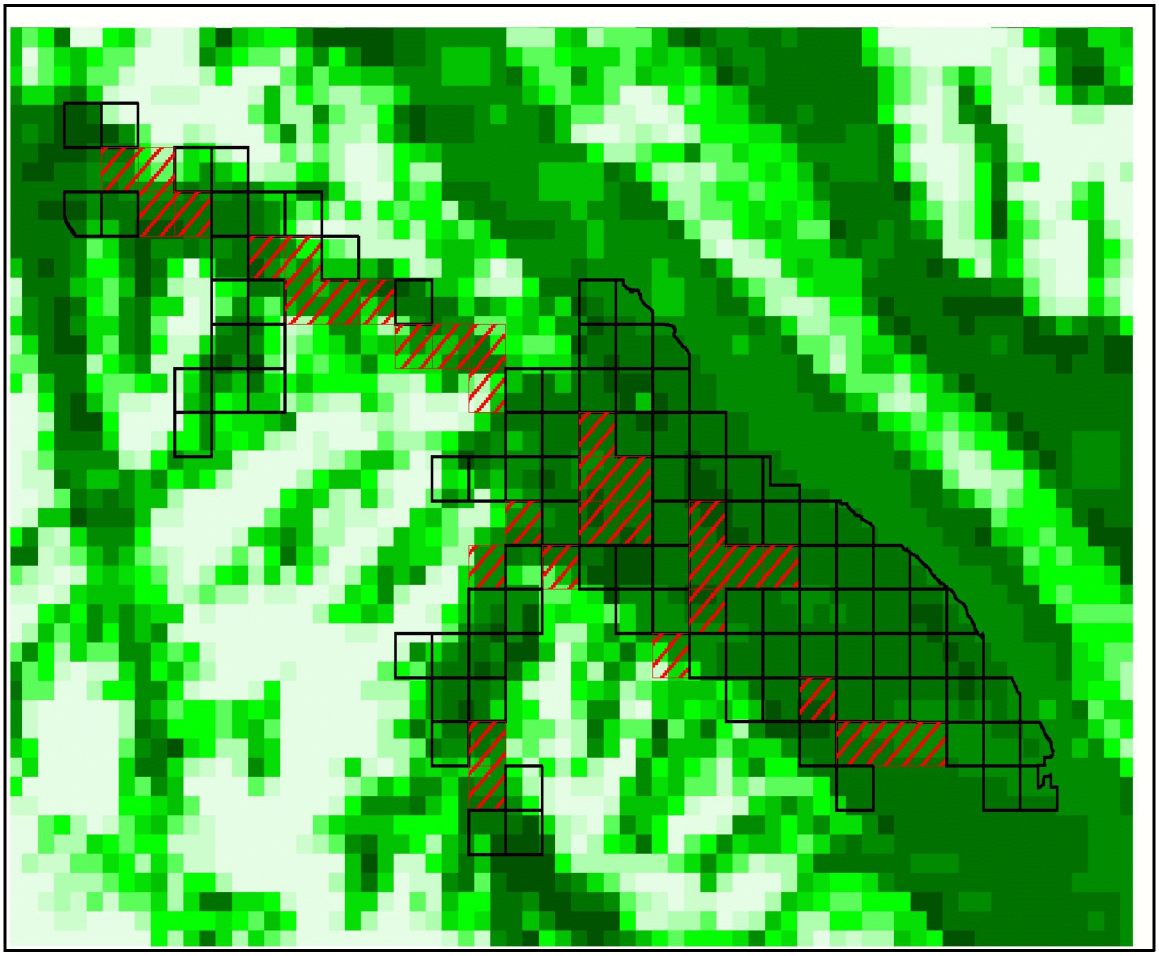


Figure 27. Results of SITES runs for eight carnivore species (static model-based, goals 40% regional, 30% local). Protected areas were not locked into portfolio.

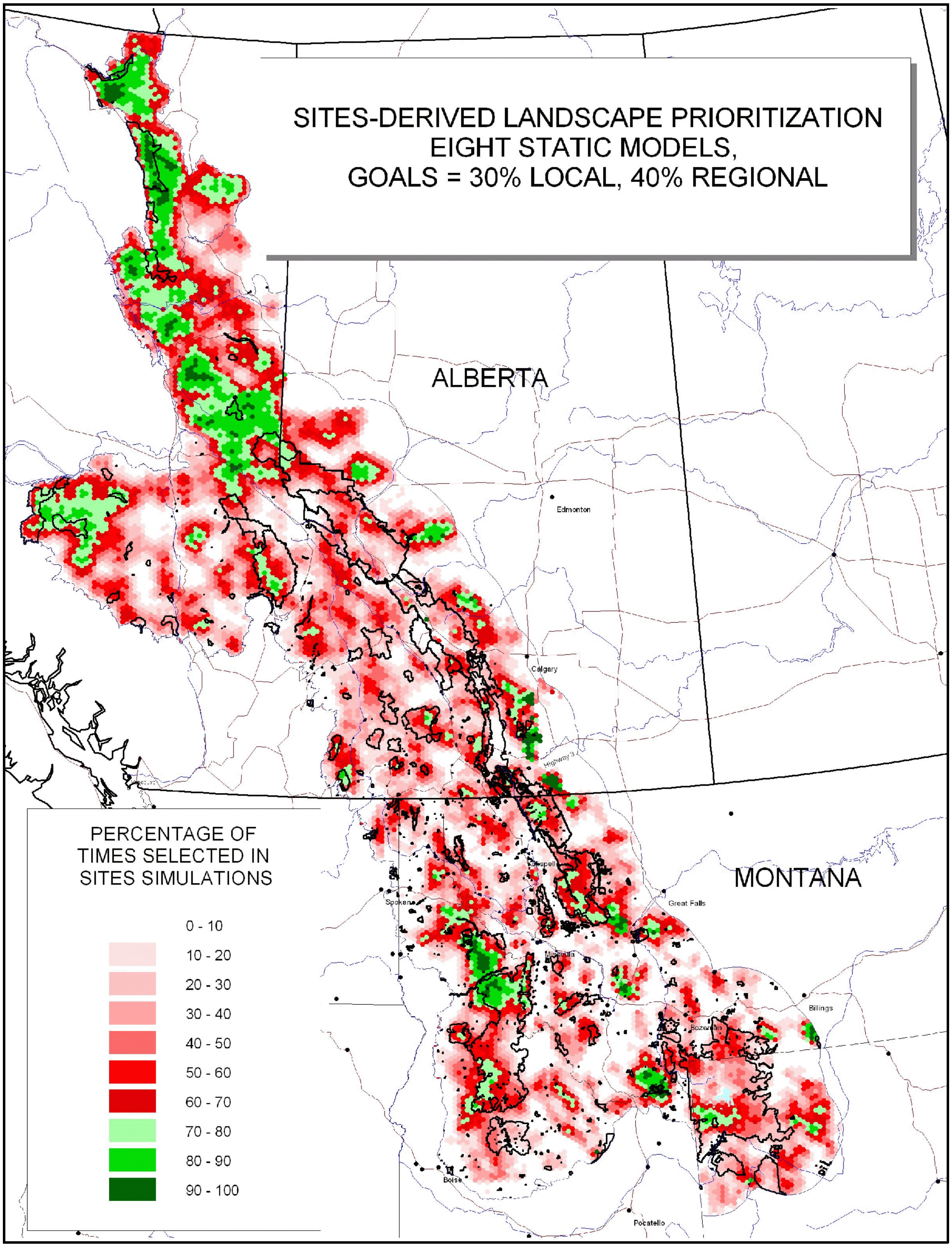


Figure 28. Example of PATCH-based goals used in SITES runs. Areas shown in red lie in Quadrant 1 (top-right) of the irreplaceability/vulnerability graph for grizzly bear, that is, areas with both high value as source habitats and high threat. Areas shown in green are the highest value source habitats, that is, the upper portions of quadrants 1 and 2 of the irreplaceability/vulnerability graph for grizzly bear.

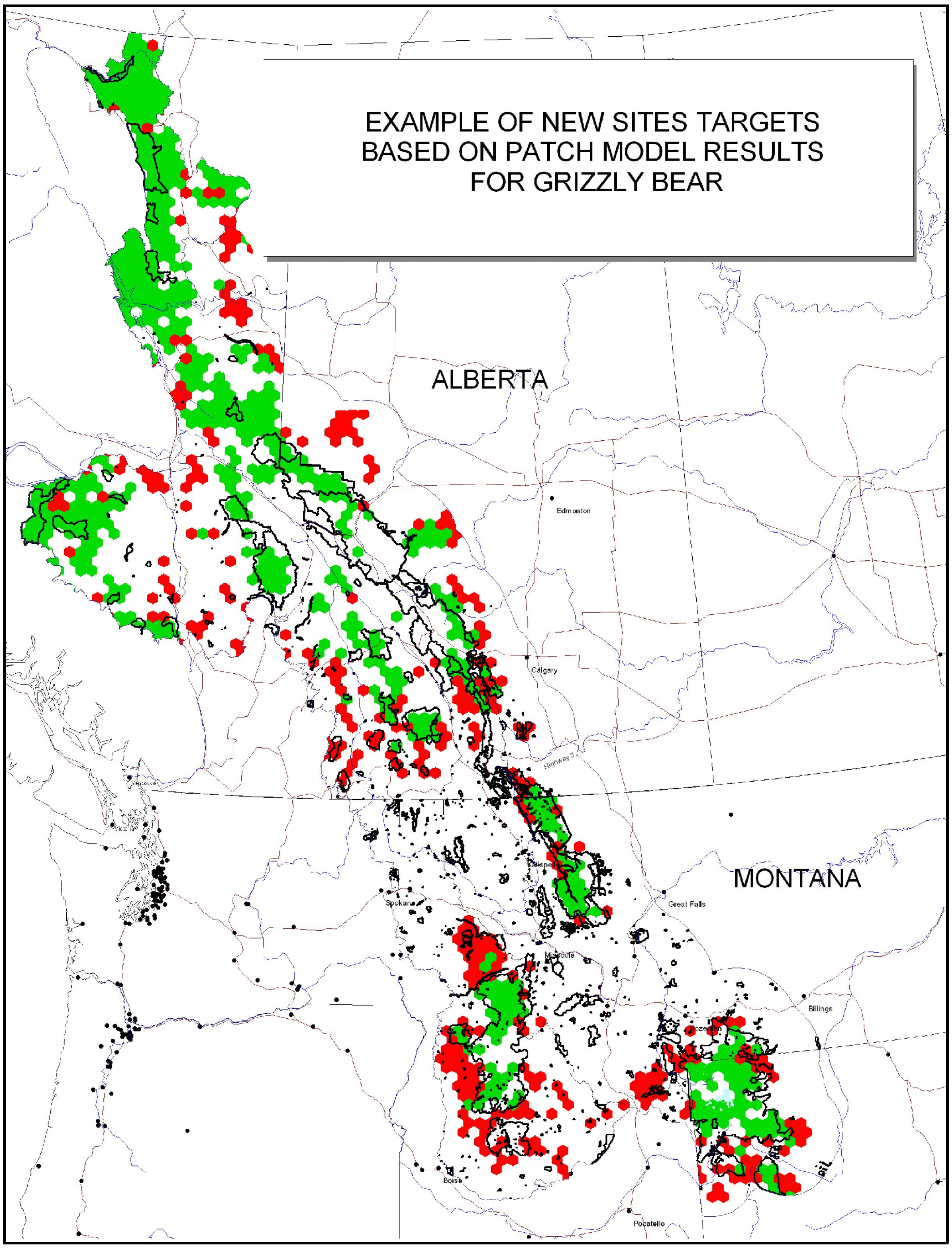


Figure 29. Contrast between SITES solutions for three carnivores species (grizzly bear, wolf, and wolverine) which based on the static habitat suitability models or the PATCH models. Areas in orange were only selected in the static model-based SITES runs (goals 35% regional/15% local), areas in green were only selected in the PATCH model-based SITES runs (goals 50% regional/30% local), and areas in red were common to both alternative cost scenarios.

