Relationships between grizzly bears and human disturbances in a rapidly changing multi-use forest landscape

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ABSTRACT

Grizzly bear (*Ursus arctos*) populations across their range are being threatened by anthropogenic development and associated increases in human-caused mortality. However, details surrounding the impact of cumulative human effects are not yet fully understood, as prior research has focused primarily on habitat selection of individual disturbance features, rather than the spatio-temporal dynamics of aggregated disturbance processes. We used grizzly bear relative-abundance information from a DNA population inventory alongside a GIS database of human footprint dynamics to gain insight into the relationships between human disturbance features and the spatial distribution of grizzly bears in west-central Alberta, Canada: a landscape experiencing heavy resource development. We used candidate model-selection techniques and zero-inflated Poisson regression models to test competing hypotheses about disturbance processes, neighborhood effect and landscape characteristics. The best model explained about 57% of the overall variation in relative grizzly bear abundance. Areas with lower 'disturbance exposure' (i.e. high mean distance to new disturbances over time), lower 'neighborhood disturbance' (i.e. disturbance density around those areas), and higher 'availability of regenerating forest', were associated with higher bear abundance. In addition, areas located further away from an adjacent protected area exhibited a higher probability of 'excess absences', accounting indirectly for the cumulative effects of disturbance and the history of human-caused mortality. Our results suggest that managing the spatio-temporal exposure of grizzly bears to new disturbance features may be an important consideration for conserving this species in rapidly changing landscapes.

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1. Introduction

Landscape modification through human-induced disturbance is a key driver of contemporary habitat loss and fragmentation, represents an ongoing threat to wildlife species, and contributes to the decline of biodiversity throughout the world (Saunders et al., 1991; Lindenmayer and Fischer, 2006; Krauss et al., 2010). The growing availability of satellite image-based time series (e.g. Woodcock et al., 2008) and the development of new strategies for handling these image data sets effectively (Linke et al., 2009; Linke and McDermid, 2011) provide new opportunities for multi-temporal remote sensing, which is broadly defined as a set of analysis techniques involving two or more time intervals, enabling the characterization of trends and dynamics of landscape modification (Gillanders et al., 2008; White et al., 2011). Such multi-temporal landscape perspectives can enhance our understanding of the relationships between species occurrence or abundance and the presence and/or extent of *disturbance features* (Burton, 2007) on the landscape; collectively referred to as the *human footprint* (Janzen, 1998; Leu et al., 2008).

In the multi-use forested regions of western Alberta, Canada, anthropogenic disturbance features associated with oil and gas extraction, forestry, and coal mining exert a strong influence on this rapidly changing landscape (Linke and McDermid, 2012; Schneider, 2002). In these same regions, grizzly bear (*Ursus arctos*) populations have been suggested to be in decline (ASRD/ACA, 2010) and the species is now officially listed as *threatened* under provincial legislation. Habitat alteration by anthropogenic development and the accompanying increase in human access are the main issues of concern for this species both in Alberta (Gibeau et al., 2002; Nielsen et al., 2004c; Roever et al., 2010) and throughout its other habitats in western North America and Eurasia (Fernández et al., 2012; Naves et al., 2003; Proctor et al., 2012).

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Whereas grizzly bears are generally thought to avoid disturbance features associated with human activity, such as towns (Martin et al., 2010; Nellemann et al., 2007), transportation corridors (Graves et al., 2011; Kaczensky et al., 2003; Wielgus and Vernier, 2003), and forestry clearcuts (Waller, 1992; McLellan and Hovey, 2001), recent studies have observed instances of preferential selection for roads (Roever et al., 2010; Northrup et al., 2012) and regenerating clearcuts (Apps et al., 2004; Nielsen et al., 2004a,b), mainly due to the availability of high-quality forage in these locations, which act as attractants (Munro et al., 2006; Nielsen et al., 2010; Roever et al., 2008). With active fire suppression having led to reduced availability of young forest stands throughout western North America (Payne, 1997), regenerating clearcuts may offer a surrogate for early seral-stage stands normally created by natural disturbances (Nielsen et al., 2004a, 2008). Together with nearby mature forest stands, which provide resting and hiding cover, these clearcuts may contribute to a landscape mosaic of high-quality grizzly bear habitat (Herrero, 1972; Blanchard, 1980; Hamer and Herrero, 1987). However, such habitat-selection behavior can heighten the threats posed to bears (Nielsen et al., 2006) by increasing the risk of human-caused mortality brought about by road networks and associated increases in human access (Benn and Herrero, 2002; Nielsen et al., 2004c; Graham et al., 2010; Roever et al., 2010). A recent study in Alberta (Berland et al., 2008) found no evidence for avoidance of even new (<1 year old) disturbance features, including clearcuts, roads, and wellsites; underscoring the high risk associated with this behavior.

With the exception of certain studies modeling occupancy abundance and human-caused mortality risk (Apps et al., 2004; Graves et al., 2011; Nielsen et al., 2010), the current body of knowledge regarding disturbance effects stems predominantly from habitat-selection and movement analyses associated with individual disturbance features. However, an important dimension that is presently lacking understanding is an explicit accounting of the cumulative effects of multiple disturbances across space and time. Whereas individual disturbance features assessed in isolation may have a negligible or even positive impact on habitat selection, their spatial and temporal accumulation may constitute a major negative impact (Theobald et al., 1997). Neighborhood effects may also exert an amplifying influence on populations (Dunning et al., 1992), whereby more disturbed neighborhoods may entail a lower provision of supplemental shelter to already disturbed sites. The effects of density, configuration, rate of change and neighborhood gradients of anthropogenic disturbance features on present grizzly bear distributions are unclear, as are the respective roles played by short-term, high-intensity disturbance events (defined by high presence of humans and/or machinery while a disturbance feature is being created, such as during road construction or forest harvesting) and long-term, medium-intensity disturbance features (defined by their permanence and consistent activity or emission, such as wellsites). Of particular conservation relevance is also the question of whether landscape characteristics, such as the availability of regenerating and mature forest stands, and landscape context, such as the presence of nearby protected areas, can counteract any potential negative impacts associated with disturbance (Graves et al., 2011; Martin et al., 2010).

