Extinction Debt of Protected Areas in Developing Landscapes

CARLOS CARROLL,* REED F. NOSS,† PAUL C. PAQUET,‡ AND NATHAN H. SCHUMAKER§

*Klamath Center for Conservation Research, Orleans, CA 95556, U.S.A., email carlos@sisqtel.net
†Department of Biology, University of Central Florida, Orlando, FL 32816, U.S.A.
‡Faculty of Environmental Design, University of Calgary, Calgary, Alberta, Canada
§U.S. Environmental Protection Agency, Corvallis, OR 97333, U.S.A.

Abstract: *To conserve biological diversity, protected-area networks must be based not only on current species distributions but also on the landscape's long-term capacity to support populations. We used spatially explicit population models requiring detailed habitat and demographic data to evaluate the ability of existing park systems in the Rocky Mountain region (U.S.A. and Canada) to sustain populations of mammalian carnivores. Predicted patterns of extirpation agreed with those from logistic-regression models based only on park size and connectedness (or isolation) for the grizzly bear (*Ursus arctos*) in developed landscapes (northern U.S. Rocky Mountains) and semideveloped landscapes (southern Canadian Rocky Mountains). The area-isolation model performed poorly where the landscape matrix contained large amounts of suitable habitat (northern Canadian Rocky Mountains). Park area and connectedness were poor predictors of gray wolf (*Canis lupus*) occurrence because of this species' broader-scale range dynamics and greater ability to inhabit the landscape matrix. A doubling of park area corresponded to a 47% and 57% increase in projected grizzly bear population persistence in developed and semideveloped landscapes, respectively. A doubling of a park's connectedness index corresponded to a 81% and 350% increase in population persistence in developed and semideveloped landscapes, respectively, suggesting that conservation planning to enhance connectivity may be most effective in the earliest stages of landscape degradation. The park area and connectivity required for population persistence increased as the landscape matrix became more hostile, implying that the relatively small combined area of parks in the boreal forest and other undeveloped regions may fall below the threshold for species persistence if parks become habitat islands. Loss of carnivores from boreal landscapes could further reduce the viability of temperate populations occupying refugia at the southern range margin. Spatially realistic population models may be more informative than simpler patch-matrix models in predicting the effects of landscape change on population viability across a continuum of landscape degradation.*

Key Words: connectivity, conservation planning, island biogeography, metapopulation, population viability analysis, Rocky Mountains, SEPM

Deuda de Extinción de Áreas Protegidas en Paisajes en Desarrollo

Resumen: *Para conservar la diversidad biológica, las redes de áreas protegidas deben basarse no solo en la distribución actual de especies sino también en la capacidad a largo plazo del paisaje para soportar poblaciones. Utilizamos modelos espacialmente explícitos, que requieren de datos demográficos y de hábitat detallados, para evaluar la habilidad de los sistemas de parques existentes en la región de las Montañas Rocallosas (E.U.A./Canadá) para sostener poblaciones de mamíferos carnívoros. Los patrones de extirpación predichos coincidieron con los modelos de regresión logística basados sólo en el tamaño y conectividad (o aislamiento) del parque obtenidos para oso grizzli (*Ursus arctos*) en paisajes desarrollados (norte de Montañas Rocallosas en E.U.A.) y semi-desarrollados (sur de Montañas Rocallosas Canadienses). El modelo área-aislamiento funcionó pobremente donde la matriz del paisaje contenía grandes extensiones de hábitat disponible (norte de*

Paper submitted February 27, 2003; revised manuscript accepted November 7, 2003.

*Montañas Rocallosas Canadienses). La superficie y conectividad del parque fueron malos predictores de la ocurrencia de lobo gris (*Canis lupus*) debido a la mayor escala en la dinámica de esta especie y su mayor habilidad para habitar en la matriz del paisaje. La duplicación de la superficie del parque correspondió a un incremento de 47% y 57% de la persistencia proyectada de las poblaciones de oso grizzli en paisajes desarrollados y semi-desarrollados, respectivamente. La duplicación del índice de conectividad de un parque correspondió a un incremento de 81% y 350% en la persistencia de la población en paisajes desarrollados y semi-desarrollados, respectivamente, lo que sugiere que la planificación de conservación para mejorar la conectividad puede ser más efectiva en las primeras etapas de degradación del paisaje. La superficie y conectividad del parque requeridas para la persistencia de la población incrementó a medida que la matriz del paisaje era más hostil, lo que implica que la superficie combinada relativamente pequeña de parques en el bosque boreal y otras regiones sin desarrollo puede quedar debajo del umbral de la persistencia de especies si los parques se vuelven islas de hábitat. La pérdida de carnívoros en paisajes boreales podría reducir aun más la viabilidad de poblaciones templadas que ocupan refugios en el margen meridional de la cadena. Los modelos poblacionales espacialmente realistas pueden ser más informativos en la predicción de efectos de cambios en el paisaje sobre la viabilidad poblacional a lo largo de un continuo de degradación del paisaje que los modelos fragmento-matriz más simples.*

Palabras Clave: análisis de viabilidad poblacional, biogeografía de islas, conectividad, metapoblación, Montañas Rocallosas, planificación de conservación, SEPM

Introduction

Human population growth and consequent conversion of habitat are among the primary threats to biological diversity (Cincotta et al. 2000). Parks and other nominally protected areas are not immune to these threats (Wilcove 1986) and have been compared to land-bridge islands within a sea of hostile habitat (Diamond 1975; Newmark 1987, 1996). The relevance of predictions based on island biogeographic theory (MacArthur & Wilson 1967) that smaller and more isolated parks will lose more species than those that are big or connected (Newmark 1987, 1996) depends on the level of contrast between the park and the landscape matrix. At establishment, most parks are embedded within a relatively benign matrix, becoming more island-like as human-associated development transforms the surrounding landscape. Long-lived vertebrate species may persist in a large landscape for some time after habitat alteration has ensured their eventual demise (Doak 1995). The number of still-extant species whose habitat needs are no longer met comprises a landscape's extinction debt (Tilman et al. 1994; Hanski & Ovaskainen 2002). Extinction debt can be quantified most easily in landscapes that resemble the ideal of a classic metapopulation of discrete habitat islands embedded within a matrix of nonhabitat (Hanski 1994, 1997; Hanski & Ovaskainen 2002). In less-fragmented landscapes, the matrix (i.e., areas outside the reserves) may still contain areas of suitable habitat that provide demographic support to park populations (Pulliam 1988; Hansen & Rotella 2002). By moving from simple patch-matrix models to models that incorporate landscape structure (Wiens 2001), we may be able to identify critical matrix habitat (e.g., corridors) before it is lost to development.

