LETTER

Landscape heterogeneity shapes predation in a newly restored predator–prey system

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Abstract

Because some native ungulates have lived without top predators for generations, it has been uncertain whether runaway predation would occur when predators are newly restored to these systems. We show that landscape features and vegetation, which influence predator detection and capture of prey, shape large-scale patterns of predation in a newly restored predator–prey system. We analysed the spatial distribution of wolf (*Canis lupus*) predation on elk (*Cervus elaphus*) on the Northern Range of Yellowstone National Park over 10 consecutive winters. The influence of wolf distribution on kill sites diminished over the course of this study, a result that was likely caused by territorial constraints on wolf distribution. In contrast, landscape factors strongly influenced kill sites, creating distinct hunting grounds and prey refugia. Elk in this newly restored predator–prey system should be able to mediate their risk of predation by movement and habitat selection across a heterogeneous risk landscape.

Keywords

Antipredator response, catchability, kill occurrence, native predator, predation risk, predator restoration, prey refugia, risk map, territoriality, trophic cascades, vulnerability.

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INTRODUCTION

Global efforts are underway to restore and conserve remnant populations of apex predators including lions (*Panthera leo*), grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) (Treves & Karanth 2003). Restoring predators to the large landscapes of their historic range has the potential to maintain biodiversity by recovering the strong but indirect species interactions inherent to these systems (Crooks & Soule 1999; Terborgh *et al.* 2001; Soule *et al.* 2005). However, such community-level benefits of carnivore restoration may come at a cost to their native ungulate prey, which form the basis of recreational and subsistence hunting by humans (Orians *et al.* 1997; Eberhardt *et al.* 2003;

Nilsen *et al.* 2004). The perception that reintroduced predators will devastate native prey is a primary concern for some stakeholders, and successful carnivore restoration efforts often hinge on resolving these and other human–carnivore conflicts (Orians *et al.* 1997; Treves & Karanth 2003).

Native ungulates that have lived without predators are expected to become naïve and less vigilant, increasing their vulnerability to predation (Berger 1999; Berger *et al.* 2001; Sand *et al.* 2006). For example, in only 4 years at least 10 adult moose (*Alces alces*) fell prey to grizzly bears at the frontier of bear recolonization in the greater Yellowstone area as compared with no records of predation where both had existed for 100+ years (Berger *et al.* 2001). The history

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of introductions of exotic predators to predator-free islands illustrates that novel predators can markedly reduce populations of native prey and cause local extinctions (Fritts & Rodda 1998; Knapp *et al.* 2001; Blackburn *et al.* 2004). If native ungulate prey are naïve and thus highly susceptible to predation wherever they encounter recolonizing native predators, similar reductions in prey numbers might be expected (Berger *et al.* 2001; Sand *et al.* 2006). Unfortunately, we know little about the ways in which native prey interact with their new predators or the mechanisms that govern these predator–prey interactions (but see Hebblewhite *et al.* 2005).

Theory suggests that native predator–prey systems persist over the long term due to heterogeneity in predation rates caused by prey refugia in space or time (Fryxell *et al.* 1988; Kareiva & Wennegren 1995; Ellner *et al.* 2001). Whether or not native prey can benefit from such refugia when their historical predators are returned will depend on the mechanisms by which prey refugia are created and the retention of the prey's ability to exploit them. Do the rates and patterns of predation by newly restored predators exhibit high levels of heterogeneity, and if so what mechanisms govern the predation process? Quantifying the spatial structure of predation by recolonizing carnivores would enhance our understanding of apex predator effects on native prey populations (Sinclair & Arcese 1995).

In this study, we quantified the spatial structure of wolf predation on elk (*Cervus elaphus*) during winter on the Northern Range (NR) of Yellowstone National Park (YNP), USA. Wolves were reintroduced to YNP in 1995 after being extirpated from this ecosystem in the 1930s (Bangs & Fritts 1996). During the 10 years since reintroduction, the NR wolf population increased from 14 wolves in three packs to 84 wolves in six packs (Fig. 1a). Over this time period, 92% of the ungulate prey taken by wolves during winter have been elk (Smith *et al.* 2004). We evaluated landscape-level variability in wolf predation on elk and found that spatial patterns of predation are more strongly influenced by landscape features than by wolf distribution.

MATERIALS AND METHODS

We quantified spatial patterns of wolf predation on NR elk by analysing the factors that influence the spatial distribution of elk killed by wolves in winter during the first 10 years of wolf recovery. We estimated the extent to which variation in kill locations (Fig. 1b) was determined by the annual distribution of wolf territories (Fig. 1a) or physical features of the landscape where elk and wolves interact. We also evaluated whether the strength of landscape variables changed through time as wolves

expanded their distribution and wolf predation on elk became less novel. The primary data for these analyses is a GIS data set of the spatial locations of elk killed by wolves during 1996–2005.

