

Linking landscape characteristics to local grizzly bear abundance using multiple detection methods in a hierarchical model

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Abstract

Few studies link habitat to grizzly bear *Ursus arctos* abundance and these have not accounted for the variation in detection or spatial autocorrelation. We collected and genotyped bear hair in and around Glacier National Park in northwestern Montana during the summer of 2000. We developed a hierarchical Markov chain Monte Carlo model that extends the existing occupancy and count models by accounting for (1) spatially explicit variables that we hypothesized might influence abundance; (2) separate sub-models of detection probability for two distinct sampling methods (hair traps and rub trees) targeting different segments of the population; (3) covariates to explain variation in each sub-model of detection; (4) a conditional autoregressive term to account for spatial autocorrelation; (5) weights to identify most important variables. Road density and per cent mesic habitat best explained variation in female grizzly bear abundance; spatial autocorrelation was not supported. More female bears were predicted in places with lower road density and with more mesic habitat. Detection rates of females increased with rub tree sampling effort. Road density best explained variation in male grizzly bear abundance and spatial autocorrelation was supported. More male bears were predicted in areas of low road density. Detection rates of males increased with rub tree and hair trap sampling effort and decreased over the sampling period. We provide a new method to (1) incorporate multiple detection methods into hierarchical models of abundance; (2) determine whether spatial autocorrelation should be included in final models. Our results suggest that the influence of landscape variables is consistent between habitat selection and abundance in this system.

Introduction

Wildlife managers from Leopold (1949) have attempted to understand how habitat influences wildlife populations. For rare and wide-ranging animals, research on this has been extremely difficult and costly to conduct at appropriate scales for reliable inference to population-level metrics. Recent advances in technology, such as non-invasive genetic and remote camera sampling, now make sampling across populations more feasible. Statistical techniques to take advantage of these improved data sources and to link habitat with abundance and other population metrics (review in Williams, Nichols & Conroy, 2002, e.g. Holmes & Miller, 2010; Kery & Royle, 2010) are still under intense development.

Our goal was to understand which landscape characteristics influence relative grizzly bear abundance. Identifying variables that best explain local variation in bear abundance

can help prioritize conservation actions to promote recovery of threatened populations. These habitat characteristics can be monitored for an early warning of a potential population decline. Habitat monitoring is one requirement for delisting this population (US Fish and Wildlife Service, 1993).

Habitat management designed to support grizzly bear population recovery has relied primarily on habitat selection studies of radio-collared individuals (e.g. Servheen 1983; Waller & Mace, 1997; Mace *et al.*, 1999; McLellan & Hovey, 2001; Nielsen *et al.*, 2004a; Ciarniello *et al.*, 2007; Nielsen *et al.* 2010).

These studies sampled a small proportion of populations and covered relatively small, homogeneous areas. Only two grizzly bear studies have linked habitat with abundance within a population. Apps *et al.* (2004) modeled abundance patterns of grizzlies in southeastern British Columbia, with animals considered either (1) present and detected; or (2) not detected. Their approach conflates non-presence and

non-detection of animals and does not permit assessment of whether habitat or effort influenced detection. This could result in biased estimates of relative abundance if detection probability varies by environment or sampling effort (Gu & Swihart, 2004; Mazerolle *et al.*, 2005; MacKenzie, 2006). Nielsen *et al.* (2010) used a zero-inflated Poisson model to estimate occupancy abundance. Their model does not distinguish between non-presence and non-detection of animals that were present, nor permit inclusion of covariates that could account for spatial or temporal heterogeneity in non-detection of present animals.

Our analysis separates the two causes of non-detection to reduce bias that could result if detection probability varies by habitat, effort or time (Royle & Dorazio, 2008), while directly estimating the influence of habitat covariates on abundance. We use an N-mixture model, which includes two levels, abundance and detection, and permits incorporation of covariates for each process. This mark–recapture model uses sites as the sampling unit, and produces estimates of abundance at each site. Royle (2004a) developed the model to estimate local abundance for birds with avian point count data. As then variations of the model have been used for many animals including amphibians (e.g. Mazerolle *et al.*, 2007), fish (Webster & Pollock, 2008), invasive species (Hooten *et al.*, 2007), wild turkeys (Rioux, Belisle & Giroux, 2009) and shrubland birds (e.g. Chandler, King & DeStefano, 2009; Riddle *et al.*, 2010).

We collected hair from the northern third of a grizzly bear population in northwest Montana and used genetic analysis to identify individuals. Our 7933 km² study included areas where bear density varied widely. We used two forms of genetic sampling to increase the number of individuals detected in a cost efficient manner and target the trap-shy individuals (Kendall *et al.*, 2008). The use of multiple detection methods

can improve abundance estimates by decreasing issues of individual heterogeneity resulting from sensitivity to a single method (Williams *et al.*, 2002; e.g. Conway & Gibbs, 2005; Dreher *et al.*, 2007). Boulanger *et al.* (2008) used this dataset to estimate overall abundance and found that precision increased with the use of multiple detection methods. Based on those findings, we extended the N-mixture model to incorporate multiple detection methods.

This approach can be used by other researchers to identify the most important habitat variables influencing abundance. Our approach will be particularly useful where (1) detection varies within the study area and is related to sampling effort, time or habitat; (2) multiple detection techniques detect different segments of the population. Our approach will also be useful when researchers want to determine the strength of spatial autocorrelation in their study area and to understand the relationship between spatial autocorrelation and habitat variables in their study area.

