

Spatial Patterns of Breeding Success of Grizzly Bears Derived from Hierarchical Multistate Models

JASON T. FISHER,* MATTHEW WHEATLEY,† AND DARRYL MACKENZIE‡

*Alberta Innovates – Technology Futures, Ecosystem Management Unit, 3-4476 Markham St, Victoria, BC V8Z 7X8, Canada, email jason.fisher@albertainnovates.ca

†Provincial Parks Division, Government of Alberta, Edmonton, AB T7X 3B4, Canada

‡Proteus Research & Consulting Ltd, P.O. Box 5193, Dunedin, New Zealand

Abstract: Conservation programs often manage populations indirectly through the landscapes in which they live. Empirically, linking reproductive success with landscape structure and anthropogenic change is a first step in understanding and managing the spatial mechanisms that affect reproduction, but this link is not sufficiently informed by data. Hierarchical multistate occupancy models can forge these links by estimating spatial patterns of reproductive success across landscapes. To illustrate, we surveyed the occurrence of grizzly bears (*Ursus arctos*) in the Canadian Rocky Mountains Alberta, Canada. We deployed camera traps for 6 weeks at 54 surveys sites in different types of land cover. We used hierarchical multistate occupancy models to estimate probability of detection, grizzly bear occupancy, and probability of reproductive success at each site. Grizzly bear occupancy varied among cover types and was greater in herbaceous alpine ecotones than in low-elevation wetlands or mid-elevation conifer forests. The conditional probability of reproductive success given grizzly bear occupancy was 30% (SE = 0.14). Grizzly bears with cubs had a higher probability of detection than grizzly bears without cubs, but sites were correctly classified as being occupied by breeding females 49% of the time based on raw data and thus would have been underestimated by half. Repeated surveys and multistate modeling reduced the probability of misclassifying sites occupied by breeders as unoccupied to <2%. The probability of breeding grizzly bear occupancy varied across the landscape. Those patches with highest probabilities of breeding occupancy—herbaceous alpine ecotones—were small and highly dispersed and are projected to shrink as treelines advance due to climate warming. Understanding spatial correlates in breeding distribution is a key requirement for species conservation in the face of climate change and can help identify priorities for landscape management and protection.

Keywords: breeding success, climate change, occupancy estimation, spatial distribution, *Ursus arctos*

Patrones Espaciales del Éxito Reproductivo de Osos Pardos, Derivados de Modelos Jerárquicos Multi-Estado

Resumen: Los programas de conservación manejan frecuentemente a las poblaciones indirectamente por medio de los terrenos en los que viven. Enlazar empíricamente al éxito reproductivo con la estructura del terreno y el cambio antropogénico es un primer paso en el entendimiento y manejo de los mecanismos espaciales que afectan a la reproducción de la extinción, pero este enlace no está suficientemente informado por datos. Los modelos jerárquicos multi-estado de ocupación pueden forjar estos enlaces al estimar la aparición de osos pardos (*Ursus arctos*) en las Montañas Rocallosas de Canadá, en la provincia de Alberta, Canadá. Desplegamos trampas-cámara durante 6 semanas en 54 sitios de sondeo en diferentes tipos de cubierta de suelo. Usamos modelos jerárquicos multi-estado de ocupación para estimar la probabilidad de detección, de ocupación por osos pardos y del éxito reproductivo en cada sitio. La ocupación por osos pardos varió entre los tipos de cubierta y fue mayor en los ecotonos herbáceos alpinos que en humedales de baja elevación o bosques de coníferas de elevación media. La probabilidad condicional del éxito reproductivo dada la ocupación fue de 30% (SE 0.14). Los osos pardos con cachorros tuvieron una probabilidad mayor de detección que los osos pardos sin cachorros, pero los sitios fueron clasificados correctamente como ocupados por hembras reproductoras 49% del tiempo basado en datos crudos y así se habrían subestimado a la mitad. Los sondeos repetidos y el modelado multi-estado redujeron la probabilidad de clasificar mal sitios ocupados

por reproductores como desocupados a <2%. La probabilidad de la ocupación de osos pardos reproductores varió a lo largo del terreno. Los fragmentos con la probabilidad más alta de ocupación por reproductores – ecotonos herbáceos alpinos – fueron pequeños y altamente dispersos y se proyecta que se encogerán conforme la línea de árboles avanza debido al cambio climático. Entender correlaciones espaciales en la distribución de la reproducción es un requerimiento clave para la conservación de especies de frente al cambio climático y puede ayudar a identificar prioridades para el manejo y la protección de terrenos.

Palabras Clave: cambio climático, distribución espacial, estimación de ocupación, éxito reproductivo, *Ursus arctos*

Introduction

Life-history characteristics, such as reproduction, survival, and movement, in combination contribute to population persistence. Conservation programs rarely target these characteristics and instead manage populations indirectly through their landscapes. Reproductive success is affected by the quality and spatial distribution of breeding habitat (Pulliam & Danielson 1991; Kurki et al. 2000), so empirically linking variability in reproductive success with landscape structure and anthropogenic change is a first step in understanding and managing the spatial mechanisms affecting reproduction. This link is not sufficiently informed by data because spatially explicit data on breeding success can be difficult to acquire. It is more difficult yet to link these data to landscape change, but this may become increasingly important, particularly as species' ranges—and hence, conservation areas—shift as the climate changes (Lawler et al. 2008, 2009).

