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## Wolverine behavior varies spatially with anthropogenic footprint: implications for conservation and inferences about declines

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### Abstract

Understanding a species' behavioral response to rapid environmental change is an ongoing challenge in modern conservation. Anthropogenic landscape modification, or “human footprint,” is well documented as a central cause of large mammal decline and range contractions where the proximal mechanisms of decline are often contentious. Direct mortality is an obvious cause; alternatively, human-modified landscapes perceived as unsuitable by some species may contribute to shifts in space use through preferential habitat selection. A useful approach to tease these effects apart is to determine whether behaviors potentially associated with risk vary with human footprint. We hypothesized wolverine (*Gulo gulo*) behaviors vary with different degrees of human footprint. We quantified metrics of behavior, which we assumed to indicate risk perception, from photographic images from a large existing camera-trapping dataset collected to understand wolverine distribution in the Rocky Mountains of Alberta, Canada. We systematically deployed 164 camera sites across three study areas covering approximately 24,000 km<sup>2</sup>, sampled monthly between December and April (2007–2013). Wolverine behavior varied markedly across the study areas. Variation in behavior decreased with increasing human footprint. Increasing human footprint may constrain potential variation in behavior, through either restricting behavioral plasticity or individual variation in areas of high human impact. We hypothesize that behavioral constraints may indicate an increase in perceived risk in human-modified landscapes. Although survival is obviously a key contributor to species population decline and range loss, behavior may also make a significant contribution.

## Introduction

Wildlife populations around the globe are experiencing declines and range contractions (Butchart *et al.* 2010) where habitat loss and fragmentation are major causes (Fahrig 1997, 2001, 2003). Human exploitation of landscapes is a consequence of increasing human populations and resource development (Woodroffe *et al.* 2005). Although expanding landscape modification, or “human footprint,” is well documented as a major cause of mammalian range contraction and declines in biodiversity (Vitousek *et al.* 1997; Laliberte and Ripple 2004), there is little research on the effects of footprint on other important aspects of species persistence such as life-history traits, population dynamics, and behavior (Frid and Dill 2002; Béchet *et al.* 2004; Ciuti *et al.* 2012a). Human landscape modification is expected to shift species’ selection to habitats possessing the highest realized suitability (Rosenzweig 1981; Petit and Petit 1996; Abrams 2000), and this can occur by inducing mortality, or by decreasing its suitability relative to other patches available for choosing. Given rapidly expanding global human footprint (Vitousek *et al.* 1997), and associated ongoing mammalian population declines (Woodroffe 2000; Laliberte and Ripple 2004), it is important to assess the effects of human footprint on species of critical conservation concern.

Testing these premises for some taxa, for example, large wide-ranging carnivores, has proved logistically difficult (but see Woodroffe 2000). However, we can make inferences by investigating shifts in behavior over large spatial scales – shifts assumed to be associated with underlying changes in human footprint. We examined spatial patterns in behavior of wolverines (*Gulo gulo*), a species of Special Concern in Canada and recently petitioned for listing under the US Endangered Species Act. Based on an analysis of camera-trap data collected to understand wolverine distribution, we formed the post hoc hypothesis that wolverines exhibit changes in behavior across areas with varying degrees of human footprint. We suggest spatial variation in behavior may indicate variation in perceived suitability, which could be contributing to decreased distribution.

Our assumptions about wolverine behavior derive from the landscape of fear (LOF) hypothesis, applied to human-modified landscapes. In LOF, habitat selected by a species consists of high- and low-risk habitat patches, characterized by the occupancy and perceived lethality of a predator (or other source of mortality) within those patches (Caraco *et al.* 1980; Baker and Brown 2010; Laundre *et al.* 2014). Predators can cause direct mortality, but predators can also affect prey distribution through sublethal effects, which may surpass mortality in impact

by manipulating prey morphology, physiology, behavior, or habitat selection (Sih *et al.* 1985; Sheriff *et al.* 2009; Ford *et al.* 2014). The LOF hypothesis predicts that patches with greater perceived risk will be less likely occupied, and if occupied, it will invoke increased behaviors indicative of perceived risk. A well-known example is the trophic cascade resulting from the risk-sensitive foraging behavior of elk following wolf re-introduction in Yellowstone National Park (Ripple and Beschta 2006). In human-modified landscapes, perceived risk can be manipulated by human presence and landscape modifications (Darimont *et al.* 2009; Ciuti *et al.* 2012a,b).

The perceived risk induced by human footprint can be assessed by quantifying animal behaviors (Lima and Dill 1990; Lima and Zollner 1996; Ciuti *et al.* 2012a) across a range of human footprints. Behavior is affected by several factors including habitat characteristics (Hollén *et al.* 2011), sex and density (Childress and Lung 2003), predator presence (Morrison 2011), and breeding season (Wolff and Van Horn 2003), but importantly it can correlate strongly to human presence (Wang *et al.* 2011). The majority of past research has been conducted on prey species, but risk concepts outlined under the LOF hypothesis could apply to carnivore species assuming they perceive cues induced by landscape modification as tradeoffs between mortality risk, competition with other carnivores, and foraging (Murphy *et al.* 1995). We tested this premise using wolverines distributed across landscapes of widely varying human footprints in the Rocky Mountains of Alberta, Canada.

Wolverines have experienced considerable reductions in much of their North American range over the last two centuries (Laliberte and Ripple 2004). In western Canada, wolverines are designated “Special Concern,” and remain listed as “Data Deficient” in Alberta (COSEWIC Annual Report 2014). Despite small and relatively isolated populations, wolverines in the USA remain unlisted under the Endangered Species Act (U.S. Fish and Wildlife Service 2014) in part due to debate over the cause of population decline. Several competing hypotheses exist. Wolverines are more likely to occur in areas of low human footprint (Krebs *et al.* 2007; Heinemeyer 2013; Fisher *et al.* 2013), implicating landscape development as a source of landscape change. Alternatively, wolverines are more likely to occur in areas of persistent spring snow (Copeland *et al.* 2010; McKelvey *et al.* 2011; Inman *et al.* 2012; Clevenger and Baruetto 2014), ostensibly because they require snow dens to raise young (Magoun and Copeland 1998). In this event, climate change may have led to population declines (Brodie and Post 2009) and may continue to do so. Hunting and trapping (Krebs *et al.* 2004; Lofroth and Ott 2007) may play a role, and emerging evidence suggests other carnivore competitors may also have an effect

(Mattisson *et al.* 2011; Heim 2015). However, the proximate cause(s) of wolverines' range contraction remain in question. Most studies have examined wolverine habitat selection or distribution, and related this to landscape characteristics such as anthropogenic disturbance as a basis for inference. We try a different approach and hypothesize that wolverine behaviors spatially vary with the degree of anthropogenic landscape footprint. We predicted that wolverines in human-modified landscapes would be more likely to express behaviors assumed to be associated with perceived risk, than those in protected landscapes with much less landscape modification.

## Materials and Methods

### Study area

We repurposed photographic data from three collaborative studies examining wolverine distribution in the Canadian Rocky Mountains, conducted in three landscapes: the Willmore Wilderness Area, Kananaskis Country, and Banff, Kootenay, and Yoho National Parks (National Parks Complex [NPC]; Fig. 1) (Fisher *et al.* 2011, 2013; Clevenger and Baruetto 2014; Fisher and Bradbury 2014; Heim 2015). All three areas exhibit rugged topography with mountains ranging above sea level from 825 m valley bottoms to 4000 m summits, and mid-elevation conifer forests in between dominated by Engelmann spruce (*Picea engelmannii*), Subalpine fir (*Abies lasiocarpa*), and Subalpine larch (*Larix lyallii*). Diverse mammalian carnivore communities and prey communities inhabit all three landscapes (Fisher *et al.* 2011; Heim 2015).

The three areas vary marginally in terms of topography, persistent spring snow, and natural landcover (Fisher *et al.* 2013; Heim 2015); they differ strikingly in the degree of anthropogenic development. The Willmore Wilderness is fully protected from landscape development and has only horse and foot trails within it, with all terrain vehicle access limited to fur trappers. The NPC is a complex of nationally protected parks with concentrated, intensive development for tourism and transportation in the valley bottoms, little to no development throughout most of the landscape, and no trapping. Adjacent to NPC, Kananaskis Country is managed by various land-use directives ranging from tourism and recreational activities to industrial development, such as petroleum extraction and forest harvesting, as well as historic and current fur trapping.

### Field protocols and data collection

We surveyed wolverines monthly at sites deployed in a systematic design comprised of  $12 \times 12$  km<sup>2</sup> grid cells imposed upon the study area. At each site, we surveyed

