Spatial decomposition of predation risk using resource selection functions: an example in a wolf–elk predator–prey system

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Predation is a fundamental ecological and evolutionary process that varies in space, and the avoidance of predation risk is of central importance in foraging theory. While there has been a recent growth of approaches to spatially model predation risk, these approaches lack an adequate mechanistic framework that can be applied to real landscapes. In this paper we show how predation risk can be decomposed into encounter and attack stages, and modeled spatially using resource selection functions (RSF) and resource selection probability functions (RSPF). We use this approach to compare the effects of landscape attributes on the relative probability of encounter, the conditional probability of death given encounter, and overall wolf and elk resource selection to test whether predation risk is simply equivalent to location of the predator. We then combine the probability of encounter and conditional probability of death into a spatially explicit function of predation risk following Lima and Dill's reformulation of Holling's functional response. We illustrate this approach in a wolf–elk system in and adjacent to Banff National Park, Alberta, Canada. In this system we found that the odds of elk being encountered by wolves was 1.3 times higher in pine forest and 4.1 times less in grasslands than other habitats. The relative odds of being killed in pine forests, given an encounter, increased by 1.2. Other habitats, such as grasslands, afforded elk reduced odds (4.1 times less) of being encountered and subsequently killed (1.4 times less) by wolves. Our approach illustrates that predation risk is not necessarily equivalent to just where predators are found. We show that landscape attributes can render prey more or less susceptible to predation and effects of landscape features can differ between the encounter and attack stages of predation. We conclude by suggesting applications of our approach to model predator–prey dynamics using spatial predation risk functions in theoretical and applied settings.

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Ecologists are increasingly recognizing that predation risk can have as important an effect as the direct effects of predation on structuring communities (Abrams et al. 1996, Schmitz 1998). Experimental studies have demonstrated that risk avoidance can increase energetic costs (Abrahams and Dill 1989), modify habitat selection (Gilliam and Fraser 1987), and change trophic flows by altering diet selection (Schmitz 1998). In most experimental studies predation risk is defined as the addition

of predators to a predator-free system (Abrahams and Dill 1989). Lima and Dill (1990) suggest, however, that predation risk is more than just predator presence, and Lima (2002) criticizes experimental approaches because they often ignore the spatial and temporal variation in predation risk that prey face. Lima and Dill (1990) provide a mechanistic approach to understanding predation risk by decomposing Hollings' (1959) disk equation of the predator functional response into its

two fundamental components: the probability of being encountered (α) and the conditional probability of being killed given an encounter (d). Similar decompositions of predation risk have been presented by Wrona and Dixon (1991) for an aquatic planarian–trichopteran predator–prey system and by Hebblewhite and Pletscher (2002) for a wolf (*Canis lupus*) –elk (*Cervus elaphus*) system, but neither of these studies focused on the spatial variation in the components of predation risk.

Several recent studies have explicitly linked predation risk to landscape attributes. Kunkel and Pletscher (2000) compared landscape features where wolves killed moose (*Alces alces*) to those at random sites, and found moose were more likely to be killed closer to roads and trails and farther from forest cover. Thogmartin and Schaeffer (2000) compared where turkeys (*Mellagris gallapavo*) lived in relation to roads to the distance at which they were killed from roads, and found they were more likely to be killed farther from roads. Cresswell and Quinn (2004) showed distance to cover influenced the success of predation by sparrowhawk (*Accipter nisus*) predation on redshanks (*Tringa totanus*). All three studies attributed these results to habitat covariates that modified vulnerability to predation. Yet, in the first two examples, these patterns could have arisen simply because of prey habitat use, and not necessarily due to landscape features because only kills and available landscape characteristics were compared. In modeling resource selection of caribou (*Rangifer tarandus*), Johnson et al. (2002) attempted to account for these differences in predation risk by weighting kill-site locations twice that of predator telemetry locations. However, they had little empirical support for these weights. More recently, Kristan and Boarman (2003) documented the spatial pattern in predation risk to common tortoises (*Gopherus agassizii*) from ravens (*Corvus corax*) by comparing attributes of sites where ravens attacked model tortoises with attributes at random sites, but they also did not account for the distribution of prey nor decompose the components of predation. In the case of tortoises, it could be argued that spatial attributes associated with encounters are similar to where they are attacked because tortoises have few antipredator strategies once encountered (Kristan and Boarman 2003). For other prey species, habitats where individuals are most likely to be encountered may not be where they are most likely to be killed. For example, deer (*Odoicoleus* spp.) frequenting open slopes can often evade predators if the slope is steep (Lingle and Pellis 2002, Kunkel et al. 2004). Therefore it seems that Lima and Dill's (1990) critique of experimental definition of predation risk is warranted, and that an approach to describe spatial and temporal variation in predation risk is required.

Here, we demonstrate how to spatially decompose the components of predation risk as a function of landscape attributes using resource selection functions (Manly et al. 2002). We combine spatial risk of encounter and kill to estimate spatial predation risk following Lima and Dill's (1990) derivation of predation risk from Hollings disc equation. We illustrate our approach for gray wolf predation on elk (wapiti) during winter in and adjacent to Banff National Park, Alberta, Canada. We address two specific questions: (1) do landscape features associated with where wolves occur differ from where wolves encounter and kill elk? (2) In which predation stage (i.e. search, encounter, kill) do landscape features express their greatest effects on predation risk? We discuss common sampling and statistical issues for applying this approach to a variety of predator–prey systems, and conclude with examples of the importance of spatially decomposing predation risk, and applications to predator–prey models in conservation and theoretical settings.

