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ARTICLE

Effects of predation risk on elk (*Cervus elaphus*) landscape use in a wolf (*Canis lupus*) dominated system

Cristina Eisenberg, David E. Hibbs, and William J. Ripple

Abstract: Food acquisition and predation avoidance are key drivers of herbivore behaviour. We investigated the interaction of top-down (predator) and bottom-up (food, fire, thermal) effects by measuring the relationship between wolf (*Canis lupus* L., 1758) predation risk perceived by elk (*Cervus elaphus* L., 1758) and elk landscape use. We conducted fecal pellet and wolf scat surveys in three valleys with three wolf population levels (Saint Mary: low; Waterton: moderate; North Fork: high). In the North Fork, 90% of quaking aspen (*Populus tremuloides* Michx.) stands burned recently; the other valleys had no fire. We created predictive models of elk pellet density that incorporated bottom-up and top-down variables. All valleys had a high elk pellet density (≥10 per 100 m^2). Wolf scat density was similar where there was no fire, but one order of magnitude greater in burned areas. Elk pellet density was lower in the North Fork, a predation-related response. In all valleys, site-specific elk density declined as impediments to detecting or escaping wolves increased, and elk avoided aspen, except for North Fork unburned areas. Models that best predicted elk density contained bottom-up and top-down effects. At local scales, high predation risk negatively influence elk occurrence, suggesting that even with minimal wolf exposure elk avoid risky sites.

Key words: elk, *Cervus elaphus*, predation risk, wolves, *Canis lupus*, trophic cascades.

Résumé : L'acquisition de nourriture et l'évitement de la prédation sont des moteurs clés du comportement des herbivores. Nous avons examiné l'interaction d'effets descendants (prédateur) et ascendants (nourriture, feu, chaleur) en mesurant le lien entre les risques de prédation par des loups (*Canis lupus* L., 1758) perçus par les wapitis (*Cervus elaphus* L., 1758) et l'utilisation du paysage par ces derniers. Nous avons effectué des levés de boulettes fécales et de fèces de loup dans trois vallées présentant des populations de loups de trois niveaux différents (Saint Mary : faible; Waterton : modérée; North Fork : élevée). Dans la vallée de la North Fork, 90 % des peuplements de trembles (*Populus tremuloides* Michx.) avaient brûlé récemment; aucun feu n'avait eu lieu dans les deux autres vallées. Nous avons créé des modèles prédictifs de la densité des boulettes de wapiti qui intègrent des variables ascendantes et descendantes. Toutes les vallées présentaient des densités de boulettes de wapiti élevées (≥10 par 100 m^2). La densité des fèces de loup était semblable là où il n'y avait pas eu de feu, mais d'un ordre de grandeur plus élevée dans les zones brûlées. La densité des boulettes de wapiti était plus faible dans la vallée de la North Fork, une réaction reliée à la prédation. Dans toutes les vallées, la densité de wapitis propres à des sites précis diminuait inversement à l'augmentation des entraves à la détection des loups ou à la fuite de ces derniers, et les wapitis évitaient les trembles, sauf dans les zones non brûlées de la North Fork. Les modèles qui prédisaient le mieux la densité des wapitis contenaient des effets ascendants et descendants. Aux échelles locales, un risque de prédation élevé exerce une influence négative sur la présence de wapitis, donnant à penser que, même si l'exposition aux loups est très faible, les wapitis évitent les sites à risque. [Traduit par la Rédaction]

Mots-clés : wapiti, *Cervus elaphus*, risque de prédation, loup, *Canis lupus*, cascades trophiques.

Introduction

Animals select habitat and move within a landscape using complex decision-making strategies. Food acquisition and quality, as well as predation, are important drivers of animal behaviour and landscape use (Brown et al. 1999). The ability of an animal to assess and behaviourally control its risk of being preyed upon strongly influences feeding decisions (Lima and Dill 1990). In a low predator-density system, herbivores will eat the most nutritionally profitable foods before browsing foods of lower nutritional value. In a high predator-density system, herbivore decisions about food consumption are mediated by avoidance of predation (Stephens and Krebs 1986). Landscape features can increase the risk of predation (Ripple and Beschta 2004; Hebblewhite et al. 2005*a*; Kauffman et al. 2007; Painter et al. 2015) and can cause prey to alter foraging decisions (Laundré et al. 2001; Hebblewhite et al. 2005*b*). For example, in Yellowstone National Park (YNP), Fortin et al. (2005) found that as the risk of encountering wolves (*Canis lupus* L., 1758) increased, elk (*Cervus elaphus* L., 1758) spent less time foraging in stands of quaking aspen (*Populus tremuloides* Michx.; hence referred to aspen). These authors found that elk respond to wolves by shifting habitat selection, utilizing more open areas when wolves are present, and spending less time browsing in aspen stands, despite the highly nutritional value of aspen for elk (Cook 2002).

The above studies suggest that by altering prey utilization of vegetation and thus changing vegetation dynamics, predation can initiate trophic cascades. Paine (1980) defined trophic cascades as food-web relationships in which a dominant (e.g., "apex") predator influences the density and (or) behaviour of its prey, and in doing so indirectly affects other taxa. Apex predators thereby create top-down influences in ecosystems (Hairston et al. 1960; Paine 1980; Schmitz et al. 2000).

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C. Eisenberg and D.E. Hibbs. College of Forestry, Oregon State University, Corvallis, OR 97331, USA.
W.J. Ripple. Department of Forest Ecosystems and Society, College of Forestry, Oregon State University, Corvallis, OR 97331, USA.
Corresponding author: Cristina Eisenberg (e-mail: cristina.eisenberg@oregonstate.edu).

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In addition to the top-down effects in ecosystems described above, energy flows through ecosystems from the bottom-up. Bottom-up effects include factors that can increase or decrease the abundance and productivity of plants, such as moisture, disturbance (e.g., fire), and solar radiation (Murdoch 1966; Menge et al. 1999). Because plants have primacy in energy production, these dynamics also structure ecosystems by influencing herbivore abundance and landscape use (Power 1992).

In North America, among the most studied wildlife habitat-selection relationships are those that focus on ungulates. Elk have been the subject of many such studies because of the economic value of this species and its impact on habitat for other taxa due to intensive consumption of resources (Wagner 2006). Factors historically linked to elk habitat use include food, climate, topography (Skovlin et al. 2002), and human disturbance (Frair et al. 2005). Scientists have linked predator presence to elk behaviour and habitat use (Ripple et al. 2001; Ripple and Beschta 2006), focusing on the potential influence of the gray wolf, the leading predator of elk (Geist 2002; Soulé et al. 2003).

The mid-1990s northern Rocky Mountain wolf reintroduction created opportunities to test these relationships observationally (Smith et al. 2003). Emerging research from YNP stimulated a scientific debate about whether wolves create behavioural changes in elk via predation risk, and if so, whether these effects are indirectly influencing other trophic levels (Creel and Christianson 2009; Kauffman et al 2010; Ripple and Beschta 2012). Optimal foraging theory predicts a shift of elk away from foraging in high predation risk sites, despite the presence of nutritious foods (Stephens and Krebs 1986). Some authors have documented, using fecal pellet counts, elk avoidance and differential use of aspen habitat in areas with a wolf population and avoidance of places with impediments to detecting and escaping wolves (White et al. 2003; Kuijper et al. 2013). Other YNP research alternatively suggests that topography and vegetation characteristics that may increase wolf predation risk have no influence on elk use of habitat (Creel and Christianson 2009; Kauffman et al 2010). A recent review highlights the complexity of wolf-related trophic cascades in YNP and Isle Royale National Park and suggests that these multicausal ecological relationships do not generate definitive answers to research questions (Peterson et al. 2014).

The objective of this study was to determine whether risk of predation by wolves influences how elk use a winter range landscape. In all ecological settings, top-down (predator-driven) effects operate along with bottom-up (resource-driven) effects, which include factors that increase or decrease plant abundance, thus changing herbivore habitat (Polis and Strong 1996). Therefore, we designed our hypotheses to explore top-down and bottom-up effects together. First, we investigated whether predation risk would be a strong driver of elk habitat use. We then examined the interaction of observed elk responses to bottom-up and top-down factors in their use of habitat on a landscape scale. We predicted that elk occurrence would increase with food palatability and landscape radiant heat, and decrease with an increase in putative impediments to detecting and escaping wolves. These hypotheses were used to generate models that contained predictive variables that best described the data collected, using an information-theoretic approach. We used these models to explore the influence of cover types (e.g., grass, aspen, shrub, conifer, bare mineral soil) on our response variable, elk pellet pile density.