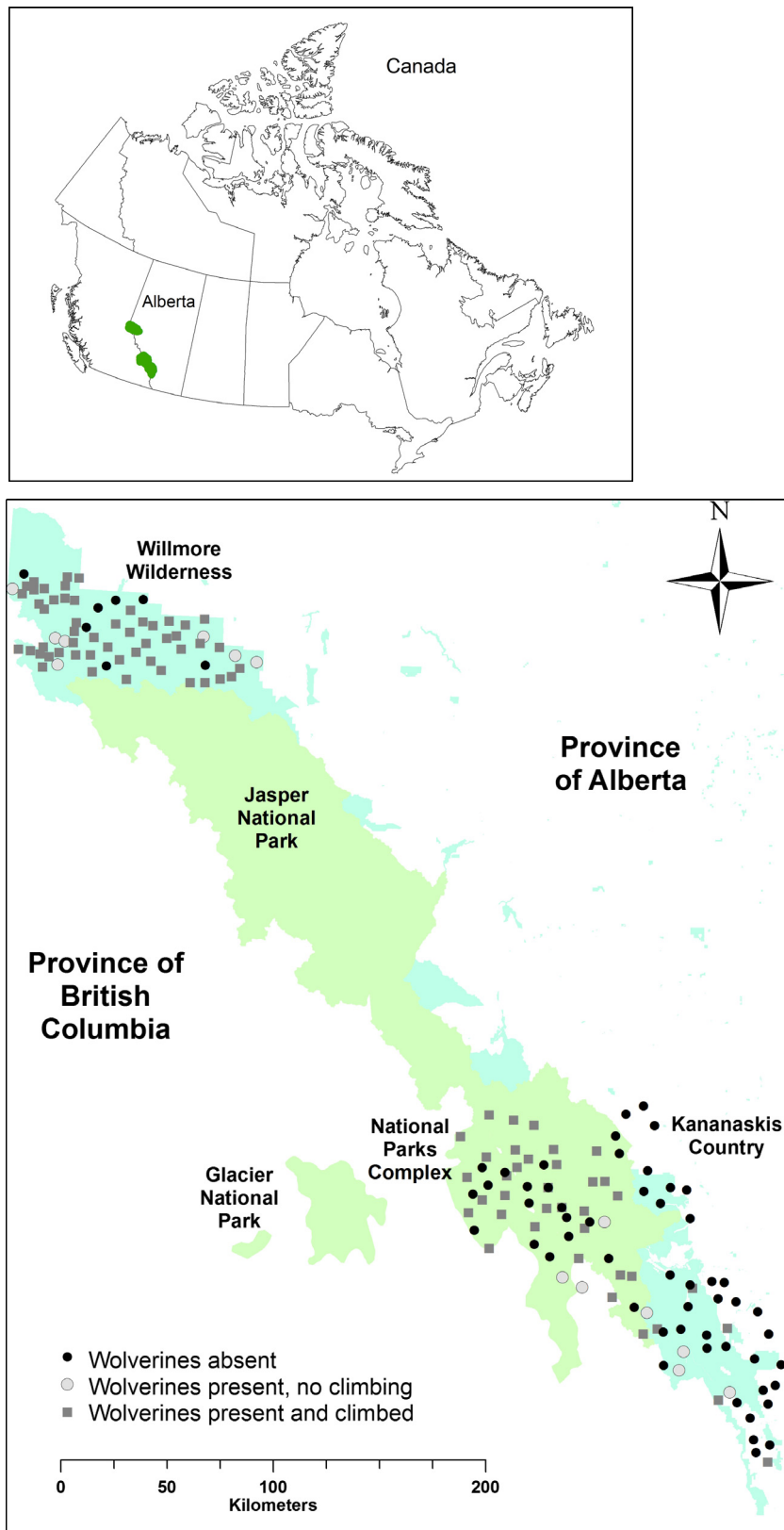
wolverines with a combination of remote camera trapping (Burton *et al.* 2015) and noninvasive genetic tagging (NGT; Waits and Paetkau 2005) wherein the camera photographed the hair trap used for capturing genetic material, as well as the surrounding area. Wolverine occurrence was recorded using Reconyx™ digital cameras triggered by heat-in-motion (models RM30, PM30, PC900; Reconyx, Holmen, WI) at sites baited with a whole frozen beaver carcass, nailed to a tree wrapped in barbed wire, to capture hair. This double-sampling approach allowed us to quantify error in NGT samples (Fisher and Bradbury 2014). Having a quantifiably low detection error (Fisher and Bradbury 2014), this technique facilitated a primary objective: estimating wolverine abundance and distribution (e.g., Fisher *et al.* 2013). However, the camera dataset also allowed us to observe the behaviors of wolverines in the vicinity of, and interacting with, the baited tree at each site.

We deployed cameras in December through March in the Willmore Wilderness (winters 2006/2007 and 2007/2008), where each site was deployed for one winter, and January through April in the NPC (2012, 2013) and Kananaskis Country (2011, 2012), where some sites were deployed for one winter and some for both. We used a dataset comprised of the first year of data from each of 164 sites across the three areas (Willmore = 66, NPC = 52, Kananaskis Country = 45), spanning 24,000 km<sup>2</sup>, with 100 uniquely identified individuals (Willmore = 28, NPC = 64, Kananaskis Country = 8) – the largest North American dataset on wolverine distribution extant (Fisher *et al.* 2013; Clevenger and Baruetto 2014; Heim 2015). We quantified behaviors from all monthly surveys at each site.

### Quantifying behaviors

Little is known about wild wolverine behavior (Banci 1994). This required that we posit four fundamental assumptions about wolverine behavior at these sites, based on established wildlife behavior theory and observations. First and most generally, we assumed that as scavenging carnivores ranging across vast areas, behavioral plasticity is a key component to wolverine life history and that individuals exhibit different behaviors under different conditions (e.g., Komers 1997; Sih *et al.* 2004a). Second, we assumed that climbing a tree to acquire the bait posed a perceived risk to wolverines. The nature of this risk is unknown; it may be due to neophobia of the trap itself, or perceived risk of being away from visual cover and escape cover, or some other unknown factor. Third, we assumed that time spent at the baited site posed a risk to wolverines. Several other (larger) carnivore species are attracted to bait (Long *et al.* 2007; Fisher *et al.* 2011) and





**Figure 1.** Wolverine occurrence and climbing of a baited tree were sampled across three large areas of varying human footprint and protection status. Provincial protected areas, in blue, include Willmore Wilderness area and Kananaskis Country. National protected areas, in green, include Banff, Kootenay, and Yoho National parks (the National Parks Complex) of Alberta, Canada.

an interspecific encounter can lead to wolverine mortality, as suggested by intraguild predation rates in Krebs *et al.* (2004). Fourth, we assumed that individual wolverine response to these risks is not static but instead varies in space as a result of behavioral plasticity Komers (1997), a natural corollary of optimization theory (Pyke *et al.* 1977; Krebs 1978).

Based on these assumptions, we quantified four metrics: (1) the probability that a wolverine detected at a site would climb the baited tree; (2) the latency (time in minutes) of a wolverine to show up at a site; (3) the latency (time in minutes) for a wolverine to climb the baited tree, given it climbed; and (4) the total time (in minutes) spent at a site. There may be other, more subtle behaviors such as “head-lifting” risk-related behaviors (e.g., Lima and Dill 1990; Lima and Bednekoff 2014) but we used these four because we contend their obviousness and ease of quantification make them conservative metrics less prone to subjectivity and observer error.

We used digital infrared remote camera images from each site to measure these four metrics. When triggered, cameras took five photographs at 1-s intervals, repeated at each detected movement. Images therefore comprise a short time-lapse video of wolverine behavior at each site and each visit. For each time series (month) of photographs, we used a standardized protocol to record the time elapsed between camera setup and wolverine detection (latency to detection; min), the time at which the wolverine climbed the tree (latency to climb; min), and the time spent at the site before moving off (total event duration; min). Although wolverines possess distinctive chest markings, our cameras were not always positioned

to identify individuals (e.g., Magoun *et al.* 2011; Fig. 2), and photographed individuals did not always leave hair for genetic identification (Clevenger and Baruetto 2014; Fisher and Bradbury 2014; Heim 2015). Thus, our question does not address individual behavior; rather we ask whether wolverine behavior, averaged across the population, changes across a gradient of human footprint. As wolverines are social scavenging carnivores with vast territories (Krebs *et al.* 2007), we assumed that an individual would consume or cache the bait within a few hours and move on to another location. Therefore, we recorded a different behavioral “event” to occur at a site after a 6-h period of site inactivity. At each event, we measured the three behavioral metrics, and averaged each metric among events, yielding a single value at each site. This conservative method makes it harder for us to find a signal (reducing Type I error) by decreasing the total variation in behavior.

### Habitat analysis

Digital map inventories from the Alberta Biodiversity Monitoring Institute (ABMI; Human Footprint Map 2012, and National and Alberta Provincial Parks’ geodatabases) were accessed to quantify 16 anthropogenic landscape features: percent area of urban landcover, cultivation, disturbed vegetation, rural residential, petroleum extraction well sites, forest harvesting cut blocks, industrial sites, mine sites, pipelines, transmission lines, petroleum exploration seismic lines, roads, and rail lines. Based on extensive exploratory analyses (Heim 2015), we merged noncollinear features in ArcGIS 9.3.1 (Environ-



**Figure 2.** Although wolverines possess distinctive chest markings (A), wildlife cameras were not always positioned to identify individuals, individuals did not always face the camera (B), and photographed individuals did not always leave hair for genetic identification.

mental systems research Institute, Redlands, CA) into one “cumulative human footprint” variable. We calculated the percent cover (% area) of human footprint at a 5000-m buffer around each site (Fisher et al. 2013). We also calculated the linear feature density of seismic lines, pipelines, transmission lines, roads, and rail lines (km/km<sup>2</sup>) around each site, at this same extent. Although there is some redundancy in the measures, linear features are the most spatially extensive form of disturbance in this region, and Heim (2015) suggests wolverines respond to linear features more strongly than patch features.

## Statistical analysis

We tested for correlations between behavioral variables and found none (Table 1). We conducted two analyses to investigate the association between wolverine behavioral variation and human footprint. First, we calculated the proportion of sites where a wolverine was present and climbed the baited tree. We used a generalized linear model (binomial error distribution, logit-link function) in R (R Foundation for Statistical Computing 2012) to estimate the probability of climbing in relation to cumulative human footprint (% area) and density of linear features (km/km<sup>2</sup>), as these variables test the hypotheses that wolverine behavior changes with increasing landscape modification. Second, we conducted two Levene's tests of equal variances (Levene 1960), using the “car” package in R (Fox and Weisber 2014), to test for behavioral variation, and variation in human footprint, among the three study areas.

To weigh support for our hypothesis, we wished to model latency to climb the tree in relation to the several landscape variables we quantified, and rank these models in an information-theoretic approach (Burnham and Anderson 2004). However, the distribution of these data did not lend themselves to any of the available generalized linear models and links (Crawley 2007), and the discrepancy in sample sizes between study areas did not lend the data to linear mixed effect models (Pinheiro et al. 2012), generalized least squares regressions (sensu Zuur et al. 2009), or nonlinear least squares regressions (Bates and

Chambers 1992). Upon inspecting the data, we instead posed the ad hoc hypothesis that these data were represented by two distributions in this dataset, representing two linear relationships between the response and predictor variables. In plain terms, we suspected that wolverines were behaving one way in response to one range of the anthropogenic footprint features, and differently to another range of these features. We tested this ad hoc hypothesis with a piecewise (or segmented) regression analysis, in the R package SiZer (Sonderegger 2015) to identify the point at which a linear model with cumulative human footprint as a predictor variable, and latency to climbing as the response variable, would have the smallest mean square error (Toms and Lesperance 2003; Sonderegger 2015). We then regressed two linear models: one using predictor data (average latency to climb) smaller than the derived break point and the other using predictor data (average latency to climb) larger than the break point, to demonstrate the change in wolverine behavior before and after this break point.