Surveys for wolf-killed elk

During each winter, ground and aerial surveys for wolf-killed prey were conducted by crews tracking the wolf packs with radiotelemetry. All of the kills used in our analysis came from two 30-day periods in the early (mid-November to mid-December) and late (March) winters of 1996–2005, when wolf packs were intensively monitored by ground and air crews. These efforts resulted in 774 locations of wolf-killed elk across the NR (Fig. 1b). Smith *et al.* (2004) used a double-count method to evaluate observation error in these surveys and found that ground crews are biased towards detecting wolf-killed elk in close proximity to the road system, with no kills found further than 7.23 km from the road. However, aerial surveys were not biased with respect to vegetation type (conifer forest vs. open sage/grasslands) or roads. While an estimated 27% of total kills went undiscovered, the two survey efforts conducted simultaneously (45% of our kills were detected from the air, 71% from the ground and 17% by both survey methods) resulted in minimal detection bias with respect to the landscape features used in our analysis (Smith *et al.* 2004).

Wolf kills are distinguished readily from kills made by other carnivores. Kills were classified as wolf-caused when wolves were observed making the kill, or evidence supported wolves as the cause (e.g. wolves were observed feeding on a fresh carcass). Necropsies were performed on the vast majority of kills ($\geq$ 90%), and evidence from the carcass site such as chase tracks and signs of struggle also were used to evaluate cause. In rare cases, cougar (*Puma concolor*) kills were usurped by wolves, but these tended to be discernible by evidence that cougars had cached a carcass. Grizzly bears occasionally kill elk, but only rarely in the winter when, for the most part, bears are denning.

Kill site model

We used logistic regression to estimate a model of the relative probability of a kill by analysing the spatial attributes of known kill locations vs. random available locations in the NR study area (Manly *et al.* 2002). We employed a matched case–control design with strata consisting of 774 kills matched to 20 control points each randomly selected from within the NR study area (Hosmer & Lemeshow 2000). Case–control logistic regression fits the following likelihood for each stratum ($k = 774$):
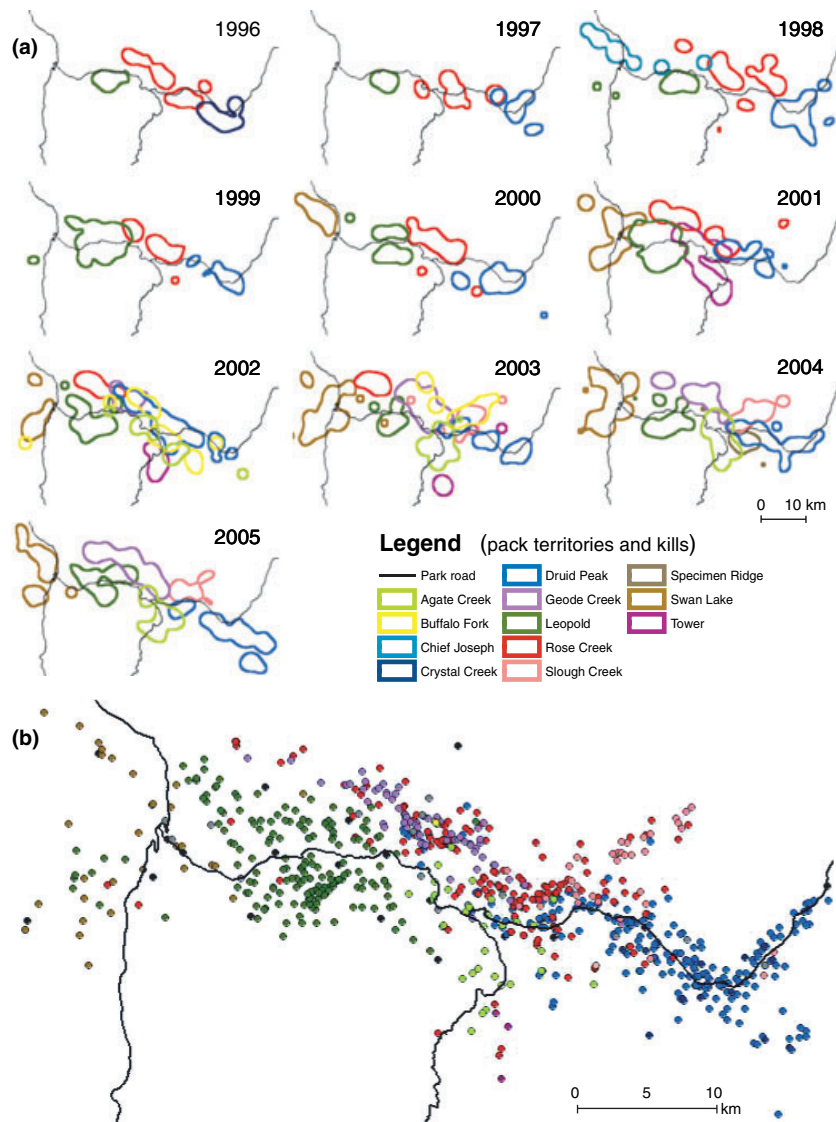
Figure 1 The spatial distribution of wolf pack territories and wolf-killed elk on Yellowstone's Northern Range, 1996–2005. Wolf pack territory boundaries (panel a) are represented by an 80% kernel home range. Wolf-killed elk (panel b) are colour coded according to the pack that made the kill. The legend in panel (a) gives the colour codes for both pack territories and kills (in panel b, grey circles = dispersers or unformed pack).