Towards a spatial decomposition of predation risk

Since Hollings' (1959) seminal work, most workers have recognized two main components of predation across systems. These are the instantaneous risk, or probability, of encounter, α, and the conditional risk of death, given an encounter, d (Fig. 1). While some authors decompose these components further, for example splitting α into the probability of detection and evasion (Lima and Dill 1990), we consider α and d to be the basic components that include finer divisions (Taylor 1984). Lima and Dill (1990) reformulated Holling's (1959) functional response to operationally define predation risk P(k), or the risk of being killed per unit time, as a function of α and d by:

$$P(k) = 1 - \exp^{-(\alpha dT)} \tag{1}$$

where α is Holling's (1959) encounter rate or probability of encounter, d is the conditional probability of the attack being successful given an encounter, and T is the time interval over which predation risk is being integrated. Equation 1 bounds predation risk, P(k), between 0 and 1, even where α and d are relative probabilities (below). For the risk of being killed per unit time, we adopt P(k) instead of Lima and Dill's (1990) P(d) for clarity; P(k) avoids having P(d) and the conditional risk of being killed, given encounter, d, in the same function. To make P(k) spatially explicit, spatial functions for α and d need to be derived and substituted into Eq. 1.

Data required to estimate the spatial risk of encounter, α, and conditional risk of death, d, will depend on the predator–prey system. Typically, the most difficult component will be estimating α not d, for many predator–prey systems. Locations of killed prey are often conspicuous and can be readily quantified, and functions describing spatial variation in mortality sites have already been developed in many systems (Kunkel

and Pletscher 2000, Nielsen et al. 2004). To estimate the spatial risk of encounter, a simple approach could be based on elementary set logic developed for measuring spatial habitat overlap for two species (Minta 1992). Extending Minta's (1992) approach to spatial models, the product of spatial predator and prey models would represent the joint probability of co-occurrence, which should be proportional to the probability of encounter (Manly et al. 2002). However, the joint probability assumes independence between predator and prey, a problem identified but not resolved by Minta (1992). Assuming independence might be reasonable for alternate prey in a two-prey, one-predator system where the predator specializes on the primary prey and predation is essentially independent for alternate prey. Assuming independence also might be justified for primitive predators with random or limited searching behavior. Independence could also be tested for by extending Minta's (1992) approach. However, for many predator – prey systems, independence may be biologically unrealistic because of dynamic feedbacks between predator and prey.

The problem of independence may be circumvented in cases where we can estimate spatial encounters directly from field data. Examples include where encounters between predators and prey can be observed directly (Fanshawe and Fitzgibbon 1993, Cresswell and Quinn 2004), or where they can be estimated indirectly, for example, via snow tracking (Hebblewhite and Pletscher 2002). New technology, such as GPS collars on predators and prey, may provide additional means to estimate encounters. Encounters also could be estimated in experimental settings such as with predation trials on prey or with artificial baits or nests (Kristan and Boarman 2003, Forstmeier and Weiss 2004). Estimating encounters directly also avoids problems of differential sampling bias between predator and prey habitat use (Rettie and McLoughlin 1999). Where the above approaches provide estimates of spatial locations of encounters and kills, all that remains is to estimate spatial functions of α and d, and then substituting these in Eq. 1 to estimate a spatial predation risk function.

Application of resource selection functions to modeling predation risk

Resource selection functions provide an efficient framework for quantifying the spatial probability of encounter and kills in ecological landscapes. A resource selection probability function (RSPF) is defined as any function that equals the probability of use of a resource unit, and is easily adapted to spatial data (Boyce and McDonald 1999, Manly et al. 2002). Logistic regression has become one of the most common statistical approaches to estimate habitat selection models with used units char-

acterized as 1 and unused units characterized as 0. In designs with used and available units, a resource selection function (RSF) is estimated using logistic regression that is proportional to the probability of use (Manly et al. 2002). The used-available design results in a relative probability because the intercept or β_0 coefficient is incorrectly scaled. This problem arises because the true population-sampling fraction is unknown (Boyce and McDonald 1999). Because the RSF is only proportional to an RSPF, the odds-ratio is also only a relative probability ratio. Recent statistical discussion highlights another potential problem with the used-available design in logistic models when the 'contamination' rate, or false-negative rate (units that were used but misclassified as available due to sampling) is high (>20%, Keating and Cherry 2004). However, in geographic information system (GIS) applications contamination rate is unlikely to be large enough to affect logistic models because of the typically large numbers of available resource units (pixels) relative to the sample of used resource units. Moreover, Manly et al. (2002, p. 177) show the assumption that an RSF is proportional to an RSPF is often valid, and used-available designs are useful in a wide array of applications (Boyce and McDonald 1999).

While resource selection approaches typically have been used for predicting the probability of use (Manly et al. 2002), they also can be used for other spatial events, such as encounters or kills. Predation is a series of discrete stages that can be characterized by binary responses. Searching predators are either successful (α) or unsuccessful ($1 - \alpha$) at encountering prey, and given an encounter, are either successful (d) or unsuccessful ($1-d$) in making a kill (Fig. 1). Thus, components of predation risk can be modeled in a sequential framework
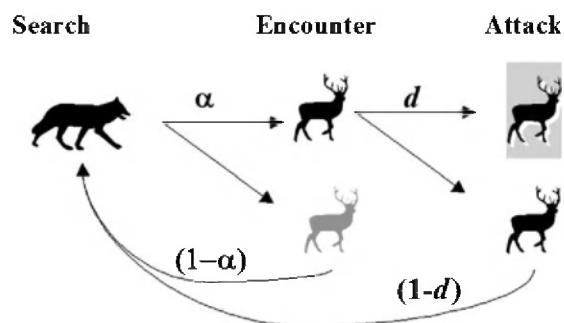

