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Spatially Explicit Power Analyses for Occupancy-Based Monitoring of Wolverine in the U.S. Rocky Mountains

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Abstract: *Conservation scientists and resource managers often have to design monitoring programs for species that are rare or patchily distributed across large landscapes. Such programs are frequently expensive and seldom can be conducted by one entity. It is essential that a prospective power analysis be undertaken to ensure stated monitoring goals are feasible. We developed a spatially based simulation program that accounts for natural history, habitat use, and sampling scheme to investigate the power of monitoring protocols to detect trends in population abundance over time with occupancy-based methods. We analyzed monitoring schemes with different sampling efforts for wolverine (Gulo gulo) populations in 2 areas of the U.S. Rocky Mountains. The relation between occupancy and abundance was nonlinear and depended on landscape, population size, and movement parameters. With current estimates for population size and detection probability in the northern U.S. Rockies, most sampling schemes were only able to detect large declines in abundance in the simulations (i.e., 50% decline over 10 years). For small populations reestablishing in the Southern Rockies, occupancy-based methods had enough power to detect population trends only when populations were increasing dramatically (e.g., doubling or tripling in 10 years), regardless of sampling effort. In general, increasing the number of cells sampled or the per-visit detection probability had a much greater effect on power than the number of visits conducted during a survey. Although our results are specific to wolverines, this approach could easily be adapted to other territorial species.*

Keywords: detection probability, occupancy, population monitoring, population trends, sampling design

Poder de Análisis Espacialmente Explícito para el Monitoreo Basado en Ocupación del Glotón (*Gulo gulo*) en las Montañas Rocallosas de Estados Unidos

Resumen: *Científicos de la conservación y administradores de recursos frecuentemente tienen que diseñar programas de monitoreo para especies que son raras o están distribuidas en fragmentos a lo largo de paisajes extensos. Tales programas frecuentemente son caros y rara vez pueden ser conducidos por una entidad. Es esencial que un análisis prospectivo de poder se lleve a cabo para asegurar que las metas de monitoreo enunciadas son factibles. Desarrollamos un programa de simulación basado en el espacio que toma en cuenta la historia natural, el uso de hábitat y el esquema de muestreo para investigar el poder de los protocolos de monitoreo para detectar tendencias en la abundancia de la población a través del tiempo con un método basado en ocupación. Analizamos esquemas de monitoreo con esfuerzos de muestreo diferentes para poblaciones de glotones (Gulo gulo) en 2 áreas de las Montañas Rocallosas de los Estados Unidos. La relación entre la ocupación y la abundancia fue no-lineal y dependía del paisaje, el tamaño de la población y los parámetros de movimiento. Con las estimaciones actuales del tamaño de población y la probabilidad de detección en las Rocallosas del norte de los Estados Unidos, la mayoría de los esquemas sólo pudieron detectar disminuciones grandes en la abundancia en las simulaciones (p. ej.: 50% de disminución a lo largo de 10 años). Para poblaciones pequeñas restableciéndose en las Rocallosas sureñas, los métodos basados en ocupación tuvieron suficiente poder para detectar tendencias de población solamente cuando las poblaciones*

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estaban incrementando dramáticamente (p. ej.: duplicándose o triplicándose en 10 años), sin importar el esfuerzo de muestreo. En general, incrementar el número de celdas muestreadas o la probabilidad de detección por visita tuvo un mayor efecto sobre el poder que el número de visitas hechas durante un muestreo. Aunque nuestros resultados son específicos para los glotones, esta aproximación puede adaptarse fácilmente a otras especies territoriales.

Palabras Clave: diseño de muestreo, monitoreo de población, ocupación, probabilidad de detección, tendencias de población

Introduction

Wildlife populations worldwide have faced major reductions in abundance and geographic range due to natural and anthropogenic causes (Butchart et al. 2010; Hoffmann et al. 2010; Rands et al. 2010; Inman et al. 2011). Currently, many populations face multiple threats, including habitat fragmentation and loss, climate change, direct and indirect exploitation, disease, invasive species, and interactions among these threats (Primack 2006; Laurance et al. 2008; Povilitis & Suckling 2010). In response, many countries have adopted legislation aimed at affording protection to species of conservation concern. Two of the more powerful pieces of legislation are Canada's Species at Risk Act and the United States' Endangered Species Act (ESA). These acts not only identify species at risk and aim to protect them from additional harm, but also stipulate mechanisms for recovery. For example, in the United States approximately half of the annual budget spent on threatened and endangered species is designated for recovery (GAO 2005; Male & Bean 2005). However, determining when a species of concern is declining or subsequently recovering requires information on trends in relevant state variables.

Most researchers who have examined trends in wildlife have based their assessments on changes in the abundance of individuals (Dennis et al. 1991; Bart et al. 2007; Foster et al. 2009; Broms et al. 2010). Although estimates of abundance are important, other measures such as changes in genetic or demographic parameters within a population or changes in geographic range size have been used to infer population trends (Gaston 1991; Schwartz et al. 2007; Marucco et al. 2009; Broms et al. 2010). Recently, more attention has been placed on estimating changes in occupancy of a species geographic range (Joseph et al. 2006; MacKenzie et al. 2006). Occupancy estimation usually requires multiple visits to a set of sample units, where detection or nondetection of species of interest is recorded during each visit. Repeat-visit data are used to simultaneously model species occupancy and detectability so as to reduce the bias induced by imperfect detection (MacKenzie et al. 2006). If occupancy estimation is conducted over multiple time intervals, trends in occupancy can be estimated (Field et al. 2005; MacKenzie 2005; Marsh & Trenham 2008).

Before launching an occupancy study, some form of power analysis should be conducted to allocate monitoring effort efficiently (Field et al. 2005; MacKenzie 2005; Rhodes et al. 2006). Most researchers base power analyses for occupancy estimation on detection of declines in occupancy over time; however, these simulations rarely consider spatial dynamics. Also, monitoring trends in occupancy is often used as a surrogate for trends in abundance, but this link is rarely evaluated (but see Rhodes et al. 2006; Rhodes & Jonzén 2011). To this end, we built a species-specific model of changes in abundance over time from which we sampled repeat detection and nondetection data to determine power to detect population trends under various scenarios.

We designed our approach to assess effort required for a large-scale wolverine (*Gulo gulo*) monitoring effort. Wolverines are a Holarctic carnivore species known for their large home ranges, low densities, and occasional long-distance movements (Lofroth & Krebs 2007; Squires et al. 2007; Inman et al. 2012). The species is currently being considered for listing under the ESA (USFWS 2010), primarily due to the large decrease in their abundance and the possibility that the species was eliminated from the contiguous United States in the early 20th century. Wolverine populations have returned to Idaho, Montana, Washington, and Wyoming, and single male wolverines have recently recolonized California and Colorado (Aubry et al. 2007; Moriarty et al. 2009). Yet, wolverines are still absent from substantial portions of their historical range. Their current abundance in the contiguous United States is likely to be at most 500 individuals.