In this study we adopted a multi-temporal landscape perspective, with the goal of better understanding the relationship between the spatial distribution of present-day grizzly bear abundance and the spatio-temporal patterns of cumulative (over several previous years) anthropogenic disturbance features. We defined five processes designed to capture broad aspects of anthropogenic disturbance, namely (a) *habitat alteration* (i.e. total cumulative human footprint), (b) *habitat degradation* (i.e. accumulation of long-term, medium-intensity disturbance features), (c) *habitat disruption* (i.e. compound density of individual short-term,

high-intensity disturbance events), (d) *disturbance exposure* (i.e. proximity to areas undergoing short-term, high-intensity disturbance events over time); and (e) *disturbance rate* (i.e. annual rate of occurrence of new disturbances). In addition, we defined another process accounting for neighborhood effects: *neighborhood disturbance* (i.e. total cumulative human footprint surrounding a given area). For landscape characteristics, we included (a) *habitat quality* (i.e. average habitat ranking); (b) *regenerating forest* (i.e. availability of clearcut originated young stands); (c) *mature forest* (i.e. availability of mature stands); and (d) *distance to park* (i.e. proximity to nearest protected area). We examined how these disturbance processes and landscape characteristics relate to the spatial variation of relative abundance in a low-density grizzly bear population unit in the rapidly changing, multi-use Rocky Mountain Foothills of Alberta, Canada (Boulanger et al., 2005; Linke and McDermid, 2012) using a candidate model-selection approach (Burnham and Anderson, 2002).

2. Study area

The 8721 km^2 study area coincides with the Yellowhead grizzly bear population unit (Fig. 1), which is one of seven genetically distinct populations in the west-central portion of Alberta, Canada (Proctor et al., 2012). The area increases in topographic elevation and complexity from east to west, ranging from around 1000 m in the east to peaks of over 2400 m along the western boundary. At lower elevations (below ∼1450 m), the area is dominated primarily by closed-canopied mixed forests, whereas the forests in the upper elevations are mainly coniferous (Strong, 1992; Beckingham et al., 1996).

The Yellowhead grizzly bear population is bounded in the north and south by highways 16 and 11, respectively, with the boundary along the east extending into agricultural lands, where bears generally no longer occur. The western boundary contains no physical barriers, except for steep and high-elevation terrain, which bears are known to traverse. The overall east/west orientation of river valleys in the study area facilitates movement of individuals from the protected area of Jasper National Park (JNP) in the west to the increasingly anthropogenic landscape in the east. A portion of a smaller provincial park, the Whitehorse Wildland (WWP), straddles about 1% of the study area along its west-central boundary. Whereas recreational use and hunting is allowed in WWP, industrial use and motorized access are not permitted. Grizzly bear abundance data was acquired in 2004 using a systematic 7 × 7-km sampling grid (Boulanger et al., 2005). Therefore, we partitioned the study area into the same grid yielding 178 square landscape cells, each 49 km^2 in size (Fig. 1).

Over the past century, the study area has been exposed to increasing levels of industrial activity, particularly coal-mining and forestry, which date back as far back as the 1910s (AAR, 2005). Forest harvesting, however, has occurred extensively only within the past few decades, and oil and gas extraction – an even more recent development – is now widespread. With the exception of two small human settlements, Robb (30 dwellings) and Cadomin (81 dwellings), the human footprint comprises cutblocks from forest clearcutting, surface mines, wellsites, pipelines, and roads.

