

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

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4 Jeremy J. Cusack

5 Department of Zoology, University of Oxford, Oxford OX1 3PS, UK

6 Current affiliation: Biological and Environmental Sciences, University of Stirling,

7 Stirling FK9 4LA, UK

8 jeremy.cusack@stir.ac.uk

9

10 Michel T. Kohl

11 Department of Wildland Resources and Ecology Center, Utah State University,

12 Logan, UT, USA

13 michel.kohl@usu.edu

14

15 Matthew C. Metz

16 Department of Ecosystem and Conservation Services, University of Montana,

17 Missoula, MT, USA

18 matthew.metz@umontana.edu

19

20 Tim Coulson

21 Department of Zoology, University of Oxford, Oxford OX1 3PS, UK

22 tim.coulson@zoo.ox.ac.uk

23

24 Daniel R. Stahler

25 Yellowstone Center for Resources, National Park Service, Yellowstone National

26 Park, WY, USA

27 dan_stahler@nps.gov

28

29 Douglas W. Smith

30 Yellowstone Center for Resources, National Park Service, Yellowstone National

31 Park, WY, USA

32 doug_smith@nps.gov

33

34 Daniel R. MacNulty

35 Department of Wildland Resources and Ecology Center, Utah State University,

36 Logan, UT, USA

37 dan.macnulty@usu.edu

38

39 Corresponding author

40 Jeremy J. Cusack – jeremy.cusack@stir.ac.uk

41 Biological and Environmental Sciences, University of Stirling, Stirling FK9 4LA, UK

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50 **Abstract**

51 1. The extent to which prey space use actively minimises predation risk
52 continues to ignite controversy. Methodological reasons that have hindered
53 consensus include inconsistent measurements of predation risk, biased
54 spatiotemporal scales at which responses are measured, and lack of robust null
55 expectations.

56 2. We addressed all three challenges in a comprehensive analysis of the
57 spatiotemporal responses of adult female elk (*Cervus elaphus*) to the risk of
58 predation by grey wolves (*Canis lupus*) during winter in northern
59 Yellowstone, USA.

60 3. We quantified spatial overlap between the winter home ranges of GPS-
61 collared elk and three measures of predation risk: the intensity of wolf space
62 use, the distribution of wolf-killed elk and vegetation openness. We also
63 assessed whether elk varied their use of areas characterised by more or less
64 predation risk across hours of the day, and estimated encounter rates between
65 simultaneous elk and wolf pack trajectories. We determined whether observed
66 values were significantly lower than expected if elk movements were random
67 with reference to predation risk using a null model approach.

68 4. Although a small proportion of elk did show a tendency to minimise use of
69 open vegetation at specific times of the day, overall we highlight a notable
70 absence of spatiotemporal response by female elk to the risk of predation
71 posed by wolves in northern Yellowstone.

72 5. Our results suggest that predator-prey interactions may not always result in
73 strong spatiotemporal patterns of avoidance.

74

75 **Key-words:** *Canis lupus*, *Cervus elaphus*, null model, predation risk, proactive
76 avoidance, reactive avoidance, spatial overlap, Yellowstone

77

78 **Introduction**

79 How, and to what extent, prey respond to the risk posed by predators are central
80 questions in behavioural and community ecology (Sih, 1984; 1998). Although many
81 types of behavioural responses, such as grouping (Hebblewhite & Pletscher, 2002;
82 Fryxell et al., 2007) or increased vigilance (Elgar, 1989; Liley & Creel, 2007; Creel,
83 Schuette & Christianson 2014; Creel et al., 2017, Dröge et al., 2017), can be studied
84 through direct observation, others are more difficult to characterise
85 unambiguously. In particular, the extent to which prey movement patterns actively
86 minimise predation risk across space and time continues to ignite controversy (Creel
87 et al., 2008). Indeed, there is a debate regarding the relative importance of proactive
88 versus reactive spatiotemporal responses by prey to predators and the risk of
89 predation (Creel, 2018). Proactive avoidance, where prey purposefully avoid areas or
90 reduce activity during times of the day in which they are more vulnerable to predation
91 (Prugh & Golden, 2014; Kohl et al., 2018), has been highlighted to a varying degree
92 in a number of systems (Heithaus & Dill 2002; Creel et al., 2005; Fortin et al., 2005;
93 Dupuch et al., 2009; Heithaus et al., 2009; Valeix et al., 2009; Padié et al., 2015). In
94 contrast, reactive responses, which involve sudden displacements following more
95 rapid changes in predation risk within the immediate surroundings have received
96 increased attention in recent years owing to advances in tracking technology (Courbin
97 et al., 2013; Middleton et al., 2013a; Basille et al., 2015; Courbin et al., 2016; Martin
98 & Owen-Smith 2016).

99 Three common challenges arise when attempting to characterise prey

100 spatiotemporal responses to predation risk. The first relates to how exactly predation
101 risk is measured (Moll et al., 2017). It has often been assumed that the spatial
102 distribution of a predator reflects a heterogeneous landscape of predation risk (Lima
103 & Dill, 1990; Searle, Stokes & Gordon, 2008; Thaker et al., 2011). However, past
104 studies have suggested prey may in fact be more likely to avoid specific habitats or
105 landscape features that increase their vulnerability to predation (Hopcraft, Sinclair &
106 Packer, 2005; Kauffman et al., 2007; Kohl et al., 2018). Predation risk may also vary
107 over time, such as increase during times of the day when predators are more active or
108 have higher hunting success rates (Palmer et al., 2017; Gehr et al., 2018; Kohl et al.,
109 2018). In this context, Moll et al. (2017) recently recommended the use of multiple
110 metrics in studies of predation risk.

