Limited evidence for proactive and reactive spatial responses of prey to an active predator

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Abstract

Predator-prey interactions are often assumed to result in spatial avoidance patterns whereby prey respond to the distribution and movement of predators, yet this assumption is rarely tested. We estimated spatial overlap between the winter trajectories of GPS-collared elk (*Cervus elaphus*) and the long-term utilisation distribution of GPS-collared grey wolf (*Canis lupus*) packs in northern Yellowstone, as well as evaluated encounter rates during a subset of winter months when the movement of both species was tracked simultaneously. We carried out a null model analysis that randomised elk trajectories according to three different formulations (rotation, rotation and shift, and correlated random walk) to test whether observed values of spatial overlap and encounter rate were less than expected by chance. Our analysis revealed 1 in 5 elk winter trajectories had lower spatial overlap than expected by chance when the less restrictive null formulation was used. Although elk encountered wolves on average once every 8.5 days, encounter rate was no different to null expectations for all but two of the 120 tested trajectories. Our study suggests that predator-prey interactions may not always result in strong spatial patterns of avoidance, and that other behavioural mechanisms may be more important in shaping long and short-term prey responses.

Keywords: elk, grey wolf, Yellowstone, spatial overlap, encounter rate, null model, northern range, avoidance

Introduction

The spatial response of prey to the distribution and movement of predators is an important component of predator-prey interactions (Sih 1984, 1998), providing valuable insights into the role of non-consumptive effects of predators in structuring mammal communities (Weissberg et al. 2014). There is, however, still much debate regarding the relative importance of proactive versus reactive spatial responses by prey to predators. Proactive predator avoidance is expected to occur over large spatial scales (i.e. several kilometres), with prey purposefully avoiding areas that are preferentially used by predators (Thaker et al. 2011). This approach generally assumes that the spatial distribution of a predator reflects a heterogeneous landscape of long-term predation risk (Lima and Dill 1990, Thaker et al. 2011, Kauffman et al. 2007, Searle et al. 2008). In contrast, reactive movement responses involve sudden displacements following detection of a predator in the immediate surroundings (Creel et al. 2008, Courbin et al. 2013, Middleton et al. 2013, Basille et al. 2015). In the case of a wide-ranging, active predator, it is generally accepted that prey should elicit reactive rather than proactive spatial responses owing to the unpredictability with which predators occur in the landscape. Although lack of a proactive response to an active predator has been highlighted in the past (Mao et al. 2005, Kittle et al. 2008, Schmitz 2008, Thaker et al. 2011), it remains unclear whether this is compensated for by a strong reactive response (Middleton et al. 2013, Courbin et al. 2015).

Global Positioning System (GPS) telemetry has become an invaluable tool with which to quantify relationships between the movement patterns of different individuals and species, often with a view to inferring intra- and inter-specific interactions, respectively (Kays et al. 2015). In particular, measures of spatial overlap and encounter rate, which respectively quantify the level of joint space use exhibited

by two individuals (Kernohan et al. 2001, Millspaugh et al. 2004, Fieberg and Kochanny 2005) and the degree to which their trajectories "meet" one another over time (Macdonald et al. 1980, Doncaster 1990), have provided intuitive indices of the potential for interaction (Benhamou et al. 2014, Long et al. 2014). Such measures have primarily been used to gain insights into competitive and social interactions between individuals of the same species (Walrath et al. 2011, Robert et al. 2012, Lührs and Kappeler 2013, Miller 2015), as well as the potential for disease transmission across species (Proffitt et al. 2010, Barasona et al. 2014, Williams et al. 2014). However, measures of spatial overlap and encounter rate have rarely been considered simultaneously when attempting to characterise avoidance behaviour in the context of predator-prey interactions (Valeix et al. 2009).

Although measures of spatial overlap and encounter rate have the potential to advance our understanding of the spatial responses of prey to predators, their interpretation is often hindered by lack of an appropriate null model of random movement with which to generate expected values (Gotelli and Graves 1996, Richard et al. 2013, Miller 2015). Typically, a null model generates a pattern based on randomisation that lacks some process or mechanism of interest to test its influence (Gotelli and Graves 1996). Recently, Richard et al. (2013) extended the application of null models used in community ecology to examine the potential for spatial interactions between female red and roe deer (*Cervus elaphus* and *Capreolus capreolus*, respectively). They did this by randomly permuting and shifting roe deer trajectories to obtain "pseudo-trajectories", re-calculating the level of overlap with the distribution of female red deer to generate an expected distribution. The authors found that spatial interaction outcomes between the two species varied depending on the formulation of the simulation procedure. However, they did not apply their null model

approach to assess whether trajectories of the two species encountered each other less than expected by chance.