Materials and methods

Our 7933 km² greater Glacier National Park (GNP) study area was centered over the park (4079 km²) and spanned the east–west range of grizzlies in the Rocky Mountains of western Montana, USA (Fig. 1). Our study covered over 30% of grizzly bear habitat in the Northern Continental Divide Ecosystem (US Fish and Wildlife Service, 1993). Vegetation transitioned with climate from Pacific maritime-influenced coniferous forests west of the Continental Divide, to drier prairie grasslands and agricultural fields along the eastern boundary. Elevations ranged from 960 to 3190 m. Our study included areas with both the highest and lowest grizzly bear densities in the ecosystem. Human density was generally low and mostly concentrated along road corridors,

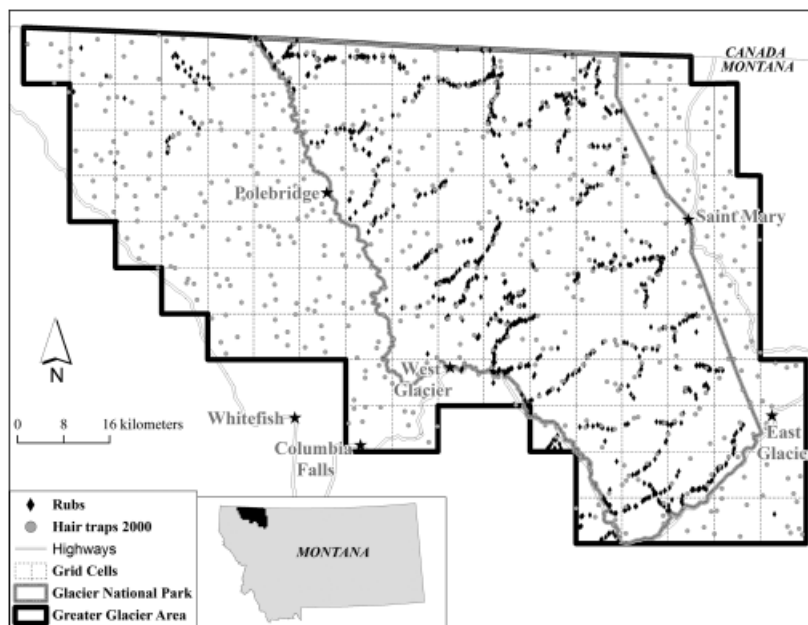


Figure 1 Hair trap and rub tree sample locations in the Greater Glacier National Park study area in northwestern Montana in 2000.

but several large towns exist. Although grizzlies, designated a threatened species, were protected throughout the study area, protective measures varied by landowner. GNP required and strictly enforced secure storage of bear attractants and prohibited firearm use. National forests enforced attractant storage guidelines as funding permitted, but much less control existed on other lands. Firearm possession was legal on all lands outside GNP.

We sampled grizzly bears in the year 2000 using two sampling methods: hair traps and rub trees (Kendall *et al.*, 2008). Hair traps consisted of a single strand of barbed wire stretched around several trees with scent lure poured on forest debris in the center. We attempted to install one hair trap in each of one hundred and twenty-six 8×8 km grid cells for each of five 14-day sample sessions May 22–August 9. However, due to logistical constraints such as high avalanche danger, 43 traps were placed in neighboring cells or during adjacent sessions, resulting in 633 ($\bar{x} = 126.2/\text{session} \pm 5.8$) hair trap sites. Traps were moved to different locations where we expected high bear use within each cell for each session. Our second sampling method involved collecting hair periodically from trees on which bears naturally rubbed, using short pieces of barbed wire to facilitate hair collection. We surveyed 907 rub trees for bear hair during May 22–October 27 along 1185 km trails, covering 5161 km², primarily in GNP (Kendall *et al.*, 2008). We visited rub trees 5.26 times on average, with median time between surveys = 15 days. Rub tree sample collections were assigned to 10 sessions based on collection date. The first five rub tree sessions corresponded to hair trap sessions. These were followed by four more 14-day sampling sessions and a final session lasting 21 days.

We genetically analyzed hair samples to determine species, sex and individual identity of bears. Species was determined with the G10J microsatellite (Mowat *et al.*, 2005; Kendall *et al.*, 2009). We determined sex using the SRY marker (Taberlet *et al.*, 1993) and a size polymorphism in the amelogenin marker (Ennis & Gallagher, 1994; Pilgrim *et al.*, 2005). We used six microsatellite loci to determine individual identity: G1A, G10B, G10C, G10L, G10M and G10P (Paetkau *et al.*, 1995). Up to 10 additional loci were analyzed for ≥ 1 sample from each individual to confirm differences between individuals with similar six-locus genotypes. We detected and reduced errors following recommendations in Paetkau (2003), Roon, Waits & Kendall (2005) and McKelvey & Schwartz (2005). For a complete description of genotyping error in our dataset, see Kendall *et al.* (2008 and 2009).

We hypothesized that variables influencing habitat selection would also influence bear abundance. We evaluated the importance of habitat descriptors like vegetation and topography, as well as measures of human disturbance, such as road and human activity density. We examined several indices of the amount and quality of plant food available to bears. The importance of greenness (an index to leaf-area; Crist & Cicone, 1984; Manley *et al.*, 1992), elevation and avalanche chutes (rich in preferred bear foods) have been supported in previous habitat selection and abundance

research (e.g. Mace *et al.*, 1996; Apps *et al.*, 2004). We created the avalanche chute variable by assigning each grid cell with ≥ 3 chutes visible on remote imagery a 1 and cells with < 3 chutes 0. Examination of the study area indicated that the cutoff of three provided a good discrimination of areas with many versus almost no avalanche chutes. We also included two new indices of vegetation. We examined per cent mesic habitat, derived from a remote sensing-based LANDFIRE cover type classification (USDOI, 2007). The cover type map was created from 2001 images, incorporates terrain and climate data (indirect indices of the vegetative component of habitat), describes sub-canopy vegetation, uses most vegetative bear foods as indicator species for the ecological classifications and should be available at 10-year intervals and thus easily available for use in monitoring. To calculate per cent mesic habitat, we extracted all riparian and mesic existing cover types, all of which contained bear foods. We also included precipitation (based on DAYMET climate models; <http://www.daymet.org>) because it will be directly influenced by climate change, and is monitored. Three-dimensional area and terrain ruggedness (Apps *et al.*, 2004) describe the space sampled better than 2-D area and should have a positive relationship with abundance if they greatly increase the quantity or variety of foods at various phenological stages.