Conservation biologists can forge these links by estimating spatial patterns of reproductive success across landscapes with the emerging technique of hierarchical multistate models (Nichols et al. 2007) informed by data from infrared remote camera (IRC) trapping (O'Connell et al. 2010). We used IRCs to survey the occurrence of grizzly bears (*Ursus arctos*) in the Canadian Rocky Mountains of Alberta, Canada. We estimated spatial patterns of grizzly bear breeding success. We defined *breeding success* (or reproductive success) as a grizzly bear with at least one attendant cub in the summer months following den emergence. This is a conservative definition that comes phenologically close to recruitment—a key component of population persistence. We related breeding success to type of land cover in this heterogeneous mountain landscape, including alpine areas that may decrease as the treeline advances as climate warms (Harsch et al. 2009).

Grizzly bears were once pan-continently distributed but their historic range has declined by over half since European colonization; they remain only in the mountain ranges and arctic of western North America (Laliberte & Ripple 2004). The eastern edge of grizzly bears' Canadian range is in the province of Alberta, where they were listed as threatened under the Wildlife Act in 2010 and had an estimated provincial-population size

of 690 individuals (ASRD 2010). Habitat loss and human encroachment into core habitat are likely the primary mechanisms of grizzly bear decline (ASRD 2010). Extensive research has examined grizzly bear population size, resource selection, and mortality (Nielsen et al. 2004a, 2004b, 2004c). Human-induced mortality is a primary cause of death (Benn & Herrero 2002; Nielsen et al. 2004b) and has been spatially linked to road density and motorized access to trails and linear features (Schwartz et al. 2006). Population persistence requires (in conjunction with other demographic parameters) recruitment rates sufficient to offset mortality, but grizzly bears have late primiparity and small, infrequent litters and hence, low reproductive potential (Weaver et al. 1996; Schwartz et al. 2003; Garshelis et al. 2005). In Alberta, a breeding female produces approximately 0.24 female cubs and recruits 0.17 females/year (Garshelis et al. 2005). Cub survival varies markedly across landscapes (Garshelis et al. 2005), and anthropogenic habitat disturbance is implicated.

Breeding success is expected to vary across heterogeneous landscapes, but how it varies remains unknown. Though females are highly philopatric (Weaver et al. 1996; Proctor et al. 2004), they have been known to shift denning in response to human activity (reviewed in Linnell et al. 2000). Further, as the climate warms and treelines advance, key alpine habitat is lost (Harsch et al. 2009). How might these changes affect spatial patterns of breeding success on a wide-ranging species already exhibiting low reproduction? We sought to answer this question by using IRCs and multistate hierarchical models to estimate the spatial fraction of the landscape in which successful grizzly bear reproduction occurs.

IRC's are a popular technique for surveying mammalian occurrence (O'Connell et al. 2006, 2010; Balme et al. 2009). Collection of hair samples for use in noninvasive genetic tagging (NGT) is invaluable for determining grizzly bear population size (e.g., Mowat & Strobeck 2000; Boulanger et al. 2002; Kendall et al. 2009), identifying individuals, and determining sex and genetic distance. However, NGT cannot yet be used to estimate reproductive success (but see Pearse et al. 2001; Kendall & McKelvey 2008). Camera data can inform estimates of breeding success by recording occurrences of grizzly bears with and without young. The challenge in IRC

surveys (as with all surveys) is false absences. When a species is not detected at a site, it may truly be absent or it may be present but undetected (MacKenzie 2005). A species' probability of occupancy at a site (ψ) can be modeled in conjunction with its probability of detection (p): the probability of detecting that species when it is, in fact, present (MacKenzie et al. 2002, 2006). Age-sex classes may also be detected imperfectly when neither age nor sex is known with accuracy. Extending the hierarchical occupancy model, sites can be classified into one of multiple states—such as sites with breeding or without breeding—which may be observed with error. With repeated surveys one can estimate the probability, for each site, that the species is absent, present without breeding, or present with breeding and the probability that a species will be detected in each of the 2 occupied states (Nichols et al. 2007; MacKenzie et al. 2009). We applied this modeling framework to estimate successfully breeding grizzly bear occurrence across a Rocky Mountain landscape.

Mammals are influenced by land cover and ecological processes occurring over large spatial scales (Fisher et al. 2011), so it is likely that breeding success is likewise driven by landscape-scale habitat composition and disturbance. Identifying components of the landscape that support successful reproduction remains a key next step in conserving grizzly bear populations (e.g., Schwartz et al. 2006). This may be particularly true in mountainous landscapes, which are important grizzly bear refuges but which face increasing political and social pressure for recreational and industrial development, as well as the threat of landscape change from climate warming. We expected grizzly bear breeding success to be spatially structured in several ways. First, grizzly bear occupancy may vary among types of land cover (Nielsen et al. 2004a, 2004b, 2006). Second, breeding success may differ among land cover types, and breeding-bear occupancy is expected to reflect these differences. Third, detectability may be influenced by site fidelity. Grizzly bear sows with cubs are expected to display greater site fidelity (Weaver et al. 1996; Proctor et al. 2004) than bears without cubs, so we expected that breeding bears would have greater detectability. Fourth, experimental design can markedly affect the detectability of species (Hirzel & Guisan 2002; McDonald 2004), particularly in highly heterogeneous mountain landscapes with rare, clustered types of land cover. We expected that a stratified design targeting rare types of cover would result in greater detectability for both states.