Fig. 1. Schematic representation of the spatial decomposition of the three main stages of predation, search, encounter, and kill, in our wolf–elk system over time, T. All elk inside the territory are available to be encountered when wolves are searching for prey, but only some of these at any particular time are successfully encountered with probability α. Conditional on encounter, elk are killed with probability, d. We randomly sampled wolf search paths with radio telemetry locations, encounters through snow tracking, kills through telemetry and snow tracking, and we characterized elk locations through telemetry during winters 1997 to 2001, Banff National Park, Alberta, Canada.

using logistic regression (e.g. logit form of $[(p)/(1-p)]$. If encounter locations are known (used units), and areas where prey were either not encountered (unused units) or areas where prey could have been encountered (available units) are known, then an RSPF or an RSF can be used to describe the probability of encounter as a function of landscape attributes. Examples of used-unused designs in estimating probability of encounter might include observational studies where a predator is known to have 'missed' an encounter, thus representing an unsuccessful encounter. In the example we present below, we consider the more common case of used-available units for observational studies where encounters are known and compared to areas in which prey were available to be encountered. Defining availability is crucial to the scope of inference of RSF models (Manly et al. 2002). We define availability for estimating the risk of encounter as all areas in which either prey or predators occur (Minta 1992). By comparing attributes at sites where prey were encountered to all areas available to predator and prey, we estimate the spatial intersection, or overlap for a suite of landscape covariates (Minta 1992).

Using a logistic regression the relative probability of encounter, $\alpha(x)$, given availability of landscape covariates (x_i) used by both predators and prey, is equivalent to Manly et al.'s (2002, p. 100) resource selection function $(w(x_i))$, and is proportional to;

$$\alpha(x) = \exp\left(\sum_{i=1}^{n} \beta_i x_i\right) \qquad (2)$$

where i = refers to landscape covariates 1 through n for encounters and available locations. Following Manly et al. (2002) we drop the denominator of the logistic form and the intercept for this relative function. (Boyce and McDonald 1999, Manly et al. 2002).

When both kill and encounter locations are known we can estimate the second term in Eq. 1, d, the conditional probability of death as a function of landscape attributes using logistic regression where 1 = kill locations (used), and 0 = encounter locations where no kill occurred (unused). In the case with known encounters, the used-unused design corresponds to a RSPF, or true probability function (equivalent to $w^*(x_i)$ of Manly et al.'s 2002, p. 83), and the conditional probability of kill given encounter is expressed as:

$$d(x) = \frac{\exp(\beta_0 + \sum_{i=1}^{n} \beta_i x_i)}{1 + \exp(\beta_0 + \sum_{i=1}^{n} \beta_i x_i)} \qquad (3)$$

where i = refers to landscape covariates 1 through n for kills and encounters. The intercept β_0 is included because the sampling probability is known and a true probability function is estimated (Manly et al. 2002). Study designs

where encounter locations might include a kill location would represent an RSF design, and would adopt Eq. 2 above.

In some situations, encounters may not be known (Kunkel and Pletscher 2000) and decomposition of predation risk components will not be possible. Comparing landscape attributes of kill locations to locations available to predator and prey using Eq. 2 may approximate relative predation risk in Eq. 1 (Nielsen et al. 2004). A spatial function of kill locations is an improvement over assuming predator locations equal risk but does not permit the derivation from Hollings' (1959) functional response in Eq. 1. Moreover, by failing to decompose predation, it is not possible to discern if changes in risk arise at the encounter or kill stage, or are due to predator or prey effects (Thogmartin and Schaeffer 2000). Decomposing predation risk into its components can reveal valuable insights into the mechanisms of predation risk.

Where we know both the spatial risk of encounter and death, we can substitute $\alpha(x)$ and $d(x)$ into Eq. 1 to estimate a spatial predation risk function, $P(k)$. When RSPF models of both encounter and kill can be estimated, Eq. 1 yields a true joint probability function for predation risk. When either α or d are relative probability functions, as in our example below, $P(k)$ remains a relative measure of predation risk bounded between 0 and 1 (Johnson et al. 2004, p. 248). In a GIS framework, because $\alpha(x)$ and $d(x)$ are functions of landscape covariates i = 1 to n, $P(k)$ is spatially explicit and maps of predation risk can be produced (Boyce and McDonald 1999). A critical assumption is that the predation risk function applies only over time period T during which data were collected. Therefore, the encounter and kill functions must be modeled at the same time scales, i.e. day, month, or season. As a useful extension, time-varying functions could be developed to test for temporal (seasonal, annual) variation in predation risk (sensu Manly et al. 2002, p. 118). Further, RSF models are scale-dependent (Boyce et al. 2003); for example between selection for location of a home range (second-order selection), and selection within a home range (third-order selection, Johnson 1980). Predation risk components from one spatial scale would be inappropriate to apply at another spatial scale.

