1   *Running head:* Predator activity and landscapes of fear

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3   *Title:* Diel predator activity drives a dynamic landscape of fear

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25

26   ABSTRACT

27   A 'landscape of fear' (LOF) is a map that describes continuous spatial variation in an animal's

28   perception of predation risk. The relief on this map reflects, for example, places that an animal

29   avoids to minimize risk. Although the LOF concept is a potential unifying theme in ecology that

30   is often invoked to explain the ecological and conservation significance of fear, quantified

31   examples of a LOF over large spatial scales are lacking as is knowledge about the daily

32   dynamics of a LOF. Despite theory and data to the contrary, investigators often assume,

33   implicitly or explicitly, that a LOF is a static consequence of a predator's mere presence. We

34   tested the prediction that a LOF in a large-scale, free-living system is a highly-dynamic map with

35   'peaks' and 'valleys' that alternate across the diel (24-hour) cycle in response to daily lulls in

36   predator activity. We did so with extensive data from the case study of Yellowstone elk (*Cervus*

37   *elaphus*) and wolves (*Canis lupus*) that was the original basis for the LOF concept. We

38   quantified the elk LOF, defined here as spatial allocation of time away from risky places and

39   times, across nearly 1000-km^2 of northern Yellowstone National Park and found that it fluctuated

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40   with the crepuscular activity pattern of wolves, enabling elk to use risky places during wolf

41   downtimes. This may help explain evidence that wolf predation risk has no effect on elk stress

42   levels, body condition, pregnancy, or herbivory. The ability of free-living animals to adaptively

43   allocate habitat use across periods of high and low predator activity within the diel cycle is an

44   underappreciated aspect of animal behavior that helps explain why strong antipredator responses

45   may trigger weak ecological effects, and why a LOF may have less conceptual and practical

46   importance than direct killing.

47

48   *Keywords:* antipredator behavior, diel activity, elk, habitat selection, landscape of fear (LOF),

49   predation risk, predator activity rhythm, predator-prey interaction, wolf, Yellowstone

50

51   INTRODUCTION

52   Fear of predation (perceived predation risk) caused by the mere presence of a predator is

53   increasingly regarded as an ecological force that rivals or exceeds that of direct killing (Preisser

54   et al. 2005). The 'landscape of fear' (LOF) concept has been advanced as a general mechanism

55   that drives the effects of fear that cascade from individuals to ecosystems (Brown and Kotler

56   2004, Schmitz 2005, Laundré et al. 2010), including changes in prey physiology (Zanette et al.

57   2014) and demography (Preisser et al. 2007), plant growth (Ford et al. 2014), and nutrient

58   cycling (Hawlena et al. 2012). Operationally, a LOF is a map that describes the continuous

59   change in predation risk that an animal perceives as it navigates the physical landscape (Brown

60   and Kotler 2004, Laundré et al. 2001, 2010). This mental map of risk overlies the physical terrain

61   like a map of soils, vegetation, or climate, and its 'peaks' and 'valleys' describe an animal's

62   perception of those locations as dangerous and safe, respectively (van der Merwe and Brown

63   2008). Risk perception is indexed by an animal's measurable response to changes in predation

64   risk (Lima and Steury 2005), and the continuous spatial patterning of this response approximates

65   a LOF as originally defined by Laundré et al. (2001, 2010). Brown and Kotler (2004) defined the

66   concept more narrowly as the spatial distribution of the foraging cost of predation, which is fear

67   measured as the energetic consequence of an animal's response, chiefly vigilance and (or) time

68   allocation. No matter its definition, the LOF concept is often cited to explain the ecological

69   effects of fear despite two important empirical shortcomings.

70   First, quantified examples of large-scale LOFs are lacking. Numerous studies have

71   measured animal response to spatial variation in predation risk (reviewed by Moll et al. 2017),

72   but few have mapped this response across physical landscapes as a continuous function of risk in

73   accord with the LOF concept. Among those that have, none mapped areas much larger than 1-

74   km^2 (Shrader et al. 2008, van der Merwe and Brown 2008, Druce et al. 2009, Willems and Hill

75   2009, Abu Baker and Brown 2010, Emerson et al. 2011, Matassa and Trussell 2011, Iribarren

76   and Kotler 2012, Coleman and Hill 2014). Conversely, some studies have mapped large-scale

77   vegetation patterns and attributed them to animal response to risk without measuring the

78   response itself (Madin et al. 2011). The response has also been overlooked in studies that define

79   a LOF solely in terms of spatial variation in predation risk (e.g., Kauffman et al. 2010, Catano et

80   al. 2016). Large-scale, quantitative examples of a LOF are probably lacking because spatially-

81   explicit data on animal response to risk across vast physical landscapes are difficult to obtain.

82   Second, little is known about LOF dynamics across the diel (24-hr) cycle. To date, many

83   ecologists have, implicitly or explicitly, assumed that a LOF is a fixed spatial pattern as long as

84   the predator is present (but see Palmer et al. 2017). The underlying rationale is that a constant

85   possibility of predation enforces a chronic state of apprehension in the prey (Schmitz et al. 1997,

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86   Brown et al. 1999). This 'fixed-risk' assumption of constant attack over time has been a

87   conceptual mainstay in the study of behavioral predator-prey interactions for decades (Lima

88   2002). Nevertheless, it neglects how predator activity and hunting ability can vary across the diel

89   cycle, and how this may foster a fluctuating acute state of apprehension in the prey and a

90   dynamic LOF despite the constant presence of predators.

91   Many predators are only active at certain times of day, and visual predators active at

92   night often cannot hunt in absolute darkness. These predatory constraints provide pulses of safety

93   during the diel cycle that may temporarily relieve an animal's fear of predation and flatten its

94   LOF. This hypothesis is broadly consistent with risk allocation theory, which predicts that

95   animals constantly exposed to predators should respond to pulses of safety with intense feeding

96   efforts (Lima and Bednekoff 1999). It also accords with numerous empirical studies that show

97   how various animals (e.g., zooplankton, rodents, and ungulates) forage in risky places during

98   periods of the diel cycle (e.g., day or night) associated with reduced predator activity and/or

99   hunting ability (reviewed by Lima and Dill 1990, Lima 1998, Brown and Kotler 2004, Caro

100   2005; see also Fischhoff et al. 2007, Tambling et al. 2012, Burkepile et al. 2013). However, these

101   studies neither tested how animal response to spatial risk is linked to measured variation in diel

102   predator behavior, nor showed how this linkage shapes the animal's LOF across the diel cycle.

103   Dichotomizing continuous variation in diel predator behavior into periods of presumed safety

104   and danger (e.g., day versus night) is potentially misleading if diel behavior does not conform to

105   these simple categories or if animals assess predation risk as a continuous variable (Creel 2011).

106   The empirical gaps in the LOF concept are exemplified by its founding case study of elk

107   (*Cervus elaphus*) in northern Yellowstone National Park (YNP) following wolf (*Canis lupus*)

108   reintroduction there in 1995-97 (Laundré et al. 2001). Although this case is frequently cited as a

5

109   well-understood example of a LOF, and is one that has motivated the proposal that the LOF is a

110   unifying concept in ecology (Laundré et al. 2010), researchers never quantified the elk LOF after

111   wolf reintroduction, nor examined its temporal dynamics in relation to diel wolf behavior.

112   Instead, the elk LOF was inferred from broad-scale, population-level data on vigilance behavior

113   (Laundré et al. 2001), fecal pellets (Hernández and Laundré 2005), and herbivory (Ripple and

114   Beschta 2004) that supported three predictions based on the LOF concept: (1) elk shifted habitat

115   use in response to wolves, including abandonment of high-risk open areas, which (2) decreased

116   diet quality and body fat, and (3) reduced browsing on woody deciduous plants in high risk areas

117   (Laundré et al. 2001, 2010). Some researchers have argued that habitat shifts also reduced elk

118   pregnancy rate (Creel et al. 2009, Christianson and Creel 2014). On the other hand, concurrent

119   fine-scale, individual-level data on movement, body condition, and pregnancy rate indicated elk

120   selected for open areas (Fortin et al. 2005, Mao et al. 2005) and maintained body fat and

121   pregnancy rate (Cook et al. 2004, White et al. 2011, Proffitt et al. 2014). Whereas Fortin et al.'s

122   (2005) 6.5-month study (2001-2002) of 13 female elk equipped with global positioning system

123   (GPS) radio collars suggested elk avoided aspen (*Populus tremuloides*) forests in response to

124   wolves, a three-year experimental study (2004-2007) of aspen demography found that elk

125   browsing was not reduced in risky places (Kauffman et al. 2010). These divergent results have

126   yet to be reconciled, and together they highlight an outstanding need to clarify the elk LOF that

127   prevailed in YNP during the initial years after wolf reintroduction.

128   The overarching purpose of this study was to improve the empirical foundation of the

129   LOF concept. Our objectives were to (1) quantify a large-scale LOF, and (2) determine how this

130   mental map of risk changes across the diel cycle in response to the daily activity pattern of a

131   predator that is always present. Because the response of Yellowstone elk to wolf reintroduction

132   is a seminal yet unresolved example of a LOF, we examined the elk LOF in northern YNP within

133   the first decade after wolves were released.

134   We defined the elk LOF as spatial allocation of time away from risky places and times.

135   This conforms to Laundré et al.'s (2001, 2010) broad definition and approximates Brown and

136   Kotler's (2004) narrower definition. The latter is possible because research indicates that

137   Yellowstone elk manage wolf predation risk mainly through time allocation, keeping vigilance

138   levels constant across habitats that vary in predation risk (e.g., near versus far from forest cover)

139   and increasing vigilance only when wolves are an immediate threat (Childress and Lung 2003;

140   Lung and Childress 2007; Winnie and Creel 2007; Creel et al. 2008; Liley and Creel 2008;

141   Gower et al. 2009; Middleton et al. 2013).

142   To assess spatial time allocation, we conducted a retrospective habitat selection analysis

143   of data from 27 GPS radio-collared female elk collected during 2001-2004. This included 13 elk

144   from Fortin et al.'s (2005) study, 2 elk from Boyce et al. (2003), 1 elk from Forester et al. (2007,

145   2009), and 11 elk whose data were never published. Together, these were the first elk GPS

146   location data collected in YNP before or after wolf reintroduction, and we used them to quantify

147   the elk LOF across 995-km^2 of northern YNP. We tested how this large-scale LOF varied across

148   the diel cycle in relation to the daily activity pattern of wolves which we estimated from direct

149   observations of hunting behavior (1995-2003) and GPS location data (2004-2013). We predicted

150   a dynamic LOF with peaks and valleys that alternated across the diel cycle in response to daily

151   lulls in wolf activity.

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153   METHODS

154   *Study Area*

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155   Our study occurred in a 995-km^2 area of northern YNP (44° 56′ N, 110° 24′ W) where the

156   climate is characterized by short, cool summers and long, cold winters (Houston 1982). Low

157   elevations (1500-2000 m) in the area create the warmest and driest conditions in YNP, providing

158   important winter range for ungulates, including elk. Vegetation includes montane forest (44%;

159   e.g., lodgepole pine [*Pinus contorta*] and Douglas fir [*Pseudotsuga menziesii*]), open sagebrush–

160   grassland (37%; e.g., Idaho fescue [*Festuca idahoensis*], blue-bunch wheatgrass

161   [*Pseudoroegneria spicata*], and big sagebrush [*Artemisia tridentata*]), upland grasslands, wet

162   meadows, and non-vegetated areas (19%) (Despain 1990).