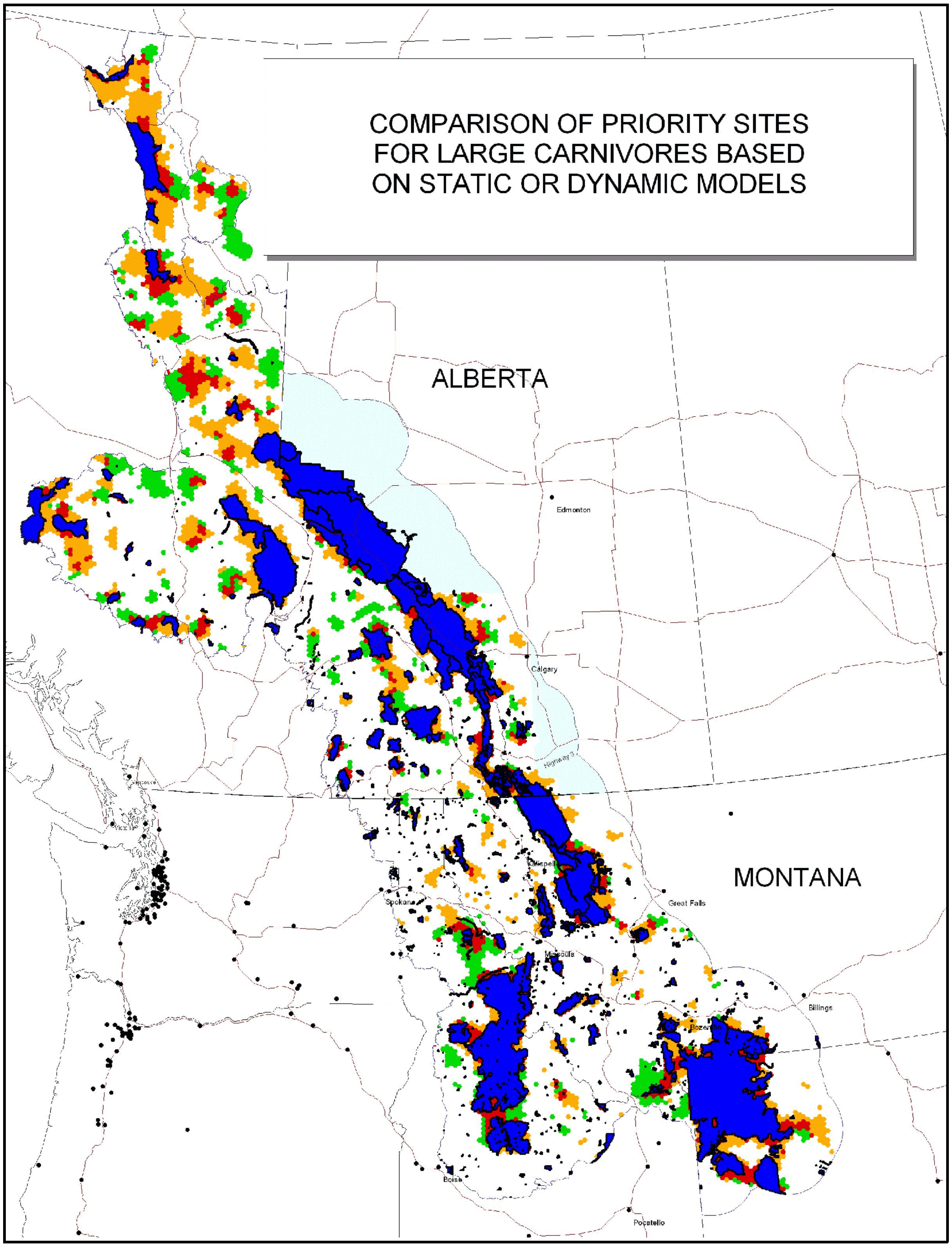


Figure 30. Response of grizzly bear and wolf populations, as predicted by the PATCH model, to SITES portfolios of varying size.

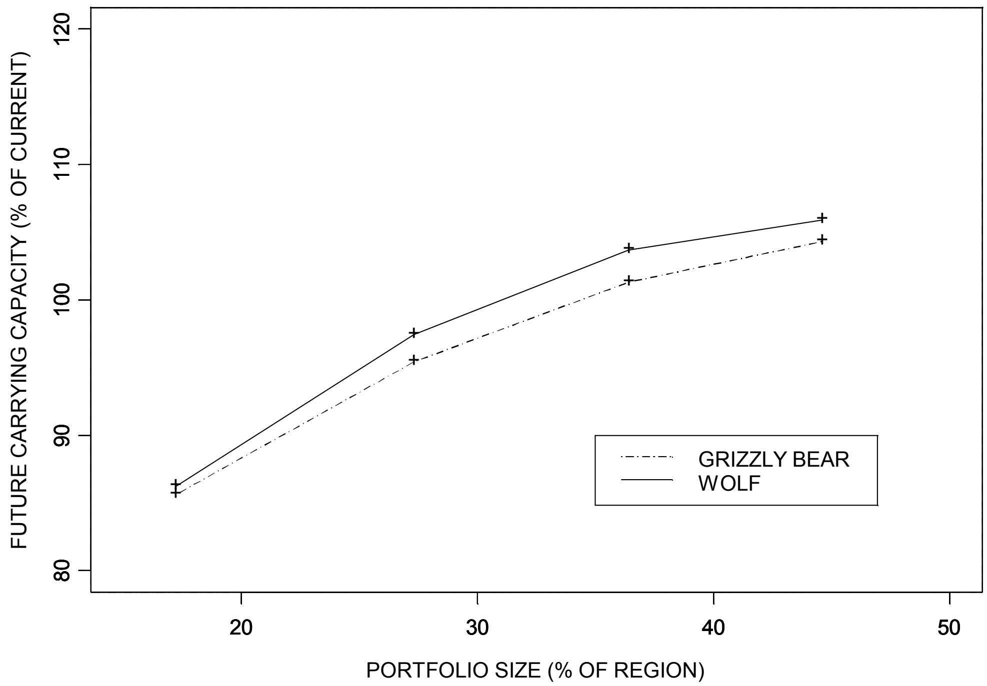


Figure 31. Contrast in potential future distribution in 2025, as predicted by the PATCH model, for A) grizzly bear, and B) wolf, under current trends (green) and the 40% regional/30% local goals portfolio (green plus red).

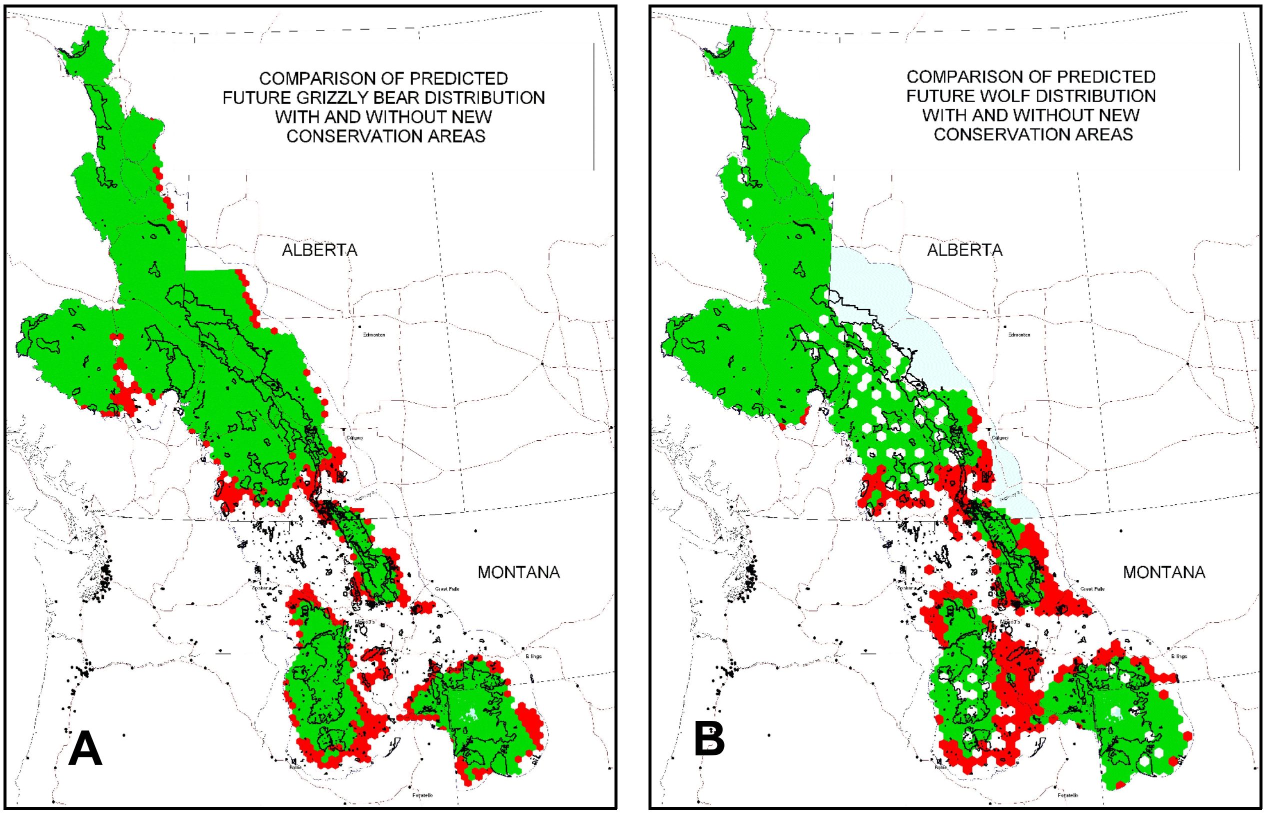


Figure 32. Comparison of final SITES portfolios with moderate goals (dark green areas) and high goals (both light and dark green areas).

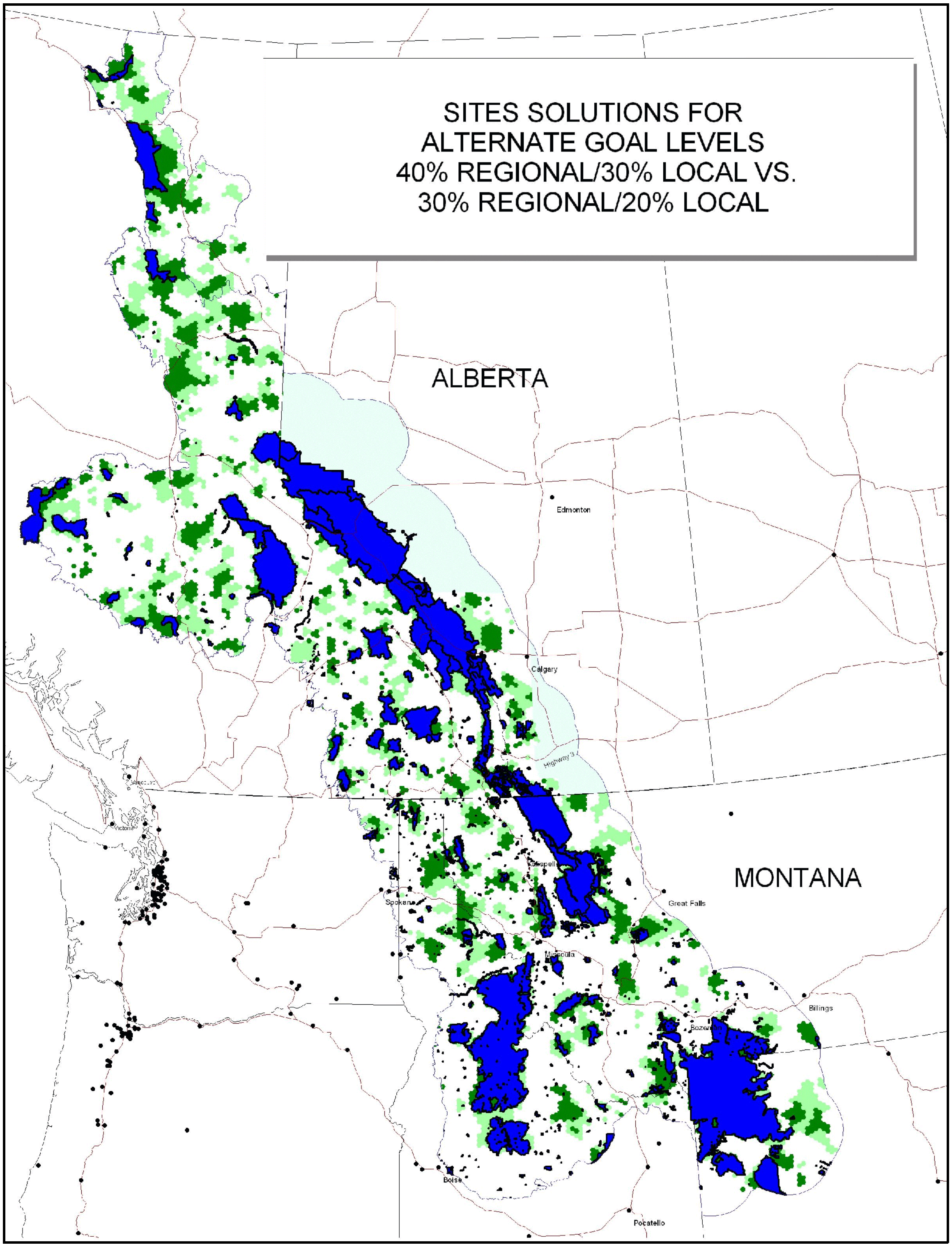


Figure 33. Variability and flexibility in SITES results for a final portfolio (goals 30% regional, 20% local). Areas included in the best solution is shown in blue hatching. Red areas were included in one or more of 100 replicate SITES solutions, with darker red indicating inclusion in a larger proportion of the 100 solutions.