Aubry et al. (2007) and Copeland et al. (2011) found that the historical distribution of wolverines is consistent with the distribution of persistent spring snow. On the basis of 7 years of satellite images of snow cover from 24 April–15 May, Copeland et al. (2011) found that >99% of wolverine den sites and >89% of year-round telemetry locations were in areas classified as having persistent spring snow. Furthermore, Schwartz et al. (2009) demonstrated that wolverine gene flow is facilitated in areas with persistent spring snow relative to areas that are free of snow.

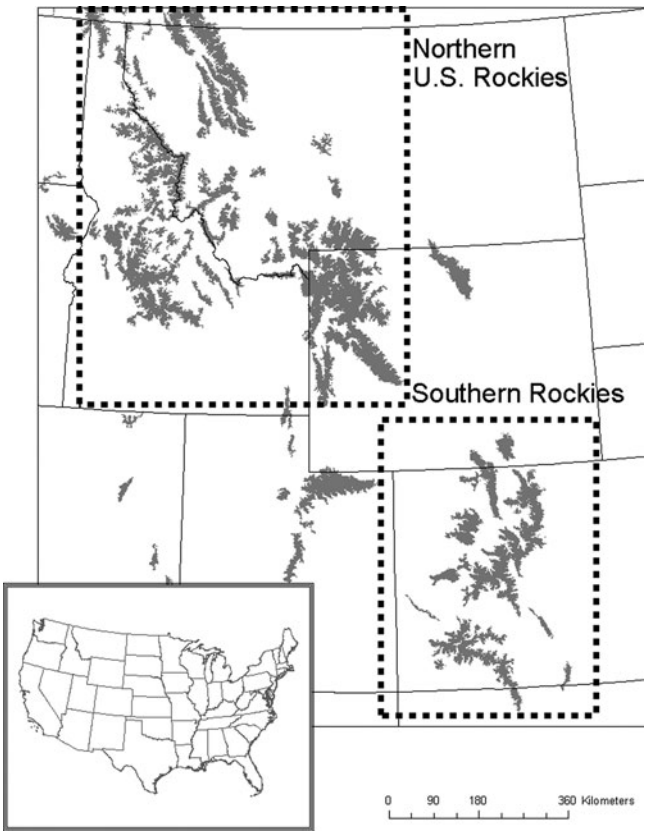

Figure 1. Study areas (dashed lines) and distribution of persistent spring snow in the U.S. Rocky Mountains (shading).

We used habitat (i.e., persistent spring snow), movement, and home range data to build a spatially based model with which to assess the power of monitoring efforts aimed at wolverine in their current range and in areas they may eventually recolonize naturally or through reintroduction.

Methods

Study Area

The primary study area was the U.S. Rocky Mountains in northern and central Idaho, western Montana, and northwest Wyoming (Fig. 1). This area is known to be occupied by wolverines; current population estimates range from 200 to 500 individuals (USFWS 2010). We allowed areas used by simulated wolverines to extend up to 50 km into Alberta and British Columbia, Canada, to account for continuous wolverine populations in the Northern Rockies, but these areas were not included in the sampling.

We included the mountainous region of the Southern Rocky Mountains as a secondary study area. This area does not currently have a population of wolverines, although wolverines are thought to have occurred there historically (Aubry et al. 2007) and there seems to be adequate habitat, including persistent spring snow (Aubry et al. 2007; McKelvey et al. 2011). Areas of persistent spring snow are more patchily distributed in the Southern Rockies and are separated from areas of persistent spring snow in the Northern U.S. Rockies by >200 km.

Individual Utilization Distributions

We randomly selected points within areas of persistent spring snow (using Copeland et al. 2010) for the center of individual home ranges for adult female, adult male, and transient male wolverines. Among these 3 groups, locations were chosen independently to allow for overlapping home ranges (Copeland 1996; Inman et al. 2011); however, within each group, selection of home range centers was constrained to reflect territoriality (Supporting Information). All home range centers were located in snow patches large enough to support at least one resident female wolverine (Krebs et al. 2007).

Once home range centers were established for a given simulated landscape, we assigned a bivariate normal utilization distribution for each individual that we based on estimated home range parameters (Supporting Information). These distributions were weighted by the availability of persistent spring snow. Thus, each of the individual utilization distributions took a unique shape on the basis of location of the home range center and availability of snow. As distance from home range center increased, probability of use decreased.

Following these rules, our program, SPACE (spatially based power analyses for conservation and ecology), created 1000 surfaces for initial populations of $N_0 = 500$ or $N_0 = 200$ individuals in the Northern Rockies landscape. These values reflected high and low estimates of wolverine population size in the study area. We simulated 10%, 20%, or 50% declines in population size over a decade ($\lambda = 0.989, 0.977, 0.933$) by randomly removing an appropriate number of individuals in each time step. We also simulated a hypothetical reintroduced or recolonizing population in the Southern Rockies. These populations were started with $N_0 = 30$ individuals and allowed to increase by 50%, 100%, or 200% over a decade ($\lambda = 1.041, 1.072, 1.116$). We initiated all populations with a 2:1:2 ratio of females:resident males:transient males (see Supporting Information for details).

Sampling

The second stage of our simulation was to create encounter histories (i.e., data necessary for occupancy estimation) for each simulated landscape. We initially divided the study area into 225-km^2 sample units (cells), an area that matches home range sizes for resident females, which is a strategy widely used for monitoring carnivores

(e.g., Zielinski & Stauffer 1996). We excluded cells that did not overlap the persistent snow layer by ≥50%, which resulted in 388 cells in the Northern U.S. Rockies study region and 128 cells in the Southern Rockies. We later explored how the size of the cell affected power by running more simulations in which the sample grid had cells that were 100, 500, and 1000 km^2. We calculated the probability of at least one wolverine being present in each cell (hereafter, probability of presence) and created simulated encounter histories for each landscape over 10 years (see Supporting Information for details). We explored the effect of changes in parameters associated with sampling on power to detect population changes by subsampling from the encounter histories (see Supporting Information for details).