163

164   *Study Population*

165   We analyzed habitat selection behavior of 27 adult (> 1 year-old) female elk that spent

166   winter in northern YNP and adjoining areas of the Yellowstone River valley outside YNP from

167   about 15 October to 31 May, 2001-2004. These elk were from a migratory population that

168   numbered from 8,300-13,400 individuals. Our sample of adult female elk was captured in

169   February (2001-2003) via helicopter net-gunning (Hawkins and Powers, Greybull, Wyoming,

170   USA; Leading Edge Aviation, Lewiston, Idaho, USA) and fitted with Telonics (Telonics, Mesa,

171   Arizona, USA) or Advanced Telemetry Systems Inc. (Isanti, Minnesota, USA) GPS radio-collars

172   ($\overline{x} \pm$ SD location error = 6.15 ± 5.24 m; Forester et al. 2007) programmed to collect locations at

173   4-6 hour intervals (5 hour intervals: $n = 23$; alternating between 4 and 6 hour intervals: $n = 4$). To

174   control for movements associated with migratory behavior, we limited our analysis to winter

175   locations collected from 1 November – 30 April. If individuals arrived on the winter range after

176   1 November, data were censored to the individual's arrival date (1-22 November). Location data

177   for each individual were collected for 30-353 days ($\overline{x} \pm$ SD = 124.5 ± 12.5) across 1-3 winters

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178   until collar failure, collar removal, or animal death. We censored location data to include only

179   high-quality locations following guidelines developed by Forester et al. (2009).

180   Elk age was estimated using cementum analysis of an extracted vestigial tooth (Hamlin et

181   al. 2000) and pregnancy was determined from a serum sample using the pregnancy-specific

182   protein B assay (Sasser et al. 1986, Noyes et al. 1997, White et al. 2011). We evaluated elk

183   nutritional condition via a rump body condition score developed for elk and maximum

184   subcutaneous rump fat thickness measured using an ultrasonograph (Cook et al. 2004). We

185   estimated ingesta-free body fat percentage using the scaled LIVINDEX for elk, which is an

186   arithmetic combination of the rump body condition score and maximum rump fat thickness

187   allometrically scaled using body mass (Cook et al. 2004).

188   Wolves in this study were members or descendants of a population of 41 radio-collared

189   wolves reintroduced to YNP in 1995-1997 (Bangs and Fritts 1996). The study occurred during a

190   time of peak wolf abundance in YNP: wolf numbers in northern YNP ranged from 70-98

191   individuals in 4-8 packs (Cubaynes et al. 2014). Each winter, 20-30 wolves, including 30-50% of

192   pups born the previous year, were captured and radio-collared (Smith et al. 2004). Wolves were

193   fitted with very high frequency (VHF; Telonics Inc., Mesa, AZ, USA) or GPS (Televilt,

194   Lindesberg, Sweden; Lotek, Newmarket, ON, Canada) radio-collars. Locations of VHF and

195   GPS-collared wolves were recorded approximately daily during two 30-day periods in early

196   (mid-November to mid-December) and late (March) winter, when wolf packs were intensively

197   monitored from the ground and fixed-wing aircraft, and approximately weekly during the rest of

198   the year. GPS collars recorded locations every hour during the 30-day periods and at variable

199   intervals outside these periods. The proportion of the Yellowstone wolf population that was

200   radio-collared ranged from 35-40%. We captured and handled wolves and elk following

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201   protocols in accord with applicable guidelines from the American Society of Mammalogists

202   (Sikes 2016) and approved by the National Park Service Institutional Animal Care and Use

203   Committee.

204

205   *Diel activity patterns*

206   We used movement rate to index diel wolf activity given that speed of locomotion is a

207   valid proxy for diel activity patterns in large mammals (Ensing et al. 2014). We estimated

208   movement rate at each hour of the day from the hourly winter positions of 21 GPS-collared

209   wolves recorded in northern YNP during 2004-2013. Wolf GPS data were unavailable prior to

210   2004. Movement rate equaled the average Euclidean distance of the preceding 1-hour or 5-hour

211   time step. We used hourly movement rate (km/hr) to describe the diel pattern in wolf activity and

212   5-hour movement rate (km/5-hrs) to test how diel wolf activity influenced elk selection of safe

213   and risky places. We used 5-hour movement rate in the habitat selection analysis to match the 5-

214   hour time interval between consecutive elk locations. To generalize the 1-hour data to 5-hour

215   data, we retained every fifth location beginning with the first 5-hour location available. We used

216   only consecutive 1-hour and 5-hour locations to calculate movement rates.

217   We estimated the population-level pattern in diel movement rate by applying a

218   generalized additive mixed model (GAMM) to both the 1-hour and 5-hour locations using the

219   mgcv package (version 1.8.0) in R 3.2.3. Because movement data were heavily right skewed

220   (e.g., Fortin et al. 2005), we fit the GAMM using the negative binomial family and incorporated

221   performance iterations such that the scale parameter was as close to 1 as possible. We applied a

222   cyclic cubic regression spline so that the first and last hour of the day matched in accordance

223   with the diel cycle. We included a random intercept for individual identity to account for

10

224   repeated measures within the study period. We were unable to distinguish between individual

225   and annual variation in wolf diel activity patterns because the number of individuals sampled

226   within years was too small (Appendix S1). Thus, our estimate of diel activity is a population-

227   level estimate calculated as a univariate function of time of day. We used the estimated 5-hour

228   movement rate as the covariate for diel wolf activity in the habitat selection analysis. We used

229   this same approach to model the diel activity pattern of GPS-collared elk, which we did for

230   illustrative purposes. All of our major inferences were based on analyses of elk habitat selection.

231   Each wolf provided an independent measure of movement rate because it was solitary, was the

232   only GPS radio-collared wolf in a pack, or rarely associated with other GPS-collared pack

233   members. The latter was limited to 3 pairs of GPS-collared wolves that were nominally in the

234   same pack during a 30-day period. The proportion of simultaneous fixes that wolves in each pair

235   were near each other (< 2 km) was low: 3%, 6%, and 22%.

236   We checked that our estimate of diel wolf activity was a valid index of diel hunting

237   pressure during the study period by comparing mean 1-hour diel movement rate to the hourly

238   distribution of daylight (0700-2000) observations of wolves encountering elk in winter from

239   1995-2003. An encounter was defined as wolves approaching, harassing, chasing, and (or)

240   grabbing elk. Details about how we observed and recorded wolf-elk encounters are described

241   elsewhere (MacNulty et al. 2007).

242   A concurrent cause-specific mortality study established that wolves were the primary

243   predator of our sample of adult female elk; only one case of cougar-caused mortality was

244   documented (Evans et al. 2006). Analyses of wolf-killed prey during our study period also

245   revealed that elk comprised 90-96% of prey species killed by wolves during winter (Smith et al.

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246   2004; Metz et al. 2012). Together, these studies indicate that the opportunity to kill elk was a key

247   driver of wolf activity in our study area during the period of interest (2001-2004).

248

249   *Spatial variation in wolf predation risk*

250   We considered multiple indices of spatial variation in wolf predation risk because it is

251   unclear how elk perceive spatial risk (Beschta and Ripple 2013, Kauffman et al. 2013, Moll et al.

252   2017). We calculated four indices of spatial risk: predicted occurrence of wolf-killed elk

253   (Kauffman et al. 2007, 2010), density of wolf-killed elk (Gude et al. 2006), openness (Creel et al.

254   2005, Fortin et al. 2005, Mao et al. 2005), and wolf density (Fortin et al. 2005, Mao et al. 2005,

255   Forester et al. 2007). Kill sites are a well-established metric of predation risk in wildlife systems

256   (e.g., Hopcraft et al. 2005; Thaker et al. 2011; Gervasi et al. 2013; Lone et al. 2014). All spatial

257   risk indices (30 x 30 m grid cell) were developed using the Geospatial Modelling Environment

258   or ArcGIS 10.1.

259

260   Predicted kill occurrence

261   We used a previously published model to predict the spatial distribution of wolf-killed

262   elk in northern YNP during each winter of our study (Fig. 1a). Kauffman et al. (2007) developed

263   this model to understand elk response to wolf predation risk in northern YNP. It estimates the

264   relative probability of a kill on the landscape compared to random locations based on the

265   landscape attributes of 774 locations of wolf-killed elk. These kills included all age and sex

266   classes and were documented in winter during a period (1996-2005) that encompassed the

267   present study. Landscape attributes included annual distribution of wolf packs (based on

268   cumulative kernel densities weighted by pack size), relative elk density (from an elk habitat

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269   model; Mao et al. 2005), proximity to streams, proximity to roads, habitat openness (forest vs.

270   grassland), slope, and snow depth. The model predicts kill occurrence with respect to the average

271   value of each landscape attribute, such that a predicted kill occurrence of 1 equals no difference

272   between the location of interest and the average landscape, whereas a predicted kill occurrence

273   of 10 equals a kill probability 10 times greater than average for a given year. This produces a

274   year-specific range of values that did not exceed 245 for any year. For example, the range in

275   winter 2000-01 was 0 – 36.5 whereas the range in winter 2001-2002 was 0 – 245.

276

277   Kill density

278   We used a kernel density estimator (KDE) to estimate the spatial distribution of wolf-

279   killed adult female and calf elk in northern YNP during each winter of our study (Fig. 1b). We

280   excluded kills of adult males because their spatial distribution differed from that of adult females

281   and calves (Pearson's correlation coefficient, $r = 0.39$; Appendix S2), and we sought to control

282   for possible behavioral responses of adult female elk to sex-specific kill distributions. A total of

283   235 wolf-killed adult female and calf elk were recorded across the 4 winters (Nov. 2000 – Apr.

284   2004) following established protocols (Smith et al. 2004). The number of kills included in each

285   annual kill density KDE ranged from 44-84. Following previous studies, we used a fixed

286   bandwidth of 3 km (Fortin et al. 2005). Annual kill density KDEs were standardized from 0 – 1.

287

288   Openness

289   We calculated openness (Fig. 1c) as the sum of non-forested cells within a 500 x 500 m

290   moving window centered on each grid cell (range 0 [deep forest] – 289 [open grassland])

291   following Boyce et al. (2003). We obtained information on the spatial distribution of vegetation

13

292   types in northern YNP from databases provided by the YNP Spatial Analysis Center. Non-

293   forested pixels were identified from a 1991 vegetation layer which accounted for vegetative

294   changes following the 1988 fires in and near YNP (Mattson et al. 1998). We used this layer to

295   calculate openness because it permitted direct comparison with contemporaneous northern

296   Yellowstone elk habitat selection studies that also utilized the 1991 vegetation layer (e.g., Boyce

297   et al. 2003, Fortin et al. 2005, Mao et al. 2005). We verified that our map of openness was

298   representative of conditions during the study period by comparing it to one calculated from a

299   2001 LANDFIRE vegetation layer (landfire.gov). We developed and analyzed a single map of

300   openness because there was no inter-annual variation in openness during the study.