The boreal forest region is relatively low in protected areas. Protected areas form 5.3% of the land area lying between 50° and 60°N, as opposed to 9.4% of the tropics (UNEP–WCMC 2002). Loss of uniquely adapted boreal populations is of concern even for widely distributed species, especially given the projected effects of climate change (Ceballos & Ehrlich 2002). We predicted population viability and distribution within protected areas for the grizzly bear (*Ursus arctos*) and gray wolf (*Canis lupus*), two species sensitive to human-induced landscape change (Weaver et al. 1996), across a spectrum of landscape conditions in the Rocky Mountain region from the Yukon–British Columbia (Canada) border to the Greater Yellowstone Ecosystem (U.S.A.) (Fig. 1).

How landscape change (e.g., an increase in road density) affects a particular local population depends on its location within the broader-scale dynamics of the species' range. We therefore compared three subregions of our larger study area that serve as examples of three contrasting landscape contexts: (1) parks as semi-isolated island populations, southern subregion; (2) parks located on the margin of the continuously inhabited range, central subregion; and (3) parks embedded within a relatively benign matrix within the "mainland" of the species distribution, northern subregion (Fig. 1). Road density, one surrogate of landscape impermeability for large carnivores, increases progressively from north to south, averaging 0.39, 0.68, and 0.83 km/km^2 in the northern, central, and southern subregions, respectively (C. C., unpublished data). However, our subregional boundaries are a somewhat arbitrary division of a more continuous gradient in landscape condition. We used the results of our comparison of the three regions to evaluate the adequacy of existing protected-area networks in the boreal forest

Figure 1. Study area in the Rocky Mountains of Canada and the United States. Protected areas are shaded. Divisions between the three subregions (northern, central, southern) compared in the text are shown. Letters a, b, and c show the location of the maps in Fig. 2.

region and the extent to which island biogeographic theory and metapopulation ecology can provide guidelines for regional conservation planning.

We modeled population dynamics with an individual-based spatially explicit population model (SEPM) (Dunning et al. 1995). We used the model's predicted occurrence of the two carnivore species rather than field data on distribution because our SEPM results closely matched the observed distribution (Mowat & Strobeck 2000; Mattson & Merrill 2002) and allowed us to assess the long-term ability of a park to support the species—the equilibrium carrying capacity—without complication from effects of time lags or past human activities. For example, although the large protected-area complex in central Idaho (U.S.A.) has among the highest potential carrying capacity of grizzly bears in our study region, the species is currently absent there as a result of past predator control efforts (Mattson & Merrill 2002). Use of the SEPM also allowed extrapolation of current trends in landscape change to predict how this equilibrium carrying capacity would change in future landscapes.

Results from complex models such as SEPMs may have limited utility for conservation because their results are often valid only for a particular landscape. We therefore analyzed our SEPM results with logistic-regression models to determine whether we could identify general principles relating area and connectivity thresholds to species persistence in landscapes with differing levels of contrast between parks and landscape matrix. We compared the SEPM results with logistic-regression models rather than more complex metapopulation models such as incidence functions because it was evident that our simulated populations violated the assumptions under which such models give informative results (Hanski 1997). For example, both the grizzly bear and wolf may occur in nonequilibrium metapopulations (Harrison 1994) in this region because of the slow equilibration of their populations to deteriorating habitat. Thus, very few successful recolonizations of vacant parks by the grizzly bear or wolf would be expected, making it difficult to estimate the colonization rate necessary for creation of an incidence model (Morris & Doak 2002). Although patch-matrix models such as incidence functions can be modified to account for how connectedness or landscape permeability vary with matrix habitat quality (Hanski 1997), they cannot incorporate the demographic contribution from occupied "matrix" habitat that may increase the effective area of parks and thus buffer their populations from extinction.

Methods

The structure of the SEPM and input habitat models are described in detail elsewhere (Schumaker 1998; Carroll et al. 2000, 2001*a*, 2001*b*, 2002, 2003*a*, 2003*b*) and are summarized here. The SEPM used here, PATCH, is a female-only model designed for studying territorial vertebrates and links the survival and fecundity of individual animals to geographic information system (GIS) data on mortality risk and habitat productivity measured at the location of the individual or pack territory (Schumaker 1998). Territories are allocated by intersecting the GIS data with an array of hexagonal cells. The pixels of the GIS maps are assigned weights based on the relative levels of fecundity and survival rates expected in the various habitat classes. Survival and reproductive rates are then supplied to the model as a population projection matrix (Caswell 2001). The model scales the matrix values based on the mean of the habitat weights within each hexagon, with lower means translating into lower survival rates or reproductive output. These "expected" demographic rates can then be used to calculate a predicted lambda, or population growth rate, for each territory. We based our analysis not on these expected lambda values, however, but on the lambda values actually observed during the model simulations. Observed lambda values are derived from: 1.0 +

(emigration − immigration), with emigration and immigration values for each hexagon expressed as per year per simulation (Schumaker 1998).

The simulations incorporate demographic stochasticity with a random number generator. In the case of survival, a uniform random number between zero and one is selected. An individual dies if this number is less than the sum of the probabilities of making a transition between the current age class and every other class. A random number is also selected to force the number of offspring in a year to take on integer values. Environmental stochasticity is incorporated by drawing each year's base population matrix from a randomized set of matrices whose elements are drawn from a truncated normal distribution. Coefficients of variation were 25% for fecundity and 23% for cub and adult mortality for the grizzly bear and 30% for fecundity, 40% for pup mortality, and 30% for adult mortality for the wolf (Ballard et al. 1987; Fuller 1989; Mattson 2000). We did not model additional catastrophic mortality events (e.g., disease outbreaks). Parameters for territory size, dispersal distance, and demographic rates used in PATCH are shown in Table 1.

Habitat rankings were calibrated to specific demographic values based on field studies from areas showing habitat quality (e.g., road density) similar to that of habitat classes in the PATCH input layers (grizzly bear: Knight & Eberhardt 1985; Hovey & McLellan 1996; Mace & Waller 1998; Pease & Mattson 1999; Mattson 2000; wolf: Ballard et al. 1987; Fuller 1989; Hayes & Harestad 2000). The grizzly bear fecundity model was based on tasseled-cap greenness, a metric derived from satellite imagery that correlates with primary productivity (Crist & Cicone 1984; Mace et al. 1999). A metric combining road density, local human population density, and interpolated human population density (Merrill et al. 1999) predicted mortality risk. The habitat variables for the wolf model were similar to those used for the grizzly bear, with the exception that the fecundity layer incorporated the negative effect of terrain (slope) on prey availability (Paquet et al. 1996). The social structure incorporated in the wolf model (Carroll et al. 2003*a*) also caused results to differ from those of the grizzly bear simulations. We modified PATCH to allow territory holders to be social, with individuals from the same pack able to replace territory holders (alpha females) that die. As pack size increases, members of a pack in the model have a greater tendency to disperse and search for new available breeding sites (Carroll et al. 2003*a*).