Estimated Occupancy

The encounter histories provided a basis for obtaining annual estimates of occupancy and detection probability for each simulated landscape and parameter set. Because the subject of our simulations was a mobile carnivore capable of moving freely among sample cells between visits, we violated the critical assumption of occupancy estimation that the system remain closed over the course of sampling (i.e., occupancy status of a given cell cannot change during the period surveys are conducted). Due to this violation, interpretation of estimated occupancy parameters was different than the usual context in which the status (occupied or unoccupied) of a given cell is static over the course of a survey. Specifically, the estimate of occupancy (Ψ) generated under this context was the probability that any given cell across the study area was used during the survey rather than occupied, and any reference to Ψ or occupancy from here on refers to probability of use (MacKenzie et al. 2006). Furthermore, the estimate of detection probability generated in this context is actually the product of detection probability (i.e., probability of detection given that the species of interest is present; this quantity is specified directly for any given simulation) and the probability that an individual is present, and thus available for detection (MacKenzie et al. 2006). We refer to the detection probability estimated by the model as p_{est} and the actual detection probability specified for the simulations as $p_{sim,}$ such that $p_{est} = p_{sim} \times$ probability of presence.

We used the R package RMark (R Development Core Team 2011) to input the encounter histories and fit a multiple season, implicit dynamics occupancy model in Program MARK (White & Burnham 1999). For each model fit, we extracted the derived occupancy estimates (i.e., on a probability scale) and their variance–covariance matrix for each year over the 10 years of each simulation. We then used the variance components procedure in RMark to fit a linear trend model to the estimates with a random effect of year (Burnham & White 2002; Laake & Rexstad 2012). This approach assumes the occupancy estimates came from a normal distribution centered along a declining trend line, and process variance (i.e., year-to-year differences) was treated separately from parameter uncertainty. As such, it may be more realistic than simply fitting a linear trend model to the data (with no random effect), which forces each of the occupancy estimates to fall directly on a line. To account for sampling effort, we applied a finite population correction to the trend estimate that reduced the sampling variance by a factor of $(N - n)/N$, where N is the total number of cells in the study area and n is the number of cells included in the sample (Supporting Information). With a significance value (α) of 0.05, a trend was detected if the 95% confidence interval of the trend parameter excluded zero and was in the correct direction. Thus, we computed the statistical power produced by a sampling scenario (i.e., probability a significant trend is detected given that a trend exists) as the percentage of simulations in which a trend was detected.

We repeated the power analysis, as described previously, across 1000 simulated landscapes produced for each combination of population change, population size, simulated detection probability (p_{sim}), number of visits, cell size, number of cells sampled, and annual or alternate year sampling schemes (Table 1). For alternate-year sampling, we fitted the linear random effect model to occupancy estimates from data in odd years only. Where applicable, all sampling was cumulative to facilitate the most meaningful contrasts between levels of a parameter. For example, a sample of 50 cells would include the same cells as a sample of 25 cells with an additional 25 cells included. We bracketed the sampling parameters (cell size, detection probability, visits) on the basis of previous efforts described in the literature (Magoun et al. 2007; Gardner et al. 2010; Magoun et al. 2011).

Our simulations were intended to be generalizations; we did not attempt to specifically define the sampling season, sampling mechanism, or what constitutes a visit. The simulations are subject to limitations. First, the manner in which we determined availability of animals to be detected (integrating the individual utilization distributions across each cell [Supporting Information]) best reflects protracted sampling over time (i.e., each visit or sampling occasion is composed of several weeks) with cameras or hair snares, which sample animals directly. Simulating other sampling methods such as aerial surveys, track surveys, or scat collection, would require treating each visit as a snapshot in time or accounting for decay of sign. With protracted sampling, the relation between occupancy and abundance may be more blurred compared to a snapshot approach due to movement of individuals within the sampling period. Second, we assumed visits were defined through time such that the availability of an animal during one visit was independent of other

Table 1. Variables and ranges of values tested in simulations of potential wolverine monitoring scenarios.

Variable	*Values tested*
Initial population size	$N_0 = 30, 200, 500$
Population growth rates	$\lambda = 0.933, 1.041, 1.072, 1.116$ for $N_0 = 30$
	$\lambda = 0.933, 1.041$ for $N_0 = 200$
	$\lambda = 0.933, 0.977, 0.989, 1.041$ for $N_0 = 500$
Limit on movement	none; 1, 2 SD from home range center
Simulated detection probability	0.2, 0.8
Number of cells sampled	10–90% of grid
Number of visits	2–7
Cell size	100, 225, 500, 1000 km^2
Sampling	annual or alternating years

visits. We did not consider cases in which replicate visits occurred over a short time such that availability did not change between visits (e.g., multiple independent observers on a single visit or clusters of cameras in relatively close proximity). Third, we assumed the population was closed demographically over the course of each annual survey and that surveys occurred at a time of year (i.e., winter) when animals generally confined their movements to a specific home range (e.g., other than those animals we defined as transients, adult animals did not make exploratory movements or disperse). Finally, we assumed that as population size changed, animal home ranges remained the same size.

Results

Due to the spacing rules among individuals that we used to reflect wolverine territoriality, the Northern Rockies landscape became saturated with approximately 850 individuals (mean [SD] across 100 simulated landscapes: 420 [6] females, 219 [4] resident males, 219 [4] transient males). For $N = 800$, the median probability of at least one wolverine per cell (i.e., probability of presence) was 0.74. This yielded, on average, 280.4 cells in which wolverines were available for detection per sampling occasion across the 388 cells in the grid. As the population size decreased, the probability of presence decreased to 0.54 (212.4 cells with wolverine available per occasion) for $N_0 = 500$ and the probability of presence was 0.05 (18.9 cells with wolverine available per occasion) for $N_0 = 30$. Assuming perfect detection ($p_{sim} = 1$), these cell-based probabilities of presence translated to an estimated occupancy (Ψ) of 0.97 [0.01] for populations with $N_0 = 500$ individuals and 0.22 [0.04] for $N_0 = 30$.

Effects of Population Size and Trend

We investigated the upper limits of power to detect population trends with occupancy estimation by examining results when detection probability was perfect ($p_{sim} = 1$) and cells were visited numerous times (5). We focused these analyses on the U.S. Northern Rockies landscape and a declining population ($\lambda = 0.933$). Even with perfect detection and intense sampling, detecting a large decline (50% over 10 years) in a large starting population ($N_0 = 500$) required a sample of 90 of 388 cells (Fig. 2) to achieve adequate power (>80% chance of detecting the trend). As the population size decreased, the amount of sampling needed to detect a 50% decline even under this best-case scenario increased dramatically. For example, for $N_0 = 200$, achieving 80% power required sampling approximately 120 cells (Fig. 2). Power to detect trends was generally lower for increasing populations relative to scenarios with decreasing populations. For example, to detect a 50% increase ($\lambda = 1.041$) with >80% confidence, the required number of cells increased from 90 to 245 for $N_0 = 500$ and 120 to 225 for $N_0 = 200$. Detecting trends in small populations ($N_0 = 30$) was difficult; a census of cells would be required to detect either a 50% increase or decrease.

