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Diel predator activity drives a dynamic landscape of fear

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Abstract. A “landscape of fear” (LOF) is a map that describes continuous spatial variation in an animal’s perception of predation risk. The relief on this map reflects, for example, places that an animal avoids to minimize risk. Although the LOF concept is a potentially unifying theme in ecology that is often invoked to explain the ecological and conservation significance of fear, little is known about the daily dynamics of an LOF. Despite theory and data to the contrary, investigators often assume, implicitly or explicitly, that an LOF is a static consequence of a predator’s mere presence within an ecosystem. We tested the prediction that an LOF in a large-scale, free-living system is a highly dynamic map with “peaks” and “valleys” that alternate across the diel (24-h) cycle in response to daily lulls in predator activity. We did so with extensive data from the case study of Yellowstone elk (*Cervus elaphus*) and wolves (*Canis lupus*) that was the original basis for the LOF concept. We quantified the elk LOF, defined here as spatial allocation of time away from risky places and times, across nearly 1,000-km² of northern Yellowstone National Park and found that it fluctuated with the crepuscular activity pattern of wolves, enabling elk to use risky places during wolf downtimes. This may help explain evidence that wolf predation risk has no effect on elk stress levels, body condition, pregnancy, or herbivory. The ability of free-living animals to adaptively allocate habitat use across periods of high and low predator activity within the diel cycle is an underappreciated aspect of animal behavior that helps explain why strong antipredator responses may trigger weak ecological effects, and why an LOF may have less conceptual and practical importance than direct killing.

Key words: antipredator behavior; diel activity; elk; habitat selection; landscape of fear (LOF); predation risk; predator activity rhythm; predator–prey interaction; wolf; Yellowstone.

INTRODUCTION

Fear of predation (perceived predation risk) caused by the mere presence of a predator within an ecosystem is increasingly regarded as an ecological force that rivals or exceeds that of direct killing (Preisser et al. 2005). The “landscape of fear” (LOF) concept has been advanced as a general mechanism that drives the effects of fear that cascade from individuals to ecosystems (Brown and Kotler 2004, Schmitz 2005, Laundré et al. 2010), including changes in prey physiology (Zanette et al. 2014) and demography (Preisser et al. 2007), plant growth (Ford et al. 2014), and nutrient cycling (Hawlena et al. 2012). Operationally, an LOF is a map that describes the continuous change in predation risk that an animal perceives as it navigates the physical landscape (Brown and Kotler 2004, Laundré et al. 2001, 2010). This mental map of risk overlies the physical terrain like a map of soils, vegetation, or climate, and its “peaks” and “valleys” describe an animal’s perception of those locations as dangerous and safe, respectively (van der Merwe and Brown 2008). Risk perception is indexed by an animal’s measurable response to changes in predation risk (Lima and Steury 2005), and the continuous spatial patterning of this response approximates

an LOF as originally defined by Laundré et al. (2001, 2010). Brown and Kotler (2004) defined the concept more narrowly as the spatial distribution of the foraging cost of predation, which is fear measured as the energetic consequence of an animal’s response, chiefly vigilance and/or time allocation. No matter its definition, the LOF concept is often invoked to explain the ecological effects of fear.

Yet little is known about LOF dynamics across the diel (24-h) cycle. To date, many ecologists have, implicitly or explicitly, assumed that an LOF is a fixed spatial pattern as long as the predator is present (but see Palmer et al. 2017). The underlying rationale is that a constant possibility of predation enforces a chronic state of apprehension in the prey (Schmitz et al. 1997, Brown et al. 1999). This “fixed-risk” assumption of constant attack over time has been a conceptual mainstay in the study of behavioral predator–prey interactions for decades (Lima 2002). Yet it neglects how predator activity and hunting ability can vary across the diel cycle, and how this may foster a fluctuating acute state of apprehension in the prey and a dynamic LOF despite the constant presence of predators.

Many predators are only active at certain times of day, and visual predators active at night often cannot hunt in absolute darkness. These predatory constraints provide pulses of safety during the diel cycle that may temporarily relieve an animal’s fear of predation and flatten its LOF. This hypothesis is broadly consistent with risk allocation theory, which

predicts that animals constantly exposed to predators should respond to pulses of safety with intense feeding efforts (Lima and Bednekoff 1999). It also accords with numerous empirical studies that show how various animals (e.g., zooplankton, rodents, and ungulates) forage in risky places during periods of the diel cycle (e.g., day or night) associated with reduced predator activity and/or hunting ability (reviewed by Lima and Dill 1990, Lima 1998, Brown and Kotler 2004, Caro 2005, see also Fischhoff et al. 2007, Tambling et al. 2012, Burkpile et al. 2013). However, these studies neither tested how animal response to spatial risk is linked to measured variation in diel predator behavior, nor showed how this linkage shapes the animal's LOF across the diel cycle. Dichotomizing continuous variation in diel predator behavior into periods of presumed safety and danger (e.g., day vs. night) is potentially misleading if diel behavior does not conform to these simple categories or if animals assess predation risk as a continuous variable (Creel 2011).

This empirical gap in the LOF concept is exemplified by its founding case study of elk (*Cervus elaphus*) in northern Yellowstone National Park (YNP) following wolf (*Canis lupus*) reintroduction there in 1995–1997 (Laundré et al. 2001). Although this case is frequently cited as a well-understood example of an LOF, and is one that has motivated the proposal that the LOF is a unifying concept in ecology (Laundré et al. 2010), researchers never quantified the elk LOF after wolf reintroduction, nor examined its temporal dynamics in relation to diel wolf behavior. Instead, the elk LOF was inferred from broad-scale, population-level data on vigilance behavior (Laundré et al. 2001), fecal pellets (Hernández and Laundré 2005), and herbivory (Ripple and Beschta 2004) that supported three predictions based on the LOF concept: (1) elk shifted habitat use in response to wolves, including abandonment of high-risk open areas, which (2) decreased diet quality and body fat, and (3) reduced browsing on woody deciduous plants in high risk areas (Laundré et al. 2001, 2010). Some researchers have argued that habitat shifts also reduced elk pregnancy rate (Creel et al. 2009, Christianson and Creel 2014). On the other hand, concurrent fine-scale, individual-level data on movement, body condition, and pregnancy rate indicated elk selected for open areas (Fortin et al. 2005, Mao et al. 2005) and maintained body fat and pregnancy rate (Cook et al. 2004, White et al. 2011, Proffitt et al. 2014). And whereas one study suggested elk avoided aspen (*Populus tremuloides*) forests in response to wolves (Fortin et al. 2005), another found that elk browsed aspen irrespective of wolf predation risk (Kauffman et al. 2010). These divergent results have yet to be reconciled, and together they highlight an outstanding need to clarify the elk LOF that prevailed in YNP during the initial years after wolf reintroduction.

The overarching purpose of this study was to improve the empirical foundation of the LOF concept. Our objective was to determine how a large-scale LOF changes across the diel cycle in response to the daily activity pattern of a predator that is always present. Because the response of Yellowstone elk to wolf reintroduction is a seminal yet unresolved example of an LOF, we examined the elk LOF in northern YNP within the first decade after wolves were released.

We defined the elk LOF as spatial allocation of time away from risky places and times. This conforms to Laundré

et al.'s (2001, 2010) broad definition and approximates Brown and Kotler's (2004) narrower definition. The latter is possible because research indicates that Yellowstone elk manage wolf predation risk mainly through time allocation, keeping vigilance levels constant across habitats that vary in predation risk (e.g., near versus far from forest cover) and increasing vigilance only when wolves are an immediate threat (Childress and Lung 2003, Lung and Childress 2007, Winnie and Creel 2007, Creel et al. 2008, Liley and Creel 2008, Gower et al. 2009, Middleton et al. 2013a).