Table 1. Parameters used in the PATCH model of carnivore population dynamics in the Rocky Mountain region (modified from Carroll et al. 2003*b*).[a]

Parameter	*Grizzly bear*	*Wolf*
Territory size (km^2)	270	504
Maximum dispersal distance (km)	56	254
Survival rates (maximum/mean)		
young/year 0	0.82/0.70	0.46/0.40
subadult/year 1	0.92/0.78	0.86/0.76
adult/>2 years	0.94/0.80	0.96/0.84
at senescence (at year in [])	n/a	0.69/0.61[8]
Fecundity rates (maximum/mean)[b]		
subadult/year 1	0/0	0/0
adult/year 2	0/0	2.29/1.26
adult/>3 years	0.55/0.44	3.21/1.77

[a] *Mean values are averaged over the entire region under current landscape conditions, including territories that did not support the species in the subsequent simulations.*
[b] *Number of female offspring per adult female or pack.*

Adult organisms are classified as either territorial or floaters. The movement of territorial individuals is governed by a site-fidelity parameter, but floaters must always search for available breeding sites. Movement decisions use a directed random walk that combines varying proportions of randomness, correlation (tendency to continue in the direction of the last step), and attraction to higher-quality habitat (Schumaker 1998). However, there is no knowledge of habitat quality beyond the immediately adjacent territories. Although results from SEPMs may be sensitive to variation in poorly known parameters such as dispersal distance (Ruckelshaus et al. 1997), this may be most evident in simplified SEPMs that lack a demographic context (South 1999), use a dispersal function that is not sensitive to landscape quality, and vary dispersal mortality across a wider range than is usually plausible for a particular species (Mooij & DeAngelis 1999). Real landscapes often contain a few large patches with very low extinction probability. The resultant mainland-island dynamics tend to stabilize metapopulations and reduce sensitivity to dispersal success (South 1999).

As evident in other realistic SEPMs (Pulliam et al. 1992; South 1999), our results were more sensitive to the demographic parameters used and how they were assigned to habitat classes than to variation in dispersal distance (Carroll et al. 2002). The SEPM predictions for large carnivores such as the grizzly bear and wolf were strongly correlated with species distributions from regional-scale field surveys (Mowat & Strobeck 2000; Poole et al. 2001; D. Smith, unpublished data), in contrast with the poorer performance of distribution models for mesocarnivores (Carroll et al. 2002). This is likely because large-carnivore distribution is strongly limited by human influences, for which easily mapped attributes such as road density are good surrogates (Carroll et al. 2001*a*).

The landscape-change scenarios we used estimated potential change in human-associated impact factors, such as roads and human population, by proportionately increasing road density 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.A.) or 1990–1996 (Canada) (U.S. Census Bureau 1991; Statistics Canada 1997). We predicted human population growth from 2000 to 2025 based on growth rates from 1990 to 1996/2000, but we adjusted the predicted 2025 population to match state- and subprovince-level predictions based on more complex socioeconomic models (U.S. Census Bureau 1991; Statistics Canada 1997). Road density was predicted to grow at 1% per year (Theobald et al. 1996).

Strictly protected parks and protected areas were treated differently from other management classes. We defined strictly protected parks as those where hunting and trapping is prohibited and assumed that in these areas an additional increment of human impacts (e.g., a road density level of 2 $\mathrm{km/km^2}$ rather than 1 $\mathrm{km/km^2}$) had an effect on large-carnivore survival that is 50% of that in other areas. These areas formed 6.5% of the overall region, whereas protected areas as a whole formed 16.5% of the region. High levels of hunting activity for other species may result in enough incidental mortality of carnivores to cause protected areas to function as population sinks (Mace & Waller 1998). In the landscape-change analysis, we also treated all protected areas—including those with hunting—differently from unprotected habitat in that we assumed no increase in road density over time.

We report equilibrium predictions rather than transient population dynamics, in that "current" predictions depict the current capacity for an area to support a carnivore species over 200 years. Equilibrium carrying capacity, or long-term occupancy as predicted by PATCH, may differ from current species distribution because human-caused habitat change is faster than the rate of response of an affected carnivore population. We performed 1000 simulations of 200 years each for each model scenario. We plotted species occurrence, as predicted by PATCH under current and future landscape conditions, on a graph of protected-area size ($\mathrm{km^2}$) and connectedness. All protected areas of >25 $\mathrm{km^2}$ were used in the analysis. Connectedness, the inverse of park isolation, was calculated as an index of the potential number of dispersers reaching a site from all other protected areas (Hanski 1997):

$$\sum_{j=1}^{n} p_j e^{-\alpha d_{ij}} A_j, \; j \neq i,$$

where A_j is the area of patch j in square kilometers, p_j is the mean probability of occupancy of territories in patch j as predicted by the PATCH model, d_{ij} is the distance between patch i and j, and α is a coefficient to the negative exponential function.

We used α values that gave a mean dispersal distance close to that observed for females of each species in field studies (grizzly bear, 30 km [Blanchard & Knight 1991]; wolf, 110 km [Wydeven et al. 1995]). However, because the exponential distribution of dispersal distances assumed by the connectedness index function may not reflect observed dispersal-distance curves for most species (Shigesada & Kawasaki 2002), we explored the effect of using α values associated with mean dispersal distances of 30, 70, 110, and 150 km for both species.

We then fit logistic-regression models to predict patch occupancy from patch area and connectedness and plotted the resulting incidence lines for a 50% probability of patch occupancy. Because wolves, unlike grizzly bears, are effectively unable to establish territories in rugged areas with extremely high snowfall (Paquet et al. 1996), these areas are not considered potential breeding habitat for wolves in the PATCH model. To assess the robustness of results to this assumption, we fit alternate logistic-regression models that based park occupancy, area, and connectedness on potential breeding habitat rather than total habitat. We compared models with corrected Akaike information criterion (AICc), an information theory–based statistic that penalizes for overfitting and adjusts for small sample size (Burnham & Anderson 1998). Models within 2 AICc (ΔAICc < 2) of the model with lowest AICc have some plausibility as alternate models (Burnham & Anderson 1998).

We adapted an approach that sets priority areas for conservation action based on their irreplaceability and vulnerability in order to minimize the loss of options for conservation planning during an interim period when new reserves are being achieved in some areas while habitat loss is occurring elsewhere (Pressey & Taffs 2001). An area's irreplaceability is the relative contribution it makes to reaching a conservation goal, here species persistence (Margules & Pressey 2000). We defined irreplaceability in this context as the relative value of an area as source habitat. This was based on models of the current landscape (before the projections of landscape change) in order to identify conservation values that might be lost in the future. Because source habitat is based on the "observed" lambda from the PATCH simulations, it depends on both the quality of a patch and its landscape context. Vulnerability, the likelihood that a site's conservation value will be reduced over time, 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. The upper right quadrant, which includes sites with high irreplaceability and high vulnerability, contains the highest-priority sites for conservation (Pressey & Taffs 2001). This is followed in priority by the upper left and lower right quadrants and, finally, by the lower left quadrant, containing sites that are relatively replaceable and face less severe threats. Areas in the lower left quadrant somewhat misleadingly show low threat values because they contain sink habitat that is becoming less influential as it becomes less likely to be occupied by the species.

