



Weak spatiotemporal response of prey to predation risk in a freely interacting system

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Abstract

1. The extent to which prey space use actively minimizes predation risk continues to ignite controversy. Methodological reasons that have hindered consensus include inconsistent measurements of predation risk, biased spatiotemporal scales at which responses are measured and lack of robust null expectations.
2. We addressed all three challenges in a comprehensive analysis of the spatiotemporal responses of adult female elk (*Cervus elaphus*) to the risk of predation by wolves (*Canis lupus*) during winter in northern Yellowstone, USA.
3. We quantified spatial overlap between the winter home ranges of GPS-collared elk and three measures of predation risk: the intensity of wolf space use, the distribution of wolf-killed elk and vegetation openness. We also assessed whether elk varied their use of areas characterized by more or less predation risk across hours of the day, and estimated encounter rates between simultaneous elk and wolf pack trajectories. We determined whether observed values were significantly lower than expected if elk movements were random with reference to predation risk using a null model approach.
4. Although a small proportion of elk did show a tendency to minimize use of open vegetation at specific times of the day, overall we highlight a notable absence of spatiotemporal response by female elk to the risk of predation posed by wolves in northern Yellowstone.
5. Our results suggest that predator–prey interactions may not always result in strong spatiotemporal patterns of avoidance.

KEYWORDS

Canis lupus, *Cervus elaphus*, null model, predation risk, proactive avoidance, reactive avoidance, spatial overlap, Yellowstone

1 | INTRODUCTION

How, and to what extent, prey respond to the risk posed by predators are central questions in behavioural and community ecology (Sih, 1984, 1998). Although many types of behavioural responses, such as grouping (Fryxell, Mosser, Sinclair, & Packer, 2007; Hebblewhite & Pletscher, 2002) or increased vigilance (Creel, Schuette, & Christianson, 2014; Creel et al., 2017; Dröge, Creel, Becker, & M'soka, 2017; Elgar, 1989; Liley & Creel, 2007), can be studied through direction observation, others are more difficult to characterize unambiguously. In particular, the extent to which prey movement patterns actively minimize predation risk across space and time continues to ignite controversy (Creel, Winnie, Christianson, & Liley, 2008). Indeed, there is a debate regarding the relative importance of proactive versus reactive spatiotemporal responses by prey to predators and the risk of predation (Creel, 2018). Proactive avoidance, where prey purposefully avoid areas or reduce activity during times of the day in which they are more vulnerable to predation (Kohl et al., 2018; Prugh & Golden, 2014), has been highlighted to a varying degree in a number of systems (Creel, Winnie, Maxwell, Hamlin, & Creel, 2005; Dupuch, Magnan, Bertolo, Dill, & Proulx, 2009; Fortin et al., 2005; Heithaus & Dill, 2002; Heithaus, Wirsing, Burkholder, Thomson, & Dill, 2009; Padié et al., 2015; Valeix et al., 2009). In contrast, reactive responses, which involve sudden displacements following more rapid changes in predation risk within the immediate surroundings, have received increased attention in recent years owing to advances in tracking technology (Basille et al., 2015; Courbin, Fortin, Dussault, Fargeot, & Courtois, 2013; Courbin et al., 2016; Martin & Owen-Smith, 2016; Middleton, Kauffman, McWhirter, Jimenez et al., 2013).

Three common challenges arise when attempting to characterize prey spatiotemporal responses to predation risk. The first relates to how exactly predation risk is measured (Moll et al., 2017). It has often been assumed that the spatial distribution of a predator reflects a heterogeneous landscape of predation risk (Lima & Dill, 1990; Searle, Stokes, & Gordon, 2008; Thaker et al., 2011). However, past studies have suggested prey may in fact be more likely to avoid specific habitats or landscape features that increase their vulnerability to predation (Hopcraft, Sinclair, & Packer, 2005; Kauffman et al., 2007; Kohl et al., 2018). Predation risk may also vary over time, such as increase during times of the day when predators are more active or have higher hunting success rates (Gehr et al., 2018; Kohl et al., 2018; Palmer, Fieberg, Swanson, Kosmala, & Packer, 2017). In this context, Moll et al. (2017) recently recommended the use of multiple metrics in studies of predation risk.

A second complication lies in defining the spatial and/or temporal scale at which fear may act on prey behaviour (Kittle, Fryxell, Desy, & Hamr, 2008). A useful framework within which to consider this question was provided by Johnson (1980) in the form of a hierarchical classification of resource selection orders (see also Boyce, 2006). Past research investigating predator–prey interactions have primarily focused on whether the avoidance of predation risk by prey occurs at the level of home range selection (2nd order) or at

the level of patches within individual home ranges (3rd order) (e.g. Courbin et al., 2013). However, few studies have considered how selection across these orders varies along a temporal dimension, for example 2nd order selection between years or 3rd order selection between different times of the day (although see Kohl et al., 2018).

A final challenge concerns how the expectation of behaviour in the absence of proactive and/or reactive responses is defined. For example, how would prey move through a given landscape if they ignored predation risk? Indeed, characterization of prey spatiotemporal responses to predation risk has often been hindered by lack of an appropriate null model with which to generate expected behaviour, such as random movement (Gotelli & Graves, 1996; Miller, 2015; Richard, Calenge, Saïd, Hamann, & Gaillard, 2013). Although step selection functions, which implement randomizations at the individual step level, provide a powerful tool to address this issue (Thurfjell, Ciuti, & Boyce, 2014), their ability to randomize at the level of entire home ranges or to incorporate the temporal dimensions of space use is currently limited (although see Cozzi, Maag, Börger, Clutton-Brock, & Ozgul, 2018). An alternative method was proposed by Richard et al. (2013), who extended the application of null models used in community ecology to examine the potential for spatial interactions. They did this by randomly permuting and shifting roe deer *Capreolus capreolus* trajectories to obtain “pseudo-trajectories,” re-calculating the level of overlap with the distribution of female red deer (*Cervus elaphus*) to generate an expected distribution. Though promising, this approach has so far never been used to measure the strength of prey responses to predation risk.

In this study, we address all three challenges in a uniquely comprehensive analysis of the spatiotemporal responses of adult female elk (*Cervus elaphus*) to the risk of predation by wolves (*Canis lupus*) during winter in northern Yellowstone, USA. Since the reintroduction of wolves to Yellowstone in 1995–1997, numerous studies have sought to characterize potential proactive versus reactive responses of elk and how these might relate to an apparent trophic cascade observed across the ecosystem (Ripple & Beschta, 2012). The majority of studies investigating movement and habitat selection responses by elk to the risk posed by wolves have revealed weak and/or inconsistent patterns (Forester et al., 2007; Fortin et al., 2005; Kohl et al., 2018; Mao et al., 2005; Middleton, Kauffman, McWhirter, Jimenez et al., 2013; Proffitt, Grigg, Hamlin, & Garrott, 2009; White et al., 2008). Despite this large body of research, which was drawn from multiple elk populations and relied primarily on movement data collected in the early years following wolf reintroduction, there remains a persistent contention that wolves have strong and consistent effects on elk space use (Beschta, Painter, & Ripple, 2018; Creel, 2018; Painter, Beschta, Larsen, & Ripple, 2018; Winnie & Creel, 2017).

In this context, we carried out a multi-scale assessment of the spatiotemporal response of GPS-collared elk to three measures of predation risk: the intensity of wolf space use, the distribution of wolf-killed elk and vegetation openness. We first considered the location of the elk winter home range within northern Yellowstone between 2012 and 2016, asking whether philopatric behaviour by elk (Houston, 1982; White et al., 2010) might reflect proactive avoidance of predation risk. We then investigated whether the configuration of

the elk winter home range within the chosen area minimizes spatial overlap with predation risk (2nd order selection). We also assessed whether elk varied their use of areas characterized by more or less predation risk across the 24-hr cycle. Lastly, we estimated encounter rates between collared elk and wolf packs during six 32-day winter periods occurring between 2013 and 2015 (3rd order selection). For all of these measures, we determined whether observed values were significantly lower than expected if elk movements were random with reference to predation risk. To do this, we implemented a set of null model formulations that represent expectations of prey movement in the absence of predation risk effects, while accounting for elevation constraints known to affect winter movements of elk.

