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LETTER

Do prey select for vacant hunting domains to minimize a multi-predator threat?

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Abstract

Many ecosystems contain sympatric predator species that hunt in different places and times. We tested whether this provides vacant hunting domains, places and times where and when predators are least active, that prey use to minimize threats from multiple predators simultaneously. We measured how northern Yellowstone elk (*Cervus elaphus*) responded to wolves (*Canis lupus*) and cougars (*Puma concolor*), and found that elk selected for areas outside the high-risk domains of both predators consistent with the vacant domain hypothesis. This enabled elk to avoid one predator without necessarily increasing its exposure to the other. Our results demonstrate how the diel cycle can serve as a key axis of the predator hunting domain that prey exploit to manage predation risk from multiple sources. We argue that a multi-predator, spatiotemporal framework is vital to understand the causes and consequences of prey spatial response to predation risk in environments with more than one predator.

Keywords

Antipredator behaviour, cougar, diel activity, elk, habitat selection, predation risk, predator facilitation, risk enhancement, synergistic predation, wolf.

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INTRODUCTION

The influence of predators on prey space use is a key mechanism by which predators structure food webs and modify ecosystem function. However, much of what is known about how prey spatially respond to predators stems from studies that consider the effects of a single predator species. A common finding is that prey avoid places where the predator is most abundant or lethal (Fig. 1a) (Lima & Dill 1990; Lima 1998a; Brown *et al*. 1999). Less is known about the effects of multiple predator species on prey habitat selection. This is problematic because almost all prey live with more than one predator (Relyea 2003; Schmitz 2007; Say-Sallaz *et al*. 2019), and how prey spatially respond to multiple predators can alter the impact of predators on prey populations and ecological communities. For example, if prey avoidance of one predator causes greater exposure to another predator and vice versa (Charnov *et al*. 1976), total prey mortality may exceed the sum of all predator-specific mortality rates (i.e., synergistic predation; Sih *et al*. 1998).

Standard hypotheses about how prey navigate multi-predator environments focus on how prey position themselves relative to the spatial domains of different predator species. Prey may select for: (1) the gap between predator spatial domains where the lethality (i.e., instantaneous probability of predator-caused mortality) of both predators is lowest (Fraser *et al*. 2004; Cresswell & Quinn 2013; Fig. 1b); (2) the spatial domain of the least lethal predator species (Relyea 2003; Morosinotto *et al*. 2010; Fig. 1c); or (3) the spatial domain of the cursorial predator assuming it leaves too few reliable environmental cues to warrant avoidance (Schmitz *et al*. 2004; Preisser *et al*. 2007; Fig. 1d). We refer to these as the '*gap*', '*lethality*' and '*hunting mode*' hypotheses, respectively. These hypotheses have provided a productive framework for exploring prey spatial response to multiple predators, but they overlook the temporal dimension of the predator hunting domain, and how it may provide additional refuge from predation (Kronfeld-Schor & Dayan 2003). We define '*predator hunting domain*' as the place(s) and time(s) where and when a predator kills its prey.

Time is a key niche axis that predators use to minimize interspecific competition across the diel (24-h) cycle (Ross 1986; Cozzi *et al*. 2012; Monterroso *et al*. 2013). Segregation of predator species over space and across the diel cycle increases the number of potential hunting domains. For example, in a system with two spatial domains (e.g., forest and grassland), the addition of two temporal domains (e.g., night and day) doubles the number of potential hunting domains available to competitively interacting predator species. It also doubles the number of potential prey refuges. Specifically, any unfilled (or minimally occupied) hunting domain provides a predictable refuge from predation in environments where every spatial domain is occupied by a predator species. Prey species living in such environments may therefore select for vacant hunting domains as a strategy to minimize predation risk (Fig. 2).

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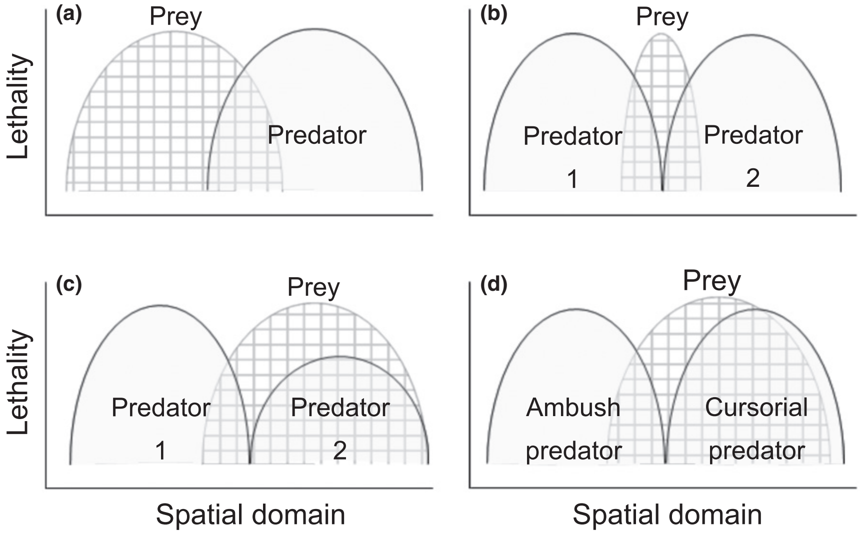