In this study, we fill this gap by characterising the spatial responses of female elk (*Cervus elaphus*) to the distribution and movement of grey wolves (*Canis lupus*) in northern Yellowstone. We first quantify spatial overlap between the winter trajectories of GPS-collared elk and a distribution of wolf space use derived from 15 winters of GPS tracking data. Secondly, we estimate encounter rates between collared elk and wolf packs during six 32-day winter periods occurring between 2013 and 2015. For both spatial overlap and encounter rate, we determine whether observed values are significantly lower than expected if elk movements were random with reference to those of wolves, respectively. To do this, we implement three different null model formulations that generate alternative elk trajectories within the same geographic locality as the observed, thus accounting for the species' philopatric behaviour (Brough 2009, Gower et al. 2008, White et al. 2012). Given the active nature of wolf hunting, we did not expect to find a proactive response, but did expect elk to actively minimise encounters with wolves. Overall, we find little evidence supporting either type of spatial response.

Materials and Methods

Study area

The northern Yellowstone winter range encompasses roughly 1,520 km^2 of mountainous terrain and open valleys, with elevation ranging from 1,500 to 3,210 m (Houston 1982). The area defines the winter range of seasonally migrating elk (White et al. 2012, Tallian et al. 2017), and is largely composed of shrub steppe, with patches of intermixed lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*),

Engelmann spruce (*Picea engelmanni*), and aspen stands (Houston 1982, Despain 1990). We consider wolf and elk trajectories recorded over the entire northern Yellowstone winter range – that is including land within Yellowstone National Park (YNP) and north of the park boundary – and hereafter refer to this as the northern range. Winters in the NR are usually cold and snowy.

Elk abundance in the northern range has shown a decrease of 70% between 1995 and 2015, which has been largely due to a reduction in elk abundance within the YNP section of the northern range (White and Garrot 2005, White et al. 2012, Tallian et al. 2017). The population currently numbers around 6000 individuals, although it is estimated that only ~1500 of these overwinter in the YNP portion of the northern range (Tallian et al. 2017). Elk are the primary prey of wolves in the study area (Smith et al. 2004, Tallian et al. 2017).

Wolf long-term space use

We used GPS collar data collected on grey wolves each winter between 2000 and 2016 to characterise long-term winter space use patterns by packs in the northern range (Fig. 1a). Wolf GPS tracking has been carried out by the Yellowstone Wolf Project since 2000, with a varying proportion of packs inside YNP sampled every year (details of collaring procedures can be found in Smith and Bangs 2009). Although the exact model of fitted GPS collars varied during this period, all were manufactured by either Telonics (Mesa, AZ, USA), Televilt (Lindeserg, Sweden) or Lotek (Newmarket, ON, Canada). Average winter fix frequency between 2000 and 2016 varied between periods of intensive monitoring of wolf movements when relocations were obtained every hour (32-day winter periods, either Early Winter [EW] period between 14th November and 15th December or Late Winter [LW] period

between 28th February and 31st March) and periods characterised by longer delays between relocations (average of 6 hours).

As a first step, we extracted wolf trajectories recorded between November 1st of a given year and 31st April of the next. To avoid duplicated trajectories derived from collared wolves belonging to the same pack, which could bias subsequent estimation of space use, we calculated an index of movement cohesion as well as the average distance between simultaneous relocations for every wolf dyad within a given winter. For movement cohesion, we used Shirabe's (2006) correlation coefficient, which measures the degree of correlation between the movement paths of two individuals as a multivariate Pearson product-moment correlation coefficient (Shirabe 2006, Long et al. 2014). The index ranges from -1 (negative correlation) to 1 (positive correlation), with 0 indicating random movement. For dyads showing a movement correlation coefficient equal to or greater than 0.5 (Long et al. 2014), we excluded the trajectory with the least number of relocations from the corresponding winter. The average distance between dyads exhibiting joint movement was used in the estimation of wolf pack space use (see below). We assumed that wolf trajectories recorded during each period reflected the movement of corresponding packs (Benson and Patterson 2015).

For each winter, we then estimated a joint wolf utilisation distribution (UD) representing the combined spatial activity of all collared wolves during that winter. The joint wolf UD was taken as the mean of individual wolf pack UDs – each of these weighted by the size of the corresponding pack (see Table S1, and Kauffman et al. 2007 for a similar procedure) – and scaled to sum to unity. Utilisation distributions were estimated over a continuous grid of cell size 1 by 1 km using a Brownian bridge movement model (BBMM) implemented in the R package BBMM (Bullard 1999,

Horne et al. 2007). The BBMM is a continuous-time stochastic movement model, where the probability of being in an area is conditioned on 1) the distance and elapsed time between successive locations, 2) a measure of location error, and 3) an estimate of the animal's mobility (the Brownian motion variance, see Horne et al. 2007). In other words, the model approximates the movement path between two subsequent locations by applying a conditional random walk. Because UD tails (i.e. beyond the 95 % isopleth) tend to be poorly estimated, we generated conditional 95 % UDs scaled to sum to unity (Benhamou et al. 2014). We used a location error of 468 m for wolf packs as this represented the average distance between joint wolf movements. We assumed that this value accounted for the position of individuals that were not collared when estimating a pack's UD.

A final joint UD representing wolf long-term space use in the northern range was then derived by averaging winter joint UDs and scaling to sum to unity. By averaging across winters – which differed in the number of packs collared (see Table S1 in Supporting Information) – we aimed to produce a space use pattern representative of where wolves were more or less likely to be encountered across the northern range. It is important to note, however, that no wolves were collared north of the YNP boundary, and thus the estimation of the wolf UD in the northern section of the elk winter range relies on excursive movement from park packs.