301

302   <u>Wolf density</u>

303   We estimated wolf density (Fig. 1d) from winter aerial wolf telemetry locations that were

304   randomly filtered to obtain a single location per pack per day. We calculated a least-squares

305   cross-validation fixed smoothing factor (H) for each pack with at least 25 locations per winter

306   using Animal Space Use 1.3. Using all non-redundant locations, we used mean H (1 km) to

307   calculate annual winter bi-weight kernel densities weighted by pack size (Forester et al. 2007).

308   Annual wolf density KDEs were standardized from 0 – 1.

309

310   *Elk habitat selection*

311   We analyzed elk habitat selection using matched case-control logistic regression (CCLR).

312   We used a 1:3 empirical sampling design (Fortin et al. 2005) where, for each end location of a

313   movement step, 3 available locations were sampled with replacement from each individual's

314   respective step-length and turning-angle distributions. Each set of 4 locations defines a unique

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315   stratum (k). Successive strata ($k = 10,199$) were not independent. Although this autocorrelation

316   does not affect estimated coefficients it does bias the associated standard errors (Fortin et al.

317   2005). We calculated robust standard errors by specifying an intragroup correlation in our model.

318   Groups were clusters of strata ($n = 1,080$ clusters) assigned sequentially to each individual each

319   winter and defined by a step-lag at which the autocorrelation was nearly zero. Autocorrelation

320   analysis indicated that this step-lag was 15 steps, such that steps separated by 75 hours were

321   independent (Basille et al. 2015).

322   We fitted the following CCLR model to all clusters using generalized estimating

323   equations (Craiu et al. 2008):

324

325                                  $$(w) = \exp(X'\beta) \tag{1}$$

326

327   where β is a vector of fitted coefficients and X is matrix of explanatory variables for all used and

328   available locations that describe the relative probability of a movement step (w), which is the

329   straight-line segment between successive locations at 5-hour intervals. Movement steps with a

330   higher score relative to the set of possible steps have higher odds of being chosen by an animal

331   (Fortin et al. 2005). The sign of the relationship between w and spatial risk indicates steps toward

332   or away from risky places: a positive relationship indicates steps toward risky places whereas a

333   negative relationship indicates steps away from risky places. Values of w that depict these

334   relationships reflect different levels of perceived predation risk that correspond to the 'peaks'

335   and 'valleys' in a LOF: minimum values identify peaks (high perceived predation risk) and

336   maximum values identify valleys (low perceived predation risk). We rescaled predicted values of

337   w to present an intuitive visualization of the elk LOF (see below).

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338   We could not estimate the main effect of mean 5-hour wolf movement rate because it did

339   not vary within a stratum owing to how used and available locations within a stratum share the

340   same point in time. Within the case-control design of our model, spatial risk variables assigned

341   to each of the three control locations came from the same year in which the use location

342   occurred. Because results did not differ between models fitted to all clusters and models fitted to

343   every other independent cluster ($n = 2$ independent datasets), we present results from the analysis

344   of all the clusters.

345   For each spatial risk index, we developed a 'space-only' habitat selection model and

346   compared it to a 'space × activity' model that included terms for the interaction between spatial

347   risk and mean 5-hr wolf movement rate. The space × activity model evaluated how elk selection

348   for risky places at the end of a 5-hour movement step was affected by the mean wolf movement

349   rate during that step. Because prey may not respond instantaneously to predator activity due to

350   imperfect knowledge (Brown et al. 1999), optimal foraging strategies (Kie 1999), shell games

351   (Mitchell and Lima 2002), large landscapes (Middleton et al. 2013a), or a combination thereof,

352   we evaluated the potential for a behavioral lag in habitat selection up to the preceding behavioral

353   step (i.e., 5 hours). We tested different forms of the relationship between habitat selection and

354   spatial risk in the space-only analysis and compared the best-fit space-only model to the best-fit

355   forms in the space × activity analysis. This was necessary to account for how elk in northern

356   YNP may tolerate low levels of spatial risk (Fortin et al. 2005, Mao et al. 2005). We tested for a

357   response threshold by comparing models with a linear effect for spatial risk to models with a

358   threshold effect specified by two linear splines. We performed a grid search of candidate CCLR

359   models to determine the presence and position of thresholds. To control for outliers, we imposed

360   constraints such that the threshold occurred within 1 – 99% of all used data points for a given

16

361   spatial risk index. This resulted in a range of candidate models (n = 41-288) depending on the

362   precision (i.e., decimal units) and scale (i.e., difference in minimum/maximum values) of the

363   spatial risk index.

364   We compared models using the quasi-likelihood under independence criteria (QIC; Pan

365   2001), which considers independent clusters of observations while also accounting for non-

366   independence between subsequent observations (Craiu et al. 2008). The most parsimonious

367   model was the one with the lowest QIC and smallest ΔQIC, which equals the QIC for the model

368   of interest minus the smallest QIC for the set of models being considered. The best-fit model has

369   a ΔQIC of zero.

370   We performed 1,000 iterations of a 5-fold cross validation for case-control design to

371   evaluate the predictive accuracy of each best-fit model (Boyce et al. 2002). Location data were

372   partitioned into five equal sets and models were fitted to each 80% partition of the data, while the

373   remaining 20% of the data were withheld for model evaluation. Within a cross-validation, the

374   estimated probabilities were binned into 10 equal bins and correlated with the observed

375   proportion of movement steps within the evaluation set. This yielded an average Spearman rank

376   correlation (r_s). Correlations > 0.70 indicate satisfactory fit of models to data (Boyce et al. 2002).

377   CCLR analyses and k-folds cross validations were performed in R 3.0.2 using the SURVIVAL

378   and HAB packages, respectively.

379

380   *Visualizing the landscape of fear*

381   We used predicted values from our best-fit space × activity step selection model to

382   visualize the LOF for elk in northern YNP. For simplicity, we focused on a single index of

383   spatial risk: kill density. We calculated the predicted relative probability of a movement step ($\hat{w}$)

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384 at each level of kill density at each hour of diel wolf activity. We rescaled these values $(1 - \hat{w})$

385 and used the results to elevate the 2-dimensional kill density layer in ArcScene 10.2. Rescaling

386 was necessary so that higher elevations indicated increasing levels of perceived predation risk as

387 per the LOF concept. We constructed a static visualization at two hours when wolf activity was

388 highest (1100: 2.80 km/5-hour) and lowest (1600: 1.42 km/5-hours), and an animated

389 visualization that showed perceived predation risk at each hour of the diel cycle (0000-2300).

390

391   RESULTS

392   Most GPS-collared wolves (19 of 21) were crepuscular such that their hourly movement

393 rates followed: morning > evening > night > day (Fig. 2a). There was less individual-level

394 variation during peak morning hours than during peak evening hours, indicating that morning

395 was a more reliably active period. The population-average pattern in hourly movement rate

396 during 2004-2013 matched the hourly distribution of directly-observed daylight wolf encounters

397 with elk ($r = 0.79$; $N = 502$ encounters; Fig. 2a) during 1995-2003. A similar and slightly

398 stronger association was evident when we limited the encounter data to actual kills ($r = 0.87$, $N =$

399 89 kills). This suggests that diel variation in wolf movement rate was a meaningful index of diel

400 variation in wolf predation risk. It also suggests, together with evidence that the crepuscular

401 pattern in Fig. 2a was consistent across years (Appendix S3), that the crepuscular pattern during

402 2004-2013 was representative of the crepuscular pattern during 2001-2004 when elk location

403 data were recorded.

404   We estimated wolf movement rate as distance travelled per 5 hours to match the time

405 interval between consecutive elk locations. This shifted the timing of wolf activity to later in the

406 day but it did not alter the crepuscular pattern (Fig. 2b). The mean diel movement rate (km/5-hrs)

18

407   of elk was similarly crepuscular except that the timing of high and low movement rates was

408   opposite that of wolves: elk movement was greatest at dusk and less at dawn (Fig. 2b).

409   Correlation between wolf and elk movement rates was moderate ($r = 0.58$).

410   Irrespective of diel wolf movement, the influence of spatial risk on elk habitat selection

411   was inescapably nonlinear. For each spatial risk index, the best-fit space-only model included a

412   linear spline for spatial risk (Appendix S4), indicating a threshold at which the effect of spatial

413   risk on habitat selection changed. Evidence against a model describing a simple linear

414   relationship between spatial risk and habitat selection was strong for predicted kill occurrence

415   (ΔQIC = 347.13), kill density (ΔQIC = 78.72), openness (ΔQIC = 16.35), and wolf density

416   (ΔQIC = 9.98; Appendix S4). The best-fit models indicated that elk preferred increasingly risky

417   places at low levels of spatial risk ($P < 0.001$; Appendix S5), perhaps due to more food in these

418   areas. At high levels of spatial risk, the effect of risk on habitat selection was negative (wolf

419   density; $P = 0.02$), positive (kill density, $P < 0.01$; openness, $P < 0.001$), or nil (predicted kill

420   occurrence; $P = 0.76$; Appendix S5).

421   Support for the best-fit space-only models was substantially weaker compared to models

422   that included space × activity interactions between mean diel movement rate (km/5-hrs) of

423   wolves (Fig. 2b) and linear splines for predicted kill occurrence (ΔQIC = 126.73), kill density

424   (ΔQIC = 95.28), openness (ΔQIC = 200.98), and wolf density (ΔQIC = 35.28; Appendix S6).

425   The best-fit space x activity model included a time lag of 2 hour (kill density, openness, wolf

426   density) or 3 hours (predicted kill occurrence; Appendix S6). Five-fold cross validation revealed

427   strong correlations between observed and predicted values for the best-fit space × activity

428   models that included predicted kill occurrence (mean Spearman-rank correlation, $r_s = 0.99$),

429   openness ($r_s = 0.99$), and kill density ($r_s = 0.97$). Correlations of this magnitude indicate that

430 these models are reliable. By contrast, the reliability of the model that included wolf density was

431 poorer ($r_s = 0.67$), consistent with earlier findings that wolf density is an inaccurate index of

432 spatial risk in northern YNP due to wolf packs displacing one another from the best hunting

433 grounds where they kill elk (Kauffman et al. 2007). We therefore excluded the wolf density

434 model from further consideration.

435   Negative space × activity interactions before or after thresholds in predicted kill

436 occurrence ($P < 0.001$; before threshold), kill density ($P < 0.001$; after threshold), and openness

437 ($P < 0.001$; before and after threshold; Appendix S7) showed that elk avoided open grasslands

438 and places where kills occurred when wolf activity was high, but selected for these places when

439 wolf activity was low (Fig. 3a-c). Habitat selection probably did not vary beyond a predicted kill

440 occurrence of 4.5 (Fig. 3a; $P = 0.87$; Appendix S7) because there were few places where the

441 predicted kill occurrence was more than 4.5 times the average kill probability; together, these

442 places comprised only 7% of the study are.

443   To assess the time of day that elk selected for risky places, we calculated the bi-hourly

444 frequency that elk steps ended in these places. A place was 'risky' if it exceeded the average

445 value of a spatial risk index measured across all available locations in the study area. For

446 example, 10.5% of 4084 elk steps ending in places that exceeded the study area's mean predicted

447 kill occurrence (4.5) happened at 0400-0500, whereas 5.5% of these steps happened at 1200-

448 1300 (Fig. 3d). Steps ending in risky places were most frequent from 2200-0500, which

449 corresponded to the nightly lull in wolf activity (Fig. 3d-f).