Materials and methods

Study area

The study setting spans the US–Canada border within Glacier National Park (GNP), Montana, USA, and Waterton Lakes National Park (WLNP), Alberta, Canada, in the Crown of the Continent Ecosystem. Within these parks we studied three geographically separate valleys (Fig. 1), all of which are elk winter range: (1) the Saint Mary Valley, in eastern GNP; (2) the Waterton Valley, in eastern WLNP; and (3) the North Fork Valley in western GNP. Ecological resources are comparable in all valleys (e.g., climate, soil, elevation), as is precipitation quantity and temporal distribution (Achuff et al. 2005; Hop et al. 2007; Parks Canada 2010; Western Regional Climate Center 2010), resulting in similar biotic communities. The valleys consist of low-elevation (1024–1700 m) grasslands dominated by rough fescue (*Festuca scabrella* Torr.) and provide elk with snow depths <0.7 m and wind protection in the winter. Secondary foods include aspen, shrubs, and conifers (Singer 1979; Achuff et al. 2005). In the North Fork, 90% of aspen stands have burned between 1988 and 2003. Measured areas included 1392, 2741, and 5705 ha for Saint Mary, Waterton, and the North Fork study areas, respectively (ArcGIS version 10.1).

Wolves are the dominant predator of elk in our study area (Kunkel et al. 1999). Other species that prey on elk include cougar (*Puma concolor* (L., 1771)), grizzly bear (*Ursus arctos horribilis* Ord, 1815), and black bear (*Ursus americanus* Pallas, 1780). However, these species did not have a large impact on elk in our study, because bears hibernate when elk are on their winter range and cougars prey mostly on deer (genus *Odocoileus* Rafinesque, 1832) in the Crown of the Continent Ecosystem (Kunkel and Pletscher 2001; Banfield 2010).

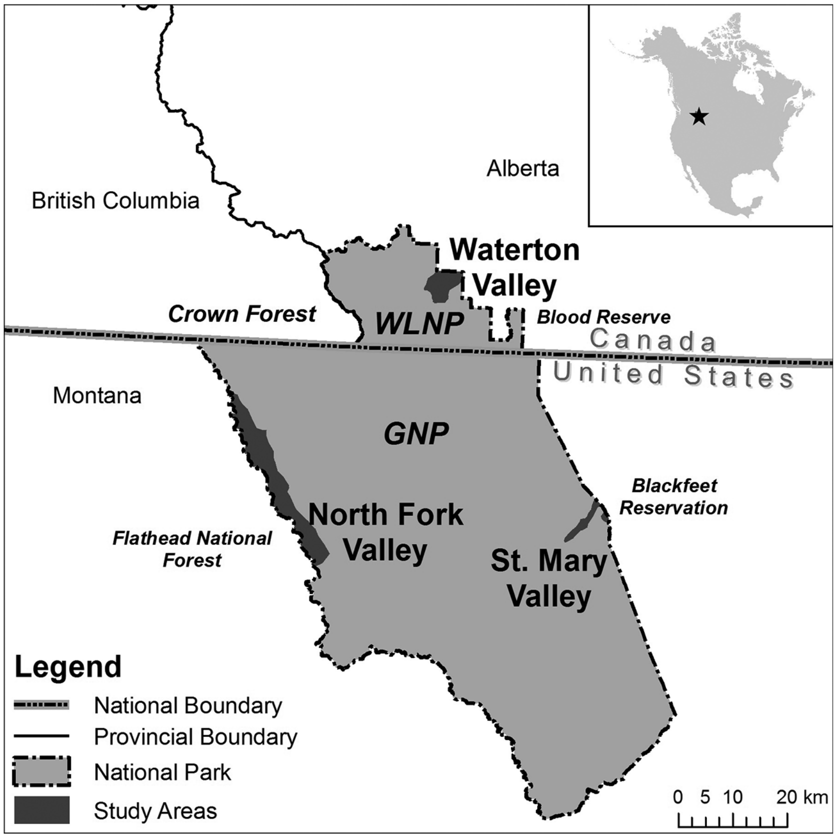
While all valleys offer similar wolf habitat, past wildlife management policies and practices have varied. This has resulted in a range of wolf population sizes among the valleys. Wolf abundance in the Crown of the Continent Ecosystem was very low from the 1880s until the mid-1970s, due to wolf extirpation. In the mid-1970s, wolves from Canada began to recolonize the ecosystem naturally and were confirmed denning in the North Fork in 1986 (Ream et al. 1990).

The three valleys had three different wolf population levels (a coarse-scale measure of wolf presence), based on breeding dynamics. We used agency reports and field observations that took place during the course of our study to characterize wolf population. We also based our assessment of wolf population level on Mech and Boitani (2003, pp. 2–29) and Fuller et al. (2003, pp. 181–191), which characterized an established population as one in which a wolf pair produces pups each year. Saint Mary had a low wolf population; although wolves have attempted to recolonize Saint Mary since the 1980s, no breeding pair or pack of wolves occurred there during our study (Sime et al. 2010), but wolves were observed occasionally passing through the area. Waterton had a moderate and variable wolf population; wolves were confirmed denning in WLNP in 1992 (Fox and Van Tieghem 1994) and have denned in that park consistently since then. Wolves are subject to legal take outside the park. During our study, wolves in Waterton averaged six individuals in the single pack that denned inside the park (Watt 2009). We characterized the North Fork as having a high wolf population. During our study, North Fork wolves averaged 38 individuals in two packs that produced multiple litters (Sime et al. 2010). These wolf population levels provided a very coarse measure of wolf activity in the three valleys. To provide a further index of wolf presence that could help inform our interpretation of our investigation of factors that influence elk habitat use, we measured wolf relative density at the same scale as the elk data that we gathered (100 m^2), as described below in the section Fecal sampling methods.

Fecal sampling methods

We used counts of ungulate fecal pellets and wolf scats to derive an index of ungulate and wolf occurrence, density, and utilization of the landscape in each valley. Pellet counts are the process of estimating, using fecal pellet piles, the relative numbers of mammals in a given area (Neff 1968). Scat counts are used to survey for carnivores (Gompper et al. 2006). While similar information can be derived via radio-collar data, the benefit of pellet-count surveys is that they can inexpensively estimate the entire observable

Fig. 1. Study areas in Glacier National Park, Montana, USA, and Waterton Lakes National Park, Alberta, Canada.



population inhabiting a site. If observer and detection bias are addressed, a sample of sufficient size is used, and counts in rapid decomposition sites (e.g., in areas of high moisture) are avoided, fecal pellet survey methods provide a reliable manner to evaluate species density and habitat use (White and Eberhardt 1980; Fuller 1991; Kunkel 1997; Sanchez et al. 2004; McComb et al. 2010).

Our surveys took place between snowmelt and green-up because snow cover and tall grass can diminish detectability of pellets and scats (Lehmkuhl et al. 1994). We surveyed Waterton and Saint Mary in spring 2007 and the North Fork in spring 2008. To reduce observer bias, a single observer conducted all counts. We confirmed identification of carnivore scats using a DNA test of randomly selected carnivore scats ($n = 11$ scats) and obtained results of 100% detection accuracy.

Decomposition rates and manipulation or consumption of scats by animals could bias studies that use scat to investigate life-history parameters (Sanchez et al. 2004). To test persistence, we observed wolf scat near known wolf dens in a variety of terrain. Wolf scats tended to persist for 1 year. They were not moved by other species during the period of observation. We assumed that carnivore scats would have similar detectability and persistence across cover types, because these scats were very large (e.g., >2 cm in diameter) and because data were collected in spring between snowmelt and green-up when vegetation did not interfere with detectability.

We sampled all patches of elk winter range within the valleys. We defined elk winter range as discrete grasslands that contain well-distributed aspen stands <1 ha in area and shrub patches <1 ha in area and have a low elevation (<1800 m) and mean snow depth of <0.7 m (Skovlin et al. 2002). Pellets were counted along transects 2 m wide and 1 km long. We refer to these transects as “pellet transects”. We used transects versus circular or square plots to best capture landscape heterogeneity and match methods used by Parks Canada in Banff National Park, Alberta (Neff 1968; Thomson 2003). Transects encompassed a variety of cover types (e.g., grass, aspen, shrubs) and geographic variation (e.g., prairie, benchland), to capture habitat available to elk.

Pellet transects were oriented on a chosen azimuth (measured with a sighting compass, 1°–360°) parallel to the elevational gradient of the landscape (Neff 1968), which trended east–west throughout all valleys. Transects began from a random start <25 m from the northern or southern edge (randomly determined) of each elk winter range patch. Thereafter, transects were positioned systematically, parallel to one another every 50 m in each patch. All transects were straight and 1 km in length. We subdivided transects into 20 contiguous 50 m subtransects and defined the sampling unit as the 50 m subtransect. At the start of each count, a transect tape was positioned along the center of the subtransect, lengthwise. From the starting end of the tape, we measured Universal Trans Mercator (UTM) grid coordinates and elevation (in metres, error ± 2–6 m), aspect (arcsine transformation ranging from 1° to 360°), and slope (percentage).

