

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 circum-boreal 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/km² (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

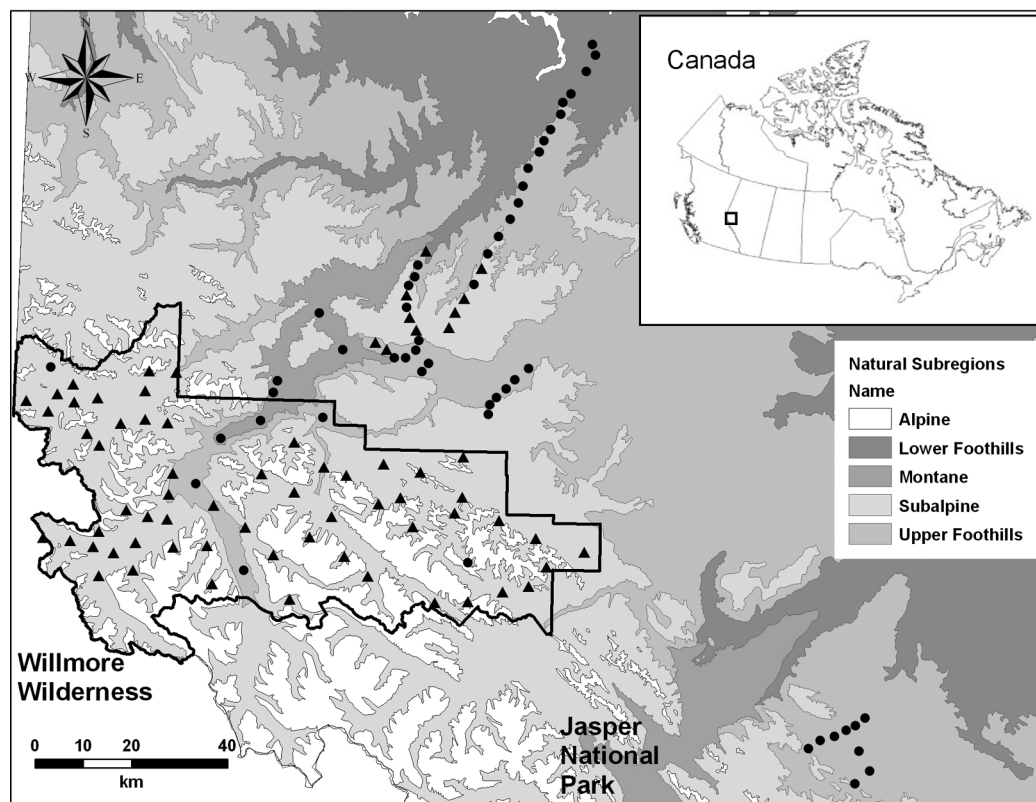
We sampled wolverine occurrence along an approximately east–west gradient (trending to northwest–southeast) spanning the Main Ranges, Front Ranges, and Upper Foothills of the Rocky Mountains in Alberta, Canada (Fig. 1). The area receives high precipitation and winter snow accumulation >2 m. The western 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 km² 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 km² 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