Measures of human disturbance that we hypothesized might affect bear abundance by indirectly elevating mortality included: road density (weighted so that roads with higher traffic volumes had higher values) and building density (primarily buildings, but also outfitter camps, mines and other point sources of activity from 1998; USFS, 2005). Bears select against areas of high road density and building density (e.g. Mace *et al.*, 1996; Wielgus, Vernier & Schivatcheva, 2002; Roever, Boyce & Stenhouse, 2010). The negative impact of human presence was also supported by Apps *et al.*'s (2004) study of bear abundance in British Columbia and Nielsen *et al.*'s (2004b) study of bear mortality in Alberta. We hypothesized two additional variables could influence bear abundance: bear protection level and historic mortality. We defined bear protection level based on the strength of regulations enacted to prevent bears from obtaining human food and garbage, enforcement of those regulations and other management efforts designed to minimize human impacts on bears. Bears that associate humans with food often require management removal to ensure human safety and are more vulnerable to illegal killing, so more stringent food storage regulations and greater enforcement of them should reduce grizzly bear mortality. Levels were assigned to ownership types based on expert opinion of bear managers: GNP = 10 (highest level of protection), US Forest Service land = 7, other state and federal agencies and Plum Creek land = 3 and private land = 0. We calculated an index of historic mortality from locations of known human-caused grizzly bear mortalities between 1970 (when consistent records began) and 1999. Bear populations have relatively slow reproductive rates. Thus historic human-caused mortality levels may affect population abundance for an extended period of time.

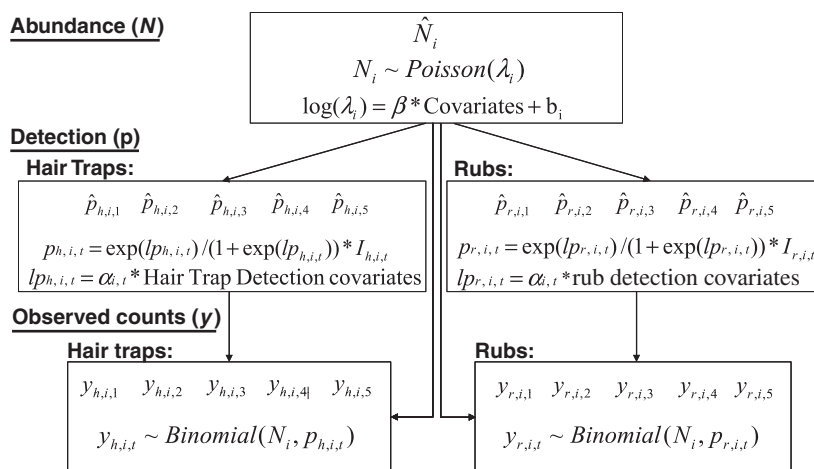


Figure 2 Diagram of the hierarchical model we used to model the influence of landscape characteristics on local grizzly bear *Ursus arctos* abundance in the Greater Glacier National Park study area in northwestern Montana in 2000. Moving from bottom to top, our data consist of observed counts of animals in cell *i*, session *t*, $y_{h,i,t}$ or $y_{r,i,t}$ (depending on sample type; *h*: hair trap, *r*: rub tree). Detection probability, $p_{r,i,t}$ or $p_{h,i,t}$, is modeled as a binomial distribution with the number of trials equal to the estimated number of animals in a grid cell, N_i . A detection probability is estimated for each cell for each session. We assumed the true number of animals in a grid cell followed a Poisson distribution, commonly used to model count data with equal mean and variance. We modeled N as the log of covariates plus a conditional autoregressive term, b_i , to account for spatial autocorrelation with neighbors. Detection is modeled using a logit link to detect covariates and is multiplied by an indicator, $I_{r,i,t}$ or $I_{h,i,t}$, of whether any sampling effort occurred that session, which constrains detection probability to 0 when no sampling occurred. Weights to determine variable importance are not shown here.

We summarized all landscape variables within each 8×8 km grid cell except mortality density, which we calculated within a 14 km-wide moving window because we thought this direct effect on abundance might have a broader area of influence (supporting information I). We used the best available data layers, but all maps are imperfect and as detailed above, some maps reflect the variable 1–2 years apart from our data collection. Our aggregation of cover types over large spatial extents and multiple categories should reduce any misclassification effects. Because we are examining relative abundance, mapping errors would only influence our results if errors are unevenly distributed across the study area, so that the values of summaries across grid cells change relative to each other.

To model spatial variation in bear abundance, we used an N-mixture model (Royle 2004a). We recorded the number of unique bears, $y_{i,t}$, captured in each grid cell, *i* (rows) in each session, *t* (columns) for each sample type: hair trap (*h*) or rub tree (*r*). We analyzed these spatial mark–recapture histories with a hierarchical model (Fig. 2) with two levels. The upper level represents true local abundance, N_i for grid cell *i*. Because we cannot count the true number of bears in the cell, we modeled N_i as random effects, and assumed they were realizations of a Poisson random variable with mean local abundance λ_i .

$$\text{Abundance : } N_i \sim \text{Poisson}(\lambda_i)$$

The lower level represents detection of bears with either hair traps or rub trees and links our counts to true local abundance. We assumed counts were binomial random variables (detected or not) based on true local abundance

and detection probability of either hair traps, $p_{h,i,t}$, or rub trees, $p_{r,i,t}$, for grid cell *i* at session *t*. Counts are linked to abundance because N_i is in both distributions.