111 A second complication lies in defining the spatial and/or temporal scale at
112 which fear may act on prey behaviour (Kittle et al., 2008). A useful framework within
113 which to consider this question was provided by Johnson (1980) in the form of a
114 hierarchical classification of resource selection orders (see also Boyce, 2006). Past
115 research investigating predator-prey interactions have primarily focused on whether
116 the avoidance of predation risk by prey occurs at the level of home range selection
117 (2nd order) or at the level of patches within individual home ranges (3rd order) (e.g.
118 Courbin et al. 2013). However, few studies have considered how selection across
119 these orders varies along a temporal dimension, for example 2nd order selection
120 between years or 3rd order selection between different times of the day (although see
121 Kohl et al., 2018).

122 A final challenge concerns how the expectation of behaviour in the absence of
123 proactive and/or reactive responses is defined. For example, how would prey move
124 through a given landscape if they ignored predation risk? Indeed, characterisation of

125 prey spatiotemporal responses to predation risk has often been hindered by lack of an
126 appropriate null model with which to generate expected behaviour, such as random
127 movement (Gotelli & Graves 1996; Richard et al., 2013; Miller, 2015). Although step
128 selection functions, which implement randomisations at the individual step level,
129 provide a powerful tool to address this issue (Thurfjell, Ciuti & Boyce, 2014), their
130 ability to randomise at the level of entire home ranges or to incorporate the temporal
131 dimensions of space use is currently limited (although see Cozzi et al., 2018). An
132 alternative method was recently proposed by Richard et al. (2013), who extended the
133 application of null models used in community ecology to examine the potential for
134 spatial interactions. They did this by randomly permuting and shifting roe deer
135 *Capreolus capreolus* trajectories to obtain “pseudo-trajectories”, re-calculating the
136 level of overlap with the distribution of female red deer (*Cervus elaphus*) to generate
137 an expected distribution. Though promising, this approach has so far never been used
138 to measure the strength of prey responses to predation risk.

139 In this study, we address all three challenges in a uniquely comprehensive
140 analysis of the spatiotemporal responses of adult female elk (*Cervus elaphus*) to the
141 risk of predation by grey wolves (*Canis lupus*) during winter in northern Yellowstone,
142 USA. Since the reintroduction of wolves to Yellowstone in 1995, numerous studies
143 have sought to characterise potential proactive versus reactive responses of elk and
144 how these might relate to the trophic cascade observed across the ecosystem (Ripple
145 & Beschta 2012). The majority of studies investigating movement and habitat
146 selection responses by elk to the risk posed by wolves have revealed weak and
147 inconsistent patterns (Fortin et al., 2005; Mao et al., 2005; Forester et al., 2007;
148 Proffitt et al., 2009; White et al., 2008; Middleton et al., 2013a; Kohl et al., 2018).
149 Despite this large body of research, which was drawn from multiple elk populations

150 and relied primarily on movement data collected in the early years following wolf
151 reintroduction, there remains a persistent contention that wolves have strong and
152 consistent effects on elk space use (Winnie & Creel, 2017; Beschta, Painter & Ripple,
153 2018; Creel et al., 2018; Painter et al., 2018).

154 In this context, we first quantify spatial overlap between the winter home
155 ranges of GPS-collared elk and three measures of predation risk: the intensity of wolf
156 space use, the distribution of wolf-killed elk and vegetation openness. We then assess
157 whether elk vary their use of areas characterised by more or less predation risk across
158 the hours of the day. Lastly, we estimate encounter rates between collared elk and
159 wolf packs during six 32-day winter periods occurring between 2013 and 2015. For
160 all of these measures, we determine whether observed values are significantly lower
161 than expected if elk movements were random with reference to predation risk. To do
162 this, we implement a set of null model formulations that represent expectations of
163 prey movement in the absence of predation risk effects, while accounting for
164 elevation constraints known to affect winter elk movements. Using this approach, we
165 answer the following questions:

166

- 167 1) Does elk choice of home range within northern Yellowstone (hereafter,
168 philopatric behaviour) reflect proactive avoidance of spatial predation risk?
- 169 2) Does elk winter home range configuration reflect proactive avoidance of spatial
170 predation risk?
- 171 3) Do elk minimise use of risky areas at specific times of the day?
- 172 4) Do elk avoid close encounters with wolf packs?

173

174

175 **Materials and Methods**

176 Study area

177 The northern Yellowstone winter range encompasses roughly 1,520 km² of
178 mountainous terrain and open valleys, with elevation ranging from 1,500 to 3,210 m
179 (Houston, 1982). The area defines the winter range of seasonally migrating elk
180 (White, Proffitt & Lemke, 2012; Tallian et al., 2017), and is largely composed of
181 shrub steppe, with patches of intermixed lodgepole pine (*Pinus contorta*), Douglas fir
182 (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmanni*), and aspen stands
183 (Houston, 1982; Despain, 1990). We consider wolf and elk trajectories recorded over
184 the entire northern Yellowstone winter range – that is including land within
185 Yellowstone National Park (YNP) and north of the park boundary – and hereafter
186 refer to this as the northern range (NR). Winter severity in the NR is highly variable
187 but in general snowfall increases from west to east due to an elevation gradient that
188 approximates the distribution of elk on winter range, hence the inclusion of elevation
189 in null model formulations (see below). Snow cover generally lasts from late October
190 to early May but has recently become more variable (Middleton et al., 2013b).

191 Elk abundance in the NR has declined ~70% between 1995 and 2015.
192 Currently, elk abundance numbers around 6000 individuals. It is estimated that only
193 ~1500 of these elk overwinter in the YNP portion of the NR (Tallian et al., 2017). The
194 decline in NR elk abundance has been largely due to a reduction in elk numbers
195 within the NR's YNP section (White & Garrot, 2005; White et al., 2012; Tallian et
196 al., 2017). Elk are the primary prey of wolves in the study area (Smith et al., 2004;
197 Tallian et al., 2017).