Figure 1 Standard hypotheses about how prey spatially avoid predators. In single-predator systems, prey select for the spatial domain where the predator is least lethal (a). In multi-predator systems, prey select for the gap between predator spatial domains where the lethality of both predators is lowest (b), the spatial domain of the least lethal predator (c), or the spatial domain of the spatially unpredictable cursorial predator (d). We term (b)–(d) the *'gap'*, *'lethality'* and *'hunting mode'* hypotheses. Shaded and hatched areas identify predator and prey domains, respectively.

We tested the extent that elk (*Cervus elaphus*) selected for vacant hunting domains to avoid predation from wolves (*Canis lupus*) and cougars (*Puma concolor*) in northern Yellowstone National Park (YNP). Wolves are cursorial predators that kill mainly in flat, open areas at morning and dusk (Kauffman *et al.* 2007; Kohl *et al.* 2018), whereas cougars are spot-and-stalk/ambush predators that kill mainly in topographically rugged, forested areas at night (Murphy *et al.* 1998; Ruth *et al.* 2019). We predicted that elk selected for flat, open areas at night (night-flat and night-open domains), and for rugged, forest areas during daylight (day-rugged and day-forest domains). We studied elk habitat selection in winter when wolves and cougars were the only major elk predators inside YNP (Evans *et al.* 2006; Barber-Meyer *et al.,* 2010), and during a period (2001–2004) when densities of both predators were highest (Cubaynes *et al.* 2014; Ruth *et al.* 2019). Our results shed new light on how multiple predators can drive prey habitat selection in a predator-rich environment, and how prey can minimize these multiple threats simultaneously.

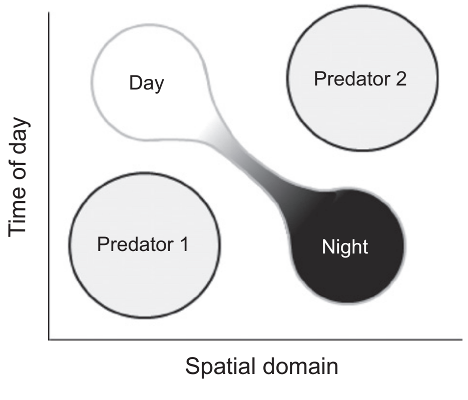

Figure 2 Vacant hunting domain hypothesis. To avoid multiple predator species, prey may select for places and times of the day where and when predators rarely kill prey (white-to-black transition). Grey-shaded circles represent the different hunting domains of two different predator species.

MATERIALS AND METHODS

Study area

Our study occurred within the northern Yellowstone elk winter range (hereafter, northern Yellowstone). This 1520-km^2 area consists of low-elevation (1500–2600 m) grasslands and shrub steppes that fan out from the Yellowstone River and its tributaries along the northern border of YNP and adjacent areas in Montana (Lemke, Mack & Houston 1998). Approximately 65% (995-km^2) of the winter range is located within the Park (hereafter, northern YNP). Most of the data in our study were collected in northern YNP (Fig. 1, 2 in Appendix S1) because wolves were concentrated there (Stahler *et al.* 2016).

Study population

We analysed habitat selection behaviour of 27 adult (> 1 year-old) female elk from the northern Yellowstone elk population, which annually occupies the winter range from about 15 October to 31 May. This population ranged from approximately 10 700 to 17 600 individuals during the study (Tallian *et al.* 2017). Adult female elk were fitted with GPS radio-collars that collected locations at 4–6 h intervals. We limited our analysis to winter locations collected from 1 November to 30 April. Appendix S1: Fig. 1 illustrates the spatial distribution of these data.

Wolf abundance in northern YNP ranged between 70 and 98 individuals in 4–8 packs (mean individuals/pack = 8.36; SE = 0.90). Each winter, 20 to 30 wolves (35–40% of northern

YNP wolf population), including 30–50% of pups born in the previous year were captured and fitted with VHF ($n = 72$ [11 unique packs], 2000–2004) or GPS radio-collars ($n = 21$ [12 unique packs], 2004–2013; Smith *et al.* 2004). Cougar abundance ranged between 26 and 42 individuals (Ruth *et al.* 2019). We monitored 54 (27 females, 27 males) radio-collared adult and independent, subadult cougars (68–93% of estimated adult cougar population; Ruth *et al.* 2011), including six GPS-collared individuals that were the focus of our activity analysis.