Sampling intensity was determined by our need to accurately capture data from species whose presence in the landscape may have been low (e.g., the carnivores) (Elton 2001). A post hoc power analysis conducted on similar pellet transect data in Banff National Park suggested a minimum sample size of one hundred and sixty 2 m × 50 m subtransects. The potential overdispersion of pellet-count data and the complexity of the models we intended to fit further indicated a robust sample size (White and Eberhardt 1980). The number of subtransects surveyed within each valley varied: 1820 subtransects (91 full transects), 2200 subtransects (110 full transects), 740 subtransects (37 full transects) for North Fork, Waterton, and Saint Mary, respectively. We evenly sampled all elk winter range in the valleys, using the same sampling intensity. The pellet and scat data that we collected in these transects

Table 1. Definition of predation risk variables.

Variable	1 (no to low)	2 (medium)	3 (high)
Debris	Grass cover type, debris found <100 m from center line of the transect consisting of shrub cover type <15 cm in height from the ground, and no downed wood or rocks ≥15 cm in diameter. No landscape characteristics that represent escape impediments for an elk (*Cervus elaphus*)	Debris found ≥50 to <100 m from center line of the transect consisting of low shrubs, occasional pieces of downed wood, trees, and occasional rocks ≥15 to <30 cm in height from the ground or diameter. Mild slopes (<5%) and drop-offs that represent moderate escape impediments for an elk	Debris found <50 m from center line of the transect consisting of shrubs, trees, and rocks ≥30 cm in height from the ground or diameter. Sharp slopes (≥5%), sharp drop-offs, or ravines that represent severe escape impediments for an elk
View	No landscape features that represent impediments within 100 m from center line of the transect that hinder visually detecting a predator for an elk	Landscape features in <180° of the viewshed of an ungulate, within ≥50 to <100 m from center line of the transect that represent impediments to visually detecting a predator for an elk	Landscape features in ≥180° of the viewshed of an ungulate, within <50 m from center line of the transect that represent impediments to visually detecting a predator for an elk

represented an index of these species' relative density at a scale of 100 m^2. This index enabled us to determine trends in wolf presence within the valleys on a scale of 100 m^2 (McComb et al. 2010, p. 144). For example, we noted predator–prey use of habitat (e.g., grass and aspen, burned and unburned sites) by examining elk and wolf scats/100 m^2 subtransects in grass and aspen habitat and in burned and unburned sites.

Each count consisted of a pile of ungulate pellets, which corresponded to a single defecation incident, or a single wolf scat. We defined a pile as five or more pellets (Neff 1968) within a transect. While diet can greatly influence elk pellet colour when fresh, as pellets age and decompose, they turn gray. In high ungulate density areas, we were reliably able to identify discrete pellet piles by colour. We did not count pellets when they were wet, as moisture darkens their colour, rendering old and new pellets indistinguishable. We only counted intact pellets. We were unable to differentiate deer pellets by species (e.g., mule deer, *Odocoileus hemionus* (Rafinesque, 1817), versus white-tailed deer, *Odocoileus virginianus* (Zimmermann, 1780)). We defined a wolf scat as a single, unbroken tubular piece of wolf fecal matter. In the event that a wolf scat was broken into two or more pieces, we counted it as one scat.

Habitat sampling

We assigned each subtransect a cover type based on a subjective estimate of the cover type most common within it (grass, aspen, shrub, and other, which are listed here in order of palatability). These cover types denoted broad food types utilized by elk in winter in the Rocky Mountains (Canon et al. 1987; Cook 2002), and specifically in Crown of the Continent Ecosystem (Wasem 1963; Singer 1979). Shrubs occurred in a mix of western serviceberry (*Amelanchier alnifolia* (Nutt.) Nutt. ex M. Roem.), western snowberry (*Symphoricarpos occidentalis* Hook.), common snowberry (*Symphoricarpos albus* (L.) S.F. Blake), and rose (genus *Rosa* L.). This shrub mix was palatable to elk but lower in palatability than aspen (Cook 2002). The "other" level was designated for cover types that offer low to negligible nutrition (Skovlin et al. 2002) and consisted of lodgepole pine (*Pinus contorta* Douglas ex Loudon), spruce (genus *Picea* A. Dietr.), rocks, and bare mineral soil.

We estimated the effect of landscape radiant heat input on elk resource utilization, heat load, which incorporates the subtransect slope, aspect, and latitude (McCune and Keon 2002). Heat load does not account for cloud cover and shading by adjacent vegetation or topography.

We designated view (impediments to detecting wolves) and debris (impediments to escaping wolves) as factors that could increase predation risk. We then rated these factors on a categorical scale as low (1), medium (2), or high (3). View impediments and debris increase predation risk because they hamper the ability of an elk to detect or escape wolves (Ripple and Beschta 2004). Table 1 describes how we defined view and debris. We based these definitions on elk adaptive behavioural strategies to avoid predation (e.g., avoidance of impediments and obstacles) (Geist 2002). We used a laser rangefinder, clinometer, and leveling rod to measure view impediments and debris.

Table 2. Specific a priori hypotheses used to develop models for Akaike's information criterion (AIC) analysis.

A priori hypotheses
Bottom-up (resources) factors
Hypothesis 1: elk (*Cervus elaphus*) pellet pile occurrence increases with food palatability
Hypothesis 2: elk pellet pile occurrence increases with solar radiation
Top-down (risk) factors
Hypothesis 3: elk pellet pile occurrence decreases with an increase in impediments to detecting wolves (*Canis lupus*) (e.g., "view")
Hypothesis 4: elk pellet pile occurrence decreases with an increase in impediments to escaping wolves (e.g., "debris")

Analysis

We evaluated summary statistics for all variables to determine trends. We calculated summary statistics (mean, 95% confidence interval (CI)) of the number of pellet piles and individual wolf scats per subtransect (100 m^2) by species. In interpreting these and other statistical analyses, we used a p value of 0.05 as the upper threshold for statistical significance (Ramsey and Schafer 2002, p. 46).

We used mean piles of ungulate pellets and the mean number of wolf scats per subtransect (100 m^2) to conduct our analysis. Using elk pellet data, we confirmed that elk are the dominant herbivore by biomass in this system. Wolves were the dominant predator of elk; therefore, we focused our analysis on elk and wolves.

We took the mean piles of elk pellets and wolf scats for each valley and stratified these data to graphically examine the effects of factors such as predation risk and food. We focused on aspen and grass cover types, because they are important food sources used by elk in the winter range that we studied (Martinka 1978; Singer 1979) and because they represent two extremes (grass = low; aspen = high) in terms of impediments to detecting or escaping wolves. Elk prefer grass over aspen and use aspen primarily after grass has been depleted in winter (Skovlin et al. 2002). We used a modeling approach to explore the influence of other cover types (e.g., shrub, conifer, bare mineral soil) on elk pellet pile density. We could only test for the effect of fire on elk use of a landscape, as measured by density of elk pellet piles, in the North Fork. Because each valley was a case study, we did not make statistical comparisons between valleys.

Table 3. Variables used in statistical analyses.

Variable	Definition	Type	No. of levels	Top-down and bottom-up factors
Cover type	Dominant vegetation cover type	Indicator	A, G, S, O	Bottom-up
Heat load	Solar radiation within transect	Index	0–1	Bottom-up
View	Impediments to elk (*Cervus elaphus*) detecting a wolf (*Canis lupus*)	Indicator	1, 2, 3	Top-down
Debris	Impediments to elk escaping a wolf	Indicator	1, 2, 3	Top-down
Easting	Easting location coordinate	Metres	Continuous	na
Northing	Northing location coordinate	Metres	Continuous	na

Note: Reference levels for categorical variables are view (*V*1, low; *V*2, medium; *V*3, high; *V*3 is the reference level), debris (*D*1, low; *D*2, medium; *D*3, high; *D*3 is the reference level), and cover type (G, grass; A, quaking aspen (*Populus tremuloides*); S, shrub; O, other; other is the reference level). View and debris reference levels are defined in Table 1. na, not available.

Table 4. Candidate models for Akaike's information criterion (AIC) analyses in each of the three valleys.