2 | MATERIALS AND METHODS

2.1 | Study area

The northern Yellowstone winter range encompasses roughly 1,520 km² of mountainous terrain and open valleys, with elevation

ranging from 1,500 to 3,210 m (Houston, 1982). The area defines the winter range of seasonally migrating elk and is largely composed of shrub steppe, with patches of intermixed lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*) and aspen (*Populus tremuloides*) (Despain, 1990; Houston, 1982). We consider wolf and elk trajectories recorded over the entire northern Yellowstone winter range—that is including land within Yellowstone National Park (YNP) and north of the park boundary—and hereafter refer to this as the Northern Range (NR). Winter severity in the NR is highly variable but in general snowfall increases from west to east due to an elevation gradient that approximates the distribution of elk on winter range, hence the inclusion of elevation in null model formulations (see below). Snow cover generally lasts from late October to early May.

Elk abundance in the NR has declined ~70% between 1995 and 2015. In 2015, elk abundance numbered around 6,000 individuals. It was estimated that only ~1,800 of these elk overwintered in the YNP portion of the NR (Tallian et al., 2017). The decline in NR elk abundance has been largely due to a reduction in elk numbers within the

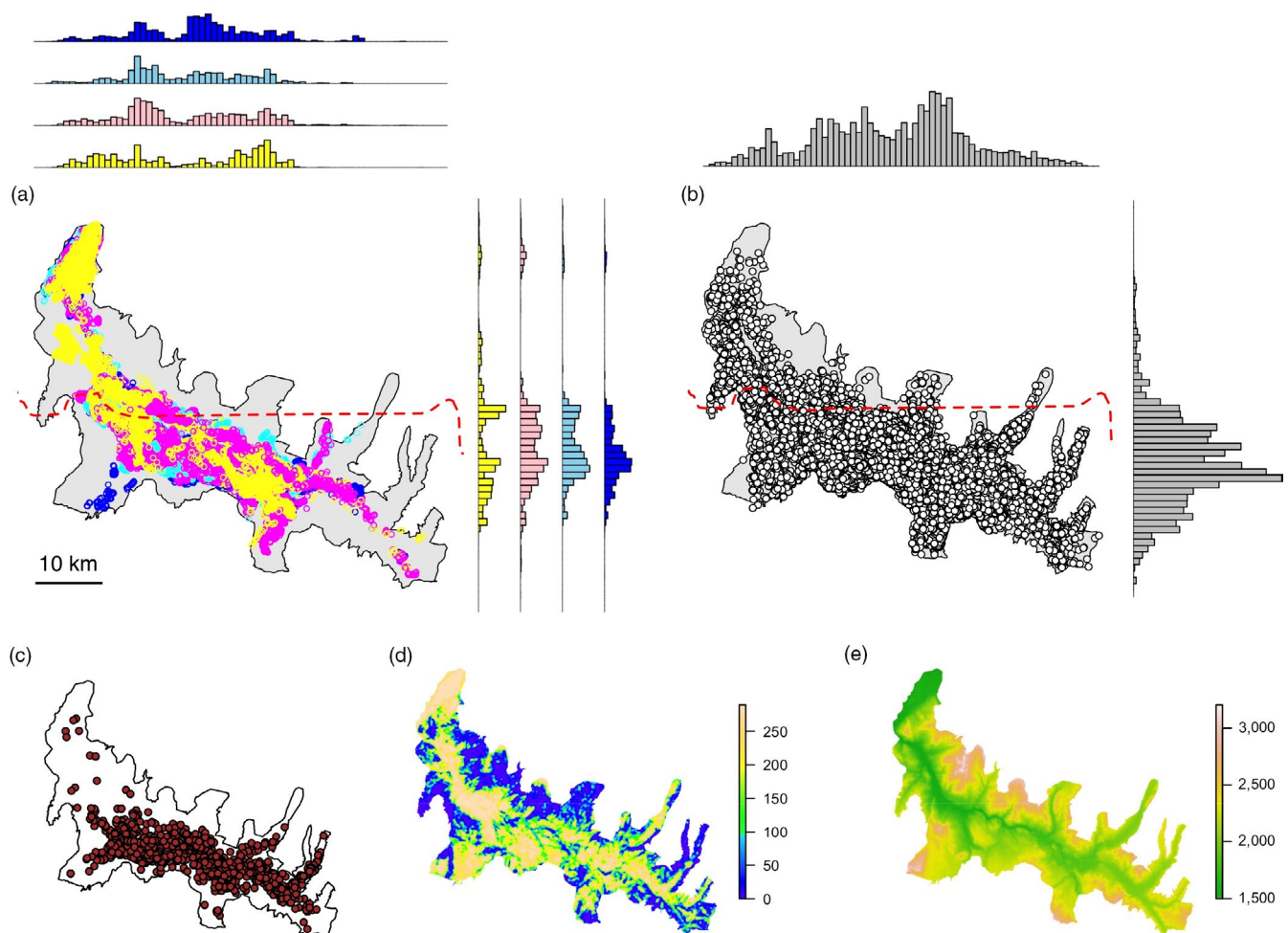


FIGURE 1 Overview of the spatial data collected across the Northern Range and used in this study. (a) Adult female elk GPS relocations for the winters of 2012 (dark blue), 2013 (light blue), 2014 (pink) and 2015 (yellow); (b) wolf GPS relocations recorded between 2004 and 2016; (c) distribution of wolf-killed adult female and calf elk recorded between 1995 and 2016; (d) vegetation openness (0 = closed, 289 = open); (e) elevation (in m). The dashed red line in (a) and (b) denotes the northern boundary of Yellowstone National Park

NR's YNP section (Tallian et al., 2017; White & Garrott, 2005; White, Proffitt, & Lemke, 2012). Elk are the primary prey of wolves in the study area (Smith, Drummer, Murphy, Guernsey, & Evans, 2004; Tallian et al., 2017). During the present study, wolf abundance within the NR of YNP varied between 34 and 50 individuals (Smith et al., 2018).

2.2 | Elk winter space use

We estimated individual-level home ranges for GPS-collared adult female elk during four winters (2012–13, 2013–14, 2014–15 and 2015–16) (Figure 1a). A winter was defined as the period between November 1st of a given year and 30th April of the next. Elk collars (Iridium TrackM 3D, Lotek Wireless Inc.) were first deployed in February 2011, with new additions and redeployments occurring each subsequent winter. Adult (>1 year old) female elk were captured using helicopter net-gunning. Recorded data were uploaded via Iridium satellite every 4–12 fixes and subsequently downloaded from a dedicated webserver. To ensure accurate representation of elk winter space use, we excluded winter movement paths for which the average fix frequency was more than five hours or the time difference between the first and last relocation was less than four months.

For each winter, we estimated the individual-level utilization distribution (UD) of each collared elk over a continuous grid of cell size 1 by 1 km using a Brownian bridge movement model (BBMM) implemented in the R package BBMM (Bullard, 1999; Horne, Garton, Krone, & Lewis, 2007). The BBMM is a continuous-time stochastic movement model, where the probability of being in an area is conditioned on (a) the distance and elapsed time between successive locations, (b) a measure of location error and (c) an estimate of the animal's mobility (the Brownian motion variance, see Horne et al., 2007). In other words, the model approximates the movement path between two subsequent locations by applying a conditional random walk. Because UD tails (i.e. beyond the 95% isopleth) tend to be poorly estimated, we generated conditional 95% UD's scaled to sum to unity (Benhamou, Valeix, Chamaillé-Jammes, Macdonald, & Loveridge, 2014). Location error for elk collars was unknown and fixed to a conservative estimate of 50 m. To avoid pseudo-replicating trajectories from collared elk belonging to the same group, we calculated an index of movement cohesion for every elk dyad within a given winter. We used Shirabe's (2006) correlation coefficient, which measures the degree of correlation between the movement paths of two individuals as a multivariate Pearson product-moment correlation coefficient (Long, Nelson, Webb, & Gee, 2014; Shirabe, 2006). The index ranges from -1 (negative correlation) to 1 (positive correlation), with 0 indicating random movement. If two elk trajectories recorded during the same winter showed a movement correlation coefficient equal to or greater than 0.5 (Long et al., 2014), the one with the least number of relocations was excluded from the analysis.

2.3 | Wolf space use intensity

We used GPS collar data collected on wolves each winter between 2004 and 2016 to characterize long-term winter space use patterns

by packs in the NR (Figure 1b). Wolf GPS tracking has been routinely carried out by the Yellowstone Wolf Project since 2004, with a varying proportion of packs inside YNP sampled every year (details of collaring procedures can be found in Smith & Bangs, 2009). Although the exact model of fitted GPS collars varied during this period, all were manufactured by either Telonics (Mesa, AZ, USA), Televilt (Lindesberg, Sweden) or Lotek (Newmarket, ON, Canada). Average winter fix frequency between 2004 and 2016 varied between periods of intensive monitoring of wolf movements when relocations were obtained every hour (32-day winter periods, either Early Winter [EW] period between 14th November and 15th December or Late Winter [LW] period between 28th February and 31st March) and periods characterized by longer delays between relocations (average of 6 hr).