Predation sampling

We searched for elk killed by wolves (Fig. 2a in Appendix S1) and cougars (Fig. 2b in Appendix S1) from 1 November to 31 May by radio-tracking VHF- and GPS-collared wolves and cougars. We excluded adult male elk from our analysis because wolves killed male and female elk in different areas (Kohl *et al.* 2018), and because GPS data were unavailable to assess male habitat selection. We analysed wolf-killed elk ($n = 400$ adult females and calves) collected from 01 November 2000 to 31 May 2004 to correspond with the winters in which we monitored elk. We analysed cougar-killed elk ($n = 257$ adult females and calves) collected during winter over a longer period (April 1998 to May 2005) to maximize sample size (Appendix S2).

Spatial variation in predation risk

We used topographic roughness (Fig. 3a in Appendix S1) and vegetation openness (Fig. 3b in Appendix S1) as separate indices of spatial variation in predation risk from wolves (Creel *et al.* 2005; Fortin *et al.* 2005; Mao *et al.* 2005; Kohl *et al.* 2018) and cougars (Atwood *et al.* 2009; Bartnick *et al.* 2013). We did not consider human harvest as an important source of predation risk because only 1.8% of all elk locations and only one of 27 collared elk occurred outside YNP. We also did not consider the effects of other spatial covariates on elk habitat selection. Nevertheless, openness plausibly indicated the influence of forage availability, thermal cover and predation risk on elk habitat selection.

We developed and analysed single maps of openness and roughness because neither varied during the study period. Both spatial risk indices (30 × 30 m grid cell) were developed using the Focal tool within the *raster* package in R 3.2.3. Openness and roughness were not highly correlated (Pearson's correlation coefficient, $r = -0.18$). We calculated openness (range 0 [dense forest] – 289 [open grassland]) as the sum of non-forested cells within a 500 × 500 m moving window centred on each grid cell following Boyce *et al.* (2003) using data from the LANDFIRE program in 2001 (Fig. 4 in Appendix S1). We calculated roughness (range 0 [flat]–1114 [cliff]) as the sum of the absolute value of the difference in elevation between each grid cell and surrounding eight neighbours (3 × 3 window) following criteria developed for Yellowstone cougars (Ruth *et al.* 2019).

To determine if openness and roughness were valid indices of predation risk, we separately modelled the relative probability of a wolf- or cougar-killed elk (adult females and calves only) as a function of openness or roughness using a resource selection function framework (RSF; Manly *et al.* 2002). We analysed wolf and cougar kill RSFs with a generalized additive model (GAM) to account for potential nonlinear effects of openness and roughness on the probability of a kill at a given location (Appendix S2).

Diel activity patterns

We used movement rate to index the diel activity patterns of wolves and cougars because speed of locomotion is a valid proxy for diel activity patterns in large mammals (Ensing *et al.* 2014; Vander Vennen *et al.* 2016). In addition, ungulates, including elk, are sensitive to temporal variation in predator locomotion (Fröhlich *et al.* 2012; Kohl *et al.* 2018). For wolves, we estimated movement rate at each hour of the day from the hourly winter positions of 21 GPS-collared animals during 2004–2013.

For cougars, we estimated movement rate at each hour of the day from winter locations collected at 3-h intervals from 6 GPS-collared individuals (2 females, 4 males) during 2001–2006. Movement rate equalled the Euclidean distance of the preceding 5-h time step for wolves and 6-h time step for cougars as these intervals most closely matched the 5-h interval between consecutive elk locations. We subsampled the wolf and cougar data to match the elk data by retaining every fifth wolf location or second cougar location. We used only consecutive 5- or 6-h locations to calculate movement rates.

We modelled the mean diel movement rate by applying a generalized additive mixed model (GAMM) to the 5-h wolf and 6-h cougar step-lengths. For wolves, we could not distinguish between individual and annual variation in diel activity due to small sample sizes within years (Kohl *et al.* 2018). For cougars, we included a fixed effect for sex to account for potential differences in movement rate between males and females (Wang *et al.* 2015; Appendix S2).

Elk habitat selection

For each spatial risk index (openness and roughness), we evaluated models that tested whether elk selection for risky and safe places was (1) independent of wolf and cougar activity ('space-only' models), (2) dependent on the activity of wolves *or* cougars ('single-predator space × activity' models), or (3) dependent on the activity of wolves *and* cougars ('multi-predator space × activity' models). Space × activity models included terms for the interaction between spatial risk and mean diel movement rate of wolves and/or cougars. These models therefore evaluated how elk selection for risky and safe places at the end of a 5-h movement step was affected by the mean movement rate of predators during that step. Because male and female cougars exhibited different diel activity patterns (see *Results*), we specified separate models for the effects of male and female cougars. Our multi-predator models considered only wolves and male cougars because the mean activity patterns of wolves and female cougars were collinear (Appendix S2).