$$\text{Detection Hair Trap : } y_{h,i,t} \sim \text{Binomial}(N_i, p_{h,i,t})$$

$$\text{Detection Tree Rub : } y_{r,i,t} \sim \text{Binomial}(N_i, p_{r,i,t})$$

At each level we evaluated whether covariates could explain the response (abundance or detection). The hierarchical approach permits estimation of both levels simultaneously. This approach is analogous to occupancy models, but in the N-mixture model variation in counts between rows (grid cells) informs the estimates of abundance rather than occupancy, while variation in counts between sessions is used to estimate detection. To account for systematic spatial variation of abundance not explained by other covariates, we also included a spatial random effect modeled by a correlated autoregressive (CAR) process. The CAR term, b_i , accounts for correlation in abundance given abundance in adjacent grid cells (Keitt *et al.*, 2002; Webster *et al.*, 2008).

$$\log(\lambda_i) = \beta_0 + \beta_1 \times \text{Covariate 1} + \dots + \beta_{11} \times \text{Covariate 11} + b_i$$

Because sampling methods have different detection probabilities, we modeled detection probabilities (and covariates relating to them) for each sampling method separately, but simultaneously (Fig. 2). We used a logistic function for the detection components of the model. We evaluated whether hair trap effort (traps/cell) influenced detection probability

for hair trap sessions. We examined two detection covariates for rub tree sessions: rub tree effort (cumulative days all rub trees within a cell could collect hair), and Julian day.

$$\text{Hair trap : logit } (p_{h,i,t}) = \alpha_{h0} + \alpha_{h1} \times \text{Hair trap effort}$$

$$\begin{aligned} \text{Rub tree : logit } (p_{r,i,t}) &= \alpha_{r0} + \alpha_{r1} \times \text{Rub tree effort} \\ &+ \alpha_{r2} \times \text{Julian day} \end{aligned}$$

We predicted higher sampling effort would positively influence detection probability. We used mean Julian day of sampling in each rub tree session to model trend in detection through time (Boulanger *et al.*, 2008). Preliminary analysis with this dataset indicated that Julian day was not important for hair trap detection. Because detection probability should equal zero when no sampling occurs, we multiplied the cell-session detection probability by an indicator (sampled or not) to force detection probability to equal 0 when no rub tree or hair trap effort occurred (supporting information II).

$$p_{h,i,t} = \exp(\text{logit}(p_{h,i,t})) / (1 + \exp(\text{logit}(p_{h,i,t}))) \times I_{h,i,t}$$

$$p_{r,i,t} = \exp(\text{logit}(p_{r,i,t})) / (1 + \exp(\text{logit}(p_{r,i,t}))) \times I_{r,i,t}$$

We used a variable identification rather than a model selection approach because we were most interested in selecting appropriate variables for long-term monitoring and management. In addition, in many hierarchical models it is unclear how to count the number of effective parameters, and thus calculate information criteria (Link & Barker, 2010). We identified the most important variables and estimated effects of those variables on detection and abundance using a Bayesian model fitted by Markov chain Monte Carlo (MCMC) in the software package WinBUGS (Lunn *et al.*, 2000). MCMC generates a sample of values from the posterior distribution of each parameter which can be used to obtain point estimates or credible intervals (McCarthy, 2007). When identifying the most important variables using likelihood-based estimation, Burnham & Anderson (2002) recommend comparing all nested sub-sets of the most complex model. In the Bayesian analog, the covariate terms, j , are multiplied by an indicator term, w_j (Kuo & Mallick, 1998; Royle & Dorazio 2008: section 2; O'Hara & Sillanpää, 2009) with a prior Bernoulli distribution ($P = 0.5$). When $w_j = 1$ the covariate was included in the model, when $w_j = 0$ the covariate was excluded from the model. Indicators are kept in the model more often when the likelihood of the variable being in the model is higher. We used a similar indicator, w_{CAR} , to compare models with and without spatial autocorrelation.

$$\begin{aligned} \log(\lambda_i) &= \beta_0 + w_1 \times \beta_1 \times \text{Road Density} \\ &+ \dots + w_{11} \times \beta_{11} \times \text{Mesic Habitat 11} + w_{CAR} \times b_i \end{aligned}$$

If spatial autocorrelation is ignored, sample sizes appear overly large, statistical significance may change, model and variable selection may change and estimates of effect size of a variable may be biased. These problems are most severe when both the response and explanatory variables have high

levels of spatial autocorrelation and results in underestimation of the variance of the sampling distribution of correlation (Richardson & Hemon, 1981). CAR models partition variance due to unmodeled environmental variables that influence abundance (Keitt *et al.*, 2002). In this system, we knew autocorrelation likely existed; bear home ranges, especially for males, extend over areas greater than the size of a grid cell.

The MCMC algorithm explores most nested sub-sets of the variables. The proportion of posterior samples that included the variable in the model, that is, the posterior mean of w_j , can thus be interpreted as the posterior probability that the variable is a component of the model. Variables with weights $> 50\%$ are considered important because this resulting median probability model has optimal predictive properties (Barbieri & Berger, 2004; supporting information II). Similarly, each model is characterized by a binary vector comprised of w_1, w_2, \dots, w_{11} , and w_{CAR} . The frequency of each unique binary vector was tabulated from the posterior simulations which yielded direct estimates of posterior model probabilities (Link & Barker, 2007).

We conducted separate, parallel analyses for male and female bears. We used program R to set up our model and data, and WinBUGS to run the MCMC simulation (supporting information II). WinBUGS was executed from program R (R Development Core Team 2010) with the package, R2WinBUGS (Gelman *et al.*, 2008). We ran three MCMC chains with: (1) randomized starting values; (2) diffuse normal priors with mean = 0 and variance = 10 or 100 (Fig. 3); (3) 10 000 burn-in iterations; (4) $\geq 120\,000$ subsequent iterations. We thinned by 20 to reduce correlation within chains. After identifying the most important variables for the model, we re-ran the best model for each sex to estimate parameters and confirm convergence.

Results

Genetic analysis of the samples from hair traps and rub trees identified 222 unique grizzly bears: 108 males and 114 females. Seventy-one per cent ($n = 809$) of the grizzly bear samples were genotyped to individual. After error checking, all individual bears differed at ≥ 4 loci including the gender locus. The probability of failing to separate two random or closely related individuals was extremely low ($P_{ID} = 0.000006$, $P_{SIB} = 0.007$, respectively; Kendall *et al.* 2008).