To avoid duplicated trajectories derived from collared wolves belonging to the same pack, which could bias subsequent estimation of space use, we also applied Shirabe's (2006) correlation coefficient to every wolf dyad in a given winter. For dyads showing a movement correlation coefficient equal to or greater than 0.5, we excluded the trajectory with the least number of relocations from the corresponding winter. The average distance between simultaneous relocations of dyads exhibiting joint movement was used in the estimation of wolf pack space use (see below).

For each winter, we estimated the joint spatial activity of all collared wolves, which we refer to as a localized density distribution (LDD; Kittle et al., 2008). The LDD was taken as the sum of individual wolf pack UD's—each of these weighted by the size of the corresponding pack (see Supporting Information Table S1, and Kauffman et al., 2007 for a similar procedure)—and scaled to sum to unity. We retained the UD's of lone wolves in the estimation of winter-specific LDDs to account for their contribution towards the risk of wolf predation. Utilization distributions were estimated using BBMMs estimated over the same spatial grid as that used for elk. We used a location error of 468 m for wolf packs as this represented the average distance between joint wolf movements. We assumed that this value accounted for the position of individuals that were not collared when estimating a pack's UD (Benson & Patterson, 2015). A final joint LDD representing wolf long-term space use in the NR was then derived by averaging winter LDDs and scaling to sum to unity. By averaging across winters—which differed in the number of packs collared (see Supporting Information Table S1)—we aimed to produce a space use pattern representative of where wolves were more or less likely to be encountered across the NR. Such a long-term pattern was necessary to test for proactive responses by elk. Our study focused on wolves collared within the YNP boundary, and thus, the estimation of the wolf LDD in the northern section of the elk winter range relied on excursive movements by park packs.

2.4 | Elk kill site density and vegetation openness

We used a long-term, spatially explicit dataset on adult female elk and calf kill sites recorded in winter between 1995 and 2016 (Figure 1c) to derive a probability surface of observed predation

by wolves. In a similar way to Kohl et al. (2018), we used a kernel density estimator implemented in the R package *adehabitatHR* to generate a smoothed spatial distribution of kill sites, setting a fixed bandwidth of 1,000 m to match the resolution of the landscape grid. Lastly, we used a layer representing vegetation openness as a third measure of predation risk (Kauffman et al., 2007; Figure 1d). Values in this layer ranged from 0 (thick forest) to 289 (open grassland) (see Kohl et al., 2018), which we subsequently standardized to sum to unity in order to ensure consistency with measures of wolf space use intensity and kill site density.

2.5 | Spatial overlap

We defined spatial overlap as the volume of intersection (VI) between the UD of a single elk during a given winter and a surface representing either one of the spatial predation risk indicators. We interpret VI as the proportion of the volume of the elk UD intersecting with a given predation risk layer (Fieberg & Kochanny, 2005; Kernohan, Gitzen, & Millspaugh, 2001). The VI index, which ranges from 0 (no overlap) to 1 (complete overlap), has been widely used to compare UDs in a range of different taxa (Fieberg & Kochanny, 2005). In our case, if UD_{Eik} and UD_{PR} are the estimated utilization distributions for an individual elk and predation risk type, respectively, then

$$VI = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \min[UD_{Eik}(x,y), UD_{PR}(x,y)] dx dy$$

We calculated the VI index based on conditional 95% UDs for elk, so as to minimize bias associated with the poorly estimated UD tails (Benhamou et al., 2014; Fieberg, 2007). We expected VI values to be low owing to the much larger spatial extent of predation risk layer values relative to that of individual elk UD values (i.e. there were many more instances of $UD_{Eik}(x,y) = 0$ across the landscape, biasing VI towards 0). Thus, low VI values in our case cannot be considered as evidence for proactive avoidance behaviour as they could just be the result of differences in the extent of the overlapped spatial distributions. This is the reason why a null model approach as implemented below is required to ascertain true avoidance behaviour.

2.6 | Hourly predation risk

To investigate whether elk use of risky areas varied across the 24-hr cycle, we modelled spatial predation risk level (wolf space use intensity, kill site density or vegetation openness) associated with a given relocation as a function of hour of the day. We used generalized additive mixed models (GAMMs) that included a term for first order auto-regressive processes (i.e. autocorrelation AR(1)) and implemented a cyclic cubic spline and Gaussian error structure (Wood, 2006). From this, we obtained a prediction for the observed predation risk level associated with a given relocation at each hour of the

day. For each type of predation risk considered, we ran one model per winter trajectory using the *gamm* function in the R package *mgcv* (Wood, 2006).

2.7 | Encounter rate

We measured the rate at which individual elk encountered wolf packs during six periods of intense monitoring (hereafter, winter periods) characterized by wolf relocations recorded every hour. We limited our analysis of encounter rate to winter periods in 2013–15 as these included a greater GPS coverage of NR wolf packs. Encounter rate was defined as ST/n where ST is the total number of recorded encounters with wolves and n represents the total number of fixes recorded for a given elk. Encounters consisted of spatially proximal and temporally simultaneous elk and wolf fixes defined according to specific distance d and time t thresholds, respectively (Long et al., 2014). We set d to 1,000 m following Middleton, Kauffman, McWhirter, Jimenez et al. (2013), who found that elk tended to increase their rates of movement, displacement and vigilance when wolves were within this distance threshold. Temporal proximity t was set to 1 hr as this represented the average length of a successful hunting bout by wolves (MacNulty, 2002). Thus, if elk and wolf relocations obtained in the same 1-hr window were observed to be within 1,000 m of one another, they constituted an encounter. Importantly, we use the term “encounter” to denote a significantly increased likelihood of wolf-caused mortality (MacNulty, Mech, & Smith, 2007), which we assume elk would actively avoid (Creel et al., 2005; Latombe, Fortin, & Parrott, 2014; Proffitt et al., 2009). We excluded elk trajectories for which the number of tracking days was less than 30. Note that incomplete winter trajectories excluded from the spatial overlap analysis could be included in the analysis of encounter rate if they spanned an entire winter period. For ease of interpretation, we present values of encounter rate per 100 elk fixes.

We modelled encounter rate as a function of the proportion of wolf packs collared within the NR of YNP using a generalized linear mixed model (GLMM). The model response consisted of the number of encounters per trajectory with an offset term to account for varying number of fixes. We set the error distribution to Poisson and included elk ID as a random intercept to control for repeated measures on the same individuals across winter periods.

2.8 | Null model formulations

We used a null model approach to determine whether the observed spatial overlaps, encounter rates and hourly predation risk levels obtained for winter and period-level elk trajectories were less than expected by chance. All null model formulations were based on a correlated random walk, which randomly sampled the distributions of step lengths and turning angles derived from the observed elk trajectory to construct an alternative trajectory. We also imposed three constraints on null trajectories to ensure realistic outcomes. The first was that the generated trajectory fit within the same elevation

range as the original trajectory (Figure 1e). This was necessary to account for how deep snowpack excludes elk from high-elevation areas during winter irrespective of predation risk (Houston, 1982). Secondly, the null trajectory had to fit within the same bounding box area as the original. This ensured that the area covered by the trajectory did not affect expected outcomes. Lastly, null relocations could not occur outside of the NR.

To test whether philopatric behaviour by elk reflected avoidance of predation risk, we generated null trajectories with starting locations sampled across the NR. Note that the starting location served as the centroid of the bounding box within which the null trajectory had to fit. We then constrained the starting location of null trajectories to a randomly sampled relocation from the observed trajectory, thus keeping the alternative elk trajectory within the same geographical area as the original. This latter formulation was also used to generate null trajectories for each winter period.

For each winter and period-level elk trajectory, we generated 1,000 null trajectories, each time re-calculating the corresponding spatial overlap and encounter rate indices with each predation risk layer and period-level wolf trajectories, respectively. Hourly predation risk levels were re-calculated using the same null trajectories as for the spatial overlap analysis. Randomizations were carried out using the *NMs.randomCRW* function in the *r* package *adehabitatLT* (Calenge, 2006). Statistical testing consisted in computing the one-tailed probability $P = (k_e + 1)/k$ of getting a value based on the null model equal to or less than the observed level, where k is the total number of null elk trajectories and k_e is the number of values $<$ observed. To control for the high number of significance tests, we applied a sequential Bonferroni correction by multiplying P by the number of elk trajectories in the corresponding winter, period or hour bin (Holm, 1979). We chose to implement a one-tailed test as we were interested in the alternative hypothesis of avoidance, which we refer to hereafter as a significant outcome. We report statistical significance at an α level of 0.05. All analyses were carried out in *R* version 3.5.0 (R Development Core Team, 2018). Data used in this study are available from the Dryad Digital Repository (<https://doi.org/10.5061/dryad.tp546d7>).