For each model, we tested different forms of the relationship between habitat selection and spatial risk to account for how elk tolerate low levels of spatial risk (Kohl *et al.* 2018). Specifically, we tested for a response threshold in elk habitat selection by comparing models with a linear effect for spatial risk to models with a threshold effect specified by two linear splines. We performed a grid search of candidate models to determine the presence and position of thresholds (Appendix S2) and identified the best-fitting model using the quasi-likelihood under independence criteria (QIC; Pan 2001). We performed 5-fold cross validation (n = 1000) for a step-selection function design to evaluate the predictive accuracy of each best-fit model (Boyce *et al.* 2002). Average Spearman rank correlations (r_s) > 0.70 indicated satisfactory fit of models to data (Boyce *et al.* 2002).

Visualizing elk selection for vacant hunting domains

We used our models of diel predator movement rate and spatial kill probability to visualize cougar and wolf hunting domains. The cougar hunting domain was based on the activity of males and the kills of males and females. We excluded female activity because it was a poor predictor of elk habitat selection (see Results), and included kills by both sexes because their spatial distributions with respect to openness and roughness were similar (Appendix S3). Using predicted mean values of diel predator movement rate and spatial kill probability, we calculated percentile-specific ellipses to illustrate the hunting domain of each predator. The 90th percentile ellipse indicated the places and times where and when predation risk was greatest. We overlaid the ellipses on a contour plot of elk habitat selection with respect to spatial risk (openness and roughness) and time of day to reveal the extent that elk selected for vacant hunting domains (see Appendix S2). This provided a visualization of elk habitat selection relative to the hunting domains of wolves and male cougars that was comparable to the vacant domain hypothesis illustrated in Figure 2. Our visualization assumes that areas occurred within the study area where all possible values of openness (0–289) or roughness (0–150) were accessible to an elk within a 5-h movement step. We demonstrate the validity of this assumption in Appendix S2.

RESULTS

Hunting domains

Wolves and cougars hunted elk (adult females and calves) in different places at different times of the day. Cougars mainly killed elk in moderately forested, rugged areas while wolves killed elk in open, flat areas (Fig. 3). And whereas cougars, especially males, hunted mainly at night, wolves hunted mainly during morning and at dusk (Fig. 4; Appendix S4). The diel activity pattern of male cougars was unimodal with a single peak in activity at 0300-h (Fig. 4a). Female cougars exhibited a bimodal pattern, with comparatively lower activity peaks at about 0400-h and 2000-h (Fig. 4a). The activity pattern of wolves was also bimodal with activity peaks at 1000-h and 2000-h (Fig. 4b). Together, cougars hunting at night in rugged forests, and wolves hunting in daylight (morning/dusk) in flat open areas indicated four vacant hunting domains: ‘night-open’, ‘night-flat’, ‘day-rough’ and ‘day-forest’.

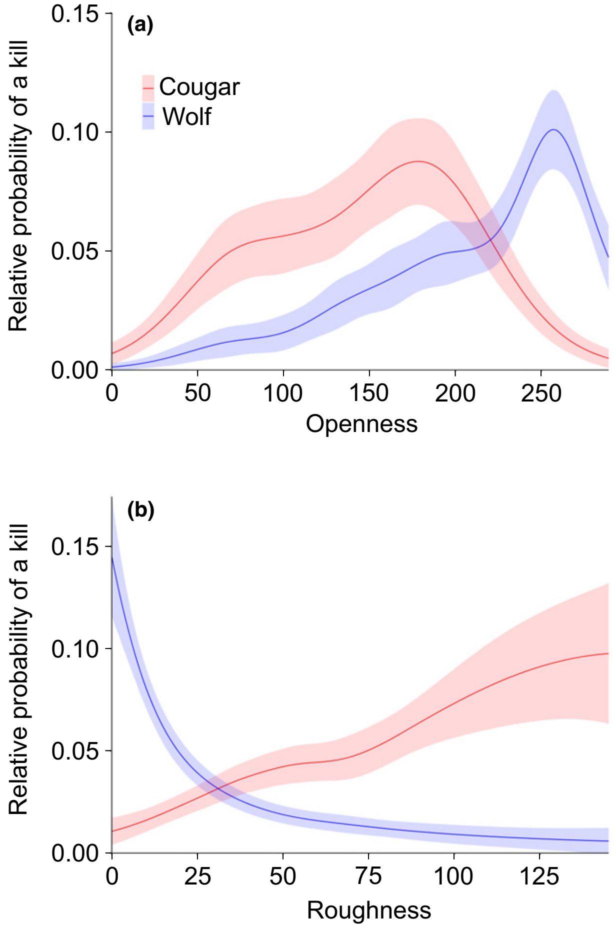

Figure 3 Spatial distribution of elk (adult females and calves) killed by wolves (2000–2004) and cougars (1998–2006) during winter in northern Yellowstone National Park relative to vegetation openness (a) and topographic roughness (b). Lines are fitted values with 95% confidence intervals (shaded areas) from four separate generalized additive models (Appendix S2).