With current population sizes ($N_0 = 500$) in the Northern Rockies, the ability to detect declines decreased dramatically as the strength of the decline decreased (Fig. 3). For a 20% decline in population size over 10 years, a census of cells with perfect detection ($p_{sim} = 1$) would be required to detect the population change with 80% power. For a 10% population decline, this effort would give <60% power. With either population increases or declines, sampling every other year substantially increased the number of cells and visits that would need to be included relative to annual sampling.

Trade-Offs in Sampling Methods

The sampling parameter that most affected power to detect change was the simulation detection probability (p_{sim}). In nearly all scenarios, relatively large gains in power were realized when p_{sim} increased from 0.2 to 0.8. For instance, a monitoring scheme that required 5 visits to each of 125 cells had approximately 10% chance of detecting a 50% decline over 10 years when $p_{sim} = 0.2$. Power for detecting that same decline under the same sampling regime increased to 80% when $p_{sim} = 0.8$ (Fig. 3, upper left panel). By comparison, for $p_{sim} = 0.2$, an increase in sample size from $n_{cells} = 125$

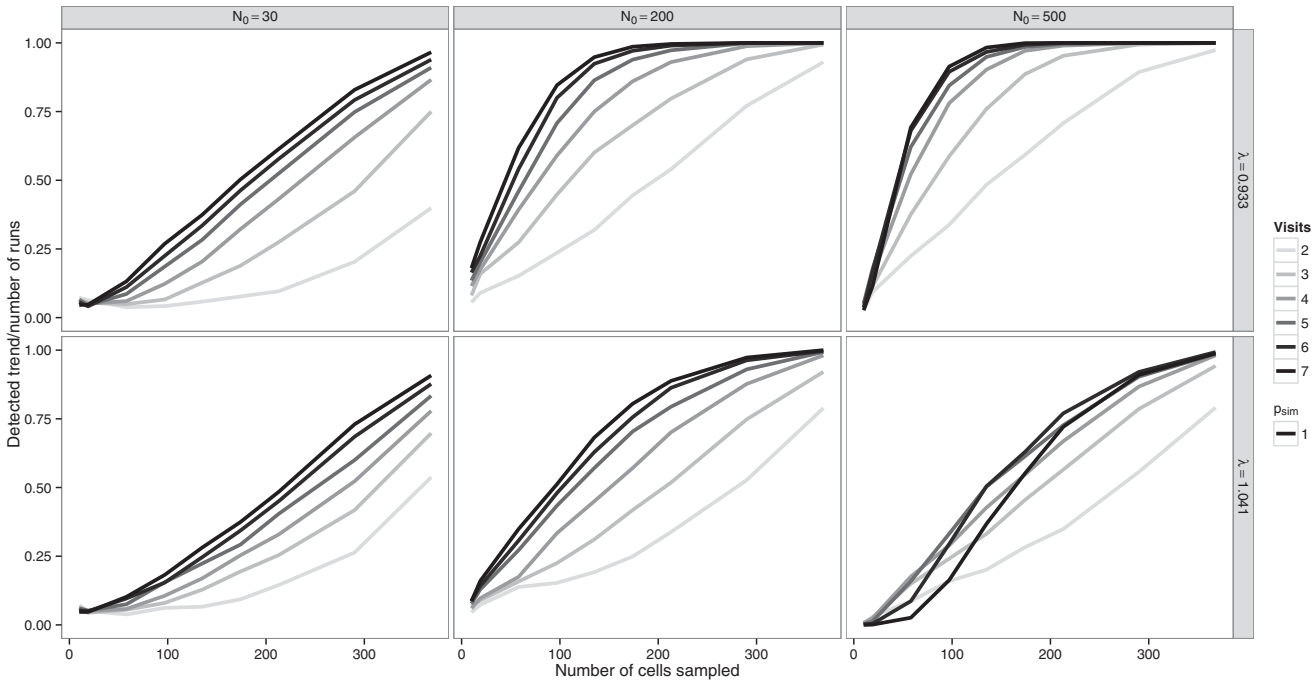

Figure 2. Effect of initial wolverine population size (N_0) on power to detect population trends in the Northern U.S. Rocky Mountains. Perfect detection is associated with sampling for a 50% decline ($\lambda = 0.933$) or a 50% increase ($\lambda = 1.041$) from initial population sizes of 30, 200, and 500 individuals. Simulated populations were sampled in a grid of 225-km^2 cells overlaid on the landscape.

to $n_{\text{cells}} = 300$ increased power to approximately 25%. Similar gains in power relative to simulation detection probability and sample size were realized in other scenarios.

The number of visits to each sample unit affected power as well, although generally to a lesser degree than population change, p_{sim}, and sample size. Even with $p_{\text{sim}} = 1$, the power to detect a trend increased with the number of visits at each grid cell due to the number of opportunities for an individual to be present. When simulation detection probability was high but imperfect (i.e., $p_{\text{sim}} = 0.8$), some gain in power was realized by visiting each sampled cell 4 times versus visiting cells 2–3 times (Fig. 3). However, there was no appreciable difference in power for 4, 5, 6, or 7 visits. When simulated detection probability was low (i.e., $p_{\text{sim}} = 0.2$), potentially greater gains in power were realized by making more visits, but it depended on the scenario (Figs. 3 and 4).

Effect of Cell Size

The number of cells and the total area that required sampling was affected by cell size (Fig. 5). Grids of 100-km^2 and 225-km^2 cells yielded similar power in terms of the percentage of the grid that needed to be sampled, although the smaller cell size required sampling more cells. Assuming 5 visits and high detection, achieving 80% power for detecting a 50% decline required 250 cells (25,000 km^2) from the small grid versus 125 cells (28,125 km^2) for the medium-sized grid. As the size of the grid increased, the power to detect trends decreased. The 1000-km^2 grid produced very low power to detect population trends. In this case, the grid in the Northern Rockies comprised only 76 cells. Including every cell in the population, with 7 visits and high detection probability, we detected a 50% population declines in <5% of the simulations. For some scenarios, we observed a phenomenon in which power was actually reduced when there were a high number of visits (Fig. 5) (500-km^2 and 1000-km^2 scenarios).