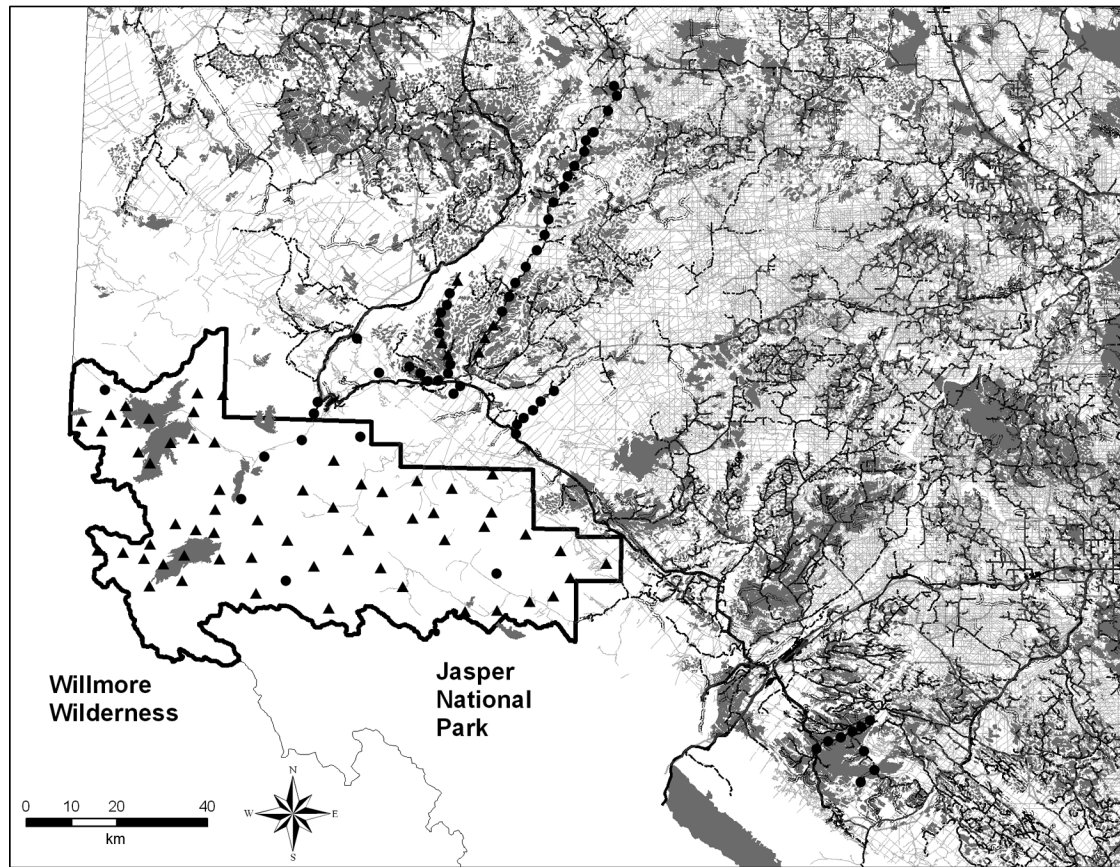
We used the Rcapture package (Baillargeon and Rivest 2007) in program R version 2.14.2 (R Development Core Team 2012) to estimate wolverine abundance. It is not feasible to relate abundance to the gradient of anthropogenic disturbance (since abundance is calculated for discrete areas, whereas the gradient 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 km² 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/km²) 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 km²) 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 (ψ) 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 ψ 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_i 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 km², we estimated density as 1 wolverine/148 km², or 6.8 wolverines/1000 km².

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 km² in 2004–2005, we estimated density as 1 wolverine/333 km², or 3 wolverines/1000 km². We sampled 2260 km² in 2005–2006 and estimated density as 1 wolverine/565 km², or 1.8 wolverines/1000 km².

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 ($pfa = 0.13$). Accounting for p , wolverines were more likely to occupy sites with increasingly rugged topography (ΣAIC weights = 0.70, $ER = 2.31$). There was weak evidence that occupancy varied with both ruggedness and seismic-line density (ΣAIC weights = 0.30, $ER = 0.43$). There was no evidence that wolverine occupancy varied with amount of regenerating area after timber harvest for fire ($ER = 0.0$).