Elk habitat selection

The effect of spatial risk on elk habitat selection was nonlinear. For each spatial risk index (openness, roughness), the top space-only model included a linear spline for spatial risk (Appendix S5, S6), indicating a threshold at which the effect of spatial risk on habitat selection changed. Evidence against a model describing a simple linear relationship between spatial risk and habitat selection was strong for openness (ΔQIC = 37.3; Appendix S5) and roughness (ΔQIC = 89.2; Appendix S6).

Support for the top space-only models was substantially weaker compared to single-predator models that included space × activity interactions between mean diel movement rate of male cougars (or wolves) and linear splines for openness (ΔQIC = 342.4–360.6; Appendix S5) or roughness (ΔQIC = 34.5–111.3; Appendix S6). Similar models including

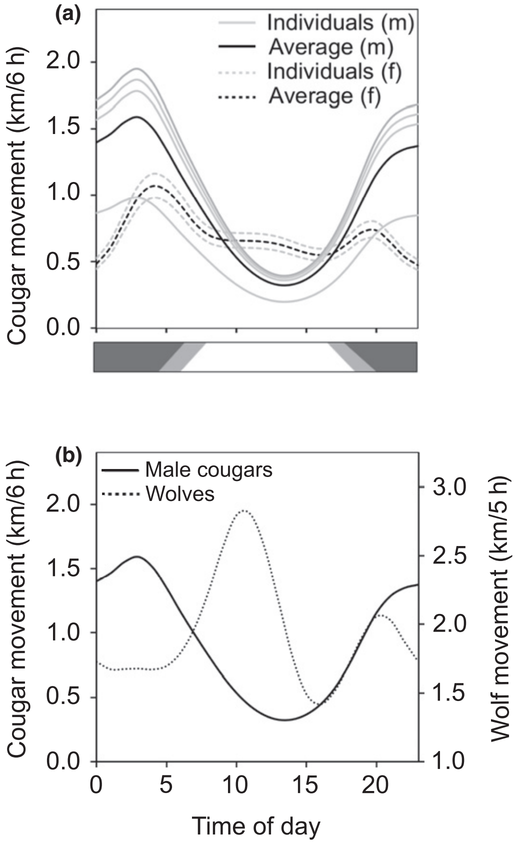

Figure 4 Diel activity pattern of cougars and wolves during winter in northern Yellowstone National Park. Mean 6-h movement rate for 6 GPS-collared cougars (2 F, 4 M) and the predicted sex-specific population means from a generalized additive mixed model (a). Predicted mean 6-h movement rate of male cougars (left ordinate) relative to the predicted mean 5-h movement rate of 21 GPS-collared wolves (right ordinate) (b). Bars represent day (white), night (black) and dawn/dusk periods (grey) from 15 Nov to 15 April.

mean diel movement rate of female cougars differed little from the top space-only model (openness: ΔQIC = 2.6; roughness: ΔQIC = −0.7; Appendix S5, S6), indicating little or possibly no effect of female cougars on elk habitat selection. Support for the single-predator wolf models was also notably weaker compared to the single-predator male cougar models (openness: ΔQIC = 18.3; roughness: ΔQIC = 76.8; Appendix S5 and S6). This suggests that male cougars had a stronger singular effect on elk habitat selection than did wolves.

However, support for the single-predator male cougar model was substantially weaker compared to multi-predator models that also included the activity of wolves (openness: ΔQIC = 38.7; roughness: ΔQIC = 10.9; Appendix S5, S6). This suggests that elk responded to both predators simultaneously. Support for models that included the activity of male and female cougars was weaker compared to the best-fit models that included the activity of male cougars and wolves (openness: ΔQIC = 13.5; roughness: ΔQIC = 1.9; Appendix S5, S6). Fivefold cross validation revealed a strong correlation between observed and predicted values for these best-fit models (openness: $r_s = 0.98$; roughness: $r_s = 0.95$). Correlations of this magnitude indicate that these models were reliable.

Coefficients for the best-fit models (Appendix S7) indicate that when male cougar activity was high and wolf activity was low, elk selected for open areas (Fig. 5a, red line) and avoided rough areas (Fig. 5b, red line). Conversely, when wolf activity was high and male cougar activity was low, elk avoided the most open areas (Fig. 5a, blue line: descending limb) and selected for rougher areas (Fig. 5b, blue line: ascending limb). The subsequent shift to avoidance with increasing levels of roughness (Fig. 5b, blue line: descending limb) may reflect a latent response to female cougars. Females were more active than males when wolf activity was high (Fig. 4a), and the level of roughness where selection switched to avoidance approximates the point beyond which the probability of cougar predation exceeded that of wolf predation (Fig. 3b).