Power to Detect Increases in Small Populations

For small populations ($N_0 = 30$), power to detect population trends was limited except for situations with large population increases and high detection probability (Fig. 4). For the purposes of comparison, there was slightly greater power for detecting trends in the Southern Rockies landscape than in the Northern Rockies, although the total sampling area in the Southern Rockies landscape was approximately one-third of the Northern Rockies. For both landscapes, a doubling of the population over 10 years ($\lambda = 1.072$) could be detected with >80% power in scenarios where a large proportion of the landscape was included with relatively high capture probability. If simulation detection probability was

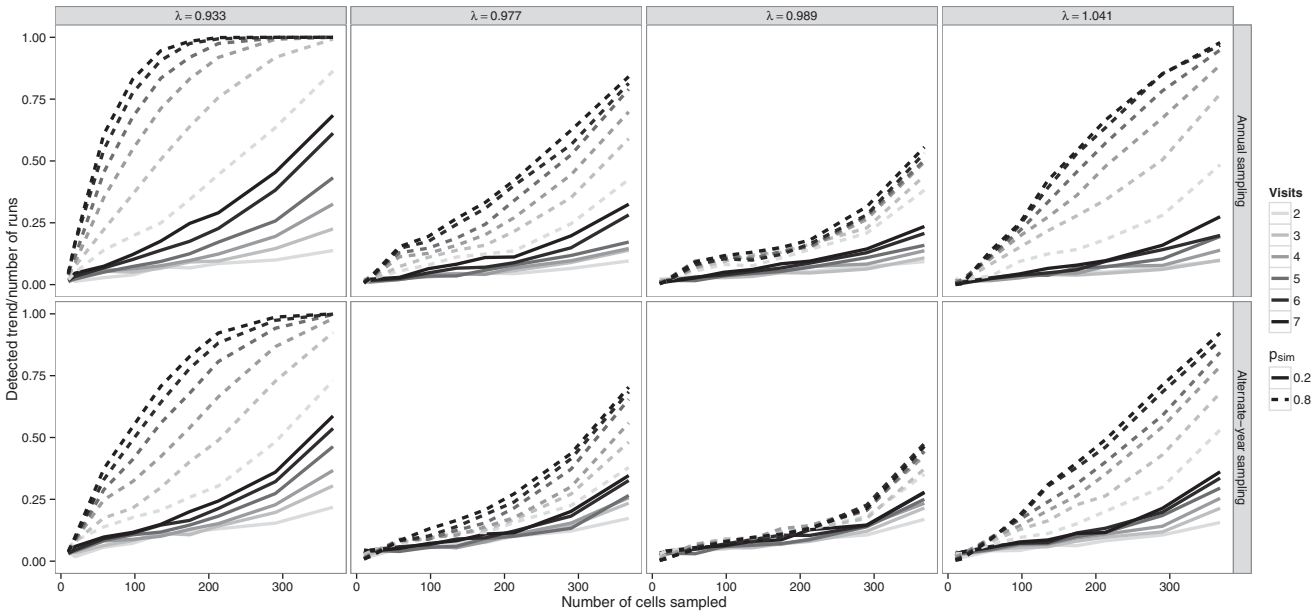

Figure 3. Results of power analyses used to assess the feasibility of using occupancy to monitor trend in the population of wolverines in the Northern U.S. Rocky Mountains ($N_0 = 500$ individuals, sampling cells size 225 km^2). Results are parsed by population growth rate ($\lambda = 0.933$, 0.977, 0.989, and 1.041, corresponding to 50%, 20%, or 10% decline or 50% increase over 10 years, respectively), sampling effort (whether sampling occurred annually or every other year), detection probability for sampling (p_{sim}), number of visits per year, and number of grid cells sampled from a total of 388. Power is based on number of detected trends in 1000 simulated populations.

low, then adequate power could only be achieved via sampling a large portion of the available landscape and making a large number (≥5) of visits to each sampled cell.

Discussion

Monitoring population trends is one of the most common challenges for management of endangered species. Using a spatially explicit simulation for wolverine in the U.S. Rocky Mountains tested the ability of occupancy-based approaches to detect trends in population size under a range of monitoring scenarios. Even for large changes in population size (e.g., 50% declines over 10 years), detecting population trends required large-scale, intensive sampling. In many scenarios, no amount of sampling could produce sufficient power to achieve monitoring goals. Our results highlight the importance of analyzing the statistical power of monitoring schemes.

Interpreting Detection Probabilities

In the case of the wolverine, work has commenced to evaluate the effectiveness of various approaches for detecting presence. These range from using fix-winged aircraft to find tracks in 100-km^2 (Magoun et al. 2007) or 1000-km^2 (Gardner et al. 2010) sampling cells to use of cameras at bait stations (Mulders et al. 2007; Magoun et al. 2011), to use of noninvasive genetic sampling (Ulizio et al. 2006; Schwartz & Monfort 2008; Magoun et al. 2011). These methods produced detection probabilities of 0.2–0.8 as bracketed in our simulations. However, matching estimates from field studies to our results requires care. Pilot analyses of detection probability derived from occupancy surveys yield p_{est}, which is not the same as p_{sim} in our analyses. Occupancy models cannot separate the effects of true detection probability (p_{sim}) and probability of presence (see Methods). Instead they estimate the product. Consequently, p_{est} returned from pilot studies will be smaller than the detection probabilities used in our simulations (p_{sim}). If pilot work indicates $p_{est} = 0.2$, power can be assumed to be better than the curves shown for $p_{sim} = 0.2$ in our figures. The exact correspondence between p_{est} and p_{sim} depends on the landscape, cell size, population size, territoriality, and home range size of the species in question. Thus, no rule of thumb holds for converting between the 2 types of detection probability. However, matching p_{est} derived from pilot work to curves for p_{sim} can still be useful; such an exercise will result in conservative estimates of power.

Pilot work specific to occupancy monitoring for wolverine in the Northern Rockies has been conducted using camera stations (R. Inman, unpublished data) and

