

Multiscale wolf predation risk for elk: does migration reduce risk?

Mark Hebblewhite · Evelyn H. Merrill

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Abstract While migration is hypothesized to reduce predation risk for ungulates, there have been few direct empirical tests of this hypothesis. Furthermore, few studies examined multiscale predation risk avoidance by migrant ungulates, yet recent research reveals that predator–prey interactions occur at multiple scales. We test the predation risk reduction hypothesis at two spatial scales in a partially migratory elk (*Cervus elaphus*) population by comparing exposure of migrant and resident elk to wolf (*Canis lupus*) predation risk. We used GPS and VHF telemetry data collected from 67 migrant and 44 resident elk over the summers of 2002–2004 in and adjacent to Banff National Park (BNP), Canada. We used wolf GPS and VHF telemetry data to estimate predation risk as a function of the relative probability of wolf occurrence weighted by a spatial density model that adjusted for varying pack sizes. We validated the predation risk model using independent data on wolf-killed elk, and showed that combining wolf presence and spatial density best predicted where an elk was likely to be killed. Predation risk on summer ranges of migrant elk was reduced by 70% compared to within resident elk summer ranges.

Because wolves avoided areas near high human activity, however, fine-scale selection by resident elk for areas near high human activity reduced their predation risk exposure to only 15% higher than migrants, a difference significant in only one of three summers. Finally, during actual migration, elk were exposed to 1.7 times more predation risk than residents, even though migration was rapid. Our results support the hypothesis that large-scale migrations can reduce predation. However, we also show that where small-scale spatial variation in predation risk exists, nonmigratory elk may equally reduce predation risk as effectively as migrants under some circumstances.

Keywords Antipredator behavior · Human–wildlife relationships · Partial migration · Predator avoidance · Resource selection

Introduction

The question of how behavioral strategies reduce predation risk while minimizing starvation risk is a central concept in ecology because of the role that predator avoidance plays in population and trophic dynamics (Houston et al. 1993; Hebblewhite et al. 2005b). Predation risk is a prime determinant of lifetime reproductive success of large ungulate herbivores (Kjellander et al. 2004), and hence ungulate life history (Geist 2002). Perhaps the most basic antipredator strategy is to spatially avoid areas with high predator density (Caro 2005), which can be achieved at several scales (Lima and Zollner 1996). For example, avoiding predation at large scales is hypothesized to be one of the key benefits of long-distance migration in ungulates

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M. Hebblewhite (✉)
Wildlife Biology Program,
Department of Ecosystem and Conservation Sciences,
College of Forestry, University of Montana,
Missoula, MT 59812, USA
e-mail: mark.hebblewhite@cfc.umt.edu

M. Hebblewhite · E. H. Merrill
Department of Biological Sciences,
University of Alberta,
Edmonton, AB T6G 2E9, Canada

(Bergerud et al. 1984; Fryxell et al. 1988). Bergerud et al. (1984) proposed that ungulate migration benefits individuals primarily by reducing predation risk, theoretically allowing migratory populations to attain higher densities because of reduced mortality (Fryxell et al. 1988).

Nonmigratory ungulates must necessarily avoid predators at smaller spatial scales, however, and adopt fine-scale behavioral strategies to do so (Caro 2005). Examples of fine-scale predator avoidance by ungulates include exploiting predation refugia created by territorial predators between territories (Lewis and Murray 1993; Anderson et al. 2005), or fine-scale avoidance of risky patches (Fortin et al. 2005; Mao et al. 2005). For example, at intermediate scales, elk (*Cervus elaphus*) reduced use of aspen stands and shallow slopes (both preferred foraging patches) when wolves (*Canis lupus*) were present (Fortin et al. 2005; Mao et al. 2005). At the finest scales, however, elk avoidance of the highest risk areas was strongest during night when wolves were most active (Beyer 2006). Human activity may also influence predation risk for ungulate prey because human-caused mortality imposes a trade-off for predators which may cause predators to avoid humans (*sensu* Frid and Dill 2002). These studies emphasize that predation risk is spatially and temporally dynamic (Lima and Zollner 1996).

The ability of ungulates to avoid risk at multiple scales begs the question: at what scale is it most effective to avoid predation risk? Large-scale risk avoidance is consistent with the predation risk avoidance hypothesis that Bergerud (1984) and others (Fryxell et al. 1988) proposed for migratory ungulates. Large-scale predation risk avoidance was also reported for other nonmigratory ungulates as well (Rettie and Messier 2000; Johnson et al. 2002a). Despite this apparent support for large-scale risk avoidance, no studies have compared both migratory and nonmigratory (resident) ungulates in order to conclusively test the predation refuge hypothesis and compare risk exposure at different spatial scales. Furthermore, numerous studies confirm smaller-scale predation risk avoidance strategies (Kunkel and Pletscher 2001; Gude et al. 2006) that involve exploiting fine-scale variation in predation risk or adopting adaptive group-living strategies (e.g. Gude et al. 2006). Thus, the consequences of risk avoidance at different scales are unclear, and tests have been hindered because of a lack of ways to model predation risk over large areas (Lima and Zollner 1996).