Methods

Study area

We illustrate our approach for a wolf–elk predator–prey system in and adjacent to Banff National Park (BNP, 51°15′/116°00′), Alberta, Canada, during winters 1997 to 2001. We defined winter as 15 October to 15 April. BNP, 6641 km^2 in area, is on the eastern slope of the continental divide in the Canadian Rocky Mountains

(1400 to 3400 m). Vegetation is dominated by closed lodgepole pine (*Pinus contorta*) forests interspersed with riparian Engelmann spruce (*Picea engelmanii*) – willow (*Salix* spp.), aspen (*Populus tremuloides*) – parkland, and dry grasslands at low elevations. Engelmann spruce-subalpine fir (*Abies lasiocarpa*) forests dominate at higher elevations, interspersed with willow-shrub meadows, subalpine grasslands, avalanche terrain, and alpine shrub-forb meadows (Holland and Coen 1983). Elk are the most abundant ungulate and are the primary prey of wolves, comprising 40–70% of wolf diet (Hebblewhite et al. 2004). Wolf predation is equally important to elk, accounting for 30–60% of adult female elk mortality (McKenzie 2001). To illustrate our approach we use data from the Cascade wolf pack, which established in 1991 inhabiting an area previously uninhabited by wolves for up to 30 years (Hebblewhite et al. 2004). Winter wolf numbers stabilized around eight wolves from 1997 to 2001. We used elk telemetry data from elk within the Cascade pack territory. The Cascade territory contained two primary elk winter ranges, the Ya Ha Tinda and Bow Valley ranges, and several smaller secondary ranges.

Wolf and elk predator–prey data

Wolf and elk research and capture methods followed approved and standard methods (Parks Canada Environmental Assessment B-1994–29, Univ. of Alberta Animal Care protocol ID# 35112). For more detailed descriptions of wolf and elk monitoring see McKenzie (2001) and Hebblewhite et al. (2004). For wolf monitoring, we used systematic (weekly) aerial relocations of radiocollared wolves to characterize the search stage of predation and to start continuous tracking sessions (Fig. 1). During continuous snow tracking of wolves we recorded spatial intersection of the tracks of wolves and elk groups (Hebblewhite and Pletscher 2002) and found elk killed by wolves (Hebblewhite et al. 2004). We defined the intersection of wolf tracks with elk tracks as an encounter, and locations of wolf-killed elk as kills (Fig. 1). Spatial differences between encounters and kills were evident from the snow tracking sequence with elk being chased an average of 262m (SD = 330.2, n = 96, range 10–1700 m, unpubl.) after an encounter. Our definition of search and encounter assumed (1) wolves always hunted while traveling (Mech and Boitani 2003) and (2) spatial intersection of wolf and elk snow tracks represented the spatial encounter location where wolf and elk tracks overlap in space (Fig. 1; Hebblewhite and Pletscher 2002). In reality, our measure of encounter may not have represented the true spatio-temporal encounter, yet for RSF models we were only interested in spatial encounters. Future extensions of our approach could include spatio-temporal encounters, but difficul-

ties remain in defining "true" spatio-temporal encounters. Resource selection of elk was determined by relocating radiocollared female elk within the Cascade territory weekly from the air or ground during winter following standard techniques at the major winter ranges in the Bow Valley and Ya Ha Tinda, and in secondary winter ranges scattered throughout the Cascade territory (McKenzie 2001, Hebblewhite, M., unpubl.).

Landscape attributes

We selected landscape attributes known from previous studies to influence wolf and/or elk resource selection and predator–prey dynamics (Kunkel and Pletscher 2000, Roloff et al. 2001, Boyce et al. 2002, Lingle and Pellis 2002). Landscape attributes measured at encounter, kills, wolf, elk, and available sites included percent slope, aspect classified as eight cardinal directions, elevation to nearest 100 m, distance (km) to roads and trails, and vegetative cover type in ARCGis 8.2 (ESRI Inc.). Topographic variables (slope, elevation) were calculated from a 100 m^2 resolution digital elevation model for the study area, whereas distance to roads and vegetation layers were measured at a 30 m^2 resolution. Roads and trails were derived from the human use atlas of the Central Rockies Ecosystem (Jevons 2001) and included active roads used by vehicles, and inactive roads and trails used by off highway vehicles, horseback riders, or by hikers. We buffered this access layer with ArcGIS 8.2 to create a distance to human access surface in km. Because the territory of the Cascade wolf pack straddled two mapping jurisdictions for vegetative cover type, we merged two landcover maps following expert advice (D. Zell, Parks Canada). Land cover types were pine, closed conifer, open conifer, avalanche path, alpine, grassland, shrub, and rock/ice. We screened for collinearity using tolerance scores following Menard (2002), which resulted in the exclusion of the rock/ice, and several aspect categories. We included categorical habitat and aspect variables in models using dummy variable coding, excluding the reference category.

Resource selection function modeling

We estimated resource selection models for the encounter (Eq. 2) and kill (Eq. 3) stages of wolf predation, and then compared these to overall wolf-search and elk RSF models (using Eq. 2) to test for differences in effects of landscape attributes between predation stages (Fig. 1). For the elk RSF, we assessed availability using a balanced number of random locations for each individual elk in the wolf territory. We calculated variance for beta coefficients in elk models by clustering data by individual elk in STATA (StataCorp 2001) to reduce autocorrelation (Pendergast et al. 1996). For the wolf-

search RSF, we compared wolf telemetry locations to 1000 random locations within the wolf territory. Wolf relocations were screened ≥ 24 h between locations to reduce autocorrelation (Otis and White 1999). Analyses with multiple packs should use an appropriate grouping by pack (Pendergast et al. 1996) to account of lack of independence among individuals within a pack. We estimated $\alpha(x)$, the encounter RSF, by comparing all elk encounters obtained from snow tracking with the same 1000 random locations as for describing resource availability within the wolf territory. Finally, we used all elk encounters and kill locations of elk in the final $d(x)$, or probability of death, RSPF model. Our analyses correspond to the third-order (Johnson 1980) or within home range scale, but our approach could easily be applied at different spatial scales (Boyce et al. 2003).