For female bear abundance, per cent mesic habitat and road density had posterior probabilities $> 50\%$, while the spatial autocorrelation component had low posterior probability (34.6%; Table 1). In the detection component of the model, rub tree effort was in all iterations after the burn-in. The top model was consistent with these rankings, but had only 21% of the weight (Table 2). As predicted, we found a negative relationship between road density and abundance and a positive relationship for mesic habitat and abundance (Table 3). All 95% credible intervals exclude 0.

For males, road density was the most important variable influencing bear abundance (Table 4). All iterations included rub tree effort and Julian day, with hair trap effort included in 80% of models. The spatial autocorrelation

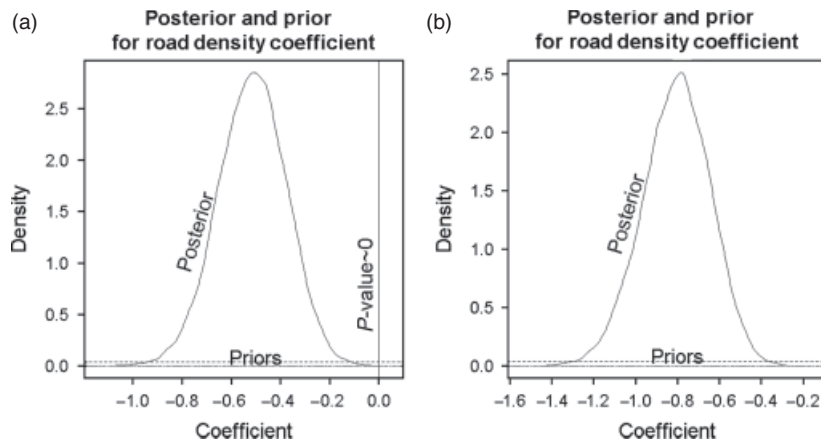


Figure 3 Prior and posterior density estimates of road density coefficient for (a) female and (b) male grizzlies *Ursus arctos* in the Greater Glacier National Park study area in northwestern Montana in 2000. The dashed line represents the prior when variance=10. Densities for variance=100 and are represented with dotted lines. Note that both are essentially flat, so the posterior density is based almost entirely on the data. Based on this analysis, Bayesian *P*-values are <0.01, so we are essentially 100% confident that the true coefficient for road density is <0 for both females and males.

Table 1 Importance (weight) of variables influencing female grizzly bear *Ursus arctos* abundance and detection probability at hair traps and bear rub trees in and around Glacier National Park, MT in 2000 based on hierarchical Markov chain Monte Carlo (MCMC) models

Model	Parameter	Variance = 100			Variance = 10		
		Mean	SD	MC error	Mean	SD	MC error
Abundance	Road density	0.879	0.326	0.018	0.755	0.430	0.021
	Mesic habitat	0.775	0.418	0.021	0.750	0.433	0.019
	Spatial autocorrelation	0.346	0.476	0.029	0.216	0.411	0.025
	Structure density	0.171	0.377	0.018	0.357	0.479	0.018
	Avalanche chute presence	0.158	0.364	0.016	0.385	0.487	0.021
	Terrain ruggedness	0.083	0.275	0.014	0.400	0.490	0.026
	Solar radiation	0.073	0.260	0.014	0.356	0.479	0.026
	Bear protection level	0.059	0.236	0.009	0.212	0.408	0.017
	Precipitation	0.039	0.193	0.006	0.073	0.260	0.005
	Greenness	0.030	0.171	0.006	0.129	0.335	0.012
	Area 3D	0.016	0.125	0.002	0.067	0.250	0.005
Detection: Rub trees	Historical mortality	0.010	0.102	0.001	0.046	0.209	0.003
	Rub tree effort	1.000	0.000	0.000	1.000	0.000	0.000
Detection: Hair traps	Julian day	0.384	0.486	0.009	0.662	0.473	0.007
	Hair trap effort	0.102	0.302	0.004	0.205	0.404	0.006

As each weight can be either 1 or 0 at each iteration, the mean represents the proportion of iterations in which the variable was included in the model. Shading highlights variables present in >50% of models. All parameters have normal priors with variances of either 100 or 10. The precision of the prior for the spatial autocorrelation parameter (τ) is 10 in all cases.

component was included in 63% of the models, supporting its incorporation in final models (Table 2). When priors had less variance (Table 4), precipitation emerged as an important variable, and autocorrelation dropped out. Because we were uncertain of the influence of these variables on abundance, we chose to use important variables identified using the most uninformative priors in the best model. More bears were present where road densities were lower and precipitation was higher (Table 5). All 95% credible intervals exclude 0.

We examined relative abundance of males and females across the study by mapping the posterior medians of

abundance, N_i in each grid cell (Fig. 4a and b). Patterns of abundance were similar to the total number of individual bears detected in each cell across the entire summer ($r = 0.72$ and 0.78 for females and males respectively) even though raw counts did not account for detection probabilities (Fig. 4 and d). Precision of abundance estimates was lowest in cells with highest predicted abundances (females: $r = 0.988$, males: $r = 0.964$). For males, positive spatial autocorrelation was highest along the eastern side of the study area (Fig. 4e). West-central GNP had high predicted abundance and high autocorrelation indicating a cluster of bears beyond the level predicted by our habitat covariates.