To assess spatial time allocation, we conducted a retrospective habitat selection analysis of data collected during 2001–2004 from 27 female elk equipped with global positioning system (GPS) radio collars. This included 13 unique elk from Fortin et al. (2005), 2 more from Boyce et al. (2003), 1 more from Forester et al. (2007, 2009), and 11 more whose data were never published. Together, these were the first elk GPS location data ever collected in YNP, and we used them to quantify the elk LOF across 995-km² of northern YNP. We tested how this large-scale LOF varied across the diel cycle in relation to the daily activity pattern of wolves, which we estimated from direct observations of hunting behavior (1995–2003) and GPS location data (2004–2013). We predicted a dynamic LOF with peaks and valleys that alternated across the diel cycle in response to daily lulls in wolf activity.

METHODS

Study area

Our study occurred in a 995-km² area of northern YNP (44°56' N, 110°24' W) where the climate is characterized by short, cool summers and long, cold winters (Houston 1982). Low elevations (1,500–2,000 m) in the area create the warmest and driest conditions in YNP, providing important winter range for ungulates, including elk. Vegetation includes montane forest (44%; e.g., lodgepole pine [*Pinus contorta*] and Douglas fir [*Pseudotsuga menziesii*]), open sagebrush-grassland (37%; e.g., Idaho fescue [*Festuca idahoensis*], blue-bunch wheatgrass [*Pseudoroegneria spicata*], and big sagebrush [*Artemisia tridentata*]), upland grasslands, wet meadows, and non-vegetated areas (19%; Despain 1990).

Study population

We analyzed habitat selection behavior of 27 adult (>1 yr old) female elk that spent winter in northern YNP and adjoining areas of the Yellowstone River valley outside YNP from about 15 October to 31 May 2001–2004. These elk were from a migratory population that numbered from 8,300 to 13,400 individuals. Our sample of adult female elk was captured in February (2001–2003) via helicopter net-gunning (Hawkins and Powers, Greybull, Wyoming, USA; Leading Edge Aviation, Lewiston, Idaho, USA) and fitted with Telonics (Mesa, Arizona, USA) or Advanced Telemetry Systems (Isanti, Minnesota, USA) GPS radio collars ($\bar{x} \pm \text{SD}$ location error = 6.15 ± 5.24 m; Forester et al. 2007) programmed to collect locations at 4–6 h intervals (5 h intervals, $n = 23$; alternating between 4 and 6 h intervals, $n = 4$). To control for movements associated with

migratory behavior, we limited our analysis to winter locations collected from 1 November to 30 April. If individuals arrived on the winter range after 1 November, data were censored to the individual's arrival date (1–22 November). Location data for each individual were collected for 30–353 d ($\bar{x} \pm \text{SD} = 124.5 \pm 12.5$) across 1–3 winters until collar failure, collar removal, or animal death. We censored location data to include only high-quality locations following guidelines developed by Forester et al. (2009).

Elk age was estimated using cementum analysis of an extracted vestigial upper canine (Hamlin et al. 2000), and pregnancy was determined from a serum sample using the pregnancy-specific protein B assay (Sasser et al. 1986, Noyes et al. 1997, White et al. 2011). We evaluated elk nutritional condition with a rump body condition score developed for elk and maximum subcutaneous rump fat thickness measured using an ultrasonograph (Cook et al. 2004). We estimated ingesta-free body fat percentage using the scaled LIVINDEX, which is an arithmetic combination of the rump body condition score and maximum rump fat thickness allometrically scaled using body mass estimated from chest girth measurements (Cook et al. 2004).

Wolves in this study were members or descendants of a population of 41 radio-collared wolves reintroduced to YNP in 1995–1997 (Bangs and Fritts 1996). The study occurred during a time of peak wolf abundance in YNP: wolf numbers in northern YNP ranged from 70–98 individuals in four to eight packs (Cubaynes et al. 2014). Each winter, 20–30 wolves, including 30–50% of pups born the previous year, were captured and radio-collared (Smith et al. 2004). Wolves were fitted with very high frequency (VHF; Telonics, Mesa, Arizona, USA) or GPS (Televilt, Lindesberg, Sweden; Lotek, Newmarket, Ontario, Canada) radio collars. Locations of VHF- and GPS-collared wolves were recorded approximately daily during two 30-d periods in early (mid-November to mid-December) and late (March) winter, when wolf packs were intensively monitored from the ground and fixed-wing aircraft, and approximately weekly during the rest of the year. Wolf GPS collars recorded locations every hour during the 30-d periods and at variable intervals outside these periods. The proportion of the Yellowstone wolf population that was radio-collared ranged from 35–40% and included all wolf packs in the study area. We captured and handled wolves and elk following protocols in accord with applicable guidelines from the American Society of Mammalogists (Sikes 2016) and approved by the National Park Service Institutional Animal Care and Use Committee.

Diel activity patterns

We used movement rate to index diel wolf activity given that speed of locomotion is a valid proxy for diel activity patterns in large mammals (Ensing et al. 2014). We estimated movement rate at each hour of the day from the hourly positions of 21 GPS-collared wolves recorded in northern YNP during early and late winter, 2004–2013. Wolf GPS data were unavailable prior to 2004. Movement rate equaled the average Euclidean distance of the preceding 1- or 5-h time step. We used hourly movement rate (km/h) to describe the diel pattern in wolf activity and 5-h movement rate (km/5-h) to test how diel wolf activity influenced elk

selection of safe and risky places. We used 5-h movement rate in the habitat selection analysis to match the 5-h time interval between consecutive elk locations. To generalize the 1-h data to 5-h data, we retained every fifth location beginning with the first 5-h location available. We used only consecutive 1- or 5-h locations to calculate movement rates.

We estimated the population-level pattern in diel movement rate with generalized additive mixed models (GAMMs) separately fitted to the 1- and 5-h locations using the mgcv package (version 1.8.0) in R 3.2.3. Because movement data were heavily right skewed (Fortin et al. 2005), we fit the GAMM using the negative binomial family and incorporated performance iterations such that the scale parameter was as close to 1 as possible. We applied a cyclic cubic regression spline so that the first and last hour of the day matched in accordance with the diel cycle. We included a random intercept for individual identity to account for repeated measurements of individuals across the study.

Each wolf provided an independent measure of movement rate because it was solitary or the sole GPS-collared wolf in a pack, or rarely associated with other GPS-collared pack members. The latter was limited to three pairs of GPS-collared wolves that were nominally in the same pack during a 30-d period. The proportion of simultaneous fixes that wolves in each pair were near each other (<2 km) was low: 3%, 6%, and 22%. We could not distinguish between individual and annual variation in wolf diel activity patterns because the number of individuals sampled within years was too small (Appendix S1: Table S1). Thus, our estimate of diel activity is a population-level estimate calculated as a univariate function of time of day. It is also a seasonal average that subsumes an approximate 3-h shift in the timing of dawn and dusk between 1 November and 30 April that may add variation to hourly measurements of activity. We used this same approach to model the average winter diel activity pattern of GPS-collared elk, which we did for illustrative purposes. All of our major inferences were based on analyses of elk habitat selection.

We used the estimated 5-h wolf movement rate as the covariate for diel wolf activity in the habitat selection analysis. We checked that our estimate of diel wolf activity was a valid index of diel hunting pressure during the study period by comparing mean 1-h diel movement rate to the hourly distribution of directly observed daylight (07:00–20:00 hours) encounters between wolves and elk in winter from 1995–2003. These behavioral data were independent of the wolf GPS data we used to calculate diel activity. An encounter was defined as wolves approaching, harassing, chasing, and (or) grabbing elk. Details about how we observed and recorded wolf-elk encounters are described elsewhere (MacNulty et al. 2007).

A concurrent cause-specific mortality study established that wolves were the primary predator of our sample of adult female elk; only one case of cougar-caused mortality was documented (Evans et al. 2006). Analyses of wolf-killed prey during our study period also revealed that elk comprised 90–96% of prey species killed by wolves during winter (Smith et al. 2004, Metz et al. 2012). Together, these studies indicate that the opportunity to kill elk was a key driver of wolf activity in our study area during the study period (2001–2004).