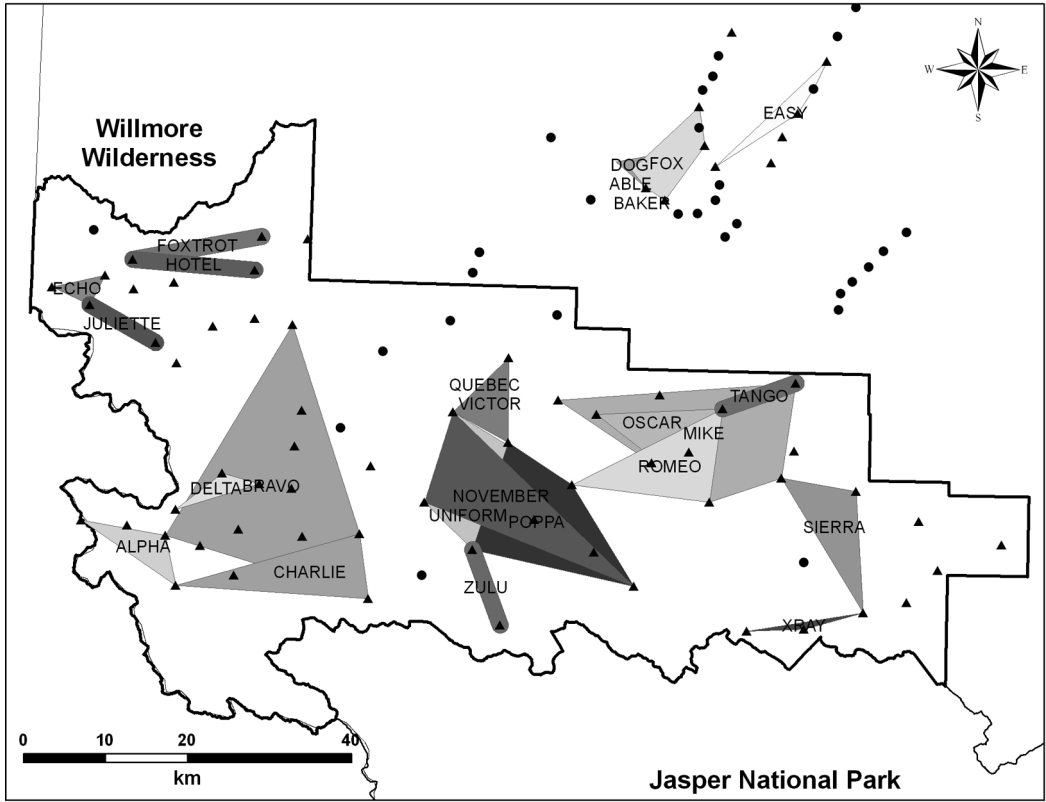
Habitat selection

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 km², 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_t ; (iii) variation through time, M_b ; (iv) variation in time and individuals, M_{th} ; (v) behavioural variation resulting in a trap effect, M_b ; 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_b	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 km² is similar to neighbouring British Columbia (6.2 wolverines/1000 km²; Lofroth and Krebs 2007) and Yukon (5.6 wolverines/1000 km²; Banci and Harestad 1990). The estimate of 2–3 wolverines/1000 km² is lower than most estimates from western North America, except for recent estimates from Montana (3.5 wolverines/1000 km²; 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 Serrouy 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.

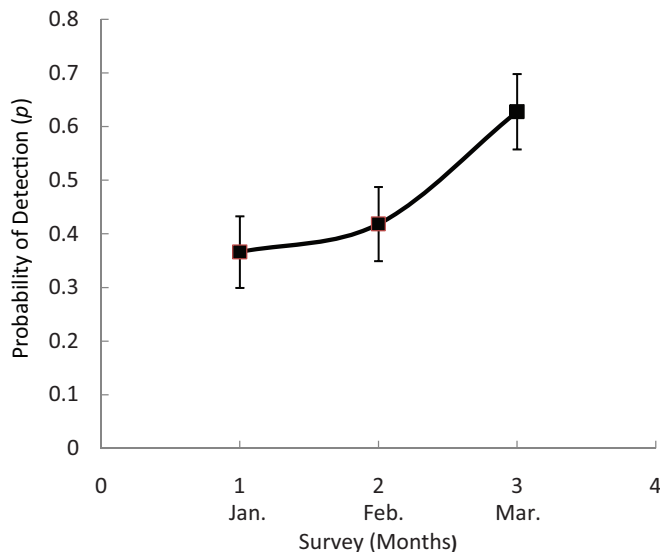
Table 3. Selection of wolverine (*Gulo gulo luscus*) occupancy models in west-central Alberta.

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 (ψ) 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 β 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 km².

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 ΔAIC scores would be smaller, and relative support for either the habitat alteration or the ruggedness models weaker, as they share variance. Instead, ΔAIC 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	25.52	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 β parameters from wolverine (*Gulo gulo luscus*) species distribution models.

Model	Parameter	Estimate	SE	<i>p</i>	RVI*
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 (RVI) 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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References

Alberta Fish and Wildlife Division. 2008. Report of Alberta’s Endangered Species Conservation Committee, June 2006. Alberta SRD, FWD, Edmonton.
Amstrup, S.C., McDonald, T.L., and Manly, B.F. 2010. Handbook of capture–recapture analysis. Princeton University Press, Princeton, N.J.