Results

The SEPM results predict that land use and human population growth trends over the period 2000–2025 result

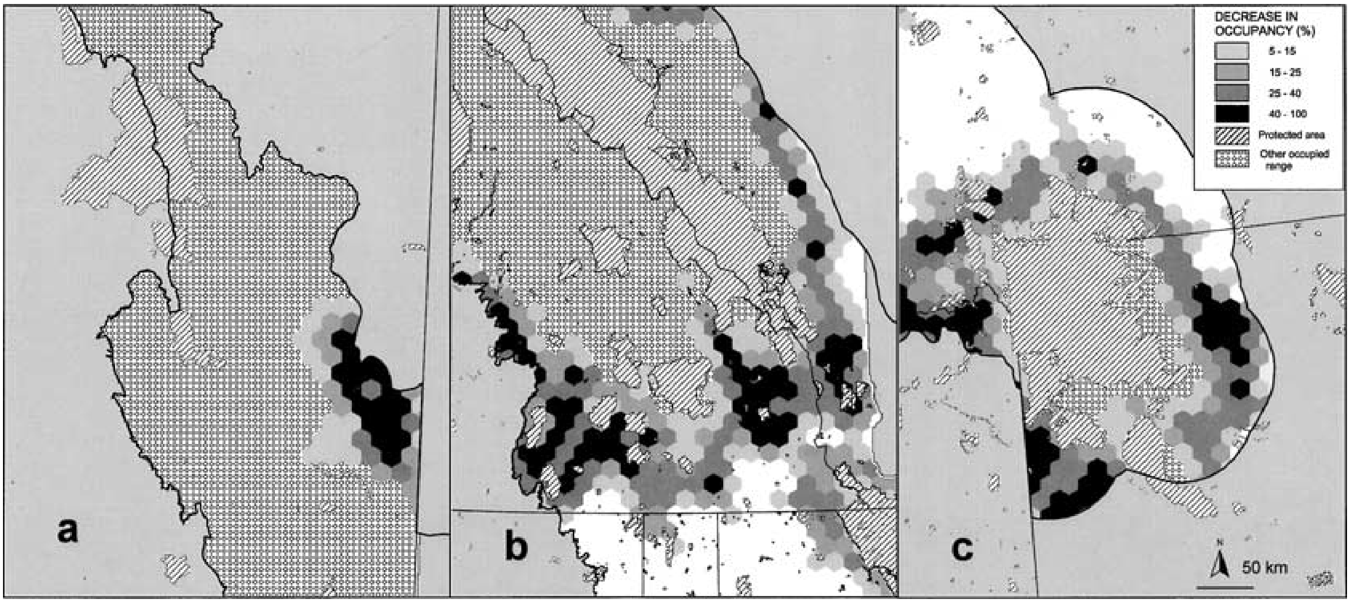

Figure 2. Maps of decline in predicted occupancy probability for grizzly bears due to landscape change for subregions of the larger study region. These show examples of the landscape context of protected areas in the (a) northern, (b) central, and (c) southern subregions.

in a regional loss in long-term carrying capacity of 12.2% for the wolf and 13.7% for the grizzly bear, due about equally to development on private lands and to degradation of habitat on public lands. Carrying capacity (long-term occupancy rate as predicted by PATCH) declined 6.0%, 11.5%, and 25.5% for the grizzly bear and 1.8%, 14.3%, and 26.4% for the wolf in the northern, central, and southern subregions, respectively. Responses of carnivore populations to landscape change varied between the northern, central, and southern subregions (Fig. 2). In the northern subregion, which lies within the mainland or continuously occupied portion of the range for boreal-associated species, the primary effect of landscape change was demographic fragmentation of the range (creation of sink habitat; Pulliam 1988) (Fig. 2a). Range contraction occurred at the interface of the undeveloped matrix with road corridors and populated areas, but this was fairly distant from protected areas. In the central subregion, which is at the margin of continuously occupied range for several boreal-associated carnivores, the primary trend was a loss of populations from the landscape matrix and smaller protected areas and a northward retreat of the range margin (Fig. 2b). In the southern subregion, the primary trend was range contraction at the margins of the large island-like refugia that still support large carnivores (Fig. 2c).

Park area and connectedness were better predictors of carnivore viability and distribution for each subregion individually than on the scale of the entire study region, and effects varied strongly by subregion (Table 2). A model based on park area and connectedness had the lowest AICc for the grizzly bear in the overall region and in the central and southern subregions (Table 2). For the wolf, the only "best" (lowest AICc) model containing covariates was a connectedness model for the central subregion (Table 2). Results from alternate wolf models based on potential breeding habitat rather than total habitat differed in that an area model performed slightly better than the null model (ΔAICc $= -0.6407$) for the overall region, and the connectedness model for the central subregion was slightly poorer (ΔAICc $= 1.0338$) than the null model. Results from models with alternate α values gave similar (wolf) or poorer (grizzly bear) results than those with the base α parameters.

Table 2. Evaluation of logistic-regression models predicting viability of grizzly bear and wolf populations inhabiting protected areas in the Rocky Mountain region based on park size and connectedness.*

Species and region	*Model* *null*	*log(area)*	*log (connectedness)*	*both factors*
Grizzly bear				
overall	16.1585	6.4806	13.2527	0
northern	0	0.9377	2.4436	3.2779
central	18.0168	16.5652	1.4405	0
southern	8.9680	5.9679	6.0361	0
Wolf				
overall	0	0.9809	2.0763	2.9112
northern	0	1.8173	2.3010	4.3560
central	1.4842	3.6088	0	2.2132
southern	0	1.2721	1.7041	2.1281

**The ΔAICc value, which represents the difference between a model and the competing model with the lowest AICc, is given for each model, and n = 106 (overall), 51 (southern), 34 (central), and 21 (northern).*