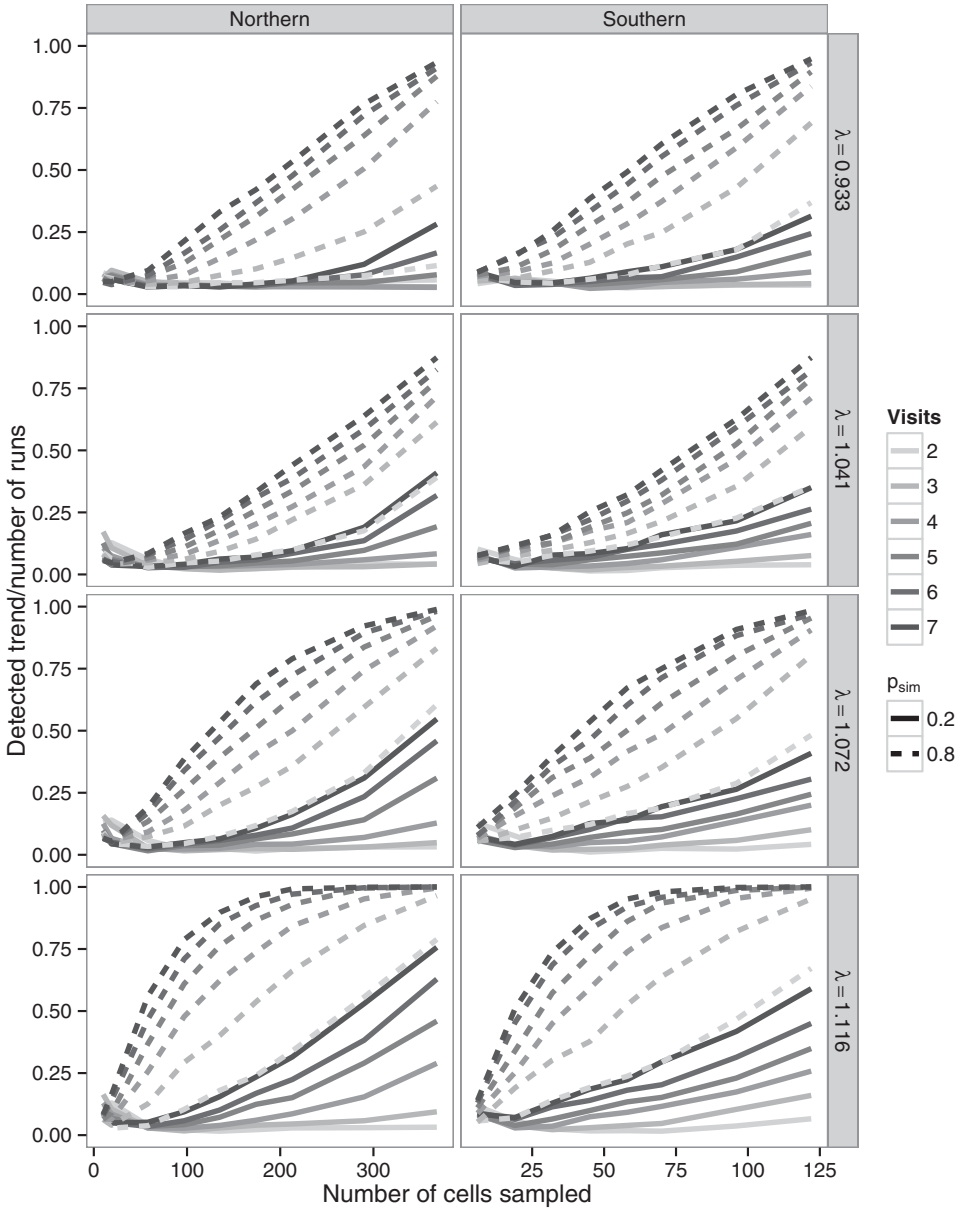

Figure 4. Power to detect population trends for N_0 = 30 wolverines in Northern U.S. Rocky Mountains compared with a population of the same size in the Southern Rocky Mountains. Population growth rates (λ = 0.933, 1.041, 1.072, 1.116) correspond to a 50% decline or 50%, 2-fold, or 3-fold increases in population size over 10 years, respectively. Sampling effort includes detection probability for sampling (p_{sim}), number of visits per year, and number of grid cells sampled from a total of 388 cells for the Northern U.S. Rocky Mountains or 128 for the Southern Rocky Mountains. Power is based on number of detected trends from 1000 simulated populations.

hair snares (J. Waller, unpublished data) in 100-km^2 sample units. Initial results from this work suggest p_{est} is approximately 0.25–0.3, which in our simulations corresponded to $p_{sim} \approx 0.8$ (i.e., $p_{est} = p_{sim} \times$ probability of presence; mean probability of presence was 0.33, therefore 0.25/0.33 ≈ 0.76). From this estimate, and assuming 3–4 visits to each sample unit (sampling occurred during 3–4 months over winter for each pilot study), our results suggest that roughly 100–150 of the 100-km^2 cells would need to be sampled per year to attain an 80% probability of detecting a 50% decline in the Northern Rockies population (Fig. 5). Thus, monitoring will require well-coordinated surveys across multiple entities and jurisdictions. Anything less than a large-scale, coordinated effort will likely be of limited or no value.

Effects of Landscape and Cell Size

Even for fixed population sizes, the effect of the underlying landscape extends to the power to detect population changes. Power to detect trends in occupancy was similar in terms of percentage of the total study area included in the sample when comparing the Northern versus Southern Rockies but very different in terms of the absolute area that needs to be sampled. For example, to detect a 3 times increase of the $N_0 = 30$ populations with a 225-km^2 grid and >80% power required sampling approximately 35% of either landscape, which translates to sampling 30,000 km^2 in the Northern Rockies versus 10,000 km^2 in the Southern Rockies. Yet, changing the size of a study area would generally also change the size of the population included, which we found substantially affected power to detect trends.