Recent developments in the application of resource selection functions (RSF, Manly et al. 2002) to model predation risk over large areas (e.g. Kristan and Boarman 2003; Hebblewhite et al. 2005a) now make

multiscale tests of the predation risk avoidance hypothesis possible. Spatial predation risk modeling approaches have assumed that either predator density (Anderson et al. 2005; Mao et al. 2005) or predator habitat use (Johnson et al. 2002a; Hebblewhite et al. 2005a) is proportional to risk. However, both Kristan and Boarman (2003) and later Hebblewhite et al. (2005a) suggested that resource selection and spatial density are both important components of risk. Spatial density of predators is likely to be particularly important for territorial species (such as wolves), where densities vary in response to social factors that are typically not included in resource selection (Fretwell 1972). Unfortunately, few studies have evaluated risk modeling approaches.

In this paper, we test the predation risk avoidance hypothesis for migrant and nonmigratory (resident) elk preyed on by wolves on the eastern slopes of Banff National Park (BNP), Alberta, Canada. We test the hypothesis that large-scale avoidance of wolves by migration has the greatest effect in reducing predation risk by comparing risk exposure of migrant and resident elk at two spatial scales: between summer home ranges (landscape scale), and between telemetry locations within summer home ranges (home range scale). We also compared predation risk during migratory movements between winter and summer ranges. However, we first address the question of what constitutes wolf predation risk for elk. Recent studies suggest that it is not merely habitat selection of predators, their spatial distribution or density that constitutes risk, but some function of all three (i.e., Kristan and Boarman 2003; Hebblewhite et al. 2005a, 2005b). We test the hypothesis that, from an elk perspective, predation risk is a function of all three factors, by combining previously developed habitat selection models for wolves (Hebblewhite 2006; Hebblewhite M, Merrill EH, Modeling wildlife–human relationships with mixed-effects habitat selection models, *Ecol Appl*, in review) with the spatial density and wolf pack size to estimate total predation risk for elk. We validated predation risk models using locations of wolf-killed elk. Finally, because our previous habitat selection model emphasized the importance of wolf avoidance of human activity (Hebblewhite M, Merrill EH, Modeling wildlife–human relationships with mixed-effects habitat selection models, *Ecol Appl*, in review), we test the hypothesis that wolf avoidance of humans at the home range scale reduced exposure of elk to predation risk. While herbivore decisions regarding predation risk avoidance are made in the context of a forage–predation trade-off, herein we focus on predation only and address the nutritional benefits of migration and the

trade-off between risk and forage elsewhere (Hebblewhite 2006).

Materials and methods

Study area

The study area is located on the eastern slopes of the Canadian Rockies in and adjacent to Banff National Park (BNP, 51°30′/115°30′). Movements of radio-collared wolves and elk from the Ya Ha Tinda (YHT) elk population defined a 7,000 km² study area. Wolves were the primary predator of elk (Hebblewhite 2006). Topography in the study area ranges from 1,400 m to 3,500 m on the western part of the study area. Climate is cold continental, with long (October–April) snowy winters, and a brief summer (May–September) (Holland and Coen 1983). The YHT winter range (Fig. 1) is one of Alberta's largest (25 km²) montane rough fes-

cue (*Festuca campestris*) grasslands, surrounded by lodgepole pine (*Pinus contorta*) forests interspersed with shrub (*Salix* spp., *Betula* spp.), riparian, and scattered grassland meadows. Elk are partially migratory, with migrants moving to summer ranges ~35 km (range 15–70 km) distant in the main ranges of BNP on ~1 June, and returning on ~1 October (Hebblewhite et al. 2006). Summer ranges are in the subalpine and alpine ecoregions, characterized by Englemann spruce (*Picea engelmanni*), shrub meadows, avalanche terrain, and subalpine grasslands, with lush alpine shrub and herbaceous communities. Resident elk remain on the YHT winter range and adjacent slopes year-round (Hebblewhite et al. 2006). Human activity was concentrated on the YHT winter range, and was lowest on migrant summer ranges inside BNP (Jevons 2001). Wolves that occupied park boundary areas or lived outside of the protection of BNP experienced higher human-caused hunting and trapping mortality (unpublished data).