We surveyed grizzly bears with IRCs deployed in 2 study designs: a systematic design and a stratified design based on remotely sensed land cover. We used hierarchical multistate models to estimate occupancy and detectability of breeding and nonbreeding bears and tested the following hypotheses: the probability of detecting grizzly bears is greater under a stratified sampling de-

sign than under a systematic sampling design; the probability of detecting grizzly bears varies among breeding states, through time, and spatially across land-cover types in a mountain landscape; and the probability of occupancy by grizzly bears in different breeding states varies spatially across land-cover types in a mountain landscape.

Methods

Study Area

We surveyed grizzly bear occurrence in the Rocky Mountains of west-central Alberta within the Willmore Wilderness Park (Fig. 1). The Willmore is a 4600-km² conservation area protected from forest harvesting, mining, seismic exploration, and roads. Public access is restricted to hikers or equestrians. The Willmore has one of the highest densities of grizzly bears in the province (ASRD 2010). Topography is rugged, with high peaks, steep-sloped ridges, and valley bottoms. Summers are cool with short growing seasons. Winter snow accumulation can exceed several meters. Alpine areas are characterized by mountain meadows of herbs and shrubs. Subalpine slopes are forested by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Lowland valley bottoms are wet and characterized by black spruce (*Picea mariana*) with extensive shrub cover.

Study Design

We implemented 2 overlapping sampling designs. First, we established a systematic sampling grid across the Willmore: 30 sampling points spaced approximately 12.3 km apart (Fig. 1). Topographic and vegetation diversity is greatest along the east-west gradient, and the grid was designed to capture this diversity. Second, we deployed 30 additional points within a stratified sampling design. This design was based on a LandSat thematic-mapped GIS land cover data set developed for grizzly bears that incorporated digital elevation models (DEMs) classified with a habitat-identification algorithm (McDermid et al. 2009). This data set yielded 16 potential habitat types, such as dense-, moderate-, and open-conifer forest; mixedwood forest; shrub-dominated areas; herbaceous-dominated areas; and regenerating areas (including both anthropogenic-origin and recently burned forested stands).

We used GIS-based systematic habitat-representation trials to calculate the probability that any given land-cover type would be sampled in a systematic design (data not shown) and identified 2 rare land-cover types—wetlands and herbaceous alpine ecotones—that were consistently undersampled in these trials. Wetlands included open and treed wetlands in high altitude depressions and in

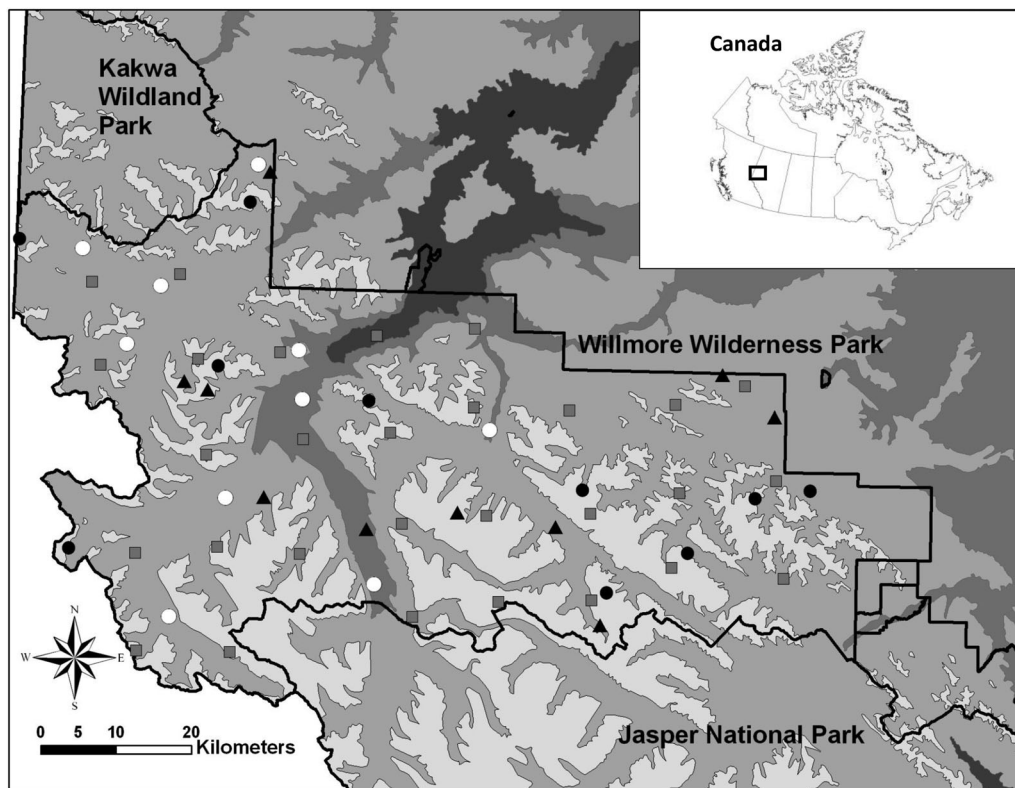


Figure 1. Willmore Wilderness area of the front and main ranges of the Rocky Mountains in west-central Alberta, Canada, where camera-trap surveys for grizzly bears were conducted. Surveys were of 2 sampling designs: a systematic design (squares) and a 3-stratum design based on remotely sensed land-cover types designated as alpine herbaceous patches (black circles), wetlands (white circles), and other (triangles, predominately conifer forest).

valley bottoms. Herbaceous areas included the relatively narrow ecotone between higher-elevation sub-alpine forests and rocky alpine patches. Both land covers differed from the upland conifer forests that dominate the region. We, therefore, identified 3 strata: wetlands, herbaceous areas, and other. The last broad category included all remaining land-cover classes but was dominated by conifer forests, so we refer to it as conifer forest. We reclassified the 16 land covers into these 3 categories. Herbaceous habitats covered 7% of the study landscape, wetlands covered 6%, and conifer forests covered 48%. We randomly assigned 10 sampling points to each stratum (Fig. 1). We surveyed half of all points (systematic and stratified) in June–August 2009 and the other half in June–August 2010. Sites were randomly assigned to years.