3 | RESULTS

3.1 | Spatial overlap

Elk winter UD's were estimated for 13, 22, 22 and 12 individuals during the winters of 2012, 2013, 2014 and 2015, respectively, totalling 69 winter trajectories. Trajectories showed a median of 181 days

of tracking (range = 134–182) and an average of 2.39 hr between relocations ($SD = 0.69$) across all winters (Table 1; Supporting Information Figure S1). Movement correlation between contemporaneous trajectories was consistently <0.5 . Wolf long-term space use across the NR was estimated from 72,454 GPS relocations obtained from 23 individual packs (a total of 61 winter trajectories) between 2004 and 2016 (Supporting Information Table S1). A total of seven pairs of wolf trajectories exhibited a movement correlation coefficient greater than 0.5, resulting in the exclusion of the same number of trajectories prior to estimation of wolf space use intensity (Figure 2a). The predation risk layer relating to elk kill site density (Figure 2b) was derived from 1,780 wolf-killed adult female and calf elk detected between 1995 and 2016 across the NR.

As expected, spatial overlap values between elk winter home ranges and predation risk layers were low, ranging from 0.004 to 0.170 for wolf space use intensity, 0.007 to 0.361 for elk kill site density and 0.006 to 0.058 for vegetation openness (see Supporting Information Tables S2 and S3). There was no evidence for proactive avoidance at the home range level when the null model formulation did not include a constraint representing philopatric behaviour, regardless of the predation risk layer (Table S2). When philopatry was included in the null model formulation, 2 out of the 69 home ranges showed significantly less than expected overlap with vegetation openness, one in the winter of 2013 and the other in 2014 (Table S3). No home range displayed a significant outcome for wolf space use intensity or elk kill site density.

3.2 | Hourly predation risk

Across all hours of the 24-hr cycle, the mean percentage of individual elk using areas with lower than expected levels of predation risk was 1.4% ($SD = 0.67$) for wolf space use intensity, 0% ($SD = 0$) for kill site density, and 10.4% ($SD = 2.4$) for vegetation openness (see Supporting Information Figures S2–S5 for observed and expected values of vegetation openness across the 24-hr cycle). For the latter metric, the proportion of significant outcomes was generally higher between 07:00 and 18:00 hrs, with a peak of 0.149 between 12:00 and 13:00 hrs (Figure 3).

3.3 | Encounter rate

We recorded a total of 453 encounter events from 36,738 elk and 13,685 wolf pack relocations recorded across the six winter periods considered (Table 2). The majority of encounters (95.8%) were

TABLE 1 Summary of winter elk trajectories

Winter	# trajectories	Total # relocations	Mean # tracking days	Mean # hours between relocations (attempted interval)
2012–13	13	18,647	177.4	3.213 (2.5)
2013–14	22	36,986	168.4	2.514 (2.5)
2014–15	22	37,757	165.5	2.523 (2.5)
2015–16	12	52,891	178.2	1.051 (1)

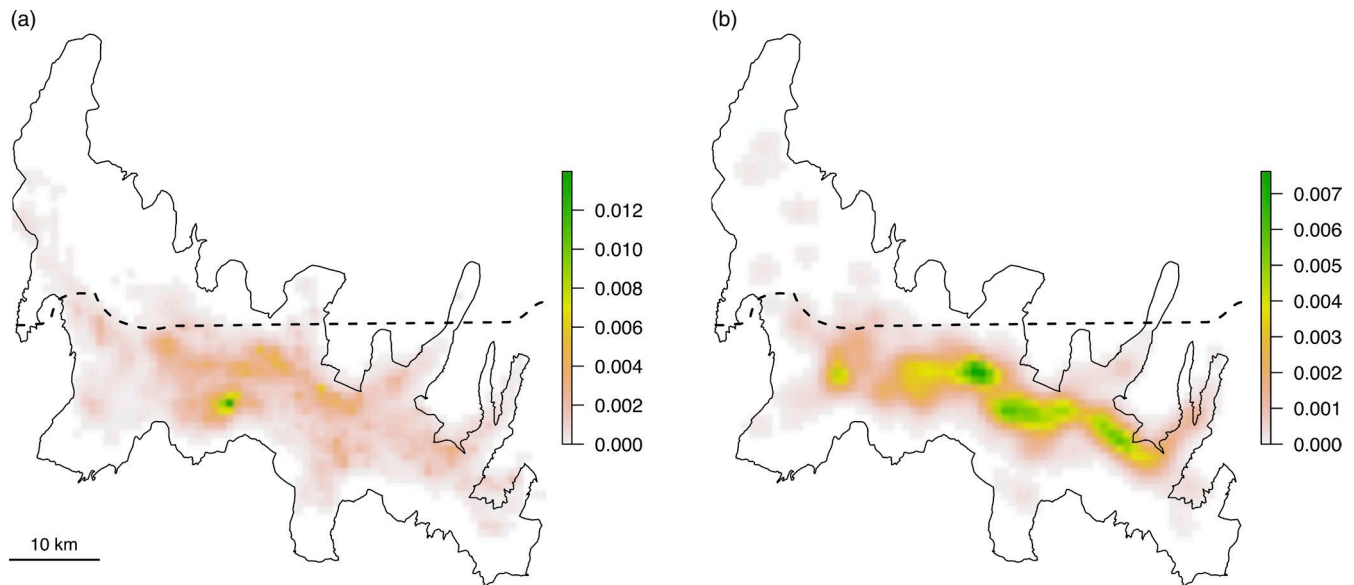


FIGURE 2 Predation risk layers representing wolf space use intensity, 2004–2016, (a) and elk kill site density, 1995–2016, (b) during winter in the Northern Range. The dashed line denotes the northern boundary of Yellowstone National Park

recorded inside YNP (Figure 4a). For those elk that did experience encounters, these occurred on average once every 9.0 days with a range of 7.1 to 11.7 days across winter periods (Table 2). The shortest recorded distance between simultaneous wolf and elk relocations was 102.5 m. From this value, encounter frequency increased at a constant rate until the threshold of 1,000 m (Figure 4b). Encounters were more likely to be recorded during morning (07:00–10:00) and

dusk (16:00–18:00) than during the middle of the day or at night (Figure 4c). Encounter rate increased significantly with the proportion of wolf packs collared within the NR of YNP (GLMM; Figure 4d and Table 2). Random intercept estimates showed a 12-fold variation across elk IDs, reflecting considerable differences in encounter rates at the individual level (Supporting Information Table S4). No elk trajectories were found to exhibit a lower than expected encounter rate with collared wolf packs. Note that a repeat of the analysis using a distance threshold of 500 m yielded the same result (see Supporting Information Table S5).

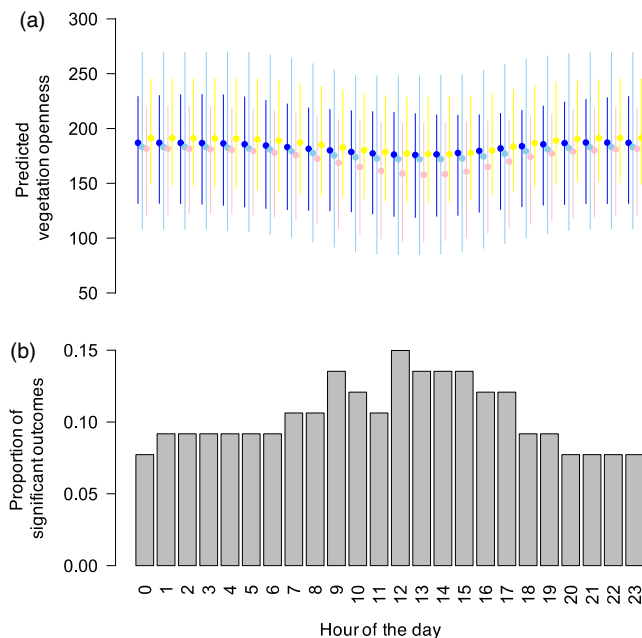


FIGURE 3 (a) Predicted mean level of vegetation openness per hour of the day. Full circles represent averages across individuals with bars showing 95% CIs. Colours indicate the different winters (dark blue for 2012, light blue for 2013, pink for 2014 and yellow for 2015). (b) Proportion of individual elk showing lower than expected mean vegetation openness per hour across all winters

4 | DISCUSSION

Our study highlights a notable absence of spatiotemporal response by adult female elk to the risk of predation posed by wolves in the Northern Range. Home range selection by elk, both at the level of the entire NR and that defined by philopatric behaviour, did not reflect proactive avoidance of wolves themselves nor of sites associated with a higher risk of being hunted successfully. Similarly, we found no evidence for reactive responses of individual elk to the presence of wolves in close proximity. Although a small proportion of elk did show a tendency to minimize use of open vegetation at specific times of the day (more so during the day than at night), in general we found a weak proactive temporal response to the different measures of predation risk. Together, these results suggest that predator–prey interactions may not always result in strong spatiotemporal patterns of avoidance.