## Results

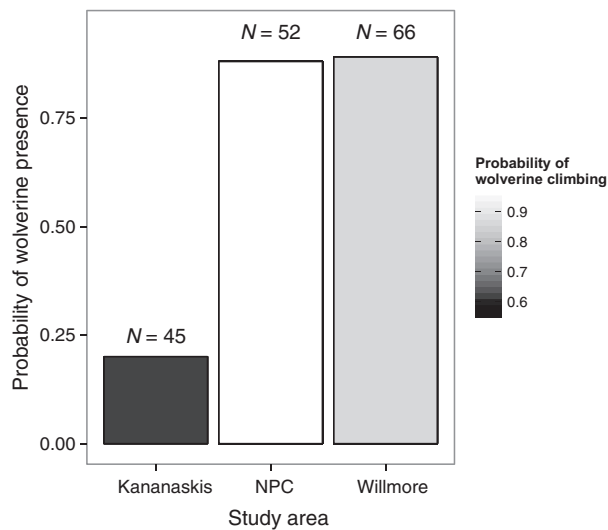
Cumulative human footprint varied among all three study areas (Levene's test:  $F_{2,160} = 51.82$ ,  $P < 0.0001$ ), with the greatest landscape modification found in the Kananaskis Country region compared with the other two areas (Kananaskis  $8.09 \pm 0.77\%$  area; NPC  $1.47 \pm 0.50\%$  area; Willmore  $0.0005 \pm 0.0001\%$  area). Wolverine climbing also varied across the three study areas, with wolverines in Kananaskis Country, the least likely to climb a baited tree when detected at a site, at 56% (5/9 sites). In the Willmore Wilderness, 88% (46/52 sites) of the wolverines detected at a site climbed the bait tree and in the NPC, 96% (44/46 sites) of those detected climbed the bait tree (Fig. 3).

Behaviors varied among all three study areas (Fig. 4). The average latency of climbing varied (Levene's test;  $F_{2,86} = 3.69$ ,  $P = 0.03$ ); climbing was the fastest and least variable in Kananaskis, and slower and more variable in Willmore. The total event duration also varied between study areas (Levene's test;  $F_{2,97} = 13.35$ ,  $P < 0.001$ ); events were fast and least variable in Kananaskis. Total event duration was the longest and most variable in the NPC (Fig. 4). In the less human-modified Willmore Wilderness and National Park Complex, wolverines displayed a greater range of behavior: there was on average 16.5 and 11.9% greater behavioral variation in their latency to climb, and 13.8 and 37.5% greater behavioral variation in the duration spent at a site (respectively) than in Kananaskis Country (Fig. 4).

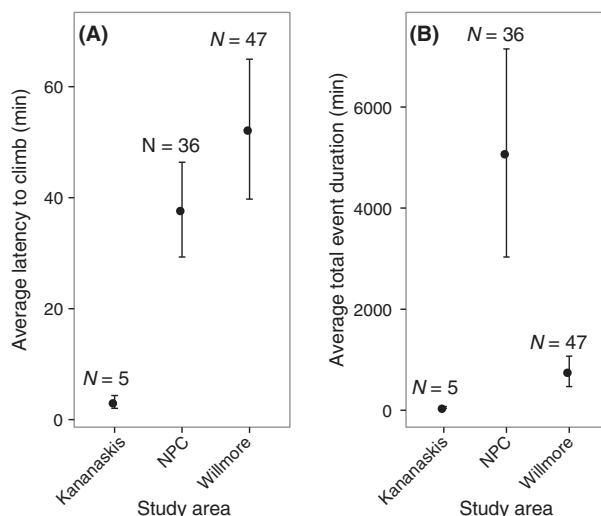
Wolverines' climbing behavior changed at 0.35% human footprint, as suggested by the piecewise linear

**Table 1.** Correlations between recorded behavioral variables collected at each study site. Numbers below the diagonal represent Pearson's correlation coefficients, where no correlation was significant ( $\alpha < 0.05$ ). Numbers above the diagonal represent degrees of freedom.

	Latency to detection	Latency to climb	Total event duration
Latency to detection		87	98
Latency to climb	−0.04		86
Total event duration	−0.03	0.05	

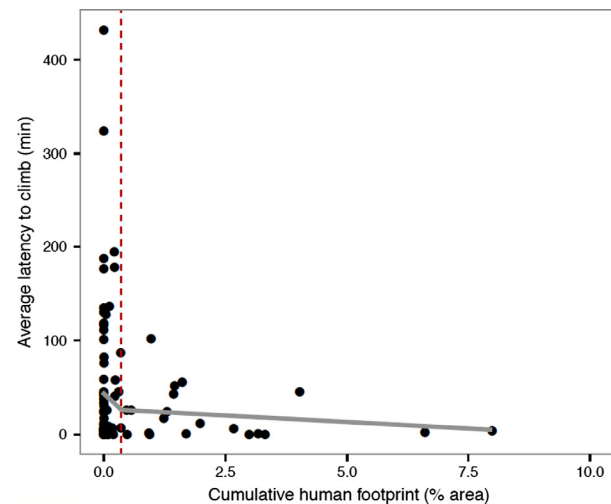


**Figure 3.** The probability of wolverine presence and climbing varied across three study areas in the Alberta Rocky Mountains, Canada. Wolverine had the lowest probability of occurrence and of climbing a baited tree in Kananaskis Country. Sample sizes indicate the number of sites sampled within each study area.



**Figure 4.** Both the absolute value (mean) and variation (SE) of the latency of a wolverine to climb a baited site (A) and the total duration of each event (B) were significantly different between landscapes with different degrees of disturbance. Sample sizes indicate the number of sites with wolverine present within each study area.

model regressing average latency to climb (min) as a function of cumulative human footprint (% area; Fig. 5). Average latency to climb decreased across the range of human footprint values, but this trend was significantly greater in areas with human footprint measuring less than 0.35%, represented by the linear model  $y = 49.87 - 50.46$



**Figure 5.** Wolverine decreased their average latency to climb across a range of human footprint values. An ecological threshold in behavior is represented by the red-dashed line; when greater than 0.35% of area is covered by human footprint, wolverine significantly change their behavior, as represented by the different slopes of the gray lines before and after this threshold.

( $x$ ), than in areas measuring more than 0.35%, represented by the linear model  $y = 23.95 - 1.00(x)$  (Fig. 5).

There was no linear relationship between cumulative human footprint and the probability of climbing the baited tree (generalized linear model:  $N = 113$ ,  $Z = -0.33$ ,  $P = 0.74$ ). Linear features correlate to human footprint ( $r = 0.37$ ,  $df = 162$ ,  $P < 0.001$ ), but also do not predict the probability for a wolverine to climb the baited tree (generalized linear model:  $N = 113$ ,  $Z = -1.33$ ,  $P = 0.19$ ).

## Discussion

Wolverines behaved differently in heavily human-modified landscapes than in lightly human-modified or protected landscapes. The time that wolverines spent at a site was less in Kananaskis Country compared with the other two areas. This difference is not subtle. In the less human-impacted Willmore Wilderness and NPC, some wolverines lingered for hours at a site, and some wolverines went in and out quickly. However, in Kananaskis Country, wolverines rarely lingered. Instead, they consistently arrived at a site quickly, climbed quickly, and left quickly. We contend that this pattern, manifested over a very large landscape, a range of human footprint, and over 100 individuals, is consistent with evidence for spatial variability in behavior correlated with increasing human footprint.



## Hypothesized drivers of wolverine behavior

In developed areas, wolverines were constrained to a behavior where they climbed quickly (if they climbed at all), and left quickly. If our assumptions are correct – that climbing an exposed baited tree and lingering at a site represent a risk – then we provide good evidence that wolverines perceive human-modified landscapes as riskier. What might wolverines be afraid of, if they are indeed afraid? Most LOF studies are based on predation risk as a direct mechanism (Laundré *et al.* 2010; Matassa and Trussell 2011). Some studies suggest the presence of humans can induce a similar response, increasing perceived mortality risk (Ciuti *et al.* 2012a). Neophobia is a common phenomenon among some taxa (Sih *et al.* 2004a,b; Real *et al.* 2007) and wolverines may experience this as well. Neophobia might explain the avoidance of roads, linear features, and other disturbed areas that are pervasive in wolverine literature (Rowland *et al.* 2003; Krebs *et al.* 2007; Fisher *et al.* 2013).

There are other contenders for mechanisms driving spatial patterns in wolverine behavior. In general, animal behavior can vary with fluctuations in population density (Sih 1984; Dantzer *et al.* 2012). Across these three study areas, variation in behavior differs, but population density is similar between two of the study areas: the Willmore Wilderness and the NPC (Fisher *et al.* 2013; Clevenger and Baruetto 2014). In contrast, wolverine occurrence (a surrogate for density) is much lower in Kananaskis Country (Heim 2015). If density were the sole driver, we may not have detected differences between the Willmore Wilderness and NPC. Because density changes with degree of human footprint, teasing these two factors apart may prove difficult.

Behavior can also vary with the degree of intraguild competition (Amarasekare 2003). Heim (2015) showed that wolverines were less likely to occur at sites with an increasing probability of coyote (*Canis latrans*) and red fox (*Vulpes vulpes*) occurrence and hypothesized that competition may be a factor influencing the differential response to human footprint between wolverine and mesocarnivores. The presence of these potentially competing species varies with human footprint, requiring more research to tease apart these mechanisms. Trapping and food availability (Pyke *et al.* 1977) may also be drivers of behavioral variation. Trapping can induce significant mortality (Krebs *et al.* 2004), and there may be selection for animals that can avoid traps. However, wolverines are trapped in both the Willmore Wilderness and Kananaskis Country, but wolverine detected in the Willmore Wilderness had a greater range of behavior than did wolverine detected in the Kananaskis Country region. Based on an assessment of camera data on prey communities, forage

availability does not significantly differ between these three study areas.

## Caveats

Variation in wolverine behavior could be caused by several sources, but we are able to rule out some competing hypotheses. First, the signal we recorded is not likely due to detection error. Given that the probability of wolverine detection (*sensu* MacKenzie 2006) via cameras approached 1.0 in the Willmore Wilderness (Fisher and Bradbury 2014), and was similar in NPC and Kananaskis Country (Clevenger and Baruetto 2014; Heim 2015), we are confident that the majority of wolverine individuals were sampled using our field methods. Second, despite relatively equal sampling efforts in all three areas, there were fewer wolverines occurring in Kananaskis Country than in the Willmore or NPC, resulting in fewer behavioral observations there. If these observations came from a nonrepresentative sample of KC wolverines more risk-averse than others, a false signal would be generated. However, we have no reason to suspect that is the case due to very high detectability of wolverine using our methods (Fisher and Bradbury 2014). Third, we recognize that our assumptions about what constitute risk-averse behavior for wolverines may be completely incorrect. If these assumptions were not upheld, we would not expect to detect a behavioral signal that varies in space. However, we did find a signal, thus providing evidence to support our assumptions, which were founded in, and consistent with, behavioral theory. Wolverine behavior in the wild has never been assessed before, and spatial variation in behavior is a newly emerging subdiscipline (Lima and Zollner 1996). Moreover, proving risk perception can sometimes be contentious, despite a great body of work on the subject (Lima and Dill 1990). It might instead be the case that wolverines are quicker to climb, and quicker to leave, when conditions are good, although we could not formulate a reasonable guess why this might be. Given this is the first examination of wolverine behavior in the wild, we contend that the spatial pattern is worth considering, and the assumptions worth testing.