Table 2 Support (weights) for models of the effect of human and habitat factors potentially influencing grizzly bear *Ursus arctos* abundance in and around Glacier National Park, MT in 2000

Abundance	CAR ^a	Detection	Weights
Females: variance = 100			
Road density, mesic habitat	No	Rub effort ^b	0.212
Road density, mesic habitat	No	Rub effort, time ^c	0.163
Road density, mesic habitat	Yes	Rub effort	0.073
Road density, mesic habitat	Yes	Rub effort, time	0.038
Road density	Yes	Rub effort	0.037
Females: variance = 10			
Road density, mesic habitat	No	Rub effort, time	0.124
Road density, mesic habitat	No	Rub effort	0.044
Road density, mesic habitat	No	Rub effort, time, HTrap effort ^d	0.034
Road density, mesic habitat, structure density	No	Rub effort, time	0.031
Road density, mesic habitat, avalanche chutes	No	Rub effort, time	0.028
Males: variance = 100			
Road density	Yes	Rub effort, time, HTrap effort	0.353
Road density	No	Rub effort, time, HTrap effort	0.112
Road density	Yes	Rub effort, time	0.101
Males: Variance = 10			
Road density	Yes	Rub effort, time, HTrap effort	0.184
Road density, Precipitation	No	Rub effort, time, HTrap effort	0.131
Road density	No	Rub effort, time, HTrap effort	0.073
Precipitation	No	Rub effort, time, HTrap effort	0.042
Road density, Precipitation	Yes	Rub effort, time, HTrap effort	0.039
Road density, precipitation, solar radiation	No	Rub effort, time, HTrap effort	0.032

We report models up to cumulative weight = 0.5 or top five models. All parameters have normal priors with variances of either 100 or 10.

^aCAR, spatial autocorrelation supported.

^bRub effort, cumulative days all rub trees could detect bears in a grid cell.

^cTime, Julian day.

^dHTrap effort, number of traps in a grid cell.

Discussion

Mesic habitat likely does a better job describing female bear abundance than greenness or precipitation because factors such as precipitation, elevation, slope and aspect that create high greenness values (an index to presence and density of green vegetation) were included in the process that created our vegetation class layer. Managers have little ability to expand the amount of mesic habitat, but could manage for vegetative bear foods. Mesic habitat may be affected by climate change and disturbances such as fires. If large changes occur, the carrying capacity of the area could change, thus monitoring mesic habitat may provide early insight into causes of changes in population abundance.

Road density explained much of the variation in male and female abundance in our study area. This is consistent with earlier nearby habitat selection studies, which found that bears selected against areas with high road density (Mace *et al.*, 1996) or used areas near roads less than expected (Waller & Servheen, 2005). In recent years, land managers such as the Flathead National Forest have closed roads to reduce road density to decrease the risk of grizzly bear mortality and bolster recovery. This study supports the assumption that closing and removing roads may increase the number of bears when mesic habitat and low road density habitat are nearby. Our results also suggest that habitat selection analyses provide a good index of grizzly bear habitat quality in this ecosystem.

Most habitat selection studies assume equal detection rates across habitat types and equal sampling effort (MacKenzie, 2006). Because overall capture rates at hair traps are typically low, most DNA-based studies select sample sites believed to increase the probability of capture (Apps *et al.*, 2004; Kendall *et al.*, 2008; Kendall *et al.*, 2009). However, if detection probability varies by habitat or effort is not equal across the study area, results will likely be biased. In our study, the number of hair samples in hair traps did not correlate well with the number of bears caught in hair traps ($r = 0.459$) and our efforts varied spatially across the study area so it was important to model variability in detection. Inclusion of a second detection method increased our sample size with respect to both sessions and detections of individual bears, likely decreasing the effect of individual heterogeneity on our estimates (Boulanger *et al.*, 2008).

Apps *et al.*'s (2004) examination of the influence of landscape on abundance did not evaluate variation in detection

Table 3 Coefficient estimates for variables in best model for female bears *Ursus arctos* in and near Glacier National Park Montana in 2000

Parameter	Mean	SD	MC error	0.025	Median	0.975
Intercept (M)	1.598	0.775	0.038	0.689	1.401	4.098
Mesic habitat	0.365	0.090	0.001	0.188	0.365	0.540
Road density	-0.806	0.163	0.001	-1.136	-0.801	-0.501
Intercept ($p_{r,i,t}$)	-4.074	0.788	0.038	-6.598	-3.877	-3.142
Rub tree effort	0.617	0.095	0.002	0.456	0.609	0.829
Intercept ($p_{h,i,t}$)	-3.590	0.792	0.039	-6.117	-3.392	-2.660

Estimation used burn-in = 10 000, thin = 20 and total iterations = 120 000. We report estimates where variance of normal priors for all covariates = 100, but parameter estimates were similar when variances equaled 10. The model has three intercepts, one each for abundance (M), rub tree detection probability ($p_{r,i,t}$) and hair trap detection probability ($p_{h,i,t}$).

Table 4 Importance (weight) of variables influencing male grizzly bear *Ursus arctos* abundance and detection probability at hair traps and bear rub trees in and around Glacier National Park, MT in 2000 based on hierarchical Markov chain Monte Carlo (MCMC) models

Model	Parameter	Variance = 100			Variance = 10		
		Mean	SD	MC error	Mean	SD	MC error
Abundance	Road density	0.830	0.376	0.013	0.853	0.354	0.009
	Spatial autocorrelation	0.629	0.483	0.023	0.452	0.498	0.025
	Precipitation	0.286	0.452	0.015	0.537	0.499	0.015
	Bear protection level	0.050	0.218	0.006	0.101	0.301	0.005
	Structure density	0.038	0.191	0.003	0.127	0.333	0.005
	Avalanche chute presence	0.025	0.156	0.003	0.081	0.273	0.003
	Solar radiation	0.021	0.142	0.002	0.113	0.317	0.005
	Historical mortality	0.019	0.136	0.001	0.052	0.223	0.002
	Greenness	0.017	0.128	0.001	0.048	0.213	0.002
	Terrain ruggedness	0.015	0.120	0.001	0.053	0.224	0.002
	Mesic habitat	0.012	0.107	0.001	0.033	0.180	0.001
Area 3D	0.009	0.092	0.001	0.026	0.160	0.001	
Detection: Rub trees	Rub tree effort	1.000	0.000	0.000	0.932	0.252	0.002
	Julian day	1.000	0.000	0.000	1.000	0.000	0.000
Detection: Hair traps	Hair trap effort	0.799	0.401	0.006	1.000	0.000	0.000

As each weight can be either a 1 or 0 at each iteration, the mean represents the proportion of iterations in which the variable was included in the model. Shading indicates variables present in > 50% of models. Variance of the prior for the autocorrelation parameter (τ) is 10.