Spatial variation in wolf predation risk

We considered multiple indices of spatial variation in wolf predation risk because it is unclear how elk perceive spatial risk (Beschta and Ripple 2013, Kauffman et al. 2013, Moll et al. 2017). We calculated four indices of spatial risk: predicted occurrence of wolf-killed elk (Kauffman et al. 2007, 2010), density of wolf-killed elk (Gude et al. 2006), openness (Creel et al. 2005, Fortin et al. 2005, Mao et al. 2005), and wolf density (Fortin et al. 2005, Mao et al. 2005, Forester et al. 2007). Kill sites are a well-established metric of predation risk in wildlife systems (Hopcraft et al. 2005, Thaker et al. 2011, Gervasi et al. 2013, Lone et al. 2014). All spatial risk indices (30 × 30 m grid cell) were developed using the Geospatial Modelling Environment or ArcGIS 10.1.

Predicted kill occurrence.—We used a previously published model to predict the spatial distribution of wolf-killed elk in northern YNP during each winter of our study (Fig. 1a). Kauffman et al. (2007) developed this model to understand elk response to wolf predation risk in northern YNP. It estimates the relative probability of a kill on the landscape compared to random locations based on the landscape attributes of 774 locations of wolf-killed elk. These kills included all age and sex classes and were documented in winter during a period (1996–2005) that encompassed the present study. Landscape attributes included annual distribution of wolf packs (based on cumulative kernel densities weighted by pack size), relative elk density (from an elk habitat model; Mao et al. 2005), proximity to streams, proximity to roads, habitat openness (forest vs. grassland), slope, and snow depth. The model predicts kill occurrence with respect to the average value of each landscape attribute, such that a predicted kill occurrence of 1 equals no difference between

the location of interest and the average landscape, whereas a predicted kill occurrence of 10 equals a kill probability 10 times greater than average for a given year. This produces a year-specific range of values that did not exceed 245 for any year. For example, the range in winter 2000–2001 was 0–36.5, whereas the range in winter 2001–2002 was 0–245.

Kill density.—We used a kernel density estimator (KDE) to estimate the spatial distribution of wolf-killed adult female and calf elk in northern YNP during each winter of our study (Fig. 1b). We excluded kills of adult males because their spatial distribution differed from that of adult females and calves (Pearson's correlation coefficient, $r = 0.39$; Appendix S1: Fig. S1), and we sought to control for possible behavioral responses of adult female elk to sex-specific kill distributions. A total of 235 wolf-killed adult female and calf elk were recorded across the 4 winters (November 2000–April 2004) following established protocols (Smith et al. 2004). The number of kills included in each annual kill density KDE ranged from 44–84. Following previous studies, we used a fixed bandwidth of 3 km (Fortin et al. 2005). Annual kill density KDEs were standardized from 0 to 1.

Openness.—We calculated openness (Fig. 1c) as the sum of non-forested cells within a 500 × 500 m moving window centered on each grid cell (range 0 [dense forest]–289 [open grassland]) following Boyce et al. (2003). We obtained information on the spatial distribution of vegetation types in northern YNP from databases provided by the YNP Spatial Analysis Center. Non-forested pixels were identified from a 1991 vegetation layer, which accounted for vegetative changes following the 1988 fires in and near YNP (Mattson et al. 1998). We used this layer to calculate openness because it permitted direct comparison with contemporaneous

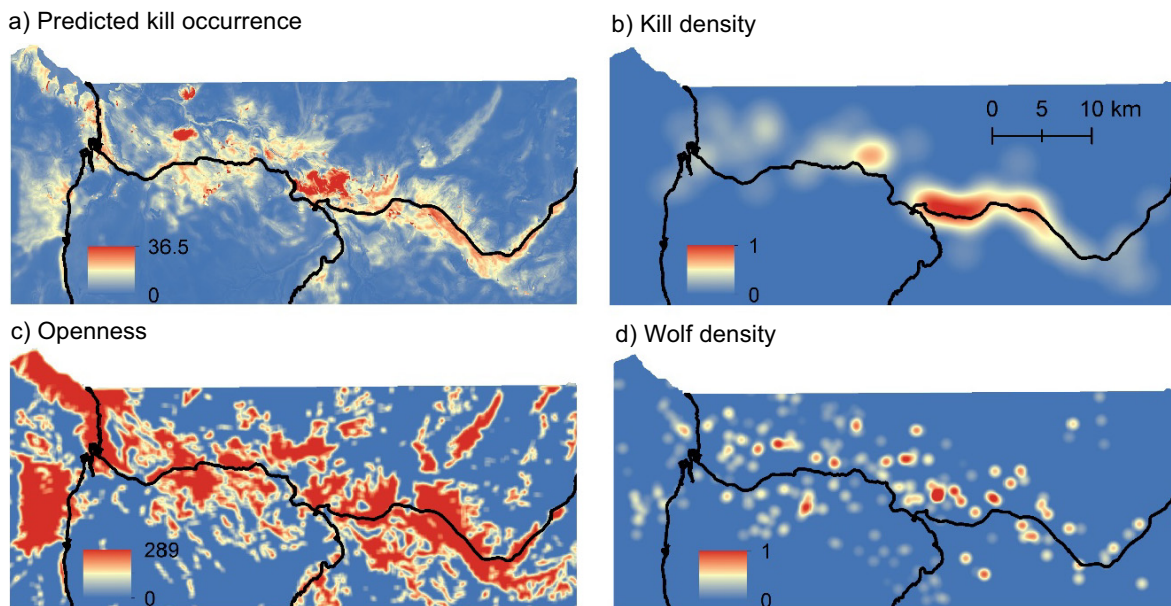


FIG. 1. Spatial variation in wolf predation risk during winter in northern Yellowstone National Park was indexed as (a) predicted occurrence of wolf-killed adult male, adult female, and calf elk, (b) density of wolf-killed adult female and calf elk, (c) openness, and (d) density of wolves. Panels a, b, and d illustrate conditions during the first year of the study (2001). Openness was consistent across years. Black lines denote roads.

northern Yellowstone elk habitat selection studies that also utilized the 1991 vegetation layer (Boyce et al. 2003, Fortin et al. 2005, Mao et al. 2005). We verified that our map of openness was representative of conditions during the study period by comparing it to one calculated from a 2001 LANDFIRE vegetation layer (landfire.gov). We developed and analyzed a single map of openness because there was no inter-annual variation in openness during the study.

Wolf density.—We estimated wolf density (Fig. 1d) from winter aerial wolf telemetry locations that were randomly filtered to obtain a single location per pack per day given that packs often included more than one radio-collared wolf. We calculated a least-squares cross-validation fixed smoothing factor (H) for each pack with at least 25 locations per winter using Animal Space Use 1.3. Using all non-redundant locations, we used mean H (1 km) to calculate annual winter bi-weight kernel densities weighted by pack size (Forester et al. 2007). Annual wolf density KDEs were standardized from 0–1.

Elk habitat selection

We analyzed elk habitat selection using matched case-control logistic regression (CCLR). We used a 1:3 empirical sampling design (Fortin et al. 2005, Forester et al. 2009) where, for each end location of a movement step, three available locations were sampled with replacement from each individual's respective step-length and turning-angle distributions. Each set of four locations defines a unique stratum (k). Successive strata ($k = 10,199$) were not independent. Although this autocorrelation does not affect estimated coefficients it does bias the associated standard errors (Fortin et al. 2005). We calculated robust standard errors by specifying an intragroup correlation in our model (Craiu et al. 2008). Groups were clusters of strata ($n = 1,080$ clusters) assigned sequentially to each individual each winter and defined by a step-lag at which the autocorrelation was nearly zero. Autocorrelation analysis indicated that this step-lag was 15 steps, such that steps separated by 75 h were independent.