198

199

200 Elk winter space use

201 We estimated individual-level home ranges for GPS-collared female elk during four
202 winters (2012-13, 2013-14, 2014-15 and 2015-16) (Fig. 1a). A winter was defined as
203 the period between November 1st of a given year and 30th April of the next. Elk
204 collars (Iridium TrackM 3D, Lotek Wireless Inc.) were first deployed in February
205 2011, with new additions and redeployments occurring each subsequent winter. Adult
206 (> 1 year old) female elk were captured using helicopter net-gunning. Recorded data
207 were uploaded via Iridium satellite every 4-12 fixes and subsequently downloaded
208 from a dedicated webserver. To ensure accurate representation of elk winter space
209 use, we excluded winter movement paths for which the average fix frequency was
210 more than five hours and the time difference between the first and last relocation was
211 less than four months.

212 For each winter, we estimated the individual-level utilisation distribution (UD)
213 of each collared elk over a continuous grid of cell size 1 by 1 km using a Brownian
214 bridge movement model (BBMM) implemented in the R package BBMM (Bullard,
215 1999; Horne et al., 2007). The BBMM is a continuous-time stochastic movement
216 model, where the probability of being in an area is conditioned on 1) the distance and
217 elapsed time between successive locations, 2) a measure of location error, and 3) an
218 estimate of the animal's mobility (the Brownian motion variance, see Horne et al.,
219 2007). In other words, the model approximates the movement path between two
220 subsequent locations by applying a conditional random walk. Because UD tails (i.e.
221 beyond the 95 % isopleth) tend to be poorly estimated, we generated conditional 95 %
222 UD's scaled to sum to unity (Benhamou et al., 2014). Location error for elk collars
223 was unknown and fixed to a conservative estimate of 50 m. To avoid pseudo-
224 replicating trajectories from collared elk belonging to the same group, we calculated

225 an index of movement cohesion for every elk dyad within a given winter. We used
226 Shirabe's (2006) correlation coefficient, which measures the degree of correlation
227 between the movement paths of two individuals as a multivariate Pearson product-
228 moment correlation coefficient (Shirabe, 2006; Long et al., 2014). The index ranges
229 from -1 (negative correlation) to 1 (positive correlation), with 0 indicating random
230 movement. If two elk trajectories recorded during the same winter showed a
231 movement correlation coefficient equal to or greater than 0.5, the one with the least
232 number of relocations was excluded from the analysis.

233

234 Wolf space use intensity

235 We used GPS collar data collected on wolves each winter between 2004 and 2016 to
236 characterise long-term winter space use patterns by packs in the NR (Fig. 1b). Wolf
237 GPS tracking has been routinely carried out by the Yellowstone Wolf Project since
238 2004, with a varying proportion of packs inside YNP sampled every year (details of
239 collaring procedures can be found in Smith & Bangs, 2009). Although the exact
240 model of fitted GPS collars varied during this period, all were manufactured by either
241 Telonics (Mesa, AZ, USA), Televilt (Lindeserg, Sweden) or Lotek (Newmarket, ON,
242 Canada). Average winter fix frequency between 2004 and 2016 varied between
243 periods of intensive monitoring of wolf movements when relocations were obtained
244 every hour (32-day winter periods, either Early Winter [EW] period between 14th
245 November and 15th December or Late Winter [LW] period between 28th February and
246 31st March) and periods characterised by longer delays between relocations (average
247 of 6 hours).

248 For each winter, we estimated a joint wolf UD representing the combined
249 spatial activity of all collared wolves during that winter. The joint wolf UD was taken

250 as the sum of individual wolf pack UD_s – each of these weighted by the size of the
251 corresponding pack (see Table S1, and Kauffman et al., 2007 for a similar procedure)
252 – and scaled to sum to unity. Utilisation distributions were estimated using BBMMs
253 estimated over the same spatial grid as that used for elk. We used a location error of
254 468 m for wolf packs as this represented the average distance between joint wolf
255 movements. We assumed that this value accounted for the position of individuals that
256 were not collared when estimating a pack’s UD (Benson et al., 2015). A final joint
257 UD representing wolf long-term space use in the NR was then derived by averaging
258 winter joint UD_s and scaling to sum to unity. By averaging across winters – which
259 differed in the number of packs collared (see Table S1 in Supporting Information) –
260 we aimed to produce a space use pattern representative of where wolves were more or
261 less likely to be encountered across the NR. Our study focuses on wolves collared
262 south of the YNP boundary, and thus the estimation of the wolf UD in the northern
263 section of the elk winter range relies on excursive movement from park packs.

264

265 Elk kill site density and vegetation openness

266 We used a long-term, spatially explicit dataset on female elk and calf kill sites
267 recorded in winter between 1995 and 2016 to derive a probability surface of observed
268 predation by wolves (Fig. 1c). In a similar way to Kohl et al. (2018), we used a kernel
269 density estimator implemented in the R package `adehabitatHR` to generate a smoothed
270 spatial distribution of kill sites, setting a fixed bandwidth of 1000 m to match the
271 resolution of the landscape grid. Lastly, we used a layer representing vegetation
272 openness as a third measure of predation risk (Fig. 1d). Values in this layer ranged
273 from 0 (thick forest) to 289 (open grassland) (see Kohl et al., 2018), which we
274 subsequently standardised to sum to unity in order to ensure consistency with

275 measures of wolf space use intensity and kill site density.