$$l_k(\beta) = \frac{e^{\beta' \mathbf{x}_{k,1}}}{e^{\beta' \mathbf{x}_{k,1}} + e^{\beta' \mathbf{x}_{k,2}} + \cdots + e^{\beta' \mathbf{x}_{k,21}}} \quad (1)$$

where β is a vector of fitted coefficients, $\mathbf{x}_{k,n}$ are the explanatory variables for observation n (1 = the kill location, 2–21 = the random locations) in stratum k. This equation is not interpretable as the probability that a predation event will occur at a given location. Rather, it is the probability that the location with data $\mathbf{x}_{k,1}$ is in fact the kill site relative to the 20 control locations. However, the set of fitted coefficients are interpretable as the odds ratio as in standard logistic regression (Hosmer & Lemeshow 2000).

Relative probability of kill occurrence was calculated with respect to a reference vector ($\mathbf{x}_r$), defined as the set of mean values for each variable within the domain of availability. The resulting odds ratio expression for a given landscape location ($\mathbf{x}$) was calculated following Keating & Cherry (2004) as:

$$\Psi(\mathbf{x}|\mathbf{x}_R) = \exp[\beta_1(x_1 - x_{1,R}) + \cdots + \beta_n(x_n - x_{n,R})]. \quad (2)$$

Because the true probability of a predation event for any individual location (30 × 30 m grid cell) on the NR is close to zero, random locations are unlikely to include kill

locations and we assume the odds ratio to be interpretable as relative probability of kill (Keating & Cherry 2004). Thus, a $\Psi(\mathbf{x}|\mathbf{x}_R) = 1$ denotes no difference between location i and the reference (mean probability on the landscape), whereas a $\Psi(\mathbf{x}|\mathbf{x}_R) = 10$ would indicate a kill probability 10 times greater than the average.

Accounting for elk distribution

One obvious driver of the spatial distribution of wolf-killed elk is the spatial distribution of elk themselves. During winter elk select south-facing grassland habitats, where the snow level is not deep or crusted enough to impede their ability to forage (Houston 1982; Skovlin et al. 2002). On the NR, it is well known that snow accumulation throughout winter (if deep enough) pushes elk to lower-elevation winter range; thus, elk distribution on the landscape changes within and among annual winter seasons. We sought to account for this by estimating the spatial distribution of elk with an existing NR habitat model derived from radiocollared elk that includes – among other habitat variables – the influence of recorded annual variability in snow accumulation (Mao et al. 2005).

Although the NR elk population has declined since wolf reintroduction (Smith et al. 2004; White & Garrott 2005), our habitat model assumed (aside from the influence of snow) that the relative distribution of elk within each year was constant. As in the original elk habitat model of Mao et al. (2005), we used the daily snow water equivalent (SWE) estimated from an existing snow model that interpolates SWE across Yellowstone National Park from 28 fixed snow measurement sites (Wockner et al. 2006). We averaged the daily SWE estimates within the four 2-week periods from which the kills were collected each winter. We used a natural log transformation of the Mao et al. (2005) Resource Selection Function (RSF) as our estimate of elk use in our kill-site analysis. Within the case–control design of our kill-site model, the elk variable assigned to each of the 20 random control locations came from the same 2-week period of the winter in which the kill occurred.

Wolf distribution

We estimated the annual spatial distribution of wolves on the basis of individual packs. To characterize pack territories in a GIS, we constructed a utilization distribution (UD) using a 95% kernel estimation (Seaman & Powell 1996) for each pack from aerial locations of radiocollared wolves (average number of locations = 31) using a Home Range extension for ArcView 3.2 (Hooge & Eichenlaub 1997). A maximum of one location per pack per day was used for kernel estimation. A smoothing factor of 1500 m was chosen because it appeared to best approximate the extent of territory boundaries known from field observations.

Aerial relocations of wolf packs known to be on a kill were excluded from the UD estimation to reduce the spatial dependence of kill sites on pack territories. Kernel percentile values were divided by the number of cells within each percentile category to approximate a probability distribution such that all 30×30 m cells within a pack UD summed to 1. To account for variation in wolf pack size (range 2–37), we multiplied each pack UD by the number of wolves observed within each pack during winter. All individual pack UDs for a given year were summed across the NR resulting in an annual composite measure of wolf use.