Grizzly Bear Detection and Analysis

We deployed one Reconyx PM30 or PM85 IRC (Reconyx, Holmen, WI, USA) at each site. We baited sites with approximately 50 mL of scent lure (O’Gorman’s, Broadus, MT, USA). Our data set consisted of 6 repeated surveys (6 weeks) from date of deployment. We assumed sites occupied by grizzly bears could exist in 1 of 2 true states:

occupied by grizzly bears without cubs (i.e., singles) or occupied by grizzly bears with cubs (i.e., breeders). Singles included both males and females because gender could not be discerned. Occurrence of grizzly bears without and with cubs were recorded from photographs (Supporting Information) and summed over weeklong survey periods. We used hierarchical models in the software Presence (version 4.2, build 120217.1107; Hines 2006) to estimate grizzly bear occupancy (ψ), detectability (p), and breeding state (R), where ψ_i is probability that site i is occupied, regardless of reproductive state; R_i is conditional probability that young occurred, given that site i is occupied; $\psi_{i(\text{breeding})}$ is unconditional probability that site i is occupied with breeding = $\psi_i * R_i$; $p(1)_{it}$ is probability that occupancy is detected for site i , period t , given that true state = 1; $p(2)_{it}$ is probability that occupancy is detected for site i , period t , given that true state = 2; and δ_{it} is probability that evidence of successful reproduction is found, given detection of occupancy at site i , period t , and successful reproduction (Nichols et al. 2007).

Hierarchical occupancy models can be considered simultaneous generalized linear models of serial detection data that are applied to each component of the model (i.e., p , ψ , and R) with binomial errors (logistic link) and fit using maximum likelihood. The study area

Table 1. Selection of single-state occupancy models of grizzly bears in the Rocky Mountains of the Willmore Wilderness in Alberta, Canada.

Model ^a	AIC ^b	Δ AIC	AIC weight	Model likelihood	No. para ^c	$-2LL^d$
ψ (land cover), p (trend)	209.13	0.00	0.49	1.00	5	199.13
ψ (land cover), p (trend + design)	210.00	0.87	0.32	0.65	6	198.00
ψ (.), p (trend)	211.47	2.34	0.15	0.31	3	205.47
ψ (land cover), p (.)	215.51	6.38	0.02	0.04	4	207.51
ψ (land cover), p (design)	216.42	7.29	0.01	0.03	5	206.42
ψ (.), p (design)	217.73	8.60	0.01	0.01	3	211.73

^aOccupancy (ψ) was either constant (.) or varied by land cover; probability of detection (p) was constant (.), varied with survey design, or varied by a linear trend through time.

^bAkaike's information criterion.

^cNumber of parameters in the model.

^dDeviance is $-2 \log$ likelihood of the model.

was assumed to be closed to species-level changes in distribution during the 6-week survey, an assumption solidly supported by camera data. With no evidence of any intraseasonal change in grizzly bear distribution in the region (ASRD 2010), models assumed that movement among sites was non-Markovian (MacKenzie et al. 2006). The models also assumed static breeding state at the species level. Cub loss is unlikely (though possible) over 6 weeks, but all breeders at a site would need to lose all of their cubs to change the breeding state of that site. Finally, camera data showed that the probabilities of detection and occupancy were independent among sites.

We conducted 2 analyses to investigate the effect of modeling 1 state (grizzly bear occupancy) versus 2 states (occupancy by grizzly singles or breeders) on conclusions about landscape use by bears. In the single-state analysis, we created competing models that assumed ψ was either constant or varied among land-cover types and that p was either constant, varied among experimental designs, varied in a trend through time, or both. In the multistate analysis, we created competing models that assumed ψ was either constant or varied among habitats; that R was either constant or varied among land-cover types, independently of ψ ; and that p_1 and p_2 were either constant, varied among experimental designs, varied in a trend through time, or varied among designs and through time.

Each model's Akaike's information criterion (AIC) score measured support for the model based on deviance explained ($-2 \log$ likelihood) and the number of parameters in the model (Burnham and Anderson 2002; Anderson 2008). We ranked each model by AIC weight (AIC_w), a normalized AIC score calculated for each model within a candidate set. We summed AIC_w and calculated evidence ratios (ER) (Anderson 2008), which describe the importance of each covariate relative to the candidate set of models; $ER = 2$ suggests there is twice the evidence for inclusion of an explanatory variable than its exclusion. We calculated model-averaged parameter estimates from top-model sets by rescaling $\sum (AIC_w) = 1$ and summing each model's contribution to the parameter estimate and its standard error (Burnham & Anderson