Elk winter space use

We estimated individual-level space use for GPS-collared elk during four winters (2012-13, 2013-14, 2014-15 and 2015-16) (Fig. 1b). Elk collars (Iridium TrackM 3D, Lotek Wireless Inc.) were first deployed in February 2012, with new additions and redeployments occurring each subsequent winter. Adult female elk were captured

using helicopter net-gunning. Recorded data were uploaded via Iridium satellite every 4-12 fixes and subsequently downloaded from a dedicated webserver. To ensure accurate representation of elk winter space use, we excluded winter trajectories for which the average fix frequency was more than five hours and the time difference between the first and last relocation less than four months. If two elk trajectories recorded during the same winter showed a movement correlation coefficient equal to or greater than 0.5, the one with the least number of relocations was excluded from the analysis. For each winter, we used BBMMs to estimate individual elk UDs. Location error for elk collars was unknown and fixed to a conservative estimate of 50 m.

Spatial overlap

We defined spatial overlap as the volume of intersection (VI) between the UD of a single elk during a given winter and the joint wolf UD representing wolf long-term space use. We interpret VI as the proportion of the volume of the elk UD taken up by the joint wolf UD (Kernohan et al. 2001, Fieberg and Kochanny 2005). The VI index, which ranges from 0 (no overlap) to 1 (complete overlap), has been widely used to compare UDs in a range of different taxa (Fieberg and Kochanny 2005). If UD_A and UD_B are the estimated utilisation distributions for individuals *A* and *B*, respectively, then

$$VI = \iint_{-\infty}^{\infty\,\infty} \min\left[UD_A(x,y), UD_B(x,y)\right] dx dy$$

We calculated the VI index based on conditional 95 % UDs, so as to minimise bias associated with the poorly estimated UD tails (Fieberg 2007, Benhamou et al. 2014). Given the substantial difference between the size of the joint wolf UD and the home

ranges of individual elk, we expected VI values to be closer to 0 than to 1. However, we stress that this in itself cannot be considered as evidence for proactive avoidance behaviour, and is the reason why we implemented a null model approach (see below).

Encounter rate

We measured the rate at which a given elk encountered wolves as *ST/n* where *ST* is the total number of recorded encounters with wolves and *n* represents the total number of fixes recorded for a given elk. Encounters consisted of spatially proximal and temporally simultaneous elk and wolf fixes defined according to specific distance *d* and time *t* thresholds, respectively (Long et al. 2014). We set *d* to 1000 m following Middleton et al. (2013), who found that elk tended to increase their rates of movement, displacement and vigilance when wolves were within this distance threshold. Temporal proximity *t* was set to 1 hour as this represented the average length of a successful hunting bout by wolves (MacNulty 2002). Thus, if elk and wolf relocations obtained in the same 1-hour window were observed to be within 1000 m of one another, they constituted an encounter. Importantly, we use the term "encounter" to denote a significantly increased likelihood of predator-caused mortality (MacNulty et al. 2007), which we assume elk would actively avoid (Creel et al. 2005, Proffitt et al. 2009, Latombe et al. 2014). We limited our analysis of encounter rate to six periods of intense monitoring (hereafter, winter periods) during which wolf collars were programmed to record one relocation every hour. We excluded elk trajectories for which the number of tracking days was less than 30. For ease of interpretation, we present values of encounter rate for 100 elk fixes.

We modelled encounter rate as a function of the proportion of collared wolf packs in northern Yellowstone using a Generalised Linear Mixed Effects (GLMM)

model. The model response consisted of the number of encounters per trajectory with an offset term to account for varying number of fixes. We set the error distribution to Poisson and included elk ID as a random intercept to control for repeated measures on the same individuals across winter periods.

Null model formulations

We used a null model approach to determine whether the observed spatial overlap and encounter rate obtained for each winter and period-level elk trajectory, respectively, were less than expected if a given elk moved randomly with reference to wolves. We implemented three different null model formulations to generate alternative elk trajectories within the study area. The first randomly rotated the observed elk trajectory around its centre of gravity (Rotation model, Fig. 1c), thus maintaining its inherent structure. The second formulation randomly rotated the trajectory, but in addition shifted its centre of gravity to a random location sampled from the original trajectory (RSH model, Fig. 1d). The third formulation randomly sampled the distributions of step lengths and turning angles derived from the observed trajectory to construct a correlated random walk (CRW model, Fig. 1e) from the original starting location. Thus, all formulations maintained alternative elk trajectories within the same geographical area as the original, thereby reflecting the species' philopatric behaviour (average annual winter home range shift in northern Yellowstone: median = 109.90 meters, n = 128; M. Kohl, unpublished data), which we hypothesised would limit their ability to modulate spatial activity over the entire northern range. Since individual elk UDs generally covered a much smaller area than the joint wolf UD, and were typically contained within the latter, our null model approach tested specifically whether elk were able to exploit gaps in wolf spatial activity within a given

geographic locality, thus minimising overall spatial overlap.