During the late 1990s and the early 2000s, human-induced disturbances have expanded rapidly, while no significant natural disturbance (e.g. wildfires) have occurred (Linke and McDermid, 2012). By the year 2004, the large majority of landscape cells in our study area contained disturbances (Fig. 2A), and the average cumulative disturbance density was 9.9 ha/km^2. The total disturbance density increased in most cells between 1998 and 2004 (Fig. 2B), with an overall mean annual rate of change of 0.6 ha/ km^2. Over these six years, cutblocks and wellsites were the
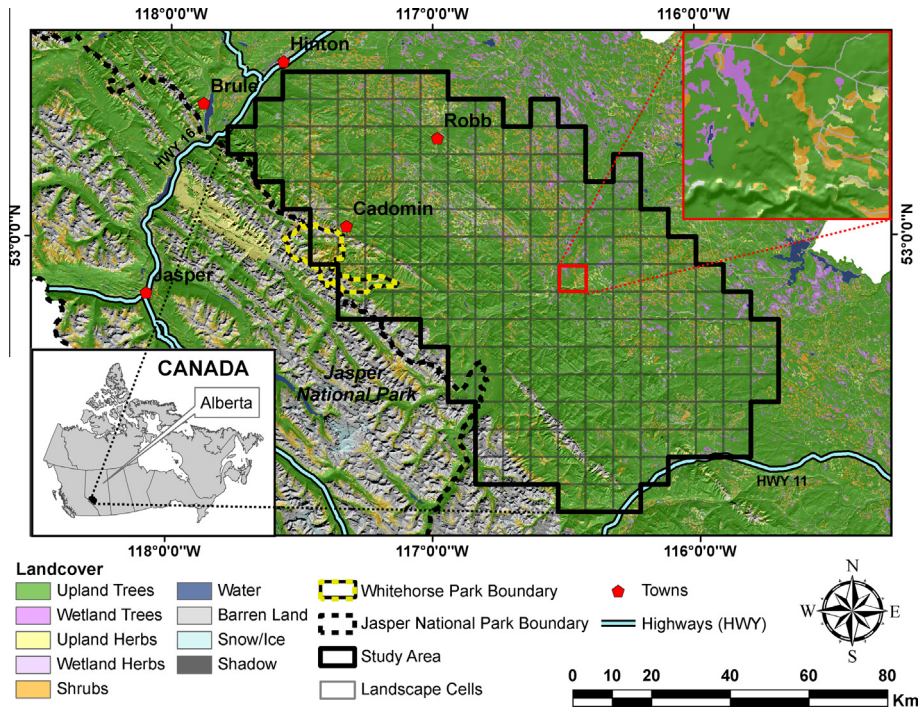
Fig. 1. Stratification of the 8721 km² study area into 49-km² landscape cells located in western-central Alberta, with one example landscape cell enlarged (landcover map generated by Linke et al., 2009).
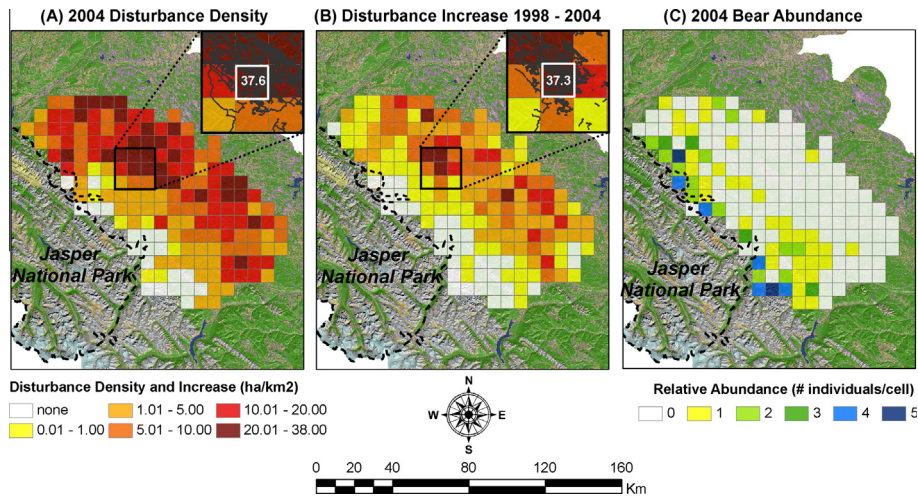

Fig. 2. Distribution of (A) cumulative disturbance density existing in the study area at year 2004, and (B) the total increase in cumulative density between the years 1998 and 2004 (B shows the net change over six years instead of the annual rate of change as stated in text for better visualization); and (C) the relative abundance of grizzly bears in the year 2004, based on repeated DNA-hair-sampling counts, across 178 landscape cells of the study area. Enlarged inserts show the underlying distribution of the actual cumulative disturbance features by 2004 (B) and of the new disturbance features gained between 1998 and 2004. Disturbance data based on data generated by Linke et al. (2009).

fastest-growing disturbance types, followed by a relatively steady and uniform growth in roads and pipelines (Linke and McDermid, 2012).

3. Materials and methods

3.1. Relative abundance of grizzly bears

The population size and spatial distribution of grizzly bears in the study area were estimated in the early summer of 2004 using a mark-recapture systematic sampling design based on hair-snag DNA techniques (Boulanger et al., 2005, 2006). The sampling was

carried out in four two-week intervals between June 6 and July 27, during the *hypophagia* and *early hyperphagia* foraging seasons. Over this time period, foraging behavior is more general and forage distribution is more evenly dispersed (Hamer and Herrero, 1987; Nielsen et al., 2010, Munro et al., 2006), thereby minimizing seasonal foraging effects on bear distribution. That study resulted in a total population estimate of 42 grizzly bears, of which 39 were captured by hair samples (Boulanger et al., 2005). We used the total number of unique individuals detected within each of the repeatedly sampled landscape cells as a measure of the relative abundance of grizzly bears for the year 2004 (Fig. 2B).

Historic distributions of grizzly bear populations in North America have demonstrated gradual declines and range contractions towards higher-elevation areas with low levels of human density (Mattson and Merrill, 2002). Whereas resource-rich, good-quality grizzly bear habitat exists throughout the Yellowhead population unit, much of it is not realized as a result of top-down (human-caused) mortality factors (Nielsen et al., 2010). Therefore, we interpreted absences and low relative-abundance values as being indicative of the effects of human use, including both the history of human-caused mortality events and industrial-based landscape disturbance and modification.

3.2. Explanatory variablesfor disturbance processes and landscape characteristics

We defined a total of 11 explanatory variables designed to describe a variety of spatio-temporal disturbance processes, neighborhood effects, and landscape characteristics (Table 1). These variables were computed for each of the 178 landscape cells in the study area using ArcGIS 9.3 (Esri, 2008). The foundation for these computations was a multi-temporal disturbance inventory which covered the six-year time span between 1998 and 2004 and contained a complete accounting of the cutblocks, mines, wellsites, pipelines, and roads that existed each year. This information was complemented with spatio-temporally coincident land-cover maps derived from 30 m-resolution Landsat imagery (Linke et al., 2009; Linke and McDermid, 2012).

To quantify *habitat alteration* concurrent and prior to the timing of the bear inventory, we calculated the total cumulative area that had been converted from mature forest to either barren ground or vegetated cover by wellsites, roads, pipelines, surface mines, and cutblocks once for each of the years 2004 (DD04) and 1998

(DD98, Table 1). For *habitat degradation*, we calculated the cumulative wellsite density in 2004 (WD04, Table 1), since these permanent features are generally characterized by frequent human presence due to regular facility checks during operation, and permit access even after abandonment (e.g. used for hunting or camping). *Habitat disruption* was characterized by the total density of all disturbance features originating less than one year prior to the bear inventory (NDD04, Table 1). *Disturbance exposure* was indicated by the average across annual mean distances to any nearest new disturbance feature for each of the six years between 1998 and 2004, as calculated from any 30 m-grid point within the landscape cell (NDP, Table 1). Large NDP values indicate low *disturbance exposure*. *Disturbance Rate* was calculated as the mean density of new features originating annually between 1998 and 2004 (ARC, Table 1). *Neighborhood disturbance* was quantified as the difference in DD04 between the outside (within a 3.5 km-square buffer of 147 km² area) and inside of each cell (NDG, Table 1).