Landscape variables

Explanatory landscape variables were derived from a GIS of the study area and included: slope, openness, proximity-to-roads, proximity-to-streams and SWE. Slope was derived from a 30-m digital elevation model of YNP (range 0–70°). Openness was calculated as per Boyce et al. (2003) using the sum of non-forested cells within a 500×500 m moving window centred on each grid cell (range 0 [deep forest]–289 [open grassland]). The proximity-to-roads measure (range 0–13 435 m) was calculated as the shortest distance between each grid cell and the nearest road. Trails and roads that were not maintained were not included in our analysis. Proximity-to-streams (range 0–2352 m) was calculated as the shortest distance to the nearest major stream or river. Snow was calculated as the average SWE for each of the four 2-week periods during each winter (40 snow layers total) and matched to kills as described for the elk variable above. All landscape variables showed relatively low levels of collinearity ($r < 0.43$), except for SWE and elk, which were negatively correlated with $r = -0.80$.

RESULTS

We began our analysis of the kill-site data by first building a set of 'encounter' models in which elk and wolf distributions alone describe the spatial distribution of kills. A model including both elk and wolf distributions fit the kill data much better than did single-term models that included the distribution of only predator or prey (likelihood ratio $\chi^2 = 88.57$, d.f. = 1, $P < 0.0001$; Table S1 in Supplementary Material). This indicates that wolves were not simply making kills on the landscape in strict proportion to the distribution of elk, or their own spatial patterns of winter territory use.

To characterize the influence of landscape features on kill occurrence, we constructed a set of 'landscape effects' models that retained the effects of wolves and elk in addition to landscape features including: proximity-to-roads, proximity-to-streams, openness, slope and snow. The best-fit landscape model included all landscape variables and

Table 1 Estimated coefficients for models used to estimate the probability of occurrence of wolf-killed elk on Yellowstone's Northern Range, 1996–2005

Effect	Landscape effects		Time-varying		Catchability	
	β	SE	β	SE	β	SE
Elk	1.238	0.131	1.238	0.132	1.331	0.131
Wolf	1682.00	197.24	4988.00	706.44		
Road	−0.00013	2.14E-05	−0.00013	2.15E-05	−0.00012	2.06E-05
Stream	−0.00078	0.00014	−0.00017	0.00032	−0.00080	0.00014
Openness	0.0026	0.0005	0.0046	0.0010	0.0028	0.0005
Slope	−0.0749	0.0175	−0.0761	0.0176	−0.0795	0.0174
Slope^2	0.0028	0.0007	0.0028	0.0007	0.0030	0.0007
Snow	0.0112	0.0018	0.0115	0.0018	0.0120	0.0018
Wolf × time			−462.95	97.01		
Openness × time			−0.00032	0.00015		
Stream × time			−0.00011	4.94E-05		

vastly outperformed the elk + wolf encounter model (likelihood ratio $\chi^2 = 270.11$, d.f. = 6, $P < 0.0001$; Table 1; Table S1). Because these models take into account the spatial distribution of elk and wolves, they indicate that landscape factors strongly shape where wolves kill elk in this newly restored predator–prey system.

To determine whether the factors controlling the distribution of kills have changed over time, we built a third set of 'time-varying' models that allowed the influence of wolves and landscape factors to vary linearly through time. Among other causes, such temporal changes could result from learned hunting patterns by wolves in new habitats, learned antipredator behaviour by elk, or intraspecific predator interference as the number of wolf packs increased. The best-supported time-varying models included a negative wolf × time interaction (likelihood ratio $\chi^2 = 23.66$, d.f. = 1, $P < 0.0001$; Table 1; Table S1), indicating that the influence of wolf distribution on kills has diminished over time. There was negligible support for temporal interactions with landscape variables, indicating that the types of habitats where wolves have killed elk have changed little over the 10 years of wolf recolonization. Likelihood ratio χ^2 values and associated P values (from nested model comparisons) were non-significant for temporal interactions with all landscape variable except for distance-to-stream (slope × time: $\chi^2 = 0.43$, $P < 0.51$; open × time: $\chi^2 = 3.42$, $P < 0.06$; road × time: $\chi^2 = 1.35$, $P < 0.25$; stream × time: $\chi^2 = 4.40$, $P < 0.04$). We do not believe that the significant stream × time interaction is indicative of a temporal change in wolf or elk behaviour with respect to streams. Rather, we believe this results from the addition of kills to our data set in the winter 2002–2003 from the newly formed Slough Creek Pack in 2002, which has been making kills ($n = 36$) near the banks of lower Slough Creek (Fig. 1).

We used k-fold cross-validation (Boyce *et al.* 2002) to evaluate the predictions of kill sites by the kill occurrence models. The kill data were partitioned into five equal sets, and models were fit to each 80% partition of the data, while the remaining 20% of the data were held out for model evaluation. In each cross-validation, the estimated probabilities were binned into 10 equal bins and correlated with the observed proportion of kills within the evaluation set. The average Spearman-rank correlations across the five partitions of the data were 0.90, 0.96 and 0.95 for the best-fit encounter, landscape effects and time-varying models, respectively. Correlations of this magnitude indicate a very good fit of models to data (Boyce *et al.* 2002).