Wolf and elk telemetry data

We estimated summer predation risk from all five wolf packs overlapping the summer range of the YHT elk herd: the Bow Valley (BV), Cascade (CA), Ranch (RA), Red Deer (RD), and Wildhorse (WH) packs. We captured 30 wolves using foot-hold traps in summer, and helicopter netgunning and aerial darting during winter (U. of Alberta Animal care protocol ID# 353112). We outfitted 14 wolves with VHF and 16 with GPS radiocollars (LMRT-3 or GPS3300sw, LOTEK Ltd., Newmarket, ON, Canada). All collared wolves were relocated aurally from a Cessna Skymaster 337 every 1–2 weeks, and wolf GPS collars attempted to collect 12 locations/day. Predation risk was modeled for three summers from 2002 to 2004; for winter predation risk, see Hebblewhite (2006). We defined summer using wolf life history as the start of denning (15 April) to the end of the rendezvous season after which pups begin traveling with the pack full time (15 October). We used only wolves with ≥15 VHF locations/summer in analyses, and excluding those wolves with <15 locations, we obtained 348 VHF locations, or ~38 VHF locations/wolf/summer. Mean error in VHF locations was 218 m based on 20 “blind” aerial trials. GPS collars collected an average of 541 GPS locations/wolf/summer. Using the Bessel function to model GPS collar location error, 50% of all locations were <34 m, and 95% were <113 m (Hebblewhite 2006).

We evaluated wolf predation risk exposure for 109 adult female elk captured using two corral traps and helicopter netgunning during winters of 2002–2004. For

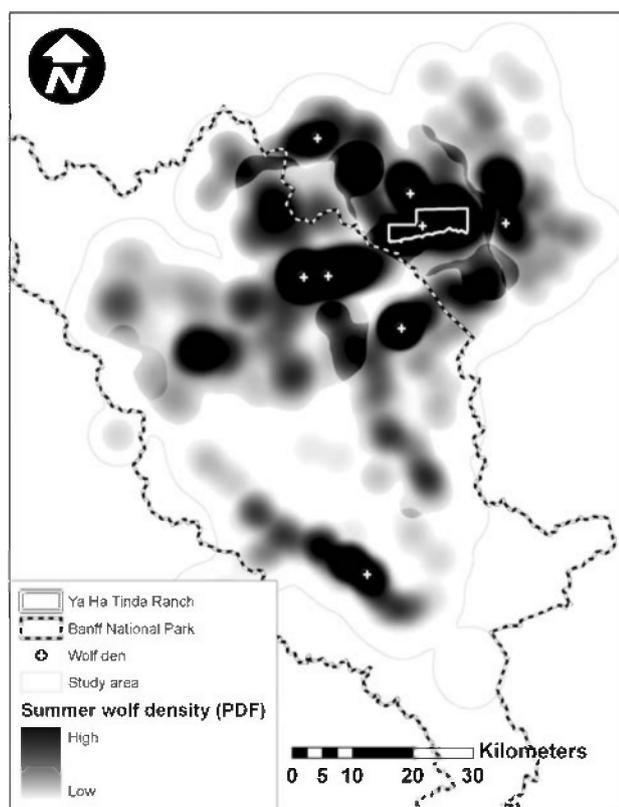


Fig. 1 Wolf (*Canis lupus*) probability density functions (PDF) during summer 2002–2004 in Banff National Park, Canada (active den sites are indicated by crosses). Density functions were calculated separately for each pack, combined, and then weighted by average seasonal wolf pack size. Thus PDFs can be >1 and are therefore reported as relative spatial density values scaled from high to low

further details on elk capture and handling, see Hebblewhite et al. (2006). We used data from 104 VHF collared and 27 GPS collared (LOTEK Ltd.) elk (some wore both) during the summer migratory period (1 June to 30 September, Hebblewhite et al. 2006) from 2002 to 2004. Of the collared sample, 65 were migrants, and 44 residents. We collected weekly VHF locations from the air or ground, but used only VHF collared elk with >10 locations/month. Elk GPS data were screened to get a consistent 2 h relocation schedule. We obtained an average of 20 and 2,347 VHF and GPS locations from each elk, respectively, in each summer.

Wolf predation risk

Numerous studies have shown that predator habitat selection can influence herbivore perception of risk (e.g. Johnson et al. 2002a, 2002b; Fortin et al. 2005; Mao et al. 2005), and other studies show that indices of spatial density influence risk (Anderson et al. 2005; Gude et al. 2006). However, few studies have considered how both factors influence predation risk, with the exception of Kristan and Boarman (2003) whose pioneering study of common raven (*Corvus corax*) predation on desert tortoises (*Gopherus agassizii*) revealed that predation risk for tortoises is a function of both raven habitat use and density. The review by Hebblewhite et al. (2005a) of nonspatial predator prey theory also supports the roles of both habitat selection and predator density in shaping predation risk. Despite this support, few studies have validated predation risk models using independent out-of-sample data, such as kill sites, to test whether our measures of predation risk measure up from the perspective of the prey species. We tested the hypothesis that wolf predation risk for elk was a function of resource selection and spatial wolf density, and validated predation risk models using locations of wolf-killed elk.