For each winter and period-level elk trajectory, as well as null model formulation, we generated 1,000 null trajectories, each time re-calculating the corresponding spatial overlap and encounter rate indices with the original joint wolf UD and period-level trajectories, respectively. Randomisations were carried out using the *NMs.randomCRW* and *NMs.randomShiftRotation* functions in the R package adehabitatLT (Calenge 2006). Statistical testing consisted in computing the one-tailed probability $P = (k_e + 1)/k$ of getting a value equal to or less than the observed level, where k is the total number of null elk trajectories and k_e is the number of values < observed. To control for the high number of significance tests, we applied a sequential Bonferroni correction by multiplying P by the number of elk trajectories in the corresponding winter or period (Holm 1979). We chose to implement a one-tailed test based on a α level of 0.05, as we were interested in the alternative hypothesis of avoidance. All analyses were carried out in R version 3.3.3 (R Development Core Team 2017).

Results

Spatial overlap

We estimated wolf long-term space use across the northern Yellowstone elk winter range from 72,454 GPS relocations obtained from 23 individual packs (a total of 61 winter trajectories) between 2000 and 2016 (Fig. 2a). A total of seven pairs of wolf trajectories exhibited a movement correlation coefficient greater than 0.5, resulting in the exclusion of the same number of trajectories prior to estimation of winter joint UDs. Elk winter UDs were estimated for 14, 22, 23 and 12 individuals during the winters of 2012, 2013, 2014 and 2015, respectively, totalling 71 winter trajectories.

Elk winter trajectories showed a median of 181 days of tracking (range = 134 – 182) and an average of 2.39 hours between relocations (SD = 0.69). Movement correlation between contemporaneous trajectories was consistently <0.5. The estimated 95% contour isopleth of the joint wolf UD covered a much larger area than the UDs estimated for individual elk (752.1 km^2 versus a range of 6.8 – 94.9 km^2 for elk), and consequently, observed spatial overlap was generally low, ranging from 0 to 0.17 across the four winters considered (Table 1, Table S2).

The three types of null model formulation resulted in expected distributions for spatial overlap that varied in their mean and variance (Fig. 2b). The CRW formulation produced values that were on average significantly higher and more varied than the Rotation and RSH models (Mann-Whitney tests: all *P*-values < 0.001). Expected distributions resulting from the latter two formulations showed similar means (W = 2498, P = 0.929) but differed in their variance (W = 1149, *P* < 0.001). The CRW null formulation resulted in the highest number of significant outcomes overall, with 19.1% of tested winter trajectories showing evidence of proactive avoidance. The number of significant outcomes was much smaller in the case of the Rotation and RSH formulations, with 5 and 4% of tested trajectories, respectively. This pattern remained the same despite differences in the number of significant outcomes across winters (Fig. 2c).

Encounter rate

We recorded a total of 424 encounter events from 36,738 elk and 13,685 wolf pack relocations recorded across the six winter periods considered (Table 2). The majority of encounters (95.8%) were recorded inside YNP (Fig. 3a). For those elk that did experience encounters, these occurred on average once every 8.5 days with a range of

7.1 to 11.7 days across winter periods (Table 2). The shortest recorded distance between simultaneous wolf and elk relocations was 102.5 m. From the latter value, encounter frequency increased at a constant rate until the threshold of 1000 m (Fig. 3b). Encounters were more likely to be recorded during the day than at night, with notable peaks between 07:00 - 10:00 and 16:00 - 19:00 (Fig. 3c). Encounter rate increased significantly with the proportion of wolf packs collared within northern Yellowstone (GLMM; Fig. 3d). Random intercept estimates showed a 12-fold variation across elk IDs, reflecting considerable differences in encounter rates at the individual level (Table S3).

Expected distributions for encounter rate resulting from the different null model formulations did not differ in their means (Kruskal-Wallis test: $\chi 2 = 1.77$, df = 2, $P = 0.412$; Fig. 4). However, distributions obtained from the Rotation model had a smaller variance than those obtained from the RSH and CRW models (Mann-Whitney tests: Rotation vs. RSH, W = 4400, $P < 0.001$; Rotation vs. CRW, W = 3731, $P < 0.001$). We detected a near absence of reactive avoidance behaviour amongst the 120 tested trajectories (Table S3). No elk trajectories were found to exhibit lower than expected encounter rate with collared wolves when the RSH and CRW formulations were used. The Rotation formulation resulted in only two trajectories showing evidence of small scale spatial avoidance.

Discussion

Behavioural responses by prey to the presence of predators are complex and often heterogeneous (Creel et al. 2008, Moll et al. 2017, Drödge et al. 2017). In this study, we chose to focus specifically on spatial responses by estimating measures of spatial overlap and encounter rate between GPS-collared elk and wolves in Yellowstone's

northern range, with the aim of characterising proactive and reactive avoidance mechanisms, respectively. We found weak evidence supporting the former, with less than 20% of tested winter home ranges showing significantly lower spatial overlap with wolves when the least restrictive null model formulation was used, and a near absence of the latter. These findings suggest that predator-prey interactions may not always result in strong spatial patterns of either proactive or reactive avoidance, and that other behavioural responses or environmental factors may play a more important role in determining space use by individual prey.