To account for variation in landscape characteristics, we computed four variables. For *habitat quality*, we calculated the mean habitat rank of each cell based on a grizzly bear resource selection function (RSF, Table 1). These values predicted the relative probability of habitat use, and were derived from a spatially explicit, 30 m-resolution RSF map of the area (Nielsen et al., 2009). For *mature forest*, we calculated the proportion of area covered by the land-cover class 'upland forest' (Fig. 1, MF, Table 1), and is intended to represent all stands aged about 40 years and older. *Regenerating forest* was calculated as the cumulative area of cutblocks existing in the year 2003 (RF, Table 1). Finally, *distance to park* was calculated as the mean nearest distance from any point within a cell to the eastern boundary of JNP and WWP (DTP, Table 1).

Table 1
A summary of the variables used to characterize disturbance processes between 1998 and 2004, neighborhood effect and landscape characteristics for occupancy abundance modeling of grizzly bears in west-central Alberta.

Process/characteristic	Variable	Definition	Variable meaning	Pre-processing details	Variable acronym
Disturbance processes					
Habitat alteration 2004	Disturbance density '04	Area of all accumulated disturbance features existing by 2004 (ha/km²)	Long-term accumulation of disturbances by 2004	transformed to log $(x + 1)$	DD04
Habitat alteration 1998	Disturbance density '98	Area of all accumulated disturbance features existing by 1998 (ha/km²)	Long-term accumulation of disturbances by 1998	transformed to log $(x + 1)$	DD98
Habitat disruption	New disturbance '04	Area of all disturbances new between 2003 and 2004 (ha/km²)	Density of short-term, high intensity disturbances in 2004	transformed to log $(x + 1)^{0.25}$	NDD04
Habitat degradation	Wellsite density	Total number of all wellsites accumulated by 2004 (100#/km²)	Accumulation of long-term, medium intensity disturbances by 2004	transformed to log $(x + 1)$	WD04
Disturbance rate	Annual rate of change	Mean annual rate of change in new disturbance density between 1998 and 2004 (ha/km²/yr)	Average rate of occurrence of new disturbances between consecutive years	transformed to $x^{0.25}$	ARC
Disturbance exposure	Proximity to new disturbance	Average across annual mean distances to any nearest new disturbance feature for each of the six years between 1998 and 2004 (m)	Spatial exposure to short-term, high-intensity disturbances over time	transformed to log $(x + 1)$	NDP
Neighborhood effect					
Neighbouhood disturbance	Neighborhood disturbance gradient	Difference in cumulative disturbance density between outside and inside landscape cell in 2004 (ha/km²)	Relative long-term accumulation of disturbances in neighborhood	None	NDG
Landscape characteristics					
Habitat quality	RSF Habitat rank	Mean value of the resource selection function habitat ranking (low 0 – high 10)	Average habitat quality	None	RSF
Mature forest	Percent area of mature forest	Total area occupied by mature forest relative to landscape cell (%/cell)	Availability of mature forest	None	MF
Regenerating forest	Percent area of regenerating forest	Total area occupied by cutblocks (older than 1 year) relative to landscape cell (%/cell)	Availability of regenerating forest	None	RF
Distance to park	Distance to protected area	Mean distance to the boundary of Jasper National and Whitehorse Park (km)	Proximity to nearest area protected from disturbances	None	DTP

3.3. Development of theoretical models

The underlying strategy of our investigation was to (1) formulate a set of theoretical models that represented alternative hypotheses concerning plausible relationships; (2) implement each as a statistical model wherein the independent variables (indicative of the various processes and/or characteristics) are functionally linked to the dependent variable (relative bear abundance); and (3) identify the best-fitting models with the smallest number of independent variables, using Akaike's Information Criterion (AIC) as a measure of goodness-of-fit (Burnham and Anderson, 2002; Johnson and Omland, 2004).

Among the 14 theoretical models we developed (Table 2), models I to IV represent global models, wherein variables from all three categories (disturbance processes, neighborhood effect, and landscape characteristics) were included. Model I represents the effect of *disturbance exposure* and the possible mitigating effects associated with the availability of regenerating forest. Model II represents the combined effects of short-term, high-intensity and long-term, medium-intensity disturbance, characterized as *habitat degradation and disruption*. Model III represents the effect of *habitat alteration* in the year 2004 with the possibility of a mitigating effect created by the availability of new, high-quality habitat. Model IV articulates the hypothesis that areas with older, established disturbances (*habitat alteration* in the year 1998) and subsequent, lower annual rates of new disturbance (*disturbance rate*) between 1998 and 2004 would positively impact abundance.

The remaining 10 models represent different combinations of disturbance processes and landscape characteristics. Models V and VIII test whether variation in bear abundance can be explained by *landscape characteristics* alone (model VIII) or combined with *neighborhood disturbance* (model V) without including within-cell disturbance processes. Models VI and VII represent the same

hypotheses as model I, but without *neighborhood disturbance* (model VII), or *landscape characteristics* (model VI). Models IX to XIII represent each of the five *disturbance processes* as sole drivers of abundance, and serve to indicate the magnitude of their relative effect. *Distance to park* is in all 14 models to account for the presumed negative gradient of bear abundance with increasing distance to the protected habitats of Jasper National Park. This gradient is readily apparent in the inventory data, with higher relative abundance clustered along the western boundary of the study area (Fig. 2A). Model XIV formulated the hypothesis that this spatial characteristic alone – *distance to park* – was driving the observed patterns of grizzly bear abundance.