In summary, we have shown that there is spatial variability in wolverine behavior, and that this variability corresponds to increases in human footprint. Potential sublethal effects, if any, that such a landscape may impact upon wolverines have yet to be investigated. More importantly however, we contend that the conservation implications of this spatial variability may shed some light on the contentious debate about the mechanisms driving wolverine decline.

## Ecological and conservation implications

Human-driven landscape-scale changes have been widespread (Vitousek *et al.* 1997) and associated with rapid mammalian population decline and range contractions across North America for the past century (Woodroffe 2000; Laliberte and Ripple 2004), with no anticipation of slowing (Woodroffe 2000; Carroll *et al.* 2004; Cumming 2007). However, for many species the ultimate causes of range contractions are still unclear. Despite a rapidly emerging body of research, the mechanisms of wolverine range contractions remain contentiously in debate, to the detriment of conservation. Wolverines have twice been denied protection under the Endangered Species Act by the United States Fish and Wildlife Service, due (in part) to this debate. Wolverines' association with persistent spring snow (Copeland *et al.* 2010; Clevenger and Baruetto 2014) has led some to contend that decreasing spring snow pack resulting from climate change primarily limits wolverine populations and distributions (Brodie and Post 2009; McKelvey *et al.* 2011; Inman *et al.* 2012). Although wolverine occurrence varies to some degree with snow pack across our study landscapes, it varies more strongly with linear features (Fisher *et al.* 2013; Heim 2015), mirroring past research showing negative responses to anthropogenic disturbance (Krebs *et al.* 2007). Before now this debate has compared spatial patterns of occurrence, which can result from multiple ecological processes. Behavior provides a different measure of response to disturbance than does occurrence. The concordance between behavioral response to linear features and large-scale distribution lends support to human footprint as a driver of habitat suitability. If wolverines were driven only by snowpack we would expect no behavioral signal.

Wolverines' behavioral shift in association with human footprint is additional evidence implicating landscape development as one of several mechanisms of population decline and range contraction. We echo others in advocating that conservation research should adopt several analytical approaches – population analysis, distribution analysis, behavioral analysis, etc. – to disentangle mechanisms of decline in complex landscapes.

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## Conflict of Interest

None declared.

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# Wolverines (*Gulo gulo luscus*) on the Rocky Mountain slopes: natural heterogeneity and landscape alteration as predictors of distribution

J.T. Fisher, S. Bradbury, B. Anholt, L. Nolan, L. Roy, J.P. Volpe, and M. Wheatley

**Abstract:** A species' occurrence can be influenced by natural and anthropogenic factors; disentangling these is a precursor to understanding the mechanisms of distribution. Anthropogenic factors may be especially important at contracting range edges. We test this premise for wolverines (*Gulo gulo luscus* L., 1758) at the edge of their Rocky Mountain range in Alberta, Canada, a mosaic of natural heterogeneity and extensive landscape development. As wolverines have a suspected negative response to human activity, we hypothesized their occurrence on the Rockies' slopes is predicted by a combination of natural and anthropogenic features. We surveyed wolverines at 120 sites along a natural and anthropogenic gradient using hair trapping and noninvasive genetic tagging. We used abundance estimation, generalized linear, and hierarchical models to determine whether abundance and occurrence was best predicted by natural land cover, topography, footprint, or a combination. Wolverines were more abundant in rugged areas protected from anthropogenic development. Wolverines were less likely to occur at sites with oil and gas exploration, forest harvest, or burned areas, even after accounting for the effect of topography. The relative paucity of wolverines in human-impacted portions of this range edge suggests that effective conservation requires managing landscape development, and research on the proximal mechanisms behind this relationship.

**Key words:** range edge, wolverine, *Gulo gulo luscus*, occupancy models, abundance estimation, habitat fragmentation, landscape scale.

**Résumé :** La présence d'une espèce en un lieu donné peut être influencée par des facteurs naturels et humains; la compréhension des mécanismes de répartition commence entre autres par la clarification des rôles de ces facteurs. Les facteurs humains peuvent s'avérer particulièrement importants aux bordures d'aires de répartition en contraction. Nous vérifions cette hypothèse pour le carcajou (*Gulo gulo luscus* L., 1758) à la bordure de son aire de répartition dans les montagnes Rocheuses de l'Alberta (Canada), une mosaïque d'hétérogénéité naturelle et de secteurs aménagés. Comme il est soupçonné que le carcajou réagit négativement à l'activité humaine, nous avons postulé que sa présence sur les pentes des Rocheuses peut être prédite par une combinaison de caractéristiques naturelles et anthropiques. Nous avons étudié des carcajous en 120 sites le long d'un gradient naturel et anthropique en utilisant le prélèvement de poils à l'aide de pièges et le marquage génétique non invasif. Nous avons utilisé l'estimation de l'abondance et des modèles linéaires généralisés et hiérarchiques pour déterminer si le meilleur prédicteur de l'abondance et de la présence en un site était la couverture naturelle du sol, le relief, l'empreinte ou une combinaison de ces facteurs. Les carcajous étaient plus abondants dans les secteurs accidentés protégés de l'aménagement humain. Ils étaient moins susceptibles d'être présents dans des sites d'exploitation pétrolière et gazière et de coupe forestière ou dans des brûlis, et ce, même en tenant compte de l'effet du relief. La rareté relative des carcajous dans les portions de cette bordure d'aire de répartition touchées par des impacts d'origine humaine laisse croire que la conservation efficace nécessite la gestion de l'aménagement du paysage et de la recherche sur les mécanismes proximaux qui sous-tendent cette relation. [Traduit par la Rédaction]

**Mots-clés :** bordure d'aire de répartition, carcajou, *Gulo gulo luscus*, modèles d'occupation, estimation de l'abondance, fragmentation de l'habitat, échelle du paysage.

## Introduction

Habitat loss, fragmentation, and alteration are a primary cause of many species' declines, and remain a pervasive anthropogenic phenomenon affecting ecological systems (Fahrig 1997, 2003). Determining the correlates of a species' spatial distribution across heterogeneous (and fragmented) landscapes is a key precursor to elucidating the ecological processes creating those patterns (e.g., Wiens et al. 1993). In particular, disentangling natural from anthropogenic correlates of distribution is a necessary requirement for effective conservation and management, and is often demanded

when species conservation potentially conflicts with economically important landscape development. This task is further complicated because pattern and process can change markedly among landscapes as ecological and spatial contexts change, potentially preventing reliable inference from other landscapes (Fisher et al. 2005; Wheatley and Johnson 2009); this may be particularly true of circumboreal species distributed over highly varied landscapes, such as wolverines (*Gulo gulo* L., 1758).

Wolverines once inhabited boreal, tundra, and mountain habitats across North America and Eurasia (Pasitschniak-Arts and Larivière 1995) but their range has contracted, and populations declined,

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since European colonization (Weaver et al. 1996; Laliberte and Ripple 2004; Aubry et al. 2007). On the eastern edge of their Rocky Mountain range in the province of Alberta, wolverines are listed as “Data deficient”, reflecting a lack of sufficient data for legal designation (Petersen 1997; Alberta Fish and Wildlife Division 2008). Historical trapping records suggest wolverines were distributed across Alberta’s Rocky Mountains, adjacent foothills, and boreal forests (Petersen 1997; Poole and Mowat 2001; Alberta Fish and Wildlife Division 2008), but their current distribution remains unknown and wolverines’ range here receives continued human perturbation.

This landscape is a topographically diverse conifer forest mosaic with oil and gas exploration, forest harvesting, coal mining, roads, and motorized recreational access. All of these impacts remove forest cover or increase human access, but of these oil and gas exploration is the most spatially extensive. It produces very narrow seismic lines—ca. 3 m wide linear corridors cut into forests—crisscrossing the landscape in densities sometimes exceeding 25 km/km<sup>2</sup> (see also Schneider et al. 2003). Seismic lines remove forest cover and increase access for industrial activities (heavy-truck haulage, well pads, and pipelines) and motorized recreation (snowmobiles and off-road vehicles). Extensive spatial linear features and accompanying human activity are known to affect the movement, distribution, and ecological interactions of other mammals in this region (Whittington et al. 2005; Muhly et al. 2011; Fisher et al. 2012; McKenzie et al. 2012).

This anthropogenic mosaic grades into rugged, high-elevation mountain landscapes largely protected from anthropogenic footprint. The current edge of wolverines’ distribution is believed to straddle this gradient (Laliberte and Ripple 2004), but the landscape features contributing to range demarcation (and by inference, range contraction) remain unknown. Natural features likely have an effect; we suspected that habitat alteration has a significant added effect that has gone unnoticed, or has been absorbed into a shifting baseline (sensu Pauly 1995) of wolverine rarity. Wolverines elsewhere avoid human-disturbed areas (Carroll et al. 2001; Rowland et al. 2003; May et al. 2006) and recreational and industrial activity (Krebs et al. 2007). Human activities such as trapping, poaching, and road mortality have accounted for 46% (North America; Krebs et al. 2004) to 52% (Scandinavia; Persson et al. 2009) of known-cause wolverine mortalities across their range. These studies focussed on individual mortality and site selection via telemetry; none have systematically examined wolverine abundance and occurrence across a gradient of landscape development and natural heterogeneity to examine the relative contribution of each in demarcating wolverine distribution. This was our objective.

We hypothesized that wolverines would be more abundant in areas without landscape development and that the probability of wolverine occurrence varies along a spatial gradient as a function of (i) land cover, (ii) topography, and (iii) the degree of landscape alteration, measured as seismic-line density and the percentage of area regenerating from forest fire and timber harvest. We predicted that wolverine abundance and occurrence would increase with land cover and topographic heterogeneity and decrease with habitat alteration.

## Materials and methods

To test these hypotheses, we used noninvasive genetic tagging (NGT) through hair trapping (Waits 2004; Kendall and McKelvey 2008) to survey spatial patterns of wolverine occurrence (e.g., Flagstad et al. 2004; Mulders et al. 2007; Hedmark and Ellegren 2007; Fisher et al. 2011; Magoun et al. 2011). For robust inference, we related these parameters to landscape composition using three approaches: abundance estimation models (Amstrup et al. 2010), species distribution models (Franklin and Miller 2009), and occupancy models (MacKenzie et al. 2002, 2006), ranked in an

information-theoretic framework, to determine those factors that best explained wolverine occurrence.