The limited proactive response of elk to the long-term distribution of wolves concurs with findings from previous studies. In their comparison of elk movement patterns before and after wolf reintroduction, Mao et al. (2005) found that elk "did not spatially separate themselves from wolves" during winter months. Rather, the availability of suitable forage, snow depth and habitat type were found to be more important factors determining elk distribution (Kittle et al. 2008). Wolf space use at the landscape-level may also be a poor indicator of predation risk. Indeed, Kauffman et al. (2007) highlighted a discrepancy between kill site occurrence and wolf distribution, which introduces the possibility that elk in our study might have been responding to the former rather than the latter. Furthermore, elk are unlikely to be aware of the precise spatial distribution of a predator known to frequently course throughout their winter range (Bergman et al. 2006, Kauffman et al. 2007, Middleton et al. 2013, Uboni et al. 2015). Instead, they may select for landscape features that reduce their vulnerability to being hunted successfully, such as increased vegetation cover (Creel et al. 2005, Fortin et al. 2005) or proximity to roads (Nelson et al. 2012).

The near absence of elk trajectories showing a lower than expected encounter rate with wolves is more surprising given the theory on prey response to active

predators (Preisser et al. 2007, Schmitz 2008). From an ecological perspective, it is possible that other factors, such as elk group size (Gower et al. 2008, White et al. 2012), switches in habitat use (Creel et al. 2005, Fortin et al. 2005, Hernández and Laundré 2005), and wolf pack size (MacNulty et al. 2012) may allow elk to minimise predation risk despite close proximity to wolves, thus dampening small scale spatial avoidance patterns. Individual elk might also tolerate close proximity to wolves because they frequently survive their encounters with wolves (MacNulty et al. 2007, Mech et al. 2015). The success of wolves hunting elk in northern YNP rarely exceeds 20% (Smith et al. 2000) and drops below 10% when wolves target adult elk (MacNulty et al. 2012). From a methodological standpoint, we also have to consider the possibility that our definition of an encounter poorly described immediate predation risk. However, Middleton et al. (2013) showed that elk tended to increase their rates of movement and displacement when wolves were within a distance threshold of 1 km, and we thus expected to see avoidance patterns emerging at this spatial scale. Although the average rate of encounter found in the present study was highly comparable – 8.5 days per encounter versus 9 for Middleton et al. (2013) – it was no different to null expectations. Furthermore, the timing of encounters recorded in this study matches the temporal patterns of wolf activity and kill rates recently reported in Vander Vennen et al. (2016, Figures 1 and 2).

Creel et al. (2013) recently reviewed sources of bias associated with the estimation of encounter rates between mobile predators and prey, some of which are relevant to the present study. Firstly, the fix frequency used to record elk movement trajectories, which averaged 2.39 hours, may have led us to overlook instances of close proximity with wolves, and even entire hunting episodes (MacNulty 2002, MacNulty et al. 2007). Although we cannot exclude this with absolute certainty, the

1-hour temporal window used to define encounters is likely to have minimised this problem. Secondly, not all of the packs active in the northern range during a given winter period were considered, which may have exacerbated the under-estimation of encounter rates. Nevertheless, our study considers movement trajectories from members of many of the dominant packs in northern YNP, and although the proportion of packs collared did positively influence observed encounter rate, it did not affect the near absence of significant outcomes. Thirdly, the encounter rate considered in this study is a point-based measure of potential interaction, meaning that the GPS data are conceptualised as discrete locations at which individuals occur. Alternative path-based measures, which typically consider the cohesiveness in movement trajectories (i.e. similar or dissimilar step lengths and turning angles), might represent yet another way of assessing the responses of prey to predators. Ultimately, however, both point and path based measures are relatively uninformative unless compared to values obtained under the assumption of random movement (Miller 2015).

Although the use of null models is widespread in community ecology (Gotelli and Graves 1996, O'Sullivan and Perry 2013), very few studies have applied them to infer on interactive behaviour between different species. Recently, Richard et al. (2013) revealed an overall absence of spatial segregation between female red and roe deer, but noted that outcomes varied depending on the null model formulation used to generate null trajectories. The fact that significant outcomes were not consistent across null model formulations in the present study supports this. In particular, null model formulations differed in the extent to which they allowed null trajectories to occupy a given geographic locality, with the CRW model likely producing trajectories over a wider area in comparison to the more restricted RSH and Rotation models.

Indeed, whilst the latter would have not changed the shape of the UD – only its relative position and orientation – CRW-based null trajectories would have resulted in UDs of varying shape and extent, which is likely to have increased overlap with the surrounding wolf joint UD. Thus, the CRW formulation may have artificially inflated the number of individuals displaying significantly lower than expected spatial overlap with wolves, which only strengthens our finding of a weak proactive response.