Anderson, D.R. 2008. Model based inference in the life sciences: a primer on evidence. Springer-Verlag, New York.
Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike’s information criterion. *J. Wildl. Manage.* **74**: 1175–1178. doi:10.2193/2009-367.
Aubry, K.B., McKelvey, K.S., and Copeland, J.P. 2007. Distribution and broadscale habitat relations of the wolverine in the contiguous United States. *J. Wildl. Manage.* **71**: 2147–2158. doi:10.2193/2006-548.
Baillargeon, S., and Rivest, L.-P. 2007. Recapture: loglinear models for capture–recapture in R. *J. Stat. Soft.* **19**: 1–31.
Banci, V.A. 1987. Ecology and behavior of wolverine in Yukon. M.Sc. thesis, Simon Fraser University, Burnaby, B.C.
Banci, V.A. 1994. Wolverine. In *The scientific basis for conserving forest carnivores*, American marten, fisher, lynx, and wolverine in the western United States. Edited by L.F. Ruggiero, K.B. Aubry, S.W. Buskirk, L.J. Lyon, and W.J. Zielinski. Gen. Tech. Rep. No. RM-254, United States Department of Agriculture, Forest Service, Rocky Mountain Range Experiment Station, Fort Collins, Colo. pp. 99–127.
Banci, V., and Harestad, A.S. 1988. Reproduction and natality of wolverine (*Gulo gulo*) in Yukon. *Ann. Zool. Fenn.* **25**: 265–270.
Banci, V., and Harestad, A.S. 1990. Home range and habitat use of wolverines *Gulo gulo* in Yukon, Canada. *Holarct. Ecol.* **13**: 195–200. doi:10.1111/j.1600-0587.1990.tb00608.x.
Bartón, K. 2012. MuMIn: Multi-model inference. R package version 1.7.2 [computer program]. Available from <http://CRAN.R-project.org/package=MuMIn> [accessed 7 June 2013].
Brøseth, H., Flagstad, Ø., Wårdig, C., Johansson, M., and Ellegren, H. 2010. Large-scale noninvasive genetic monitoring of wolverines using scats reveals density dependent survival. *Biol. Conserv.* **143**: 113–120. doi:10.1016/j.biocon.2009.09.012.
Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information–theoretic approach. 2nd ed. Springer-Verlag, New York.
Carroll, C., Noss, R.F., and Paquet, P.C. 2001. Carnivores as focal species for conservation planning in the Rocky Mountain region. *Ecol. Appl.* **11**: 961–980. doi:10.1890/1051-0761(2001)011[0961:CAFSFC]2.0.CO;2.
Chao, A. 1987. Estimating the population size for capture–recapture data with unequal catchability. *Biometrics*, **43**: 783–791. doi:10.2307/2531532. PMID: 3427163.
Copeland, J.P., Peek, J.M., Groves, C.R., Melquist, W.E., McKelvey, K.S., McDaniel, G.W., Long, C.D., and Harris, C.E. 2007. Seasonal habitat associations of the wolverine in central Idaho. *J. Wildl. Manage.* **71**: 2201–2212. doi:10.2193/2006-559.
Copeland, J.P., McKelvey, K.S., Aubry, K.B., Landa, A., Persson, J., Inman, R.M., Krebs, J., Lofroth, E., Golden, H., Squires, J.R., Magoun, A., Schwartz, M.K., Wilmot, J., Copeland, C.L., Yates, R.E., Kojola, I., and May, R. 2010. The bioclimatic envelope of the wolverine (*Gulo gulo*): do climatic constraints limit its geographic distribution? *Can. J. Zool.* **88**(3): 233–246. doi:10.1139/Z09-136.
Cormack, R.M. 1989. Log-linear models for capture–recapture. *Biometrics*, **45**: 395–413. doi:10.2307/2531485.
Crawley, M. 2007. *The R book*. John Wiley and Sons Ltd., Chichester, U.K.
Dalerum, F., Shults, B., and Kunkel, K. 2008. Estimating sustainable harvest in wolverine populations using logistic regression. *J. Wildl. Manage.* **72**: 1125–1132. doi:10.2193/2007-336.
Darroch, J.N., Fienberg, S.E., Glonek, G.F.V., and Junker, B.W. 1993. A three-