450   To illustrate the effects of diel wolf activity on the elk LOF, we focused on kill density in

451 a portion of our study area (Fig. 4a). Using our best-fit space × activity model for this index (Fig.

452 4b), we show that places where kills were densely concentrated were valleys (low perceived

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453   predation risk) when wolf activity was low (Fig. 4c) and peaks (high perceived predation risk)

454   when wolf activity was high (Fig. 4d). Wolf downtime allowed elk to use places where wolves

455   were more likely to kill them, flattening the LOF every night for about 12 hours (Fig. 3d-f, Video

456   S1). This may explain why prime-aged (2-11 years-old) elk in our sample were in excellent body

457   condition (% ingesta-free body fat; $\bar{x} \pm \mathrm{SE} = 10.12 \pm 0.18$, $n = 13$) with high pregnancy rates

458   (0.89 ± 0.11, $n = 15$) when radio-collared at midwinter.

459

460   DISCUSSION

461   The LOF has been proposed as a possible unifying concept in ecology that explains

462   animal behavior, population dynamics, and trophic interactions across diverse ecosystems

463   (Brown and Kotler 2004, Schmitz 2005, Heithaus et al. 2009, Laundré et al. 2010; Catano et al.

464   2016). It has also been argued that effective ecological restoration may depend on reestablishing

465   landscapes of fear because fear may be as or more important than direct killing in structuring

466   food webs and modifying ecosystem function (Manning et al. 2009, Suraci et al. 2016). Doubts

467   about the conceptual and practical importance of the LOF stem from a dearth of information

468   about it how it operates across large spatial scales in free-living systems involving apex predators

469   and highly mobile prey (Hammerschlag et al. 2015). We addressed this gap with extensive data

470   from the Yellowstone elk-wolf case study that was the original basis for the LOF concept.

471   An important aspect of our study is that we measured the LOF as a spatial mapping of

472   time allocation (avoiding risky places and times). This approach accords with the original and

473   widely applied definition of a LOF as a spatial mapping of "any measure of fear" (Laundré et al.

474   2001, 2010), but differs from the definition of a LOF as a spatial mapping of an animal's

475   foraging cost of predation (Brown and Kotler 2004). The latter is calculated from giving-up

476   densities which are difficult to measure across vast landscapes like the one we studied (see

477   Bedoya-Perez et al. 2013 for details about the practical uses of giving-up densities). Reconciling

478   the two definitions is important because analyses of a single fear response may describe a

479   landscape that is qualitatively different from a landscape of predation foraging cost, which is an

480   integrative measure of fear that accounts for potential differences in how animal vigilance and

481   time allocation vary with predation risk. For example, if an animal increases its vigilance while

482   foraging in risky places, these places will appear as valleys in a map of time allocation and as

483   peaks in a map of predation foraging cost, thus masking potential ecological effects of fear.

484   Alternatively, if an animal manages risk mainly with time allocation (keeping vigilance constant

485   across safe and risky places), or if vigilance and time allocation respond similarly to temporal

486   variation in risk (decreasing vigilance while foraging in risky places at safe times; Lima and

487   Bednekoff 1999), then the two maps will agree. Constant vigilance provides perfect agreement

488   (Brown 1999), whereas vigilance that covaries with time allocation may provide relatively less

489   relief (lower peaks, shallower valleys) in the map of time allocation, thus underestimating the

490   foraging cost of predation.

491   Evidence that adult female elk in northern Yellowstone (and adjacent areas) maintain

492   constant vigilance levels across habitats that vary in wolf predation risk (high vs. low wolf

493   densities, near vs. far from forest cover: Childress and Lung 2003; Lung and Childress 2007;

494   Winnie and Creel 2007; Creel et al. 2008; Liley and Creel 2008) suggests our map of time

495   allocation (Fig. 4c-d) matches a map of predation foraging cost. These elk increase vigilance

496   levels only when wolves are an immediate threat (Winnie and Creel 2007; Creel et al. 2008; Lily

497   and Creel 2008; Gower et al. 2009; Middleton et al. 2013) because they can simultaneously

498   process their food and scan their surroundings (Fortin et al. 2004; Gower et al. 2009) as well as

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499   escape wolves that attack them (MacNulty et al. 2012; Mech et al. 2015). In general, animals,

500   especially food-limited ones, are expected to use little or no vigilance when they can escape

501   predators in the absence of vigilance (Brown 1999).

502   On the other hand, if elk vigilance is sensitive to short-term (≤ 24 hours) temporal

503   variation in wolf predation risk as many studies report (Winnie and Creel 2007; Creel et al. 2008;

504   Lily and Creel 2008; Gower et al. 2009; Middleton et al. 2013), then elk may increase vigilance

505   in risky places during periods of the diel cycle when wolves are most active. This is an open

506   question because studies have yet to test how spatial variation in elk vigilance changes across the

507   diel cycle. Nevertheless, theory predicts that an animal's vigilance level (and its predation

508   foraging cost) should track its predator encounter rate which is itself a function of predator

509   activity level (Houston et al. 1993; Brown 1999; Lima and Bednekoff 1999). If so, elk should

510   reduce vigilance when foraging in risky places during lulls in wolf activity when encounters are

511   infrequent (Fig. 2a) leading to a map of predation foraging cost with more relief than is evident

512   in our map of time allocation (Fig. 4c-d).

513   We make three important advances with our results. First, we provide a quantified

514   example of a LOF at an unprecedented large scale. Quantified examples are rarer than a casual

515   survey of the literature may suggest because authors often misdefine a LOF as spatial variation

516   in predation risk (e.g., Kauffman et al. 2010, Catano et al. 2016) or an animal's unmapped

517   response to spatial risk (e.g., Avgar et al. 2015, Hammerschlag et al. 2015, Lyly et al. 2015).

518   Relatively few studies have quantified a spatially-explicit map of an animal's response to

519   predation risk in accord with the LOF concept. These focused on marine invertebrates (Matasa

520   and Trussell 2011), rodents (van der Merwe and Brown 2008; Abu Baker and Brown 2010),

521   ungulates (Shrader et al. 2008; Druce et al. 2009, Iribarren and Kotler 2012), and primates

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522   (Willems and Hill 2009, Emerson et al. 2011, Coleman and Hill 2014) at small spatial scales (< 2

523   km^2). Our example is the only one that spans a large-scale (1000-km^2) landscape. We

524   accomplished this by combining movement data from individually-marked, wide-ranging

525   animals and spatial data describing continuous change in landscape attributes associated with

526   predation risk (kill site locations, vegetation cover). Moving forward, animal-borne transmitters,

527   especially those with accelerometers that permit fine-scale behavioral inferences (Mosser et al.

528   2014, Collins et al. 2015), together with remotely-sensed spatial risk data (e.g., vegetation cover)

529   may provide the most practical method to estimate landscapes of fear across ecologically-

530   relevant scales.

531   Second, we demonstrate that diel predator activity is a crucial driver of a LOF. In the

532   large-scale, free-living system we studied, the mere presence of a predator was a necessary but

533   insufficient condition to stimulate a LOF. Had we adopted the classic fixed risk assumption of

534   constant attack over time (Lima 2002) by ignoring diel predator activity, we would have

535   concluded, incorrectly, that our focal prey population had little fear of risky places (Appendix

536   S5). Instead, our consideration of diel predator activity revealed a LOF with peaks and valleys

537   that oscillated across the diel cycle according to the predator's activity rhythm (Fig. 4, Video

538   S1). This temporally-sensitive response aligns with the 'risk allocation hypothesis' (Lima and

539   Bednekoff 1999) which predicts that animals in high-risk environments take maximal advantage

540   of safe times to forage in risky places, and with numerous day-night and light-dark comparisons

541   that show how many taxa (e.g., zooplankton, rodents, and ungulates) use risky places at times of

542   the day when predator activity or hunting ability is minimal (Lima and Dill 1990, Lima 1998,

543   Brown and Kotler 2004, Caro 2005, Fischhoff et al. 2007, Tambling et al. 2012, Burkepile et al.

544   2013, Palmer et al. 2017).

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545   However, previous studies of diel predator effects on prey habitat use neither quantified a

546   LOF nor linked it to measured variation in diel predator activity as we did. These studies only

547   compared habitat use between day and night, or light and dark periods. This approach would

548   have obscured our results because wolf activity was a complex function of time of day that did

549   not neatly fit the conventional dichotomy of safe and dangerous periods (Fig. 2). As far as we

550   know, our study is the first to quantify how continuous variation in spatial predation risk (Fig. 1)

551   and diel predator activity (Fig. 2) interact with one another to affect an animal's habitat selection

552   (Appendix S7, Fig. 3) and, ultimately, its LOF (Fig. 4, Video S1). Ecologists have only recently

553   started to investigate the influence of diel predator activity on animal habitat selection (Fischhoff

554   et al. 2007, Tambling et al. 2012, Burkepile et al. 2013). Many of the classic studies of diel

555   predator effects, including zooplankton diel vertical migration (Iwasa 1982) and rodent response

556   to moonlight (Kotler et al. 1991), considered diel changes in the ocular capability of visual

557   predators (Gibson et al. 2009, Upham and Hafner 2013) rather than diel predator activity per se.

558   This aspect of predator-prey interactions deserves more attention because the prevalence of diel

559   activity patterns in apex predators across diverse ecosystems (e.g., Theuerkauf et al. 2003, Roth

560   and Lima 2007, Whitney et al. 2007, Andrews et al. 2009, Cozzi et al. 2012) suggests that it is a

561   potentially common driver of landscapes of fear.

562   Diel predator activity was an important driver of the landcape of fear in the system we

563   studied because it was a valid source of risk that prey could evidently perceive. Wolves are

564   cursorial hunters that find and select prey by actively searching the environment and visually

565   identifying vulnerable prey that are safe to kill (MacNulty et al. 2007, Mech et al. 2015). As a

566   result, the risk of wolf predation is low when wolves are not highly active. This is illustrated in

567   our data by how the frequency at which wolves encountered, attacked, and killed elk mirrored

568 changes in wolf activity levels (Fig. 2a). The low levels of nightime activity that we documented

569 is consistent with the hypothesis that wolves avoid hunting at night because their vision is best

570 adapted to crepuscular light (Kavanau and Ramos 1975, Roper and Ryan 1977, Theurerkauf

571 2009). This may explain why wolves in Yellowstone and most other regions exhibit a

572 crepuscular activity pattern (Theurerkauf et al. 2003, Theurerkauf 2009).

573   The strong statistical association between elk habitat selection and diel wolf activity

574 across three different measures of spatial risk (Appendix S7, Fig. 3) implies that elk perceived

575 diel variation in wolf activity. How elk did this is not obvious from our data. The lagged

576 influence of wolf activity on elk habitat selection (Appendix S7, Fig. 3d-f) suggests that elk did

577 not perfectly perceive changes in wolf activity. Or it could reflect a deliberate tradeoff between

578 safety and food in which elk accepted a higher likelihood of wolf encounter in exchange for

579 more time in preferred foraging habitats. Support for this hypothesis is given by the temporal

580 distribution of elk steps in risky places, which shows that elk minimized their steps in risky

581 places after wolf activity peaked in the morning and started increasing their steps back into these

582 places before wolf activity dipped in the afternoon (Fig. 3d-f). Elk probably tolerate a modest

583 likelihood of wolf encounter because they often survive encounters (MacNulty et al. 2007, Mech

584 et al. 2015). The success of wolves hunting elk in northern YNP during the study period rarely

585 exceeded 20% (Smith et al. 2000, Mech et al. 2001) and dropped below 10% when wolves

586 selected adult elk (MacNulty et al. 2012).