Model type	Models without location coordinates
Full model	(1) Cover type, heat load, view, debris, view × debris, cover type × debris
Single-factor bottom-up model	(2) Cover type
	(3) Heat load
Single-factor top-down models	(4) View
	(5) Debris
Two-factor bottom-up model	(6) Cover type, heat load
Two-factor top-down model	(7) View, debris
Two-factor bottom-up and top-down models	(8) Cover type, view
	(9) Cover type, debris
	(10) Heat load, view
	(11) Heat load, debris
Three-factor bottom-up and top-down models	(12) Cover type, heat load, view
	(13) Cover type, heat load, debris
	(14) Cover type, view, debris
	(15) Heat load, view, debris
Four-factor bottom-up and top-down model	(16) Cover type, heat load, view, debris
Multifactor bottom-up and top-down models with interaction	(17) View, debris, view × debris
	(18) Cover type, view, debris, view × debris
	(19) Heat load, view, debris, view × debris
	(20) Cover type, heat load, view, debris, view × debris
Null model	Intercept only

Note: A second set of models (models 21–40) have the same components as models 1–20, but add location coordinates.

In model selection, we used mean elk pellet piles as the response variable. Explanatory variables included bottom-up effects (cover type, heat load), top-down effects (view, debris), and location effects (northing, easting). We categorized heat load as a bottom-up effect because in winter range, elk tend to use south-facing slopes that retain more heat and are the first to become snow-free, which can increase plant availability (Chen et al. 2002).

We tested for normality and found the data (number of pellet piles) non-normally distributed. Because the data were skewed and were count data (not continuous data), we used a gamma distribution to fit a generalized linear model to describe $G(\mu)$, elk mean piles of elk pellets, with a mean/variance relationship (σ^2/μ^2) (McCullagh and Nelder 1989).

We used model selection based on Akaike's information criterion (AIC) (Burnham and Anderson 2002). We generated a set of specific hypotheses (Table 2), which guided us in developing variables (Table 3). We developed a set of 40 biologically plausible models from our hypotheses and fit the same models in each valley. Models included bottom-up variables cover type and heat load, top-down variables view (impediments to detecting wolves) and debris (impediments to escaping wolves), and location coordinates (northing, easting) (Table 4). We included models testing specific interactions. For example, we incorporated interactions between view and debris, to determine whether these effects worked together, because both factors can affect the ability of an elk to avoid wolf predation (Ripple and Beschta 2004) and may be collinear. We also tested the interaction between cover type (i.e., palatability, food) and impediments to escaping wolves (debris), because cover type may contribute to impediments to escaping wolves (e.g., grass, shrub, and aspen provide different terrain). Sources of variation were all nonfixed effects (i.e., cover type, heat load), view, and debris. We could not use wolf scat density for multivariate analyses because low wolf scat density would have created orthogonality issues (e.g., inadequate representation in models when all other levels of all other variables were considered). Instead, we examined wolf effects via predation risk factors.

The subtransects were likely subject to spatial autocorrelation, due to elk herding behaviour (White and Eberhardt 1980). We tested for independence of the data and obtained a Moran's *I* statistics of $p < 0.00001$ in all valleys. While this test showed evidence of spatial autocorrelation, because of a large sample size our findings can be used to identify trends in the factors influencing elk habitat use of the valleys. To further address spatial autocorrelation issues with these data, we fitted an additional set of models that included the UTM grid coordinates (northing and easting).

We tested model goodness-of-fit by using an information-theoretic approach (AIC). We used a mixed model approach and quasi-likelihood estimation methods (QAIC) to account for potential overdispersion (Burnham and Anderson 2002). We evaluated all variables in the models within 4 ΔAIC values of the best model. We lacked a sufficient sample size to permit separate AIC model-fitting for North Fork unburned subtransects. We used TIBCO Spotfire S+ and SAS version 9.1 (SAS Institute Inc., Cary, North Carolina, USA) software for analyses.

Results

We evaluated relative densities (absolute pile and scat densities) of elk, deer, moose (*Alces alces* (L., 1758)), and wolves (Figs. 2*a*–2*d*, 3*a*, 3*b*).

Fig. 2. Elk (*Cervus elaphus*) pellet pile and wolf (*Canis lupus*) scat densities by predation risk. We characterized these densities by impediments to viewing (*a*, *b*) and escaping (*c*, *d*) predators as defined in the text. For impediments to viewing predators, we have used the following categorical levels: *V*1, low; *V*2, medium (med); *V*3, high. For impediments to escaping predators (debris), we have used the following categorical levels: *D*1, low; *D*2, medium (med); *D*3, high. These reference levels are defined in Table 1. These data represent piles of elk pellets and single wolf scats counted in 100 m² subtransects, expressed as a density. Error bars represent 95% confidence intervals. Overlap in error bars among categorical variables in each valley is interpreted as lack of statistical significance.

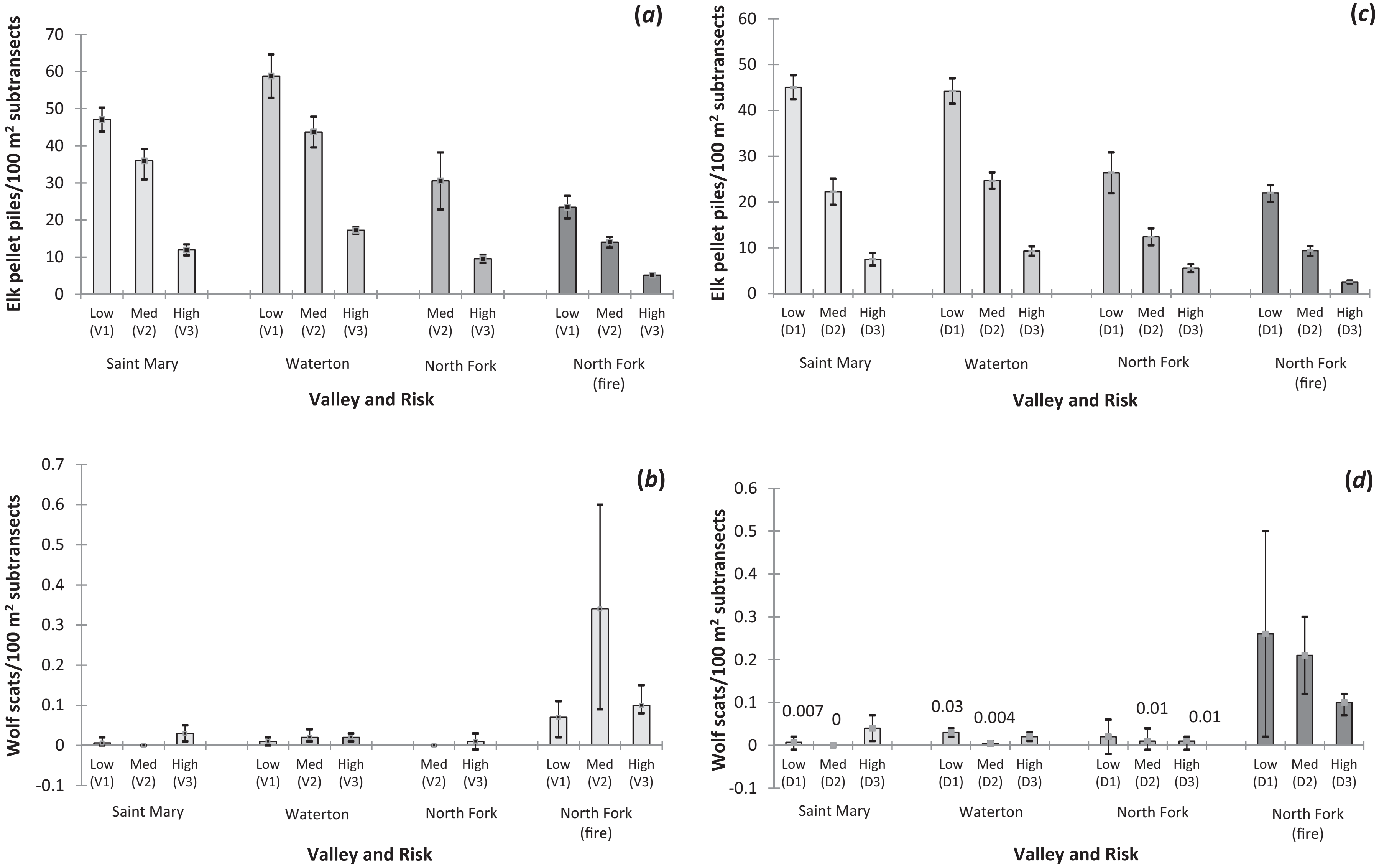
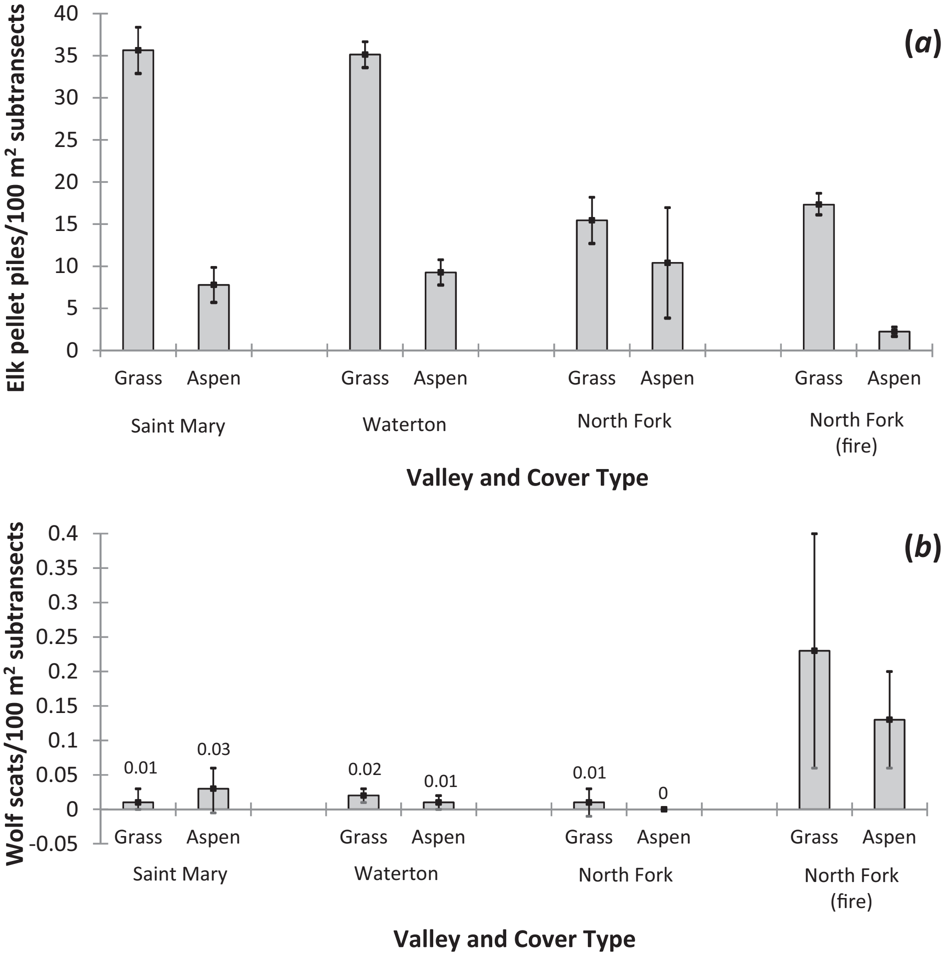