- sample multiple-recapture approach to census population estimation with heterogeneous catchability. *J. Am. Stat. Assoc.* **88**: 1137–1148. doi:10.1080/01621459.1993.10476387.
- D'Eon, R.G., and Serrouya, R. 2005. Mule deer seasonal movements and multi-scale resource selection using global positioning system radiotelemetry. *J. Mammal.* **86**: 736–744. doi:10.1644/1545-1542(2005)086[0736:MDSMAM]2.0.CO;2.
- Downing, D.J., and Pettapiece, W.W. 2006. Natural Regions Committee 2006. Natural Regions and Subregions of Alberta. Publ. No. T/852. Government of Alberta, Edmonton.
- Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *J. Wildl. Manage.* **61**: 603–610. doi:10.2307/3802168.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* **34**: 487–515. doi:10.1146/annurev.ecolsys.34.011802.132419.
- Festa-Bianchet, M. 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. *Oecologia*, **75**: 580–586. doi:10.1007/BF00776423.
- Fisher, J.T., and Wilkinson, L. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal Rev.* **35**: 51–81. doi:10.1111/j.1365-2907.2005.00053.x.
- Fisher, J.T., Boutin, S., and Hannon, S.J. 2005. The protean relationship between boreal forest landscape structure and red squirrel distribution at multiple spatial scales. *Landscape Ecol.* **5**: 73–82. doi:10.1007/s10980-004-0677-1.
- Fisher, J.T., Anholt, B., and Volpe, J.P. 2011. Body mass explains characteristic scales of habitat selection in terrestrial mammals. *Ecol. Evol.* **1**: 517–528. doi:10.1002/ecs3.45. PMID:22393519.
- Fisher, J.T., Anholt, B., Bradbury, S., Wheatley, M., and Volpe, J.P. 2012. Spatial segregation of sympatric martens and fishers: the influence of landscapes and species-scapes. *Ecography*, **35**: 1–9. doi:10.1111/j.1600-0587.2012.07556.x.
- Flagstad, Ø., Hedmark, E., Landa, A., Brøseth, H., Persson, J., Andersen, R., Segerstrom, P., and Ellegren, H. 2004. Colonization history and noninvasive monitoring of a re-established wolverine population. *Conserv. Biol.* **18**: 676–688. doi:10.1111/j.1523-1739.2004.00328.x-11.
- Franklin, J., and Miller, J.A. 2009. Mapping species distributions: spatial inference and prediction. Cambridge University Press, Cambridge, U.K.
- Gardner, B., Royle, J.A., and Wegan, M.T. 2009. Hierarchical models for estimating density from DNA mark-recapture studies. *Ecology*, **90**: 1106–1115. doi:10.1890/07-2112.1. PMID:19449704.
- Golden, H.N., Henry, J.D., Becker, E.F., Goldstein, M.I., Morton, J.M., Frost, D., Sr., and Poe, A.J. 2007. Estimating wolverine *Gulo gulo* population size using quadrat sampling of tracks in snow. *Wildl. Biol.* **13**(Suppl. 2): 52–61.
- Gustine, D.D., Parker, K.L., Lay, R.J., Gillingham, M.P., and Heard, D.C. 2006. Calf survival of woodland caribou in a multi-predator ecosystem. *Wildl. Monogr.* **165**: 1–32. doi:10.2193/0084-0173(2006)165[1:CSOWCI]2.0.CO;2.
- Hedmark, E., and Ellegren, H. 2007. DNA-based monitoring of two newly founded Scandinavian wolverine populations. *Conserv. Genet.* **8**: 843–852. doi:10.1007/s10592-006-9231-9.
- Hines, J.E. 2006. PRESENCE—Estimates patch occupancy and related parameters. Version 3.0 Build 100317.0949 Beta [computer program]. USGS-PWRC. Available at <http://www.mbr-pwrc.usgs.gov/software/presence.html> [accessed 13 June 2013].
- Hornocker, M.G., and Hash, H.S. 1981. Ecology of the wolverine in northwestern Montana. *Can. J. Zool.* **59**(7): 1286–1301. doi:10.1139/z81-181.
- Inman, R.M., Packila, M.L., Inman, K.H., McCue, A.J., White, G.C., Persson, J., Aber, B.C., Orme, M.L., Alt, K.L., Cain, S.L., Fredrick, J.A., Oakleaf, B.J., and Sartorius, S.S. 2012. Spatial ecology of wolverines at the southern periphery of distribution. *J. Wildl. Manage.* **76**: 778–792. doi:10.1002/jwmg.289.