To illustrate the patterns of predation revealed by our analysis, we used our best-fitting (time-varying) model to map relative annual probability of kill occurrence onto the NR landscape for the 2005 winter (Fig. 2a). We modified these model predictions at each landscape location to approximate per capita predation risk by scaling each probability of kill occurrence by the relative probability (log transformed RSF) of elk occurrence from the Mao *et al.* (2005) elk habitat model. In rescaling the probabilities in this manner, we assume that elk density across the study area is proportional to habitat use as estimated by Mao *et al.* (2005). In 2005, the influence of landscape features created a predation-risk landscape that was highly variable, with areas of low and high risk varying by nearly two orders of magnitude (Fig. 2a). In the early years after wolf reintroduction, wolf distribution also created considerable spatial variation in risk. For example, comparing a risky area with a refuge area, we found that an increase in wolf density that caused a 10-fold increase in risk (relative to mean annual risk) in 1996 caused only a 1.25-fold increase in risk in 2005 (Fig. 2b). Thus, during the first 10 years of wolf population expansion in Yellowstone, wolf distribution became less
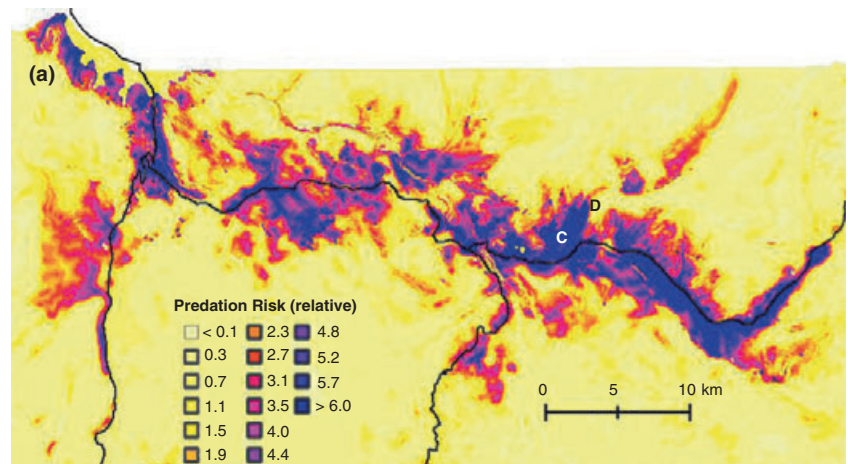
Figure 2 Relative risk of wolf predation for elk on Yellowstone's Northern Range, 2005 (panel a). Spatial variation in predation risk is largely driven by landscape features, which create a limited number of hunting grounds where predation risk is often 10 times higher than the landscape average (a map value of 1 denotes average risk). When first reintroduced, wolf pack distribution also strongly influenced predation risk (panel b), but this influence has largely diminished after 10 years of wolf population expansion. By 2005, variation in predation risk is largely determined by landscape features that create risky (location C in risk map) and refuge (location D in risk map) habitats.
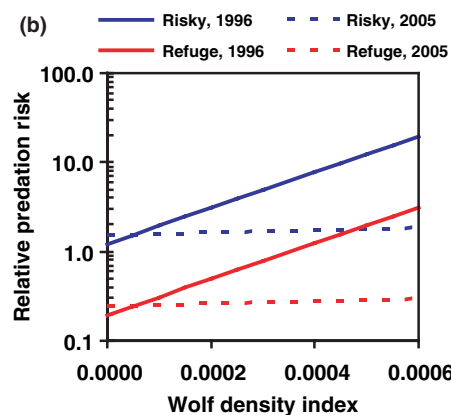
important in determining variation in predation risk relative to landscape features.

Logistic regression models such as the one we used are sensitive to spatial variation in explanatory variables. If the variability of a spatial attribute decreases through time, so too will the strength of its influence (Garshelis 2000). Therefore, we assessed whether the wolf distribution had become less variable over the 10-year study period and found that no temporal decline in the variance of the wolf density index was evident (see Fig. S1). Rather, an increase in overall variance was observed, in part because of the emergence of areas of high wolf use where several packs overlapped (Fig. 1a). These data, and our case–control design that took account of the annual change in wolf distribution, suggest that the decoupling of kills from wolf distribution was not an artefact of an increasingly homogenized wolf distribution.

Attenuation of wolf territory influence on kill distribution

Because we did not find evidence for a temporal change in the types of habitats where wolves killed elk, we believe that profound shifts in elk behaviour or habitat use are not responsible for the attenuating influence of wolves on kill locations. Similarly, the per-capita kill rate for wolves on the NR has not declined sharply over the study period (D.W. Smith, unpublished data), suggesting that wolf packs maintained a relatively constant annual kill rate. Given this, it seems unlikely that a predator-dependent functional response is responsible for the decoupling of predation from predator distribution. To further examine the decoupling of kill sites from wolf distribution, we conducted *post-hoc* analyses to explore a potential mechanism for this phenomenon. We hypothesized that as the wolf population increased, wolves shifted their territories away from the areas where they were most successful at hunting elk (dark blue patches in Fig. 2a) to reduce inter-pack conflict and mortality. Thus, we investigated a mechanism whereby at high densities wolf social structure and aggression avoidance constrains the ability of packs to defend territories where they make most of their kills.