We estimated the wolf resource selection function (RSF) component of predation risk elsewhere (Hebblewhite M, Merrill EH, Modeling wildlife–human relationships with mixed-effects habitat selection models, Ecol Appl, in review). Hebblewhite and Merrill (Modeling wildlife–human relationships with mixed-effects habitat selection models, Ecol Appl, in review) used mixed-effects RSF models (Gillies et al. 2006) that allowed wolf selection for human activity to change as a function of availability of pack-level human activity (e.g. a functional response, Mysterud and Ims 1998). Summer wolf RSF models were developed during day and night to adjust for spatiotemporal variations in wolf avoidance of human activity (Therkauf et al. 2003). RSFs were modeled based on spatial covariates at a pixel resolution of 30 m². Mixed-

effects models provide population- or conditional (i.e., pack-level) resource selection inferences (Skrondal and Rabe-Hesketh 2004; Gillies et al. 2006). Because Hebblewhite and Merrill (Modeling wildlife–human relationships with mixed-effects habitat selection models, Ecol Appl, in review) showed that pack-level RSF models were required to capture within-pack differences in wolf responses to human activity, we use their pack-level RSF models to estimate predation risk for elk.

The spatial density of wolves reflected differential territory use, introduced, for example, by proximity to the denning site (Rosenberg and McKelvey 1999), that could not be captured with habitat covariates in the RSF. Instead of including distance to a central place in the RSF model (i.e., Rosenberg and McKelvey 1999), we modeled the spatial component separately following Kristan and Boarman (2003), because wolves used multiple den/rendezvous sites during summer, and because individuals varied in central place affinity, which would influence risk. We estimated the relative spatial density of wolves using a kernel density estimator (KDE, Worton 1989) in Hawthtools 3.19 (Beyer 2005) using one randomly selected location per day per VHF or GPS collared wolf and pooled data across years to minimize effects of autocorrelation and sample size differences among packs (Girard et al. 2002). Pooling data across three summers was justified because the spatial distributions of wolf packs during summer were very stable (Hebblewhite 2006). KDE represented a relative spatial probability density function (PDF, sums to 1) for each wolf pack, which were added together to account for territorial overlap. Recent studies illustrate the “art” of selecting an appropriate smoothing factor, h , or grid cell size, to estimate KDEs (Hemson et al. 2005). Because our objective was to derive large-scale spatial density in order to refine finer-scale RSF values, we used the largest LSCV h estimate obtained across all wolf packs, 4,250 m.

Spatial density may be inadequate, however, for social predators like wolves because predation rate (and hence risk) is also a function of pack size (Hebblewhite et al. 2005a). To account for this, we estimated summer pack sizes (including pups) from ground and aerial sightings, snow tracking (e.g. in May snowstorms) and den observations. Pups were included to account for the extra predation required to feed larger litters (Mech and Boitani 2003). Pack sizes varied between wolf packs (4–18), and the total number of wolves in the study area ranged from 50 in 2002 to 62 in 2004 (7.1–8.9 wolves/1,000 km²), not including lone wolves (Table 1). Because predation rate is not a linear function of pack size (Mech and Boitani 2003), we

Table 1 Wolf pack sizes (including pups) during the summers of 2002–2004, on the eastern slopes of Banff National Park, Alberta, which were used for weighting predation risk for a partially migratory elk population

Pack size	2002	2003	2004
Bow valley (BV)	4	3	5
Cascade (CA)	11	9	13
Red deer (RD)	14	16	16
Ranch (RA)	14	17	18
Wildhorse (WH)	7	7	10
Total	50	52	62

modeled the non-linear relationship between kill rate per day (KR) and wolf-pack size (X) using data from Hebblewhite et al. (2004) for the same study area. Using a model selection approach (unpublished data), the best nonlinear model was $KR = 0.385 \times (1.00 - 0.726^X)$, $r^2 = 0.40$, $F_{(1,25)} = 15.85$, $P < 0.0005$). We used this regression to calculate expected kill rates for each pack size (Table 1), and calculated KR_p as the increase in kill rate relative to a pack size of two. We used two wolves to ensure risk was scaled relative to the minimum risk expected with wolves present. We then used KR_p to weight each pixel in a particular pack's territory for each summer, adding KR_p from adjacent packs together in areas of territorial overlap. We assigned a minimum pack size of 1 to pixels in areas outside wolf territories to account for lone wolves. Unlike KDE, which we assumed was constant during the three summers, KR_p adjusted spatial density to be summer-specific.

We then modeled total predation risk (PR_i) in each 30×30 m pixel i for elk as a multiplicative function of these three components following:

$$PR_i = RSF_i \cdot KDE_h \cdot KR_p \quad (1)$$

where RSF_i is the relative probability of use by wolves for a 30×30 m pixel, KDE_h is the spatial density of wolves within area h , defined by the kernel density estimator cell size (h is 4,250 m), and KR_p is an index to potential predation rate relative to a minimum pack size of two, whose territory includes pixel i .