587   Our third key advance is that we provide the first approximation of the elk LOF that

588 prevailed in northern YNP following wolf reintroduction in 1995-1997. This matters to the

589 discipline of ecology and the practice of conservation because this particular case study is an

590 empirical cornerstone in the LOF concept (Laundré et al. 2001, 2010). Moreover, this case study

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591   is a seminal example in the broader debates about the ecological consequences of fear (Ripple

592   and Beschta 2004, Zanette et al. 2011) and the importance of apex predators to the structure and

593   function of ecosystems (Terborgh and Estes 2010, Dobson 2014). Our central finding is that

594   wolves established an elk LOF that was not as relentlessly intimidating as originally proposed

595   and subsequently argued. On the contrary, our results indicate that wolves established a dynamic

596   LOF that shifted hourly with the ebb and flow of wolf activity. Whereas previous studies

597   reported that elk behaviorally abandoned risky places in response to the mere presence of

598   wolves, our research reveals that elk maintained regular use of these areas during nightly lulls in

599   wolf activity. This finding is important because many hypotheses about the ecological effects of

600   the elk LOF in the Greater Yellowstone Ecosystem (GYE) assume that elk abandon risky places

601   when wolves are present.

602   For example, the 'predator-sensitive food hypothesis' that fear of wolves decreases elk

603   pregnancy rate via increased over-winter fat loss assumes that elk move into the protective cover

604   of nutritionally-improverished forests when wolves are present, reducing their use of preferred

605   grassland foraging habitats that have high predation risk (Creel et al. 2009). Although our study

606   is the first to show how elk can safely use grasslands when wolves are present, prior studies of

607   243 radiocollared elk across four GYE populations (northern Yellowstone, Madison headwaters,

608   Lower Madison, Clarks Fork) have already demonstrated that wolf presence does not prevent elk

609   from using grassland habitats (Fortin et al. 2005, Mao et al. 2005, Proffitt et al. 2009, White et al.

610   2009a, Middleton et al. 2013a). Evidence that wolves exclude elk from grasslands is limited to a

611   6.5-month study of 14 GPS-collared elk across two winters (2002-2003) in the Gallatin

612   population (Creel et al. 2005), and a two-month study of elk fecal pellet density across two

613   summers (1998-1999) in northern Yellowstone (Hernandez and Laundré 2005). Decreased elk

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614   pellet density with distance from forest edge has been interpreted as evidence that "elk made a

615   significant shift toward the forest edge" following wolf reintroduction (Laundré et al. 2010). This

616   inference is questionable because fecal pellet counts are prone to bias from observer error and

617   variation in fecal disappearance rates (e.g., Campbell et al. 2004, Jenkins and Manly 2008). It

618   also has little bearing on the predator-sensitive food hypothesis which concerns changes in

619   winter habitat use (Creel et al. 2009).

620   Fortin et al.'s (2005) 7-month study of 13 GPS-collared elk across two winters (2001-

621   2002) in northern YNP is also frequently cited as evidence that wolves exclude elk from

622   grasslands (e.g., Schmitz et al. 2008, Creel et al. 2009, Creel and Christianson 2009, Creel et al.

623   2011). However, its results are more ambiguous than often acknowledged. Elk were found to

624   prefer conifer forests to grasslands where wolves were numerous, but they were also *more* likely

625   to use grasslands as local wolf densities increased (Fortin et al. 2005: Fig. 3). Confusing matters

626   further, our 26-month study of 27 GPS-collared elk across four winters (2001-2004), which

627   included the 13 animals from Fortin et al. (2005), indicated that wolf density was an unreliable

628   predictor of elk habitat selection (Appendix S6) likely because wolf density was itself an

629   inaccurate gauge of wolf predation risk (Kauffman et al. 2007). These issues highlight the

630   preliminary quality of the results from Fortin et al. (2005).

631   In winter, our sample of 27 adult female elk used grasslands in northern YNP at night

632   when wolves were relatively inactive (Fig. 3c, 3f). Body fat and blood serum data taken from

633   these elk when radiocollared at mid-winter were consistent with the hypothesis that nocturnal use

634   of preferred grassland foraging habitats was sufficient to offset the effects of wolf presence on

635   elk over-winter fat loss and pregnancy rate. Prime-aged (2-11 yrs-old) animals carried enough

636   body fat (10%) in February to maintain a high rate of pregnancy (89%) contrary to the predator-

637   sensitive food hypothesis. Although our sample is small (<16), the results agree with those from

638   a larger sample of radiocollared elk (>90) from the same population and time period that

639   included the sample we analyzed (Cook et al. 2004; White et al. 2011). They also agree with

640   fetal data from 13,550 adult female, northern Yellowstone elk harvested in Montana (outside

641   YNP) during the 1985-2008 late-season (Dec-Feb) antlerless hunts that indicated pregnancy rate

642   was independent of wolf predation pressure (Proffitt et al. 2014).

643   Nocturnal use of grasslands may explain how other elk populations utilized these

644   preferred foraging habitats, and why they too maintained relatively high levels of over-winter

645   nutrition and/or pregnancy rate despite wolf presence (Hamlin et al. 2009; White et al. 2009b;

646   Middleton et al. 2013a, b). Counter arguments are based on a potentially unreliable fecal-based

647   pregnancy test of 4 elk populations (Creel et al. 2007, Garrott et al. 2009, White et al. 2011), a

648   snow urine nutritional assay of the Gallatin population over an unspecified time period

649   (Christianson and Creel 2010), and reviews of (un)published data (Creel et al. 2011, 2013). The

650   latter includes a 32% drop in pregnancy rate in the Madison headwaters population (Garrott et al.

651   2009) that was unrelated to nutrition (White et al. 2009b) and likely an artifact of small sample

652   size and uncontrolled effects of age, which have a profound influence on elk pregnancy rate

653   (Cook et al. 2004, Middleton et al. 2013b, Proffitt et al. 2014). Finally, the consistently

654   crepsucular pattern of wolf activity (Fig. 2, Appendix S3; Theurerkauf 2009) suggests a degree

655   of predictability in wolf predation risk that may explain why wolves have no effect on elk

656   reproduction via chronic stress (Creel et al. 2009, Boonstra 2013).

657   Elk behavioral abandonment of risky places is also a key mechanism in the behaviorally

658   mediated trophic cascade hypothesis, which asserts that fear of wolves increases productivity of

659   palatable woody deciduous plants in risky places via reductions in elk browsing (Ripple and

660   Beschta 2004, Beyer et al. 2007, Kauffman et al. 2010, Winnie 2012, Peterson et al. 2015).

661   Although population reduction via direct killing could also reduce elk browsing, evidence of an

662   apparent trophic cascade in northern YNP in the decade after wolf reintroduction has been

663   attributed to behavioral mechanisms in part because elk numbers remained high during that

664   period (Ripple et al. 2001, Ripple and Beschta 2004, Ripple and Beschta 2006, Beyer et al. 2007,

665   Ripple and Beschta 2012). We scrutinized the movements of every GPS-collared elk that was

666   tracked in that area during that decade, including 11 previously unreported animals, and our

667   results demonstrate that elk maintained access to aspen (*Populus tremuloides*) and willow (*Salix*

668   spp.) within risky places during daily wolf downtimes. This inference contradicts initial reports

669   from fecal pellet surveys and 13 GPS-collared elk indicating elk avoided aspen where wolves

670   were numerous (Ripple et al. 2001, Fortin et al. 2005). However, it agrees with a winter habitat

671   selection analysis of 80 VHF-collared elk followed in 2000-2002, concurrent to the 13 GPS-

672   collared elk tracked by Fortin et al. (2005), and compared with 94 VHF-collared elk followed

673   before wolf reintroduction in 1985-1990 (Mao et al 2005). This study found that elk *preferred*

674   aspen where wolves were numerous depending on slope and snow levels, and that "elk showed

675   no significant change in selection of aspen, which was highly preferred during winter in both

676   pre- and post-wolf reintroduction periods" (Mao et al. 2005: Table 6). Assessing results from

677   Fortin et al. (2005) and Mao et al. (2005) is difficult, however, because both studies relied on an

678   unreliable index of spatial risk (wolf density; Appendix S6) and an unvalidated GIS layer for

679   aspen.

680   Nevertheless, elk nocturnal use of areas of high predicted kill occurrence in 2001-2004

681   (Fig. 3d) accords with separate aspen data taken in 2004-2007 that showed aspen in these same

682   areas did not escape browsing (Kauffman et al. 2010). Similarly, elk avoided riparian areas with

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683   willow only during dawn periods (Beyer 2006). This behavior may explain why many willow

684   also did not escape browsing (Bilyeu et al. 2008, Marshall et al. 2013, 2014; but see Beyer et al.

685   2007). Persistent browsing on aspen and willow was probably also related to how many of these

686   plants existed outside of high-risk areas as defined by our indices of spatial risk (Appendix S8).

687   These results, together with evidence that wolf-caused changes in elk distribution arise from

688   wolves removing individuals rather than elk redistributing themselves (White et al. 2009a, 2010,

689   2012), support the hypothesis that any indirect effect of wolves on woody deciduous plants is

690   mainly the result of a density-mediated trophic cascade (Creel and Christianson 2009, Kauffman

691   et al. 2010, Winnie 2012, Marshall et al. 2014, Painter et al. 2015).

692   Although our data are the best available information about the role of wolves in shaping

693   the elk LOF in northern YNP during the first decade of wolf recovery, they are limited in at least

694   three ways. First, the 5-hour interval between consecutive elk locations was coarse and a

695   potential source of bias. This possibility is minimized by the fact that several studies have

696   analyzed subsets of our data and established that the 5-hour interval provides a valid basis for

697   understanding elk movement and habitat selection (Boyce et al. 2003, Fortin et al. 2005, Forester

698   et al. 2007, 2009). Second, our estimated diel wolf activity pattern (Fig. 2) was derived from

699   wolf GPS data collected over a 10-year period (2004-2013) that only partially overlapped our elk

700   study period (2001-2004). This was necessary because GPS data for wolves in YNP were not

701   available until 2004, and the number of wolves equipped with GPS collars each year was small

702   (2-5 animals; Appendix S1). Nevertheless, our estimated diel pattern was most likely

703   representative of the diel pattern during the non-overlapping years because it was: (1) correlated

704   with the time of day that we directly observed wolves encountering ($r = 0.79$) and killing ($r =$

705   0.87) elk during the non-overlapping years (Fig. 2a); (2) consistent across the years in which it

706 was measured (Appendix S3); and (3) similar to diel patterns described for other wolf

707 populations (Eggermann et al. 2009, Theuerkauf et al. 2003, 2009, Vander Vennen et al. 2016).

708   Although wolves were the primary source of mortality for our study population (Evans et

709 al. 2006), our study, like others before it, ignored the possibility that the elk LOF was shaped by

710 multiple predator species (e.g., wolves and cougars). One reason this may be important is if

711 different predator-specific activity schedules (crespuscular versus nocturnal) create conflicting

712 spatiotemporal patterns of predation risk that require prey to prioritize their response to one

713 predator at the expense of increasing their risk to another. In addition, our analysis did not

714 address the long-term dynamics of the elk LOF. Our results could be an artifact of the potentially

715 unique conditions that prevailed during our study period including a large and growing wolf

716 population, a large but shrinking elk population, and moderate to severe drought conditions.