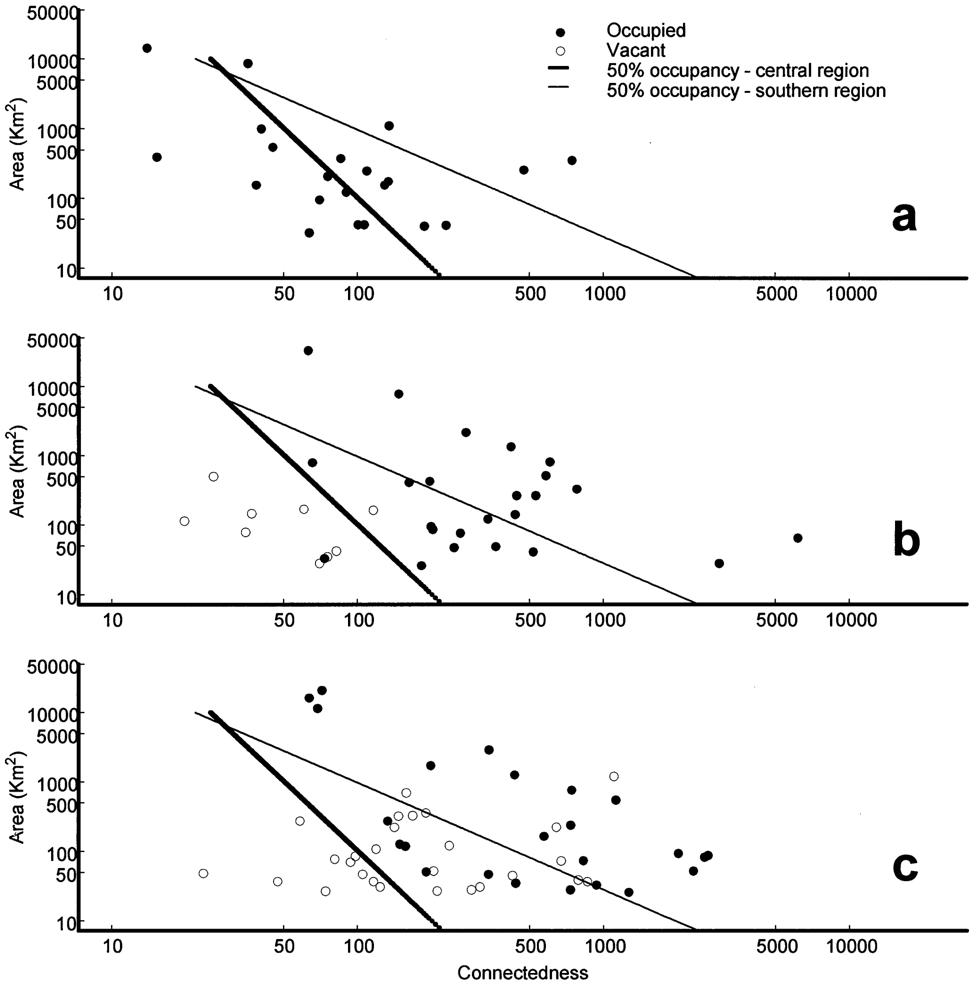

Figure 3. Grizzly bear occurrence (probability >50%, as predicted by the PATCH model) within protected areas in the three subregions (a, northern; b, central; and c, southern) of the Rocky Mountains plotted on a logarithmic scale of protected-area size and connectedness (index described in text). Incidence lines for 50% probability of patch (park) occupancy from logistic-regression models for the central (b) and southern (c) subregions are shown on all three graphs for comparison of effects between subregions. All protected areas in the northern (a) subregion were predicted to be occupied under current conditions.

The levels of area and connectedness at which occupancy fell below 50% differed by subregion, as expected, with higher area and connectedness necessary in the southern subregion with a more hostile matrix (Fig. 3). Most protected areas in the northern subregion, although predicted by the SEPM to be viable under current conditions (Fig. 3a), fell below the 50% occupancy incidence lines of more developed landscapes (the central and southern subregion), where protected areas more closely represent habitat islands. Those protected areas in the central subregion that fell between the incidence lines for the central and southern subregions (Fig. 3b) would be predicted to fall below 50% occupancy probability if located in the southern subregion. These are small parks located at the southern edges of the range margin.

The odds ratios from the models shown in Table 3 predict that a doubling of a park's area, with connectedness held constant, would result in a 50.85%, 57.00%, and 47.05% increase in probability of occupancy of that park by grizzly bear in the overall, central, and southern regions, respectively. A doubling of a park's connectedness metric with area held constant would result in a 45.07%,

Table 3. Coefficients and standard errors of logistic-regression models shown in Table 1 that included area or connectedness terms and showed lower Akaike information criterion than the null model ("best" model).

	Model term		
Species and region	*intercept*	*log(area)*	*log(connectedness)*
Grizzly bear			
overall	−5.1704(1.4807)	0.5931(0.1785)	0.5367(0.1961)
central	−13.0031(4.4985)	0.6508(0.4224)	2.1701(0.7645)
southern	−7.7596(2.4981)	0.5563(0.2139)	0.8539(0.3315)
Wolf			
central	−15.0216(8.9107)		1.8360(1.0859)

350.05%, and 80.74% increase in the probability of grizzly bear occupancy in the overall, central, and southern regions, respectively, and a 257.02% increase in probability of wolf occupancy in the central region.

Results from the landscape-change scenarios were not used in the above analysis but are reported separately for comparison. Effects of projected landscape change between 2000 and 2025 caused 21 protected areas to drop below 50% occupancy probability for the wolf, versus 14 for the grizzly bear. A graph of the irreplaceability versus vulnerability of specific sites (predicted lambda under current landscape conditions versus reduction in lambda from current to future landscapes) (Fig. 4) showed that northern protected areas generally fell into the category of secure source, with fewer threatened sources (Fig. 4, upper left quadrants). Protected areas in the central region were more variable, but many fell in the threatened source category (upper right quadrant). Southern protected areas that were not unoccupied (intersection of axes) or nearing that state (lower-left quadrant) were divided between a few threatened sources and many threatened sinks for grizzly bears (Fig. 4a). For the wolf, southern protected areas were predominantly threatened sources rather than sinks (Fig. 4b). As the landscape matrix became more degraded, parks moved clockwise through the irreplaceability-vulnerability graph from secure source to threatened source to threatened sink and ultimately to uninhabited area (intersection of axes). When protected areas in the central subregion that fell between the two incidence lines shown in Fig. 3 were plotted in terms of their irreplaceability and vulnerability (Fig. 4a), they were generally highly threatened sinks.