We validated predation risk components and total risk (PR_i) using out-of-sample locations of wolf-killed elk. We considered using kill sites (instead of in-sample wolf telemetry locations) as a strong form of model validation because kills were not used to develop predation risk models (Vaughan and Ormerod 2005), but they obviously equate to risk of death (Hebblewhite et al. 2005a). We compared all three predation risk components from Eq. 1 (RSF_i , KDE_j , KR_p) to wolf-kill locations as well as the total predation risk model (PR_i)

to determine the best predictor of elk predation risk. Between 1999 and 2005, we collected 67 locations of wolf-killed elk during summer (72% were adult female) through either snow backtracking, concurrent radio-collared elk mortality studies, or summer aerial telemetry on collared wolves (Hebblewhite 2006) to validate predation risk models against. Because the time of death was unknown for most kills, we validated average predation risk for night and day during summer. For model validation, we used the area-adjusted frequency of available predation risk components and total risk measured in ten deciles and compared this to the frequency of wolf-killed elk within the same bins (Boyce et al. 2002). The correspondence between the ranked RSF-availability bins and frequency of wolf-killed elk was assessed using Spearman's rank correlation (r_s). Values of >0.90 were considered to indicate high predictive accuracy (Boyce et al. 2002).

Multiscale predation risk for elk

We compared elk exposure to predation risk at the two spatial scales: between home ranges (landscape scale), and within home range scales (home range scale), as well as along migratory movement paths. At the landscape scale, we compared average values of the total risk and the predation risk components between 67 migrant and 44 resident elk home ranges. We estimated a 100% MCP summer range for each elk using locations from all three years because they showed high summer range fidelity. We calculated summer range average values using the zonal statistics function of Hawthtools 3.19 (Beyer 2005). Overall differences in mean values of the multivariate risk components (RSF, KDE, KR and total risk) were tested using MANOVA (StataCorp 2003) between migrant and resident home ranges. Predation risk components were then tested individually using a one-way ANOVA, correcting for multiple comparisons using the Bonferroni correction, in order to test which components were driving overall differences.

At the within home range scale, we determined total predation risk at telemetry (VHF and GPS) locations of migrant and resident elk corresponding to those appropriate for the time of day (i.e., summer night). We only considered total predation risk as the dependent variable because model validation revealed that it was the best measure of predation risk (see "Results"). To test for differences in total risk exposure (PR) between migrants and residents, we used a linear mixed-effects model (Skrondal and Rabe-Hesketh 2004) with a random effect for each elk, an AR1 (one time lag) autocorrelation term within each elk that accounted

for sequential locations being more similar, and dummy variables for migratory behavior, year, and year \times migrant interactions using XTREGAR in STATA 8.0 (Baltagi and Wu 1999; Stata Corp 2003) following:

$$\text{PR}_{j,t} = \beta_0 + \beta_M X_{1j} + \beta_2 X_{2i} + \dots + \beta_n X_{j,t} + \beta_M X_t + \gamma_j + \rho \varepsilon_{j,t-1} + \eta_{j,t} \quad (2)$$

where $\text{PR}_{j,t}$ is the mean predation risk for elk j during year t , β_M is the average effect of migrant elk, $\beta_{2..t}$ are the seasonal coefficients (spring 2002, etc.), $\beta_M X_t$ is the vector of season \times migrant status interactions, γ_j is the random effect of elk i , $\rho \varepsilon_{j,t-1}$ is the first-order autocorrelation, and $\eta_{j,t}$ is the random error. XTREGAR is robust to unbalanced observations in both j and t and seasonal gaps in t for j (Baltagi and Wu 1999). We used backwards-stepwise model selection to select the best model.

Finally, we compared exposure to predation risk at locations en route to and from summer ranges for GPS-collared migrant elk. We identified migratory movements by defining a 95% kernel home range for winter and summer, and then identified locations between these ranges for each elk (Craighead et al. 1972). Migratory movements were so definitive and rapid that more sophisticated methods (Johnson et al. 2002b) failed to improve this simple approach (unpublished data). We identified 443 GPS locations during migratory movements for 17 GPS-collared elk with ≥ 5 locations during migration. Each elk had an average of 23.5 GPS locations (range 5–149). We pooled migratory data from spring and fall migrations and compared predation risk exposure to that experienced on summer ranges using a paired t -test.

Results

Landscape-scale predation risk

At the landscape scale, resident and migrant summer home ranges differed for all predation risk components (MANOVA $F_{102} = 20.31$, $P < 0.0005$, Wilks' $\lambda = 0.3455$) even after adjusting for multiple comparisons (Table 2). Wolf pack size did not differ between home ranges of migrant and resident elk (Table 2), where pack sizes averaged 11.4 and 13.8 wolves, respectively. Relative (to a pack size of 2) wolf-kill rates (KR_p) ranged from 1 (i.e., a pack size of 2) to a maximum of 2.30 (18). While wolf pack size did not differ, spatial wolf density was different between migrant and resident elk. Spatial wolf density was much lower in the western study area because wolf dens were located along the eastern boundary of BNP (Fig. 1). The lower spatial density of wolves (KDE_j) on migrant ranges resulted in a spatial density averaging $\sim 70\%$ lower than residents (Table 2). During model validation, spatial wolf density predicted that the frequency of wolf-killed elk was the poorest of the risk components ($r_s = 0.775$, $P = 0.02$).