We used a CCLR (where each observed step was compared to a sample of available steps that originated from the same starting location) to estimate the parameters of a resource selection function, $\exp(\mathbf{Z}'\boldsymbol{\beta})$, where \mathbf{Z} is a vector of environmental covariates, and $\boldsymbol{\beta}$ is a vector of selection coefficients (Forester et al. 2009, Merkle et al. 2017). The CCLR model describes the relative probability of a movement step, p , which is the straight-line segment between successive locations at 5-h intervals. Movement steps with a higher score relative to the set of possible steps have higher odds of being chosen by an animal (Fortin et al. 2005). The sign of the relationship between p and spatial risk indicates steps toward or away from risky places: a positive relationship indicates steps toward risky places, whereas a negative relationship indicates steps away from risky places. Values of p that depict these relationships reflect different levels of perceived predation risk that correspond to the peaks and valleys in an LOF: minimum values identify peaks (high perceived predation risk) and maximum values identify valleys (low perceived predation risk). We rescaled predicted values of p to present an intuitive visualization of the elk LOF (see *Visualizing the landscape of fear*).

Our step selection model does not estimate behavioral state per se (e.g., rest, forage, and travel) because our data derive from first-generation GPS radio collars that provided only location data. We assume elk were foraging when they selected for open areas because in our system elk are mainly grazers that feed in open grasslands and rest in wooded areas (Houston 1982, Creel et al. 2005, Mao et al. 2005, Christianson and Creel 2007, 2009). Current GPS radio collars that also provide accelerometer data will allow future studies to link step selection with direct estimates of behavioral state (Mosser et al. 2014, Collins et al. 2015).

We could not estimate the main effect of mean 5-h wolf movement rate because it did not vary within a stratum owing to how used and available locations within a stratum share the same point in time. Within the case-control design of our model, spatial risk variables assigned to each of the three control locations came from the same year in which the use location occurred. Because results did not differ between models fitted to all clusters and models fitted to every other independent cluster ($n = 2$ independent data sets), we present results from the analysis of all the clusters.

For each spatial risk index, we developed a 'space-only' habitat selection model and compared it to a 'space \times activity' model that included terms for the interaction between spatial risk and mean 5-h wolf movement rate. The space \times activity model evaluated how elk selection for risky places at the end of a 5-h movement step was affected by the mean wolf movement rate during that step. Because prey may not respond instantaneously to predator activity due to imperfect knowledge (Brown et al. 1999), optimal foraging strategies (Kie 1999), shell games (Mitchell and Lima 2002), large landscapes (Middleton et al. 2013a), or a combination thereof, we evaluated the potential for a behavioral lag in habitat selection up to the preceding behavioral step (i.e., 5 h). We tested different forms of the relationship between habitat selection and spatial risk in the space-only analysis and compared the best-fit space-only model to the best-fit forms in the space \times activity analysis. This was necessary to account for how elk in northern YNP may tolerate low levels of spatial risk (Fortin et al. 2005, Mao et al. 2005). We tested for a response threshold by comparing models with a linear effect for spatial risk to models with a threshold effect specified by two linear splines. We performed a grid search of candidate CCLR models to determine the presence and position of thresholds. To control for outliers, we imposed constraints such that the threshold occurred within 1–99% of all used data points for a given spatial risk index. This resulted in a range of candidate models ($n = 41$ –288) depending on the precision (i.e., decimal units) and scale (i.e., difference in minimum/maximum values) of the spatial risk index. We compared models using the quasi-likelihood under independence criteria (QIC; Pan 2001), which considers independent clusters of observations while also accounting for non-independence between subsequent observations (Craiu et al. 2008).

We performed 1,000 iterations of a five-fold cross validation for case-control design to evaluate the predictive accuracy of each best-fit model (Boyce et al. 2002, Merkle et al. 2017). Location data were partitioned into five equal sets and models were fitted to each 80% partition of the data, while the remaining 20% of the data were withheld for model

evaluation. Within a cross-validation, the estimated probabilities were binned into 10 equal bins and correlated with the observed proportion of movement steps within the evaluation set. This yielded an average Spearman rank correlation (r_s). Correlations >0.70 indicate satisfactory fit of models to data (Boyce et al. 2002). CCLR analyses and k -folds cross validations were performed in R 3.0.2 (R Core Team 2017) using the SURVIVAL and HAB packages, respectively.

Visualizing the landscape of fear

We used predicted values from our best-fit space \times activity step-selection model to visualize the elk LOF in a region of northern YNP that we sampled as available. For simplicity, we focused on a single index of spatial risk: kill density. We calculated the predicted relative probability of a movement step, p , at each level of kill density at each hour of diel wolf activity. We rescaled these values ($1 - p$) and used the results to elevate the two-dimensional kill density layer in ArcScene 10.2 (Esri, Redlands, California, USA). Rescaling was necessary so that higher elevations indicated increasing levels of perceived predation risk as per the LOF concept. We constructed a static visualization at two hours when wolf activity was highest (11:00, 2.80 km/5 h) and lowest (16:00, 1.42 km/5 h), and an animated visualization that showed perceived predation risk at each hour of the diel cycle (00:00–23:00).

RESULTS

Most GPS-collared wolves (19 of 21) were crepuscular such that their hourly movement rates followed: morning $>$ evening $>$ night $>$ day (Fig. 2a). There was less individual-level variation during peak morning hours than during peak evening hours, indicating that morning was a more reliably active period. The population-average pattern in hourly movement rate during 2004–2013 matched the hourly distribution of directly observed daylight wolf encounters with elk ($r = 0.79$; $N = 502$ encounters; Fig. 2a) during 1995–2003. A similar and slightly stronger association was evident when we limited the encounter data to actual kills ($r = 0.87$, $N = 89$ kills). This suggests that diel variation in wolf movement rate was a meaningful index of diel variation in wolf predation risk. It also suggests, together with evidence that the crepuscular pattern in Fig. 2a was consistent across years (Appendix S1: Fig. S2), that the crepuscular pattern during 2004–2013 was representative of the crepuscular pattern during 2001–2004 when elk location data were recorded.

We estimated wolf movement rate as distance travelled per 5 h to match the time interval between consecutive elk locations. This shifted the timing of wolf activity to later in the day but it did not alter the crepuscular pattern (Fig. 2b). The mean diel movement rate (km/5 h) of elk was similarly crepuscular except that the timing of high and low movement rates was opposite that of wolves: elk movement was greatest at dusk and less at dawn (Fig. 2b). Correlation between wolf and elk movement rates was moderate ($r = 0.58$).

Irrespective of diel wolf movement, the influence of spatial risk on elk habitat selection was inescapably nonlinear. For each spatial risk index, the best-fit space-only model included a linear spline for spatial risk (Appendix S1:

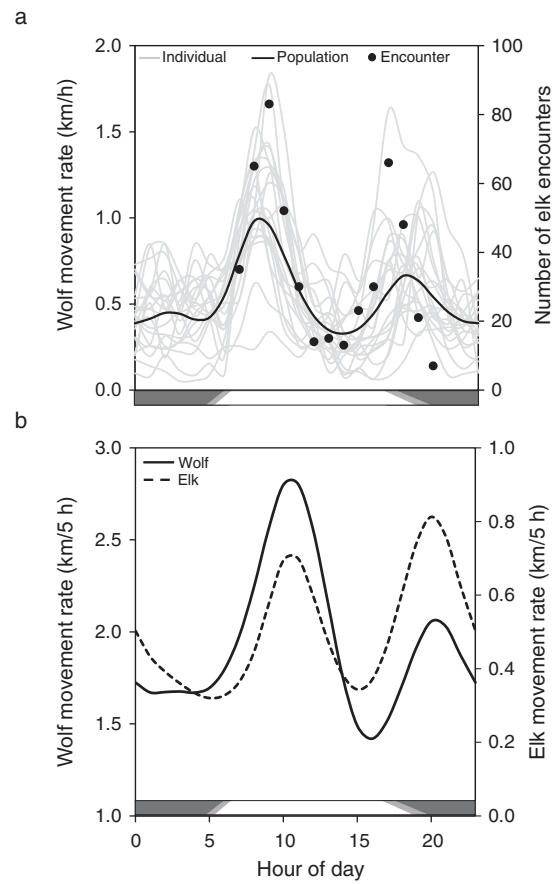


FIG. 2. Diel activity patterns of wolves and elk during winter in northern Yellowstone National Park. (a) Mean hourly movement rates for 21 GPS-collared wolves and predicted population mean from a generalized additive mixed model (left ordinate) and hourly number of directly observed daylight encounters between wolves and elk (right ordinate). (b) Predicted 5-h movement rates across 21 GPS-collared wolves (left ordinate) and 27 GPS-collared elk (right ordinate). Bars represent day (white), night (black), and variation in dawn/dusk periods (gray) from 15 October–31 May.