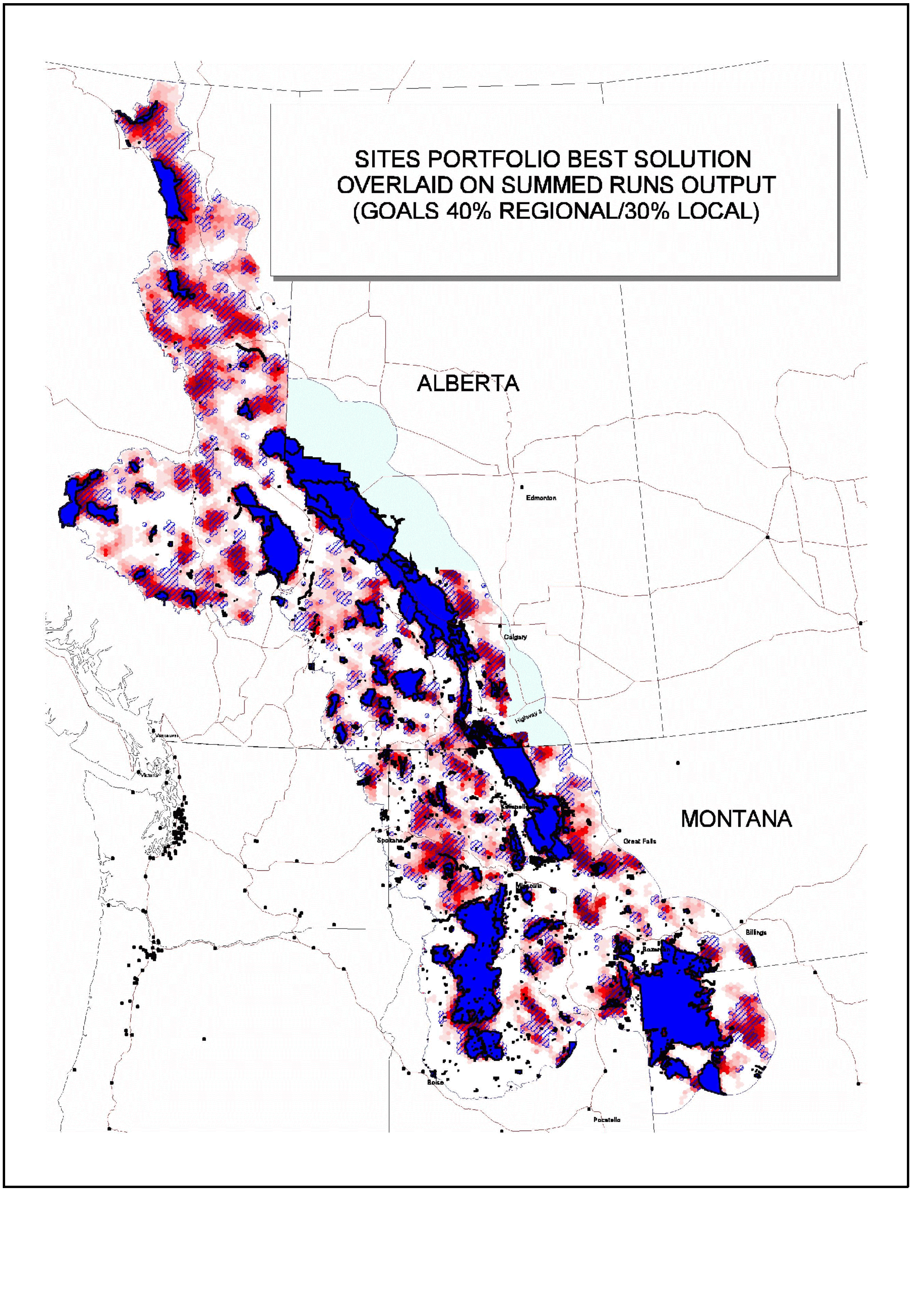


Figure 34. Conceptual diagram of threshold responses of populations of large carnivores to increasing protected area designation. Responses vary between the three major subregions of the overall study area.

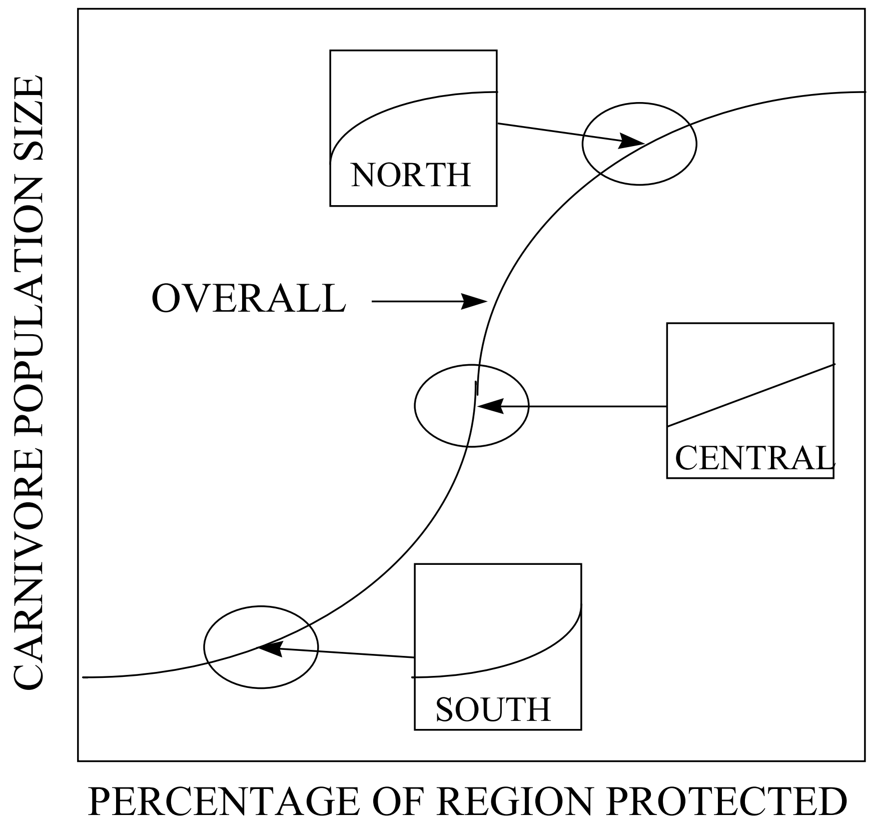


Figure 35. Contrasts between SITES portfolios based on carnivore goals and special elements and representation goals in the CanRock ecoregion. Areas in green were selected only in the carnivore-based portfolio, areas in orange only in the special elements/representation portfolio, and areas in blue in both portfolios.

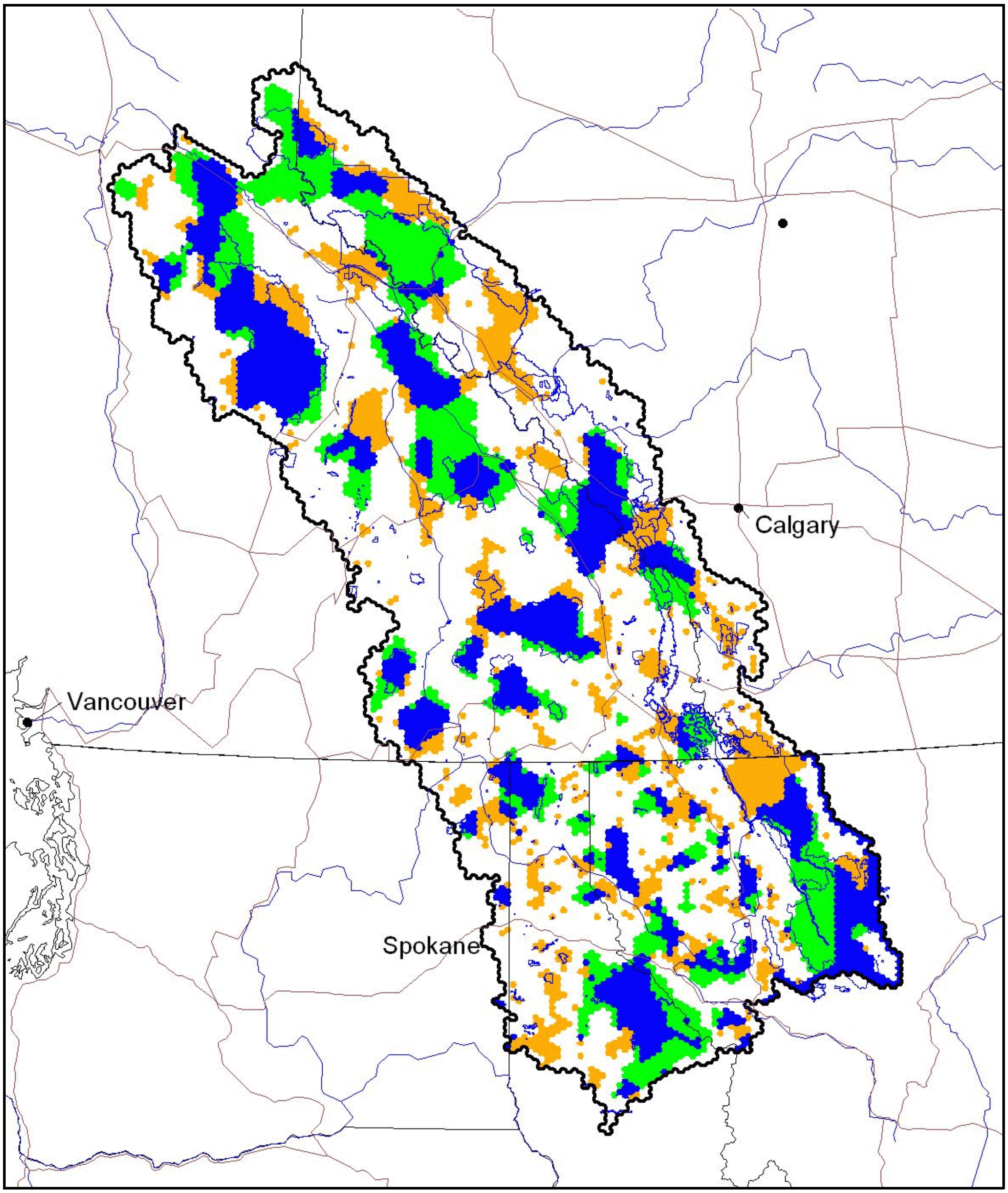


Figure 36. Comparison of SITES portfolios incorporating differing levels of carnivore habitat goals. Protected areas were not locked into the portfolio. See text for explanation of color key.