Because our objective was to compare how the different stages of predation (search, encounter, and kill) and elk distribution were affected by landscape attributes, we used a constrained model selection approach to select a constant set of parameters to compare across models. Without consistency among variables, coefficients would not be comparable because the covariance matrix adjusts coefficients differently with different combinations of covariates (Hosmer and Lemeshow 1989, McCullough and Nelder 1989). Therefore, we first created candidate sets of hypothesized models and then fit RSF or RSPF models for each component (wolf search, encounter, kill; elk), and used AIC_c to rank models based on Akaike weights, w_i for each model (Burnham and Anderson 1998). We then used the sum of all Akaike weights for each covariate to rank covariates in order of importance following Burnham and Anderson (1998, p. 140). We selected a consistent set of landscape attributes to build comparative RSF models for each predation stage from this ranked set of variables in the top models. In addition to assessing overall model fit, we compared estimated beta coefficients for each covariate for effect size and significance using 90% confidence intervals (we set $P = 0.10$) to determine at which predation stage landscape features had the largest effect. Using these models we mapped $\alpha(x)$ and $d(x)$ using Eq. 2 and 3 in ArcGIS 8.2 at the resolution of 30 m^2 pixel^{-1}. We then substituted the spatial RSF probabilities $\alpha(x)$ and $d(x)$ into Eq. 1 using map calculator in ArcGIS 8.2 to estimate the relative predation risk surface for our study area. All figures are displayed with a histogram smoother in ArcGIS 8.2.

Evaluating performance of RSF models based on normal logistic regression diagnostics (i.e. ROC, R^2, etc) are flawed in use-availability designs (Fielding and Bell 1997, Boyce et al. 2002). Therefore, we evaluated the predictive performance of all models using k-folds cross-validation (Boyce et al. 2002), where k-partitions of the dataset are made following a test to training ratio of

20%, or five subsets. Predictive capacity of partitioned models were evaluated against the withheld training data using Spearman rank correlations (r_s) between training and test data grouped within ten bins (Fielding and Bell 1997, Boyce et al. 2002). We conducted all statistical analyses in STATA 7.0 (StataCorp 2001).

Results

Data and model assessment

During four winters from 1997 to 2001 we collected 119 telemetry locations ≥ 24 h apart on six different wolves in the Cascade pack, snow backtracked wolves approximately 1250 km finding 77 groups of elk tracks encountered by wolves, and sampled 119 elk that were killed by wolves. Elk killed by wolves included 29 adult female, 52 adult male, 7 yearlings, 9 calves, and 31 unknown female age classes. We collected 4890 telemetry locations on 104 radiocollared adult female elk in both the Bow Valley and Ya Ha Tinda winter ranges between 1997 and 2001, with an average of 29 telemetry locations/elk/winter.

Six covariates, distance to human access, slope, elevation, and the cover types of grassland, pine, and open conifer were consistently retained in top-ranked models for all predation stages (Table 1, 2). Where model selection uncertainty arose, such as for the kill stage (Table 1, 2), ΔAIC_c scores suggested a close tie between the lower ranked, full six covariate model, and other top models (Table 1, 2). With the exception of the kill-stage RSPF, most models containing the top six covariates were consistently ranked first or second out of all competing models (Table 1, 2), despite some model selection uncertainty (i.e. w_i from 0.15 to 0.38). Therefore, we felt justified in comparing the importance of these six covariates among predation stages. Using these six covariates, RSF models for elk occurrence, wolf search, and wolf-encounter $\alpha(x)$ had good model fit (Table 2, all likelihood ratio-test χ^2 P-values < 0.0005, and high Nagerleke's $R^2 > 0.22$). By contrast, the RSPF predicting $d(x)$ had poor model fit, and many of the predictor variables were not selected for (Table 2, likelihood ratio-test χ^2 P-value $= 0.12$, Nagerleke's $R^2 = 0.10$). Similarly, the Spearman rank correlation from the k-fold cross-validation was lower (0.52 ± 0.05, SE) for $d(x)$ than the other models (0.67 ± 0.08 to 0.86 ± 0.01, Table 2). Based on Akaike weights, simpler models for the kill stage with less than the six covariates did not greatly improve model fit (unpubl., Table 1).

Elk and wolf occurrence

Probability of elk occurrence within the territory of the Cascade wolf pack decreased with increasing distance to

Table 1. Akaike weights (w_i) for covariates in the four predation stage RSF models: for elk, wolf-search, wolf-encounter, and wolf-kill in Banff National Park, Alberta, winters 1997–2001. Shown are the Akaike weights for each covariate, along with the averaged weight across all four predation stages and the average rank of covariate importance.

Covariate	Elk	Wolf-search	Wolf-encounter	Wolf-kill	Average Akaike weight, w_i	Average rank
Elevation	0.952	1.000	0.983	0.996	0.983	1
Distance to human access	0.952	0.921	0.983	0.996	0.963	2
Slope	0.614	1.000	1.000	1.000	0.903	3
Grassland	0.925	0.917	1.000	0.740	0.895	4
Open conifer	0.710	0.530	0.226	0.870	0.584	6
Pine	0.520	0.936	1.000	0.572	0.757	5
Closed conifer	0.483	0.233	0.440	0.459	0.404	7
Shrub	0.338	0.081	0.296	0.137	0.213	8
Avalanche	0.027	0.115	0.000	0.000	0.036	11
Deciduous	0.044	0.081	0.000	0.563	0.172	9
South aspects	0.000	0.000	0.247	0.000	0.062	10

roads ($\beta = -0.377$), and increased at lower elevations ($\beta = -0.219$) and on shallower slopes ($\beta = -0.017$) during winter (presented as relative odds ratios in Table 3, and as beta coefficients in Fig. 2). Probability of elk using grasslands ($\beta = 2.05$) and open conifer ($\beta = 1.65$) was high while probability of elk use of pine forests ($\beta = -0.125$) was low. The probability of a resource unit being used by wolves at the search stage decreased with increasing elevation ($\beta = -0.380$), slope ($\beta = -0.021$) and distance to roads ($\beta = -0.703$). Wolf use was higher in grasslands ($\beta = 1.255$) and pine forests ($\beta = 0.44$), but decreased in open conifer ($\beta = -0.204$, Table 3).