3.4. Statistical modeling approach and evaluation

With 66% of the 178 landscape cells containing *zero* counts, the abundance data, like many other species data sets (e.g. Melles et al., 2010; Nielsen et al., 2010), was *zero-inflated*. We therefore used zero-inflated Poisson (ZIP) regression (Lambert, 1992; Martin et al., 2005), which treats the count data as a mixture of a point-mass at zero and a Poisson distribution. This regression model yields final parameter estimates as separate terms: one set of independent variables and coefficients to explain 'excess absences' (e.g. logistic process), and the other set to explain the 'counts' (Poisson process). Several of the 11 variables were transformed to remove positive or negative skew in their distribution (Table 1), and all were subsequently standardized to z-scores (Quinn and Keough, 2002). Correlated variables ($r > 0.7$; Table 3) were never used jointly within any given model. *Distance to park* (DTP) was entered in the ZIP model component for 'excess absences', whereas all other variables were entered in the 'count' model component.

The ZIP models were constructed using the 'pscl' package with the 'zeroinfl' function (Jackman, 2010; Zeileis et al., 2008) of the R

Table 2
Main disturbance processes, neighborhood effect, landscape characteristics expected to affect grizzly bear relative abundance within the Yellowhead population unit in west-central Alberta in 2004. The theoretical model names indicate the specific processes or characteristics tested; since 'distance to park' is used across all models, it is omitted in model names. (See Table 1 for definitions and acronyms.).

Theoretical models	Distance to park	Landscape characteristics (L) Habitat quality and forest area	Disturbance processes (D) Disturbance exposure	Habitat degradation	Habitat disruption	Cumulative *habitat alteration*	Disturbance rate	Neighborhood effect (N) Neighborhood disturbance gradient
Model I: Global L-D-N (Disturbance exposure × RF)	X	X	X					X
Model II: Global L-D-N (degradation & disruption)	X	X		X	X			X
Model III: Global L-D-N (habitat alteration '04 × RSF)	X	X				X		X
Model IV: Global L-D-N (habitat alteration'98 × Dist. Rate)	X	X				X	X	X
Model V: L-N	X	X						X
Model VI: D-N (disturbance exposure)	X		X					X
Model VII: L-D (disturbance exposure x RF)	X	X	X					
Model VIII: L only	X	X						
Model IX: D only (disturbance exposure)	X		X					
Model X: D only (habitat degradation)	X			X				
Model XI: D only (habitat disruption)	X				X			
Model XII: D only (Habitat Alteration)	X					X		
Model XIII: D only (disturbance rate)	X						X	
Model XIV: distance to park only	X							

Table 3
Pearson's correlation coefficients between the explanatory variables used for occupancy-abundance modeling of grizzly bears in west-central Alberta. (Correlations with an $r > |0.7|$ are highlighted in bold.).

	DD98	DD04	NDD	WD04	ARC	NDP	NDG	DTP	RSF	AF	RF
DD98	1.00										
DD04	**0.91**	1.00									
NDD	0.27	0.49	1.00								
WD04	0.52	0.61	0.54	1.00							
ARC	0.61	**0.85**	0.65	0.63	1.00						
NDP	−0.60	**−0.72**	−0.65	**−0.75**	**−0.85**	1.00					
NDG	0.21	0.24	0.16	0.35	0.30	−0.37	1.00				
DTP	0.53	0.59	0.37	0.53	0.50	−0.60	0.34	1.00			
RSF	−0.04	−0.08	−0.17	−0.22	−0.17	0.26	−0.18	−0.59	1.00		
MF	−0.17	−0.18	0.01	0.08	−0.13	−0.09	0.12	0.05	−0.09	1.00	
RF	**0.79**	**0.87**	0.32	0.42	**0.71**	−0.62	0.16	0.52	−0.10	−0.28	1

statistical computing environment (version 2.10.1, R Development Core Team, 2009). For any fitted model, only the independent variables with significant coefficients ($p < 0.1$) were retained. The relative support of each statistical model was assessed using Akaike's Information Criterion index of model fit for small sample sizes (AIC$_c$), with corresponding AIC differences (Δ_i), Akaike weights (w_i), and evidence ratios (Burnham and Anderson, 2002). Models were identified as 'best-fitting' when Δ_i fell between 0 and 2, as having 'lower but some support' when Δ_i ranged between 2 and 7, and having essentially 'no support' when $\Delta_i > 10$.

The relative improvement of zero-inflated Poisson models over standard Poisson generalized linear model was assessed using Vuong's closeness tests (Vuong, 1989) under the null hypothesis that the models were indistinguishable. We also tested zero-inflated negative binomial (ZINB) models, to account for potential overdispersion in the dependent variable, which would violate the assumptions of a true Poisson process, but model parameters remained virtually unchanged, ruling out the need for a ZINB.

Whereas not used for model selection but rather as an indicator of explanatory power, we estimated a pseudo-R^2 measure for each of the fitted models, which we calculated as the percentage of the maximally achievable, potential log-likelihood gain that was attained with the inclusion of the independent variables in the particular model (Cameron and Trivedi, 1998). To summarize the behavior of independent variables in relation to bear abundance across all models that they are used in, we also documented the relative signs of their coefficient estimates. We reported model coefficients for just those models that ranked 'best' and had 'lower but some empirical support'.