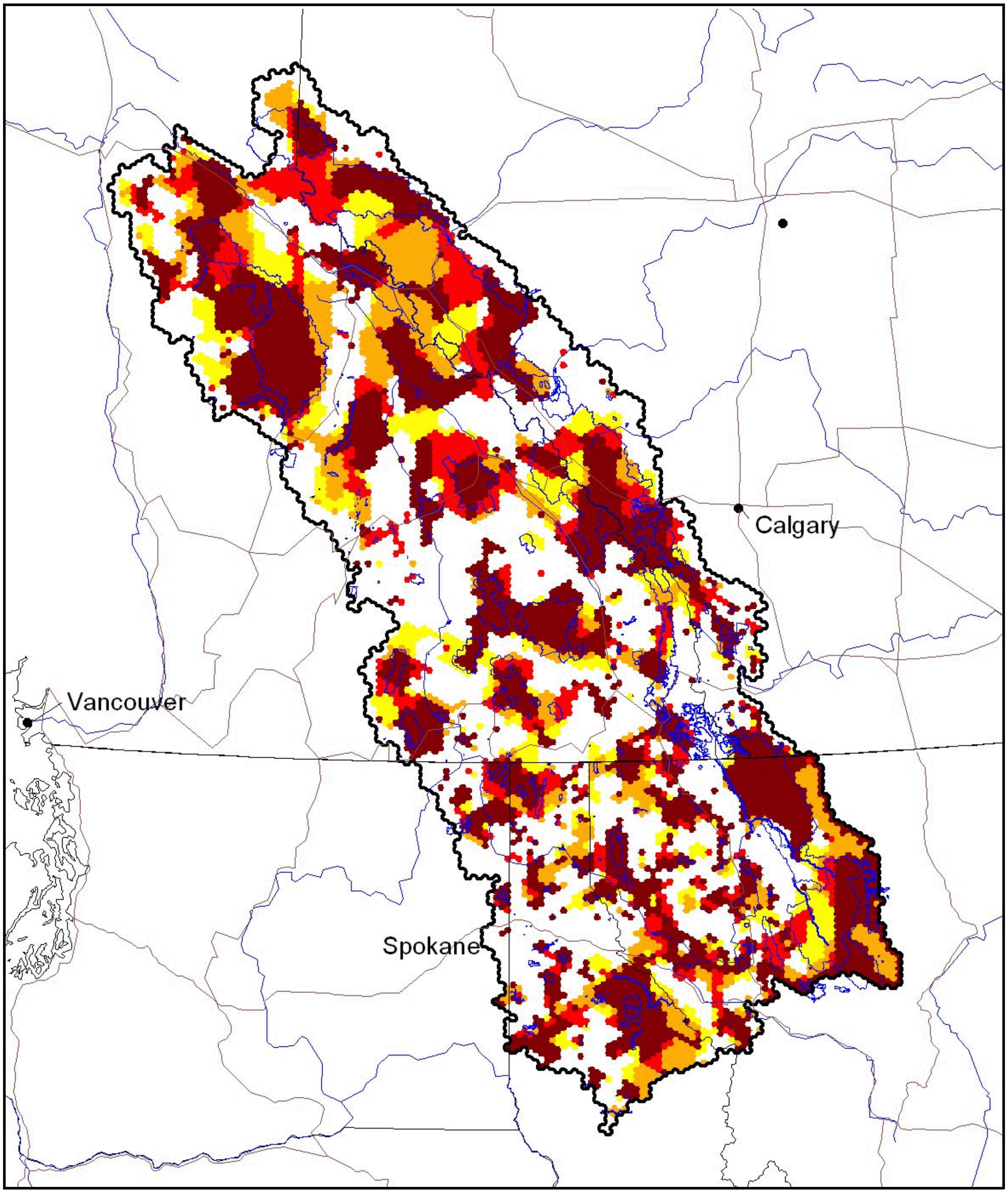


Figure 37. Comparison of SITES portfolios incorporating differing levels of carnivore habitat goals. Protected areas were locked into the portfolio. See text for explanation of color key.

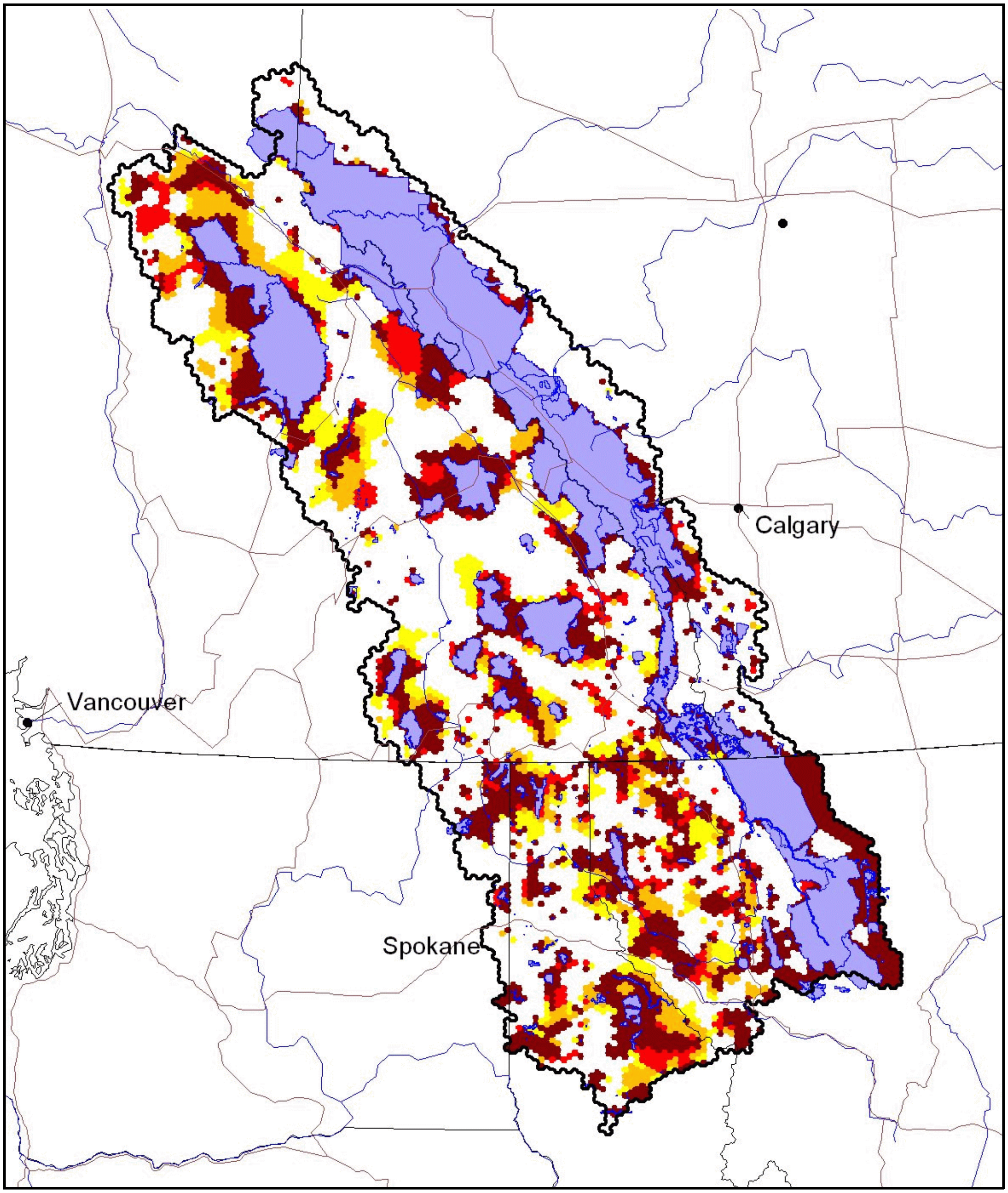


Figure 38. Response of grizzly bear and wolf populations, as predicted by the PATCH model, to CanRock SITES portfolios of varying size (locked, carnivore goals 0-50%).

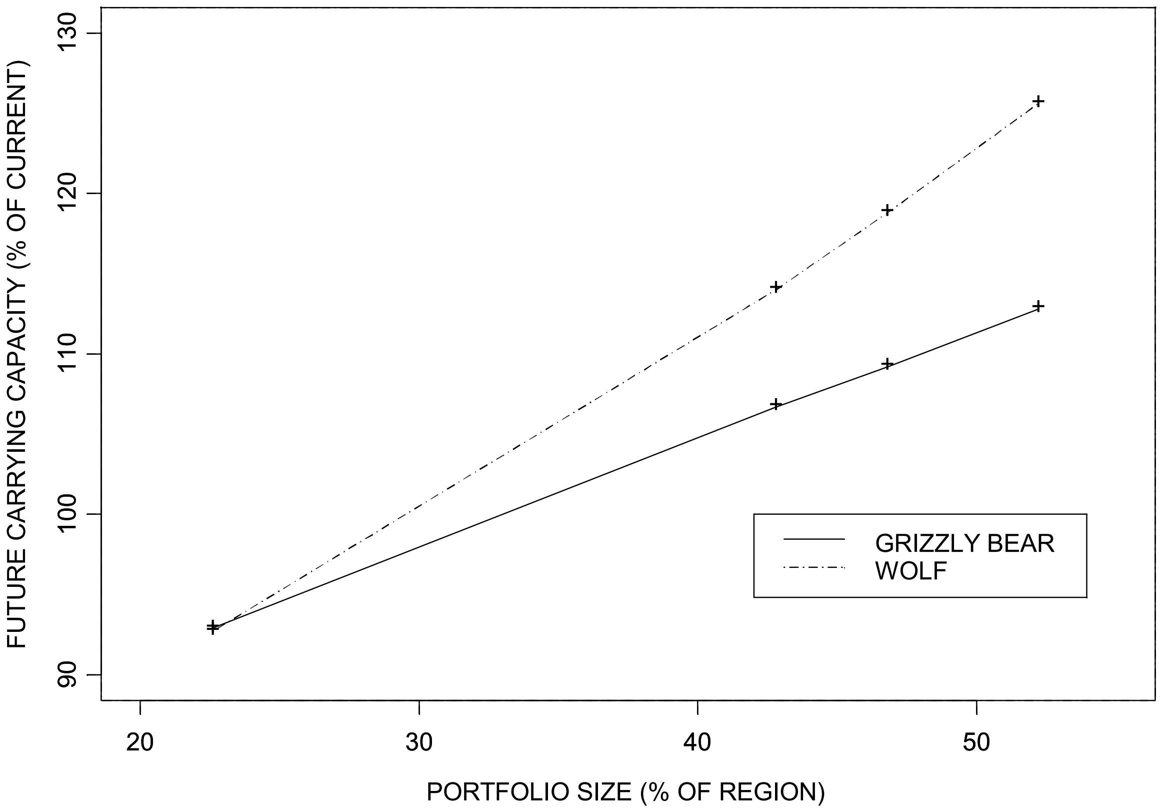


Figure 39. Contrast in potential future distribution in 2025, as predicted by the PATCH model, for A) grizzly bear, and B) wolf, under current trends (green) and the carnivore 40% locked portfolio (green plus red).

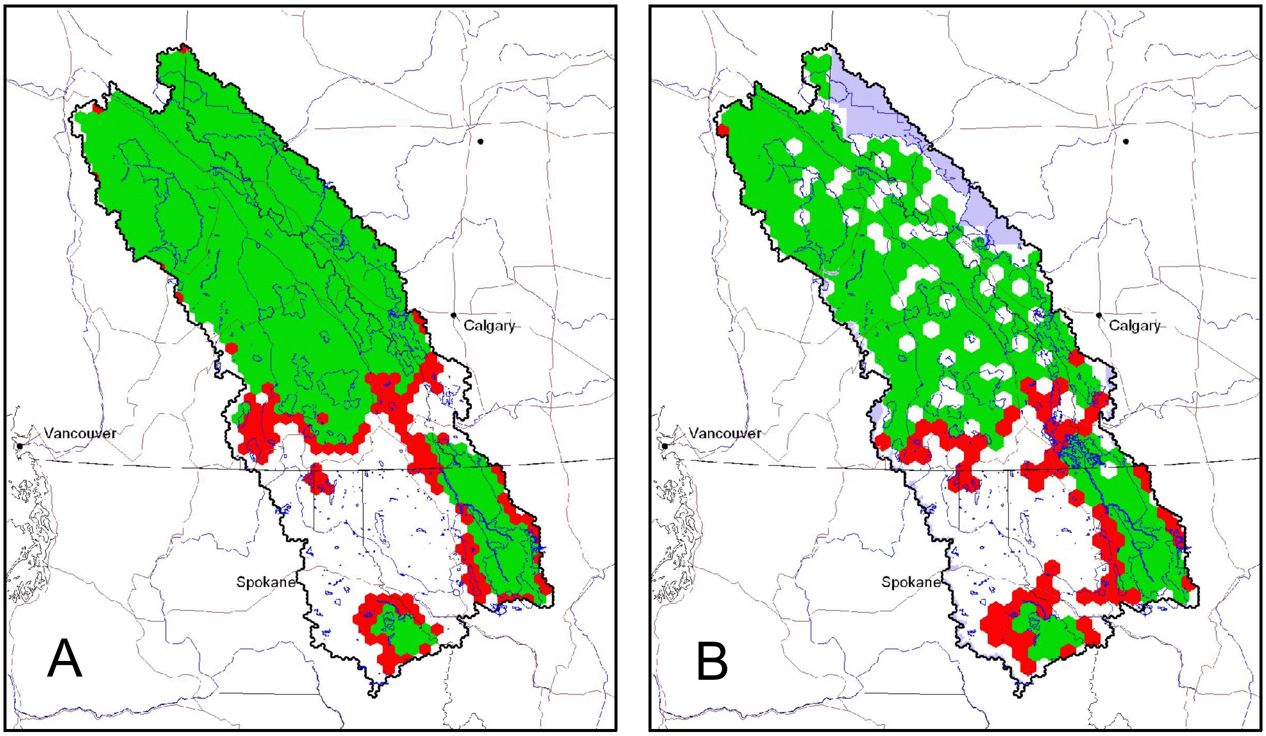


Figure 40. Variability in SITES results for the carnivore 40% non-locked portfolio. Areas included in the best solution is shown in blue hatching. Red areas were included in one or more of 100 replicate SITES solutions, with darker red indicating inclusion in a larger proportion of the 100 solutions.