276

277 Spatial overlap

278 We defined spatial overlap as the volume of intersection (VI) between the UD of a
279 single elk during a given winter and a surface representing either one of the spatial
280 predation risk indicators. We interpret VI as the proportion of the volume of the elk
281 UD intersecting with a given predation risk layer (Kernohan, Gitzen & Millspaugh,
282 2001; Fieberg & Kochanny, 2005). The VI index, which ranges from 0 (no overlap) to
283 1 (complete overlap), has been widely used to compare UDs in a range of different
284 taxa (Fieberg & Kochanny, 2005). In our case, if UD_{Elk} and UD_{PR} are the estimated
285 utilisation distributions for an individual elk and predation risk type, respectively,
286 then

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

287 We calculated the VI index based on conditional 95 % UDs for elk, so as to minimise
288 bias associated with the poorly estimated UD tails (Fieberg, 2007; Benhamou et al.,
289 2014). We expected VI values to be low owing to the much larger spatial extent of
290 predation risk layer values relative to that of individual elk UD values (i.e. there were
291 many more instances of $UD_{Elk}(x,y) = 0$ across the landscape, biasing VI towards 0).
292 However, we stress that this in itself cannot be considered as evidence for proactive
293 avoidance behaviour, and is the reason why we implemented a null model approach
294 (see below).

295

296 Hourly predation risk

297 To investigate whether elk use of risky areas varied across the 24-hour cycle, we

298 modelled spatial predation risk level (wolf space use intensity, kill site density or
299 vegetation openness) associated with a given relocation as a function of hour of the
300 day. We used generalised additive mixed models (GAMMs) that included a term for
301 first order auto-regressive processes (i.e. auto-correlation AR(1)), and implemented a
302 cyclic cubic spline and Gaussian error structure (Wood, 2006). From this we obtained
303 a prediction for the observed predation risk level associated with each hour of the day.
304 For each type of predation risk considered, we ran one model per winter trajectory
305 using the *gamm* function in the R package *mgcv*.

306

307 Encounter rate

308 We measured the rate at which individual elk encountered wolf packs during six
309 periods of intense monitoring (hereafter, winter periods) characterised by wolf
310 relocations recorded every hour. Encounter rate was defined as ST/n where ST is the
311 total number of recorded encounters with wolves and n represents the total number of
312 fixes recorded for a given elk. Encounters consisted of spatially proximal and
313 temporally simultaneous elk and wolf fixes defined according to specific distance d
314 and time t thresholds, respectively (Long et al., 2014). We set d to 1000 m following
315 Middleton et al. (2013a), who found that elk tended to increase their rates of
316 movement, displacement and vigilance when wolves were within this distance
317 threshold. Temporal proximity t was set to 1 hour as this represented the average
318 length of a successful hunting bout by wolves (MacNulty, 2002). Thus, if elk and
319 wolf relocations obtained in the same 1-hour window were observed to be within
320 1000 m of one another, they constituted an encounter. Importantly, we use the term
321 “encounter” to denote a significantly increased likelihood of wolf-caused mortality
322 (MacNulty, Mech & Smith, 2007), which we assume elk would actively avoid (Creel

323 et al., 2005; Proffitt et al., 2009; Latombe, Fortin & Parrott, 2014). We excluded elk
324 trajectories for which the number of tracking days was less than 30. For ease of
325 interpretation, we present values of encounter rate for 100 elk fixes.

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

332

333 Null model formulations

334 We used a null model approach to determine whether the observed spatial overlaps,
335 encounter rates and hourly predation risk levels obtained for winter and period-level
336 elk trajectories were less than expected by chance. All null model formulations were
337 based on a correlated random walk, which randomly sampled the distributions of step
338 lengths and turning angles derived from the observed elk trajectory to construct an
339 alternative trajectory. We also imposed three constraints on null trajectories to ensure
340 realistic outcomes. The first was that the generated trajectory fit within the same
341 elevation range as the original trajectory (Fig. 1e). This was necessary to account for
342 how deep snowpack excludes elk from high-elevation areas during winter irrespective
343 of predation risk (Houston, 1982). Secondly, the null trajectory had to fit within the
344 same bounding box area as the original. This ensured that the area covered by the
345 trajectory did not affect expected outcomes. Lastly, null relocations could not occur
346 outside of the NR.

347 To test whether philopatric behaviour by elk reflected avoidance of predation

348 risk (Question 1), we generated null trajectories with starting locations sampled across
349 the NR. Note that the starting location served as the centroid of the bounding box
350 within which the null trajectory had to fit. We then constrained the starting location of
351 null trajectories to a randomly sampled relocation from the observed trajectory, thus
352 keeping the alternative elk trajectory within the same geographical area as the original
353 (Questions 2 and 3). This latter formulation was also used to generate null trajectories
354 for each winter period (Question 4).