Fig. 3. Densities of (*a*) elk (*Cervus elaphus*) pellet piles and (*b*) wolf (*Canis lupus*) scats in quaking aspen (*Populus tremuloides*) and grass. Data represent piles of elk pellets and individual wolf scats counted in 100 m² subtransects. Error bars represent 95% confidence intervals. Overlap in error bars among categorical variables in each valley is interpreted as lack of statistical significance.



The mean elk pile density was 24.2 ± 1.3 per 100 m² subtransects (mean ± 95% CI) in Saint Mary, 28.3 ± 1.5 per 100 m² subtransects in Waterton, 11.1 ± 1.5 per 100 m² subtransects with no fire in North Fork, and 9.9 ± 0.7 per 100 m² subtransects with fire in North Fork. The mean deer pile density was <2 per 100 m² in all valleys. Deer defecate at approximately the same daily rate as elk (~12.5 times per day); therefore, the number of piles of deer pellets and the number of piles of elk pellets can be compared to estimate the relative density of deer and elk with respect to one other (Neff et al. 1965). Based on this comparison, elk were the dominant herbivore in the study area. Moose densities were <0.1 per 100 m² in all valleys, very low relative to the other ungulate species surveyed, so we omitted this species from further analysis. We found mean wolf scat densities of 0.02 ± 0.01 per 100 m² subtransects (mean ± 95% CI) in Saint Mary and Waterton, 0.01 ± 0.01 per 100 m² subtransects with no fire in North Fork, and 0.17 ± 0.1 per 100 m² subtransects with fire in North Fork. Mean elk pile density was highest in low predation risk areas, intermediate in medium predation risk areas, and lowest in high predation risk areas (Figs. 2*b*, 2*d*).

To examine predator and prey use of habitat, we plotted elk and wolf scat per 100 m² in grass and aspen habitats (Figs. 3*a*, 3*b*). Saint Mary and Waterton subtransects showed similar trends, in which elk use of grass was significantly higher than aspen. However, in North Fork subtransects with no fire, there was no significant difference between elk use of grass and aspen. In North Fork subtransects with fire, elk use of grass was significantly higher than aspen. Lack of a difference in elk use of grass versus aspen in North Fork subtransects with no fire represents a deviation from the pattern of elk use of cover type in the valleys. Wolf use of grass versus aspen did not differ within any of the valleys, nor with fire in the North Fork (Fig. 3*b*).

Several themes emerged from the model selection. Cover type did not occur in any of the top models in Saint Mary, the valley with the least number of wolves (Table 5), thus failing to support a priori hypothesis 1 that elk pellet pile occurrence increases with food palatability (Table 2). In Waterton and the North Fork, aspen had a large negative effect on the number of elk pellet piles compared with the other levels of cover type (Table 5; Figs. 4*a*, 4*b*), also failing to support a priori hypothesis 1 (Table 2). Heat load appeared in half of the top models in all valleys, but was not statistically significant, and thus failed to support a priori hypothesis 2 that elk pellet pile occurrence would increase with solar radiation (Tables 2 and 5). In all valleys, in models in which view and debris appeared without an interaction of the two variables, a negative relationship existed between each predictor of predation risk and the density of elk pellet piles (Figs. 5*a*–5*c*), thus providing support for a priori hypothesis 3 that elk pellet pile occurrence decreases with an increase in impediments to detecting wolves (e.g., "view") and a priori hypothesis 4 that elk pellet pile occurrence decreases with an increase in impediments to escaping wolves (e.g., "debris") (Table 2). Location coordinates occurred in all the top models in all valleys (Table 5), reflecting elk herding behaviour.

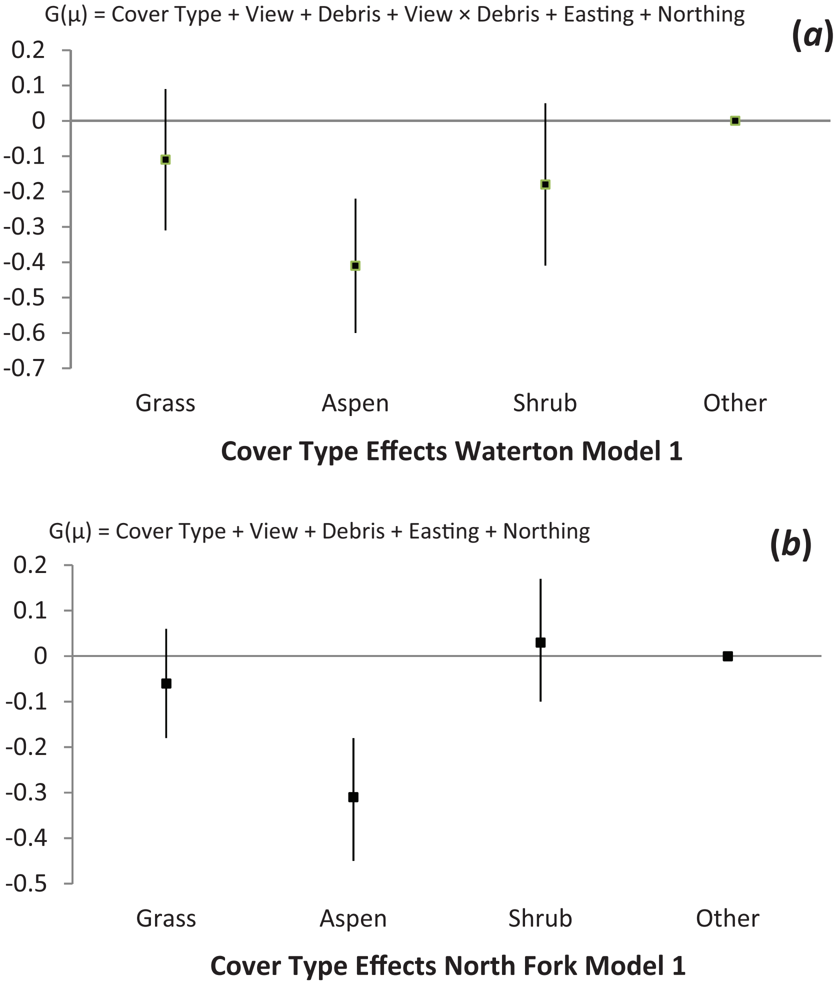
The interaction between view and debris appeared in the third- and fourth-ranked Saint Mary models and in all the top-ranked

Table 5. Results of Akaike's information criterion (AIC) model selection for density of elk (*Cervus elaphus*) pellet piles in three valleys: Saint Marry, Waterton, and North Fork.