- James, A.R.C., and Stuart-Smith, A.K. 2000. Distribution of caribou and wolves in relation to linear corridors. *J. Wildl. Manage.* **64**: 154–159. doi:10.2307/3802985.
- Johnson, W., and O'Brien, S.J. 1997. Phylogenetic reconstruction of the Felidae using 16S rRNA and NADH-5 mitochondrial genes. *J. Mol. Evol.* **44**(Suppl. 1): S98–S116. doi:10.1007/PL00000060.
- Kendall, K.C., and McKelvey, K.S. 2008. Hair collection. In *Noninvasive survey methods for carnivores*. Edited by R. Long, P. Mackay, J. Ray, and W. Zielinski. Island Press, Washington, D.C. pp. 141–182.
- Krebs, J., Lofroth, E., Copeland, J., Banci, V., Cooley, D., Golden, H., Magoun, A., Mulders, R., and Shults, B. 2004. Synthesis of survival rates and causes of mortality in North American wolverines. *J. Wildl. Manage.* **68**: 493–502. doi:10.2193/0022-541X(2004)068[0493:SOSRAC]2.0.CO;2.
- Krebs, J., Lofroth, E.C., and Parfitt, I. 2007. Multiscale habitat use by wolverines in British Columbia, Canada. *J. Wildl. Manage.* **71**: 2180–2192. doi:10.2193/2007-099.
- Kyle, C.J., and Strobeck, C. 2001. Genetic structure of North American wolverine (*Gulo gulo*) populations. *Mol. Ecol.* **10**: 337–347. doi:10.1046/j.1365-294x.2001.01222.x. PMID:11298949.
- Kyle, C.J., and Strobeck, C. 2002. Connectivity of peripheral and core populations of North American wolverines. *J. Mammal.* **83**: 1141–1150. doi:10.1644/1545-1542(2002)083<1141:COPACP>2.0.CO;2.
- Laliberte, A.S., and Ripple, W.J. 2004. Range contractions of North American carnivores and ungulates. *BioScience*, **54**: 123–138. doi:10.1641/0006-3568(2004)054[0123:RCONAC]2.0.CO;2.
- Landa, A., Strand, O., Linnell, J.D.C., and Skogland, T. 1998. Home-range sizes and altitude selection for arctic foxes and wolverines in an alpine environment. *Can. J. Zool.* **76**(3): 448–457. doi:10.1139/z97-209.
- Lofroth, E.C., and Krebs, J. 2007. The abundance and distribution of wolverines in British Columbia, Canada. *J. Wildl. Manage.* **71**: 2159–2169. doi:10.2193/2007-094.
- Lofroth, E.C., and Ott, P.K. 2007. Assessment of the sustainability of wolverine harvest in British Columbia, Canada. *J. Wildl. Manage.* **71**: 2193–2200. doi:10.2193/2007-095.
- Lofroth, E.C., Krebs, J.A., Harrower, W.L., and Lewis, D. 2007. Food habits of wolverine *Gulo gulo* in montane ecosystems of British Columbia, Canada. *Wildl. Biol.* **13**(Suppl. 2): 31–37. doi:10.2981/0909-6396(2007)13[31:FHOWGG]2.0.CO;2.
- Long, R., and Zielinski, W. 2008. Designing effective noninvasive carnivore surveys. In *Noninvasive survey methods for carnivores*. Edited by R. Long, P. Mackay, J. Ray, and W. Zielinski. Island Press, Washington, D.C. pp. 8–44.
- MacKenzie, D.I., and Kendall, W.L. 2002. How should detection probability be incorporated into estimates of relative abundance? *Ecology*, **83**: 2387–2393. doi:10.1890/0012-9658(2002)083[2387:HSDPBI]2.0.CO;2.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A., and Langtimm, C.A. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, **83**: 2248–2255. doi:10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2.
- MacKenzie, D.I., Nichols, J.D., Sutton, N., Kawanishi, K., and Bailey, L.L. 2005. Improving inferences in population studies of rare species that are detected imperfectly. *Ecology*, **86**: 1101–1113. doi:10.1890/04-1060.
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., and Hines, J.E. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier, New York.
- Magoun, A.J., and Copeland, J.P. 1998. Characteristics of wolverine reproductive den sites. *J. Wildl. Manage.* **62**: 1313–1320. doi:10.2307/3801996.