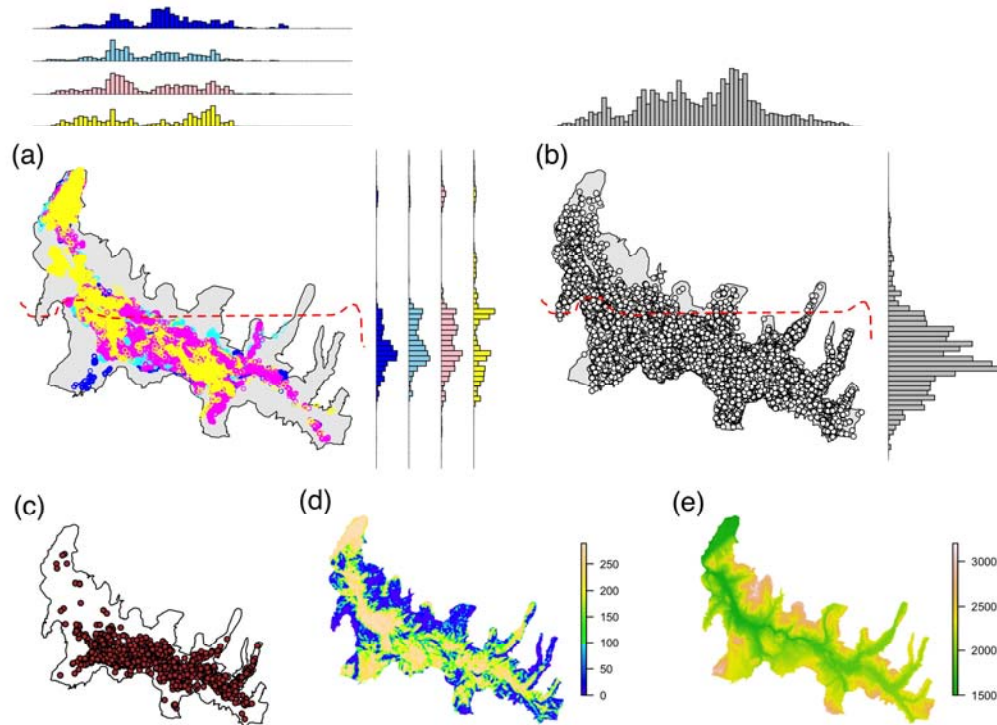
355 For each winter and period-level elk trajectory, we generated 1,000 null
356 trajectories, each time re-calculating the corresponding spatial overlap and encounter
357 rate indices with each predation risk layer and period-level wolf trajectories,
358 respectively. Hourly predation risk levels were re-calculated using the same null
359 trajectories as for the spatial overlap analysis. Randomisations were carried out using
360 the *NMs.randomCRW* function in the R package *adehabitatLT* (Calenge, 2006).
361 Statistical testing consisted in computing the one-tailed probability $P = (k_e + 1)/k$ of
362 getting a value equal to or less than the observed level, where k is the total number of
363 null elk trajectories and k_e is the number of values $<$ observed. To control for the high
364 number of significance tests, we applied a sequential Bonferroni correction by
365 multiplying P by the number of elk trajectories in the corresponding winter, period or
366 hour bin (Holm, 1979). We chose to implement a one-tailed test as we were interested
367 in the alternative hypothesis of avoidance, which we refer to hereafter as a significant
368 outcome. We report statistical significance at an α level of 0.05. All analyses were
369 carried out in R version 3.5.0 (R Development Core Team, 2018).

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375 **Figure 1.** Overview of the spatial data collected across the Northern Range and used in this
376 study. (a) Female elk GPS relocations for the winters of 2012 (yellow), 2013 (pink), 2014
377 (light blue) and 2015 (dark blue); (b) wolf GPS relocations recorded between 2004 and 2016;
378 (c) distribution of elk female and calf kill sites; (d) vegetation openness (0=closed,
379 289=open); (e) elevation (in m). The dashed red line in (a) and (b) denotes the northern
380 boundary of Yellowstone National Park.

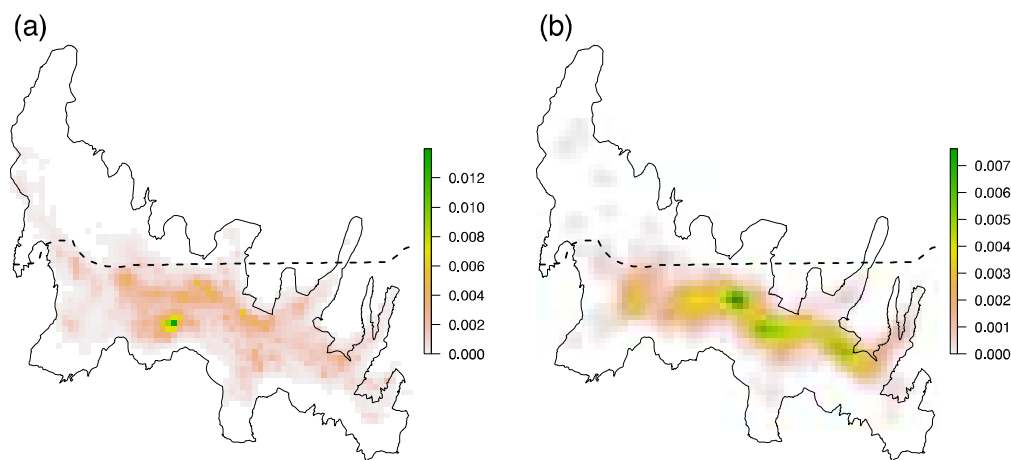
381

382 **Results**

383 **Spatial overlap**

384 Elk winter UD_s were estimated for 13, 22, 22 and 12 individuals during the winters of
385 2012, 2013, 2014 and 2015, respectively, totalling 69 winter trajectories. Trajectories
386 showed a median of 181 days of tracking (range = 134 – 182) and an average of 2.39
387 hours between relocations (SD = 0.69) across all winters (Table 1, Figure S1).

388 Movement correlation between contemporaneous trajectories was consistently <0.5 .
389 Wolf long-term space use across the northern Yellowstone elk winter range was
390 estimated from 72,454 GPS relocations obtained from 23 individual packs (a total of
391 61 winter trajectories) between 2004 and 2016 (Table S1). A total of seven pairs of
392 wolf trajectories exhibited a movement correlation coefficient greater than 0.5,
393 resulting in the exclusion of the same number of trajectories prior to estimation of
394 wolf space use intensity (Fig. 2a). The predation risk layer relating to elk kill site
395 density (Fig. 2b) was derived from 1,780 wolf-killed elk detected between 1995 and
396 2016 across northern Yellowstone.
397



398
399 **Figure 2.** Predation risk layers representing wolf space use intensity (a) and elk kill site
400 density (b). The dashed line denotes the northern boundary of Yellowstone National Park.