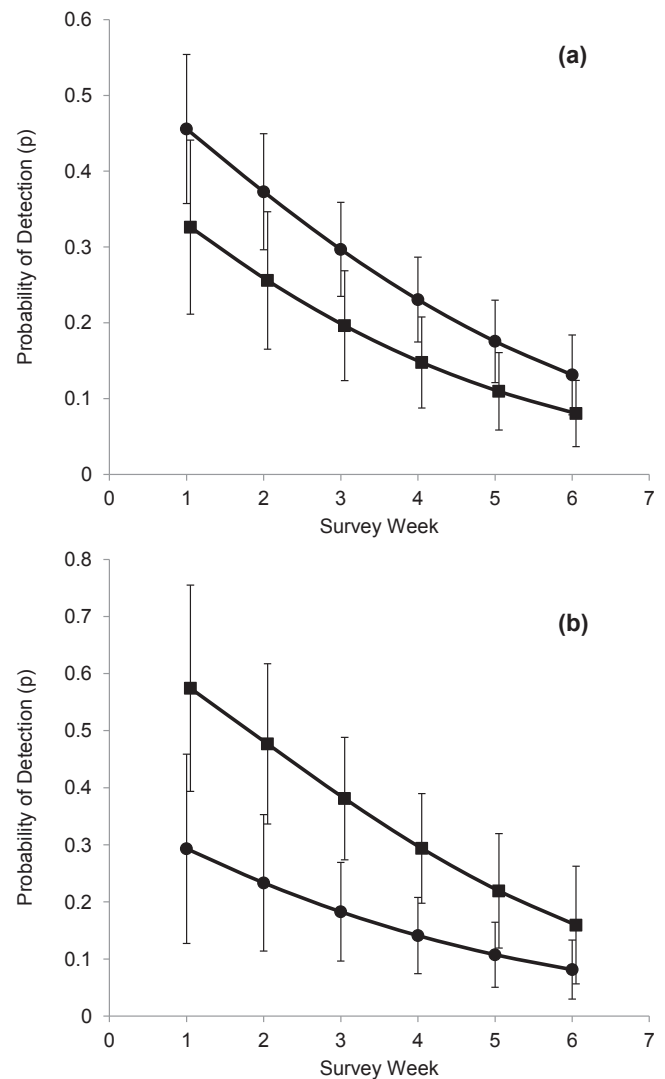


Figure 2. The probability of detecting a grizzly bear, given it was present, in the Rocky Mountains of Alberta, Canada, (a) without discerning breeding state (circle, stratified experimental design; square, systematic sampling design) and (b) in sites with single individuals (circles) and breeders (squares).

Table 2. Selection of multistate occupancy models of grizzly bears in the Rocky Mountains of the Willmore Wilderness in Alberta, Canada.

<i>Model^a</i>	<i>AIC^b</i>	<i>ΔAIC</i>	<i>AIC weight</i>	<i>Model likelihood</i>	<i>No. para^c</i>	<i>−2LL^d</i>
ψ (land cover), R , $p1$ (trend + design), $p2$ (trend + design), δ (.)	253.67	0.00	0.30	1.00	11	231.67
ψ (land cover), R , $p1$ (trend), $p2$ (trend), δ (.)	254.20	0.53	0.23	0.77	9	236.20
ψ , R (land cover), $p1$ (trend), $p2$ (trend), δ (.)	254.86	1.19	0.17	0.55	9	236.86
ψ , R , $p1$ (trend), $p2$ (trend), δ (.)	256.54	2.87	0.07	0.24	7	242.54
ψ (land cover), R (land cover), $p1$ (trend), $p2$ (trend), δ (.)	257.15	3.48	0.05	0.18	11	235.15
ψ , R (land cover), $p1$ (design), $p2$ (design), δ (.)	257.43	3.76	0.05	0.15	9	239.43
ψ (land cover), R , $p1$ (design), $p2$ (design), δ (.)	258.07	4.40	0.03	0.11	9	240.07

^aOccupancy (ψ) and conditional probability of occupancy with breeding (R) was either constant (.) or varied with land cover. Probability of detection of grizzly bear singles ($p1$) and grizzly bears with cubs ($p2$) was constant (.), varied with experimental design, or varied by a linear trend through time.

^bAkaike's information criterion.

^cNumber of parameters in the model.

^dDeviance is $-2 \log$ likelihood of the model.

2002). The probability of breeding-site misclassification through the 6 weeks of camera trapping was calculated as $\Pi (1-p2[t]*\delta[t])$, $t = 1:6$. We multiplied unconditional breeding occupancy estimates (ψ_{breeding}) by the percent cover of each land-cover type in the Willmore Wilderness to estimate the proportion of the landscape occupied by successfully breeding females.

Results

Fifty-four sites were successfully surveyed. Camera loss and malfunctions and logistics prevented collection of data at the other 6 sites. Grizzly bears were photographed at 21 (39%) sites; of these, cubs were photographed at 6 sites (29%). In all events involving cubs, both mother and cubs were observed (Supporting Information).

When we modeled occupancy and detectability for all grizzly bears without discerning breeding state, grizzly bear occupancy varied among land-cover types (ER = 3.17; Table 1). Model-averaged estimates indicated that grizzly bears were more likely to occur in patches of herbaceous cover ($\psi = 0.73$, SE 0.14) than in wetlands ($\psi = 0.40$, SE 0.17) or in conifer forests ($\psi = 0.29$, SE 0.12). Grizzly bears' detectability varied in a trend through time (ER = 13.97; Table 1). It was highest immediately upon deployment of the cameras and decreased weekly (Fig. 2a). Detectability under the stratified sampling design was always greater than under the systematic sampling design, though the 2 sampling designs had overlapping standard errors (Fig. 2a) and low model support (ER = 0.50).