Table 5 Coefficient estimates for variables in best model (with prior variance = 100) for male bears *Ursus arctos* in Glacier National Park Montana in 2000.

Parameter	Mean	SD	MC error	0.025	Median	0.975
Intercept (N)	1.918	0.438	0.024	1.236	1.854	2.965
Road density	-0.515	0.139	0.002	-0.794	-0.513	-0.250
τ (CAR)	11.130	264.100	5.540	0.575	1.675	15.400
Intercept ($p_{r,i,t}$)	-2.919	0.476	0.026	-4.059	-2.855	-2.172
Rub tree effort	0.568	0.068	0.002	0.441	0.565	0.706
Julian day	-0.436	0.067	0.001	-0.568	-0.436	-0.306
Intercept ($p_{h,i,t}$)	-3.876	0.470	0.026	-4.997	-3.813	-3.129
Hair trap effort	0.284	0.082	0.002	0.132	0.281	0.452

Estimation used for burn-in = 10 000, thin = 20 and total iterations = 120 000. Parameter estimates were similar among different variances of priors for coefficients and for τ . Prior variance for coefficients = 100, prior variance for τ = 10 and prior variance for detection intercepts = 10. The model has three intercepts, one each for abundance (N), rub tree detection probability ($p_{r,i,t}$), and hair trap detection probability ($p_{h,i,t}$).

probability due to effort or habitat, but did assess habitat influences on abundance at multiple scales. Their analyses followed research that investigated the influence of scale on habitat selection (Mace *et al.*, 1996). Because our mark-recapture dataset was sparse, we did not examine this. Other researchers (e.g. Karanth *et al.*, 2004; Garcia & Kittlein, 2005; Mowat *et al.*, 2005) have compared mark-recapture abundance estimates from multiple study areas to understand the habitat-abundance relationships. However, landscape heterogeneity, continuous distribution of bears, large home ranges and relatively low recapture rates do not make this a viable approach for assessing variability in density of grizzly bears within a population or at relatively fine scales.

Model assumptions

Our model assumed that the population of individuals exposed to capture in each grid cell remained constant from

session to session, that is, the number of animals that 'used' the grid cell remained the same (Royle 2004b; MacKenzie *et al.*, 2006). We assumed that movement in and out of each grid cell was random. Although the type and location of grizzly bear foods varied across the summer sampling period, grid cells were large, bears are omnivorous and all grid cells contained some food in all sessions. In this context, estimated abundance for a grid cell represents the relative total number of bears with home ranges that overlap that grid cell. In our study area, even the average female typically occupies multiple grid cells: the average seasonal minimum convex polygon home range of adult females was 231 km² ($n = 40$, range: 42–1199 km²; R. Mace, pers. comm.). Because males have larger home ranges they will be counted in more cells, which explains why predicted male abundance is similar to predicted female abundances although the area has only 40 males for every 60 females overall (Kendall *et al.*, 2008).