4. Results

The relative-abundance map of Fig. 2C shows an obvious general trend: bears were more abundant along the western study area boundary, in high-elevation, less disturbed areas near the protected parklands. All theoretical models accounted for this trend, exhibiting a significant relationship between *distance to park* (DTP) and the logistic process of bear abundance (Table 4), wherein the probability of excess absences was always positively associated with increasing DTP (Tables 5 and A1). However, the map also shows considerable variation in relative abundance along the western boundary and across portions of the more-disturbed portions in the east of the study area (Fig. 2A). Among the 14 competing hypotheses, models I and VII clearly stood out as best-fitting (Table 4). The highest-ranking model was model I, which fitted a global model using *disturbance exposure* (NDP) as the disturbance process, but it only exhibited a slightly higher Akaike weight ($w_I = 0.51$) than the second-ranked, competing model VII ($w_{VII} = 0.41$), which is the same as model I but excluding *neighborhood disturbance* (NDG) (Tables 2 and 4). The standardized coefficients for these best-ranking models were consistent, and demonstrated strong positive relationships between the probability of excess absences and *distance to park* (DTP) and, as well as moderate and lower positive associations between relative abundance and both *disturbance exposure* (NDP) and *regenerating forest* (RF), respectively (Table 5). NDP and RF also exhibited a positive interaction for both models, indicating a moderately accelerating effect of RF on the positive relationship between NDP and abundance (Table 5). The need for a zero-inflated process was confirmed for these two highest-ranking competing models by significant

Table 4
Small-sample adjusted AICc, Akaike weights, model likelihood, and evidence ratios of all 14 tested zero-inflated Poisson generalized linear models (ZIPs) related to relative abundance of grizzly bears in west-central Alberta in 2004, ordered from highest to lowest AIC weight (AICc for the null model = 378.0; best-ranking models appear in bold; models with lower but some support, as indicated by $\Delta_i < 7$ appear in italics; k stands for the total number of parameters incl. the intercepts). See Table 1 for variable definitions and acronyms.

Model	Variables	k	AIC$_c$	Δi	Model Likeli-hood	Akaike weight (w_i)	Evidence ratio
ZIP I	**RF + NDP + RF × NDP + NDG | DTP**	**7**	**300.05**	**0**	**1.00**	**0.51**	**1.0**
ZIP VII	**RF + NDP + RF × NDP | DTP**	**6**	**300.46**	**0.41**	**0.81**	**0.41**	**1.3**
ZIP VI	*NDP + NDG|DTP*	*5*	*304.95*	*4.9*	*0.09*	*0.04*	*14.3*
ZIP IX	*NDP|DTP*	*4*	*305.23*	*5.18*	*0.08*	*0.04*	*15.6*
ZIP II	MF + WD + NDD + NDG|DTP	7	309.90	9.85	0.01	0.00	138.2
ZIP V	RF + MF + RSF + NDG|DTP	7	316.19	16.14	0.00	0.00	3212.8
ZIP IV	DD98 + ARC + DD98 × ARC + MF + NDG|DTP	8	317.11	17.06	0.00	0.00	4602.7
ZIP VIII	RSF + MF + RF|DTP	6	318.01	17.96	0.00	0.00	9412.1
ZIP X	WD|DTP	4	319.57	19.52	0.00	0.00	21,535.7
ZIP III	RSF + DD04 + DD04 × RSF + NDG|DTP	7	324.20	24.15	0.00	0.00	>100,000
ZIP XI	NDD|DTP	4	326.18	26.13	0.00	0.00	
ZIP XIII	ARC|DTP	4	329.90	29.85	0.00	0.00	
ZIP XII	DD04|DTP	4	331.56	31.51	0.00	0.00	
ZIP XIV	|DTP	3	336.15	36.05	0.00	0.00	

Table 5
Standardized coefficients, standard errors, pseudo-R^2 and Vuong's closeness tests for the four highest-ranking zero-inflated Poisson (ZIP) regression models explaining relative abundance of grizzly bear in west-central Alberta in 2004. (Models I and VII are best-ranking models, and Models VI and IX are models with lower but some support, see Table 5 for AIC statistics). All reported estimates of coefficients are significant ($p < 0.1$) and those significant with a $p < 0.01$ are indicated with a star (*). See Table 1 for variable definitions and acronyms.

Variables for each of the ZIP model components	Model I		Model VII		Model VI		Model IX	
	β	SE	β	SE	β	SE	β	SE
Model for 'Counts' (poisson process)								
(Intercept)	−0.49*	0.16	−0.44*	0.16	−0.63*	0.16	−0.59*	0.16
NDP	1.22*	0.23	1.28*	0.23	0.62*	0.12	0.69*	0.11
NDG	−0.28	0.17	–	–	−0.23	0.16	–	–
RF	0.22	0.15	0.24	0.15	–	–	–	–
RF × NDP	0.56*	0.21	0.52*	0.21	–	–	–	–
Model for 'Excess Absences' (logistic process)								
(Intercept)	−2.37*	1.14	−2.18*	1.08	−2.23	1.19	−2.06	1.12
DTP	3.08*	1.19	3.03*	1.16	3.19*	1.21	3.12*	1.15
Vuong test (V, P) (zip > poisson GLM)	V = 1.67 (p < 0.05)		V = 1.51 (p < 0.05)		V = 1.21 (= 0.11)		V = 1.01 (p = 0.15)	
Pseudo-R^2 of overall model (%):	57		55		51		49	

Vuong tests ($p < 0.05$). Overall, the two models explained between 55% and 57% the variation in grizzly bear abundance, as indicated by the pseudo-R^2 values (Table 5). In comparison, the lowest-ranked alternative model, which only fitted the logistic process using *distance to park* (DTP, model XIV, Tables 3 and 5), had a pseudo-R^2 value of 27% (Table A2). This result indicates that a third of the variation in bear abundance was explained by factors other than *distance to park* (models I and VII).

In combination with *disturbance exposure* (NDP), *regenerating forest* (RF) played an important role in explaining grizzly bear abundance. This is highlighted by comparing the likelihood, relative to the best model, of models that excluded either *regenerating forest* (model VI, evidence ratio 14.3:1) or both *regenerating forest* and *neighborhood disturbance* (NDG) (model IX, evidence ratio 15.6) (Table 4). Both of these alternative models (models VI and IX) were among the four highest-ranked models and carried lower but some support ($\Delta_i < 7$, Table 4), explaining between 49% and 51% of the variation in bear abundance. However, since there was only a minor change in likelihood between models I and VII, resulting in very similar evidence ratios, *neighborhood disturbance* (NDG) explained abundance considerably less than *regenerating forest* (RF), as also indicated by its low standardized coefficient estimate (Table 4).