Table S2), indicating a threshold at which the effect of spatial risk on habitat selection changed. Evidence against a model describing a simple linear relationship between spatial risk and habitat selection was strong for predicted kill occurrence ($\Delta\text{QIC} = 347.13$), kill density ($\Delta\text{QIC} = 78.72$), openness ($\Delta\text{QIC} = 16.35$), and wolf density ($\Delta\text{QIC} = 9.98$; Appendix S1: Table S2). The best-fit models indicated that elk preferred increasingly risky places at low levels of spatial risk ($P < 0.01$; Appendix S1: Table S3) perhaps due to more food in these areas. At high levels of spatial risk, the effect of risk on habitat selection was negative (wolf density; $P = 0.02$), positive (kill density, $P < 0.01$; openness, $P < 0.001$), or nil (predicted kill occurrence; $P = 0.76$; Appendix S1: Table S3).

Support for the best-fit space-only models was substantially weaker compared to models that included space \times activity interactions between mean diel movement rate (km/5 h) of wolves (Fig. 2b) and linear splines for predicted kill occurrence ($\Delta\text{QIC} = 126.73$), kill density ($\Delta\text{QIC} = 95.28$), openness ($\Delta\text{QIC} = 200.98$), and wolf density ($\Delta\text{QIC} = 35.28$; Appendix S1: Table S4). The best-fit space \times activity model

included a time lag of 2 h (kill density, openness, wolf density) or 3 h (predicted kill occurrence; Appendix S1: Table S4). Five-fold cross validation revealed strong correlations between observed and predicted values for the best-fit space \times activity models that included predicted kill occurrence (mean Spearman-rank correlation, $r_s = 0.99$), openness ($r_s = 0.99$), and kill density ($r_s = 0.97$). Correlations of this magnitude indicate that these models are reliable. By contrast, the reliability of the model that included wolf density was poorer ($r_s = 0.67$), consistent with earlier findings that wolf density is an inaccurate index of spatial risk in northern YNP due to wolf packs displacing one another from the best hunting grounds where they kill elk (Kauffman et al. 2007). We therefore excluded the wolf density model from further consideration.

Negative space \times activity interactions before or after thresholds in predicted kill occurrence ($P < 0.001$; before threshold), kill density ($P < 0.001$; after threshold), and openness ($P < 0.001$; before and after threshold; Appendix S1: Table S5) showed that elk avoided open grasslands and places where kills occurred when wolf activity was high, but selected for these places when wolf activity was low (Fig. 3a–c). Habitat selection probably did not vary

beyond a predicted kill occurrence of 4.5 (Fig. 3a; $P = 0.87$; Appendix S1: Table S5) because there were few places where the predicted kill occurrence was more than 4.5 times the average kill probability; together, these places comprised only 7% of the study area.

To assess the time of day that elk selected for risky places, we calculated the frequency that elk steps ended in these places at two hour intervals. A place was risky if it exceeded the average value of a spatial risk index measured across all available locations in the study area. For example, 10.5% of 4084 elk steps ending in places that exceeded the study area's mean predicted kill occurrence (4.5) happened at 04:00–05:00, whereas 5.5% of these steps happened at 12:00–13:00 (Fig. 3d). Steps ending in risky places were most frequent from 22:00–05:00, which corresponded to the nightly lull in wolf activity (Fig. 3d–f).

To illustrate the effects of diel wolf activity on the elk LOF, we focused on kill density in a portion of our study area (Fig. 4a). Using our best-fit space \times activity model for this index (Fig. 4b), we show that places where kills were densely concentrated were valleys (low perceived predation risk) when wolf activity was low (Fig. 4c) and peaks (high

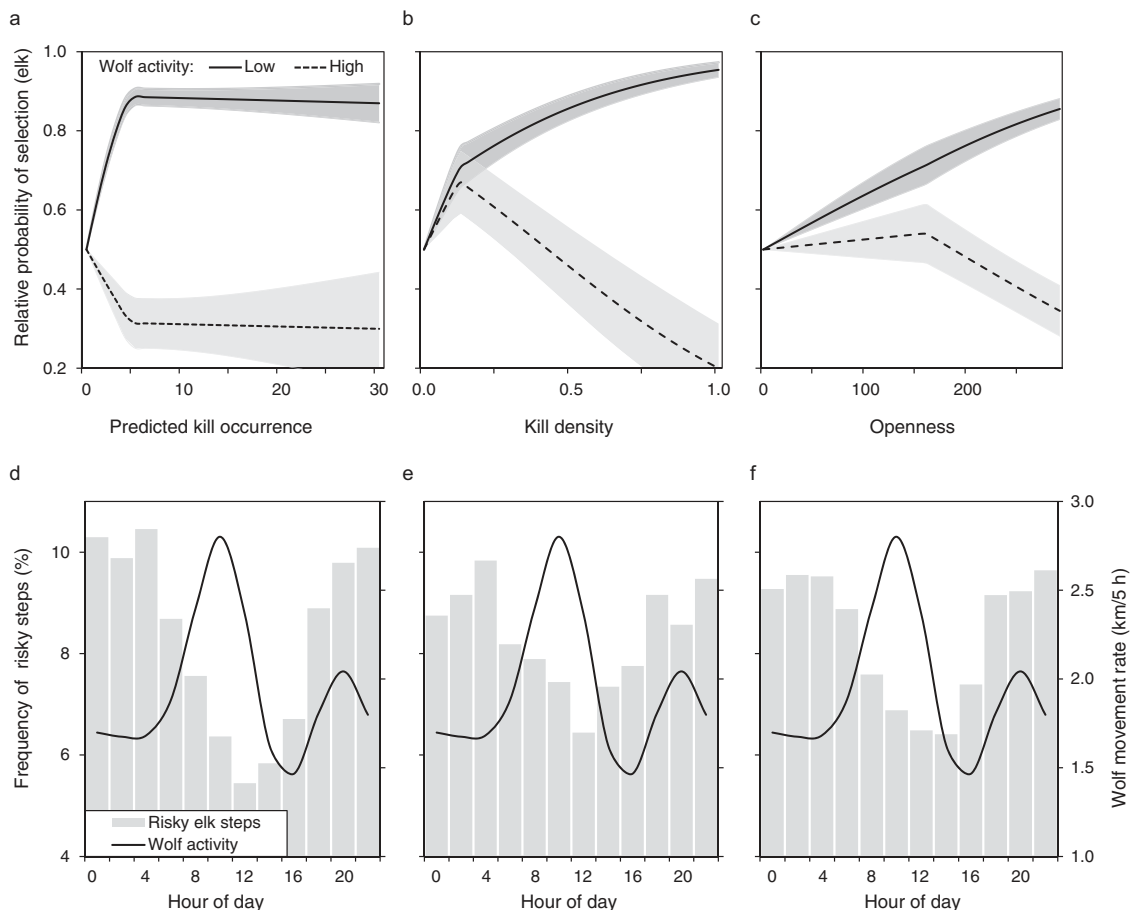


FIG. 3. Effects of diel wolf activity (predicted 5-h wolf movement rate) on elk habitat selection in northern Yellowstone National Park, 2001–2004. (a–c) Elk were more likely to select risky places (areas where kills occurred and open grasslands) when wolf activity was low (1.42 km/5 h) than when it was high (2.80 km/5 h); lines are population-averaged fitted values with 95% confidence intervals (shaded areas) from the best-fit space \times activity models (Appendix S1: Table S5). (d–f) Frequency of elk steps ending in risky places (locations $>$ mean spatial risk: predicted kill occurrence = 4.5; kill density = 0.22; openness = 194; left ordinate) was greatest at night when wolf activity (mean 5-h movement rate at 2-h intervals; right ordinate) was low.