Elk−wolf encounters and kills

In our study area there were important statistical differences in the effects of landscape attributes on wolf predation risk stages for elk (Table 3, Fig. 2). The relative odds of an elk being killed in grasslands (1.34) were about five times less than the odds of elk being encountered in grasslands (7.65). Once an elk was encountered, odds of being killed in pine stands (1.45)

was about a third more likely than being encountered (1.07), while the odds of being killed in open conifer stands (0.35) was about half that of being encountered (0.66). Similarly, elk were about fifth again more likely to be killed in high elevation areas (0.83) than being encountered (0.71). There was no difference in the odds of elk being encountered and killed near roads or on slopes of varying steepness (Table 3).

Predation risk

The spatial functions of relative probability of encounter (Fig. 3a) and probability of kill (Fig. 3b) from the equations in Table 2 illustrate the spatial application of predation risk in real landscapes (Fig. 3c). Wolves avoided high elevation and steep slope areas more than elk (Table 3, Fig. 2), concentrating elk−wolf encounters in valley bottoms (Fig. 3a). The strength of the topographic effect on encounter overwhelmed effects of other variables once translated onto the real ecological landscape in Fig. 3a. However, given an encounter, habitat appeared to have the strongest effects on risk of being killed (Fig. 2, 4b, Table 3), with risk of death being

Table 2. Model fit for predicting the relative probabilities of resource use by elk, p(elk), wolves, p(wolf), encounters between wolves and elk, $\alpha(x)$, and the true conditional probability of elk being killed by wolves, given an encounter, d(x), within the Cascade pack wolf territory during winters 1997–2001, Banff National Park, Alberta. Models are shown with corresponding number of parameters k_i, ΔAIC_c, Akaike weight (w_i), Nagerleke's R^2, and the Spearman rank correlation (r_s) obtained from k-folds cross validation (see text) as a means of evaluating model predictive performance shown with SE. See text for statistical modeling details.

Model	N^a	k_i	ΔAIC_c^b	w_i^b	Model rank[c]	R^{2d}	Likelihood ratio X^2	Likelihood ratio P-value	k-folds cross validation r_s^e
Elk	9780	7	0.61	0.15	2	0.22	139.12	<0.0005	0.86±0.01
Wolf	1190	7	0.60	0.20	2	0.32	295.70	<0.0005	0.82±0.05
Encounter $=\alpha(x)$	1077	7	0.00	0.38	1	0.28	144.10	<0.0005	0.67±0.08
Kill[f] $=$ d(x)	189	7	0.02	0.11	4	0.10	11.41	0.0700	0.52±0.05

a- Sample size including 4890 random locations for elk, 1000 for wolf and encounter, and 77 encounters and 119 kills for the probability of kill model.
b- AIC_c and weights are reported for each model of the top model set for each predation stage, and are not comparable across the different stages. They are presented to allow evaluation of their strength.
c- Model rank among candidate models set based on ΔAIC_c, from Table 1.
d- Nagerleke's pseudo − R^2 value.
e- Spearmans rank correlation coefficient for k-folds procedure averaged from five partitions. See text for details.
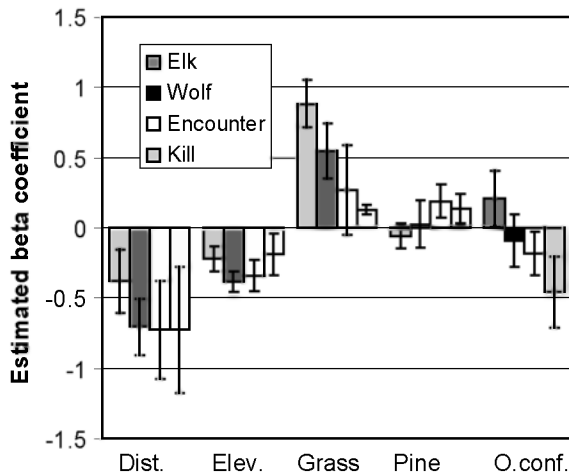f- Conditional on encounter.

Fig. 2. Beta-coefficients for distance to human access (km), elevation (in 100 m intervals), grassland, pine, and open conifer habitat's from logistic regression resource selection function models for elk, wolves, wolf encounters with elk, and wolf-killed elk in Banff National Park, Alberta. Estimates are presented with 90% confidence intervals, and non-overlapping significant differences are also indicated in Table 3. Slope is not shown because of the large Y-axis scale relative to the estimates of effect sizes for slope (Table 3).

reduced in grasslands and open conifer relative to other habitats. Combined in Eq. 1, the conditional nature of the risk of death on encounter is clearly illustrated (Fig. 3c). For example an elk's risk of death in pine forests is modified by its topographic position in Fig. 3c because of the dominant effect of topography on risk of encounter.