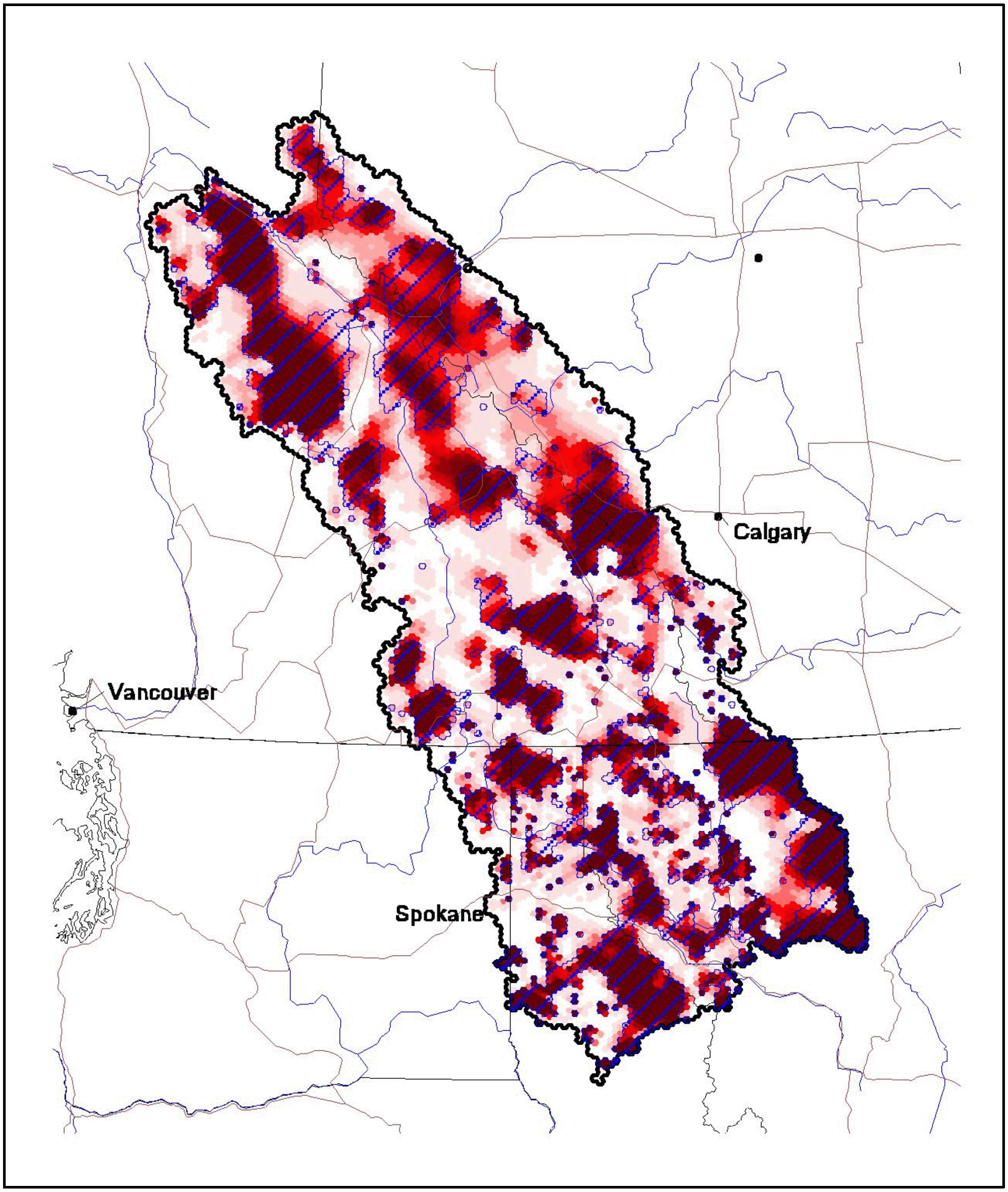


Figure 41. Contrast between SITES solutions (carnivore 40% non-locked) with differing methods for estimating the "cost" of potential portfolio sites. Areas in orange were only selected when we used the number of hectares in a site as its cost, areas in green were only selected when we also included increased land cost due to development, and areas in blue were common to both alternative cost scenarios.

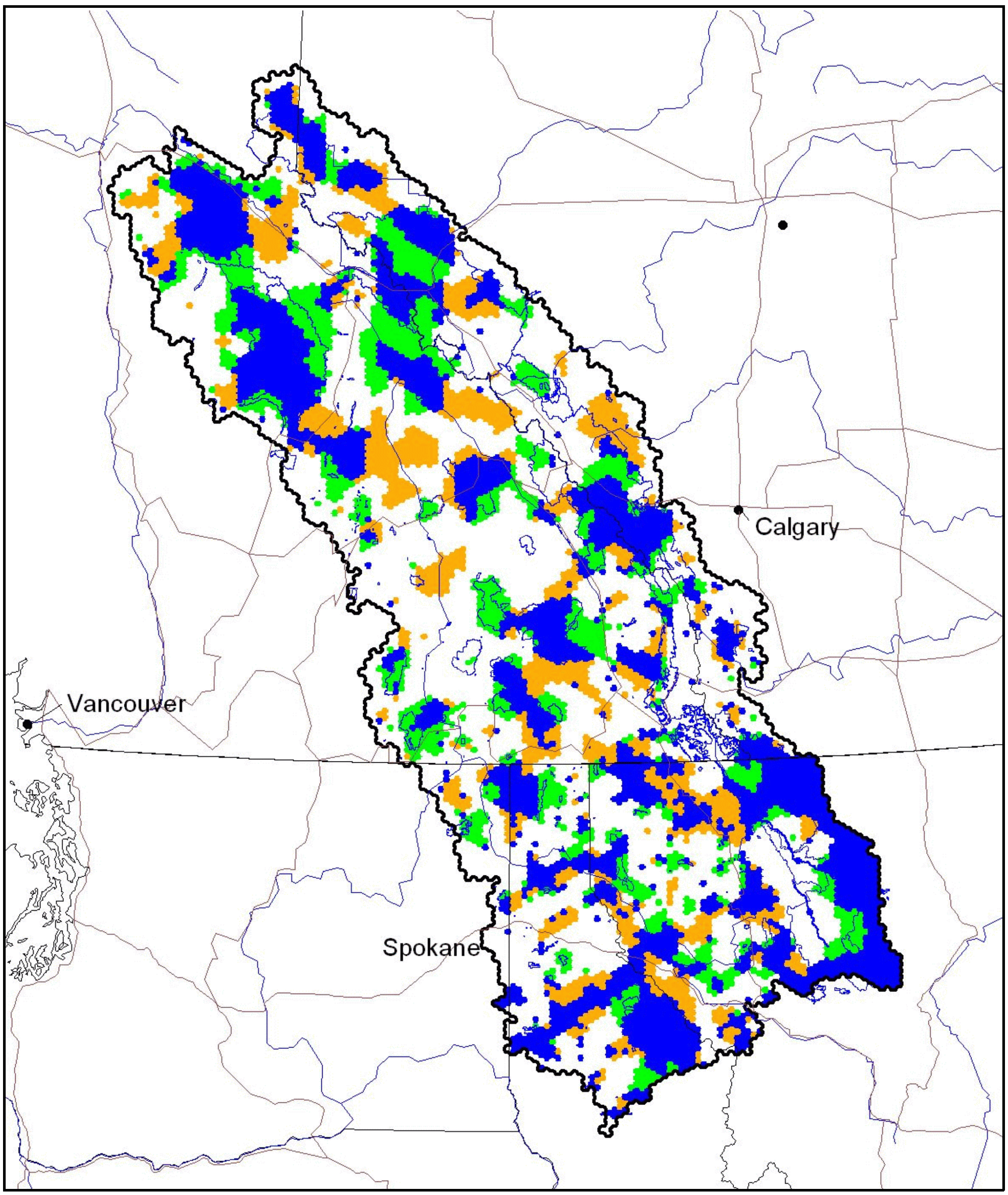


Figure 42. Contrast between SITES solutions (carnivore 40% non-locked) with differing options for stratifying the carnivore habitat goals. Areas in orange were only selected when we set one overall regional habitat goal for each species, areas in green were only selected when we also included separate goals by ecosection, and areas in blue were common to both alternative scenarios.

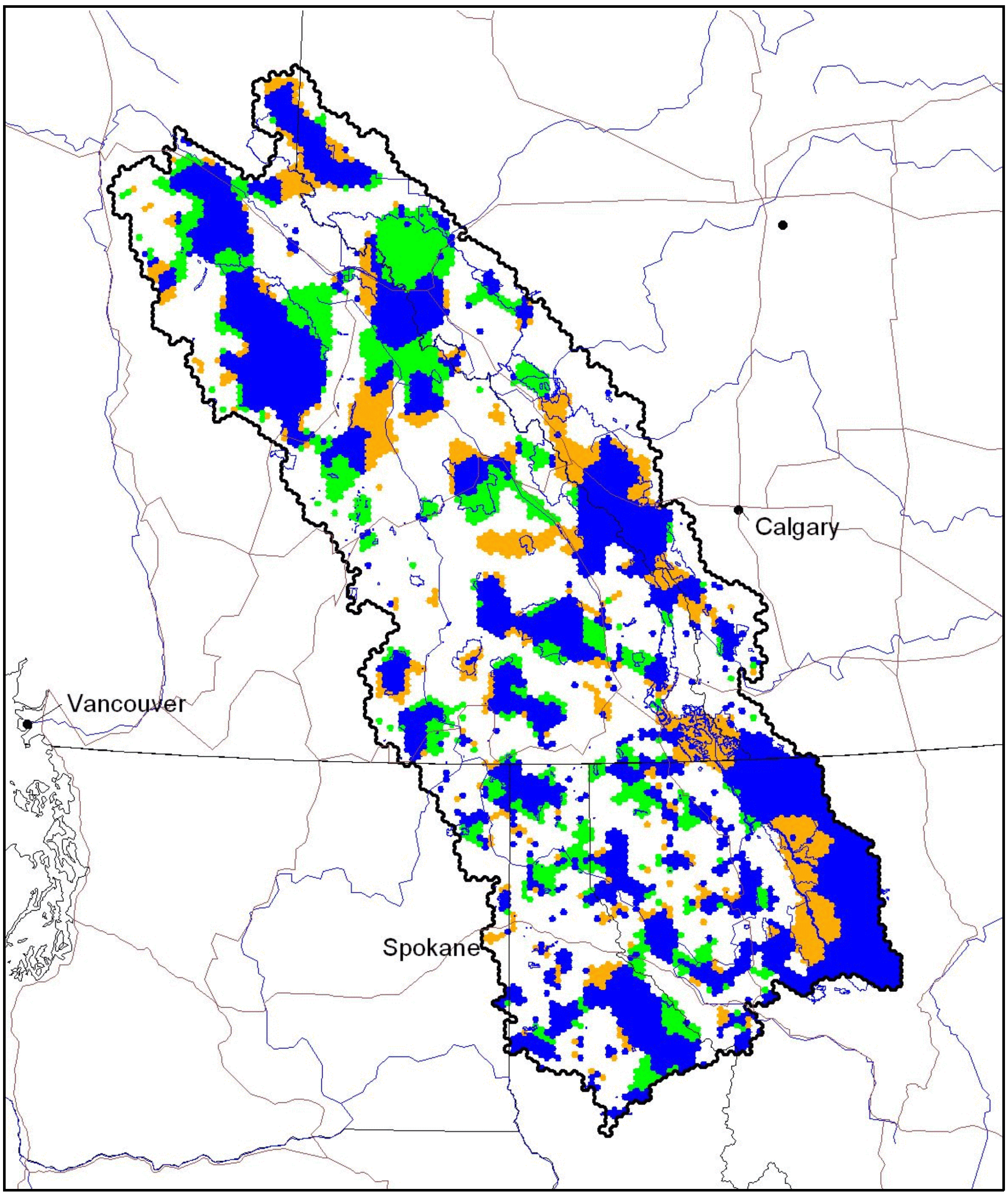


Figure 43. Map of the case study focal area in the Canada/U.S. transboundary region, showing proposed conservation areas involving Waterton Park expansion and Southern Rocky Mountains Conservation Area (SRMCA).