The limited proactive response of elk to wolf space use intensity concurs with findings from previous studies. White et al. (2010) likewise reported that most elk maintained the same wintering areas after wolf reintroduction. The overriding need for quality winter

TABLE 2 Summary of winter period elk trajectories and encounter rates with GPS-collared wolves

Period	# trajectories	Total # relocations	Mean # hours between relocations	Total # encounters	Encounter rate ^a median [range]	Mean # days per encounter	# wolf packs collared (proportion of active) ^b
LW 2013	18	5,613	2.48	108	0.82 [0–5.56]	8.4	2 [0.66]
EW 2013	18	5,452	2.54	75	0.98 [0–4.22]	9.2	3 [0.52]
LW 2014	15	4,691	2.46	87	0.33 [0–3.91]	11.7	3 [0.44]
EW 2014	24	7,300	2.52	92	1.14 [0–6.17]	7.1	4 [0.75]
LW 2015	23	7,008	2.52	76	0.50 [0–4.56]	9.1	4 [0.97]
EW 2015	22	6,674	2.53	15	0.31 [0–1.05]	8.3	2 [0.33]

Notes. LW: Late Winter; EW: Early Winter.

^aEncounter rate per 100 fixes, i.e. the number of instances in which elk and wolf relocations within the same 1-hr window were within 1,000 m of each other multiplied by 100. ^bProportion of packs collared out of the ones known to be active within the Northern Range of Yellowstone National Park.

forage most likely explains why elk resist moving their winter home ranges in response to wolves. In their comparison of elk movement patterns before and after wolf reintroduction, Mao et al. (2005) found that elk “did not spatially separate themselves from wolves” during winter months. Another reason for this could be that elk are unlikely to be aware of the precise spatial distribution of a predator known to frequently course throughout their winter range (Bergman et al., 2006; Middleton, Kauffman, McWhirter, Jimenez et al., 2013; Uboni, Smith, Mao, Stahler, & Vucetich, 2015). However, Kauffman et al. (2007) highlighted a discrepancy between kill site occurrence and wolf distribution, making the more general point that predator density may not be a good indicator of predation risk. To counter this criticism, we considered two additional measures of predation risk (Moll et al., 2017). These reflected the notion that elk might select for sites that reduce their vulnerability to being hunted successfully, such as areas of increased vegetation cover (Creel et al., 2005; Fortin et al., 2005). Yet, contrary to previous work, we did not find any evidence to support a proactive response to any of the predation risk measures, thus strengthening the idea that home range selection by elk in our study did not reflect avoidance of predation risk.

Recent work on the responses of prey to predators has highlighted the importance of time in modulating spatial relationships between prey movements and predation risk (Creel et al., 2008; Palmer et al., 2017). In particular, Kohl et al. (2018) revealed a dynamic landscape of fear, whereby elk use of risky areas in northern Yellowstone was dependent on wolf diel activity. Although the proportion of elk using open vegetation less than expected by chance did vary across the 24-hr cycle in the present study, this behaviour only concerned a small proportion of the individuals tested each hour of the day. However, in a similar way to Kohl et al. (2018), the detected avoidance response tended to be stronger during daylight hours, when wolves were more likely to be actively hunting. The weaker patterns observed in the present study could be due to its coarser scale and/or changes in elk behaviour towards wolves. For example, wolf and elk numbers in the NR were much higher during the early years of wolf re-colonization (MacNulty, Stahler, Wyman, Ruprecht, & Smith, 2016; Smith et al., 2018), when more elk could have been more sensitive to the risk of wolf predation. It is also important to note that the kill site layer was derived from long-term data that overlapped with the 2001–2004 study period, during which a stronger response was found. Although we believe that our predation risk layers accurately characterize long-term patterns needed to test for proactive responses, this highlights the need to consider appropriate time-scales when measuring long-term predation risk.

The near absence of elk trajectories showing a lower than expected encounter rate with wolves is a surprising outcome of our study. From an ecological perspective, it is possible that other factors not considered here, such as elk group size (Gower et al., 2008; White et al., 2012), switches in habitat use (Creel et al., 2005; Fortin et al., 2005; Hernández & Landré, 2005) and wolf pack size (MacNulty, Smith, Mech, Vucetich, & Packer, 2012) allow individual elk to minimize predation risk despite close proximity to wolves,

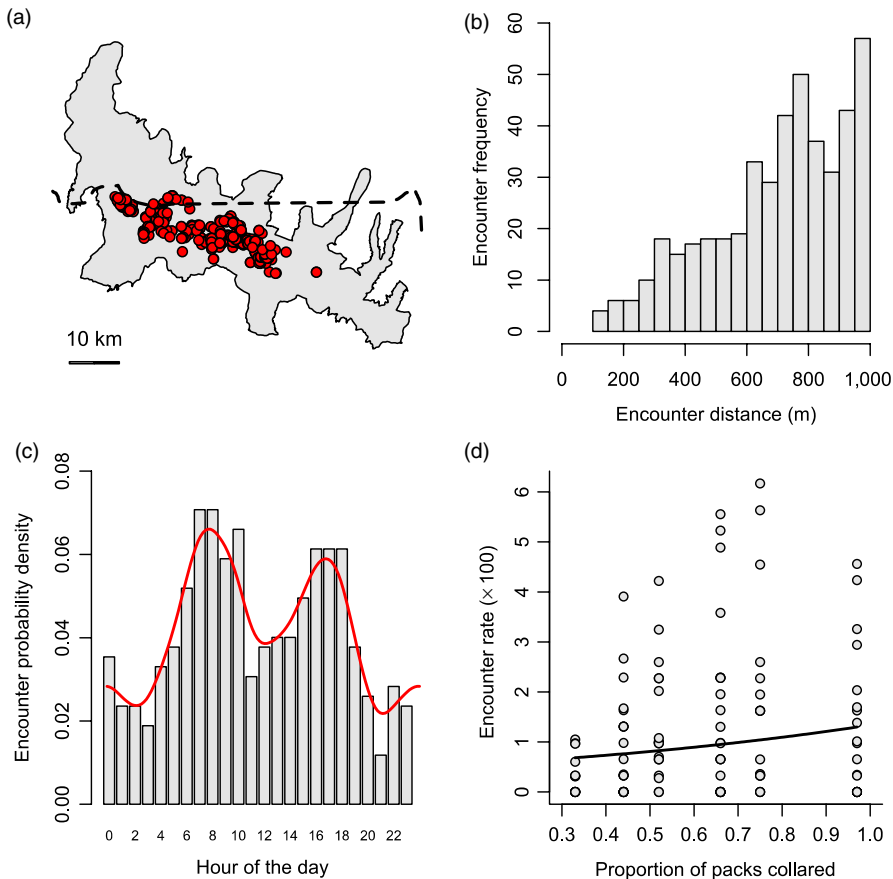


FIGURE 4 Details of encounter events recorded between GPS-collared elk and wolves in the Northern Range during six 32-day winter periods, 2013–2015. These include the spatial distribution of recorded encounters (a), the frequency distribution of encounter distances (b), the probability density function of encounter times (c), and the relationship between encounter rate and the proportion of wolf packs collared within the Northern Range of Yellowstone National Park (d). Encounters were defined as wolf and elk relocations obtained during the same 1-hr window and observed to be within 1,000 m of one another. The dashed line in (a) denotes the northern boundary of Yellowstone National Park. The red curve in (c) represents the fitted density function. The fitted line in (d) was obtained from a Poisson generalized linear mixed model with the number of encounters as response variable, the proportion of collared wolves as explanatory variable, the number of fixes as an offset term, and elk ID as a random intercept. Encounter rate is expressed per 100 elk fixes

thus dampening small-scale spatial avoidance patterns. Individual elk—and adult females in particular—might also tolerate close proximity to wolves because they frequently survive their encounters with them (MacNulty et al., 2007, 2012; Mech, Smith, & MacNulty, 2015). From a methodological standpoint, we also have to consider the possibility that our definition of an encounter poorly described immediate predation risk, and that reactive avoidance occurs at a spatial scale <500 m. Few high-resolution relocation datasets are currently available that combine simultaneous predator–prey trajectories, and our study is valuable in developing a methodological framework within which these could be considered once they become more widely available.