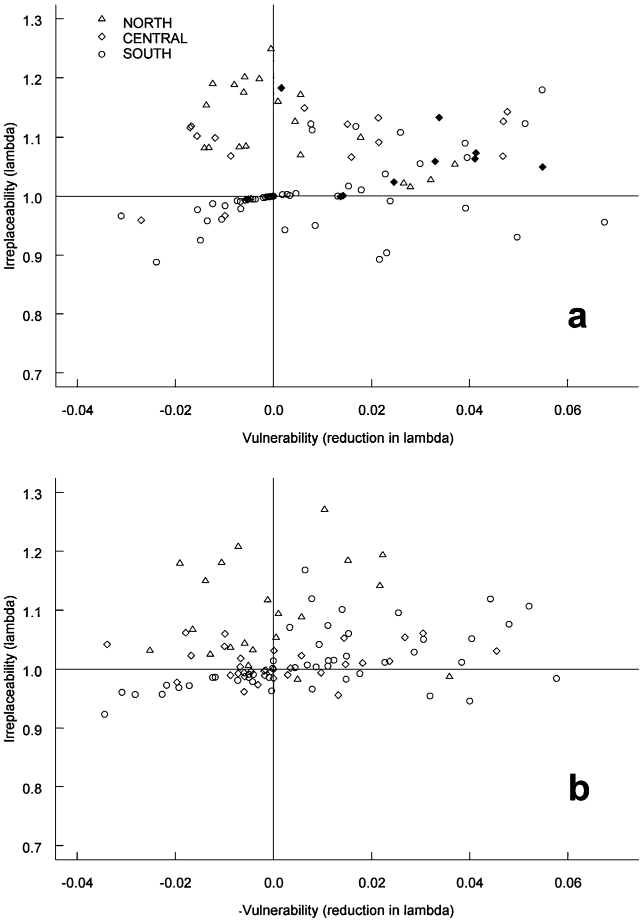

Figure 4. Irreplaceability versus vulnerability (following the procedure of Margules and Pressey [2000]) for the (a) grizzly bear and (b) wolf. Irreplaceability (y-axis) in this context is the relative value of an area as source habitat (lambda, or population growth rate). Vulnerability (x-axis) is measured here as the predicted decline in demographic value (lambda) over the next 25 years. In panel a, filled diamond symbols (◆) represent those protected areas in the central subregion that fall between the two incidence lines in Fig. 3b and thus would fall below 50% occupancy probability if located in the southern subregion.

Discussion

To effectively conserve biological diversity, protected-area networks must be based not only on current species distributions but also the landscape's long-term capacity to support populations (Cabeza & Moilanen 2001; Carroll et al. 2003*b*). Whereas relatively simple tools are adequate for identifying hotspots for narrow endemic species, quantitative evaluation of persistence thresholds for area-sensitive species requires the integration of large-scale spatial data (e.g., satellite imagery) and spatially explicit population models (SEPM). In these more complex landscape contexts, SEPMs may provide novel information on extinction debt, viability thresholds (Carroll et al. 2003*b*), and the processes driving species extirpation. These tools allow us to move beyond qualitative guidelines for reserve design (e.g., Diamond 1975) toward a quantitative integration of ecological theory and conservation planning.

The three subregions examined here (Fig. 1) present case studies in this progression from population source to extirpation as seen in the irreplaceability-vulnerability analysis (Fig. 4). Northern protected areas generally fall into the category of secure source because most development there is still occurring in the landscape matrix. Protected areas in the central region are more variable, but many fall in the threatened source category, which is the highest priority for immediate conservation action (Margules & Pressey 2000). Landscape change in this subregion appears to be fragmenting formerly continuous grizzly bear range into isolated populations more typical of the southern subregion (Paetkau et al. 1998). In the southern subregion, species loss has progressed to the stage that only the largest refugia retain all native carnivore species. Southern protected areas, if occupied, are divided between a few sources and many threatened sinks for the grizzly bear. Even the Greater Yellowstone Ecosystem (GYE), which is among the world's largest protected-area complexes, is vulnerable to the effects of fragmentation by development because high-productivity habitat there is generally unprotected (Hansen & Rotella 2002; Noss et al. 2002). Placing questions about the design of protected areas within the framework of the three landscape contexts (Fig. 2) may make our results generally applicable outside the boreal region.

Extinction debt can be estimated by the difference between the current known carnivore distribution (Mowat & Strobeck 2000; Mattson & Merrill 2002) and areas where the species are predicted to persist over time given current habitat conditions. Under this definition, extinction debt is highest in small refugia in the central subregion of the Rocky Mountains (Fig. 1) because of the rapid rate of recent landscape change and the vulnerable position of refugia on the range margin. However, the increase in area and connectivity thresholds between the long-fragmented southern subregion (Fig. 3c) and the recently fragmented central subregion (Fig. 3b) suggests a broader definition of extinction debt that anticipates the effects over time of an increasingly inhospitable landscape matrix. In less-developed landscapes, demographic rescue from matrix habitat helps buffer park populations from extinction by increasing their effective area and decreasing their effective isolation. Without this rescue effect (Brown & Kodric-Brown 1977), the minimum area required for sustaining viable populations of large carnivores is much greater than that of most current boreal reserves.

By comparing area and connectedness thresholds (Fig. 3), we effectively seek to anticipate future landscape change by comparing adjacent regions that are currently in different stages of landscape degradation. Those protected areas in the central subregion that fall between the two incidence lines (Fig. 3b) would be expected to fall below 50% occupancy probability if located in a landscape similar to that of the southern subregion, that is, with a higher contrast between parks and the landscape matrix. These are small protected areas located along the U.S.–Canada border at the southern fringe of the retreating range margin. They currently hold small, highly endangered grizzly bear populations such as the Selkirk, Cabinet-Yaak (U.S.), and Granby populations (USFWS 1993).

The relatively large effect of changes in connectivity on population viability in our models seems to contradict the fact that few recolonizations of parks by large carnivores have been documented in the region. Grizzly bears have expanded their range in the GYE since 1980 but appear to have only recolonized areas immediately adjacent to previously occupied range (Schwartz 2002). The wolf appears able to recolonize more isolated parks (Ream et al. 1991). For both species, however, the greater effect of connectedness in the central versus the southern subregion suggests that most effects of connectivity in these species occur through demographic rescue of existing populations rather than through recolonization events. Landscape connectivity may have the greatest effect at the range margin where formerly continuous populations are just beginning to break up into isolates and before the landscape can credibly be characterized by island-matrix models. The similarity between habitat suitable for dispersal and that suitable for occupancy for these species, especially the grizzly bear (Schwartz 2002), implies that any subdivided population with continuing interchange between populations will also receive a substantial demographic contribution from matrix habitat. Therefore, connectivity planning must focus on ensuring functional connectivity in a broader landscape context rather than on linear corridors.

The comparison of the area-connectedness models included only results from PATCH simulations based on current landscape conditions. We can compare those parks highlighted as at-risk by the area-connectedness models with those identified from PATCH simulations in future landscapes. The irreplaceability-vulnerability analysis (Fig. 4) showed that the at-risk parks identified previously form a subset of a larger group of parks (Fig. 4, upper left quadrant) categorized by both high conservation value and high threat. The comparison of area-connectedness models failed to highlight parks primarily threatened by broad-scale range dynamics rather than those of the local landscape. The irreplaceability-vulnerability analysis (Fig. 4) was also more informative than the simpler models (Fig. 3) about levels of threat for parks in the relatively undeveloped northern subregion.

The failure of the wolf simulation results to conform to the area-connectedness framework may be explained by two factors. The larger territory size and longer dispersal distances of the wolf, compared with those of the grizzly bear (Table 1), result in broader-scale range dynamics in this species that uncouple the viability of a park from its local landscape context. Second, because the wolf is more able to persist in semideveloped matrix habitat and, conversely, is less able to use the high-elevation habitat of many Rocky Mountain parks, there may be less contrast between parks and the landscape matrix. Although wolves are currently able to occupy a broader spectrum of the landscape, especially in the southern subregion, most source habitat there appears to be threatened by landscape change (Fig. 4b). Wolves may currently form a "patchy" metapopulation in that subregion, but landscape change will likely move the species toward the nonequilibrium metapopulation typical of the grizzly bear (Harrison 1994).