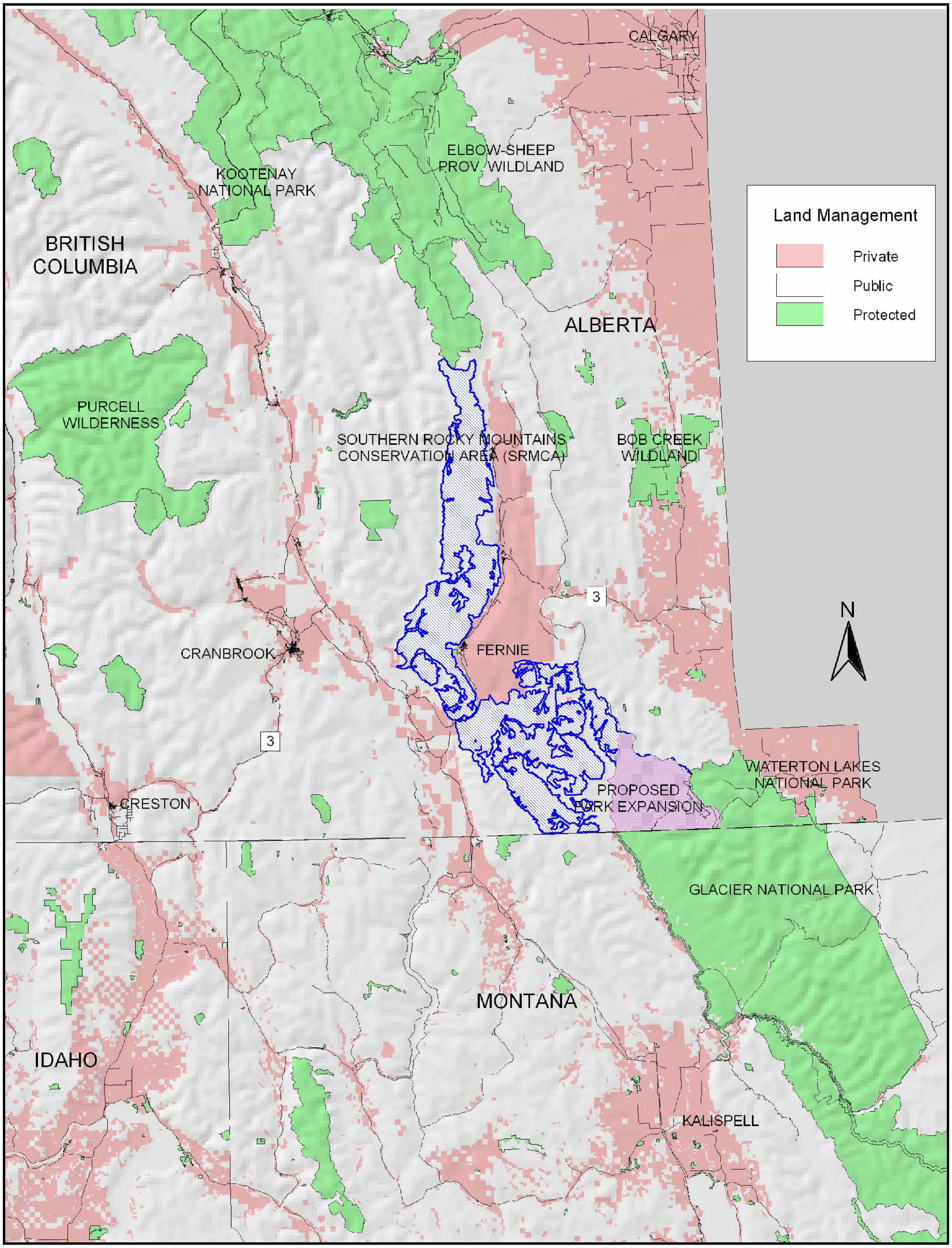


Figure 44. Potential distribution of grizzly bears in the Canada/U.S. transboundary region under (a) current and (b) future landscape conditions (2025), assuming road development on both private and public lands, as predicted by the PATCH model simulations.

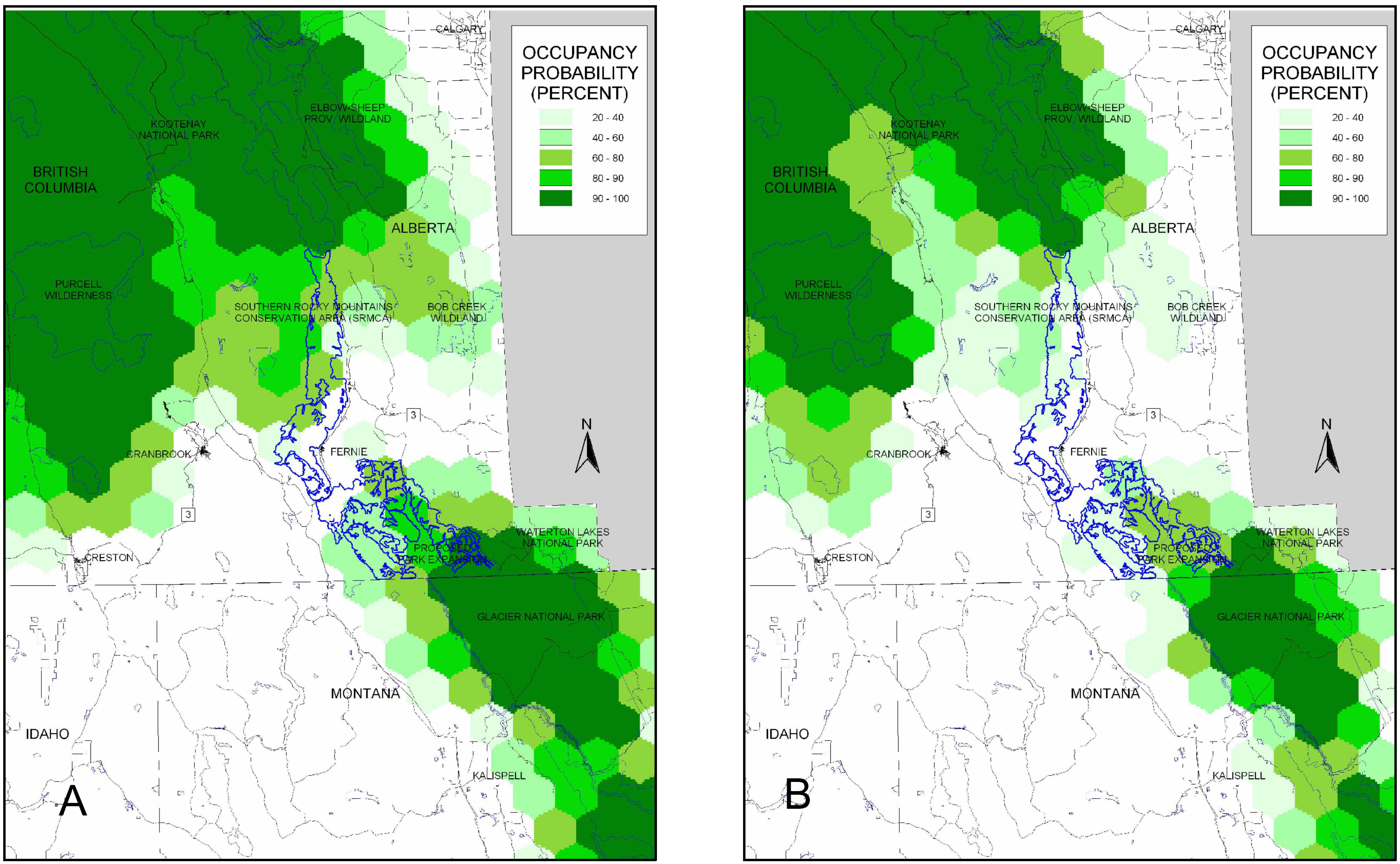


Figure 45. Demographic potential of grizzly bears in the Canada/U.S. transboundary region under current landscape conditions as predicted by the PATCH model simulations. Only areas with greater than 20% probability of occupancy are shown.

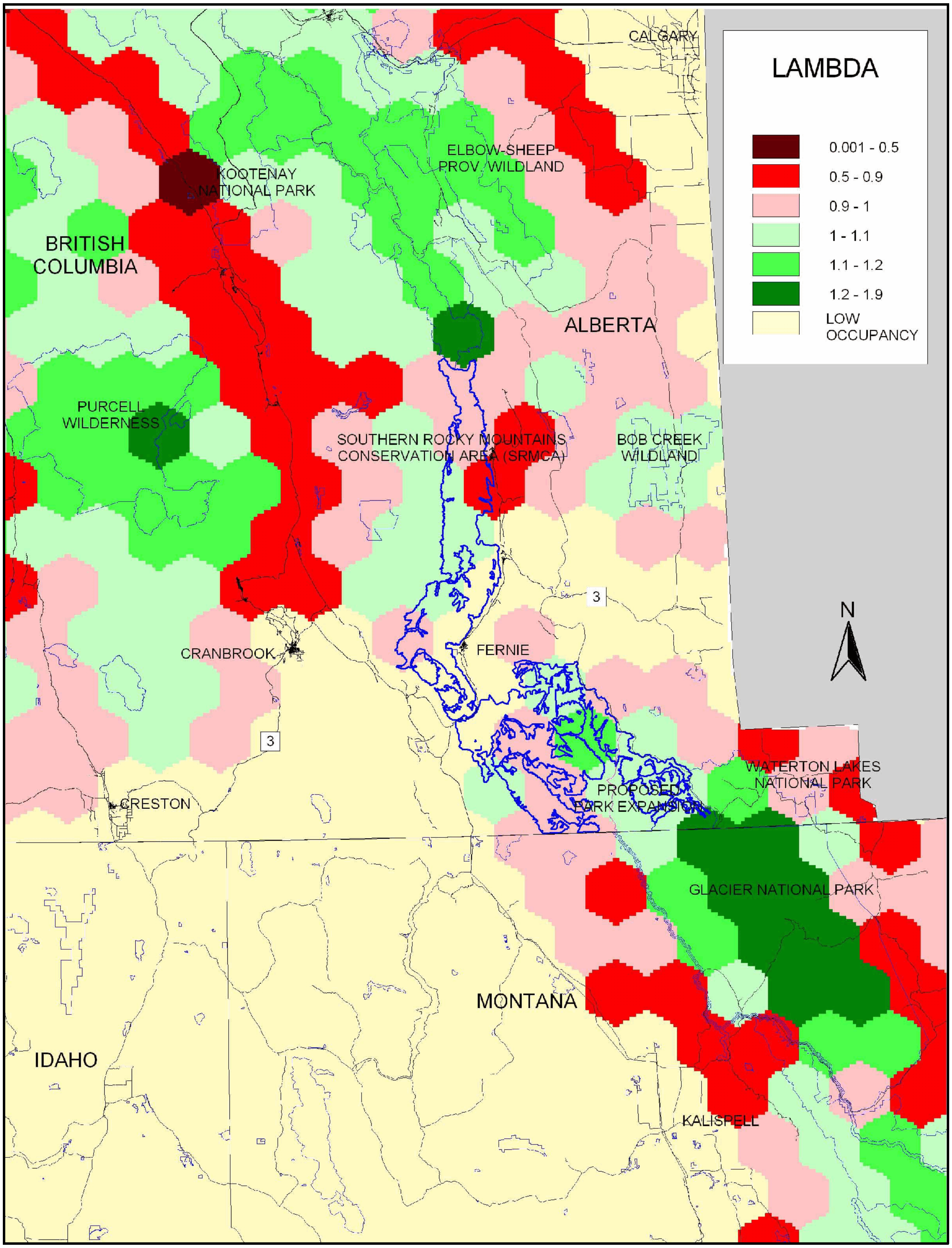


Figure 46. Change in demographic potential of grizzly bears in the Canada/U.S. transboundary region between current landscape conditions and future landscape conditions (2025), assuming road development on both private and public lands, as predicted by the PATCH model simulations. Only areas with greater than 20% probability of occupancy are shown.