717 Further research is necessary to determine if and how our estimate of the elk LOF may have

718 changed during the second decade of wolves in northern YNP.

719   In summary, our major insight is that an animal's spatially-explicit perception of

720 predation risk (i.e., its 'landscape of fear') over a large physical landscape tracks the daily

721 activity pattern of its primary predator, enabling the animal to utilize risky places during predator

722 downtimes, which in turn mitigates the impact of fear on animal resource use, nutritional

723 condition, and reproduction. Our results highlight how a LOF in a large scale, behaviorally-

724 sophisticated system like northern YNP is not a simple, unconditional function of a predator's

725 mere presence. To assume so may overestimate the threat of predation, underestimate the ability

726 of prey to efficiently manage this threat, and exaggerate the ecological effects of fear. We

727 encourage investigators to recognize the potential for free-living animals to adaptively allocate

728 habitat use across periods of high and low predator activity within the diel cycle. This

32

729   underappreciated aspect of animal behavior can help explain why strong antipredator responses

730   (e.g., movement, vigilance) may have weak ecological effects, and why these effects may not

731   rival those of direct killing. It also provides a basis for understanding why a LOF may have less

732   relevance to conservation and management than direct killing.

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1116

1117   FIGURES

1118   **Figure 1** Spatial variation in wolf predation risk during winter in northern Yellowstone National

1119   Park was indexed as (a) predicted occurrence of wolf-killed adult male, adult female, and calf

1120   elk, (b) density of wolf-killed adult female and calf elk, (c) openness, and (d) density of wolves.

1121   (a, b, and d) illustrate conditions during the first year of the study (2001). Openness was

1122   consistent across years. Black lines denote roads.

1123

1124   **Figure 2** Diel activity patterns of wolves and elk during winter in northern Yellowstone National

1125   Park. (a) Mean hourly movement rates for 21 GPS-collared wolves and predicted population

1126   mean from a general additive mixed model (left ordinate), and hourly number of directly-

1127   observed daylight encounters between wolves and elk (right ordinate). (b) Predicted 5-hr

1128   movement rates across 21 GPS-collared wolves (left ordinate) and 27 GPS-collared elk (right

1129   ordinate). Bars represent day (white), night (black), and variation in dawn/dusk periods (grey)

1130   from 15 Oct. – 31 May.

1131

1132   **Figure 3** Effects of diel wolf activity (predicted 5-hr wolf movement rate) on elk habitat

1133   selection in northern Yellowstone National Park, 2001-2004. (a-c) Elk were more likely to select

1134   risky places (areas where kills occurred and open grasslands) when wolf activity was low (1.42

1135   km/5-hrs) than when it was high (2.80 km/5-hrs); lines are population-averaged fitted values

1136   with 95% confidence intervals (shaded areas) from the best-fit space × activity models

1137   (Appendix S7). (d-f) Frequency of elk steps ending in risky places (locations > mean spatial risk:

1138   predicted kill occurrence = 4.5; kill density = 0.22; openness = 194; left ordinate) was greatest at

1139   night when wolf activity (mean 5-hr movement rate at 2-hr intervals; right ordinate) was low.

1140

1141   **Figure 4** Visualization of how diel wolf activity shaped the landscape of fear for adult female elk

1142   in northern Yellowstone National Park, 2001-2004. We examined kill density in one part of our

1143   study area, (a), and used the corresponding best-fit space × activity step-selection model, (b), to

1144   calculate elk avoidance across this area when wolf activity was low (1.42 km/5-hrs) and high

1145   (2.80 km/5-hrs). Risky places where kills were densely concentrated were valleys when wolf

1146   activity was low, (c), and peaks when wolf activity was high, (d). Black lines in (a,c, and d)
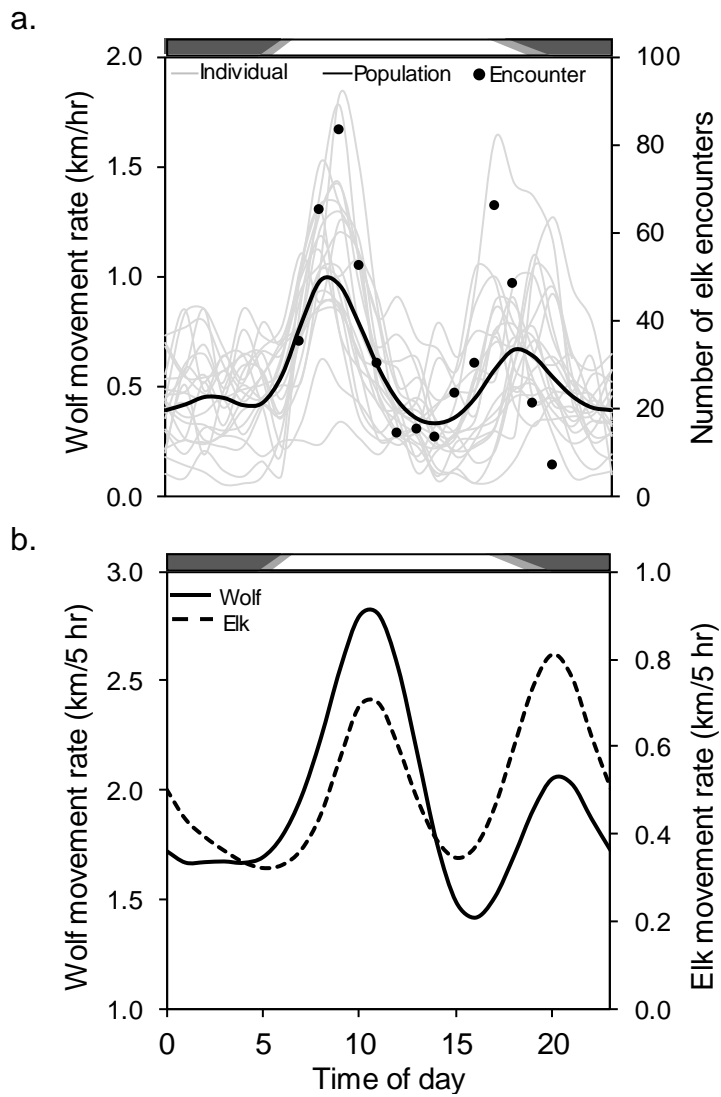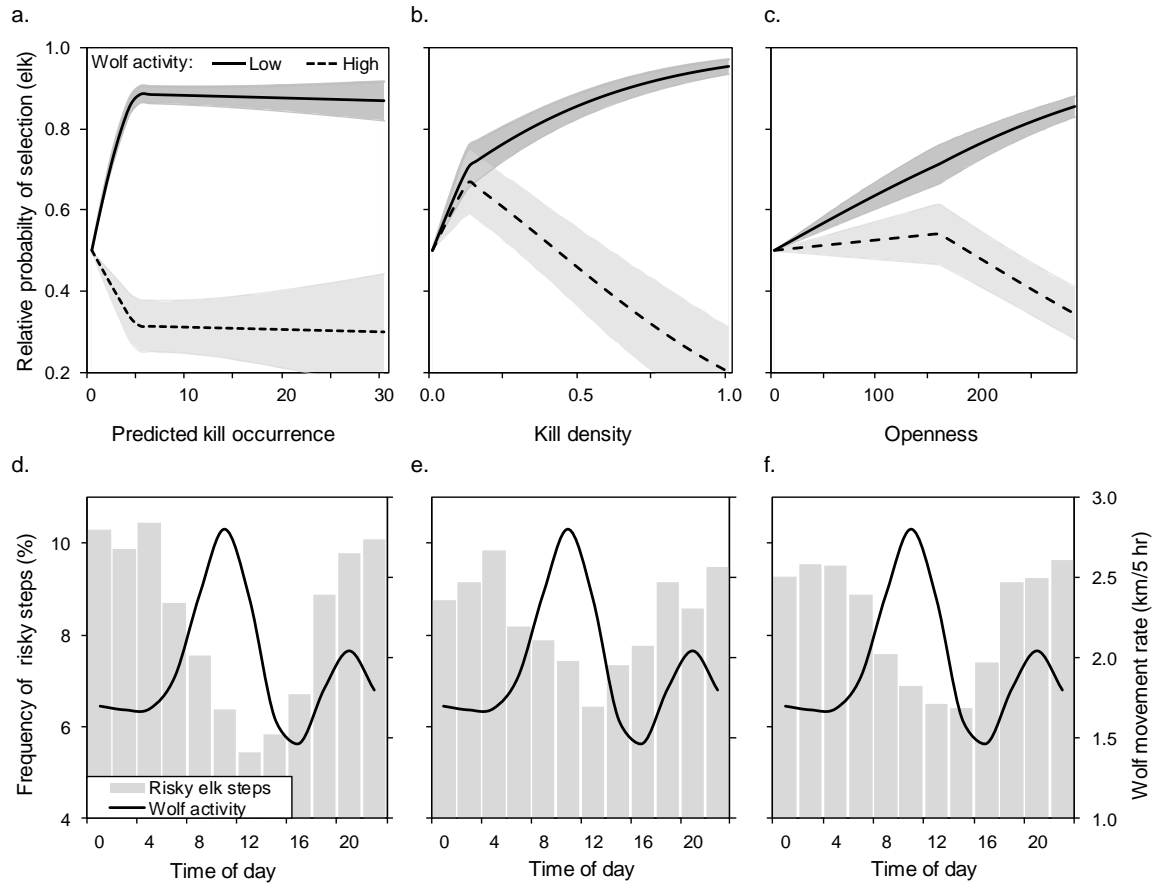
1147   denote roads.
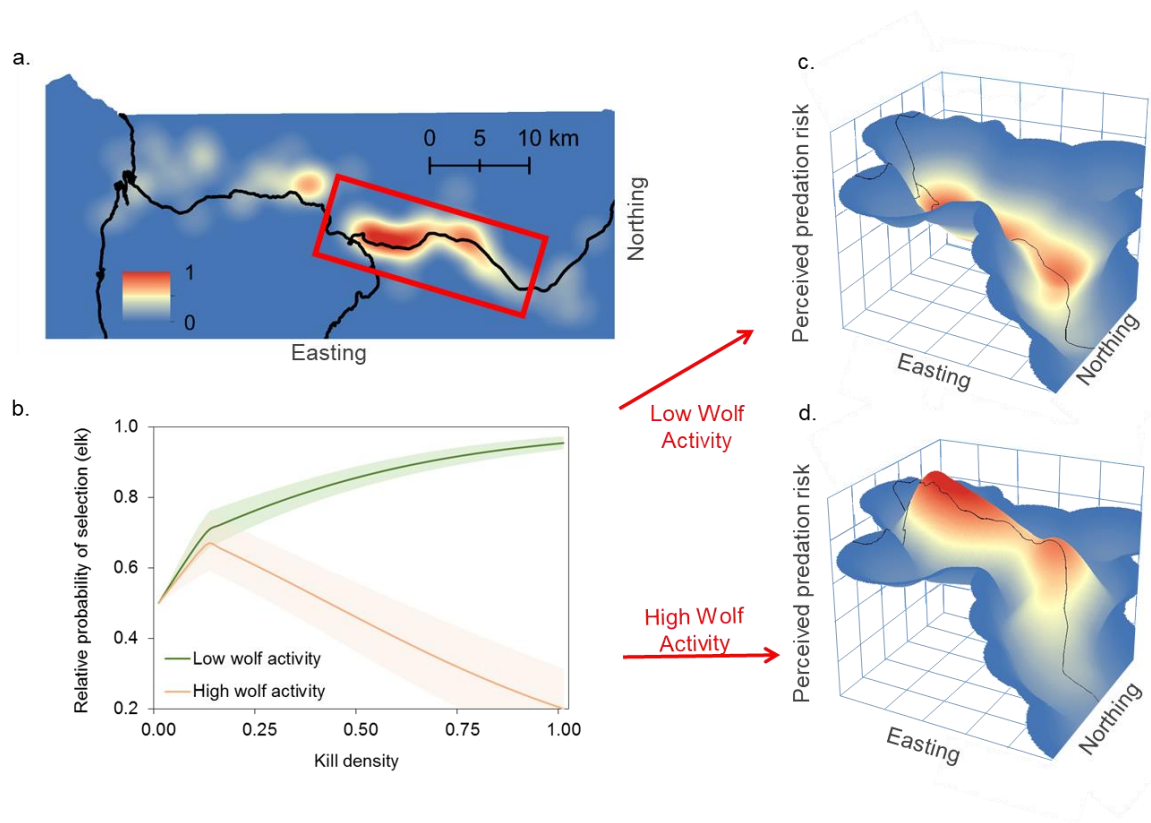
1148 **Figure 1.**
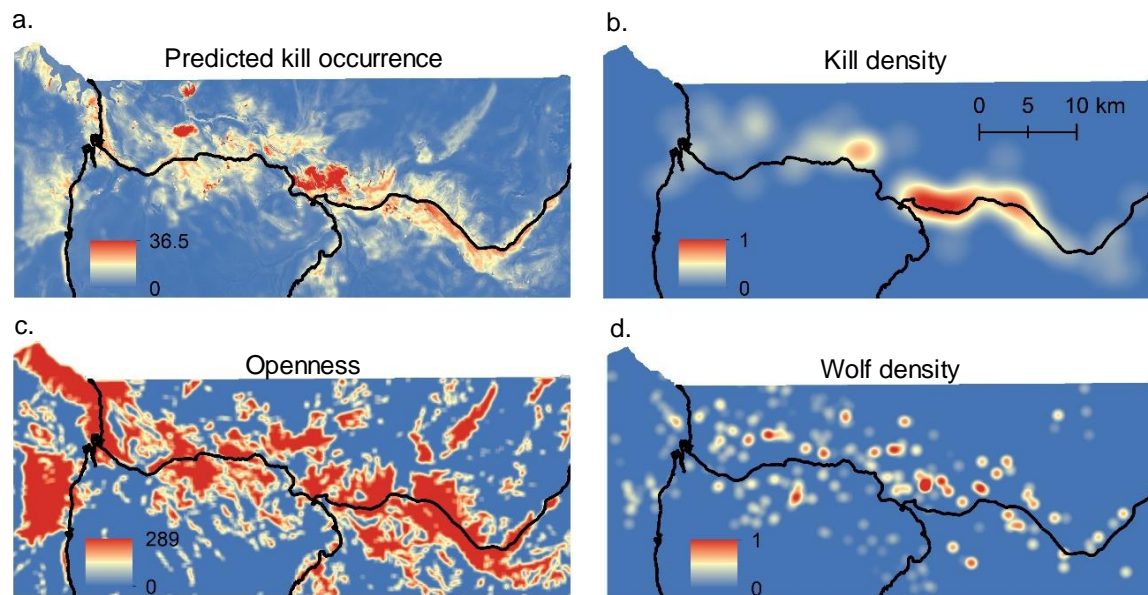
1149