Selection for vacant predator hunting domains

Figure 6 illustrates the four vacant hunting domains: day-forest (< ~200 openness), night-open (> ~200 openness) (Fig. 6a), day-rough (> ~75 roughness) and night-flat (< ~75 roughness) (Fig. 6b). The best-fit model for openness (Appendix S7a) indicated that elk selected for the day-forest and night-open domains (Fig. 6a), and the best-fit model for roughness (Appendix S7b) indicated that elk selected for the night-flat domain but not the day-rough domain (Fig. 6b). During daylight hours, elk tended to select for rougher areas outside the riskiest wolf domain (90th percentile) and within the lower risk wolf domains (70–80th percentile).

DISCUSSION

Most prey species live in environments with more than one predator species, yet few empirical studies have tested the simultaneous effects of multiple predators on prey space use, especially in free-living vertebrate systems (Say-Sallaz *et al.* 2019). And whereas most predators exhibit predictable fluctuations in activity across the diel cycle (Kronfeld-Schor & Dayan 2003), previous multi-predator studies neither measured continuous variation in diel predator activity nor linked it to prey habitat selection as we did. These studies only compared prey space use between light and dark periods (e.g., Kotler *et al.* 1992, Clark *et al.* 2003, Lone *et al.,* 2017). This approach would have obscured our results because wolf and cougar activity patterns were complex functions of time of day that did not neatly fit the conventional dichotomy of safe and dangerous periods. As far as we know, our study is the first to quantify how continuous variation in spatial risk (Fig. 3) and diel activity (Fig. 4) of more than one predator simultaneously affects the habitat selection of a shared prey. Our results advance understanding about the spatial ecology of predator–prey interactions in two important ways.

First, we demonstrate how it is perilous to assume that prey habitat selection in a multi-predator environment is sensitive to just one predator species. When wolves were reintroduced to Yellowstone National Park in 1995–1997 (Bangs & Fritts 1996), they joined a system that was already populated by other predators of elk, including growing numbers of grizzly

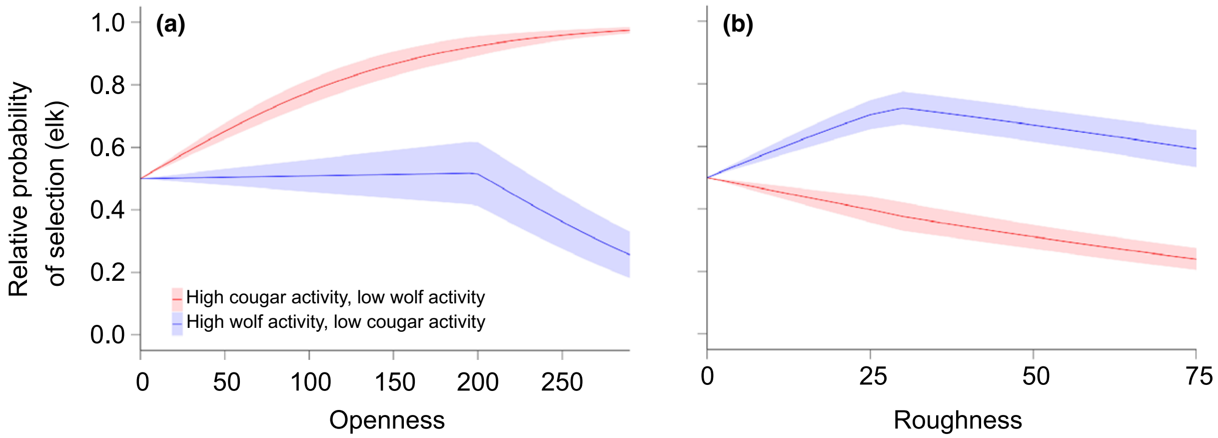

Figure 5 Effects of diel predator activity (predicted movement rates of wolves and cougars [Fig. 4b]) on elk habitat selection in northern Yellowstone National Park, 2001–2004. Red line indicates that when cougar activity was high (1.59 km/6-h) and wolf activity was low (1.42 km/5-h), elk selected for open areas (a), and avoided rough areas (b). Blue line indicates that when wolf activity was high (2.80 km/5-h) and cougar activity was low (0.33 km/6-h), elk avoided open areas > 199 (a), and selected for rough areas < 28 (b). Lines are population-averaged fitted values with 95% confidence intervals (shaded areas) from the best-fit multi-predator space × activity models (Appendix S7).

bears (*Ursus arctos,* Kamath *et al.* 2015) and cougars (Ruth *et al.* 2019). Despite this predator diversity, subsequent research and commentary about elk space use in and around Yellowstone have assumed, implicitly or explicitly, that wolves are the only (or primary) predator that elk respond to (e.g., Ripple & Larsen 2000; Laundré *et al.* 2001; Creel *et al.* 2005; Fortin *et al.* 2005; Mao *et al.* 2005; Middleton *et al.,* 2013a, 2013b; Kohl *et al.* 2018; Cusack *et al.* 2019). Our study is the first to test this long-held assumption, and our results suggest it is false. We found strong evidence that elk habitat selection was shaped by the risk of predation from wolves *and* cougars. Specifically, our top wolf-only models of elk habitat selection performed poorly compared to our best-fit models that included wolves and male cougars (openness: ΔQIC = 57.0; roughness: ΔQIC = 87.7; Appendix S5, S6).