When we modeled sites in 2 states—occupied by grizzly bears with or without cubs—strong evidence showed a temporal trend in detectability (Table 2; ER = 4.61). The probability of detecting a single grizzly and of detecting a grizzly with cubs declined each survey week (Fig. 2b). The probability of detecting breeding bears' occupancy at a site was greater than for nonbreeding bears (Fig. 2b).

There was low model support that $p1$ or $p2$ varied among experimental designs (ER = 0.72). Modeling of pilot data (J.T.F., unpublished data) showed no evidence that p varied with land-cover type, so this was omitted from candidate models.

Multistate models showed total occupancy (ψ) varied among land-cover types (ER = 1.91; Table 2) and weakly showed that R —the conditional probability of breeding occurring given occupancy—varied among land-cover types ($R = 0.30$, SE 0.14; ER = 0.33). Model-averaged estimates of unconditional occupancy, ψ_i , (SE) were 0.81 for herbaceous cover (0.24), 0.47 for conifer forest (0.30), and 0.54 for wetlands (0.30). Multiplying ψ and R , both grizzly bear singles and grizzly bears with cubs were more likely to occur in patches of herbaceous cover than in wetlands or conifer forests (Fig. 3a). Sites were more likely occupied by single breeders. Herbaceous patches had the highest breeding occupancy, 24%, and were more likely to be occupied by grizzly bear with cubs than were wetlands and conifer forests (Fig. 3a).

The model-averaged estimate of the conditional probability that a site would be correctly assigned as being occupied by a breeder (δ) was 0.49 (SE 0.19). The distribution of breeding females was underestimated by about half when only raw camera data were used. The probability of misclassifying sites occupied by breeders dropped from 51% in week 1 to < 2% in week 6 (Fig. 3b). Approximately 16% of the Willmore Wilderness was occupied by breeding grizzly bears. The spatial distribution of habitats occupied by breeding bears was highly heterogeneous (Fig. 4).

Discussion

Grizzly Bear Breeding Success

Grizzly bears live at high densities in the Rocky Mountains' Willmore Wilderness relative to the rest of Alberta

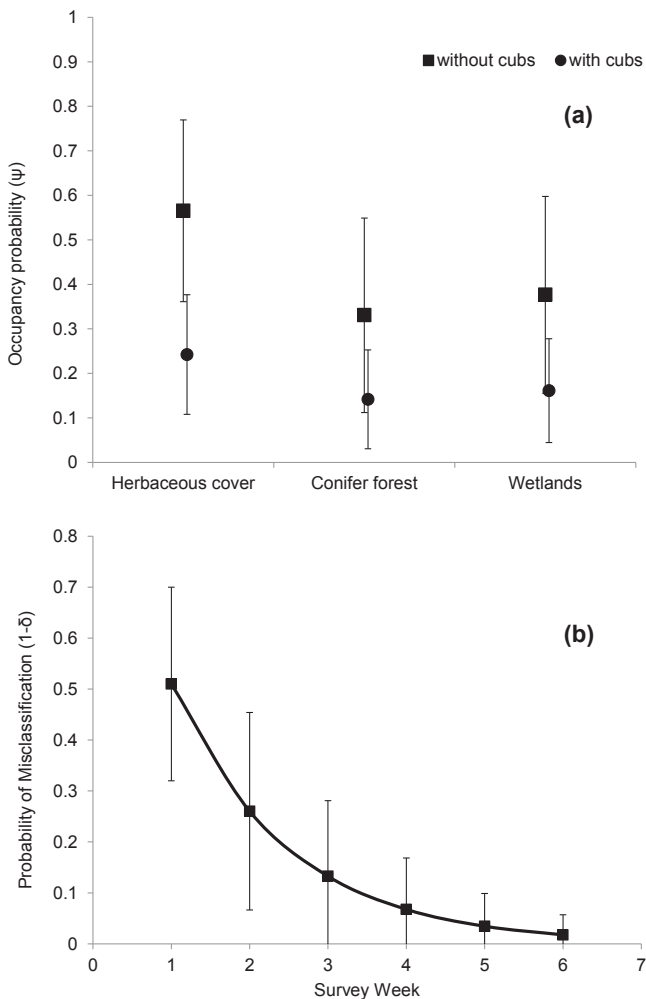


Figure 3. (a) The occupancy probability of grizzly bears with and without cubs based on hierarchical multistate occupancy models of camera-trapping data and (b) the probability of misclassifying a grizzly bear breeding site as nonbreeding, given detection of occupancy at a site (the δ parameter with standard errors shown).

(ASRD 2010), and this was reflected in the high occupancy rates we observed; occupancy is (in part) a product of density (Mackenzie et al. 2002, 2006). Grizzly bears were widespread throughout the study area, occurring in herbaceous ecotones, conifer forests, and wetlands. However, among these land-cover types, we observed marked temporal and spatial variability in occupancy and detectability for both grizzly bear singles and breeders.

Sites were occupied by single grizzly bears twice as often as by females with cubs. Herbaceous land cover was most highly selected (i.e., occupied with highest relative probability) by breeders relative to other land-cover types, suggesting these open alpine meadows were particularly important for the breeding population. Breed-

ing grizzlies occupied wetlands more often than conifer forests, emphasizing the importance of these rarer habitat types in this mountain landscape. Multiplying occupancy rates in each land-cover type by their frequency in the landscape, we estimated that less than one-fifth of this protected mountain landscape is occupied by breeding female grizzly bears—a small percentage for one of the province's most populous protected mountain landscapes.