In summary, our study emphasises the challenges of making inferences on the nature of anti-predator responses displayed by prey from spatial data alone. Whilst our analyses provide some support for proactive avoidance by elk, other ecological factors such as habitat type, or characteristics of the individual prey such as vigilance levels or body condition, may interact to blur more intricate spatial responses. Although our data were based on a system that has undergone extensive study over the past two decades, the considerations we highlight are particularly relevant to telemetry studies carried out in poorly known landscapes, in which spatial data are increasingly the first to be collected. In such cases, a clear understanding of species interactions, such as the proactive and reactive responses of prey to predators, may have to be gained through a combination of high-resolution GPS telemetry and direct observation.

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Author contributions

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

Data accessibility

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

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Tables

Table 1. Summary of winter elk trajectories and spatial overlap with collared wolves.

Winter	# trajectories	Total # relocations	Mean # tracking days	Mean # hours between relocations	Spatial overlap range
2012-13	14	18,647	177.4	3.213	0.012 - 0.143
2013-14	23	36,986	168.4	2.514	0.005 - 0.120
2014-15	24	37,757	165.5	2.523	0.004 - 0.169
2015-16	13	52,891	178.2	1.051	0.011 - 0.103

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)

*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 of each other multiplied by 100

†Proportion of packs collared out of the ones known to be active in northern Yellowstone

Figures

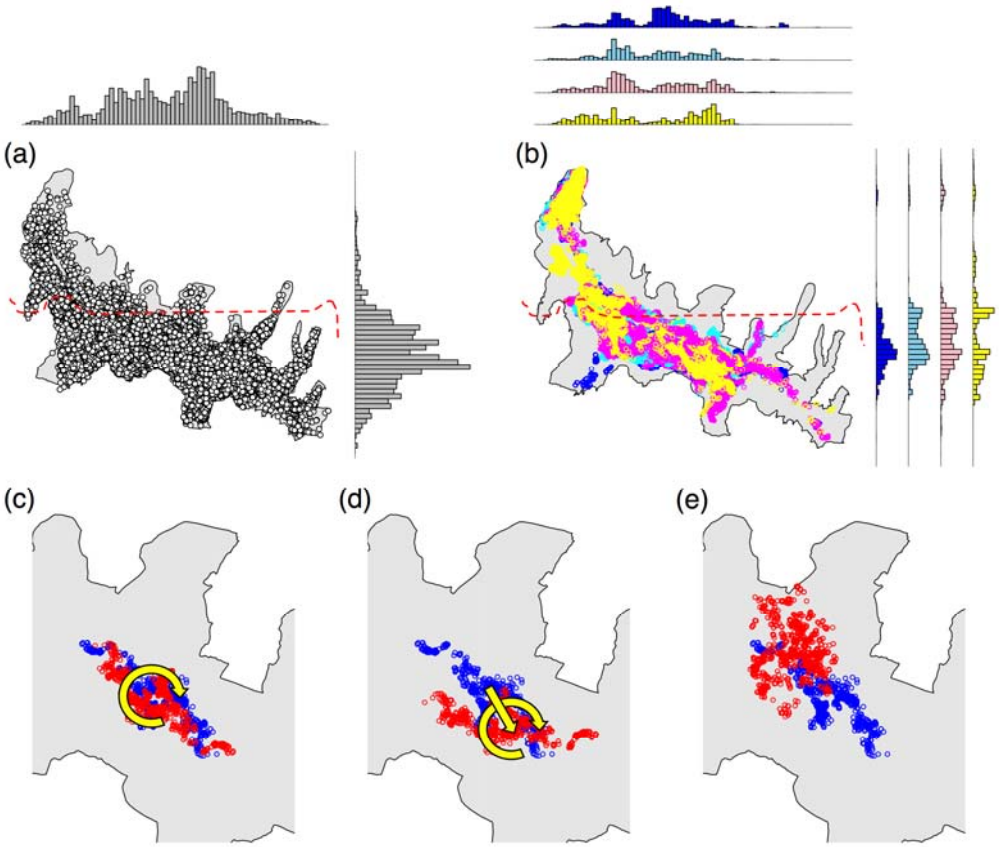

Figure 1. Distribution of wolf and elk GPS collar relocations across the northern Yellowstone elk winter range and illustration of the three null model formulations used to randomize elk trajectories. In (a) and (b), histograms show the distribution of wolf and elk X and Y coordinates, with dark blue, light blue, pink and yellow colors in the case of elk representing the winters of 2012-13, 2013-14, 2014-15 and 2015-16, respectively. The dashed red line denotes the northern boundary of Yellowstone National Park. Panels (c)-(d) illustrate the Rotation, Rotation and Shift, and Correlated Random Walk model formulations. The blue and red dots represent original and randomized trajectories, respectively, for an example elk trajectory.