Model	Partial equation showing parameter estimates of covariates with *p* values and 95% confidence intervals in parentheses	Scale parameter	AIC	Δ
Saint Mary Valley				
Model 1: heat load + view + debris + easting + northing	0.5148·heat load (0.1052; –0.11, 1.14) + 0.3709·*V*1 (0.0027; 0.13, 0.61) + 0.3657·*V*2 (0.0017; 0.14, 0.59) + 1.3258·*D*1 (<0.0001; 1.10, 1.55) + 0.7507·*D*2 (<0.0001; 0.54, 0.96) + [–0.0001·easting (<0.0001; –0.0002, –0.0001)] + 0.0002·northing (<0.0001; 0.0001, 0.0002)	0.87	5 641.9	0.00
Model 2: view + debris + easting + northing	0.3851·*V*1 (0.0019; 0.14, 0.63) + 0.3715·*V*2 (0.0015; 0.14, 0.60) + 1.3219·*D*1 (<0.0001; 1.1, 1.55) + 0.7284·*D*2 (<0.0001; 0.52, 0.94) + [–0.0001·easting (<0.0001; –0.0002, –0.0001)] + 0.0002·northing (<0.0001; 0.0001, 0.0002)	0.87	5 642.7	0.79
Model 3: heat load + view + debris + view × debris + easting + northing	0.4458·heat load (0.1648; –0.18, 1.07) + [–1.1776·*V*1 (0.0303; –2.24, –0.11)] + [–0.1242·*V*2 (0.8200; –1.19, 0.95)] + 1.3093·*D*1 (<0.0001; 1.05, 1.57) + 0.6916·*D*2 (<0.0001; 0.45, 0.93) + 1.5751·*V*1*D*1 (0.0055; 0.46, 2.69) + 1.6258·*V*1*D*2 (0.0075; 0.43, 2.82) + 0.4629·*V*2*D*1 (0.4198; –0.66, 1.59) + 0.5855·*V*2*D*2 (0.3036; –0.53, 1.70) + [–0.0001·easting (<0.0001; –0.0002, –0.0001)] + 0.0002·northing (<0.0001; 0.0001, 0.0002)	0.87	5 643.3	1.33
Model 4: view + debris + view × debris + easting + northing	–1.2207·*V*1 (0.0246; –2.29, –0.16) + [–0.2225·*V*2 (0.6811; –1.28, 0.83)] + 1.3040·*D*1 (<0.0001; 1.04, 1.57) + 0.6697·*D*2 (<0.0001; 0.43, 0.91) + 1.6324·*V*1*D*1 (0.0039; 0.52, 2.74) + 1.6809·*V*1*D*2 (0.0056; 0.49, 2.87) + 0.5674·*V*2*D*1 (0.3188; –0.55, 1.68) + 0.6937·*V*2*D*2 (0.2187; –0.41, 1.8) + [–0.0001·easting (<0.0001; –0.0002, –0.0001)] + 0.0002·northing (<0.0001; 0.0001, 0.0002)	1.04	5 643.3	1.36
Waterton Valley				
Model 1: cover type + view + debris + view × debris + easting + northing	–0.4080·A (<0.0001; –0.60, –0.22) + [–0.1072·G (0.2893; –0.31, 0.09)] + [–0.1804·S (0.1227; –0.41, 0.05)] + 1.7067·*V*1 (0.0457; 0.03, 3.38) + 1.2249·*V*2 (<0.0001; 0.85, 1.6) + 0.9707·*D*1 (<0.0001; 0.83, 1.11) + 0.6080·*D*2 (<0.0001; 0.47, 0.74) + [–0.8797·*V*1*D*1 (0.3044; –2.56, 0.8)] + [–0.5995·*V*1*D*2 (0.4889; –2.3, 1.09)] + [–0.8762·*V*2*D*1 (<0.0001; –1.3, –0.49)] + [–0.8167·*V*2*D*2 (<0.0001; –1.24, –0.4)] + [–0.0001·easting (<0.0001; –0.0001, –0.00010)] + 0.0001·northing (0.0001; 0.0001, 0.0002)	1.38	16 874.8	0.00
Model 2: cover type + heat load + view + debris + view × debris + cover type × debris + easting + northing (full model)	–0.3314·A (0.0012; –0.53, –0.13) + 0.0716·G (0.5443; –0.16, 0.30) + 0.1473·S (0.2851; –0.42, 0.12) + 0.3413·heat load (0.1019; –0.07, 0.75) + 1.5890·*V*1 (0.0630; –0.09, 3.26) + 1.1777·*V*2 (<0.0001; 0.8, 1.55) + 1.0271·*D*1 (<0.0001; 0.57, 1.49) + 1.1516·*D*2 (<0.0001; 0.61, 1.69) + [–0.7662·*V*1*D*1 (0.3714; –2.45, 0.91)] + [–0.4735·*V*1*D*2 (0.5851; 2.17, 1.23)] + [–0.8263·*V*2*D*1 (<0.0001; –1.22, –0.43)] + [–0.8199·*V*2*D*2 (0.0002; –1.25, –0.39)] + [–0.0849·A*D*1 (0.7996; –0.74, 0,57)] + [–0.4383·A*D*2 (0.1699; –0.06, 0.19)] + [–0.1584·G*D*1 (0.5148; –0.64, 0.32)] + [–0.6722·G*D*2 (0.0171; –1.22, –0.12)] + [–0.4064·S*D*2 (0.2014; –1.03, 0.22)] + [–0.0001·easting (<0.0001; –0.0001, –0.0001)] + 0.0001·northing (<0.0001; 0.0001, 0.0002)	1.38	16 875.6	1.20
North Fork Valley				
Model 1: cover type + view + debris + easting + northing	–0.3139·A (<0.0001; –0.45, –0.18) + [–0.0571·G (0.3537; –0.18, 0.06)] + 0.0345·S (0.6163; –0.1, 0.17) + 0.2353·*V*1 (0.0024; 0.08, 0.38) + 0.1179·*V*2 (0.0267; 0.01, 0.22) + 1.1671·*D*1 (<0.0001; 1.02, 1.31) + 0.6414·*D*2 (<0.0001; 0.53, 0.75) + [–0.0004·easting (<0.0001; –0.0004, –0.0004)] + [–0.0002·northing (<0.0001; –0.0003, –0.0002)]	0.72	9 984.4	0.00
Model 2: cover type + heat load + view + debris + easting + northing	–0.3123·A (<0.0001; –0.45, –0.18) + [–0.0560·G (0.3628; –0.18, 0.06)] + 0.0359·S (0.6022; –0.09, 0.17) + 0.8106·heat load (0.3676; –0.95, 2.57) + 0.2400·*V*1 (0.0020; 0.09, 0.39) + 0.1222·*V*2 (0.0221; 0.02, 0.23) + 1.1676·*D*1 (<0.0001; 1.03, 1.31) + 0.6403·*D*2 (<0.0001; 0.53, 0.75) + [–0.0004·easting (<0.0001; –0.0004, –0.0004)] + [–0.0002·northing (<0.0001; –0.0003, –0.0002)]	0.72	9 985.7	1.21

Note: Only models with Δ < 4 and better than the null model are shown. Parameters listed under the model column indicate the additional covariates added to the null model. Parameter estimates, scale parameters, and *D* values are shown. Categorical variable levels are defined in Table 2.

Fig. 4. Influence of cover type in model 1 in two valleys: (*a*) Waterton and (*b*) North Fork. Cover type did not appear in any of the candidate models (ΔAIC < 4, where AIC is Akaike's information criterion) in the Saint Mary Valley. The *y* axis represents the β values for each of the four levels of this variable (influence on log mean elk (*Cervus elaphus*) pellet piles). The "other" category represents the reference level. Error bars represent 95% confidence intervals.



Waterton models. It did not appear in any North Fork models. The relationship between view and debris was not independent in Waterton (Fig. 5*b*). The relationship between cover type and debris was not independent in the second Waterton model (Fig. 6).

The majority of the top models included a combination of bottom-up and top-down effects (Table 5). Only the second- and fourth-ranked models in Saint Mary, the valley with the lowest wolf population, contained top-down variables alone (view and debris and their interaction). None of the models with ΔAIC < 4 consisted of bottom-up variables alone.