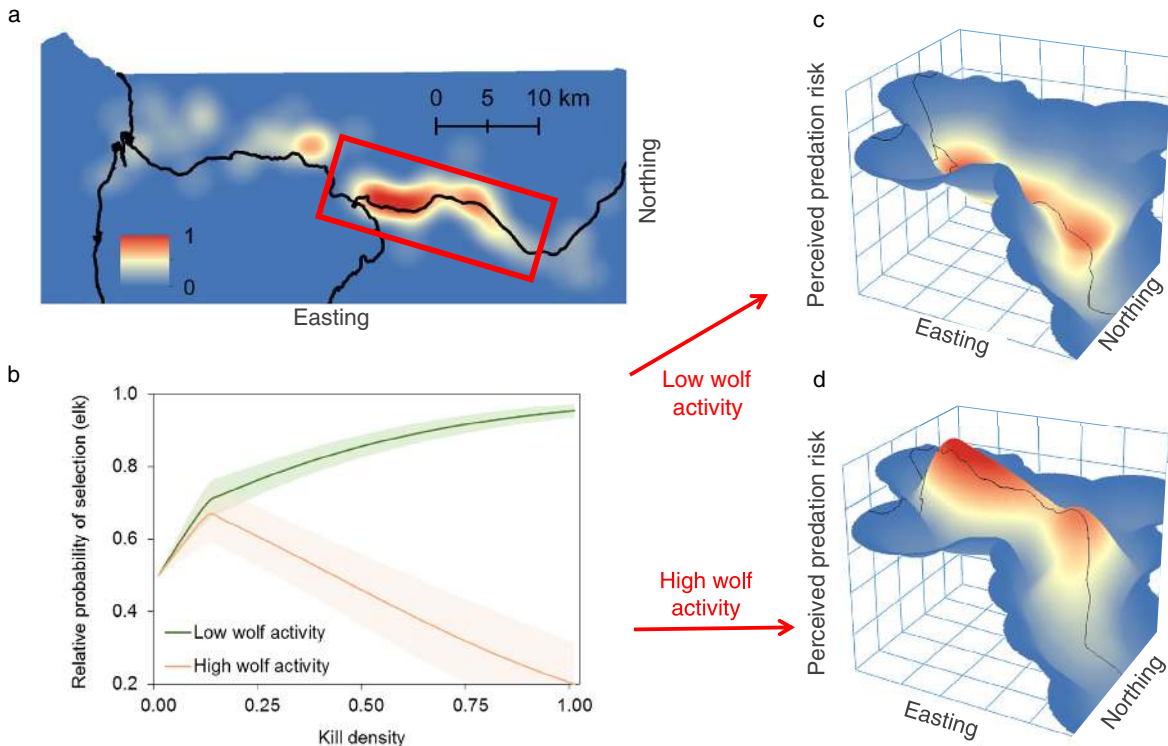


FIG. 4. Visualization of how diel wolf activity shaped the landscape of fear for adult female elk in northern Yellowstone National Park. (a) We examined kill density during the first year of the study (2001) within a portion of our study area (red rectangle), and used (b) the corresponding best-fit space \times activity step-selection model to calculate elk perception of wolf predation risk across this subregion when wolf activity was (c) low (1.42 km/5 h) and (d) high (2.80 km/5 h). Risky places where kills were densely concentrated were valleys when wolf activity was (c) low, and peaks when wolf activity was (d) high. Black lines in panels a, c, and d denote roads.

perceived predation risk) when wolf activity was high (Fig. 4d). Wolf downtime allowed elk to use places where wolves were more likely to kill them, flattening the LOF every night for about 12 h (Fig. 3d–f; Video S1). This may explain why prime-aged (2–11 yr-old) elk in our sample were in excellent body condition (percent ingesta-free body fat; $\bar{x} \pm \text{SE} = 10.12 \pm 0.18$, $n = 13$) with high pregnancy rate (0.89 ± 0.11 , $n = 15$) when radio-collared at midwinter.

DISCUSSION

The landscape of fear (LOF) has been proposed as a possible unifying concept in ecology that explains animal behavior, population dynamics, and trophic interactions across diverse ecosystems (Brown and Kotler 2004, Schmitz 2005, Heithaus et al. 2009, Laundré et al. 2010, Catano et al. 2016). It has also been argued that effective ecological restoration may depend on reestablishing landscapes of fear because fear may be as or more important than direct killing in structuring food webs and modifying ecosystem function (Manning et al. 2009, Suraci et al. 2016). Doubts about the conceptual and practical importance of the LOF stem from a dearth of information about it how it operates across large spatial scales in free-living systems involving apex predators and highly mobile prey (Hammerschlag et al. 2015). We addressed this gap with extensive data from the Yellowstone elk–wolf case study that was the original basis for the LOF concept.

An important aspect of our study is that we measured the LOF as a spatial mapping of time allocation (avoiding risky

places and times). This approach accords with the original and widely applied definition of an LOF as a spatial mapping of “any measure of fear” (Laundré et al. 2001, 2010), but differs from the definition of an LOF as a spatial mapping of an animal’s foraging cost of predation (Brown and Kotler 2004). The latter is calculated from giving-up densities, which are difficult to measure across vast landscapes like the one we studied (see Bedoya-Perez et al. [2013] for details about the practical uses of giving-up densities). Reconciling the two definitions is important because analyses of a single fear response may describe a landscape that is qualitatively different from a landscape of predation foraging cost, which is an integrative measure of fear that accounts for potential differences in how animal vigilance and time allocation vary with predation risk. For example, if an animal increases its vigilance while foraging in risky places, these places will appear as valleys in a map of time allocation and as peaks in a map of predation foraging cost, thus masking potential ecological effects of fear. Alternatively, if an animal manages risk mainly with time allocation (keeping vigilance constant across safe and risky places), or if vigilance and time allocation respond similarly to temporal variation in risk (decreasing vigilance while foraging in risky places at safe times; Lima and Bednekoff 1999), then the two maps will agree. Constant vigilance provides perfect agreement (Brown 1999), whereas vigilance that covaries with time allocation may provide relatively less relief (lower peaks, shallower valleys) in the map of time allocation, thus underestimating the foraging cost of predation.

Evidence that adult female elk in northern Yellowstone (and adjacent areas) maintain constant vigilance levels across habitats that vary in wolf predation risk (high vs. low wolf densities, near vs. far from forest cover; Childress and Lung 2003, Lung and Childress 2007, Winnie and Creel 2007, Creel et al. 2008, Liley and Creel 2008) suggests our map of time allocation (Fig. 4c, d) matches a map of predation foraging cost. These elk increase vigilance levels only when wolves are an immediate threat (Winnie and Creel 2007, Creel et al. 2008, Liley and Creel 2008, Gower et al. 2009, Middleton et al. 2013a) because they can simultaneously process their food and scan their surroundings (Fortin et al. 2004, Gower et al. 2009) as well as escape wolves that attack them (MacNulty et al. 2012, Mech et al. 2015). In general, animals, especially food-limited ones, are expected to use little or no vigilance when they can escape predators in the absence of vigilance (Brown 1999).