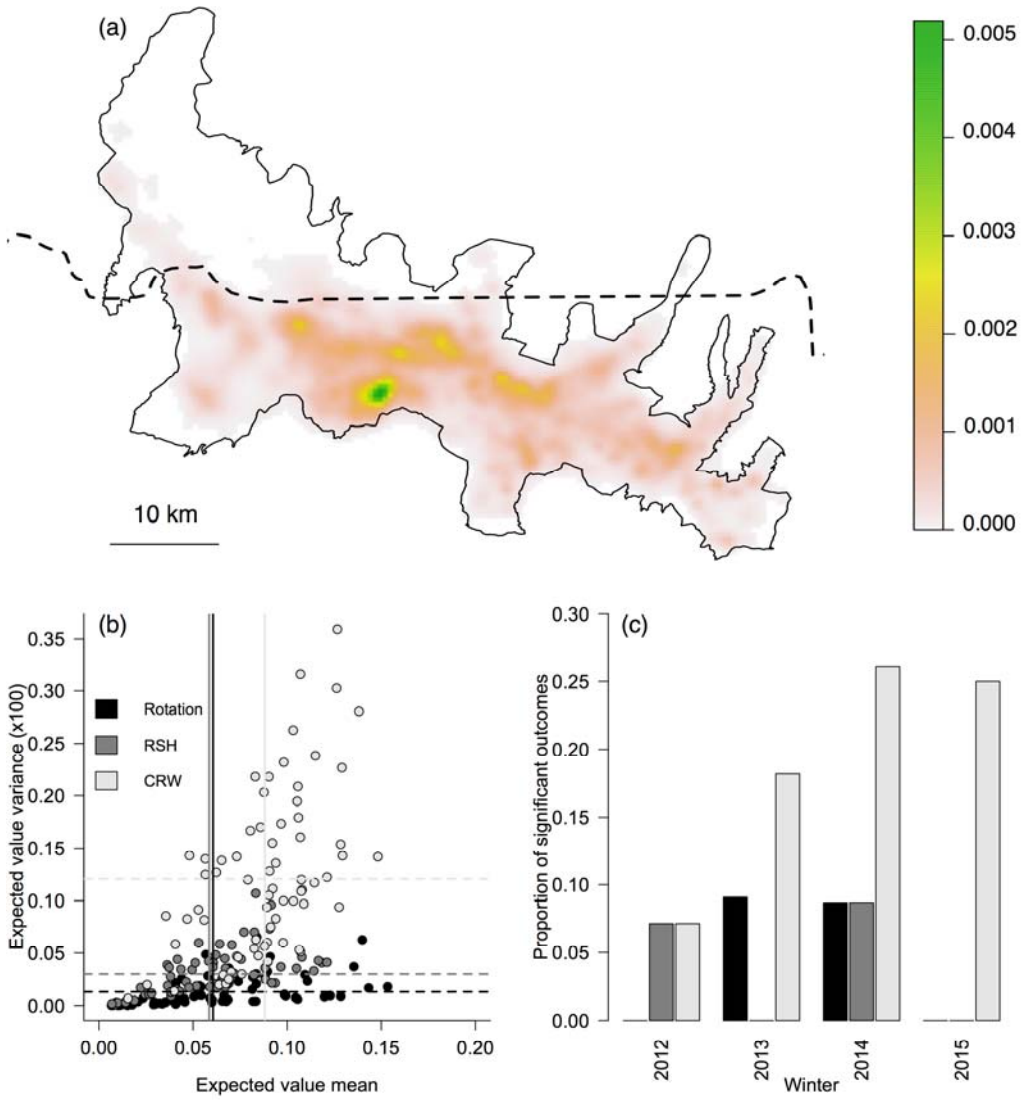

Figure 2. Joint wolf utilization probability distribution, describing the spatial activity of wolves across the northern Yellowstone elk winter range, and outputs from the null model analysis of spatial overlap. The dashed black line in (a) denotes the northern boundary of Yellowstone National Park. The color gradient describes the relative probability of finding a wolf pack in a given grid cell contained within the estimated 95% contour isopleth (see text). The UD was estimated by averaging the spatial activity of wolf packs GPS-collared within Yellowstone National Park during the winters 2000-01 to 2015-16. Panel (b) shows the mean and variance of expected

values of spatial overlap obtained from the three different types of null model formulations. A single point refers to the mean and variance of expected values derived from 1,000 randomizations of the corresponding elk winter trajectory according to one of the three null model formulations. Full vertical and dashed horizontal lines denote mean values of X and Y axes, respectively. Panel (c) presents the proportion of elk trajectories within each winter that showed less than expected spatial overlap with the joint wolf utilization distribution assuming the long-term movements of elk were random with respect to wolves.