Alpine ecotones with high breeding success were highly dispersed in this landscape (Fig. 4). Moreover, these alpine ecotones have been significantly reduced from past historical landscape change because treelines are higher in elevation (reviewed in Harsch et al. 2009; Supporting Information). As the climate warms, treelines are expected to continue advancing in altitude (Grace et al. 2002), further reducing these small and isolated patches. The sum impact of shrinking alpine habitats on grizzly bear population persistence has yet to be comprehensively modeled and understood, but we hypothesize that as habitats with highest breeding success are lost, then reproductive potential may drop across the landscape unless success in other habitats concomitantly increases.

Spatial differences in occupancy between breeders and singles may reflect differential resource (food) selection between the 2 groups; alternatively, they may reflect interspecific processes, such as spatial segregation of females with cubs from adult males (e.g., Wielgus & Bunnell 2000). Spatial patterns of breeding success estimated from multistate models provide a scientific basis for future investigation of underlying mechanisms. We used simplistic land-cover categories to illustrate the ecological applications of this technique; higher-resolution GIS analysis can produce more detailed occupancy estimates across a greater range of habitat types.

Probability of Detecting Breeding Grizzlies

Maximizing p is a key goal of an occupancy survey (Bailey et al. 2007). Providing a novel olfactory cue brings individuals into the detection radius of an IRC, thus increasing p . Probability of detection declined through time, irrespective of breeding state. This trend is consistent with detection probability for other mammals (J.T.F., unpublished data). Two possibilities emerge: scent-lure efficacy decreased through time or bears investigated the novel olfactory cue (Doty 1986) then became habituated over time. We expect that habituation is more likely because even human noses could detect the lure after 6 weeks.

Stratifying the landscape increased p for grizzly bears in both states. This effect was not strong but was consistent among models and similar for other mammals (J.T.F., unpublished data). We posit that p may vary with sampling design due to differing site fidelity among

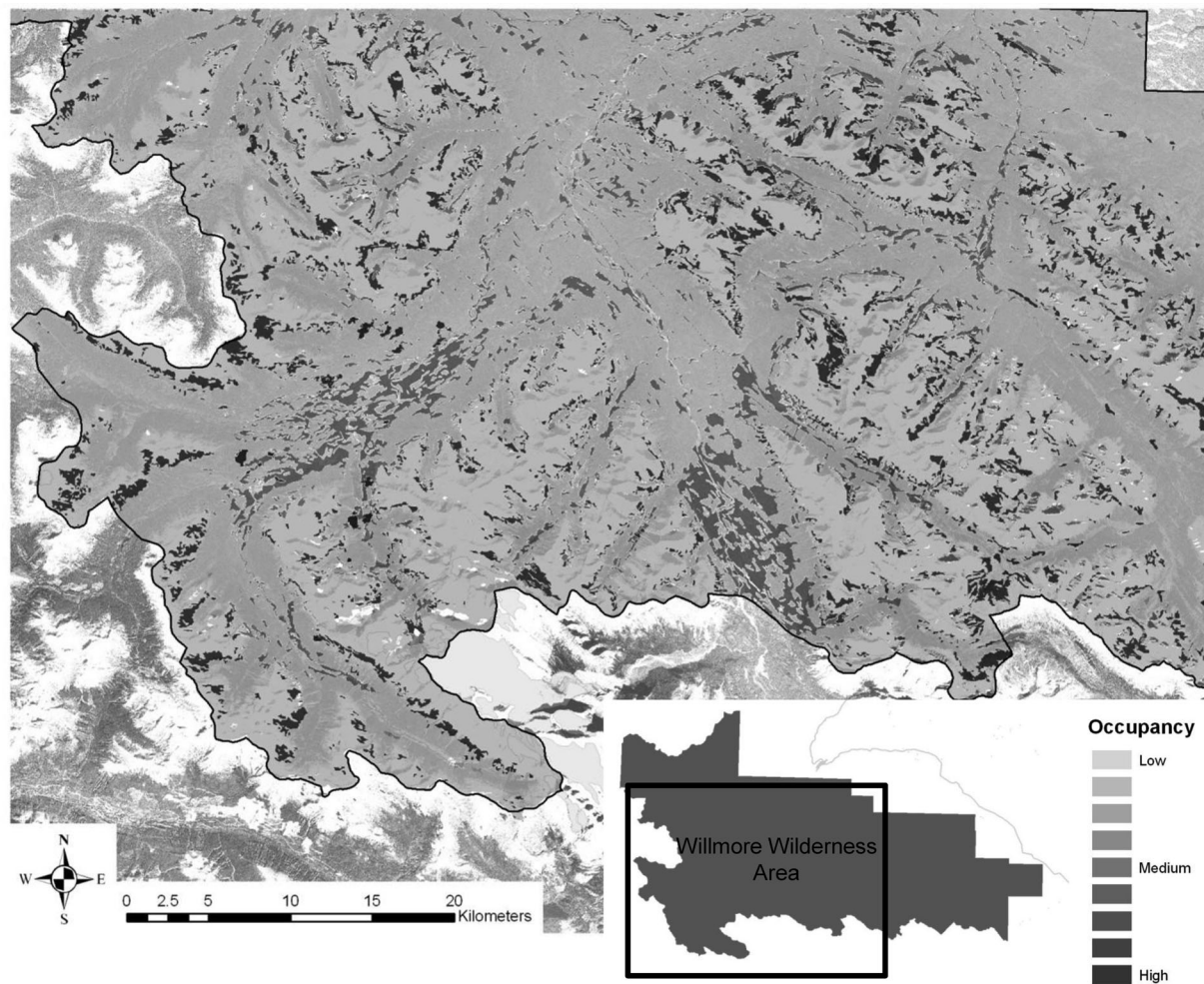


Figure 4. Relative probability of breeding grizzly bear occupancy across habitat types in the mountain landscape of the Willmore Wilderness, Alberta, Canada. Occupancy estimates range from 0.14 (low) to 0.24 (high).