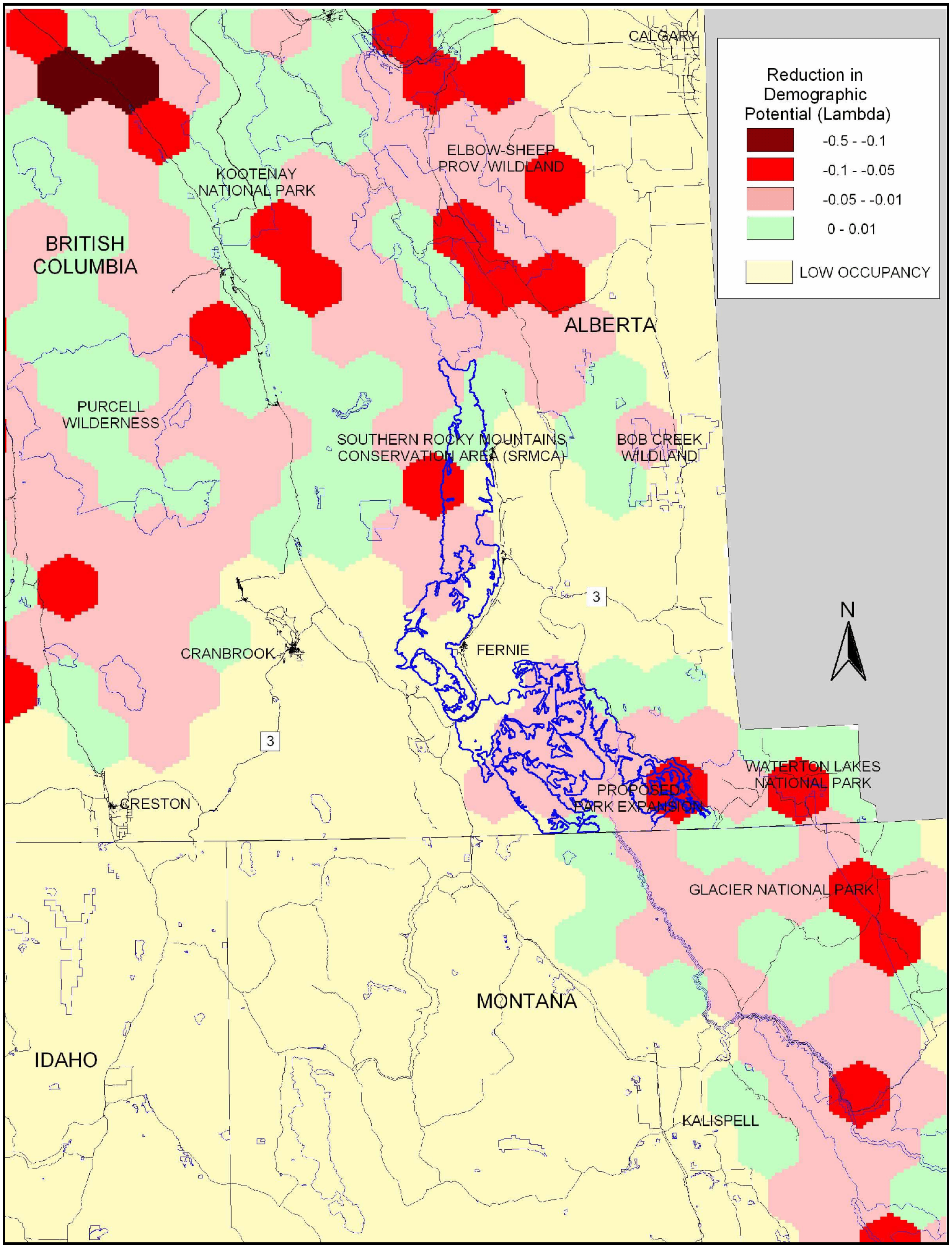


Figure 47. Reduction in potential grizzly bear carrying capacity in the Canada/U.S. transboundary region from 2000-2025 as predicted by the PATCH model, assuming road development on both private and public lands (a), or assuming road development on private lands only (b). Areas in dark red show greatest reduction in potential occupancy due to expected human population growth and landscape change.

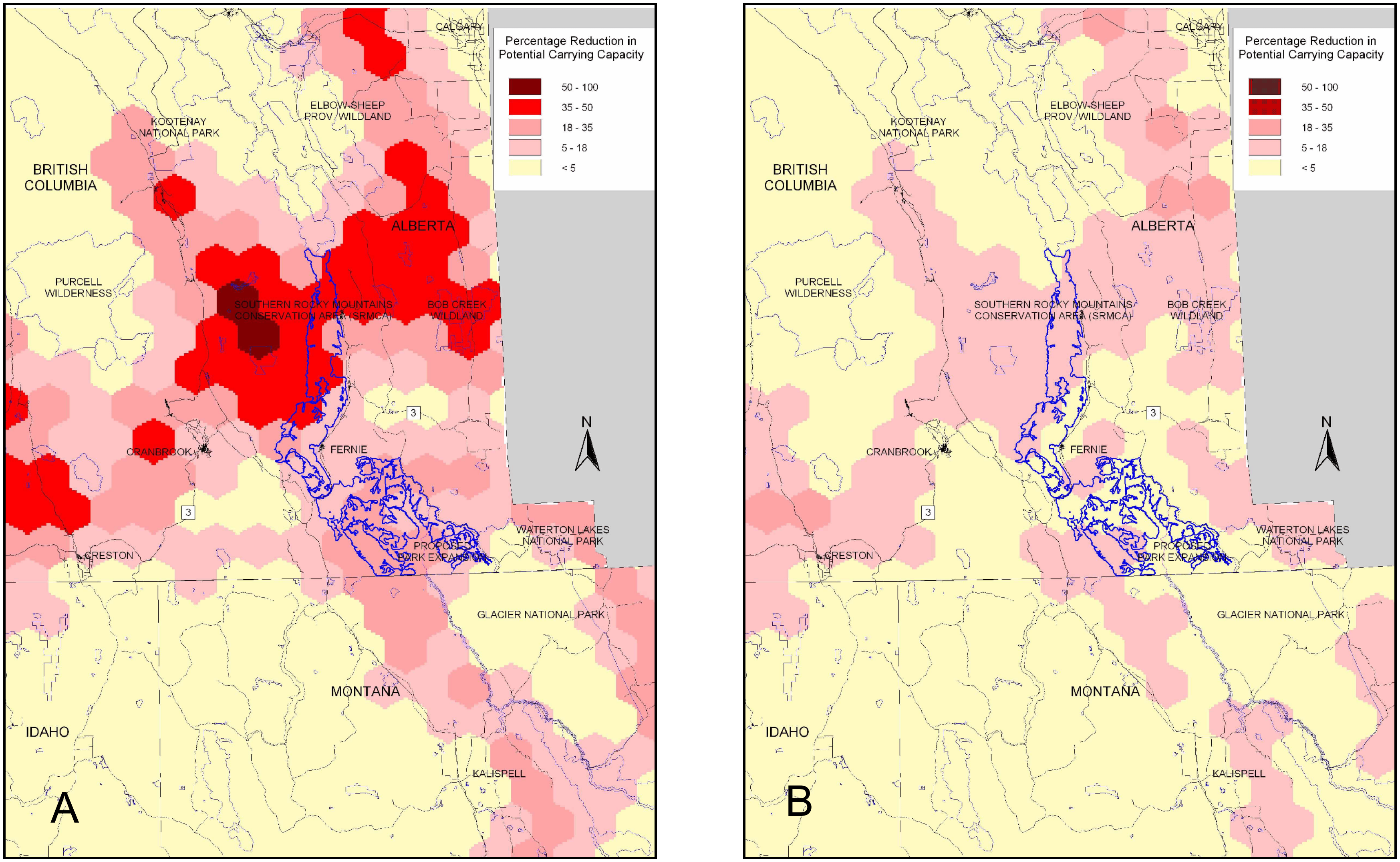


Figure 48. Increase in potential grizzly bear carrying capacity in the Canada/U.S. transboundary region under future landscape conditions (2025), assuming road development on both private and public lands, given park expansion within the proposed Waterton expansion area (a), or SRMCA area (b).

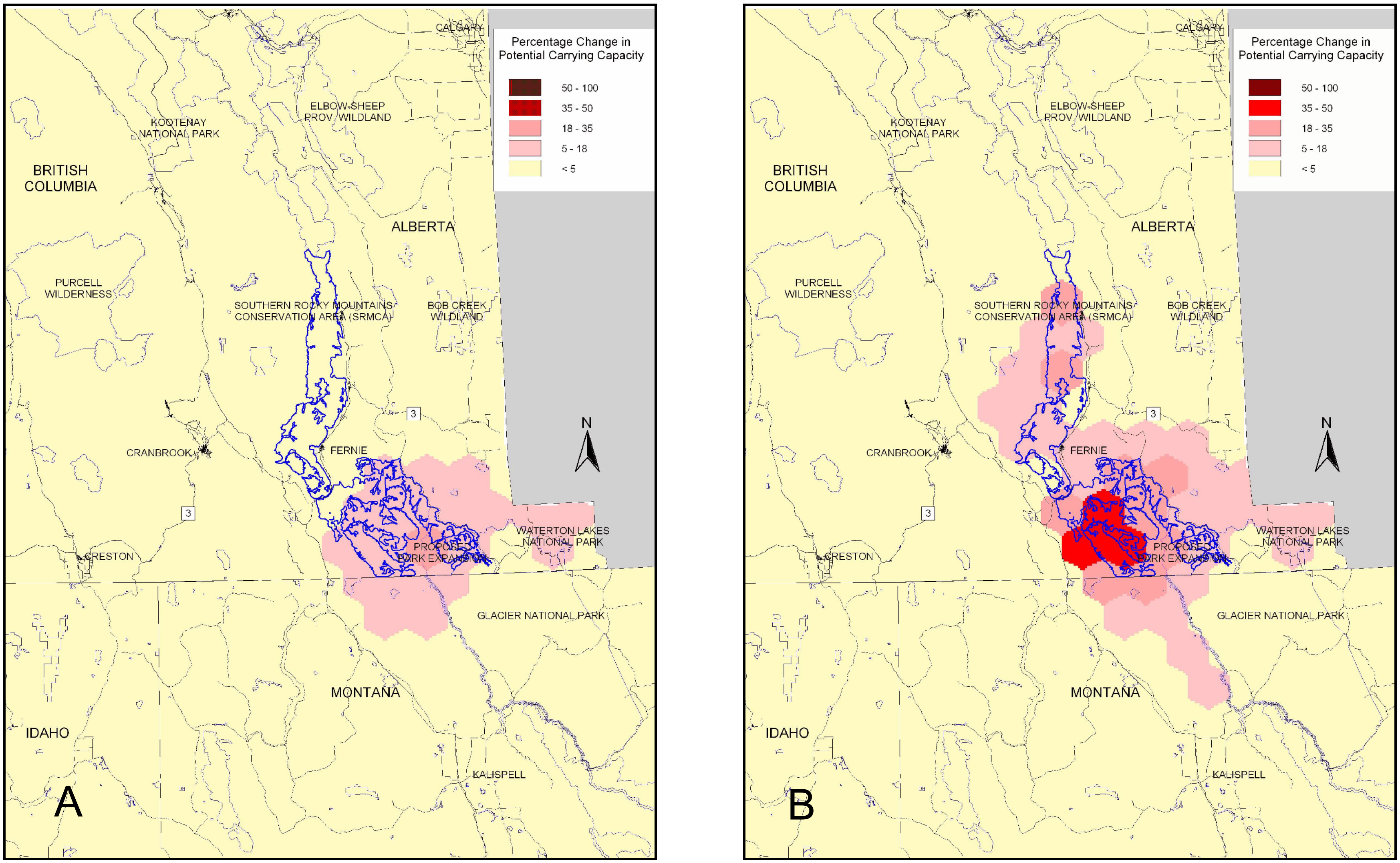


Figure 49. Potential distribution of wolves in the Canada/U.S. transboundary region under (a) current and (b) future landscape conditions (2025), assuming road development on both private and public lands, as predicted by the PATCH model simulations.