Pack conflict

There is ample evidence that inter-pack conflict has increased as the density of NR wolf packs has increased. Long-term monitoring in this system has recorded 2.8 (±0.8

SE) aggressive inter-pack interactions (i.e. intraspecific chase/flee, attack or kill) per year during the first half of the study period (1996–2000) and 11.8 (±2.6 SE) such interactions per year during the latter half of the study (2001–2005). Confirmed intraspecific killing by wolves increased over the same period, from 0.8 (±0.3 SE) per year to 2.5 (±1.0 SE) per year (D.W. Smith, unpublished data). This increase in pack–pack aggression over the study period represents an increasingly important spatial constraint on wolf territory selection and hunting patterns.

Estimating catchability across the Northern Range

To evaluate whether wolves have established their territories in poorer hunting habitats through time, we estimated the 'catchability' of the landscape occupied by each wolf pack in each year. We defined catchability as the relative probability of kill occurrence that was due to elk density and habitat features. We estimated catchability by fitting kill occurrence models without wolf distribution as an explanatory variable. We first fit a new model analogous to our best-fit landscape effects model including elk distribution and all landscape variables (but not wolf presence). Our catchability model is thus a composite measure of prey availability and the landscape attributes that influence wolf hunting success. Annual catchability maps were derived from the odds ratio of the catchability model coefficients (Table S2) using eqn 2. Mean values across the NR were used as the reference for each static variable, while the annual means were used for the time-varying terms (elk and snow). We assumed that annual catchability maps roughly approximate the relative quality of wolf habitat as it relates to their likelihood of successfully finding and killing elk.

We then sought to estimate the average catchability of each pack's winter territory as an index of territory quality. We estimated mean catchability for each pack territory (Fig. 3) as the sum of all catchability scores within the area of the pack UD weighted by the UD values. The UDs of a few wolf packs extended beyond the study area in some years, so in these cases we rescaled the pack UD so that it summed to one within the study area.

After controlling for pack size, a decline through time in the average catchability of elk within each pack's winter territory was evident (multiple regression; pack size: $t = -2.48$, $P = 0.0166$; year: $t = -3.47$, $P = 0.0011$), with a significant pack size × time interaction ($t = 2.33$, $P = 0.0238$) whereby large packs had access to high-quality hunting grounds and small packs were relegated to poor hunting grounds over time (Fig. 3). A few large, competitively dominant packs retained access to the best hunting grounds over the 10 years, but the majority of pack territories shifted away from the best hunting grounds as wolf density increased. These results are consistent with our hypothesis that individual wolf packs shifted their winter
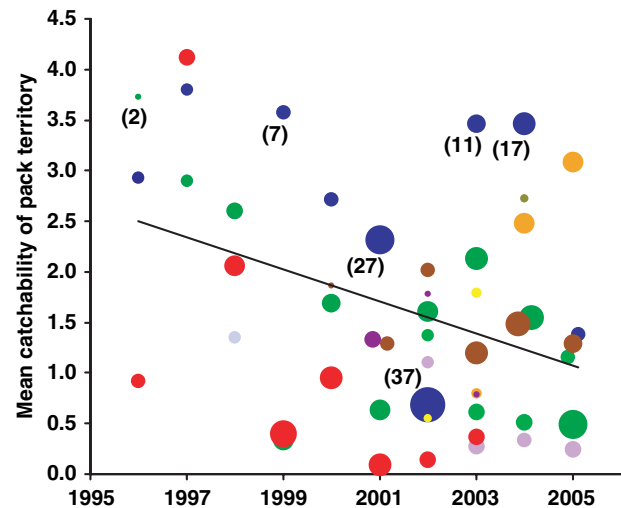

Figure 3 The distribution of wolf packs on the Northern Range of Yellowstone National Park in relation to elk catchability (≈ wolf territory quality), 1996–2005. Wolf packs have responded to the increase in the number of neighbouring packs by selecting habitat that minimizes interpack conflict, resulting in pack territories with significantly poorer catchability over time. Catchability scores were standardized within years to account for the dependency of elk distribution on observed snow levels (in all years, average catchability = 1). Bubble size scales with winter wolf pack size (representative sizes shown in parentheses), and bubbles are colour coded by pack according to the legend in Fig. 1.

territories away from but adjacent to the best hunting grounds, thus decoupling kill locations from wolf distribution.