401
402 As expected, spatial overlap values between elk winter home ranges and predation
403 risk layers were low, ranging from 0.004 to 0.170 for wolf space use intensity, 0.007
404 to 0.361 for elk kill site density, and 0.006 to 0.058 for vegetation openness (see
405 Tables S2 and S3). There was no evidence for proactive avoidance at the home range
406 level when the null model formulation did not include a constraint representing

407 philopatric behaviour, regardless of the predation risk layer. When philopatry was
408 included in the null model formulation, 2 out of the 69 home ranges showed
409 significantly less than expected overlap with vegetation openness, one in the winter of
410 2013 and the other in 2014. No home range displayed a significant outcome for wolf
411 space use intensity or elk kill site density.

412

413 Hourly predation risk

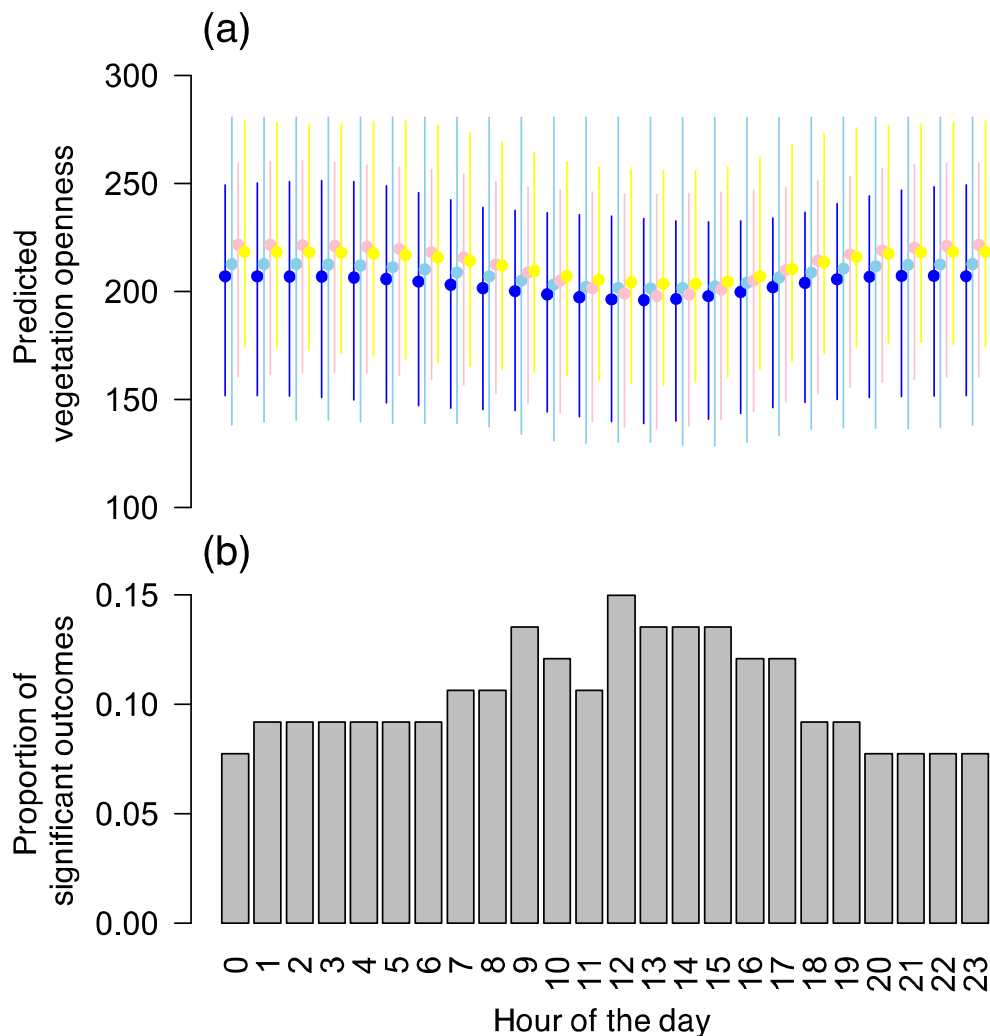
414 Across all hours of the 24-hour cycle, the mean percentage of individual elk using
415 areas with lower than expected levels of predation risk was 1.4% (SD = 0.67) for wolf
416 space use intensity, 0% (SD = 0) for kill site density, and 10.4% (SD = 2.4) for
417 vegetation openness. For the latter metric, the proportion of significant outcomes was
418 generally higher between 0700 and 1800, with a peak of 0.149 between 1200 and
419 1300 (Fig. 3).

420

421 Encounter rate

422 We recorded a total of 424 encounter events from 36,738 elk and 13,685 wolf pack
423 relocations recorded across the six winter periods considered (Table 2). The majority
424 of encounters (95.8%) were recorded inside YNP (Fig. 4a). For those elk that did
425 experience encounters, these occurred on average once every 8.5 days with a range of
426 7.1 to 11.7 days across winter periods (Table 2). The shortest recorded distance
427 between simultaneous wolf and elk relocations was 102.5 m. From the latter value,
428 encounter frequency increased at a constant rate until the threshold of 1000 m (Fig.
429 4b). Encounters were more likely to be recorded during dawn (07:00 - 10:00) and
430 dusk (16:00 - 19:00) than during the middle of the day or at night (Fig. 4c). Encounter
431 rate increased significantly with the proportion of wolf packs collared within northern