We also found that male cougars, not wolves, exerted the most pressure on elk habitat selection. The evidence for this is twofold. First, there was substantially less support for our top wolf models compared to our top male cougar models (Appendix S5, S6). Had we ignored the simultaneous effects of wolves and male cougars, we would have concluded that wolves had no effect on elk habitat selection. Second, when we accounted for these simultaneous effects, we found that the magnitude of the male cougar effect was 25–80% greater than that of the wolf effect (Appendix S7). These findings suggest that a fixation on wolves in systems with cougars could lead to misleading conclusions about the causes and consequences of elk response to predation risk. This problem may apply to other multi-predator systems where one predator species is assumed primary to another.

We are uncertain why the strong cougar effect was linked to the activity of males and not females. Poor support for the female cougar models relative to the space-only models that excluded all predator activity (Appendix S5, S6) suggests that elk were insensitive to female cougars. Yet models that included male and female cougars ranked second to our best-fit models that included male cougars and wolves (Appendix S5, S6). Near equal support for these models with respect to roughness (ΔQIC = 1.9; Appendix S6) indicates that we cannot rule out an influence of female cougars. We expected such an influence because adult females were more than three times as abundant as resident adult males, females with kittens had a higher kill rate than males (Ruth *et al.* 2019), and at least one female in our sample had kittens. On the other hand, the tendency for females, which are smaller than males, to focus their predation on elk calves (Murphy *et al.* 1998; Ruth *et al.* 2019), together with the possibility that few radio-collared elk had a calf at heel due to a scarcity of calves at the time (Proffitt *et al.* 2014), might have diminished the pressure of female cougars on elk habitat selection.

Our second important advance is that we show how the diel activity patterns of predators provide crucial insight to how prey species manage threats from multiple predators. These patterns clarified how it is possible for prey to be safe from multiple predator species simultaneously. Had we ignored diel predator activity, we would have concluded, incorrectly, that avoiding one predator necessarily increased exposure to the other. Recognizing that wolves and cougars hunted in different places *and* at different times revealed how elk could simultaneously minimize threats from both predators. Movement out of the forest and into the open to avoid cougars, for example, did not result in greater risk from wolves and vice versa because these predators were active at different times of day. Cougars were most active at night, whereas wolves were most active in the morning and at dusk (Fig. 4), and these temporal differences allowed elk to safely use open areas at night when cougars were a threat in the forest and wolves were little threat in the open (Fig 6a). Thus, two apparently conflicting predator-specific prey defenses (select open vegetation to avoid cougars vs. select forest cover to avoid wolves; Atwood *et al.* 2009) were actually compatible after accounting for diel predator activity.

Strong elk habitat selection for the night-open domain (Fig. 6a) and night-flat domain (Fig. 6b) provided the clearest