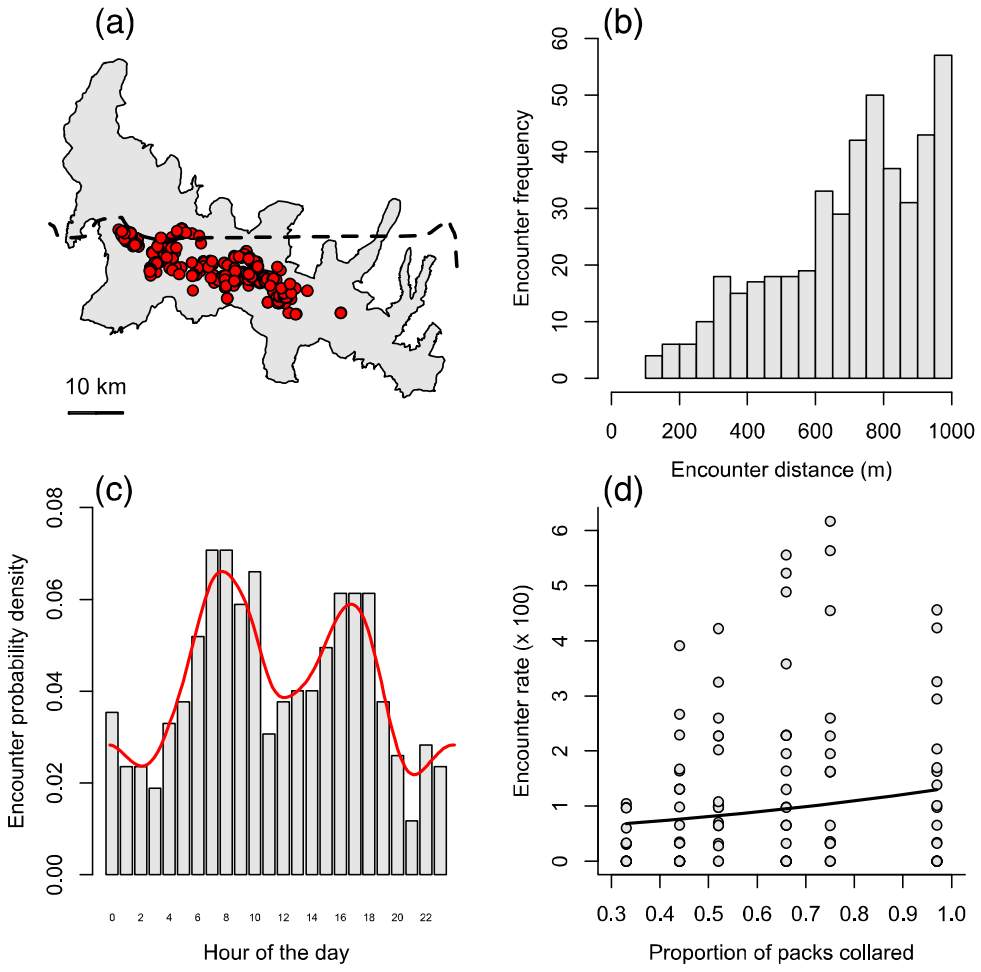

Figure 3. Details of encounter events recorded between GPS-collared elk and wolves in northern Yellowstone during six 32-day winter periods. These include the spatial distribution of recorded encounters (a), the frequency distribution of encounter distances (b), the probability density function of encounter times (c), and the relationship between encounter rate and the proportion of packs collared in northern Yellowstone (d). Encounters were defined as wolf and elk relocations obtained during the same 1-hour window and observed to be within 1000 m of one another. The dashed line in (a) denotes the northern boundary of Yellowstone National Park. The red curve in (b) represents the fitted density function. The fitted line in (d) was obtained from a Poisson generalized linear mixed model with the number of

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

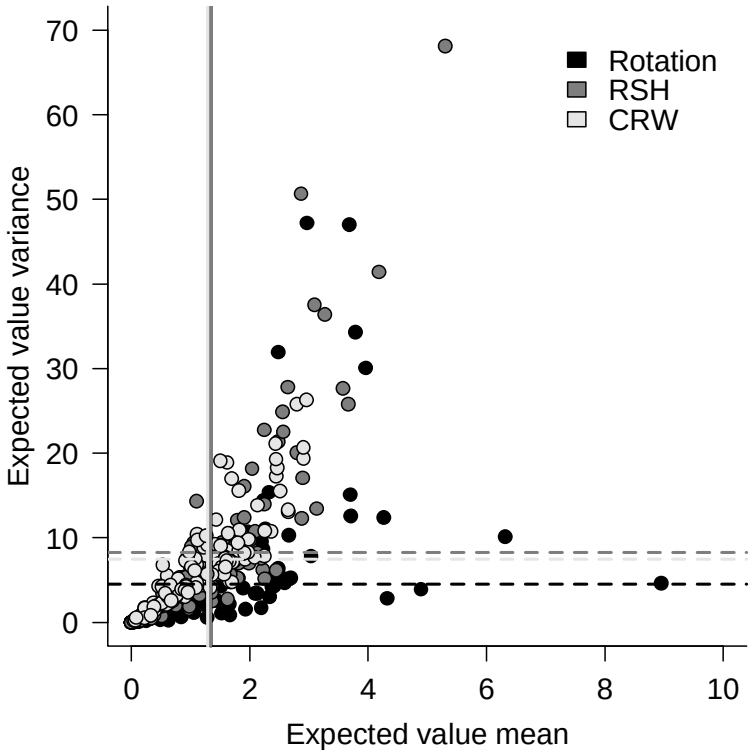

Figure 4. Mean and variance of expected values of encounter rate derived from 1,000 randomisations of corresponding elk trajectories according to one of the three null model formulations. Encounter rate is expressed per 100 elk fixes. Full vertical and dashed horizontal lines denote mean values of X and Y axes, respectively.