DISCUSSION

In this newly restored wolf-ungulate system, we found a striking degree of spatial variability in predation at the landscape level. Most of this variability appears to be caused by physical features of the landscape where prey and predator interact. Because we found a strong influence of landscape variables on kill-site occurrence after accounting for the distribution of predator and prey, we believe that habitat mediates predation by influencing the occurrence or outcome of wolf–elk encounters. Although the precise mechanisms for a strong landscape influence on patterns of predation in this system are unclear, we believe such spatially heterogeneous rates of predation to be a general feature of native (or restored) predator–prey systems. Our study suggests that hunting grounds – habitat patches with physical features favourable to hunting success of wolves – exist on the NR, and that their distribution on the landscape influences both territorial space used by wolves and spatial variation in predation risk for elk. Further, the decoupling of kill occurrence from predator distribution calls into question

the common assumption that predator distribution drives predation risk. In this system, territorial constraints on predator habitat selection and movement were the most likely mechanisms for the spatial decoupling of predator and kill sites.

Hunting grounds on the NR were flat, snow-covered grasslands close to streams and roads. Such habitat features can influence spatial patterns of predation by influencing either pre- or post-encounter interactions between predators and prey (Hebblewhite et al. 2005), and we believe both mechanisms play a role in conferring riskiness to the NR hunting grounds. The risky influence of these habitat features for elk is consistent with the cursorial (as opposed to stalking) hunting strategy of wolves. Streams and roads provide convenient travel corridors that likely increase prey encounter rates (Kunkel & Pletscher 2000), while open habitats likely facilitate prey detection (Kunkel & Pletscher 2000; Creel et al. 2005). With few visual barriers, open habitats could also enhance the wolves' ability to sort through an elk group and scan its members for vulnerable individuals to attack (Mech et al. 1998; MacNulty et al. 2007) (mean chase distance for a subset of kills was 978.20, SE ±141.73 m). Deep snow also favours wolves after encounters because it can hinder ungulate locomotion (Huggard 1993; Post et al. 1999). Similarly, streams and associated channels and ravines provide physical obstacles that may impede elk escape (Bergman et al. 2006). Overall, the physical attributes of the hunting grounds identified in this study are consistent with the natural history of wolf hunting behaviour. This work suggests that in addition to the well-documented pattern of wolf selection of prey made vulnerable due to sex, age or body condition (Mech & Peterson 2003), habitat may also influence predation rates by mediating the successful identification, pursuit and capture of vulnerable prey.

Hunting grounds of the NR are used by multiple wolf packs, a situation that does not conform to the widely held conceptual model of distinct territorial boundaries with interstitial prey refuges that has been suggested on an empirical (Mech 1977) and theoretical (Lewis & Murray 1993) basis. In Minnesota, boundaries between wolf pack territories appear to function as buffers where most inter-pack killings occur (Mech 1994) and where ungulate prey densities are elevated (Hoskinson & Mech 1976). By contrast, wolf territory overlap is high in the NR system, and territory buffers do not appear to reduce the likelihood of kill occurrence. Instead, the relative high density of wolf and elk populations on the NR and the strong landscape influence on predation success interact to create a pattern of high territorial overlap where the best hunting opportunities exist. In this system, it appears necessary that multiple packs maintain access to some of the same hunting grounds.

Predator distribution has been commonly used as a surrogate for predation risk in ecological studies (e.g. Ripple et al. 2001; Creel et al. 2005; Fortin et al. 2005); however, our findings indicate that risk is a function of both predator distribution and habitat features, with habitat playing the larger role at high predator densities. Hopcraft et al. (2005) found similar patterns for Serengeti lions (Panthera leo), whereby lion kills were more closely associated with good hunting habitats (in this case, stalking cover) than areas of high prey abundance. In a study that was able to decompose the stages of predation, Hebblewhite et al. (2005) found that topographic features determined patterns of wolf–elk encounters, while habitat (i.e. vegetation) mediated post-encounter outcomes. Wolves are inefficient predators with generally low hunting success ($\approx 20\%$; Smith et al. 2000) due, in part, to the large size and defensive capabilities of their prey. In wolf-ungulate systems, as in other large mammal systems (Sinclair & Arcese 1995), prime-age adult prey are largely invulnerable to predation, and predators are highly selective, targeting the young, old or weak (Mech & Peterson 2003). Our finding of strong landscape effects on predation suggests that landscape features may often 'tip the balance' in predator–prey encounters, thus influencing post-encounter outcomes. In addition to the constraint of landscape and habitat on predation in the NR system, the influence of the annual wolf distribution on kill occurrence was weakened by the social interactions and territory selection of the predators themselves. Lima (2002) has encouraged ecologists to evaluate the influence of predator behaviour on predator–prey interactions, especially those occurring over large landscapes. Our findings suggest that the manner in which predators organize themselves on the landscape to reduce conflict with conspecifics may obscure the relationship between predator distribution and predation risk. We suspect that this phenomenon may be especially important in predator–prey systems where patterns of predation are strongly determined by landscape or habitat features.