- Magoun, A.J., Long, C.D., Schwartz, M.K., Pilgrim, K.L., Lowell, R.E., and Valkenburg, P. 2011. Integrating motion-detection cameras and hair snags for wolverine identification. *J. Wildl. Manage.* **75**: 731–739. doi:10.1002/jwmg.107.
- Mattisson, J., Andrén, H., Persson, J., and Segerström, P. 2011a. Influence of intraguild interactions on resource use by wolverines and Eurasian lynx. *J. Mammal.* **92**(6): 1321–1330. doi:10.1644/11-MAMM-A-099.1.
- Mattisson, J., Persson, J., Andrén, H., and Segerström, P. 2011b. Temporal and spatial interactions between an obligate predator, the Eurasian lynx (*Lynx lynx*), and a facultative scavenger, the wolverine (*Gulo gulo*). *Can. J. Zool.* **89**(2): 79–89. doi:10.1139/Z10-097.
- May, R., Landa, A., van Dijk, J., Linnell, J.D.C., and Andersen, R. 2006. Impact of infrastructure on habitat selection of wolverines *Gulo gulo*. *Wildl. Biol.* **12**: 285–295. doi:10.2981/0909-6396(2006)12[285:IOI0HS]2.0.CO;2.
- May, R., van Dijk, J., Wabakken, P., Swenson, J.E., Linnell, J.D.C., Zimmermann, B., Odden, J., Pedersen, H.C., Andersen, R., and Landa, A. 2008. Habitat differentiation within the large-carnivore community of Norway's multiple-use landscapes. *J. Appl. Ecol.* **45**: 1382–1391. doi:10.1111/j.1365-2664.2008.01527.x. PMID:19330031.
- McDermid, G.J., Hall, R.J., Sanchez-Azofeifa, G.A., Franklin, S.E., Stenhouse, G.B., Kobliuk, T., and LeDrew, E.F. 2009. Remote sensing and forest inventory for wildlife habitat assessment. *For. Ecol. Manage.* **257**: 2262–2269. doi:10.1016/j.foreco.2009.03.005.
- McKenzie, H.W., Merrill, E.H., Spiteri, R.J., and Lewis, M.A. 2012. How linear features alter predator movement and the functional response. *Interface Focus*, **2**(2): 205–216. doi:10.1098/rsfs.2011.0086.
- Muhly, T.B., Semeniuk, C., Massolo, A., Hickman, L., and Musiani, M. 2011. Human activity helps prey win the predator-prey space race. *PLoS ONE*, **6**: e17050. doi:10.1371/journal.pone.0017050. PMID:21399682.
- Mulders, R., Boulanger, J., and Paetkau, D. 2007. Estimation of population size for wolverines *Gulo gulo* at Daring Lake, Northwest Territories, using DNA based mark-recapture methods. *Wildl. Biol.* **13**(Suppl. 2): 38–51. doi:10.2981/0909-6396(2007)13[38:EOPSFV]2.0.CO;2.
- Paetkau, D. 2004. The optimal number of markers in genetic capture-mark-recapture studies. *J. Wildl. Manage.* **68**: 449–452. doi:10.2193/0022-541X(2004)068[0449:TONOMI]2.0.CO;2.
- Pasitschniak-Arts, M., and Larivière, S. 1995. *Gulo gulo*. *Mamm. Species*, **499**: 1–10.
- Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. *Trends Ecol. Evol.* **10**: 430. doi:10.1016/S0169-5347(00)89171-5. PMID:21237093.
- Persson, J. 2005. Female wolverine (*Gulo gulo*) reproduction: reproductive costs and winter food availability. *Can. J. Zool.* **83**(11): 1453–1459. doi:10.1139/z05-143.
- Persson, J., Landa, A., Andersen, R., and Segerström, P. 2006. Reproductive characteristics of female wolverines (*Gulo gulo*) in Scandinavia. *J. Mammal.* **87**: 75–79. doi:10.1644/04-1.
- Persson, J., Ericsson, G., and Segerström, P. 2009. Human caused mortality in the endangered Scandinavian wolverine population. *Biol. Conserv.* **142**: 325–331. doi:10.1016/j.biocon.2008.10.028.
- Petersen, S. 1997. Status of the Wolverine, *Gulo gulo*, in Alberta. Wildlife Status Report No. 2, Alberta Environmental Protection, Wildlife Management Division, Edmonton.
- Poole, K., and Mowat, G. 2001. Alberta Furbearer Harvest Data Analysis. Alberta Species at Risk Report No. 31, Alberta Sustainable Resource Development, Fish and Wildlife Division, Edmonton.