## Study area

We sampled wolverine occurrence along an approximately east–west gradient (trending to northwest–southeast) spanning the Main Ranges, Front Ranges, and Upper Foothills of the Rocky Mountains in Alberta, Canada (Fig. 1). The area receives high precipitation and winter snow accumulation >2 m. The western end of the gradient is topographically rugged with peaks up to 3000 m, steep-sloped ridges, and wide valley bottoms. Slopes are forested by Engelmann spruce (*Picea engelmanni* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). The mountains grade eastward into subalpine, upper foothills, and montane natural subregions (Downing and Pettapiece 2006), with elevations ranging to 1700 m. Forests are commonly mixed mature lodgepole pine (*Pinus contorta* Douglas ex Loudon) with white spruce (*Picea glauca* (Moench) Voss) or balsam fir (*Abies balsamea* (L.) Mill.). The west is protected from development within the Willmore Wilderness Area, a 4600 km<sup>2</sup> conservation area exempt from forest harvesting, mining, petroleum exploration, roads, and motorized transport, though with recreation, off-road trails, and large burns. From the Willmore, the landscape grades into an increasingly intensive network of roads and seismic lines for petroleum exploration (Fig. 2); conifer forests have been harvested since approximately 1955. This is a mosaic landscape of different forest stand ages, habitat alteration, motorized access, and industrial and recreational human activity. Fur trapping occurs across both landscapes with about <5 animals taken each year (Petersen 1997; Poole and Mowat 2001).

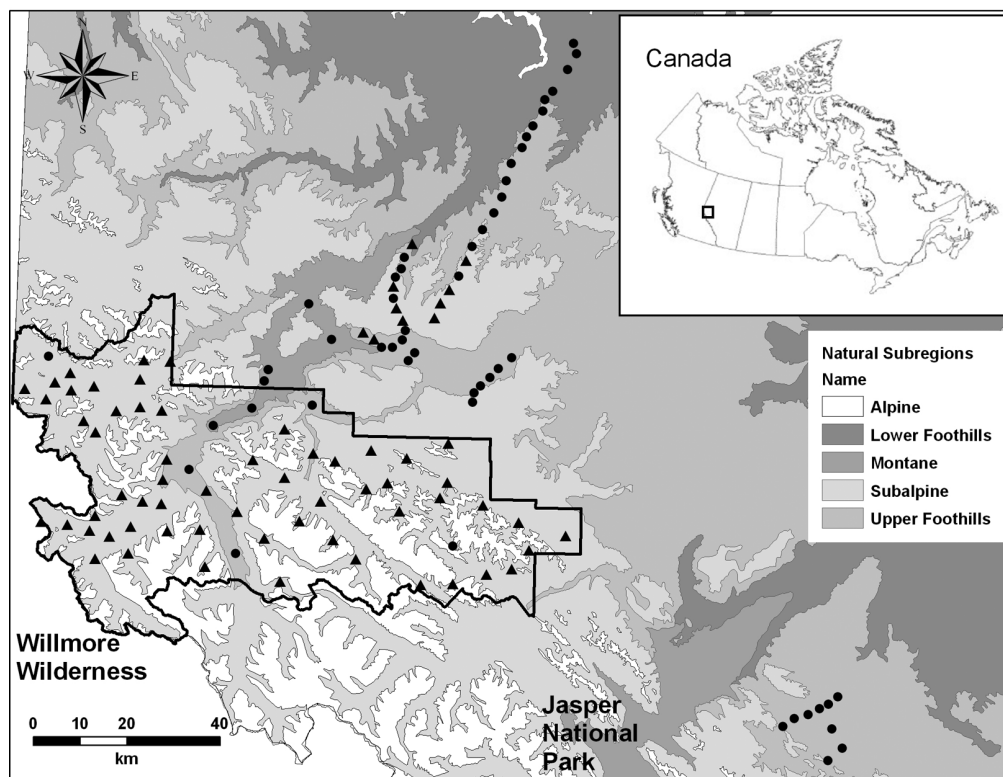
## Experimental design

Methods and design mirror Fisher et al. (2011, 2012). Wolverine occurrence was sampled with noninvasive genetic tagging (NGT) via hair sampling at 120 survey sites (Fig. 3). Hair traps consisted of a tree loosely wrapped with Gaucho® barbed wire (Bekaert, Brussels, Belgium). We baited this tree with a large (ca. 15 kg) skinned beaver carcass and O’Gorman’s LDC extra scent lure (O’Gorman’s Co., Montana, USA). Sampling sites were deployed in early December and sampled monthly through the end of March—a period when food is scarce and bait is most effective in attracting mammals. We sampled within a systematic probabilistic design. Where no motorized access exists, we employed a systematic design constrained by helicopter access and avalanche risk. Sixty-six sites were placed 5727 ± 1574 m (mean ± SD) apart; 30 were sampled in 2006–2007 and 36 in 2007–2008, for a total area of ~4200 km<sup>2</sup> sampled. Where motorized access exists, this systematic design was constrained by road and trail access. Fifty-four foothills sites were deployed 4335 ± 5218 m (mean ± SD) apart. We sampled from early December through March 2004–2005, and again in 2005–2006; the first year’s data were used in abundance estimation only.

Hair samples were collected monthly from the barbed-wire hair traps using sterile techniques. Species were identified from follicular DNA (Wildlife Genetics International, Nelson, British Columbia, Canada). DNA was extracted from hairs using QIAGEN®’s DNEasy™ Tissue Kits (QIAGEN, Hilden, Germany) and analysed to identify species using sequence-based analysis of the 16S rRNA gene of mitochondrial DNA (mtDNA) (sensu Johnson and O’Brien 1997), then compared with a DNA reference library of known mammal species. Samples identified as wolverine were assayed using microsatellite analysis to identify unique individuals using seven microsatellite markers, a number considered adequate for genetic capture–mark–recapture studies (Paetkau 2004). We summed wolverine presences across 3 months (Dec.–Jan., Jan.–Feb., Feb.–Mar.) to yield a 0–3 count of species occurrences at each site—the dependent data for species distribution models. Monthly



**Fig. 1.** Presence (triangles) and absence (circles) of wolverines (*Gulo gulo luscus*) at 120 hair-trapping stations in the Front Ranges, Main Ranges, and Foothills of the Rocky Mountains of west-central Alberta, Canada. This landscape is a mosaic of high-elevation alpine patches, mid-elevation subalpine forests, and montane and foothills forests. The western portion of the study area is protected from anthropogenic development within the Willmore Wilderness Area (black border).



occurrences by individuals informed capture histories for abundance estimation models.

#### Abundance estimation

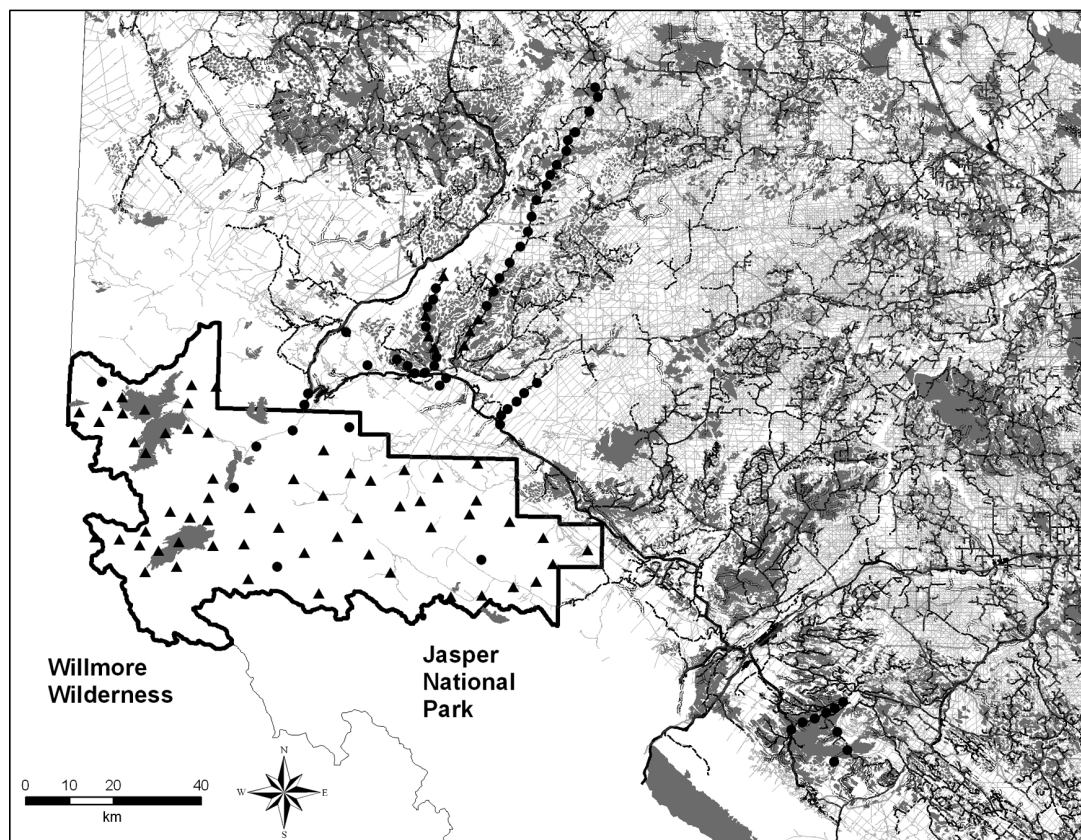
We used the Rcapture package (Baillargeon and Rivest 2007) in program R version 2.14.2 (R Development Core Team 2012) to estimate wolverine abundance. It is not feasible to relate abundance to the gradient of anthropogenic disturbance (since abundance is calculated for discrete areas, whereas the gradient is continuous). However, legislated landscape protection plays a role in the degree of disturbance (together with surface accessibility, existing land tenures, underlying geomorphology, and petroleum prices), so we asked whether wolverine abundance differed between the protected and the unprotected portions of the gradient. Models assumed a demographically closed population: mortality rates among a small population of large carnivores are expected to be near-zero over a 3-month period; our sampling period pre-dates mean kit emergence; dispersal occurs in this period (Inman et al. 2012), but there is no evidence that immigration differs from emigration. Rcapture calculates loglinear mark-recapture models (Cormack 1989) based on flexible assumptions of (i) no variation in hair-trap capture probability among individuals,  $M_0$ ; (ii) variation in space,  $M_{11}$ ; (iii) variation through time,  $M_t$ ; (iv) variation in time and space,  $M_{th}$ ; (v) behavioural variation resulting in a trap effect,  $M_b$ . Chao's (1987), Darroch et al.'s (1993), and Poisson (Rivest and Baillargeon 2007) model variants were also calculated. We selected the model with assumptions (heterogeneity, behaviour, temporal variability) that adequately fit the modelled data—a key requirement of abundance models (Baillargeon and Rivest 2007) that is reflected in low standard errors—balanced by model deviance and parsimony (Akaike's information criterion (AIC) score; Burnham and Anderson 2002). The foothills provided a sample

size too small for mark-recapture analysis. Because wolverine detectability was the same in each study area (see Results), we could assume the ratio of detected animals inside and outside the Willmore approximated the ratio of total animals in these two areas and applied MacKenzie and Kendall's (2002) equation, which estimates relative abundances by adjusting for detection probabilities from occupancy models. In both cases, we divided the abundance estimate from this model by the estimated effective sampling area (e.g., Williams et al. 2002), calculated in GIS (ArcGIS version 9.3; ESRI, Inc., Redlands, California, USA) by buffering points in the sampling array with a 100 km<sup>2</sup> circle, approximating half a mean adult wolverine home range in Canadian mountain landscapes (Banci 1987, 1994).