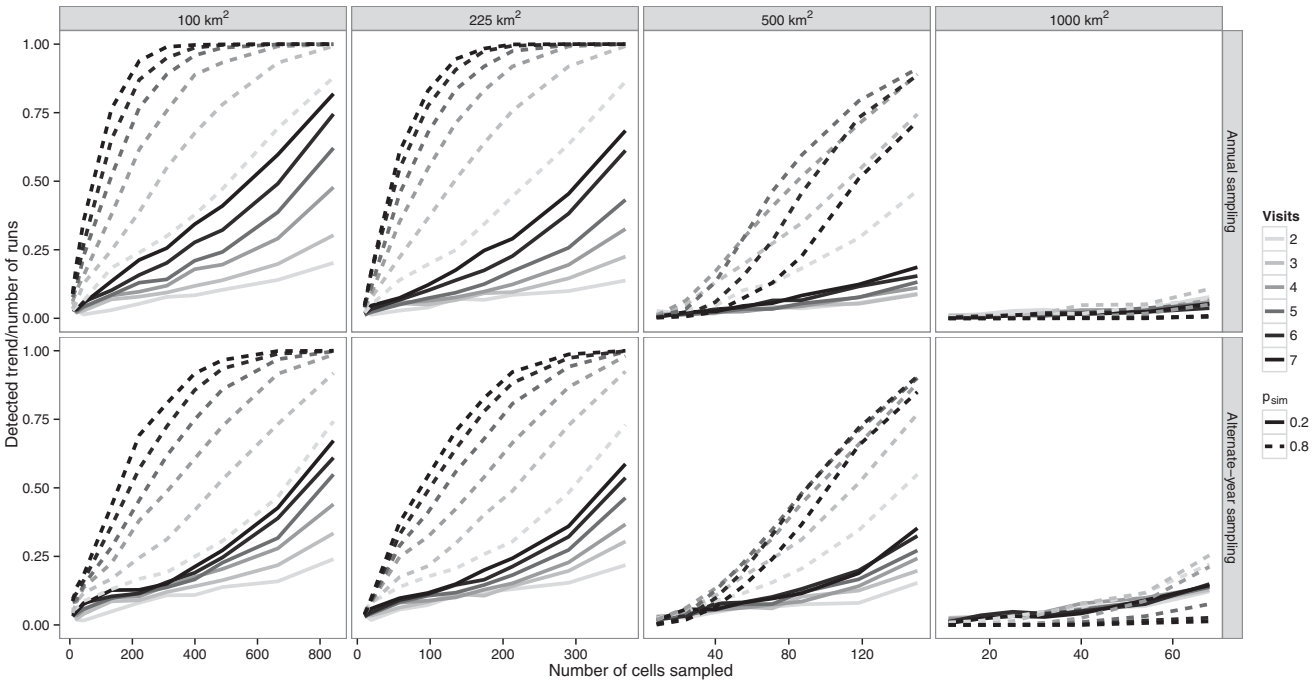

Figure 5. Effect of grid size (100–1000 km^2) on power to detect population trends in the wolverine population (N_0 = 500) in the Northern Rocky Mountains on the basis of occupancy. Sampling effort includes detection probability for sampling (p_{sim}) and number of visits per year.

To date, most authors have designed occupancy surveys for mobile species such that the cell size is equal to or greater than the typical home range (e.g., Hines et al. 2010; O'Connell & Bailey 2011). Our results indicate this type of design (i.e., cell size = 225 km^2) would work well, although power to detect declines in estimated occupancy could be somewhat better when cell size was actually smaller than a typical home range (i.e., 100 km^2). Efford and Dawson (2012) explore the relation between home range size, animal density, and occupancy and found that similar occupancy estimates can be derived from very different underlying densities, depending on home range size. They suggest this confounding is minimized when cell sizes are much larger (i.e., 10 times larger or more) than the typical home range size. However, when the sole objective is to detect trends in occupancy estimates through time, we found that very large cell sizes (500 or 1000 km^2) resulted in poor power. This is likely because home ranges for many individuals would be included in any large cell. Occupancy is less sensitive to the underlying number of animals on the landscape, and relatively large declines in a population could occur before cells would become unoccupied. Regardless of cell size used for a survey, our results depend critically on the assumption that home range size remains relatively constant, whereas abundance changes (Efford & Dawson 2012). If declines are related to changes in habitat quality, this assumption may be tenuous, although we argue that at some point a declining population will be reflected in occupancy estimates because the loss of individuals will swamp any compensation in home range size.

Relation of Number of Visits to Power

For some scenarios, we note a counterintuitive anomaly in which conducting more visits actually decreased power. This phenomenon was likely due to 2 characteristics of our simulations. First, we allowed transient males to range widely over the course of the survey period such that technically each cell was used in each year and true $\Psi = 1.0$ for all years. Thus, if we sampled long enough (made more visits), estimates of Ψ all tended toward 1.0, and power was lost because there was no trend. Second, our simulation was set up to reflect a scenario where visits occurred over a protracted period (3–4 months), and availability was independent between visits; thus, it was possible to sample transient animals almost everywhere. If all visits were made simultaneously, availability would be instantaneous and fixed across visits. In that case occupancy should track abundance more closely, and conducting more visits during this snapshot in time should increase power as expected.

Final Considerations

Using a spatially based framework to evaluate the power of monitoring efforts, we were able to quantify the effects

of sampling effort on the ability to detect population trends. Our simulations did not include cost functions, so trade-offs in sampling effort are currently missing an important real-world consideration. For instance, in a given situation, it may be easy to complete more visits to a site, but extremely costly to improve capture probability. Therefore, managers may opt to make more visits to improve power even though intensifying effort (visits) by a given percentage may be inferior to improving detection probability by a similar percentage. Thus, managers should superimpose cost and logistics over these statistical results to make informed decisions about monitoring.

Most studies base power analyses for occupancy estimation solely on detecting various simulated declines in occupancy. Here, we used a more mechanistic, spatially based approach in which we applied simulations to force declines or increases in the real parameter of interest (abundance). We then determined whether occupancy estimation could detect those changes. This approach also sets the stage for direct comparisons between occupancy and estimation of other metrics (e.g., abundance) that could potentially be used to monitor populations. Although our results can be used directly to guide the monitoring of wolverine or similar species, the largest contribution is the framework, which can be used for making decisions about the design of large-scale monitoring efforts, provided information on movement and habitat use is available. Our goals were to establish this framework to encourage cost-effective decisions in designing monitoring programs and to inspire well-coordinated surveys across multiple entities and jurisdictions. Without such coordination our analyses convincingly show that most efforts for species like the wolverine will be wasted.

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Supporting Information

Detailed methods for program SPACE (Appendix S1) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

Aubry, K. B., K. S. McKelvey, and J. P. Copeland. 2007. Distribution and broadscale habitat relations of the wolverine in the contiguous United States. The Journal of Wildlife Management **71:**2147–2158.

Bart, J., S. Brown, B. Harrington, and R. I. G. Morrison. 2007. Survey trends of North American shorebirds: population declines or shifting distributions? Journal of Avian Biology **38:**73–82.

Broms, K., J. R. Skalski, J. J. Millspaugh, C. A. Hagen, and J. H. Schulz. 2010. Using statistical population reconstruction to estimate demographic trends in small game populations. The Journal of Wildlife Management **74:**310–317.

Burnham, K. P., and G. C. White. 2002. Evaluation of some random effects methodology applicable to bird ringing data. Journal of Applied Statistics **29**:245–264.

Butchart, S. H. M., et al. 2010. Global biodiversity: indicators of recent declines. Science **328:**1164–1168.

Copeland, J. P. 1996. Biology of wolverine in central Idaho. University of Idaho, Moscow.

Copeland, J. P., et al. 2010. The bioclimatic envelope of the wolverine (*Gulo gulo*): Do climatic constraints limit its geographic distribution? Canadian Journal of Zoology-Revue Canadienne De Zoologie **88:**233–246.

Dennis, B., P. L. Munholland, and J. M. Scott. 1991. Estimation of growth and extinction parameters for endangered species. Ecological Monographs **61:**115–143.

Efford, M. G., and D. K. Dawson. 2012. Occupancy in continuous habitat. Ecosphere 3:1–15.

Field, S. A., A. J. Tyre, and H. P. Possingham. 2005. Optimizing allocation of monitoring effort under economic and observational constraints. The Journal of Wildlife Management **69:**473–482.

Foster, C. R., A. F. Amos, and L. A. Fuiman. 2009. Trends in abundance of coastal birds and human activity on a Texas barrier island over three decades. Estuaries and Coasts **32:**1079–1089.

GAO (U.S. Government Accountability Office). 2005. Fish and Wildlife Service generally focuses recovery funding on high priority species, but needs to periodically assess its funding decisions. Report GAO-05-211.GAO, Washington, D.C.