On the other hand, if elk vigilance is sensitive to short-term (≤ 24 h) temporal variation in wolf predation risk as many studies report (Winnie and Creel 2007, Creel et al. 2008, Liley and Creel 2008, Gower et al. 2009, Middleton et al. 2013a), then elk may increase vigilance in risky places during periods of the diel cycle when wolves are most active. This is an open question because studies have yet to test how spatial variation in elk vigilance changes across the diel cycle. Nevertheless, theory predicts that an animal's vigilance level (and its predation foraging cost) should track its predator encounter rate, which is itself a function of predator activity level (Houston et al. 1993, Brown 1999, Lima and Bednekoff 1999). If so, elk should reduce vigilance when foraging in risky places during lulls in wolf activity when encounters are infrequent (Fig. 2a) leading to a map of predation foraging cost with more relief than is evident in our map of time allocation (Fig. 4c, d).

The large scale of our estimated LOF is also notable. Among studies that have mapped animal response to spatial variation in predation risk in accord with the LOF concept, none mapped areas much larger than 1-km² (Shrader et al. 2008, van der Merwe and Brown 2008, Druce et al. 2009, Willems and Hill 2009, Abu Baker and Brown 2010, Emerson et al. 2011, Matassa and Trussell 2011, Iribarren and Kotler 2012, Coleman and Hill 2014). Many maps purported to describe an LOF are not based on measurements of animal response to spatial risk (Kauffman et al. 2010, Madin et al. 2011, Catano et al. 2016). A common misconception is that spatial risk by itself defines an LOF.

The role of diel predator activity

We make two important advances with our results. First, we demonstrate that diel predator activity is a crucial driver of an LOF. In the large-scale, free-living system we studied, the mere presence of a predator was a necessary but insufficient condition to stimulate an LOF. Had we adopted the classic fixed risk assumption of constant attack over time (Lima 2002) by ignoring diel predator activity, we would have concluded, incorrectly, that our focal prey population had little fear of risky places (Appendix S1: Table S3). Instead, our consideration of diel predator activity revealed an LOF with peaks and valleys that oscillated across the diel cycle according to the predator's activity rhythm (Fig. 4;

Video S1). This temporally sensitive response aligns with the risk allocation hypothesis (Lima and Bednekoff 1999), which predicts that animals in high-risk environments take maximal advantage of safe times to forage in risky places, and with numerous day–night and light–dark comparisons that show how many taxa (e.g., zooplankton, rodents, and ungulates) use risky places at times of the day when predator activity or hunting ability is minimal (Lima and Dill 1990, Lima 1998, Brown and Kotler 2004, Caro 2005, Fischhoff et al. 2007, Tambling et al. 2012, Burkepile 2013, Palmer et al. 2017).

However, previous studies of diel predator effects on prey habitat use neither quantified an LOF nor linked it to measured variation in diel predator activity as we did. These studies only compared habitat use between day and night or light and dark periods. This approach would have obscured our results because wolf activity was a complex function of time of day that did not neatly fit the conventional dichotomy of safe and dangerous periods (Fig. 2). As far as we know, our study is the first to quantify how continuous variation in spatial predation risk (Fig. 1) and diel predator activity (Fig. 2) interact with one another to affect an animal's habitat selection (Fig. 3; Appendix S1: Table S5) and, ultimately, its LOF (Fig. 4; Video S1). Ecologists have only recently started to investigate the influence of diel predator activity on animal habitat selection (Fischhoff et al. 2007, Tambling et al. 2012, Burkepile 2013). Many of the classic studies of diel predator effects, including zooplankton diel vertical migration (Iwasa 1982) and rodent response to moonlight (Kotler et al. 1991), considered diel changes in the ocular capability of visual predators (Gibson et al. 2009, Upham and Hafner 2013) rather than diel predator activity per se. This aspect of predator–prey interactions deserves more attention because the prevalence of diel activity patterns in apex predators across diverse ecosystems (Theuerkauf et al. 2003, Roth and Lima 2007, Whitney et al. 2007, Andrews et al. 2009, Cozzi et al. 2012) suggests that it is a potentially common driver of landscapes of fear.

Diel predator activity was an important driver of the landscape of fear in the system we studied because it was a valid source of risk that prey could evidently perceive. Wolves are cursorial hunters that find and select prey by actively searching the environment and visually identifying vulnerable prey that are safe to kill (MacNulty et al. 2007, Mech et al. 2015). The risk of wolf predation is therefore low when wolves are not highly active. This is illustrated in our data by how the frequency at which wolves encountered, attacked, and killed elk mirrored changes in wolf activity levels (Fig. 2a). The low levels of nighttime activity that we documented is consistent with the hypothesis that wolves avoid hunting at night because their vision is best adapted to crepuscular light (Kavanau and Ramos 1975, Roper and Ryon 1977, Theuerkauf 2009). This may explain why wolves in Yellowstone and most other regions exhibit a crepuscular activity pattern (Theuerkauf et al. 2003, Theuerkauf 2009).

The strong statistical association between elk habitat selection and diel wolf activity across three different measures of spatial risk (Fig. 3a–c; Appendix S1: Table S5) implies that elk perceived diel variation in wolf activity. How elk did this is not obvious from our data. The lagged influence of wolf activity on elk habitat selection (Fig. 3d–f;

Appendix S1: Table S5) suggests that elk did not perfectly perceive changes in wolf activity. Or it could reflect a deliberate trade-off between safety and food in which elk accepted a higher likelihood of wolf encounter in exchange for more time in preferred foraging habitats. Support for this hypothesis is given by the temporal distribution of elk steps in risky places, which shows that elk minimized their steps in risky places after wolf activity peaked in the morning and started increasing their steps back into these places before wolf activity dipped in the afternoon (Fig. 3d–f). Elk probably tolerate a modest likelihood of wolf encounter because they often survive encounters (MacNulty et al. 2007, Mech et al. 2015). The success of wolves hunting elk in northern YNP during the study period rarely exceeded 20% (Smith et al. 2000, Mech et al. 2001) and dropped below 10% when wolves hunted adult elk (MacNulty et al. 2012). After accounting for herd size, success rate per elk was as low as 1–3% (Mech et al. 2001).

The landscape of fear in northern Yellowstone

Our second key advance is that we provide the first approximation of the elk LOF that prevailed in northern YNP following wolf reintroduction in 1995–1997. This matters to the discipline of ecology and the practice of conservation because this particular case study is an empirical cornerstone in the LOF concept (Laundré et al. 2001, 2010). Moreover, this case study is a seminal example in broader debates about the ecological consequences of fear (Ripple and Beschta 2004, Zanette et al. 2011) and the importance of apex predators to the structure and function of ecosystems (Terborgh and Estes 2010, Dobson 2014). Our central finding is that wolves established an elk LOF that was not as relentlessly intimidating as originally proposed and subsequently argued. On the contrary, our results indicate that wolves established a dynamic LOF that shifted hourly with the ebb and flow of wolf activity. Whereas previous studies reported that elk behaviorally abandoned risky places in response to the mere presence of wolves, our research reveals that elk maintained regular use of these areas during nightly lulls in wolf activity. This finding is important because many hypotheses about the ecological effects of the elk LOF in the Greater Yellowstone Ecosystem (GYE) assume that elk abandon risky places when wolves are present.

For example, the predator-sensitive food hypothesis that fear of wolves decreases elk pregnancy rate via increased over-winter fat loss assumes that females move into the protective cover of nutritionally impoverished forests when wolves are present, reducing their use of preferred grassland foraging habitats that have high predation risk (Creel et al. 2009). Although our study is the first to show how female elk can safely use grasslands when wolves are present, prior studies of 243 females across four GYE elk populations (northern Yellowstone, Madison headwaters, Lower Madison, Clarks Fork) have shown that wolf presence does not exclude female elk from grasslands (Fortin et al. 2005, Mao et al. 2005, Proffitt et al. 2009, White et al. 2009a, Middleton et al. 2013a). Counter evidence is limited to one study of fewer than 14 females in one GYE elk population (Gallatin Canyon; Creel et al. 2005), and a gender-blind study of fecal pellet distributions in northern Yellowstone during summer

(Hernández and Laundré 2005) when predator-sensitive food effects are not expected (Creel et al. 2009).