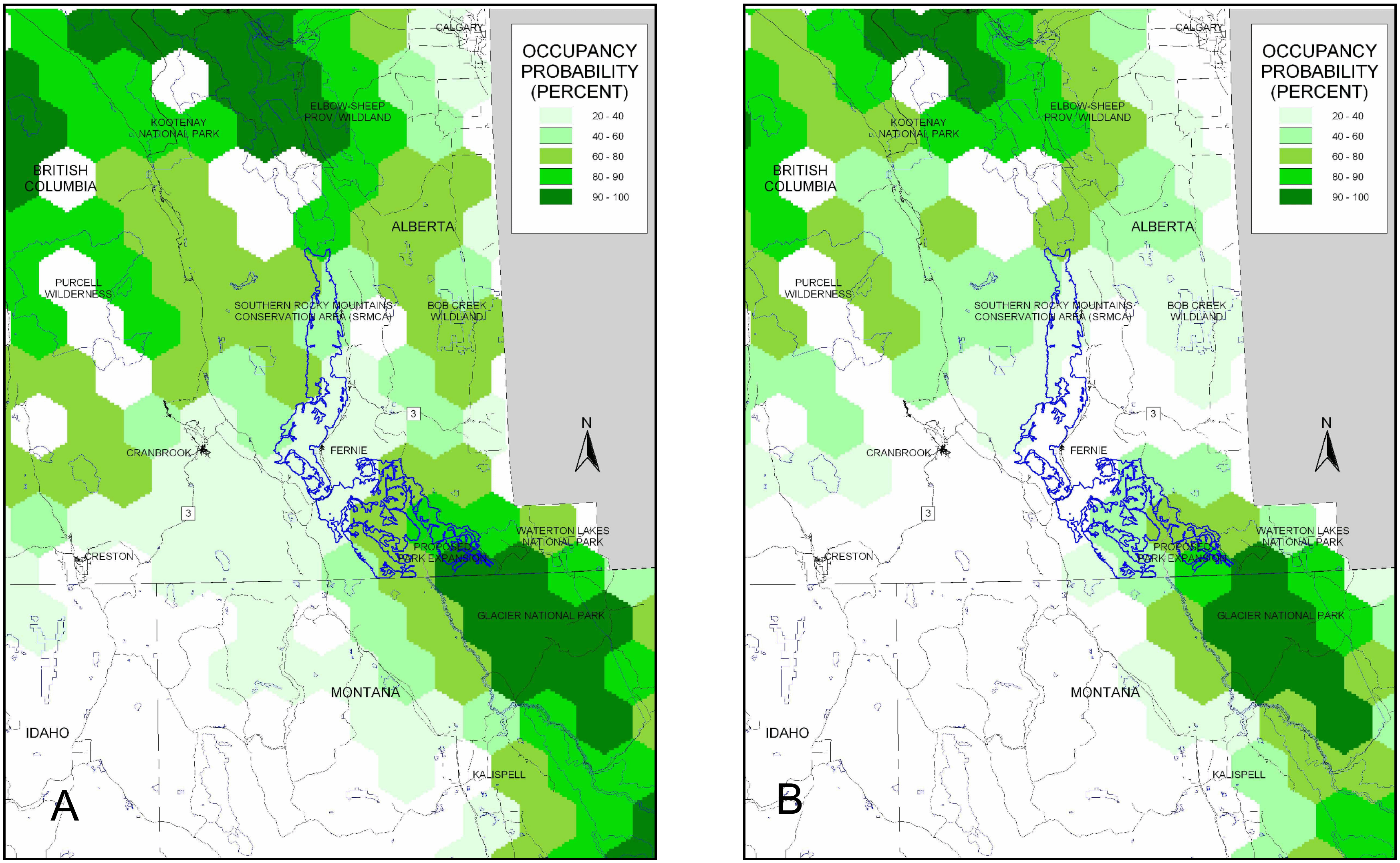


Figure 50. Reduction in potential wolf carrying capacity in the Canada/U.S. transboundary region from 2000-2025 as predicted by the PATCH model, assuming road development on both private and public lands (a), or assuming road development on private lands only (b). Areas in dark red show greatest reduction in potential occupancy due to expected human population growth and landscape change.

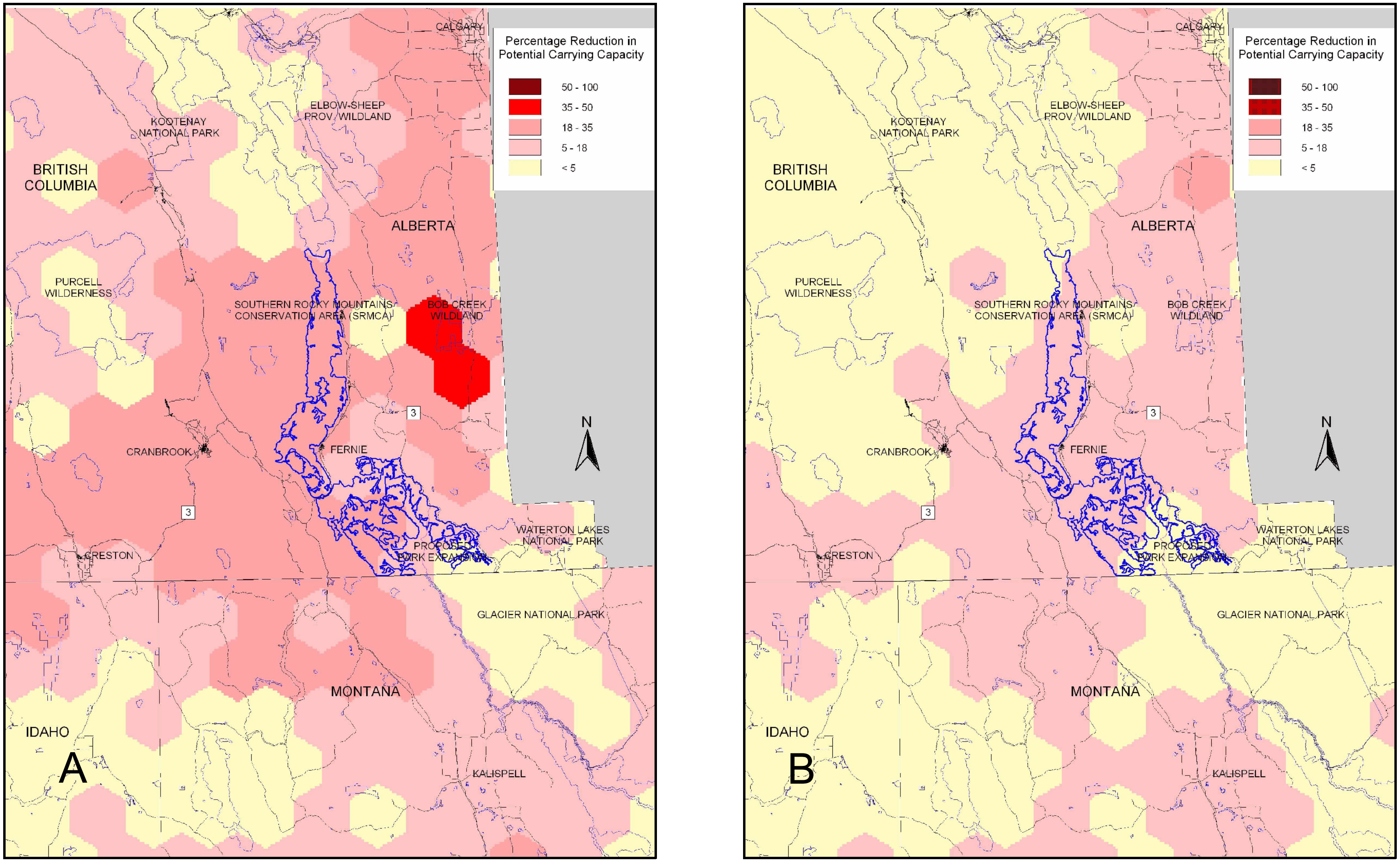


Figure 51. Increase in potential wolf carrying capacity in the Canada/U.S. transboundary region under future landscape conditions (2025), assuming road development on both private and public lands, given park expansion within the proposed Waterton expansion area (a), or SRMCA area (b).

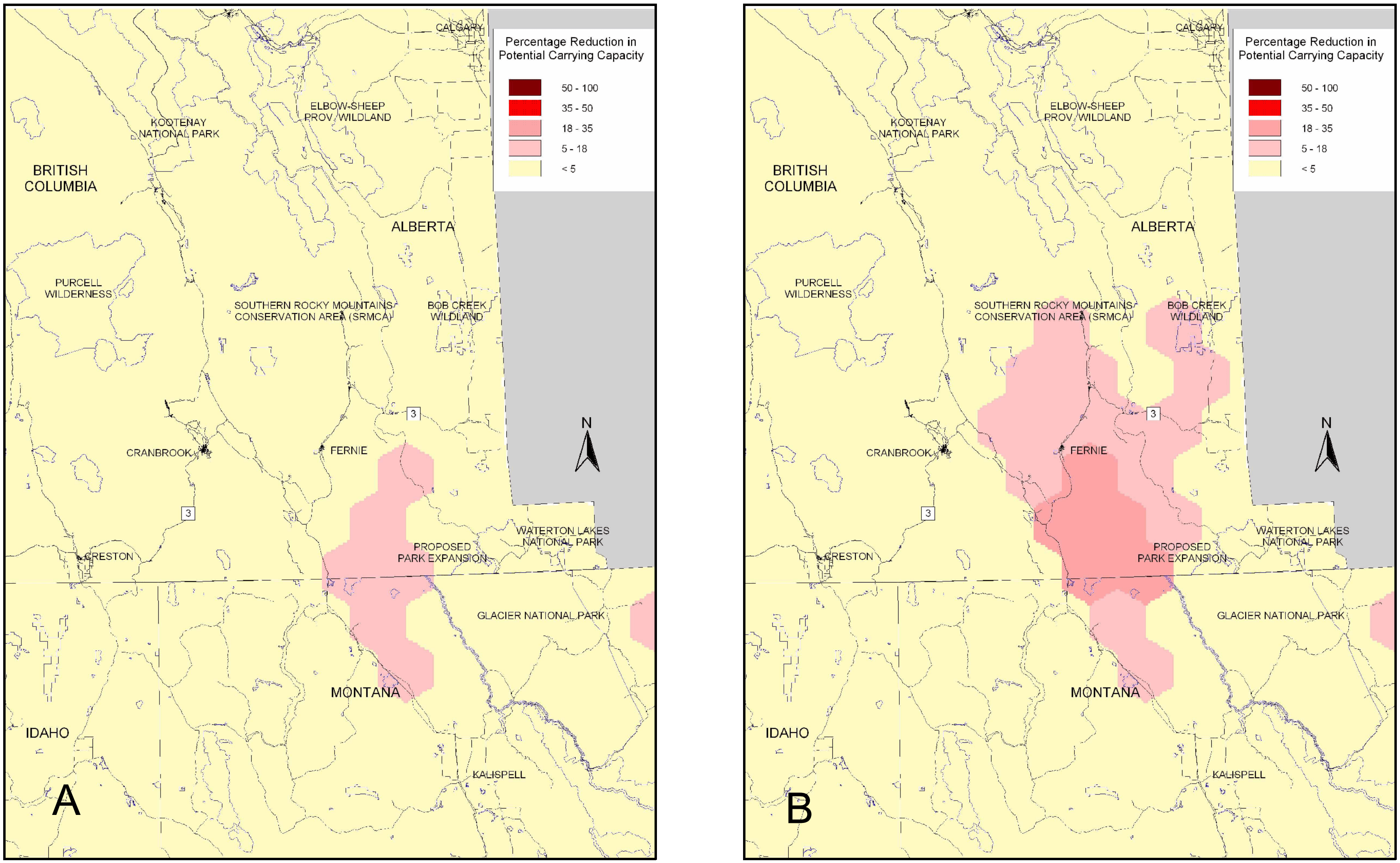


Figure 52. Reduction in potential grizzly bear carrying capacity (a) or demographic potential (b) in northeastern British Columbia from 2000-2025 as predicted by the PATCH model, assuming road development on both private and public lands.