Whereas evidence ratios and AICs values constituted the main basis for assessing our central research objective, other model parameters provide additional insights into the relative effects of investigated disturbance processes and landscape characteristics (Tables 4, A1 and A2). Consistent model coefficients across the remaining 10 theoretical models suggest for example: (1) negative additive effects of *habitat degradation* (WD) and *disruption* (NND) (model II); (2) positive effect of *habitat alteration* of older disturbances (i.e. DD98), if *disturbance rates* (ARC) are low in later years (model IV); and (3) negative effects of concurrent *habitat alteration* (DD04), which are mitigated by the availability of better *habitat quality* (RSF) (model III) (Tables 4 and A1). *Mature forest* (MF) was negatively related to bear abundance across all of the models it was used (models II, V, VIII, Tables 4 and A1). *Regenerating forest* (RF) had a consistent positive effect on bear abundance when fitted together with disturbance processes (models I and VII), but had a consistent negative effect when fitted together with other variables of landscape characteristics (models V and VIII, Tables 4 and A1).

5. Discussion

This study adopted a multi-temporal landscape perspective to investigate the relationships between spatio-temporal patterns of anthropogenic disturbance and the spatial distribution of relative abundance for a low-density grizzly bear population unit within a multi-use forest landscape. Without including more proximate variables such as mating-behavior driven associations (Stenhouse et al., 2005) and bottom-up regulatory processes such as local food distribution (Nielsen et al., 2010), our most-supported theoretical model (model I) was able to explain a large portion of the variability in abundance (~57%) with *disturbance exposure* (NDP), *neighborhood disturbance* (NDG) and *landscape characteristics* (i.e. RF). As expected from the visual assessment of the abundance data (Fig. 2C), our analysis confirmed that the probability of excess absences of grizzly bears increased with increasing *distance to park* (DTP). DTP is positively correlated ($r = 0.59$, Table 4) with *habitat alteration* (DD04), which represents variation in cutblock and road density (Linke and McDermid, 2012). Therefore the higher probability of excess absences further away from protected areas may be caused by the increased risks of human-caused mortality (Nielsen et al., 2004c), brought about by the preferential foraging use of such 'attractive sinks' (Naves et al., 2003; Nielsen et al., 2006).

Our study found that relative abundance increased with greater mean distances to new, annual disturbances (i.e. high NDP), suggesting that relatively more bears tended to be present in landscape cells that, on average and over time, exhibited a lower degree of spatial exposure to disturbances associated with short-term, high-intensity human activities, such as road construction, forest harvesting, drilling of well sites, or expansion of mine sites. This effect was larger with greater availability of *regenerating forest* (RF). This suggests that in areas of low *disturbance exposure*, more *regenerating forest* could increase the foraging opportunities and hence result in a higher relative number of bears in the area: an observation consistent with individual habitat-selection patterns noted in previous studies (Nielsen et al., 2004a; Stewart et al., 2012). In contrast, this also suggests that the generally positive foraging effect of *regenerating forest* may have been counteracted in areas of high *disturbance exposure* (low NDP i.e. short mean distance to new disturbances over time), leading to even lower bear abundance than in areas with less *regenerating forest*. This may arguably be further related to the general inverse association between the area covered by *regenerating forest* and the distribution of contiguous mature forest, where the latter may provide security and cover for resting and hiding (Apps et al., 2004; Blanchard, 1980; Herrero, 1972; Gibeau et al., 2001). Therefore, in cases where *disturbance exposure* is high, the amount of *regenerating forest* may be acting as limiting factors for the amount of secure areas and lead to even lower abundance; a result further underscoring the complex relationship between grizzly bears and their use of regenerating forests (Nielsen et al., 2004a; Stewart et al., 2012).

These findings are consistent with many studies that documented avoidance and displacement from localized areas with human presence associated with recreational or industrial activity (e.g. Gibeau et al., 2002; Graves et al., 2011; Mace et al., 1999; Martin et al., 2010; McLellan, 1989; Nellemann et al., 2007). However, they also contribute further insight into the spatio-temporal patterns of the anthropogenic disturbance features related to industrial activity at the landscape level, and hence may offer relevant information for the design of integrated landscape management regimes more favorable for grizzly bear populations. Whereas areas with high *disturbance exposure* (i.e.low NDP) generally also contain high *regenerating forest* (RF, r = −0.62, Table 4), suggesting that these two variables work in concert, variations in the size and/or distribution of these new disturbances can lead to very different values for NDP even if the total disturbed and subsequently regenerating area are similar. For example, several medium-sized but densely clustered cutblocks introduced to an area over time may exhibit greater mean distances to new disturbance, and therefore indicate low *disturbance exposure*, but at the same time contain high *regenerating forest.* Therefore these variables are distinct. This work highlights the importance of considering interaction effects on relative abundance in land use planning efforts. Specifically, limiting *disturbance exposure* (NDP) may offer an important new avenue for controlling negative impacts of human and industrial presence by managing the spatial distribution of new disturbances over space and time. This may be most relevant in multi-use forest landscapes, where ongoing industrial activity can only be managed but not restrained, and where high human access represents an increased risk of bear mortality (Noss et al., 1996; Benn and Herrero, 2002; Nielsen et al., 2004c, 2006).

Another important factor included in the best model was *neighborhood disturbance* (NDG). Grizzly bear abundance was found to decrease with increasing NDG. Higher densities of disturbances in the surrounding neighborhood than within the landscape cell may restrict movement to that cell and therefore negatively impact local abundance there, which may also offer some management implications. Notwithstanding, *neighborhood disturbance* (NDG) had the lowest contribution to the explanatory power in the best model, as judged from the second-ranked theoretical model that excluded this factor (model VII), and yet remained equally likely than the most-supported model (evidence ratio 1.3:1, Table 5).