There is little evidence that a temporal change in elk antipredator behaviour provides an alternative explanation for the decoupling of kills from predator distribution. A potentially naïve prey responding to a predator might undergo such changes, but studies conducted so far on the NR do not yield empirical support for profound elk behavioural shifts relative to wolves. Several studies have shown that elk respond to the risk of predation by wolves by increasing vigilance levels (Laundre et al. 2001) or shifting habitat use temporally (Creel et al. 2005; Gude et al. 2006). However, these antipredator behaviours have not brought about landscape-level changes in the distribution or behaviour of elk required to explain the results of our kill-site analysis. This contention is supported by an NR study evaluating elk habitat selection before and after wolf

reintroduction (Mao *et al.* 2005) that found that elk did not shift their distribution away from wolf territories during winter. In fact, wolf territory locations were a positive predictor of elk habitat use (i.e. wolf and elk distributions closely overlap). Also, elk increased their winter use of open areas post-wolf reintroduction, despite our finding that such habitats are more risky than forested areas. Further, an analysis of GPS (Global Positioning System) collared elk on the NR (Fortin *et al.* 2005) found that elk did not avoid the core areas of wolf territories. Lastly, we found little support for changes in the types of habitats where wolves have killed elk over 10 years, a response we would expect if elk have altered their habitat selection and movement patterns to avoid encountering and being killed by wolves.

Visualizing our kill-site model as a map of relative predation risk (Fig. 2a) provides some insights into how the spatial scale of safe and risky patches influences the ability of prey to manage the risk of predation while foraging, moving and selecting habitats (Brown & Kotler 2004). The mosaic of risky and safe habitat patches available to NR elk suggests that elk can reduce their risk of wolf predation by making movements on the order of 1–2 km, easily achieved within daily movements (Fortin *et al.* 2005). This notion is supported by recent findings showing that elk move out of open areas when wolves are near (Creel *et al.* 2005) or likely to occur (Fortin *et al.* 2005), and aggregate in increasingly larger groups in open areas the longer wolves are absent (Creel & Winnie 2005). The ability of elk to mediate predation risk in such a dynamic way may explain why elk do not avoid the riskiest habitat patches (Mao *et al.* 2005). Unlike the highly vulnerable native prey of introduced predators, the heterogeneity of the landscape that elk historically shared with wolves should allow them to mediate their risk of predation from this newly restored predator.

Our map of relative kill occurrence indicates that refugia for elk of considerable size exist on the NR. The availability of these refugia for elk, and their ease of accessing them, should buffer the population from extreme levels of predation. The existence of prey refugia also is likely to influence long-term wolf and elk dynamics by reducing predator-caused fluctuations in elk numbers, as found in theoretical studies (Kareiva & Wennegren 1995). Since wolf reintroduction, the NR elk population has declined by an average of 8% annually (White & Garrott 2005), resulting in much debate about the long-term equilibrium size of the elk herd (Eberhardt *et al.* 2003; Vucetich *et al.* 2005; Varley & Boyce 2006). The highly heterogeneous pattern of predation found in this system offers a measure of assurance that economically and socially valuable ungulate populations will not suffer runaway predation as occurs with many exotic predator invasions (Fritts & Rodda 1998; Knapp *et al.* 2001).

These results have implications for the potential of restored predators to initiate trophic cascades by changing the habitat-selection patterns or foraging behaviour of their prey (i.e. behaviourally mediated trophic cascades; Schmitz *et al.* 2004). Several studies on Yellowstone's NR have suggested that wolves are affecting willow (*Salix* spp.), cottonwood (*Populus* spp.) and aspen (*P. tremuloides*) communities by changing the behaviour of elk that heavily browse these woody plants during winter (Ripple *et al.* 2001; Ripple & Beschta 2004; Beyer *et al.* 2007). However, in our view, a rigorous test has been hindered thus far by the lack of an empirical assessment of landscape-level predation risk. We note that the strength of such behaviourally mediated cascades will depend on the cost and benefits of antipredator behaviour (i.e. avoiding or foraging less efficiently in risky areas; Schmitz *et al.* 2004). Our study makes clear that NR elk in winter face a clear trade-off between forage quality and predation risk: most of these browse communities are found in open, flat areas near rivers and roads, which are risky places for elk. However, we think it is unlikely to be optimal for elk to simply avoid these resources, because many of them provide forage during the critical winter months (Creel *et al.* 2005; Mao *et al.* 2005) when NR elk (and other northern ungulates) experience diminishing fat reserves (Cook *et al.* 2001). This need for winter forage most likely explains why elk have not made broad-scale changes in winter habitat selection as a means of avoiding encounters with wolves (Fortin *et al.* 2005; Mao *et al.* 2005). How elk perceive and manage the trade-off between food and safety will ultimately determine the existence and strength of a behaviourally mediated trophic cascade in the NR system.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Table S1 Spatial variance in wolf density index through time.
Figure S1 Model selection results for models of kill occurrence.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2007.01059.x

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