#### Landscape quantification

Landscape composition (habitat availability) was quantified using a LandSat thematic-mapped GIS land-cover data set incorporating a digital elevation model, with a habitat-identification algorithm that classified 16 land-cover types (McDermid et al. 2009). Eight natural land-cover variables occurred sufficiently often in the study area to allow modelling: closed conifer forest, moderate conifer forest, open conifer forest, mixedwood forest, open wetland, upland shrubs, upland herbaceous habitats, and regenerating areas (for descriptions see McDermid et al. 2009). We calculated a topographic ruggedness index (TRI; Riley et al. 1999) based on a 25 m digital elevation model data from the Alberta Base Data set. Seismic line density (km/km<sup>2</sup>) obtained from government digital map inventory was used as a surrogate for anthropogenic habitat alteration and human activity. Seismic lines mark current and past oil and gas exploration, are correlated with current industrial activity (wellpads, drill sites, and pipelines), and provide recreational motorized access. They are also spatially

**Fig. 2.** Presence (triangles) and absence (circles) of wolverines (*Gulo gulo luscus*) at 120 hair-trapping stations in the Front Ranges, Main Ranges, and Foothills of the Rocky Mountains of west-central Alberta, Canada. The protected area of the Willmore Wilderness (black border) has two large burns (grey patches), whereas the landscape outside is a mosaic of trails and off-road motorized access, seismic lines for oil and gas development (thin lines), roads (thick lines), and forest harvesting (grey patches).



extensive, so lend themselves to modelling habitat alteration at large spatial scales. We used ArcGIS version 9.3 Spatial Analyst, spatial analysis routines, and the Regional Analysis function of Patch Analyst to calculate the percentage of each variable within a 5000 m radius buffer (78.5 km<sup>2</sup>) around each sampling site. This area produces best-fit models for wolverines among a range of scales, and although some overlap among buffers exists, there is no evidence of inflation of type I error or biased estimates (Fisher et al. 2011).

### Hierarchical occupancy modelling

Species detection is often imperfect and decreases with increasing rarity (MacKenzie et al. 2005, 2006). Species occupancy at a site ( $\psi$ ) can be modelled in conjunction with its probability of detection ( $p$ ): the probability of detecting that species if present (MacKenzie et al. 2006). If wolverine  $p$  differed between the design constraints (avalanche vs. trail), this might confound the habitat selection analysis. To ensure that data from across the entire study area could be reliably combined in generalized linear models for the habitat selection analysis, we tested whether  $p$  varied among design constraints, or through time, and whether significant landscape predictors of wolverine occupancy would mirror those from generalized linear models. We used custom single-season hierarchical occupancy models in software PRESENCE version 4.9 (Hines 2006). Detection histories comprised monthly wolverine detections and nondetections at each site, repeated across 3 months. Models assumed  $\psi$  was either constant, or varied with topographic ruggedness, seismic-line density, regenerating fire and cutblocks, or a combination of ruggedness and seismic-

line density. Models further assumed that  $p$  was either constant, or differed among sampling constraints, or through time, or a combination of these. We ranked models by AIC weights and calculated evidence ratios (ERs) to weigh support for each covariate. From per-survey estimates of  $p$ , we calculated the probability of false absence (pfa) for a given survey duration as  $(1 - p)^t$  (Long and Zielinski 2008), with  $t = 3$  independent surveys.

### Habitat selection

We used generalized linear models to test hypotheses about wolverines' relationship to landscape composition, since these are more flexible than occupancy models for this purpose. Because there were no differences in detectability among sites, the response variable was the frequency of monthly wolverine detections and nondetections at each site (0–3), across the study area. Habitat selection varies with habitat availability, and we had no a priori hypotheses about wolverines' relationships with natural landscape features in this landscape, with the exception of regenerating areas. To reduce the seven nondisturbance land-cover variables for model selection (Burnham and Anderson 2002), we used generalized linear models (Poisson errors, log link; R version 2.14.2) and the minimum adequate model approach (Crawley 2007) to identify which land-cover variables best explained wolverine occurrence data. The percentage of mixedwood forest was the only significant land-cover predictor. We additionally retained the "regenerating areas" variable—which included burned and harvested areas greater than ~10 years old—to test hypotheses about disturbed habitat. We then formulated 12 competing hypotheses about the importance of elevation, landscape ruggedness,



**Fig. 3.** Occurrence of wolverines (*Gulo gulo luscus*) was sampled with noninvasive genetic tagging via hair sampling in the Rocky Mountains of Alberta, Canada. Hair traps consisted of a tree loosely wrapped with barbed wire, baited with a large skinned beaver carcass and scent lure. Cameras placed on traps showed this method was effective at detecting wolverines.



mixedwood forest cover, seismic-line density, and regenerating areas in explaining wolverine occurrence (Table 1). We ranked models based on AIC scores and normalized AIC weights (which describe the weight of evidence in support of each model; Burnham and Anderson 2002). We summed AIC weights and calculated ERs (Anderson 2008) to summarize the overall importance of each variable in explaining wolverine occurrence; ER = 2 suggests there is twice the evidence for inclusion of an explanatory variable than its exclusion. We averaged the parameter estimates of the top models using R package MuMIn (Bartón 2012).

## Results

### Abundance

We identified 26 wolverines within the Willmore Wilderness Park (12 males, 14 females, at 66 sites), with overlapping space use (Fig. 4). The  $M_1$  model had low AIC score and low SE (1.3), estimating 27.2 wolverines. However, wolverine capture probability was heterogeneous and varied through time, thus fitting the  $M_{th}$  Chao model assumptions (Table 2), which estimated 28 wolverines (SE = 2.2) in this protected area. Other models' assumptions were unsupported by data, had higher AIC scores, or produced imprecise parameter estimates (Table 2). With 28 wolverines in an effective sampling area of 4140 km<sup>2</sup>, we estimated density as 1 wolverine/148 km<sup>2</sup>, or 6.8 wolverines/1000 km<sup>2</sup>.

In the developed landscape to the east of the Willmore Wilderness, we detected five wolverines in year 1 (two males, three females, at 54 sites). Following pipeline installation through some sites, only three of these were detected in year 2 (Fig. 4). We estimated seven wolverines in this landscape in 2004–2005 and four wolverines in 2005–2006. With an effective sampling area of

2334 km<sup>2</sup> in 2004–2005, we estimated density as 1 wolverine/333 km<sup>2</sup>, or 3 wolverines/1000 km<sup>2</sup>. We sampled 2260 km<sup>2</sup> in 2005–2006 and estimated density as 1 wolverine/565 km<sup>2</sup>, or 1.8 wolverines/1000 km<sup>2</sup>.

### Occupancy and probability of detection

Wolverine detectability did not vary between the two sampling design constraints. There was little evidence that  $p$  varied with sampling constraint alone (ER = 0.03) or with a combination of survey period and sampling constraint (ER = 0.37; Table 3). This evidence indicates that wolverines were equally detectable, when present, regardless of whether the systematic design was constrained by avalanche or road access. Equal detectability among sites justifies the use of combined data across the entire study area within species distribution models for habitat selection analysis. There was some evidence that the probability of wolverine detection increased January through March (ER = 1.22; Fig. 5). The best-supported model suggests that after 3 months of hair-trap surveys, there was an 87% probability of correctly assigning a site as occupied via hair-trapping ( $p_{fa} = 0.13$ ). Accounting for  $p$ , wolverines were more likely to occupy sites with increasingly rugged topography ( $\Sigma AIC$  weights = 0.70, ER = 2.31). There was weak evidence that occupancy varied with both ruggedness and seismic-line density ( $\Sigma AIC$  weights = 0.30, ER = 0.43). There was no evidence that wolverine occupancy varied with amount of regenerating area after timber harvest for fire (ER = 0.0).

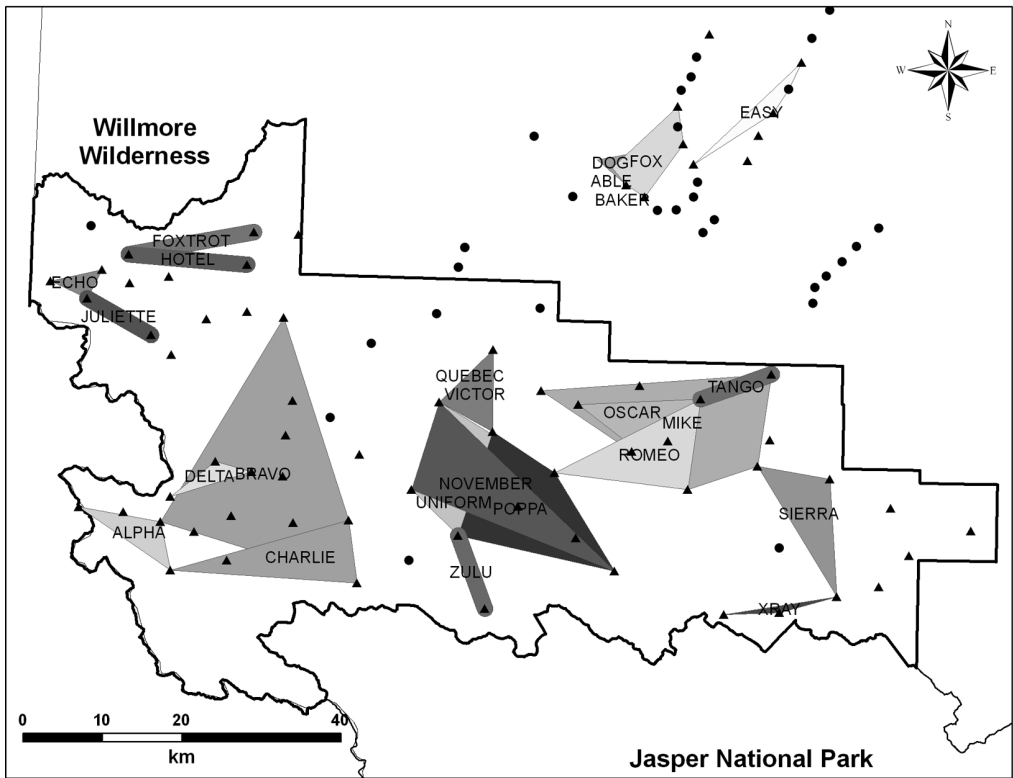
### Habitat selection

Wolverines were more likely to occur in more topographically rugged terrain and areas where industrial activity and habitat

**Table 1.** Hypotheses about association of wolverines (*Gulo gulo luscus*) with features of the Alberta landscape and the corresponding models used to assess the explanatory variables.