Importantly, our findings are consistent with two key predictions of the predator–prey shell game occurring in a freely interacting system (Lima, 1998; Mitchell & Lima, 2002). One of these relates to attempts by predators to get closer to prey. In a system such as the NR where the winter movement of elk is constrained by philopatric behaviour and snow cover (Houston, 1982; White et al., 2010), wolves may be better able to align their space use with that of their prey. A consequence of this would be the dampening of any potential avoidance patterns displayed by elk (as per Sih, 1984, 2005), which might explain their overall absence in the present study. Another prediction states that prey should attempt to be unpredictable in space, and the lack of consistent movement patterns observed in the present study could be interpreted as a reflection of this. We emphasize that the methodology presented here, combined with other

approaches such as step selection functions (e.g. Cozzi et al., 2018), could be used to assess behavioural responses on both sides of the predator–prey race.

We must acknowledge the potential limitations of our study. In particular, Creel, Winnie, and Christianson (2013) recently reviewed sources of bias associated with the estimation of encounter rates between mobile predators and prey, some of which are relevant to the present study. First, the fix frequency used to record elk movement trajectories, which averaged 2.39 hr across winters, may have led us to overlook instances of close proximity with wolves, and even entire hunting episodes (MacNulty, 2002; MacNulty et al., 2007). Although we cannot exclude this with absolute certainty, the 1-hr temporal window used to define encounters is likely to have minimized this problem. Second, not all of the packs active in the Northern Range during a given winter period were considered, which may have exacerbated the under-estimation of encounter rates. Nevertheless, our study considers movement trajectories from members of many of the dominant packs in the Northern Range, and although the proportion of packs collared did positively influence observed encounter rate, it did not affect the absence of significant outcomes. Third, we did not make use of more complex measures of dynamic interaction between simultaneous trajectories (reviewed by Long et al., 2014). Instead, we chose to use a more intuitive measure of encounter rate, which we complemented with an assessment of significance based on values obtained under the assumption of random movement (Miller, 2015).

In summary, not only does our study provide a comprehensive assessment of the spatiotemporal response of individual prey to predation risk, but it also extends the use of null models to infer on interactive behaviour between different species. In doing so, it emphasizes the challenges of detecting strong spatiotemporal responses by prey and suggests that other factors relating to both predator and prey behaviour may be more important in shaping observed outcomes. Although our data were based on a system that has undergone extensive study over the past two decades, the considerations we highlight are particularly relevant to telemetry studies carried out in poorly known landscapes, in which spatial data are increasingly the first to be collected. In such cases, a clear understanding of species interactions, such as the proactive and reactive responses of prey to predators, may have to be gained through a combination of high-resolution GPS telemetry and direct observation.

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AUTHORS' CONTRIBUTIONS

J.J.C. designed the study; M.T.K., M.C.M., D.R.S., D.W.S. and D.R.M. collected and shared the data; J.J.C. and T.C. performed the modelling work and analysed output data. J.J.C. wrote the manuscript, and all authors contributed substantially to revisions.

DATA ACCESSIBILITY

Data used is available in the Dryad Digital Repository <https://doi.org/10.5061/dryad.tp546d7> (Cusack et al., 2019).

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REFERENCES

- Basille, M., Fortin, D., Dussault, C., Bastille-Rousseau, G., Ouellet, J. P., & Courtois, R. (2015). Plastic response of fearful prey to the spatiotemporal dynamics of predator distribution. *Ecology*, 96, 2622–2631. <https://doi.org/10.1890/14-1706.1>
- Benhamou, S., Valeix, M., Chamaillé-Jammes, S., Macdonald, D. W., & Loveridge, A. J. (2014). Movement-based analysis of interactions in African lions. *Animal Behaviour*, 90, 171–180. <https://doi.org/10.1016/j.anbehav.2014.01.030>
- Benson, J. F., & Patterson, B. R. (2015). Spatial overlap, proximity, and habitat use of individual wolves within the same packs. *Wildlife Society Bulletin*, 39, 31–40. <https://doi.org/10.1002/wsb.506>
- Bergman, E. J., Garrott, R. A., Creel, S., Borkowski, J. J., Jaffe, R., & Watson, F. G. R. (2006). Assessment of prey vulnerability through analysis of wolf movements and kill sites. *Ecological Applications*, 16, 273–284. <https://doi.org/10.1890/04-1532>
- Beschta, R. L., Painter, L. E., & Ripple, W. J. (2018). Trophic cascades at multiple spatial scales shape recovery of young aspen in Yellowstone. *Forest Ecology and Management*, 413, 62–69. <https://doi.org/10.1016/j.foreco.2018.01.055>
- Boyce, M. S. (2006). Scale for resource selection functions. *Diversity and Distributions*, 12, 269–276. <https://doi.org/10.1111/j.1366-9516.2006.00243.x>
- Bullard, F. (1999). *Estimating the home range of an animal: a Brownian bridge approach*. Thesis, University of North Carolina, Chapel Hill, USA.
- Calenge, C. (2006). The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197, 516–519. <https://doi.org/10.1016/j.ecolmodel.2006.03.017>
- Courbin, N., Fortin, D., Dussault, C., Fargeot, V., & Courtois, R. (2013). Multi-trophic resource selection function enlightens the behavioural game between wolves and their prey. *Journal of Animal Ecology*, 82, 1062–1071. <https://doi.org/10.1111/1365-2656.12093>
- Courbin, N., Loveridge, A. J., Macdonald, D. W., Fritz, H., Valeix, M., Makuwe, E. T., & Chamaillé-Jammes, S. (2016). Reactive responses of zebras to lion encounters shape their predator–prey space game at large scale. *Oikos*, 125, 829–838. <https://doi.org/10.1111/oik.02555>
- Cozzi, G., Maag, N., Börger, L., Clutton-Brock, T. H., & Ozgul, A. (2018). Socially informed dispersal in a territorial cooperative breeder. *Journal of Animal Ecology*, 87, 838–849. <https://doi.org/10.1111/1365-2656.12795>
- Creel, S. (2018). The control of risk hypothesis: Reactive vs. proactive antipredator responses and stress-mediated vs. food-mediated costs of response. *Ecology Letters*. <https://doi.org/10.1111/ele.12975>
- Creel, S., Dröge, E., M'soka, J., Smit, D., Becker, M., Christianson, D., & Schuette, P. (2017). The relationship between direct predation and antipredator responses: A test with multiple predators and multiple prey. *Ecology*, 98, 2081–2092. <https://doi.org/10.1002/ecs.1885>
- Creel, S., Schuette, P., & Christianson, D. (2014). Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behavioral Ecology*, 25, 773–784. <https://doi.org/10.1093/beheco/aru050>
- Creel, S., Winnie, J. A., & Christianson, D. (2013). Underestimating the frequency, strength and cost of antipredator responses with data from GPS collars: An example with wolves and elk. *Ecology and Evolution*, 3, 5189–5200. <https://doi.org/10.1002/ece3.896>
- Creel, S., Winnie, J. A., Christianson, D., & Liley, S. (2008). Time and space in general models of antipredator response: Tests with wolves and elk. *Animal Behaviour*, 76, 1139–1146. <https://doi.org/10.1016/j.anbehav.2008.07.006>
- Creel, S., Winnie, J. Jr, Maxwell, B., Hamlin, K., & Creel, M. (2005). Elk alter habitat selection as an antipredator response to wolves. *Ecology*, 86, 3387–3397. <https://doi.org/10.1890/05-0032>
- Cusack, J. J., Kohl, M. T., Metz, M. C., Coulson, T., Stahler, D. R., Smith, D. W., & MacNulty, D. R. (2019). Data from: Weak spatiotemporal response of prey to predation risk in a freely interacting system. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.tp546d7>
- Despain, D. G. (1990). *Yellowstone vegetation: Consequences of environment and history in a natural setting*. Boulder, CO: Roberts Rinehart Publishers.
- Dröge, E., Creel, S., Becker, M. S., & M'soka, J. (2017). Risky times and risky places interact to affect prey behaviour. *Nature Ecology and Evolution*. <https://doi.org/10.1038/s41559-017-0220-9>
- Dupuch, A., Magnan, P., Bertolo, A., Dill, L. M., & Proulx, M. (2009). Does predation risk influence habitat use by northern redbelly dace