Carnivore populations inhabiting parks within developing landscapes appear generally vulnerable to decline or extirpation because current protected areas are too small and isolated and biased toward less productive habitat, paralleling results documented for other taxa (Hansen & Rotella 2002). Biologically productive habitats are often the first targeted for development, and these habitats form proportionally less of the landscape with increasing latitude and elevation. Therefore, boreal and montane protected areas are especially vulnerable to both direct human influences such as development and indirect influences such as climate change. Refugia such as the GYE that still retain carnivores at their southern range limits are large and fairly productive. Newly created protected areas in the subboreal regions, because they are likely to be less biologically productive, may need to have greater area and connectivity than those to the south. This factor accentuates the inadequacies of the current boreal protected-area system identified in the area-isolation models.

To prevent the northward retreat of carnivore populations, our results suggest that substantial conservation commitments will be necessary to sustain small populations at the range margin and to maintain their functional connections with more northerly populations. Over the longer term, our results suggest that seemingly secure boreal carnivore populations are inadequately protected from the foreseeable effects of human-associated development. This finding may be relevant for areas within the boreal forest of Canada and Russia, which are experiencing rapid development for resource extraction, and for less-developed regions in the tropics that still support wide-ranging species. Spatially explicit population models not only make us aware of the extinction debt held by current park systems, they also give us the tools to design protected-area networks that are more resilient to landscape change.

Acknowledgments

This study was funded by World Wildlife Fund–Canada and The Nature Conservancy and their contributors, with additional support provided by The Wilburforce Foundation, the Kendall Foundation, The Yellowstone to Yukon Initiative, Parks Canada, and the Calgary Foundation. Environmental Systems Research Institute, Inc. (Redlands, California) provided software. The information in this document has been funded in part by the U.S. Environmental Protection Agency. It has been subjected to the agency's peer and administrative review and has been approved for publication as a document of the Environmental Protection Agency. Mention of trade names or commercial products does not constitute endorsement or recommendation for use. We are grateful to G. Mowat, M. Gibeau, and D. Smith for sharing unpublished field data. We thank the following individuals for assistance: A. Hackman, S. Price, S. Alexander, M. Andrews, M. Austin, M. Badry, V. Banci, B. Butterfield, D. Carr, J. Copeland, L. Craighead, C. Daly, S. Donelon, D. Gilbride, B. Hall, S. Herrero, D. Hillary, M. Jalkotzy, K. Kunkel, P. Lee, M. Mahr, D. Mattson, T. Merrill, M. Quinn, R. Redmond, B. Robinson, I. Ross, C. Rumsey, B. Runnels, D. Sachs, A. Shilsky, C. Stewart, J. Weaver, C. White, J. Wierzchowski, J. Williams, and M. Wood. J. Dunning, K. Crooks, M. Burgman, R. Pressey, and two anonymous reviewers provided helpful reviews of the manuscript.

Literature Cited

Ballard, W. B., J. S. Whitman, and C. L. Gardner. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildlife Monographs **98**.

Blanchard, B. M., and R. R. Knight. 1991. Movements of Yellowstone grizzly bears. Biological Conservation **58:**41–67.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology **58:**445–449.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information theoretic approach. Springer-Verlag, New York.

Cabeza, M., and A. Moilanen. 2001. Design of reserve networks and the persistence of biodiversity. Trends in Ecology & Evolution **16(5):**242–248.

Carroll, C., R. F. Noss, and P. C. Paquet. 2000. Carnivores as focal species for conservation planning in the Rocky Mountain region. World Wildlife Fund Canada, Toronto, Ontario. Available from http://www.wwf.ca/en/res_links/rl_resources.asp (accessed December 2002).

Carroll, C., R. F. Noss, and P. C. Paquet. 2001*a*. Carnivores as focal species for conservation planning in the Rocky Mountain region. Ecological Applications **11:**961–980.

Carroll, C., R. F. Noss, N. H. Schumaker, and P. C. Paquet. 2001*b*. An evaluation of the biological feasibility of restoring wolf, wolverine, and grizzly bear to Oregon and California. Pages 23–46 in D. Maehr, R. Noss, and J. Larkin, editors. Large mammal restoration: ecological and sociological implications. Island Press, Washington, D.C.

Carroll, C., R. F. Noss, and P. C. Paquet. 2002. Rocky Mountain Carnivore Project: final report. World Wildlife Fund Canada. Toronto, Ontario. Available from http://www.wwf.ca/en/res_links/rl_resources.asp (accessed December 2002).

Carroll, C., M. K. Phillips, N. H. Schumaker, and D. W. Smith. 2003*a*. Impacts of landscape change on wolf restoration success: planning a reintroduction program using dynamic spatial models. Conservation Biology **17:**536–548.

Carroll, C., R. F. Noss, P. C. Paquet and N. H. Schumaker. 2003*b*. Use of population viability analysis and reserve selection algorithms in regional conservation plans. Ecological Applications **13:**1773–1789.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Sunderland, Massachusetts.

Ceballos, G., and P. R. Ehrlich. 2002. Mammal population losses and the extinction crisis. Science **296:**904–907.

Cincotta, R. P., J. Wisnewski, and R. Engelman. 2000. Human population density in the biodiversity hotspots. Nature **404:**990–992.

Crist, E. P., and R. C. Cicone. 1984. Application of the tasseled cap concept to simulated thematic mapper data. Photogrammetric Engineering and Remote Sensing **50:**343–352.

Diamond, J. M. 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural preserves. Biological Conservation **7:**129–146.

Doak, D. 1995. Source-sink models and the problem of habitat degradation: general models and applications to the Yellowstone grizzly. Conservation Biology **9:**1370–1379.

Dunning, J. B., Jr., D. J. Stewart, B. J. Danielson, B. R. Noon, T. L. Root, R. H. Lamberson, and E. E. Stevens. 1995. Spatially explicit population models: current forms and future uses. Ecological Applications **5:**3–11.

Fuller, T. K. 1989. Population dynamics of wolves in north-central Minnesota. Wildlife Monographs **105:**.

Hansen, A. J., and J. J. Rotella. 2002. Biophysical factors, land use, and species viability in and around nature reserves. Conservation Biology **16:**1112–1122.

Hanski, I. 1994. A practical model of metapopulation dynamics. Journal of Animal Ecology **63:**151–162.

Hanski, I. 1997. Metapopulation dynamics: from concepts and observations to predictive models. Pages 69–92 in I. Hanski and M. E. Gilpin, editors. Metapopulation biology: ecology, genetics & evolution. Academic Press, London.

Hanski, I., and O. Ovaskainen. 2002. Extinction debt at extinction threshold. Conservation Biology **16:**666–673.

Harrison, S. 1994. Metapopulations and conservation. Pages 111–128 in P. J. Edwards, R. M. May, and N. R. Webb, editors. Large-scale ecology and conservation biology. Blackwell Scientific Publications, Cambridge, Massachusetts.