Discussion

Our example clearly illustrates the importance of carefully defining predation risk for prey, and demonstrates the utility of our approach to spatially decompose predation risk for revealing the behavioral aspects of

predation risk in real landscapes. For example, encounters were driven largely by topographic variables slope and elevation (Fig. 3a), whereas habitat covariates had the greatest effects on the risk of death, given an encounter (Fig. 3b) for our study area. Important trends in predation risk between stages were also revealed. For example, grasslands and open conifer consistently reduced risk as predation escalates from search to encounter to kill, while the opposite occurred in pine stands and with decreasing elevation (Fig. 3). Broader analyses will be required to determine whether these patterns hold across different wolf territories. Nevertheless, in this example if we had defined predation risk simply as those areas used by wolves, we would have overestimated risk by 60% in grasslands and open conifer, and underestimated risk by 20% in pine and at higher elevations (Fig. 2, Table 3). Thus, predation risk for elk was a function of not only where wolves were, but of landscape attributes that rendered elk more or less vulnerable to predation once encountered. Studies that assume predation risk is equivalent to predator habitat use may be misleading. Similarly, if a landscape attribute decreased the encounter risk but increased vulnerability once encountered, studies that do not distinguish between encounter and kill may not uncover the attributes that influence predation because the components negate each other.

By distinguishing between components of predation, mechanisms driving the observed statistical patterns may be hypothesized and tested using field experiments or further analyses. For example, the safety afforded to elk in grasslands may result from increased predator detection and vigilance in open habitat (Dehn 1990) or larger group sizes. Elk group sizes are typically greater in grasslands, and while wolf encounter and attack rates may increase for large herds, individual elk predation risk declines with increasing group size because of dilution effects (Hebblewhite and Pletscher 2002). Indeed, our decomposition of predation risk results suggests elk reduce predation risk the most in grasslands,

Table 3. Parameter estimates presented as relative odds-ratios, standard errors (SE), and associated p-values for independent variables in RSF models for elk, wolf search, wolf encounter, and wolf kill models. Statistically significant differences (at P =0.10) between different predation stages (elk, wolf, encounter, kill) within a covariate are marked with different letters (a, b, c, etc).

| Variable	Distance to road	Elevation	Slope	Grassland	Pine	Open conifer
Elk	0.685[a]	0.803 [a]	0.983 [a]	7.655 [a]	0.882 [a]	1.635 [a]
SE	0.1257	0.0479	0.0136	2.5212	0.3175	0.5202
P-value	0.005	<0.0006	0.203	<0.0005	0.728	0.122
Wolf	0.495 [a]	0.684 [b]	0.979 [a]	3.508 [b]	1.553 [a]	0.815 [a]
SE	0.1154	0.0375	0.0116	1.2333	0.3919	0.2485
P-value	0.003	<0.0005	0.077	<0.0005	0.081	0.503
Encounter	0.485 [a]	0.711 [b]	0.965 [b]	1.862 [b]	1.066 [a]	0.661 [a]
SE	0.1627	0.0530	0.0173	0.9681	0.3599	0.2620
P-value	0.031	<0.0005	0.047	0.232	0.85	0.297
Kill	0.4833 [a]	0.838 [a]	0.971 [b]	1.346 [b]	1.451 [b]	0.350 [b]
SE	0.4770	0.0970	0.0153	0.7556	0.3941	0.1458
P-value	0.43	0.071	0.058	0.597	0.265	0.012
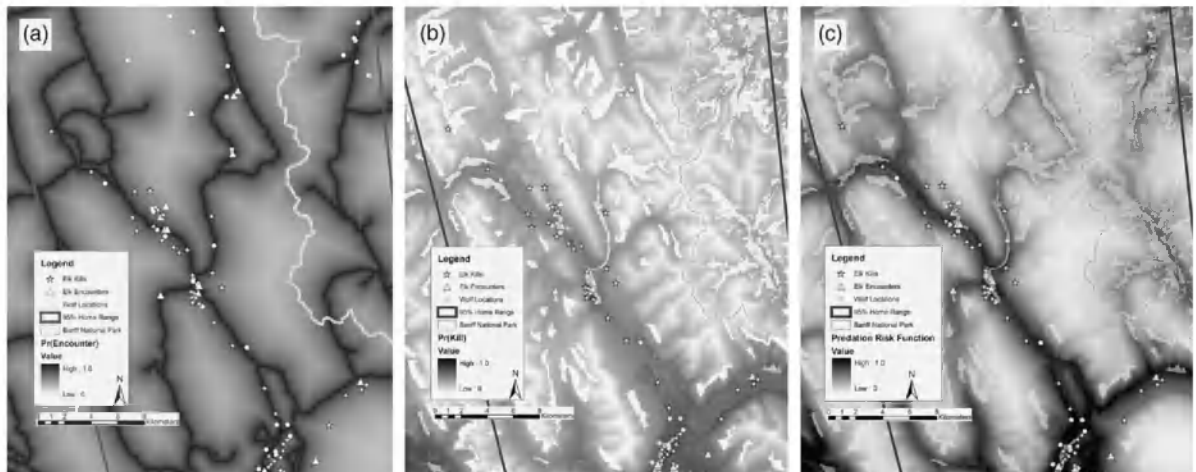
Fig. 3. Spatial maps of the decomposition of the components of predation, illustrated using wolf predation on elk in the Cascade valley portion of the Cascade pack wolf pack territory from 1997–2001 in Banff National Park (light boundary). Predation risk decomposes into (a) probability of encounter, given availability, (b) probability of kill, given encounter, and the product of (a) and (b) equal the relative probability of death, (c) P(k) following Lima and Dill (1990) where $P(k) = 1 - \exp^{-(\alpha dT)}$. Shown are wolf telemetry locations (●, n = 119), encounters with elk (▲, n = 77), and wolf killed elk (☆, n = 118). Relative probabilities were derived using resource selection functions (Manly et al. 2002).