Based on the low evidence ratio for any model that excluded direct disturbance processes (models V, VIII, XIV, Table 4), we could effectively rule out *landscape characteristics* and *neighborhood disturbance* as main drivers for abundance in this landscape. With the exception of *disturbance exposure* (NDP), we could equally rule out any of the other four disturbance processes – *habitat degradation* (WD04), *habitat disruption* (NDD04), *habitat alteration* (DD04) and *disturbance rate* (ARC) – as forming leading explanations for abundance on their own (models X, XI, XII, XIII, Table 4). Even if considered in interaction with *habitat quality* (RSF) (model III) or if qualified by older regenerating disturbance (DD98) interacting with rates of change of subsequent disturbances (ARC) (model IV), *habitat alteration* (DD) provided essentially no explanation for abundance with our data (Table 4). The only alternative model that excluded *disturbance exposure*, and which could be considered marginally supported by the given data (Δ_i = 9.85), was the hypothesized complementing negative effects of *habitat degradation* and *habitat disruption* (model II), wherein long-term, medium-intensity disturbance (WD) and short-term, high-intensity disturbance (NDD) are both indicative of frequent presence of humans and industrial equipment. Nevertheless, the likelihood that these processes explained abundance better than the global model with *disturbance exposure* was still very low (i.e. evidence ratio 138:1, Table 4) and could therefore be dismissed in this study area.

Although the main findings in this study are corroborated by other research, the drawn inferences should still be interpreted within the context of the data used to model both disturbances and bear abundance. There is little uncertainty associated with the disturbance data set, whose detection and disturbance classification accuracy was very high (Linke et al., 2009). However, it could be argued that *habitat alteration* was represented conservatively, since all disturbance-feature types were treated with the same relative importance, as measured by their areal extent. For example, the areal coverage of a linear disturbance features such as a road is on average much lower than the area occupied by a cutblock, though the importance of roads regarding its potential negative factors through human access is likely higher. However, it is not expected that this leads to a significant bias, since cutblock and linear feature magnitude are highly correlated, and are generally accounted for by *habitat alteration*.

A common concern for estimates of relative abundance is habitat or sampling-effort related variabilities in detection probability (e.g. Mazerolle et al., 2005; MacKenzie et al., 2006). A recent Montana study accounted for detections in estimating local grizzly bear abundance and found that sampling effort and none of their investigated landscape characteristic to be the only variable strongly influencing detection rates, urging for even sampling designs across sessions and space (Graves et al., 2011). Whereas we did not account for probability of detection in this study, sampling effort was even across sampling sessions and space (Boulanger et al., 2005) which limited detection biases of our estimates of local relative abundance. Considering that (1) the sample grid cells (49 km^2) covered at minimum a quarter of each bears' home range (smallest home range 200 km^2), (2) each of the 178 cells was sampled four times with movement to different locations every 2 weeks, (3) only 3 of the 42 individuals of the population unit were missed during sampling (Boulanger et al., 2005), and that (4) secondary DNA analysis of the hairsamples (Stenhouse, unpublished results) confirmed the absence of any family groups (i.e. females with cubs) in the inventory of counts, we anticipate that the detection probability in our study was fairly high and the reported relative abundance were representative. Therefore we expect that explicitly modeling detection would not have changed our identification of the main variables influencing local occupancy and abundance. It is likely that any impact would be limited to the accuracy and precision of estimated model coefficients; an important consideration for future studies aimed at predictions rather than inference alone.

Ideally, we would have evaluated these cumulative effects with multi-temporal bear data in addition to the multi-temporal disturbance data we used. However, since the inventory was performed across resource-rich, good-quality habitat (Nielsen et al., 2010) within the current extent of ocurrence (Mackenzie et al., 2006) of grizzly bears in Alberta (ASRD/ACA, 2010), we assumed that absences and low relative-abundance values reflected the cumulative effects of human activity, including both the history of human-caused mortality events and displacement associated with industrial development. The collection of multi-temporal bear data in this region, and in other less-disturbed regions, would help to build further insight into the detected relationships. Nevertheless, the strong support for disturbance exposure (NDP) emphasizes at the very least the need to examine the effect that the spatio-temporal distribution of disturbance features poses on the observed abundance of grizzly bears.

6. Conclusions and implications for future research on management and conservation

A multi-temporal remote-sensing based analysis of anthropogenic disturbances enabled an investigation on the relative

importance of select spatio-temporal disturbance processes on a low-density grizzly bear population unit in the rapidly changing forest landscape of west-central Alberta. Rather than focusing on the presence and absence of human-footprint features alone, this study investigated the varying densities of anthropgenic disturbance features across the study area. The inclusion of the multi-temporal dimension further allowed the differentiation among different disturbance processes that may act upon the resident population. Whereas we found *distance to park* to be the main driver for broad occupancy patterns, *disturbance exposure* and *regenerating forest* largely explained remaining patterns of relative abundance. Overall, the variation in abundance was low and zero-inflated, but with 57% explained variability, the findings of this study provide strong empirical support for the argument that the current low densities and distribution of this population unit are associated with human-induced spatio-temporal disturbance patterns. Areas characterized with lower *disturbance exposure*, greater *regenerating forest*, and lower *neighborhood disturbance* were related to higher relative abundance of grizzly bears. Managing the *disturbance exposure* by controlling the spatio-temporal distribution of new annual disturbance features may be an important consideration for conserving this species in multi-use forest landscapes. Since such landscapes are expected to experience continued anthropogenic modifications in the future, additional useful insights would be gained by repeating similar studies in other grizzly bear population units, especially in areas where cumulative habitat alteration is lower and population densities higher.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.06.012.

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