The mean relative probabilities of wolf occurrence derived from wolf RSF models (Hebblewhite M, Merrill EH, Modeling wildlife–human relationships with mixed-effects habitat selection models, Ecol Appl, in review) were 25–46% less for migrant than for resident summer ranges during the day and night, respectively (Table 2). There was only a 10% difference in exposure during day (RSF = 0.044) and night (RSF = 0.040) to predation risk for migrants, but residents were exposed to 27% more risk at night (RSF = 0.076) than during the day (RSF = 0.060)

Table 2 Landscape-level differences in total wolf predation risk and its components between migrant ($n = 67$) and resident ($n = 44$) elk summer ranges, 2002–2004

	Migrant		Resident		% M/R	Univariate ANOVAs ^b		
	Mean	SD	Mean	SD		F	P -value	r^2
Wolf pack size (N)	11.4	6.79	13.8	6.09	83	5.2	0.062	0.09
Wolf KDE ^a	0.172	0.148	0.596	0.203	29	161.4	<0.0005	0.59
Wolf RSF—day	0.045	0.020	0.060	0.018	75	15.3	<0.0005	0.12
Wolf RSF—night	0.040	0.017	0.074	0.033	54	48.4	<0.0005	0.31
Total wolf risk	0.037	0.036	0.129	0.065	30	112.8	<0.0005	0.46

The percentage that the migrant predation risk component is lower than the resident is given. All ANOVA F -statistics are at $df_1 = 1$, $df_2 = 109$

^a KDE is the spatial probability density function

^b Univariate ANOVA results for each covariate. P -value evaluated at an experiment-wise error rate adjusting for multiple comparisons of $P = 0.05/5 = 0.01$

(Table 2). The wolf RSF model, excluding spatial density effects, ranked second in terms of predictive ability (RSF; $r_s = 0.895$, $P = 0.0015$).

Total predation risk was concentrated in valley bottoms surrounding wolf dens along the more productive eastern part of the study area (Fig. 2), and it illustrates the effects of combining spatial density (Fig. 1) with an RSF model that revealed strong avoidance of steeper slopes by wolves (Hebblewhite M, Merrill EH, Modeling wildlife–human relationships with mixed-effects habitat selection models, Ecol Appl, in review). When all three components were combined, migrants had a 70% reduction in total predation risk (Table 2). At this scale, the difference was driven mostly by the spatial density of wolves, not wolf resource selection (Table 2). The total predation risk model (PR_i) from Eq. 1 was the best predictor of wolf-killed elk locations based on Spearman rank correlation ($r_s = 0.972$, $P < 0.0005$).

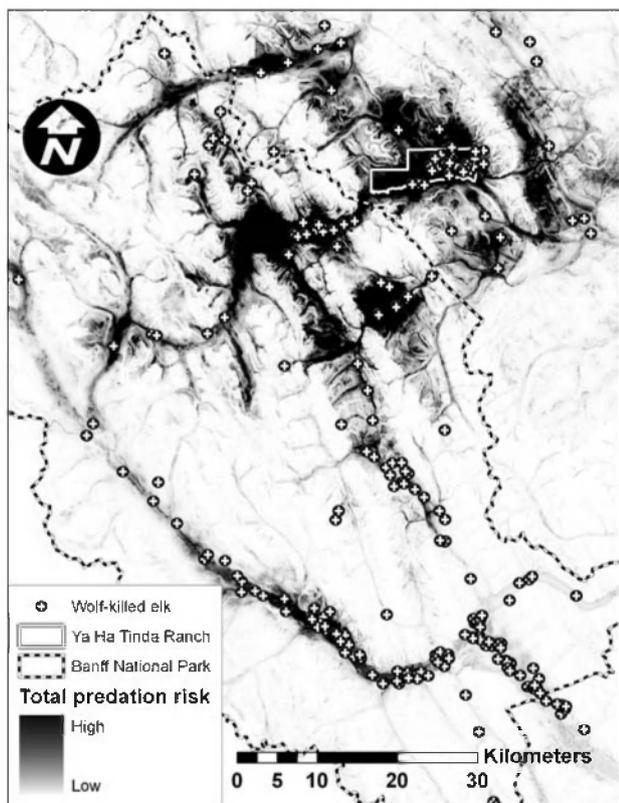


Fig. 2 Total predation risk (PR_i) during summer (average of both night and day) as a combination of spatial wolf density, pack size (Fig. 1), and pack-level wolf resource selection for 2002–2004 in Banff National Park, Alberta. Locations of the wolf-killed elk (indicated with a cross) were used for model validation and they showed that the total predation risk model had the highest predictive capacity ($r_s = 0.972$, $P < 0.0005$, see text for details)

Home-range scale predation risk

At the home-range scale, exposure of migrant elk to predation risk within summer ranges was 9, 28, and 8% lower during 2002–2004, respectively (linear-mixed effects model Wald $\chi^2 = 14.85$, overall model $P < 0.007$, Fig. 3). The only statistical difference in risk exposure, however, was lower migrant predation risk during summer 2003 (effect of migrant on overall risk $\beta = -0.02$, SE = 0.004). This statistical difference translated to a relative total risk reduction for migrants of only 15%, which was only significantly different in one of three summers (Fig. 3).