- Phoxinus eos* at different spatial scales? *Journal of Fish Biology*, 74, 1371–1382. <https://doi.org/10.1111/j.1095-8649.2009.02183.x>
- Elgar, M. A. (1989). Predator vigilance and group size in mammals and birds: A critical review of the empirical evidence. *Biological Reviews*, 64, 13–33. <https://doi.org/10.1111/j.1469-185X.1989.tb00636.x>
- Fieberg, J. (2007). Kernel density estimators of home range: Smoothing and the autocorrelation red herring. *Ecology*, 88, 1059–1066. <https://doi.org/10.1890/06-0930>
- Fieberg, J., & Kochanny, C. O. (2005). Quantifying home-range overlap: The importance of the utilization distribution. *Journal of Wildlife Management*, 69, 1346–1359. [https://doi.org/10.2193/0022-541X\(2005\)69\[1346:QHOTIO\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2005)69[1346:QHOTIO]2.0.CO;2)
- Forester, J. D., Ives, A. R., Turner, M. G., Anderson, D. P., Fortin, D., Beyer, H. L., ... Boyce, M. S. (2007). State–space models link elk movement patterns to landscape characteristics in Yellowstone National Park. *Ecological Monographs*, 77, 285–299. <https://doi.org/10.1890/06-0534>
- Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., & Mao, J. S. (2005). Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, 86, 1320–1330. <https://doi.org/10.1890/04-0953>
- Fryxell, J. M., Mosser, A., Sinclair, A. R., & Packer, C. (2007). Group formation stabilizes predator–prey dynamics. *Nature*, 449, 1041–1043. <https://doi.org/10.1038/nature06177>
- Gehr, B., Hofer, E. J., Ryser, A., Vimercati, E., Vogt, K., & Keller, L. F. (2018). Evidence for nonconsumptive effects from a large predator in an ungulate prey? *Behavioral Ecology*, 29, 724–735. <https://doi.org/10.1093/beheco/ary031>
- Gotelli, N. J., & Graves, G. R. (1996). *Null models in ecology*. Washington, DC: Smithsonian Institution Press.
- Gower, C. N., Garrott, R. A., White, P. J., Watson, F. G., Cornish, S. S., & Becker, M. S. (2008). Spatial responses of elk to wolf predation risk: Using the landscape to balance multiple demands. In R. A. Garrott, P. J. White, & F. G. R. Watson (Eds.), *The ecology of large mammals in central Yellowstone: Sixteen years of integrated field studies* (pp. 373–400). San Diego, CA: Elsevier Academic Press. [https://doi.org/10.1016/S1936-7961\(08\)00218-2](https://doi.org/10.1016/S1936-7961(08)00218-2)
- Hebblewhite, M., & Pletscher, D. H. (2002). Effects of elk group size on predation by wolves. *Canadian Journal of Zoology*, 80, 800–809. <https://doi.org/10.1139/z02-059>
- Heithaus, M. R., & Dill, L. M. (2002). Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology*, 83, 480–491. [https://doi.org/10.1890/0012-9658\(2002\)083\[0480:FAATSP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[0480:FAATSP]2.0.CO;2)
- Heithaus, M. R., Wirsing, A. J., Burkholder, D., Thomson, J., & Dill, L. M. (2009). Towards a predictive framework for predator risk effects: The interaction of landscape features and prey escape tactics. *Journal of Animal Ecology*, 78, 556–562. <https://doi.org/10.1111/j.1365-2656.2008.01512.x>
- Hernández, L., & Laundré, J. W. (2005). Foraging in the ‘landscape of fear’ and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *Bison bison*. *Wildlife Biology*, 11, 215–220. [https://doi.org/10.2981/0909-6396\(2005\)11\[215:FITLOF\]2.0.CO;2](https://doi.org/10.2981/0909-6396(2005)11[215:FITLOF]2.0.CO;2)
- Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, 6, 65–70.
- Hopcraft, J. G. C., Sinclair, A. R. E., & Packer, C. (2005). Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*, 74, 559–566. <https://doi.org/10.1111/j.1365-2656.2005.00955.x>
- Horne, J. S., Garton, E. O., Krone, S. M., & Lewis, J. S. (2007). Analyzing animal movements using Brownian bridges. *Ecology*, 88, 2354–2363. <https://doi.org/10.1890/06-0957.1>
- Houston, D. G. (1982). *The northern Yellowstone elk: Ecology and management*. New York, NY: Macmillan Publishing.
- Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 61, 65–71. <https://doi.org/10.2307/1937156>
- Kauffman, M. J., Varley, N., Smith, D. W., Stahler, D. R., MacNulty, D. R., & Boyce, M. S. (2007). Landscape heterogeneity shapes predation in a newly restored predator–prey system. *Ecology Letters*, 10, 690–700. <https://doi.org/10.1111/j.1461-0248.2007.01059.x>
- Kernohan, B. J., Gitzen, R. A., & Millspaugh, J. J. (2001). Analysis of animal space use and movements. In J. J. Millspaugh & J. M. Marzluff (Eds.), *Radiotracking and animal populations* (pp. 125–166). San Diego, CA: Academic Press. <https://doi.org/10.1016/B978-012497781-5/50006-2>
- Kittle, A. M., Fryxell, J. M., Desy, G. E., & Hamr, J. (2008). The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates. *Oecologia*, 157, 163–175. <https://doi.org/10.1007/s00442-008-1051-9>
- Kohl, M. T., Stahler, D. R., Metz, M. C., Forester, J. D., Kauffman, M. J., Varley, N., ... MacNulty, D. R. (2018). Diel predator activity drives a dynamic landscape of fear. *Ecological Monographs*. <https://doi.org/10.1002/ecm.1313>
- Latombe, G., Fortin, D., & Parrott, L. (2014). Spatio-temporal dynamics in the response of woodland caribou and moose to the passage of grey wolf. *Journal of Animal Ecology*, 83, 185–198. <https://doi.org/10.1111/1365-2656.12108>
- Liley, S., & Creel, S. (2007). What best explains vigilance in elk: Characteristics of prey, predators, or the environment? *Behavioural Ecology*, 19, 245–254. <https://doi.org/10.1093/beheco/arm116>
- Lima, S. L. (1998). Nonlethal effects in the ecology of predator–prey interactions. *BioScience*, 48(1), 25–34. <https://doi.org/10.2307/1313225>
- Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, 68, 619–640. <https://doi.org/10.1139/z90-092>
- Long, J. A., Nelson, T. A., Webb, S. L., & Gee, K. L. (2014). A critical examination of indices of dynamic interaction for wildlife telemetry studies. *Journal of Animal Ecology*, 83, 1216–1233. <https://doi.org/10.1111/1365-2656.12198>
- MacNulty, D. R. (2002). *The predatory sequence and the influence of injury risk on hunting behavior in the wolf*. Thesis, University of Minnesota, Minneapolis and St. Paul.
- MacNulty, D. R., Mech, L. D., & Smith, D. W. (2007). A proposed ethogram of large-carnivore predatory behavior, exemplified by the wolf. *Journal of Mammalogy*, 88, 595–605. <https://doi.org/10.1644/06-MAMM-A-119R1.1>
- MacNulty, D. R., Smith, D. W., Mech, L. D., Vucetich, J. A., & Packer, C. (2012). Nonlinear effects of group size on the success of wolves hunting elk. *Behavioural Ecology*, 23, 75–82. <https://doi.org/10.1093/beheco/arr159>
- MacNulty, D. R., Stahler, D. R., Wyman, C. T., Ruprecht, J., & Smith, D. W. (2016). The challenge of understanding northern Yellowstone elk dynamics after wolf reintroduction. *Yellowstone Science*, 24, 25–33.
- Mao, J. S., Boyce, M. S., Smith, D. W., Singer, F. J., Vales, D. J., Vore, J. M., & Merrill, E. H. (2005). Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. *Journal of Wildlife Management*, 69, 1691–1707. [https://doi.org/10.2193/0022-541X\(2005\)69\[1691:HSBEBA\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2005)69[1691:HSBEBA]2.0.CO;2)
- Martin, J., & Owen-Smith, N. (2016). Habitat selectivity influences the reactive responses of African ungulates to encounters with lions. *Animal Behaviour*, 116, 163–170. <https://doi.org/10.1890/08-0606.1>
- Mech, L. D., Smith, D. W., & MacNulty, D. R. (2015). *Wolves on the hunt: The behavior of wolves hunting wild prey*. Chicago, IL: University of Chicago Press. <https://doi.org/10.7208/chicago/9780226255286.001.0001>
- Middleton, A. D., Kauffman, M. J., McWhirter, D. E., Jimenez, M. D., Cook, R. C., Cook, J. G., ... White, P. J. (2013). Linking anti-predator behaviour to prey demography reveals limited risk effects of an actively hunting large carnivore. *Ecology Letters*, 16, 1023–1030. <https://doi.org/10.1111/ele.12133>
- Miller, J. A. (2015). Towards a better understanding of dynamic interaction metrics for wildlife: A null model approach. *Transactions in GIS*, 19, 342–361. <https://doi.org/10.1111/tgis.12149>