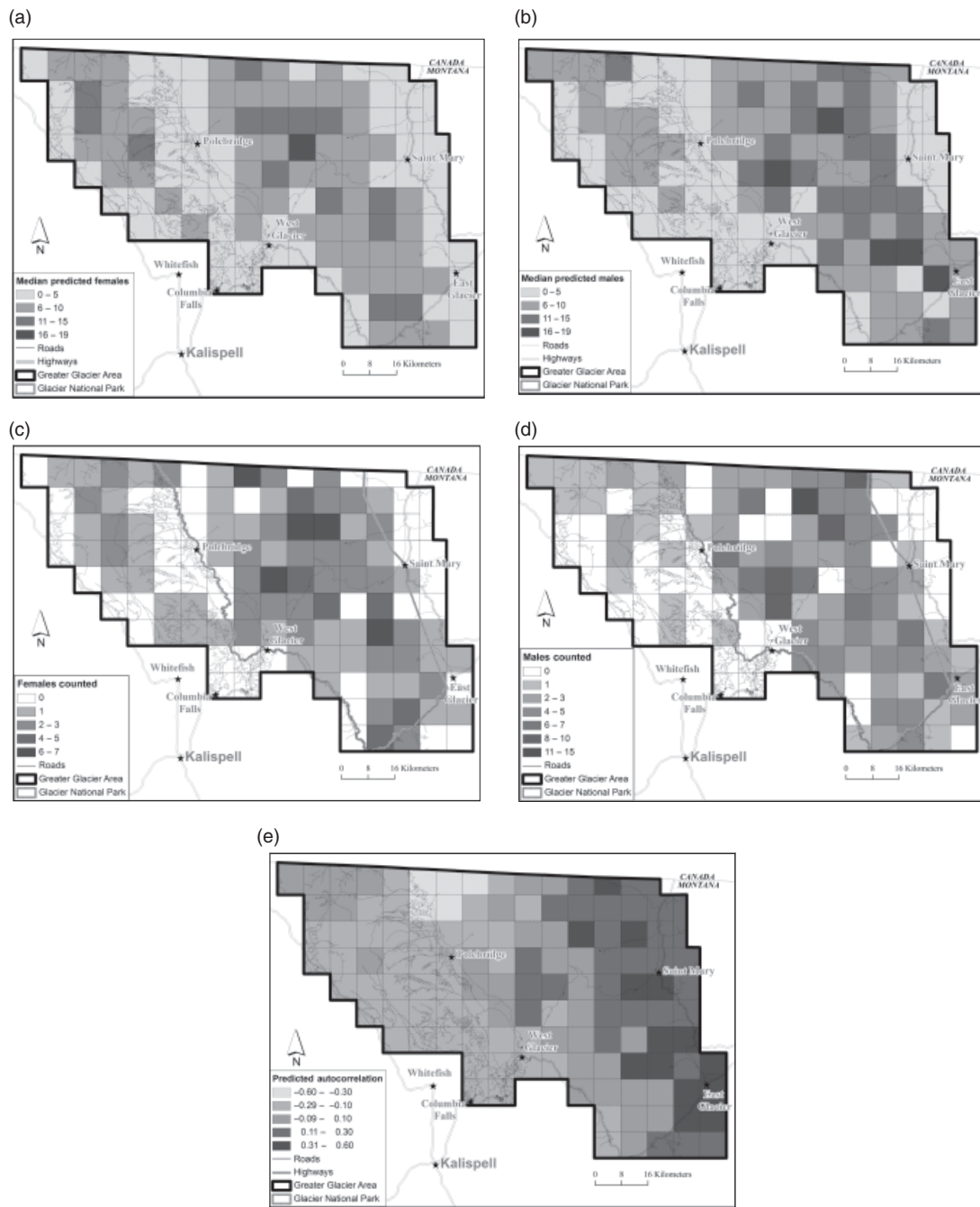


Figure 4 Posterior median of abundance in each grid cell for (a) female and (b) male bears *Ursus arctos* in and near Glacier National Park Montana in 2000. Actual number of individual (c) females and (d) males observed across the summer. (e) Posterior mean autocorrelation for males.

Analyses describing the effect of habitat on population abundance assume abundance is correlated with habitat quality (Van Horne, 1983). From the perspective of providing useful wildlife management insight, this is an improvement over the typical assumption that habitat selection is correlated with habitat quality. Given that bears are typically long-lived and long movements outside of their home-ranges are rare except during dispersal as sub-adults,

abundance is likely a good index of habitat quality. While measurement of reproduction, survival, emigration and immigration rates would detect failure of this assumption directly (i.e. ecological traps; Battin, 2004), abundance can be viewed as the net result of these processes (Nichols & Hines, 2002). Violations of this assumption could occur in areas of high density where less dominant animals are relegated to poorer habitat, which would decrease our

ability to differentiate between high and low quality habitat. Ecological traps could occur around human developments with poor attractant management or poaching (Pulliam, 1988; Nielsen *et al.*, 2006). If these occur, our predictions would be wrong, but other research demonstrates that human presence influences both abundance and mortality (Apps *et al.*, 2004; Nielsen *et al.*, 2004b; Falcucci *et al.*, 2009). We included recorded historical mortality and activity density to address this assumption but we could not account for unrecorded mortality or variable reproduction within the study area, which could mask impacts of previous mortality. If better estimates of mortality, measures of people's attitudes toward bears, or better detection covariates were available, they may describe additional variability in counts, particularly in cells where we observed fewer bears than expected. Examining population change through time and across additional seasons, particularly through the use of an explicit dynamic model may reduce additional heterogeneity resulting from seasonal habitat selection and abundance in previous years (Nichols, 2010).

Model performance

With 125 grid cells, low detection probabilities per grid cell per session, a large number of estimated parameters and 806 of 1250 (64%) rub cell sessions without rub tree sampling effort, our dataset was relatively sparse, which can contribute to slow mixing among chains. Despite our sparse data, the covariates identified as most important and the direction of coefficient estimates were insensitive to different priors and starting values except for precipitation/autocorrelation in the male models as discussed above. Predictions of the relative number of animals were consistent, though relatively imprecise across best models. We believe the slow mixing was primarily due to a high posterior correlation between the intercept terms of the abundance and detection model, that is, insufficient data to separate estimates of abundance and detection, which means our results solely reflect relative abundances. In test simulations where we imputed data to test the effect of missing data, mixing was faster (T. A. Graves, unpubl. data). Therefore, we recommend sampling as evenly as possible across sessions and space.

Maximum likelihood estimation could be substituted for MCMC estimation (Kery, Royle & Schmid, 2005). However, likelihood methods are impractical when the model possesses a CAR component (Diggle, Tawn & Moyeed, 1998) while Bayesian analysis using MCMC simulations have proven effective (Diggle *et al.*, 1998; Royle *et al.*, 2007; Webster *et al.*, 2008). Our approach provided a way of determining whether spatial autocorrelation was an important effect. The degree and nature of spatial autocorrelation of the explanatory variables could change the variables identified as most important. This likely occurred with male model selection using more precise priors. Precipitation explained some of the variation that had been absorbed by the spatial autocorrelation term.

Traditional capture–recapture techniques permit inclusion of spatial data only as a summary for an individual and

inclusion of temporal data only as a summary for a single trapping session. They also typically draw inference from a small proportion of the population. Occupancy studies often sample across a larger area and give insight into distribution, but do not work well where >90% of the area is occupied (MacKenzie *et al.*, 2006) because little difference exists in occupancy across the habitat sampled (Royle & Nichols, 2003; Dorazio, 2007). Occupancy analyses define the limits of distribution and the mechanisms driving occupancy may differ from those driving abundance (Nielsen *et al.*, 2005). Using spatially referenced local counts as the response variable at the population level is analogous to a resource selection or resource utilization function, which describe the relationship of habitat and animal use across a range of values. Therefore, where individual counts can be obtained, greater understanding of the relationship between landscape characteristics and abundance can be realized. This type of information will guide and predict the impact of management efforts in complex systems.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Additional details about creation of covariates used in analysis of grizzly bear local abundance for the year 2000 in the northern third of the Northern Continental Divide Ecosystem in northwestern Montana.

Appendix S2. R code used to identify variables important to local grizzly bear abundance for the year 2000 in the northern third of the Northern Continental Divide Ecosystem in northwestern Montana.

Appendix S3. Supplementary information on the contributions of each author to 'Linking landscape characteristics to local grizzly bear abundance using multiple detection methods in a hierarchical model'.

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