habitats. Individuals move on and off survey sites, and this movement is assumed to be nonMarkovian (MacKenzie et al. 2006), an assumption borne out by our imagery data. Where site fidelity is high, repeat visits are more likely. With greater variability among land-cover types (and by inference, habitat quality) in the systematic design than the stratified design, lower site fidelity among land-cover types may have contributed to the lower detectability on the systematic grid. Singh et al. (2009) also found that a stratified-random design improved estimates from surveys of Tibetan argali (*Ovis ammon*) in mountain landscapes. Hirzel and Guisan (2002) found that an equal-strata design provides model estimates that are more robust and precise than a proportional-strata design for simulated data. Similarly, breeding grizzly bears were more detectable than single grizzly bears, possibly due to relatively higher site fidelity in mothers with cubs (Weaver et al. 1996; Proctor et al. 2004) than with nonbreeders. The effect of variability in home-range size (which changes among individuals and as

cubs mature) on species' detectability has yet to be researched.

Multistate Hierarchical Models for Conservation Biology

Hierarchical multistate models informed by camera-trapping data make it possible to estimate, map, and analyze spatial patterns of successful breeding. We used grizzly bears as an example, but this approach has applications for any mammalian species detectable via camera trapping for which young remain with the mother through the sampling period. Moreover, this method is transferable to myriad other ecosystems and to multiple species because IRCs survey multiple species simultaneously (Fisher et al. 2011).

The importance of accounting for imperfect detections of young in remote surveys is highlighted by our example. We found that grizzly bears with cubs were correctly identified in IRC surveys only about half of the time when we used raw camera data. Estimation of breeding

state (Nichols et al. 2007; Mackenzie et al. 2009) is, thus, critical to IRC-based monitoring of occupancy and reproduction. Unless effort is made to estimate the undetected component of sites occupied by successful breeders, determining fecundity, and population growth rates through remote surveys may be negatively biased. State estimation provides the additional advantage of allowing spatially explicit inferences about the distribution of successfully breeding females, providing a platform for inferences about those spatial mechanisms that facilitate—or inhibit—recruitment.

We demonstrated the application of IRC data and multi-state models to estimating breeding success, but more opportunities exist to examine demographics. Combining state estimates with NGT-derived abundance data (e.g., Boulanger et al. 2002, 2006; Kendall et al. 2009), may allow estimates of recruitment. Alternatively, if individuals could be identified from photographs (Mace et al. 1994), or if GPS-collared animals occurred within the camera array, then hierarchical Bayesian analysis (Royle et al. 2009, 2011) could be applied to estimate population size and the number of breeding females. If more information could be garnered from photographs—such as multiple age classes, sex, lactation status of marked individuals—these data could help refine spatial patterns of breeding success across the landscape. Multiple data sources, such as combining cameras and NGT (Fisher et al. 2012; J.T.F., unpublished) would overcome some of the limitations of camera-only data. Informed by such spatial data, multistate hierarchical models allow one to partition variance among multiple demographic states and identify landscape elements that maximize reproduction—a long-recognized component of conservation (Shaffer 1981) not always implemented in conservation policy.

Applications for Conservation

Landscape changes have been prevalent over the last century (Laliberte & Ripple 2004); climate models suggest more significant changes are coming (Grace et al. 2002; Harsch et al. 2009). Landscape changes can directly impact mammalian populations, which, in turn, can affect entire ecosystems (Terborgh & Estes 2010; Estes et al. 2011). Conservation policy is often aimed at managing landscape change, either through restoration, mitigation, or protection (Lawler et al. 2008; Hole et al. 2011), so linking demography and landscapes is vital. However, for many species an understanding of the linkages between spatial habitat complexity and population vital rates has arrived late and is now limited to documenting the tail end of a long-term population decline. The shape of that tail—further decline, stabilization, or increase—depends on scientifically based management of populations and their landscapes that aims to stem mortality and facilitate reproduction.

In a protected Rocky Mountains landscape—one of the most densely populated grizzly-bear areas remaining in this edge of its range—about one-fifth is currently occupied by breeding females. Patches with highest breeding occupancy were small and highly dispersed in this heterogeneous mountain ecosystem and are expected to shrink as a result of climate warming. Losing some of these patch types may lower mean grizzly bear breeding success across the entire landscape. Estimating spatial patterns of breeding success and its correlates is a necessary precursor to understanding the demographic spatial structure of a population—a key requirement for conservation policy that aims to maximize breeding success and conserve species affected by past and future landscape change.

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Supporting Information

A camera-trap photograph of a grizzly bear female and cub (Appendix S1) and repeat imagery of Jones Pass, Alberta, in the central Rocky Mountains in 1923 (left; Wheeler Survey, Library and Archives Canada) and in 2008 (right; Mountain Legacy Project, University of Victoria) showing treeline advance (Appendix S2) 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.

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