Fortin et al.'s (2005) study is frequently cited as evidence that wolves exclude elk from grasslands (Schmitz et al. 2008, Creel et al. 2009, 2011, Creel and Christianson 2009). However, its results are more ambiguous than often acknowledged. Elk were found to prefer conifer forests to grasslands where wolves were numerous, but they were also *more* likely to use grasslands as local wolf densities increased (Fortin et al. 2005: Fig. 3). Confusing matters further, our study, which included the elk studied in Fortin et al. (2005), indicated that wolf density was an unreliable predictor of elk habitat selection (Appendix S1: Table S4) likely because wolf density was itself an inaccurate gauge of wolf predation risk (Kauffman et al. 2007). These issues highlight the preliminary quality of the results from Fortin et al. (2005).

In winter, the female elk we analyzed used grasslands at night when wolves were relatively inactive (Fig. 3c, f). Body fat and blood serum data taken from these elk when assayed at mid-winter were consistent with the hypothesis that nocturnal use of preferred grassland foraging habitats was sufficient to offset the effects of wolf presence on elk over-winter fat loss and pregnancy rate. Prime-aged (2–11 yr-old) females carried enough body fat (10%) in February to maintain a high rate of pregnancy (89%) contrary to the predator-sensitive food hypothesis. These results agree with those from a larger sample of elk (>90) from the same population and time period that included the sample we analyzed (Cook et al. 2004, White et al. 2011). They also agree with fetal data from thousands of females in this population that indicated pregnancy rate was independent of wolf predation pressure (Proffitt et al. 2014). Nocturnal use may explain how females from other elk populations maintained access to grasslands, and why they too maintained relatively high levels of over-winter nutrition and/or pregnancy rate despite wolf presence (Hamlin et al. 2009, White et al. 2009b, Middleton et al. 2013a, b). Finally, the consistently crepuscular pattern of wolf activity (Fig. 2; Appendix S1: Fig. S2; Theuerkauf 2009) suggests a degree of predictability in wolf predation risk that may explain why wolves have no effect on elk reproduction via chronic stress (Creel et al. 2009, Boonstra 2013).

Elk behavioral abandonment of risky places is also a key mechanism in the behaviorally mediated trophic cascade hypothesis, which asserts that fear of wolves increases productivity of palatable woody deciduous plants in risky places via reductions in elk browsing (Ripple and Beschta 2004, Beyer et al. 2007, Kauffman et al. 2010, Winnie 2012, Peterson et al. 2014). Although population reduction via direct killing could also reduce elk browsing, evidence of an apparent trophic cascade in northern YNP in the decade after wolf reintroduction has been attributed to behavioral mechanisms in part because elk numbers remained high during that period (Ripple et al. 2001, Ripple and Beschta 2004, 2006, Beyer et al. 2007, Ripple and Beschta 2012). Our results suggest that elk maintained access to aspen and willow (*Salix* spp.) within risky places during daily wolf downtimes. This inference contradicts initial reports that elk avoided aspen where wolves were numerous (Ripple et al. 2001, Fortin et al. 2005). However, it agrees with a winter habitat selection analysis of 80 VHF-collared elk followed in

2000–2002, concurrent to the elk tracked by Fortin et al. (2005), and compared with 94 VHF-collared elk followed before wolf reintroduction (Mao et al. 2005). This study found that elk *preferred* aspen where wolves were numerous depending on slope and snow levels, and that “elk showed no significant change in selection of aspen, which was highly preferred during winter in both pre- and post-wolf reintroduction periods” (Mao et al. 2005: Table 6). Assessing results from Fortin et al. (2005) and Mao et al. (2005) is difficult, however, because both studies relied on an unreliable index of spatial risk (wolf density; Appendix S1: Table S4) and an unvalidated GIS layer for aspen.

Nevertheless, elk nocturnal use of areas of high predicted kill occurrence (Fig. 3d) aligns with how aspen in these same areas did not escape browsing (Kauffman et al. 2010). Evidence that our collared elk selected for willow riparian areas at night (Beyer 2006) may also explain why many willow also did not escape browsing (Bilyeu et al. 2008, Marshall et al. 2013, 2014, but see Beyer et al. 2007). Persistent browsing on aspen and willow was probably also related to how many of these plants existed outside of high-risk areas as defined by our indices of spatial risk (Appendix S1: Fig. S3). These results, together with evidence that wolf-caused changes in elk distribution arise from wolves removing individuals rather than elk redistributing themselves (White et al. 2009a, 2010, 2012), support the hypothesis that any indirect effect of wolves on woody deciduous plants is mainly the result of a density-mediated trophic cascade (Creel and Christianson 2009, Kauffman et al. 2010, Winnie 2012, Marshall et al. 2014, Painter et al. 2015).

Data limitations

Although our data are the best available information about the role of wolves in shaping the elk LOF in northern YNP during the first decade of wolf recovery, they are limited in at least four ways. First, the 5-h interval between consecutive elk locations was coarse and a potential source of bias. This possibility is minimized by the fact that several studies have analyzed subsets of our data and established that the 5-h interval provides a valid basis for understanding elk movement and habitat selection (Boyce et al. 2003, Fortin et al. 2005, Forester et al. 2007, 2009). Second, our estimated diel wolf activity pattern (Fig. 2) was derived from wolf GPS data collected over a 10-yr period (2004–2013) that only partially overlapped our elk study period (2001–2004). This was necessary because GPS data for wolves in YNP were not available until 2004, and the number of wolves equipped with GPS collars each year was small (two to five animals; Appendix S1: Table S1). Nevertheless, our estimated diel pattern was most likely representative of the diel pattern during the non-overlapping years because it was (1) correlated with the time of day that we directly observed wolves encountering ($r = 0.79$) and killing ($r = 0.87$) elk during the non-overlapping years (Fig. 2a); (2) consistent across the years in which it was measured (Appendix S1: Fig. S2); and (3) similar to diel patterns described for other wolf populations (Theuerkauf et al. 2003, Eggermann et al. 2009, Theuerkauf 2009, Vander Vennen et al. 2016).

Although wolves were the primary source of mortality for our study population (Evans et al. 2006), our study, like

others before it, ignored the possibility that the elk LOF was shaped by multiple predator species (e.g., wolves and cougars). One reason this may be important is if different predator-specific activity schedules (crepuscular vs. nocturnal) create conflicting spatiotemporal patterns of predation risk that require prey to prioritize their response to one predator at the expense of increasing their risk to another. In addition, our analysis did not address the long-term dynamics of the elk LOF. Our results could be an artifact of the potentially unique conditions that prevailed during our study period including a large and growing wolf population, a large but shrinking elk population, and moderate to severe drought conditions. Further research is necessary to determine if and how our estimate of the elk LOF may have changed during the second decade of wolves in northern YNP.

CONCLUSIONS

In summary, our major insight is that an animal’s spatially explicit perception of predation risk (i.e., its landscape of fear) over a large physical landscape tracks the daily activity pattern of its primary predator, enabling the animal to utilize risky places during predator downtimes, which in turn mitigates the impact of fear on animal resource use, nutritional condition, and reproduction. Our results highlight how an LOF in a large scale, behaviorally sophisticated system like northern YNP is not a simple, unconditional function of a predator’s mere presence. To assume so may overestimate the threat of predation, underestimate the ability of prey to efficiently manage this threat, and exaggerate the ecological effects of fear. We encourage investigators to recognize the potential for free-living animals to adaptively allocate habitat use across periods of high and low predator activity within the diel cycle. This underappreciated aspect of animal behavior can help explain why strong antipredator responses (e.g., movement, vigilance) may have weak ecological effects, and why these effects may not rival those of direct killing. It also provides a basis for understanding why an LOF may have less relevance to conservation and management than direct killing.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecm.1313/full>

DATA AVAILABILITY

GPS data associated with this study are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.mr0rg45>