Hayes, R. D., and A. S. Harestad. 2000. Demography of a recovering wolf population in the Yukon. Canadian Journal of Zoology **78:**36–48.

Hovey, F. W., and B. N. McLellan. 1996. Estimating population growth of grizzly bears from the Flathead River drainage using computer simulations of reproductive and survival rates. Canadian Journal of Zoology **74:**1409–1416.

Knight, R. R., and L. L. Eberhardt. 1985. Population dynamics of Yellowstone grizzly bears. Ecology **66:**323–334.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

Mace, R. D., and J. S. Waller. 1998. Demography and population trend of grizzly bears in the Swan Mountains, Montana. Conservation Biology **12:**1005–1016.

Mace, R. D., J. S. Waller, T. L. Manley, K. Ake, and W. T. Wittinger. 1999. Landscape evaluation of grizzly bear habitat in western Montana. Conservation Biology **13:**367–377.

Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. Nature **405:**243–253.

Mattson, D. J. 2000. Causes and consequences of dietary differences among Yellowstone grizzly bears (*Ursus arctos*). Ph.D. dissertation. University of Idaho, Moscow.

Mattson, D. J., and T. Merrill. 2002. Extirpations of grizzly bears in the contiguous United States, 1850–2000. Conservation Biology **16:**1123–1136.

Merrill, T., D. J. Mattson, R. G. Wright, and H. B. Quigley. 1999. Defining landscapes suitable for restoration of grizzly bears (*Ursus arctos*) in Idaho. Biological Conservation **87:**231–248.

Mooij, W. M., and D. L. DeAngelis. 1999. Error propagation in spatially-explicit population models: a reassessment. Conservation Biology **13:**930–933.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland, Massachusetts.

Mowat, G., and C. Strobeck. 2000. Estimating population size of grizzly bears using hair capture, DNA profiling, and mark-recapture analysis. Journal of Wildlife Management **64:**183–193.

Newmark, W. C. 1987. A land-bridge island perspective on mammalian extinctions in western North America parks. Nature **325:**430–432.

Newmark, W. D. 1996. Insularization of Tanzanian Parks and the local extinction of large mammals. Conservation Biology **10:**1549–1556.

Noss, R. F., C. Carroll, K. Vance-Borland, and G. Wuerthner. 2002. A multicriteria assessment of the irreplaceability and vulnerability of sites in the Greater Yellowstone Ecosystem. Conservation Biology **16:**895–908.

Paetkau, D., L. P. Waits, P. L. Clarkson, L. Craighead, E. Vyse, R. Ward, and C. Strobeck. 1998. Variation in genetic diversity across the range of North American brown bears. Conservation Biology **12:** 418–429.

Paquet, P. C, J. Wierzchowski, and C. Callaghan. 1996. Effects of human activity on gray wolves in the Bow River Valley, Banff National Park, Alberta. Chapter 7 in J. Green, C. Pacas, S. Bayley, and L. Cornwell, editors. A cumulative effects assessment and futures outlook for the Banff Bow Valley. Banff Bow Valley Study, Department of Canadian Heritage, Ottawa.

Pease, C. M., and D. J. Mattson. 1999. Demography of the Yellowstone grizzly bears. Ecology **80:**957–975.

Poole K. G., G. Mowat, and D. A. Fear. 2001. DNA-based population estimate for grizzly bears *Ursus arctos* in northeastern British Columbia, Canada. Wildlife Biology **7:**105–115.

Pressey, R. L., and K. H. Taffs. 2001. Scheduling conservation action in production landscapes: priority areas in western New South Wales defined by irreplaceability and vulnerability to vegetation loss. Biological Conservation **100:**355–376.

Pulliam, H. R., J. B. Dunning Jr., and J. Liu. 1992. Population dynamics in complex landscapes: a case study. Ecological Applications **2:**165–177.

Pulliam, R. 1988. Sources, sinks, and population regulation. The American Naturalist **132:**652–661.

Ream, R. R., M. W. Fairchild, D. K. Boyd, and D. H. Pletscher. 1991. Population dynamics and home range changes in a colonizing wolf population. Pages 349–366 in R. B. Keiter and M. S. Boyce, editors. The greater Yellowstone ecosystem: redefining America's wilderness heritage. Yale University Press, New Haven, Connecticut.

Ruckelshaus, M., C. Hartway, and P. Kareiva. 1997. Assessing the data requirements of spatially explicit dispersal models. Conservation Biology **11:**1298–1306.

Schumaker, N. H. 1998. A user's guide to the PATCH model. EPA/600/R-98/135. U.S. Environmental Protection Agency, Environmental Research Laboratory, Corvallis, Oregon. Available from www.epa.gov/wed/pages/models.htm (accessed May 2004).

Schwartz, C. C., M. A. Haroldson, K. A. Gunther, D. Moody. 2002. Distribution of grizzly bears in the greater Yellowstone ecosystem, 1990–2000. Ursus **13:**203–212.

Shigesada, N., and K. Kawasaki. 2002. Invasion and the range expansion of species: effects of long-distance dispersal. Pages 350–373 in J. M. Bullock, R. E. Kenward, and R. S. Hails, editors. Dispersal ecology. Blackwell Science, Malden, Massachusetts.

South, A. 1999. Dispersal in spatially-explicit population models. Conservation Biology **13:**1039–1046.

Statistics Canada. 1997. A national overview: 1996 census of Canada. Publication 93-357-XPB. Industry Canada, Ottawa.

Theobald, D. M., H. Gosnell, and W. E. Riebsame. 1996. Land use and landscape change in the Colorado mountains. II. A case study of the East River Valley, Colorado. Mountain Research and Development **16:**407–418.

Tilman D., R. M. May, C. L. Lehman, and M. A. Nowak 1994. Habitat destruction and the extinction debt. Nature **371:**65–66.

U.S. Census Bureau (USCB). 1991. Census of the United States: 1990. USCB, Washington, D.C.

U.S. Fish and Wildlife Service (USFWS). 1993. Grizzly bear recovery plan. USFWS, Missoula, Montana.

United Nations Environment Programme–World Conservation Monitoring Centre (UNEP-WCMC). 2002. Protected areas database, version 5.0. UNEP–WCMC, Cambridge, United Kingdom.

Weaver, J. L., P. C. Paquet, and L. F. Ruggiero. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. Conservation Biology **10:**964–976.

Wiens, J. A. 2001. The landscape context of dispersal. Pages 96–109 in J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. Dispersal. Oxford University Press, Oxford, United Kingdom.

Wilcove, D. S., and R. M. May. 1986. National park boundaries and ecological realities. Nature **324:**206–207.

Wydeven, A. P., R. N. Schultz, and R. P. Thiel. 1995. Monitoring a recovering gray wolf population in Wisconsin, 1979–1991. Pages 147–156 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Occasional publication number 35. Canadian Circumpolar Institute, Edmonton.