Finally, predation risk exposure was 1.75 times higher during migratory movements ($\bar{x} = 0.201$, SE = 0.023) than on migrant summer ranges ($\bar{x} = 0.115$, SE = 0.015, paired t -test $t_{\alpha = 0.05/2, 16} = -1.92$, $P = 0.07$) on average for all 17 elk, though five of the 17 elk had higher risk on summer ranges than during migration.

Discussion

Our study provided conflicting support for the hypothesis that migration reduced risk for elk across spatial scales, because migrant and resident elk exploited trade-offs between wolf predation risk and human activity differently across spatial scales. At the landscape scale, migrant predation risk was 70% lower, consistent with the predation refuge hypothesis (Bergerud et al. 1984; Fryxell et al. 1988). This was

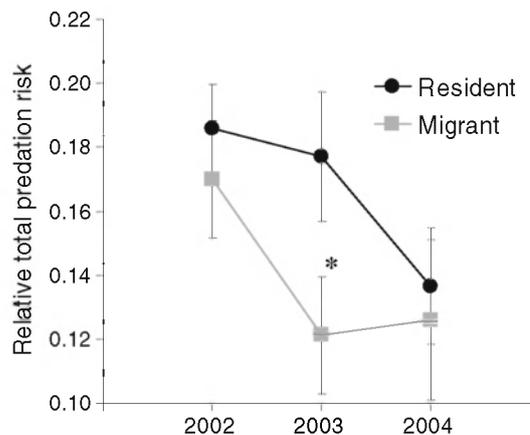


Fig. 3 Relative predation risk (mean ± SE) for resident (filled circles) and migrant (filled gray squares) elk from the partially migratory Ya Ha Tinda elk herd, summers (1 June to 30 September) 2002–2004. Statistically significant differences (at $P = 0.05$) between migrants and residents from a linear mixed effects model accounting for individual elk and autocorrelation are marked with an asterisk (see text)

because migrants moved away from low-elevation valley bottoms close to wolf dens in the eastern study area where spatial wolf density was highest, rather than avoiding habitats where wolf RSF values were higher. Also, reductions in the spatial density of wolves had a greater relative effect than the reduced RSF probability of use by wolves. In contrast, residents were exposed to higher predation risk by remaining on low-elevation winter ranges year-round, in close proximity to wolf den sites. Thus, at the landscape scale, our quantitative results support the predation refuge hypothesis, similar to the findings of Bergerud et al. (1984) for mountain caribou.

When we compared predation risk exposure within summer ranges, however, the predation risk reduction benefits of migration declined to only 15% lower risk for migrants, and benefits were significant in only one of three summers. This was because residents exploited small-scale predation refugia caused by wolf avoidance of human activity, which was captured in the RSF model (Hebblewhite M, Merrill EH, Modeling wildlife–human relationships with mixed-effects habitat selection models, *Ecol Appl*, in review). The small differences in RSF values during day and night at the large landscape scale (Table 2) magnified into much larger differences at the within home range scale because residents avoided fine-scale risk whereas migrants did not (Table 2, Hebblewhite 2006; Hebblewhite M, Merrill EH, Modeling wildlife–human relationships with mixed-effects habitat selection models, *Ecol Appl*, in review). Because wolves themselves faced a trade-off between food and human-caused mortality (*sensu* Frid and Dill 2002), wolves avoided human activity, especially in the day and near the winter range where residents summered and human activity was higher (Hebblewhite M, Merrill EH, Modeling wildlife–human relationships with mixed-effects habitat selection models, *Ecol Appl*, in review). Wolf avoidance of human activity has been described in many other systems (Thurber et al. 1994; Theuerkauf et al. 2003; Kaartinen et al. 2005; Whittington et al. 2005), but our study is novel in that we show that ungulates can exploit this to reduce their own predation risk. Because ungulates must balance predation and starvation risk, wolf avoidance of humans created spatial refugia that resident elk exploited to reduce predation risk according to the proverb “an enemy of my enemy is my friend.” Because humans can alter the interactions between wolves and their prey, future studies addressing ungulate trade-offs between predation and starvation risk should pay particular attention to the effects of human activities (Frid and Dill 2002).