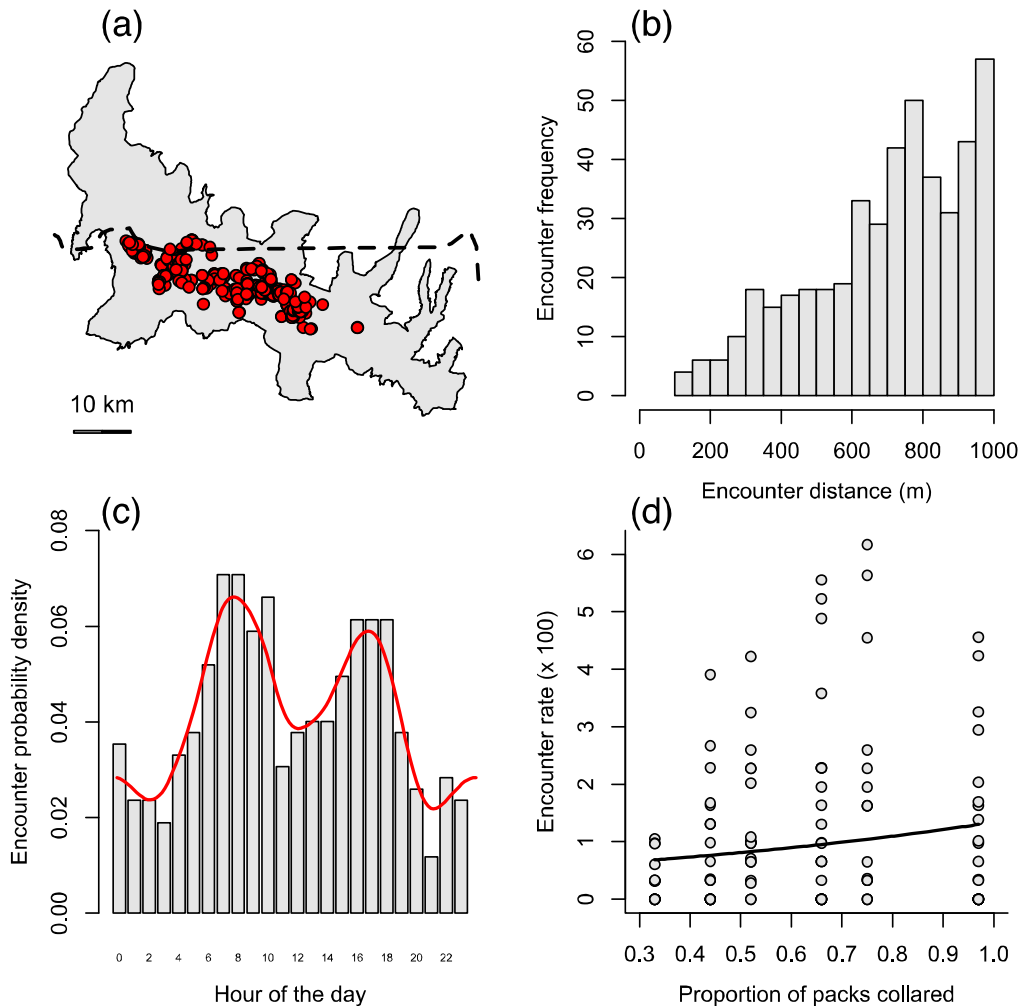
432 Yellowstone (GLMM; Fig. 4d and Table 2). Random intercept estimates showed a
433 12-fold variation across elk IDs, reflecting considerable differences in encounter rates
434 at the individual level (Table S4). No elk trajectories were found to exhibit a lower
435 than expected encounter rate with collared wolf packs. Note that a repeat of the
436 analysis using a distance threshold of 500 m yielded the same result.
437



438
439 **Figure 3.** (a) Predicted mean level of vegetation openness per hour of the day. Full circles
440 represent averages across individuals with bars showing the range of values. Colours indicate
441 the different winters (yellow for 2012, pink for 2013, light blue for 2014 and dark blue for
442 2015). (b) Proportion of individual elk showing lower than expected mean vegetation

443 openness per hour across all winters.

444



445

446 **Figure 4.** Details of encounter events recorded between GPS-collared elk and wolves in

447 northern Yellowstone during six 32-day winter periods. These include the spatial distribution

448 of recorded encounters (a), the frequency distribution of encounter distances (b), the

449 probability density function of encounter times (c), and the relationship between encounter

450 rate and the proportion of packs collared in northern Yellowstone (d). Encounters were

451 defined as wolf and elk relocations obtained during the same 1-hour window and observed to

452 be within 1000 m of one another. The dashed line in (a) denotes the northern boundary of

453 Yellowstone National Park. The red curve in (c) represents the fitted density function. The

454 fitted line in (d) was obtained from a Poisson generalized linear mixed model with the

455 number of encounters as response variable, the proportion of collared wolves as explanatory
456 variable, the number of fixes as an offset term, and elk ID as a random intercept. Encounter
457 rate is expressed per 100 elk fixes.

458

459 **Discussion**

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

471 The limited proactive response of elk to wolf space use intensity concurs with
472 findings from previous studies. In their comparison of elk movement patterns before
473 and after wolf reintroduction, Mao et al. (2005) found that elk “did not spatially
474 separate themselves from wolves” during winter months. One reason for this could be
475 that elk are unlikely to be aware of the precise spatial distribution of a predator known
476 to frequently course throughout their winter range (Bergman et al., 2006; Middleton
477 et al., 2013a; Uboni et al., 2015). However, Kauffman et al. (2007) highlighted a
478 discrepancy between kill site occurrence and wolf distribution, making the more
479 general point that predator density may not be a good indicator of predation risk. To

480 counter this criticism, we considered two additional measures of predation risk (Moll
481 et al., 2017). These reflected the notion that elk might select for sites that reduce their
482 vulnerability to being hunted successfully, such as areas of increased vegetation cover
483 (Creel et al., 2005; Fortin et al., 2005). Yet, contrary to previous work, we did not find
484 any evidence to support a proactive response to any of the predation risk measures,
485 thus strengthening the idea that home range selection by elk in our study did not
486 reflect avoidance of predation risk.