- Mitchell, W. A., & Lima, S. L. (2002). Predator-prey shell games: Large-scale movement and its implications for decision-making by prey. *Oikos*, 99, 249–259. <https://doi.org/10.1034/j.1600-0706.2002.990205.x>
- Moll, R. J., Redilla, K. M., Mudumba, T., Muneza, A. B., Gray, S. M., Abade, L., ... Montgomery, R. M. (2017). The many faces of fear: A synthesis of the methodological variation in characterizing predation risk. *Journal of Animal Ecology*, 86, 749–765. <https://doi.org/10.1111/1365-2656.12680>
- Padié, S., Morellet, N., Hewison, A. M., Martin, J. L., Bonnot, N., Cargnelutti, B., & Chamaillé-Jammes, S. (2015). Roe deer at risk: Teasing apart habitat selection and landscape constraints in risk exposure at multiple scales. *Oikos*, 124, 1536–1546. <https://doi.org/10.1111/oik.02115>
- Painter, L. E., Beschta, R. L., Larsen, E. J., & Ripple, W. J. (2018). Aspen recruitment in the Yellowstone region linked to reduced herbivory after large carnivore restoration. *Ecosphere*, 9, e02376. <https://doi.org/10.1002/ecs2.2376>
- Palmer, M. S., Fieberg, J., Swanson, A., Kosmala, M., & Packer, C. (2017). A 'dynamic' landscape of fear: Prey responses to spatiotemporal variations in predation risk across the lunar cycle. *Ecology Letters*, 20, 1364–1373. <https://doi.org/10.1111/ele.12832>
- Proffitt, K. M., Grigg, J., Hamlin, K., & Garrott, R. A. (2009). Contrasting effects of wolves and human hunters on elk behavioural responses to predation risk. *Journal of Wildlife Management*, 73, 345–356. <https://doi.org/10.2193/2008-210>
- Prugh, L. R., & Golden, C. D. (2014). Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. *Journal of Animal Ecology*, 83, 504–514. <https://doi.org/10.1111/1365-2656.12148>
- R Development Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. www.rproject.org
- Richard, E., Calenge, C., Saïd, S., Hamann, J., & Gaillard, J. M. (2013). Studying spatial interactions between sympatric populations of large herbivores: A null model approach. *Ecography*, 36, 157–165. <https://doi.org/10.1111/j.1600-0587.2012.07604.x>
- Ripple, W. J., & Beschta, R. L. (2012). Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. *Biological Conservation*, 145, 205–213. <https://doi.org/10.1016/j.biocon.2011.11.005>
- Searle, K. R., Stokes, C. J., & Gordon, I. J. (2008). When foraging and fear meet: Using foraging hierarchies to inform assessments of landscapes of fear. *Behavioural Ecology*, 19, 475–482. <https://doi.org/10.1093/beheco/arn004>
- Shirabe, T. (2006). Correlation analysis of discrete motions. In M. Raubal, H. J. Miller, A. U. Frank, & M. F. Goodchild (Eds.), *GIScience 2006, LNCS 4197* (pp. 370–382). Berlin, Germany: Springer-Verlag.
- Sih, A. (1984). The behavioural response race between predator and prey. *The American Naturalist*, 123, 143–150. <https://doi.org/10.1086/284193>
- Sih, A. (1998). Game theory and predator-prey response races. In L. A. Dugatkin & H. K. Reeve (Eds.), *Game theory and animal behaviour* (pp. 221–238). Oxford, UK: Oxford University Press.
- Sih, A. (2005). Predator-prey space use as an emergent outcome of a behavioral response race. In P. Barbosa & I. Castellanos (Eds.), *Ecology of predator-prey interactions* (pp. 240–255). Oxford, UK: Oxford University Press.
- Smith, D. W., & Bangs, E. E. (2009). Reintroduction of wolves to Yellowstone National Park: History, values, and ecosystem restoration. In M. W. Hayward & M. J. Somers (Eds.), *Reintroduction of top-order predators* (pp. 92–125). Oxford, UK: Wiley-Blackwell. <https://doi.org/10.1002/9781444312034>
- Smith, D. W., Drummer, T. D., Murphy, K. M., Guernsey, D. S., & Evans, S. B. (2004). Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995–2000. *Journal of Wildlife Management*, 68, 153–166. [https://doi.org/10.2193/0022-541X\(2004\)068\[0153:WPSAEO\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2004)068[0153:WPSAEO]2.0.CO;2)
- Smith, D. W., Stahler, D. R., Cassidy, K., Stahler, E., Metz, M. C., Cassidy, B., ... Cato, E. (2018). Yellowstone National Park Wolf Project Annual Report 2017. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, WY, USA, YCR-2018-03.
- Tallian, A., Smith, D. W., Stahler, D. R., Metz, M. C., Wallen, R. L., Geremia, C., ... MacNulty, D. R. (2017). Predator foraging response to a resurgent dangerous prey. *Functional Ecology*, 31, 1418–1429. <https://doi.org/10.1111/1365-2435.12866>
- Thaker, M., Vanak, A. T., Owen, C. R., Ogden, M. B., Niemann, S. M., & Slotow, R. (2011). Minimizing predation risk in a landscape of multiple predators: Effects on the spatial distribution of African ungulates. *Ecology*, 92, 398–407. <https://doi.org/10.1890/10-0126.1>
- Thurfjell, H., Ciuti, S., & Boyce, M. S. (2014). Applications of step-selection functions in ecology and conservation. *Movement Ecology*, 2, 4. <https://doi.org/10.1186/2051-3933-2-4>
- Uboni, A., Smith, D. W., Mao, J. S., Stahler, D. R., & Vucetich, J. A. (2015). Long-and short-term temporal variability in habitat selection of a top predator. *Ecosphere*, 6, 1–16. <https://doi.org/10.1890/ES14-00419.1>
- Valeix, M., Loveridge, A. J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., ... Macdonald, D. W. (2009). Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use. *Ecology*, 90, 23–30. <https://doi.org/10.1890/08-0606.1>
- White, P. J., & Garrott, R. A. (2005). Northern Yellowstone elk after wolf restoration. *Wildlife Society Bulletin*, 33, 942–955. [https://doi.org/10.2193/0091-7648\(2005\)33\[942:NYEAWR\]2.0.CO;2](https://doi.org/10.2193/0091-7648(2005)33[942:NYEAWR]2.0.CO;2)
- White, P. J., Garrott, R. A., Cherry, S., Watson, F. G., Gower, C. N., Becker, M. S., & Meredith, E. (2008). Changes in elk resource selection and distribution with the reestablishment of wolf predation risk. *Terrestrial Ecology*, 3, 451–476. [https://doi.org/10.1016/S1936-7961\(08\)00221-2](https://doi.org/10.1016/S1936-7961(08)00221-2)
- White, P. J., Proffitt, K. M., & Lemke, T. O. (2012). Changes in elk distribution and group sizes after wolf restoration. *The American Midland Naturalist*, 167, 174–187. <https://doi.org/10.1674/0003-0031-167.1.174>
- White, P. J., Proffitt, K. M., Mech, L. D., Evans, S. B., Cunningham, J. A., & Hamlin, K. L. (2010). Migration of northern Yellowstone elk: implications of spatial structuring. *Journal of Mammalogy*, 91, 827–837. <https://doi.org/10.1644/08-MAMM-A-252.1>
- Winnie, J. Jr, & Creel, S. (2017). The many effects of carnivores on their prey and their implications for trophic cascades, and ecosystem structure and function. *Food Webs*, 12, 88–94. <https://doi.org/10.1016/j.fooweb.2016.09.002>
- Wood, S. N. (2006). *Generalized additive models: An introduction with R*. London, UK: Chapman and Hall/CRC. <https://doi.org/10.1201/9781420010404>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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