The highest predation risk exposure occurred during migration, when migrants were exposed to >1.7 times more risk (mean wolf RSF relative probability = 0.201, SE = 0.06) than on winter or high elevation summer ranges (e.g., compared to that in Fig. 3). This was because elk migrated through low-elevation valley bottoms past wolf dens (Fig. 1). Migration was associated with a high frequency of death from wolves (42% of all mortalities, $n = 39$ total) and grizzly bears (Hebblewhite 2006). Of all migrant elk killed by wolves ($n = 19$), 63% occurred during migratory months (May/June, September/October), and, conservatively, 25% probably occurred during migration itself (Hebblewhite 2006), emphasizing the fitness costs of migration. This is one of the first reports of elevated predation risk during migration for ungulates (see also Nelson and Mech 1991). Migratory shorebirds reduced time spent at important stopover foraging locations with increasing predation risk (Lank et al. 2003; Schmaljohann and Dierschke 2005). To test for similar predation-induced migratory changes in elk, we compared migratory duration during this study and 25 years previous when wolves were absent (Morgantini and Hudson 1988). Prior to wolf recolonization, elk used low-elevation (and hence high predation risk, Fig. 2) “intermediate” ranges for >30 days (Morgantini and Hudson 1988). During the present study, the mean duration of migratory movements of 17 GPS collared elk averaged only ~5 days (unpublished data), supporting a risk-mediated change in migration behavior. Also, Hebblewhite et al. (2006) reported that fall migration occurred one month earlier than prior to wolf recolonization, further supporting risk-mediated changes in migratory behavior. The importance of elevated risk during migration to demography is unknown, but density-dependent mortality during migration could regulate migratory elk density, reducing per capita risk.

Multiscale analyses have shown that fine-scale behavioral strategies may mitigate predation risk as successfully as large-scale migration (Johnson et al. 2002a, 2002b; Anderson et al. 2005). Had we not examined predation at multiple scales, we would have missed the importance of fine-scale avoidance of human activity. Although no other studies have specifically compared migrant and resident predation risk, some have compared predation risk avoidance across spatial scales. Similar to our migrants, Johnson et al. (2002b) found that caribou movements indicated that they avoided wolf predation risk at larger scales, but not at fine scales, in contrast to our residents, because large-scale movements exposed caribou to higher predation risk. Rettie and Messier (2000) also found that

migratory woodland caribou avoided wolves at the largest spatial scales. Dussault et al. (2005) showed that nonmigratory moose were able to make trade-offs between predation risk and forage within a finer spatial scale, similar to resident elk in our study. In Wisconsin, introduced elk behaved more similarly to our residents, avoiding areas of high predation risk at the within home range scale (Anderson et al. 2005). A simultaneous analysis of trade-offs between forage and predation risk in this partially migratory population (e.g., Dussault et al. 2005) would help test whether trade-offs were occurring between or within spatial scales differently for migrants or residents. This is especially important, because migration is hypothesized to enhance access to forage resources that would be expected to increase fitness (Fryxell et al. 1988). Based on these previous studies, we predict that migrant ungulates will trade-off between scales (e.g., Rettie and Messier 2000; Johnson et al. 2002b), whereas nonmigratory ungulates will trade-off between risk and forage within the home range scale when predator territoriality or human activity provides fine-scale predation refugia (Anderson et al. 2005; Dussault et al. 2005). Simultaneous analysis of forage–predation risk trade-offs by Hebblewhite (2006) have confirmed this hypothesis in our partially migratory elk population.

Future studies of behavior in ecological landscapes (Lima and Zollner 1996) will benefit from our approach to estimating predation risk. Results from our model validation reveals that spatial density models of predation risk alone will be insufficient for refined inferences about the ecological effects of predation risk. Instead, combining fine-scale habitat selection patterns with large-scale spatial density (Fig. 2) best predicted predation risk, similar to the recommendations of Kristan and Boarman (2003) and Hebblewhite et al. (2005a). Other approaches to model predation risk have examined real spatial variations in the risk of mortality using landscape-linked survival modeling (Frair et al. 2007), but these approaches require large numbers of mortalities and do not reveal the mechanisms of the different components of predation (Hebblewhite et al. 2005a). Thus, we recommend that future predation risk studies combine habitat selection and spatial density across spatial scales, and conduct model validation as a matter of course to ensure inferences are as robust as possible.

Our study has clearly illustrated that differences in predation risk at different spatial scales can have dramatic consequences for elk. While we found support for the idea that migration reduces predation risk, resident elk reduced their predation risk substantially by taking advantage of wolf avoidance of humans at

small spatial scales. If resident elk employed other anti-predator strategies that were not examined in this study, such as diluting risk by living in larger group sizes than migrants in summer (Hamilton 1971), residents may be able to completely mitigate predation benefits by migrating. As human activities across the landscape increase, we expect that modifying behaviors to avoid predation risk will have implications in terms of meeting forage intake requirements and the long-term dynamics of predator–prey systems and their ecosystems. The growing appreciation of indirect effects in food webs (Fortin et al. 2005) suggests that indirect effects between wolves and humans will structure trophic relationships. Future studies would therefore benefit by explicitly including humans as part of the trophic food web.

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