- Pulliam, H.R. 1988. Sources, sinks, and population regulation. *Am. Nat.* **132**: 652–661. doi:10.1086/284880.
- Pulliam, H.R., and Danielson, B.J. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *Am. Nat.* **137**(Suppl. 1): S5–S66. doi:10.1086/285139.
- R Development Core Team. 2012. R: a language and environment for statistical computing. Version 2.14.2 [computer program]. R Foundation for Statistical Computing, Vienna, Austria. Available from <http://www.r-project.org/>.
- Reed, D.H., O'Grady, J.J., Brook, B.W., Ballou, J.D., and Frankham, R. 2003. Estimates of minimum viable population sizes for vertebrates and factors influencing those estimates. *Biol. Conserv.* **113**: 23–34. doi:10.1016/S0006-3207(02)00346-4.
- Riley, S.J., DeGloria, S.D., and Elliot, R. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. *Intermountain J. Sci.* **5**: 1–4.
- Rivest, L.P., and Baillargeon, S. 2007. Applications and extensions of Chao's moment estimator for the size of a closed population. *Biometrics*, **63**: 999–1006. doi:10.1111/j.1541-0420.2007.00779.x. PMID:17425635.
- Rowland, M.M., Wisdom, M.J., Johnson, D.H., Wales, B.C., Copeland, J.P., and Edelman, F.B. 2003. Evaluation of landscape models for wolverines in the interior Northwest, United States of America. *J. Mammal.* **84**: 92–105. doi:10.1644/1545-1542(2003)084<0092:EOLMFV>2.0.CO;2.
- Schneider, R.R., Stelfox, J.B., Boutin, S., and Wasel, S. 2003. Managing the cumulative impacts of land-uses in the Western Canadian Sedimentary Basin: a modeling approach. *Conserv. Ecol.* **7**: 8.
- Schneider, R.R., Hauer, G., Adamowicz, W.L., and Boutin, S. 2010. Triage for conserving populations of threatened species: the case of woodland caribou in Alberta. *Biol. Conserv.* **143**: 1603–1611. doi:10.1016/j.biocon.2010.04.002.
- Schwartz, M.K., Copeland, J.P., Anderson, N.J., Squires, J.R., Inman, R.M., McKelvey, K.S., Pilgrim, K.L., Waits, L.P., and Cushman, S.A. 2009. Wolverine gene flow across a narrow climatic niche. *Ecology*, **90**: 3222–3232. doi:10.1890/08-1287.1. PMID:19967877.
- Sorensen, T., McLoughlin, P.D., Hervieux, D., Dzus, E., Nolan, J., Wynes, B., and Boutin, S. 2008. Determining sustainable levels of cumulative effects for boreal caribou. *J. Wildl. Manage.* **72**: 900–905. doi:10.2193/2007-079.
- Traill, L.W., Brook, B.W., Frankham, R.R., and Bradshaw, C.J.A. 2010. Pragmatic population viability targets in a rapidly changing world. *Biol. Conserv.* **143**: 28–34. doi:10.1016/j.biocon.2009.09.001.
- van Dijk, J., Andersen, T., May, R., Andersen, R., Andersen, R., and Landa, A. 2008a. Foraging strategies of wolverines within a predator guild. *Can. J. Zool.* **86**(9): 966–975. doi:10.1139/Z08-073.
- van Dijk, J., Gustavsen, L., Mysterud, A., May, R., Flagstad, Ø., Brøseth, H., Andersen, R., Andersen, R., Steen, H., and Landa, A. 2008b. Diet shift of a facultative scavenger, the wolverine, following recolonization of wolves. *J. Anim. Ecol.* **77**(6): 1183–1190. doi:10.1111/j.1365-2656.2008.01445.x. PMID:18657209.
- Waits, L.P. 2004. Using noninvasive genetic sampling to detect and estimate abundance of rare wildlife species. In *Sampling rare or elusive species*. Edited by W.L. Thompson. Island Press, Washington, D.C. pp. 211–228.
- Weaver, J.L., Paquet, P.C., and Ruggiero, L.F. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. *Conserv. Biol.* **10**: 964–976. doi:10.1046/j.1523-1739.1996.10040964.x.
- Wheatley, M., and Johnson, C. 2009. Factors limiting our understanding of ecological scale. *Ecol. Complex.* **6**: 150–159. doi:10.1016/j.ecocom.2008.10.011.
- Wheatley, M., Larsen, K.W., and Boutin, S. 2002. Does density reflect habitat quality for North American red squirrels during a spruce-cone failure? *J. Mammal.* **83**: 716–727. doi:10.1644/1545-1542(2002)083<0716:DDRHQF>2.0.CO;2.
- Whittington, J., St. Clair, C.C., and Mercer, G. 2005. Spatial responses of wolves to roads and trails in mountain valleys. *Ecol. Appl.* **15**: 543–553. doi:10.1890/03-5317.
- Wiens, J.A., Stenseth, N.C., Van Horne, B., and Ims, R.A. 1993. Ecological mechanisms and landscape ecology. *Oikos*, **66**: 369–380. doi:10.2307/3544931.
- Williams, B.K., Nichols, J.D., and Conroy, M.J. 2002. Analysis and management of animal populations. Academic Press, New York.