1150

1151 **Figure 2.**

a.

b.

1152

1153 **Figure 3.**

1154

1155   **Figure 4.**

1156

1157

1159   Appendix S1. Sample size of movement steps used to calculate diel activity pattern for 21 GPS-collared wolves in northern
1160 Yellowstone National Park, 2004-2013. Values represent the steps calculated from consecutive 1-hour (outside parentheses) and 5-
1161 hour (inside parentheses) locations.

1162

		Winter									
Wolf ID	Sex	2004-05	2005-06	2006-07	2007-08	2008-09	2009-10	2010-11	2011-12	2012-13	2013-14
227	M	580 (120)									
470	F	629 (120)									
525	F		670 (135)	1387 (272)							
527	F		629 (127)								
593	F			438 (81)							
625	F				718 (144)	714 (140)					
627	M				714 (144)						
642	F						714 (142)	709 (144)			
685	M					714 (144)	1413 (282)				
692	F					620 (120)					
693	F					692 (140)	708 (144)				
752	F							704 (142)			
775	M							704 (140)	700 (138)		
777	M							708 (139)	1416 (282)		
829	F								712 (144)		
832	F								715 (144)	506 (100)	
889	F									533 (108)	652 (128)
890	M										714 (144)
907	F										694 (138)
910	M										694 (138)
SW763	M									698 (144)	1417 (275)
Total 1-Hr Steps		1209	1299	1825	1432	2740	2835	2825	3543	1737	4171
Total 5-Hr Steps		240	262	353	288	544	568	565	708	352	823

1163

1164   Appendix S2. Distribution of wolf-killed (a) adult male elk, and (b) adult female and calf elk

1165   during winter in northern Yellowstone National Park, 2001-2004. Contours are 10% kernel

1166   isopleths from a kernel density estimator applied to kill locations pooled across years. Red

1167   represents the highest density of kills and black lines denote roads.

1168

a.
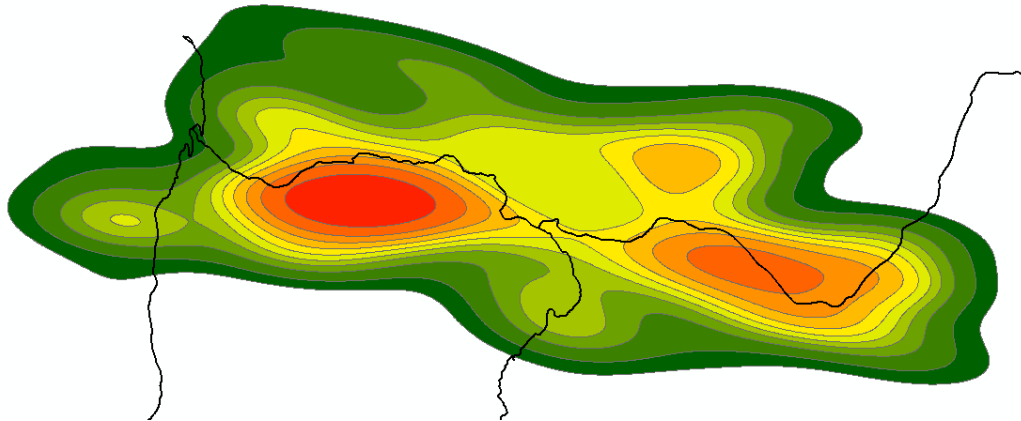
b.
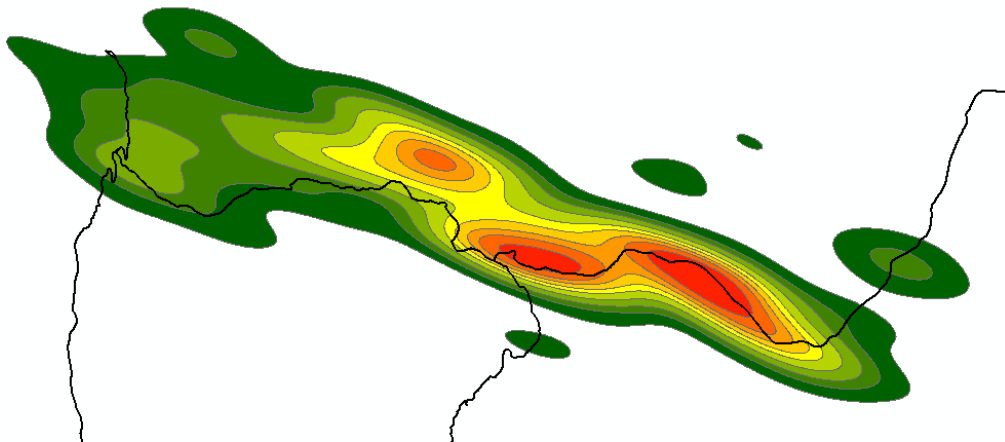
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1170

1171   Appendix S3. Annual diel activity patterns of wolves during winter in northern Yellowstone
1172   National Park, 2004-2013. Mean hourly movement rate for each of 10 years (2-5 GPS-collared
1173   wolves per year; Appendix S1) and predicted population mean from a general additive mixed
1174   model (left ordinate), and hourly number of directly-observed daylight encounters between
1175   wolves and elk (right ordinate). Bars represent day (white), night (black), and variation in
1176   dawn/dusk periods (grey) from 15 Oct. – 31 May.
1177
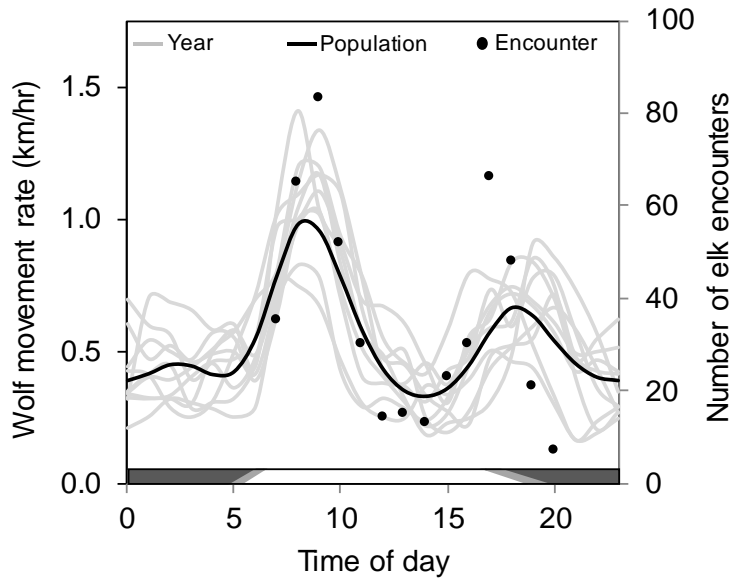
1179   Appendix S4. Model selection results for matched case-control logistic regression models
1180 describing the relationship between elk habitat selection and four indices of spatial risk
1181 (predicted kill occurrence [a], kill density [b], openness [c], and wolf density [d]) in northern
1182 Yellowstone National Park, 2001-2004. Variables risk1 and risk2 contain a linear spline for
1183 spatial risk at the indicated threshold. The simple linear model (risk) includes no threshold.
1184 Number of parameters (K), QIC, and differences in QIC compared to the best model (ΔQIC) are
1185 given for each model. The best model for each spatial risk index is in bold face.
1186