Model	Hypothesis: wolverine occurrence is predicted by
1	Global model: proportion of mixedwood forest cover, proportion of regenerating areas, seismic-line density, landscape ruggedness, and sample-site elevation
2	Mixedwood forest cover, regenerating areas, seismic-line density, and landscape ruggedness
3	Mixedwood forest cover, regenerating areas, and seismic-line density
4	Mixedwood forest cover and regenerating areas
5	Regenerating areas only
6	Regenerating areas and seismic-line density
7	Regenerating areas, seismic-line density, and landscape ruggedness
8	Seismic-line density and landscape ruggedness
9	Landscape ruggedness only
10	Mixedwood forest and landscape ruggedness
11	Mixedwood forest and seismic-line density
12	Mixedwood forest, seismic-line density, and landscape ruggedness

**Fig. 4.** Minimum convex polygons (MCP) of “spatial detection ranges” of wolverine (*Gulo gulo luscus*) individuals (identified by names) detected at >1 site in the Main Ranges, Front Ranges, and Foothills of the Rocky Mountains of west-central Alberta, Canada. Twenty-six wolverines were detected within the Willmore Wilderness Park (black border); outside the Park, we detected 5 wolverines in 2004–2005 (shown) and only 3 of these again in 2005–2006. Wolverines were detected but not identified, or detected only once, at triangles outside MCPs and undetected at circles.



alteration was low. Wolverine occurrence was negatively related to seismic-line density ( $ER = 499$ ) and was positively related to landscape ruggedness ( $ER = 61.5$ ) (Table 4). Regenerating areas was related to wolverine occurrence ( $ER = 249$ ), but this relationship is more difficult to decipher. The parameter estimate for REGEN was unstable in the multivariate model; it was negative in the single-variable model, but positive in the multi-variable model (Table 5), since regenerating areas and ruggedness were negatively correlated (see Caveats). Additional variables did not sufficiently improve explanatory power to warrant the penalty for an added parameter (Arnold 2010).

## Discussion

### Wolverine abundance differed between landscapes

The rugged, undeveloped end of the study area had 2–3 times the wolverine density of the less-rugged, developed end. By comparison, with 80% of the spatial effort (but twice the temporal effort) we identified only five wolverines outside the undeveloped Willmore Wilderness. Wolverine densities vary widely across western North America, ranging from 3 to 20 wolverines/1000 km<sup>2</sup>, depending on location, trapping pressure, and habitat quality (Hornocker and Hash 1981; Banci and Harestad 1990; Lofroth and Krebs 2007; Golden et al. 2007; Inman et al. 2012). Many of these

**Table 2.** Estimated abundance of wolverines (*Gulo gulo luscus*) in the Rockies of west-central Alberta, based on Rcapture models with flexible assumptions of (i) no variation in hair-trap capture probability among individuals,  $M_0$ ; (ii) variation among individuals only,  $M_h$ ; (iii) variation through time,  $M_t$ ; (iv) variation in time and individuals,  $M_{th}$ ; (v) behavioural variation resulting in a trap effect,  $M_{\tau}$ ; and Chao's (1987), Darroch et al.'s (1993), and Poisson (Rivest and Baillargeon 2007) model variants.

Model	Abundance estimate	SE	Model deviance	df	AIC score
$M_0$	27.8	1.7	17.09	5	39.72
$M_t$	27.2	1.3	6.58	3	33.21
$M_h$	51.7	38.0	4.36	4	28.99
$M_{bh}$	35.0	23.6	3.98	3	30.61
$M_{th}$ Chao	28.2	2.2	4.75	2	33.38
$M_{th}$ Darroch	33.2	10.9	4.75	2	33.38
$M_{th}$ Poisson	30.0	4.7	4.75	2	33.38

Note: SE, standard error; df, degrees of freedom; AIC, Akaike's information criterion.

estimates are now 20–30 years old and none examines density estimates across landscapes with a marked gradient of habitat alteration. Our estimated 6.8 wolverines/1000 km<sup>2</sup> is similar to neighbouring British Columbia (6.2 wolverines/1000 km<sup>2</sup>; Lofroth and Krebs 2007) and Yukon (5.6 wolverines/1000 km<sup>2</sup>; Banci and Harestad 1990). The estimate of 2–3 wolverines/1000 km<sup>2</sup> is lower than most estimates from western North America, except for recent estimates from Montana (3.5 wolverines/1000 km<sup>2</sup>; Inman et al. 2012). The low density was unexpected, since wolverine populations have supported trapping throughout this region in past decades (Poole and Mowat 2001). Density differences inside and outside the protected area should be considered in the context of their close proximity (Fig. 3), which are <10–20 km apart in some places—much closer than wolverine home-range movements.

We used a standard method for estimating effective sampling area, but newly developed hierarchical models—which model encounter rates on spatial capture arrays as a basis for estimating effective sampling area—provide density estimates that sometimes differ from standard methods (Gardner et al. 2009). A hierarchical density estimator may have changed our conclusions if wolverine densities had differed only slightly inside and outside the park; however, the magnitude of the differences that we observed lends strong support to our conclusions.

#### Wolverines occupied rugged and undeveloped sites

Wolverines were more likely to occur at sites with rugged topography and low anthropogenic footprint. Similarly, May et al. (2006) found that Scandinavian wolverine home-range locations were better predicted by human infrastructure than by habitat. Wolverines avoid roads and other human development in British Columbia (Krebs et al. 2007), Norway (May et al. 2008), Idaho (Copeland et al. 2007), Montana (Carroll et al. 2001), and throughout the northwestern United States (Rowland et al. 2003). Inferences from range retractions coinciding with European colonization may also suggest wolverines are sensitive to human development at continental scales (Laliberte and Ripple 2004; Aubry et al. 2007).

We used seismic lines as an indicator of anthropogenic landscape alteration that causes habitat fragmentation and loss of forest canopy. Fragmentation is not synonymous with a barrier effect, as wolverines often cross these linear features (J.T. Fisher, unpublished snow-tracking data). Fragmentation can, however, alter ecological processes that indirectly affect species' distributions. We hypothesize that interspecific interactions play a role. Wolverines have a broad prey base (Hornocker and Hash 1981; Banci and Harestad 1990; Lofroth et al. 2007) including caribou neonates (Gustine et al. 2006), but reproductive rates are driven by winter availability of ungulate carcasses (Persson 2005). Anthro-

pogenic activity may provide predation refuges for ungulates (e.g., Muhly et al. 2011) thereby reducing carcass availability. Alternatively, competition among carnivores may increase with fragmentation and human activity; seismic lines can alter movement by wolves (*Canis lupus* L., 1758), increasing encounter rates with other species and predation rates (James and Stuart-Smith 2000; Whittington et al. 2005; McKenzie et al. 2012), a factor implicated in the declines of Alberta woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788)) (e.g., Sorensen et al. 2008; Schneider et al. 2010). Seismic lines may therefore increase competition or intraguild predation for wolverines. In Scandinavia, wolves and Eurasian lynx (*Lynx lynx* (L., 1758)) are important influences on wolverine habitat selection (Mattisson et al. 2011a, 2011b; van Dijk et al. 2008a, 2008b). However, interspecific processes have never been examined in the markedly more predator-diverse North American landscape, where wolverines coexist with multiple ursid, canid, felid, and large mustelid species (Fisher et al. 2011); this remains a significant gap.

Habitat alteration and accompanying human activity may degrade habitat quality and depress naturally late-onset reproduction, low reproductive rates, juvenile survival, and population growth rates (Banci and Harestad 1988; Krebs et al. 2004; Persson et al. 2006). Low adult survival in harvested populations (Krebs et al. 2004) shows that anthropogenic mortality is typically additive, often leading to population declines (Lofroth and Ott 2007; Dalerum et al. 2008). Natural predation on wolverines is also higher in trapped than untrapped landscapes (Krebs et al. 2004). Human activity may therefore increase mortality through increased natural or human predation; alternatively denning and rearing areas may be abandoned owing to perceived risk. Whatever the mechanism, we show that the probability of wolverine occurrence decreases across a gradient of increasing anthropogenic landscape development.

Wolverine occurrence also increases with topographic ruggedness, where there is a combination of low- and high-elevation habitats. Bighorn sheep (*Ovis canadensis* Shaw, 1804) (Festa-Bianchet 1988), mule deer (*Odocoileus hemionus* (Rafinesque, 1817)) (D'Eon and Serrouya 2005), and other ungulates winter at lower elevations; in Scandinavia, wolverines showed significant selection for lower-elevation habitats during winter months (Landa et al. 1998). It is possible that wolverines require lower elevations for foraging and higher elevations for predation refuge. Persistent spring snow cover has been hypothesized as important (Schwartz et al. 2009; Copeland et al. 2010) but is not a good predictor at this scale, since spring snow cover was sufficiently persistent across our study landscape to prevent modelling but wolverine occurrence still varied. Finally, rugged areas may offer more den sites in steep, snow-covered slopes with large talus boulders (Magoun and Copeland 1998) and such den sites may be limiting factors for breeding females. However, wolverines also den in flatter landscapes in lower foothills, boreal forest, and arctic tundra.

#### Caveats

Wolverine detectability was imperfect and varied through time. For large mobile organisms, detectability is affected by movement in and out of sites that is assumed to be non-Markovian (Mackenzie et al. 2006). Variable wolverine detectability could result from changes in mobility owing to snow conditions or female denning (which occurs in this period). Understanding the relationship between mobility and detectability is an ongoing area of research. Notably, if wolverine detectability had differed among design constraints—avalanche risk vs. trail access—then estimates from species distribution models could be affected. In fact, all evidence from occupancy models showed that there was no effect of design constraint on wolverine detectability, indicating that the results observed from habitat selection models (which used the same data) were due to ecological signal, not an artefact of sampling, providing confidence in the conclusions.