consistent with earlier non-spatial work on predation risk (Hebblewhite and Pletscher 2002). In contrast to grasslands, dense cover in pine forests may render elk more vulnerable to predation by wolves because detection distance may be reduced or woody deadfall may slow escape of fleeing prey (Kunkel and Pletscher 2000). Because our analysis was conducted at a resolution of a 30-m pixel we did not measure deadfall, but resource attributes at the microsite level (<30 m) could be measured to test more mechanistic hypotheses (Kunkel and Pletscher 2004).

Insights into the mechanisms of predation may have important management and conservation implications. For example, endangered mountain caribou (*Rangifer tarandus tarandus*) are thought to spatially separate from predators by migrating to high elevations to reduce the risk of encountering wolves (Seip 1992). Recent caribou declines are hypothesized to arise from the combined effects of a numeric response in wolves from increasing alternative prey (moose) density as a result of early seral habitats from forestry (Terry et al. 2000) and/or increased encounter rates by wolves due to human-modified trails (Seip 1992). Cause-specific survival data support the hypothesis that predation plays a key role in caribou decline (Seip 1992, Kinley and Apps 2001). However, demonstrating whether roads increase encounter rates, or that roads or attributes associated with roads themselves make prey more susceptible to predation once encountered may require different mitigating actions. Without the decomposition of predation risk, these and other mechanistic hypotheses about landscape effects on predation risk would be difficult to test. Decomposition of predation risk can focus conservation

actions on the predation stage that had the greatest effect or flexibility to management.

Our objective was to illustrate the importance of decomposing predation risk. In applications where predicting predation risk for management or conservation is the main priority, the need to model predation risk with a consistent set of covariates would not unnecessary. One would simply select the best model for each predation stage, or where model selection uncertainty arose, adopt a model averaging approach (Burnham and Anderson 1998). Total predation risk over the landscape would then result from the combined effects of the best encounter and kill models. Furthermore, if information about encounters were unavailable, predation risk could be approximated using a direct comparison of kills and availability of habitats to predators and prey. One important caveat is that we focused on a single wolf territory and ignored density in our example because wolf numbers over the study were relatively constant. Thus our relative spatial predation risk function would be valid for the Cascade pack we modeled. Yet, total predation risk is not only related to the spatial predation risk function, but to the numeric, or spatial density of predators (Messier 1994, Kristan and Boarman 2003). This is similar to non-spatial predator-prey dynamics where total predation rate is a function of both the functional and numeric responses (Messier 1994). Thus, while the predation risk function (Eq. 1) will identify risky habitats, for example, pine for elk, predation risk may vary across pack territories dependent on the number of predators, wolf pack size in our example. To incorporate the effect of density on predation risk, Kristan and Boarman (2003) weighted predation risk for tortoises by raven density to estimate

total predation risk. Therefore, for situations of multiple predators or packs, different packs should be weighted according to pack size, although this assumes predation risk responds linearly to predator density, which may not always be the case (Messier 1994). Assessing the functional response of predation risk as a function of predator density (sensu Mysterud and Ims 1998) using this approach would provide a considerable advance in our understanding of spatial predation risk.

We believe the most exciting opportunities for this approach is in their application to spatial models of predator–prey dynamics. Predator–prey dynamics have been modeled spatially using lattice-networks (Tobin and Bjornstad 2003), heuristic simulation models (Donalson and Nisbet 1999), and individually-based models (McCauley et al. 1993), to name a few approaches. Most models simplify landscape structure into a few patch types, and model predator–prey dynamics in these different patches. Our approach can provide spatially explicit functions of predation risk based on landscape attributes (Lima and Zollner 1996) that are proportional to probability of encounter (α) and attack (d) (Manly et al. 2002, p. 177), and thus should be proportional to the predator functional response (Holling 1959, Messier 1994). Messier (1994) combined the functional and numeric response to estimate the total population-level predation response of wolves preying on moose. If the spatially explicit risk of predation in Fig. 3c (i.e. a relative functional response) is combined with the spatial density response (numeric response) to generate a spatially explicit total predation function (sensu Messier 1994), this total predation risk function should be proportional to the number of prey expected to be killed by predators in a landscape, and could be used for a number of applied and theoretical purposes. For example, one could adapt the Boyce and McDonald (1999) approach whereby a RSF is used to distribute a known number of animals (from some other data source) on a landscape using a GIS for predator–prey modeling. Instead of distributing a known number of animals on a landscape (Boyce and McDonald 1999), the predation risk function could distribute a known number of kills across the landscape, which could be then combined with RSF models for prey species to examine relative predation rates across a landscape. Moreover, pack-size kill-rate relationships (Mech and Boitani 2003) or mechanistic models of predator functional responses (Messier 1994) could be used to rescale the relative encounter probability $\alpha(x)$ to a true probability in combination with prey density data. In this fashion, landscape-level prey simulation models (Turner et al. 1994) could be combined with predation risk functions to model the effects of landscape on predator–prey dynamics (Iwasa et al. 1981). Thus, spatial predation risk functions will help bridge the gap between behavioral ecology and landscape ecology in real ecological landscapes (Lima and Zollner 1996, Lima 2002).

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