Model set	Threshold	*K*	QIC	ΔQIC
(a) Predicted kill occurrence				
risk	n/a	1	27560.52	347.13
risk1 + risk2	2.50	2	27214.47	0.83
risk1 + risk2	**2.60**	**2**	**27213.61**	**0.00**
risk1 + risk2	2.70	2	27214.12	0.48
(b) Kill density				
risk	n/a	1	28052.84	78.72
risk1 + risk2	0.11	2	27974.83	0.71
risk1 + risk2	**0.12**	**2**	**27974.12**	**0.00**
risk1 + risk2	0.13	2	27976.56	2.44
(c) Openness				
risk	n/a	1	27392.60	16.35
risk1 + risk2	1.00	2	27376.26	0.01
risk1 + risk2	**2.00**	**2**	27376.25	**0.00**
risk1 + risk2	3.00	2	27377.97	1.72
(d) Wolf density				
risk	n/a	1	28109.00	9.98
risk1 + risk2	0.40	2	28099.19	0.17
risk1 + risk2	**0.41**	**2**	**28099.02**	**0.00**
risk1 + risk2	0.42	2	28099.13	0.11

1187

1188

1189   Appendix S5. Best-fit matched case-control logistic regression models for the effects of four
1190 indices of spatial risk (predicted kill occurrence [a], kill density [b], openness [c], and wolf
1191 density [d]) on elk habitat selection in northern Yellowstone National Park, 2001-2004.
1192 Variables risk1 and risk2 are the slopes before and after each index-specific threshold. Model
1193 selection results are presented in Appendix S4. Confidence intervals were computed using robust
1194 standard errors.
1195

Parameter	Threshold	β	SE	P	[95% confidence interval]	
(a) Predicted kill occurrence						
risk1	2.60	0.479	0.030	<0.001	0.421	0.536
risk2		-0.001	0.003	0.755	-0.006	0.004
(b) Kill density						
risk1	0.12	6.82	0.62	<0.01	-13.25	13.49
risk2		0.67	0.13	<0.01	-1.321	1.321
(c) Openness						
risk1	2.00	0.1630	0.0400	<0.001	0.0760	0.2500
risk2		0.0025	0.0002	<0.001	0.0021	0.0029
(d) Wolf density						
risk1	0.41	0.84	0.18	<0.01	0.49	1.19
risk2		-2.06	0.84	0.02	-3.71	-0.40

1196

1197

1198   Appendix S6. Model selection results for matched case-control logistic regression models
1199 describing the interactive effect of spatial risk (predicted kill occurrence [a], kill density [b],
1200 openness [c], and wolf density [d]) and diel wolf activity (WA; km travelled/5-hr) on elk habitat
1201 selection in Yellowstone National Park, 2001-2004. Variables risk1 and risk2 contain a linear
1202 spline for spatial risk at the indicated threshold. Space-only models (risk1 + risk2) are the best-fit
1203 models from Appendix S5. Space x activity models are the top models from a grid search of
1204 thresholds for each hourly lag ($\leq$ 5) in diel wolf activity. Number of parameters (K), QIC, and
1205 differences in QIC compared to the best model (ΔQIC) are given for each model. Average
1206 Spearman-rank correlation between observed and predicted values calculated from K-fold cross
1207 validation (r_s) is given for the best-fit model (identified in bold).
1208

| Model set	Threshold	Lag	K	QIC	ΔQIC	r_s
(a) Predicted kill occurrence						
risk1 + risk2	2.60	NA	2	27213.61	126.73	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	3.40	0	4	27167.92	81.04	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	4.40	1	4	27126.15	39.27	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	4.50	2	4	27092.01	5.13	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	**4.50**	**3**	**4**	**27086.88**	**0.00**	**0.99**
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	4.20	4	4	27117.72	30.84	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	3.40	5	4	27171.30	84.42	
(b) Kill density						
risk1 + risk2	0.12	NA	2	27974.12	95.28	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	0.12	0	4	27906.66	27.82	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	0.12	1	4	27885.45	6.61	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	**0.12**	**2**	**4**	**27878.84**	**0.00**	**0.97**
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	0.12	3	4	27884.87	6.03	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	0.12	4	4	27909.96	31.12	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	0.12	5	4	27948.24	69.40	
(c) Openness						
risk1 + risk2	2.0	NA	2	27376.25	200.98	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	145.0	0	4	27257.81	82.54	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	147.0	1	4	27208.14	32.87	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	**159.0**	**2**	**4**	**27175.27**	**0.00**	**0.99**
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	165.0	3	4	27185.38	10.11	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	2.0	4	4	27242.36	67.09	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	2.0	5	4	27319.06	143.79	
(d) Wolf density						
risk1 + risk2	0.41	NA	2	28099.02	35.28	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	0.01	0	4	28077.67	13.93	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	0.02	1	4	28069.14	5.40	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	**0.02**	**2**	**4**	**28063.74**	**0.00**	**0.67**
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	0.03	3	4	28064.41	0.67	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	0.03	4	4	28071.01	7.27	
risk1 + risk2 + (risk1 x WA) + (risk2 x WA)	0.03	5	4	28086.39	22.65	

1209

1210

1211   Appendix S7. Best-fit matched case-control logistic regression models for the interactive
1212 effects of spatial risk (predicted kill occurrence [a], kill density [b], and openness [c]) and diel
1213 wolf activity (WA; km travelled/5-hr) on elk habitat selection in northern Yellowstone National
1214 Park, 2001-2004. Variables risk1 and risk2 are the slopes before and after each index-specific
1215 threshold. Model selection results are presented in Appendix S6. Confidence intervals were
1216 computed using robust standard errors.

1217

Parameter	Threshold	Lag	β	SE	P	[95% confidence interval]	
(a) Predicted kill occurrence							
risk1			1.103	0.072	<0.001	0.96	1.24
risk2	4.50	3	-0.009	0.028	0.744	-0.07	0.05
risk1 x WA			-0.456	0.036	<0.001	-0.53	-0.39
risk2 x WA			0.002	0.015	0.873	-0.03	0.03
(b) Kill density							
risk1			8.65	3.28	0.008	2.22	15.08
risk2	0.12	2	7.44	0.86	<0.001	5.75	9.13
risk1 x WA			-0.95	1.65	0.564	-4.18	2.28
risk2 x WA			-3.51	0.44	<0.001	-4.38	-2.64
(c) Openness							
risk1			0.011	0.002	<0.001	0.006	0.015
risk2	159.00	2	0.020	0.002	<0.001	0.016	0.024
risk1 x WA			-0.003	0.001	0.001	-0.005	-0.001
risk2 x WA			-0.009	0.001	<0.001	-0.011	-0.007

1218

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1220   Appendix S8. Aspen and willow distribution in northern Yellowstone National Park in
1221   relation to spatial variation in wolf predation risk (predicted kill occurrence [a], kill density [b],
1222   and openness [c]). Predation risk values in [a] and [b] are the average predicted kill occurrence
1223   and kill density at willow and aspen locations from 2000-2004. Aspen location data are from the
1224   1999 Northern Range Vegetation Layer of Yellowstone National Park (Spatial Analysis Center
1225   at Yellowstone National Park). Willow location data are from a comprehensive field mapping
1226   and inventory that concluded in 2010 (M. Tercek; http://www.yellowstoneecology.com/).
1227   Openness data are from a 1991 vegetation layer that accounted for vegetative changes follow the
1228   1988 fires (Mattson et al. 1998).
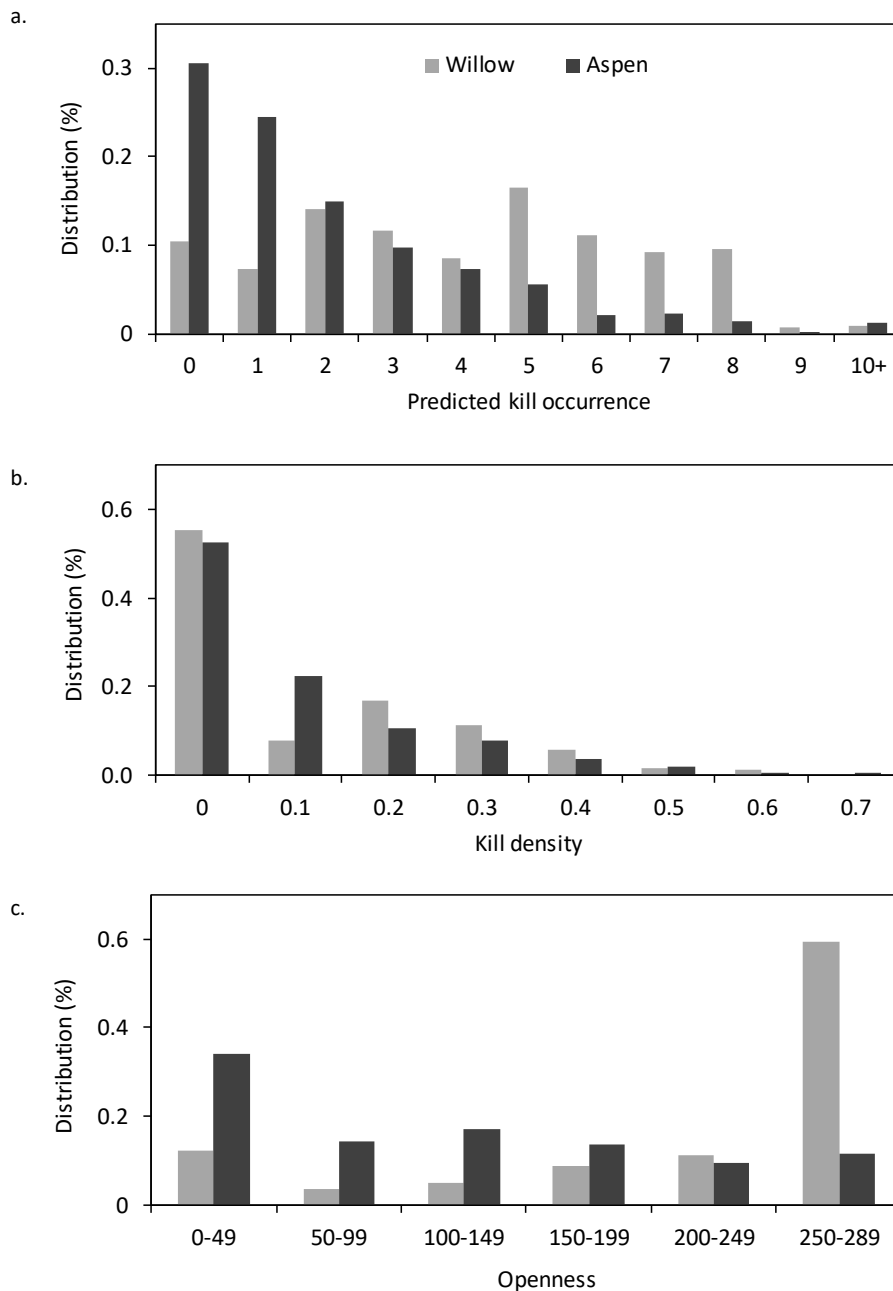
1229

1230   Video S1. Animated visualization of how diel wolf activity shaped the landscape of fear for
1231   adult female elk in northern Yellowstone National Park, 2001-2004. We examined kill density in
1232   one part of our study area, (a), and used the corresponding best-fit space × activity habitat
1233   selection model, (b), to calculate elk avoidance across this area throughout the diel cycle. Risky
1234   places where kills were densely concentrated are represented in red. Peaks identify risky places
1235   elk avoided; valleys represent safe places they utilized. Black lines denote roads.