487 Recent work on the responses of prey to predators has highlighted the
488 importance of time in modulating spatial relationships between prey movements and
489 predation risk (Creel et al., 2008, Palmer et al., 2017). In particular, Kohl et al. (2018)
490 recently revealed a dynamic landscape of fear, whereby elk use of risky areas in
491 northern Yellowstone was dependent on wolf diel activity. Although the proportion of
492 elk using open vegetation less than expected by chance did vary across the 24-hour
493 cycle in the present study, this behaviour only concerned a very small proportion of
494 the individuals tested each hour of the day. Interestingly, however, the detected
495 avoidance response tended to be stronger during daylight hours, when wolves are
496 more likely to be actively hunting (Vander Vennen et al., 2016; Kohl et al., 2018).
497 The study by Kohl et al. (2018) used elk relocation data collected over the period
498 2001-2004 and it is possible that changes in elk behaviour towards wolves might have
499 led to the weaker patterns observed in the present study. Elk numbers in northern
500 Yellowstone were also much higher during the early years of wolf re-colonisation
501 (MacNulty et al., 2016), when elk could have been using riskier habitats as a means to
502 avoid safer but more crowded ones (i.e. density dependent effect).

503 The near absence of elk trajectories showing a lower than expected encounter
504 rate with wolves is a surprising outcome of our study. From an ecological perspective,

505 it is possible that other factors not considered here, such as elk group size (Gower et
506 al., 2008; White et al., 2012), switches in habitat use (Creel et al., 2005; Fortin et al.,
507 2005; Hernández & Laundré, 2005), and wolf pack size (MacNulty et al., 2012) allow
508 individual elk to minimise predation risk despite close proximity to wolves, thus
509 dampening small scale spatial avoidance patterns. Individual elk – and adult females
510 in particular – might also tolerate close proximity to wolves because they frequently
511 survive their encounters with them (MacNulty et al., 2007; MacNulty et al., 2012;
512 Mech, Smith & MacNulty, 2015). From a methodological standpoint, we also have to
513 consider the possibility that our definition of an encounter poorly described
514 immediate predation risk, and that reactive avoidance occurs at a spatial scale < 500
515 m. Few high resolution relocation datasets are currently available that combine
516 simultaneous predator-prey trajectories, and our study is valuable in developing a
517 methodological framework within which these could be considered once they become
518 more widely available.

519 Importantly, our findings are consistent with two key predictions of the
520 predator-prey shell game occurring in a freely interacting system (Lima 1998;
521 Mitchell & Lima, 2002). One of these relates to attempts by predators to get closer to
522 prey. In a system such as northern Yellowstone where the winter movement of elk is
523 constrained by philopatric behaviour and snow cover (Nelson et al. 2012), wolves
524 may be better able to align their space use with that of their prey. A consequence of
525 this would be the dampening of any potential avoidance patterns displayed by elk (as
526 per Sih 1984; 2005), which might explain their overall absence in the present study.
527 Another prediction states that prey should attempt to be unpredictable in space, and
528 the lack of consistent movement patterns observed in the present study could be
529 interpreted as a reflection of this. We emphasise that the methodology presented here,

530 combined with other approaches such as step selection functions (e.g. Cozzi et al.,
531 2018), could be used to assess behavioural responses on both sides of the predator-
532 prey race.

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

552 In summary, not only does our study provide a comprehensive assessment of
553 the spatiotemporal response of individual prey to predation risk, but it also extends
554 the use of null models to infer on interactive behaviour between different species. In

555 doing so, it emphasises the challenges of detecting strong spatiotemporal responses by
556 prey, and suggests that other factors relating to both predator and prey behaviour may
557 be more important in shaping observed outcomes. Although our data were based on a
558 system that has undergone extensive study over the past two decades, the
559 considerations we highlight are particularly relevant to telemetry studies carried out in
560 poorly known landscapes, in which spatial data are increasingly the first to be
561 collected. In such cases, a clear understanding of species interactions, such as the
562 proactive and reactive responses of prey to predators, may have to be gained through
563 a combination of high-resolution GPS telemetry and direct observation.

564

565

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574

575 **Authors' contributions**

576 JC designed the study; MK, MM, DRS, DWS and DM collected and shared the data;
577 JC and TC performed the modelling work and analysed output data. JC wrote the
578 manuscript, and all authors contributed substantially to revisions.

579

580 **Data accessibility**

581 Data used in this study will be made available on a Dryad repository upon acceptance.

582

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863 **Tables**

864 **Table 1.** Summary of winter elk trajectories.

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

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871 **Table 2.** Summary of winter period elk trajectories and encounter rates with collared wolves.

Period*	# trajectories	Total # relocations	Mean # hours between relocations	Total # encounters	Encounter rate [†] median [range]	Mean # days per encounter	# wolf packs collared (proportion of active [§])
LW 2013	18	5613	2.48	108	0.82 [0 – 5.56]	8.4	2 (0.66)
EW 2013	18	5452	2.54	75	0.98 [0 – 4.22]	9.2	3 (0.52)
LW 2014	15	4691	2.46	87	0.33 [0 – 3.91]	11.7	3 (0.44)
EW 2014	24	7300	2.52	92	1.14 [0 – 6.17]	7.1	4 (0.75)
LW 2015	23	7008	2.52	76	0.50 [0 – 4.56]	9.1	4 (0.97)
EW 2015	22	6674	2.53	15	0.31 [0 – 1.05]	8.3	2 (0.33)

872 *LW = Late Winter, EW = Early Winter

873 [†]Encounter rate per 100 fixes, i.e. the number of instances in which elk and wolf relocations within the same 1-hour window were within 1000 m
 874 of each other multiplied by 100

875 [§]Proportion of packs collared out of the ones known to be active in northern Yellowstone.