Discussion

In evaluating whether risk of predation by wolves influenced how elk use a winter range landscape, we examined whether top-down (predator-driven) effects operate along with bottom-up (resource-driven) effects. To do so, we began by identifying trends and patterns in elk and wolf densities among the valleys. Elk were the dominant herbivore, present in high density in the three valleys, although their density differed among valleys, and was lowest in the North Fork Valley, which had the most-established wolf population. Wolves were present in low density in all areas that had not burned. However, the North Fork wolf scat density in subtransects with fire was more than one order of magnitude higher than in subtransects with no fire (Fig. 2*b*). This finding is key in evaluating trophic dynamics in this study. Similar wolf scat densities in Saint Mary and Waterton reflect our field observations of transient wolves moving through Saint Mary. Burned areas typically contain more down wood and large debris than unburned areas (Pedlar et al. 2002). This may make it more difficult for elk to escape wolves (Halofsky et al. 2008) and may give wolves, which are able to maneuver through forests more easily than elk, an advantage (Kauffman et al. 2007).

Trends in elk pellet pile density show some correspondence to wolf scat density. The lower mean density of elk pellet piles in the North Fork (9.94 ± 0.71 elk pellet piles per 100 m^2 subtransects) than in the other two valleys, while still high (White et al. 2003), may be attributable to increased wolf predation in this valley versus in valleys with a lower wolf population (Waterton) or no established wolf population (Saint Mary). While wolf predation on elk, a density-mediated (mortality) response, alone does not suggest trophic cascades, density-mediated responses are a necessary component of such food-web relationships (Paine 1980). Density-mediated responses have been observed where wolves have returned (Peterson 2007; White et al. 2012). Other factors (e.g., climate and habitat) that could be linked to a decline in elk density were comparable in the valleys (Vucetich et al. 2005).

Elk landscape-use trends were similar in the valleys, with one exception. In all valleys, predation risk factors negatively influenced elk density (Figs. 2*a*, 2*c*). Regardless of wolf population level, elk avoided aspen. Survey results from 1973 to 1974, a pre-wolf and

Fig. 5. View by debris in model 1 in three valleys: (*a*) Saint Mary, (*b*) Waterton, and (*c*) North Fork. Predation risk categories are defined in Table 1. The *y* axis represents the β values for each of the three levels of view and debris (influence on log mean elk (*Cervus elaphus*) pellet piles). Categorical variables are described in Table 3. The "*V*3" and "*D*3" categories represent reference level of these variables. Error bars represent 95% confidence intervals.

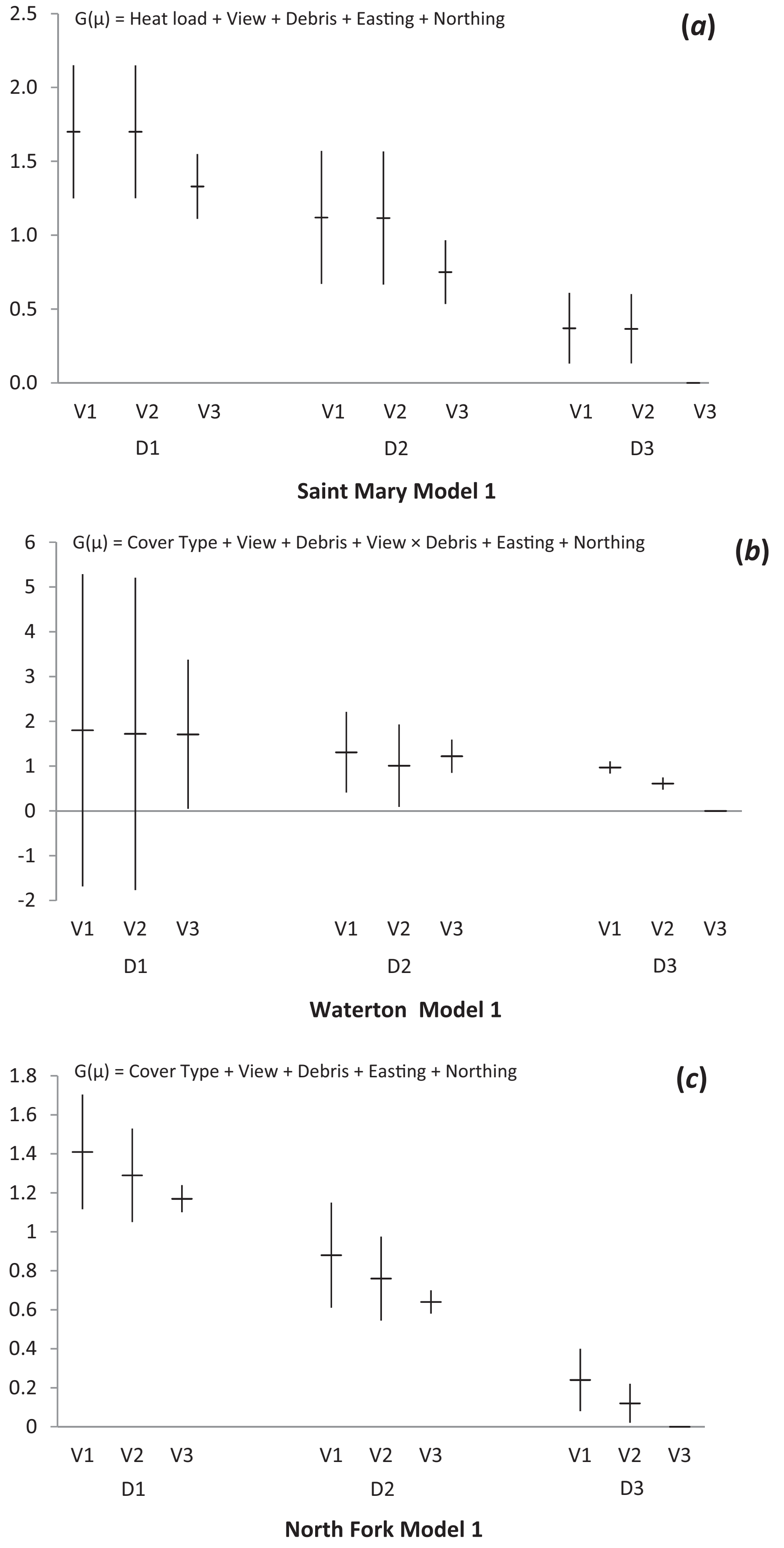
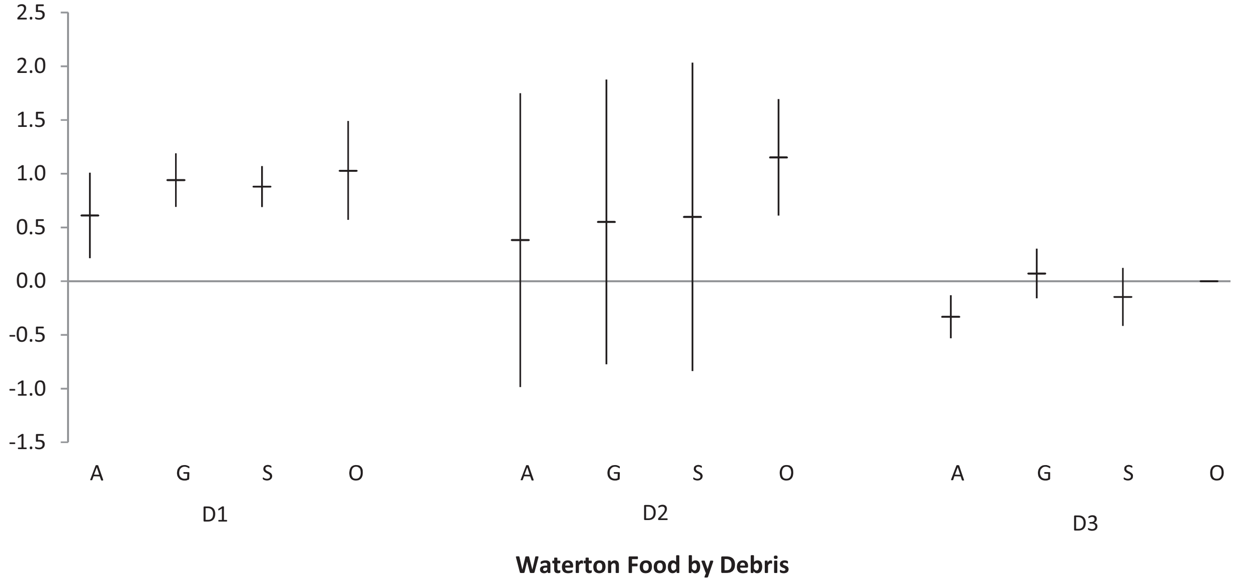


Fig. 6. Interaction of cover type and debris. The *y* axis represents the β values for each of the four levels of the interaction of these variables (influence on log mean elk (*Cervus elaphus*) pellet piles). This interaction only appeared in model 2 in the Waterton Valley. Categorical variable levels are described in Table 3. The "other" and "*D*3" categories represent the reference level of these variables. Error bars represent 95% confidence intervals.



pre-fire period (e.g., no wolves since 1910 and no fire since 1890), indicated a similar pattern: 88% versus 3% utilization of grass versus aspen in the North Fork (Singer 1979). The fact that predation risk variables that provided impediments to detecting or escaping wolves had a negative influence on occurrence of elk (pellet piles), regardless of wolf population, may be a contra-indicator to a top-down effect. An elk may have higher energetic needs when moving through coarse woody debris versus open ground. Therefore, in the absence of wolves as well as in the presence of wolves, elk may avoid areas with significant coarse woody debris to conserve energy (Seager et al. 2013).