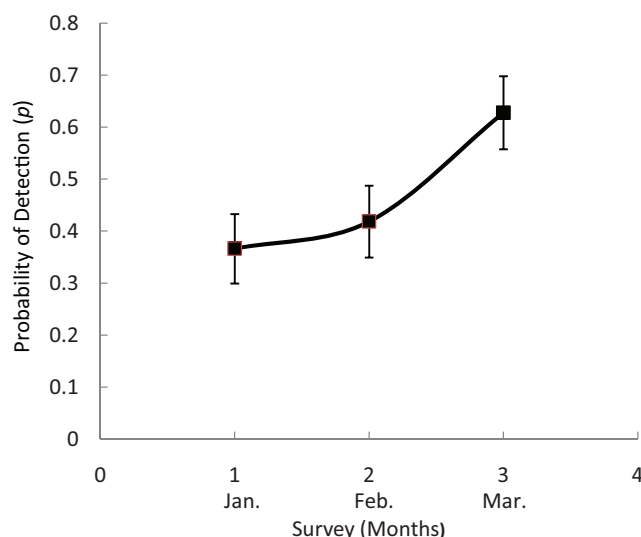
**Table 3.** Selection of wolverine (*Gulo gulo luscus*) occupancy models in west-central Alberta.

Model	AIC	ΔAIC	AIC weight	Model likelihood	No. of parameters*	-2(log likelihood)
$\psi(\text{RUGGED}), p(\text{SURVEY})$	298.96	0.00	0.38	1.00	5.00	288.96
$\psi(\text{RUGGED}), p(\text{SURVEY}+\text{CONSTRAINT})$	299.71	0.75	0.26	0.69	6.00	287.71
$\psi(\text{RUGGED}+\text{SEISMIC}), p(\text{SURVEY})$	300.56	1.60	0.17	0.45	6.00	288.56
$\psi(\text{RUGGED}+\text{SEISMIC}), p(\text{SURVEY}+\text{CONSTRAINT})$	301.50	2.54	0.11	0.28	7.00	287.50
$\psi(\text{RUGGED}), p(.)$	303.79	4.83	0.03	0.09	3.00	297.79
$\psi(\text{RUGGED}), p(\text{CONSTRAINT})$	304.54	5.58	0.02	0.06	4.00	296.54
$\psi(\text{RUGGED}+\text{SEISMIC}), p(.)$	305.41	6.45	0.02	0.04	4.00	297.41
$\psi(\text{RUGGED}+\text{SEISMIC}), p(\text{CONSTRAINT})$	306.36	7.40	0.01	0.02	5.00	296.36
$\psi(\text{SEISMIC}), p(\text{SURVEY}+\text{CONSTRAINT})$	315.83	16.87	0.00	0.00	6.00	303.83
$\psi(\text{SEISMIC}), p(\text{SURVEY})$	318.38	19.42	0.00	0.00	5.00	308.38
$\psi(.), p(\text{SURVEY}+\text{CONSTRAINT})$	319.44	20.48	0.00	0.00	5.00	309.44
$\psi(\text{SEISMIC}), p(\text{CONSTRAINT})$	320.31	21.35	0.00	0.00	4.00	312.31
$\psi(\text{REGEN}), p(\text{SURVEY}+\text{CONSTRAINT})$	320.42	21.46	0.00	0.00	6.00	308.42
$\psi(\text{SEISMIC}), p(.)$	323.10	24.14	0.00	0.00	3.00	317.10
$\psi(.), p(\text{CONSTRAINT})$	323.77	24.81	0.00	0.00	3.00	317.77
$\psi(\text{REGEN}), p(\text{CONSTRAINT})$	324.80	25.84	0.00	0.00	4.00	316.80
$\psi(\text{REGEN}), p(\text{SURVEY})$	352.11	53.15	0.00	0.00	5.00	342.11
$\psi(.), p(\text{SURVEY})$	356.05	57.09	0.00	0.00	4.00	348.05
$\psi(\text{REGEN}), p(.)$	356.80	57.84	0.00	0.00	3.00	350.80
$\psi(.), p(.)$	360.67	61.71	0.00	0.00	2.00	356.67

**Note:** Occupancy ( $\psi$ ) could be constant ( $.$ ), vary with topographic RUGGEDness, SEISMIC line density, or REGENerating forest fires and cutblocks within a 5 km radius. Probability of detection ( $p$ ) could differ by sampling design CONSTRAINTs or among SURVEYs.

\*Number of estimated  $\beta$  parameters in the model.

**Fig. 5.** Wolverines (*Gulo gulo luscus*) were imperfectly detected via hair trapping in the mountain landscape of west-central Alberta, Canada. The probability of detecting wolverines, when present at a site, increased monthly from Dec. through Mar. After three surveys, the probability of false absence was reduced to ~13%. Bars represent standard errors.



After accounting for differences in land cover and topography, developed landscapes with human activity resulted in fewer wolverines across this natural and anthropogenic gradient spanning 30 individuals and an area in excess of 6000 km<sup>2</sup>.

Topography and habitat alteration are unavoidably correlated on this edge of wolverines' distribution. Rugged areas are less likely to be developed, and topographic ruggedness was negatively correlated with both seismic-line density (Pearson's  $r = -0.765$ ,  $p < 0.0001$ ) and regenerating areas (Pearson's  $r = -0.503$ ,  $p < 0.0001$ ). Sampling design could not avoid this correlation, as no large tracts of undeveloped areas remain in subalpine and foothills landscapes (Fig. 2), and the alpine remains primarily undeveloped. This begs the question: is topography masking some

signal from anthropogenic development, or vice versa? Generalized linear modelling provided strong evidence that this correlation does not obfuscate the signal that we detected, as the effects of seismic-line density and regenerating areas remained even after accounting for topographic ruggedness (model 9 vs. model 7,  $\Delta\text{AIC} = 17.33$ ; Table 5). If otherwise, model  $\Delta\text{AIC}$  scores would be smaller, and relative support for either the habitat alteration or the ruggedness models weaker, as they share variance. Instead,  $\Delta\text{AIC}$  and evidence ratios are high—strong support for including both seismic-line density and topography in the model. Hierarchical models provided similar evidence, though the effect of habitat alteration was weaker because some of the variance was attributed to temporal changes in detectability. The response of wolverines to regenerating areas requires more investigation, as multicollinearity among variables changed the direction of this relationship in our models.

#### Implications for wolverine landscape ecology

Wolverine occurrence decreases with increasing anthropogenic landscape development at this range margin, and wolverine density changes very abruptly. Alone, the 30 wolverines in the protected landscape would not likely persist long term (e.g., Reed et al. 2003; Traill et al. 2010), but Alberta wolverines' high genetic variability indicates that they are connected to, and exchanging DNA within, a larger population (Kyle and Strobeck 2001, 2002). However, connectivity may prove detrimental. To the west, wolverines are overharvested and in decline (Lofroth and Ott 2007) and are subject to anthropogenic habitat loss (Krebs et al. 2007). If in addition anthropogenic habitat alteration at the eastern range margin creates a population sink (sensu Pulliam 1988; Pulliam and Danielson 1991), together these may result in population decline. Moreover, though Rocky Mountain wolverine densities are (comparatively) high, density does not equal quality (Wheatley et al. 2002); Brøseth et al. (2010) suggest wolverine population growth rates can decrease as density increases.

We have shown a large-scale spatial correlation between wolverine occurrence and habitat fragmentation on this edge of their range. If fragmentation is altering ecological processes resulting in reduced wolverine distribution and wolverine declines, then identifying the mechanisms responsible should be the next target for investigation. As wolverines exist at very low densities, and

**Table 4.** Selection of wolverine (*Gulo gulo luscus*)–habitat models in west-central Alberta.

Model	Habitat variables	Residual deviance*	Residual df	AIC score	ΔAIC	AIC weight
7	REGEN+SEISMIC+RUGGED	90.4	116	220.23	0	0.539
2	MIXED+REGEN+SEISMIC+RUGGED	89.5	115	221.32	1.09	0.312
1	MIXED+REGEN+SEISMIC+RUGGED+ELEV	89.2	114	223.02	2.79	0.133
3	MIXED+REGEN+SEISMIC	98.4	116	228.19	7.96	0.010
6	REGEN+SEISMIC	103.8	117	231.67	11.44	0.002
12	MIXED+SEISMIC+RUGGED	102.0	116	231.79	11.56	0.002
8	SEISMIC+RUGGED	104.5	117	232.32	12.09	0.001
10	MIXED+RUGGED	105.1	117	232.90	12.67	0.001
11	MIXED+SEISMIC	108.2	117	236.05	15.82	0.000
9	RUGGED	111.7	118	237.56	17.33	0.000
4	MIXED+REGEN	119.7	117	247.49	25.26	0.000
5	REGEN	152.9	118	278.75	27.26	0.000

**Note:** AIC, Akaike's information criterion. MIXED is the proportion of area in mixedwood (co-dominant deciduous and coniferous); REGEN is the proportion of area regenerating (fires and cutblocks <20 years old); SEISMIC is the seismic-line density in kilometres of seismic line per square kilometre of area; RUGGED is the topographic ruggedness index; ELEV is the elevation of the sample site (metres above sea level). Wolverine occurrence counts were modeled against GIS habitat data measured at a 5000 m radius using generalized linear models. The best-supported model suggests regenerating areas, seismic-line density, and topographic ruggedness best explain wolverine occurrence.

\*Null model deviance is 161.7 on 119 degrees of freedom (df).

**Table 5.** Estimated  $\beta$  parameters from wolverine (*Gulo gulo luscus*) species distribution models.

Model	Parameter	Estimate	SE	p	RV1*
7, 2 averaged	Intercept	-3.074	1.082	0.0049	
	REGEN	6.225	1.806	0.0006	1.00
	SEISMIC	-1.874	0.546	0.0007	1.00
	RUGGED	0.002	0.001	0.0013	1.00
	MIXED	-2.692	2.974	0.3704	0.35
5	Intercept	-0.231	0.115	0.0438	
	REGEN	-1.457	0.754	0.0534	

**Note:** Generalized linear models of wolverine occurrence in foothills and mountain landscapes suggest wolverines were positively predicted by topographic ruggedness and negatively predicted by seismic-line density, regenerating areas, and mixedwood forest. SE, standard error.

\*Relative variable importance (RV1) is the sum of AIC weights over all models (Bartón 2012).

over vast areas, and across landscapes with markedly different ecological characteristics and disturbance regimes, multiple inferences from landscape-scale studies will be needed to derive the ecological mechanisms caused by human use of shared landscapes.

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