Gardner, C. L., J. P. Lawler, J. M. V. Hoef, A. J. Magoun, and K. A. Kellie. 2010. Coarse-scale distribution surveys and occurrence probability modeling for wolverine in interior Alaska. The Journal of Wildlife Management **74:**1894–1903.

Gaston, K. J. 1991. How large is a species' geographic range? Oikos **61:**434–438.

Hines, J., J. Nichols, J. Royle, D. MacKenzie, A. Gopalaswamy, N. S. Kumar, and K. Karanth. 2010. Tigers on trails: occupancy modeling for cluster sampling. Ecological Applications **20:**1456–1466.

Hoffmann, M., et al. 2010. The impact of conservation on the status of the world's vertebrates. Science **330:**1503–1509.

Inman, R. M., et al. 2012. Spatial ecology of wolverines at the southern periphery of distribution. The Journal of Wildlife Management **76:**778–792.

Joseph, L. N., S. A. Field, C. Wilcox, and H. P. Possingham. 2006. Presence-absence versus abundance data for monitoring threatened species. Conservation Biology **20:**1679–1687.

Krebs, J., E. C. Lofroth, and I. Parfitt. 2007. Multiscale habitat use by wolverines in British Columbia, Canada. The Journal of Wildlife Management **71:**2180–2192.

Laake, J. L., and E. Rexstad. 2012. RMark—an alternative approach to building linear models in MARK. In E. Cooch and G. C. White, editors. Program MARK: a gentle introduction. Available at http://www.phidot.org/software/mark/docs/book/pdf/app_3.pdf.

Laurance, W. F., S. G. Laurance, and D. W. Hilbert. 2008. Long-term dynamics of a fragmented rainforest mammal assemblage. Conservation Biology **22:**1154–1164.

Lofroth, E. C., and J. Krebs. 2007. The abundance and distribution of wolverines in British Columbia, Canada. The Journal of Wildlife Management **71:**2159–2169.

MacKenzie, D. I. 2005. What are the issues with presence-absence data for wildlife managers? The Journal of Wildlife Management **69:**849–860.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier, Amsterdam.

Magoun, A. J., C. D. Long, M. K. Schwartz, K. L. Pilgrim, R. E. Lowell, and P. Valkenburg. 2011. Integrating motion-detection, cameras, and hair snags for wolverine identification. The Journal of Wildlife Management **75:**731–739.

Magoun, A. J., J. C. Ray, D. S. Johnson, P. Valkenburg, F. N. Dawson, and J. Bowman. 2007. Modeling wolverine occurrence using aerial surveys of tracks in snow. The Journal of Wildlife Management **71:**2221–2229.

Male, T. D., and M. J. Bean. 2005. Measuring progress in US endangered species conservation. Ecology Letters **8:**986–992.

Marsh, D. M., and P. C. Trenham. 2008. Current trends in plant and animal population monitoring. Conservation Biology **22:**647–655.

Marucco, F., D. H. Pletscher, L. Boitani, M. K. Schwartz, K. L. Pilgrim, and J.-D. Lebreton. 2009. Wolf survival and population trend using non-invasive capture-recapture techniques in the Western Alps. Journal of Applied Ecology **46:**1003–1010.

McKelvey, K. S., J. P. Copeland, M. K. Schwartz, J. S. Littell, K. B. Aubry, J. R. Squires, S. A. Parks, M. McGuire Elsner, and G. S. Mauger. 2011. Predicted effects of climate change on wolverine distribution and movement in western North America. Ecological Applications **21:**2882–2897.

Moriarty, K. M., et al. 2009. Wolverine confirmation in California after nearly a century: Native or long-distance immigrant? Northwest Science **83:**154–162.

Mulders, R., J. Boulanger, and D. Paetkau. 2007. Estimation of population size for wolverines *Gulo gulo* at Daring Lake, Northwest Territories, using DNA based mark-recapture methods. Wildlife Biology **13:**38–51.

O'Connell, A. F., and L. L. Bailey. 2011. Inference for occupancy and occupancy dynamics. Pages 191–205 in A. F. O'Connell, J. D. Nichols, and K. U. Karanth, editors. Camera traps in animal ecology. Springer, New York.

Povilitis, A., and K. Suckling. 2010. Addressing climate change threats to endangered species in U.S. recovery plans. Conservation Biology **24:**372–376.

Primack, R. B. 2006. Essentials of conservation biology. Sinauer Associates, Sunderland, Massachusetts.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rands, M. R. W., et al. 2010. Biodiversity conservation: challenges beyond 2010. Science **329:**1298–1303.

Rhodes, J. R., and N. Jonzén. 2011. Monitoring temporal trends in spatially structured populations: How should sampling effort be allocated between space and time? Ecography **34:**1040–1048.

Rhodes, J. R., A. J. Tyre, N. Jonzén, C. A. McAlpine, and H. P. Possingham. 2006. Optimizing presence-absence surveys for detecting population trends. The Journal of Wildlife Management **70:** 8–18.

Schwartz, M. K., J. P. Copeland, N. J. Anderson, J. R. Squires, R. M. Inman, K. S. McKelvey, K. L. Pilgrim, L. P. Waits, and S. A. Cushman. 2009. Wolverine gene flow across a narrow climatic niche. Ecology **90:**3222–3232.

Schwartz, M. K., G. Luikart, and R. S. Waples. 2007. Genetic monitoring as a promising tool for conservation and management. Trends in Ecology & Evolution **22:**25–33.

Schwartz, M. K., and S. L. Monfort. 2008. Genetic and endocrine tools for carnivore surveys. Pages 228–250 in R. A. Long, P. MacKay, J. C. Ray, and W. J. Zielinski, editors. Noninvasive survey methods for North American carnivores. Island Press, Washington, D.C.

Squires, J. R., J. Copeland, T. J. Ulizio, I. K. Schnvartz, and L. F. Ruggiero. 2007. Sources and patterns of wolverine mortality in western Montana. The Journal of Wildlife Management **71:**2213–2220.

Ulizio, T. J., J. R. Squires, D. H. Pletscher, M. K. Schwartz, J. J. Claar, and L. F. Ruggiero. 2006. The efficacy of obtaining genetic-based identifications from putative wolverine snow tracks. Wildlife Society Bulletin **34:**1326–1332.

USFWS (U.S. Fish and Wildlife Service). 2010. Endangered and threatened wildlife and plants; 12-month finding on a petition to list the North American wolverine as endangered or threatened. Federal Register **75:**78030–78061.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation for populations of marked animals. Bird Study **46:**120–138.

Zielinski, W. J., and H. B. Stauffer. 1996. Monitoring Martes populations in California: survey design and power analysis. Ecological Applications **6:**1254–1267.