The fact that elk avoided aspen regardless of wolf population level furnishes evidence that our predation risk variables (view and debris) were not related to either perceived or actual predation risk. It is possible that our finding that elk pellets were more abundant in areas with less view impediments and debris reflects a potential negative relationship between view impediments and debris and a nutritious cover type (grass) in the more open areas. Our data support this alternative hypothesis, with the exception of our North Fork Valley data, which contains both burned and unburned aspen.

In North Fork subtransects with no fire, we found a very different pattern; here elk use of aspen was similar to their use of grass (Fig. 2*a*). It is possible elk were using unburned aspen in a valley with a high wolf population because unburned stands are safer than burned aspen (e.g., less large down wood and debris on the forest floor) and provide valuable food in winter, when grass has been depleted as a food source (Cook 2002; Pedlar et al. 2002). Furthermore, it is possible that elk were using unburned aspen as cover to minimize detection by wolves in a high wolf area (the North Fork). Similar elk responses to wolf presence have been identified in other studies (Creel et al. 2005). Elk use of forest cover has been widely found to be unrelated to thermal cover and is primarily related to food and hiding from predators. While one could also argue that elk may use impediments and debris as cover from wolves, and this counters the idea that these variables increase predation risk, the fact that elk were not using unburned aspen in Saint Mary or Waterton invalidates such an argument. Even in places like the North Fork, elk may sometimes consider starvation a greater threat than wolf predation (Cook et al. 1998). In assessing and behaviourally controlling their risk of being preyed upon, herbivores use adaptive decision-making processes (Lima and Dill 1990). The presence of both burned and unburned sites in a valley changed wolf behaviour, and elk consequently moderated their behaviour to stay alive.

Did the food-web relationships that we found link elk landscape use, wolf landscape use, and fire, thus indicating trophic cascades? To evaluate this, one must consider the cover-type component of this food-web relationship. In North Fork stands with no fire, aspen stem densities were similar to those in Waterton and Saint Mary. Additionally, in North Fork stands with and without fire, relative stem density of browsable aspen was similar in the size class of aspen most easily accessible to elk in winter (stems >1 to <2.5 m in height), as was shrub height and percent cover. Grass cover did not dominate the understory of any aspen stands in this study, whether burned or unburned (Cook 2002; White et al. 2003; C. Eisenberg, unpublished data). Collectively, the above indicates that elk selection of unburned aspen was not a food effect (e.g., more browsable food in unburned North Fork aspen). However, North Fork unburned stands only represented 10% of aspen available to elk in this valley. Yet wolves were largely in the other 90% (burned aspen), forcing elk to use only 10% of all aspen in this valley. This may explain the higher pellet density in unburned aspen (although elk still preferred grass), but raises a question about why wolves were not selecting the unburned aspen where there was significant elk activity. In the other valleys, because all the aspen were unburned and thus perhaps did not have the same predation risk factor as burned aspen, the elk were more generally distributed throughout a larger population of aspen.

Bottom-up factors alone were not driving the trend that we found in elk landscape use. While the choice of where elk spend their time could be influenced by the lower amount of forage available in areas with a high elk density, we do not think this was an important factor in this study. We found the same patterns of elk use of habitat in all areas that did not have fire, regardless of elk density (Figs. 2*a*–2*d*, 3*a*, 3*b*) or nutritional value of forage (Cook 2002). In Waterton and the North Fork, which have well-established wolf populations, elk use of aspen cover type was lower than all other cover types (Figs. 4*a*, 4*b*). Wolf scat density was similar in all valleys in unburned aspen. However, research has found weaker responses by ungulates to wolf presence where a wolf population is temporally less well established, despite periodic presence (Berger 2007). Our findings suggest that high elk use of unburned aspen in the North Fork may be a top-down effect moderated by bottom-up effects.

The fact that wolves were spending far more time in North Fork subtransects that had burned is not fully indicative of top-down effects. Elk densities were not lower overall in the North Fork where there were more wolves, although their density was lower in aspen that had burned (Figs. 3*a*, 3*b*). As predicted by optimal foraging theory, wolves may have been capitalizing on elk vulnerability in such sites (Stephens and Krebs 1986). Wolves make hunting decisions based on minimizing effort involved in killing prey (Mech and Boitani 2003). However, beyond this, we did not find food-web patterns in which wolves spent more time in high-risk areas in any valley (Fig. 2*d*). Thus, wolf decision making may have been influenced by a combination of elk vulnerability and elk density, or factors that we did not measure (Fig. 3*b*).

Taken together, our findings create a picture of differential use of landscapes by elk driven by a suite of factors. Elk decision making appeared to be influenced by both top-down (predation risk) and bottom-up (food availability) factors. For example, elk avoided aspen, a valuable food source, with the exception of unburned aspen stands in a valley where wolves spent most of their time in burned areas—a bottom-up effect that produces a top-down effect on elk. Had we only studied the North Fork, we would have possibly concluded that in this valley, we observed a strong top-down effect. However, because we studied three valleys whose differences (e.g., fire, elk density, wolf density) were quantifiable, we were able to observe the complexity of what on the surface seemed like a simple food-web relationship (e.g., elk using unburned aspen versus burned aspen) (Fig. 3*a*). In summary, our results suggest that a suite of bottom-up and top-down factors work together in valleys that contain well-established wolf populations. These factors may work together to a lesser degree in a valley with a low wolf population (Table 5). Alternatively, these putative risk factors may not really function as risk factors for elk. For example, avoiding the interior of an aspen stand could be an innate foraging response by elk. We note that our low wolf area, Saint Mary, may have had enough of a wolf presence to generate a behavioural response by elk, thus potentially explaining the similar view and debris risk factor results among the three valleys (Figs. 2*a*–2*d*). Saint Mary and Waterton had exactly the same mean wolf scat densities (0.02 ± 0.01 wolf scats per 100 m^2 subtransects; mean ± 95% CI) and both were higher than the unburned area of the North Fork (0.01 ± 0.01 wolf scats per 100 m^2 subtransects; mean ± 95% CI). Further research is needed to determine risk factors and associated elk behaviour in the presence of wolves.

One of our objectives was to determine the effect of wolf population on elk landscape use. We are not certain that wolves had a strong effect on elk landscape use because of the many similarities that we found between elk landscape use and the models that had the best fit in all valleys. Elk response to predation risk variables was similar in all models in all valleys (Figs. 2*a*, 2*c*). This suggests that (*i*) a low number of wolves may alter elk landscape use via predation risk, (*ii*) what have been identified as risk factors in the scientific literature (e.g., impediments) are not really risk factors, and (*iii*) other factors, such as fire, moderate the effects of wolf population.

Studies in other ecosystems have found a variety of elk responses to predation risk. In YNP, elk moved into forested areas when wolves were present. This reduced their use of grasslands, which contained preferred forage and high predation risk when wolves where moving through the area (Creel et al. 2005). Also in YNP, predation risk from wolves to elk may operate at multiple spatial scales (Painter et al. 2015). In Banff National Park and the Ya-Ha-Tinda Ranch of central Alberta, elk avoided predation risk during the day by staying far from timber in open grassland areas, which had high human activity and low wolf presence during the day. At night, when wolves moved into the grasslands, some elk moved into the timber for cover from wolves (Robinson et al. 2010). These human-habituated elk utilized a different set of strategies at different times to avoid being preyed on by wolves. (The elk in our study site were not human-habituated, so did not approach areas with high human activity for safety.) These examples illustrate that assessing predation risk may be a complicated challenge.

Food webs involve highly complex energy flows (Strong 1992). Accordingly, we did not find a simple explanation of elk landscape use. While the structure of the food web that we studied (apex predator → dominant herbivore → plants) was simple, the influences along the pathways that link these components were not. As with any faunal species in any setting, the threat of predation alone did not drive elk landscape-use decisions (Borer et al. 2005). Further study is needed to elucidate these complex interactions.

Acknowledgements

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