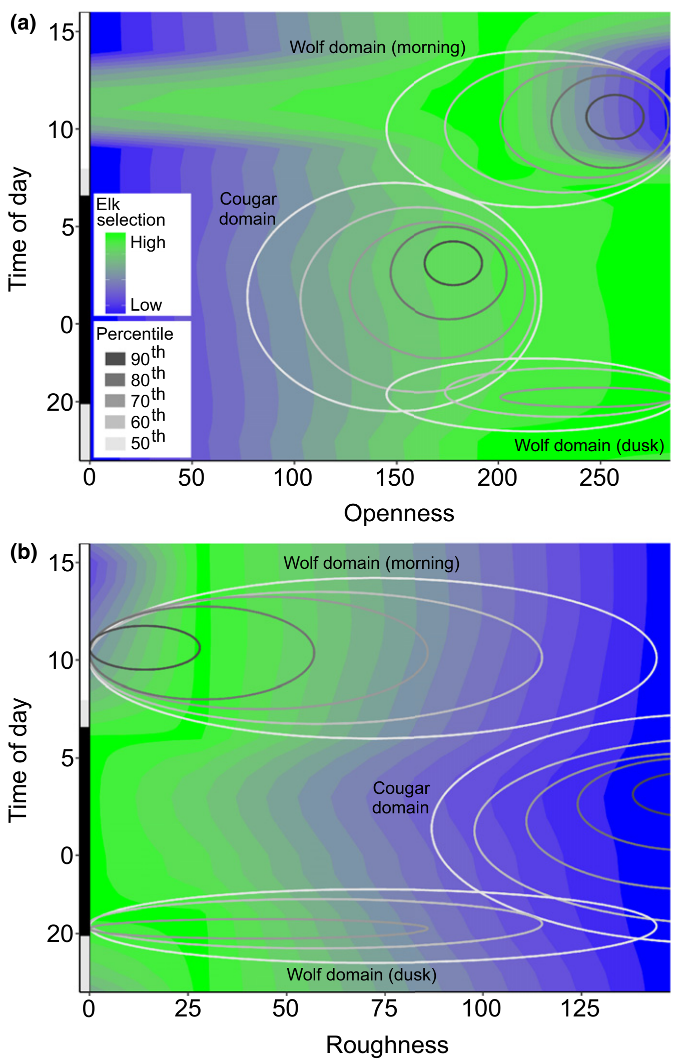

Figure 6 Elk habitat selection relative to the hunting domains of wolves and cougars with respect to vegetation openness (a) and topographic roughness (b) in northern Yellowstone National Park, 2001–2004. Blue-green contours are fitted values from the best-fit multi-predator space × activity models (Appendix S7); bright green contours indicate where and when elk habitat selection was highest. Grey-black ellipses are the top five percentiles of the fitted values from the models of spatial kill probability (Fig. 3) and diel predator activity (Fig. 4b); small black ellipses indicate where and when predation risk was highest. Y-axis bars denote approximate day (white), night (black) and dawn/dusk periods (grey) from 15 Nov to 15 April.

support for our vacant hunting domain hypothesis. At night (*c*. 2300–0500 h), the most open and flat areas of the landscape were outside the high-risk (90th percentile) and low-risk (50th percentile) predator hunting domains. As night turned to day, elk selected for more forested and rugged areas outside the high-risk wolf domains. Although this included selection for the vacant day-forest domain, selection for vegetation openness was highest within the low-risk wolf domains. Similarly, selection for rough areas was concentrated at the edge of the high-risk wolf domain. Elk may have tolerated these areas because they corresponded to places where the probability of wolf predation was too low (< 0.05; Fig. 3) to warrant selection for denser forests and rougher topography. These patterns suggest that in some cases elk selected for hunting domains that were effectively vacant rather than totally vacant. This is consistent with an animal that seeks to minimize predation risk without sacrificing other critical activities, such as feeding (Lima 1998b).

Our findings are consistent with the ‘gap’ hypothesis (Fig. 1b) insofar as elk habitat selection was concentrated outside the high-risk predator domains. The ‘gaps’ in our system, however, were a function of temporal and spatial variation in predation risk, and we would have overlooked them had we ignored diel variation in predator activity. After accounting for this variation, we found no uniform support for the ‘lethality’ or ‘hunting mode’ hypotheses (Fig. 1c-d). Assuming wolves were more lethal and less predictable than cougars, elk selection for lightly forested areas within the cougar domain (Fig. 6a) was consistent with ‘lethality’ but not ‘hunting mode’, whereas elk selection for flatter areas within the wolf domain (Fig. 6b) was consistent with ‘hunting mode’ but not ‘lethality’.

Wolves were plausibly more lethal than cougars during our study given evidence from a concurrent study that radio-collared female elk, including some from our study, were more likely killed by wolves than by cougars (Evans *et al*. 2006). On the other hand, snow-tracking and direct observation suggest that cougars may be more successful hunters than are wolves (Hornocker 1970; MacNulty *et al*. 2012). Ambiguous support for the hunting mode hypothesis may reflect how the cursorial mode of wolves was no less predictable than the spot-and-stalk/ambush mode of cougars in space (Fig. 3) or time (Fig. 4). Nevertheless, the overall stronger response of elk to cougars accords with the general notion that predator identity affects the strength of antipredator responses due to differences in functional traits of the predators (Schmitz *et al*. 2004; Preisser *et al*. 2007). Our results suggest that the effect of predator identity can arise from functional differences among predators unrelated to their spatiotemporal predictability.

Our findings are broadly relevant to ecology and conservation because they reveal a novel mechanism that may dampen the ecological effects of predators in at least three ways. First, a prey species that avoids one predator without increasing its risk to another reduces the potential for synergistic effects, where combined predators kill more prey than expected by their individual effects (also termed predator facilitation or risk enhancement; Sih *et al*. 1998; McCoy *et al*. 2012). Although conflicting prey defenses are not the sole cause of synergistic predation (Sih *et al*. 1998), our findings may help explain why synergistic predation is rare in natural systems (Schmitz 2007).

Second, prey that can simultaneously forage and be safe from multiple predators are less reliant on energetically costly antipredator defenses (e.g., vigilance, habitat shifts) that reduce survival and/or reproduction (termed non-consumptive or risk effects). In the elk we studied, high-body fat levels and correspondingly high-pregnancy rates (Cook *et al*. 2004; White *et al*. 2011; MacNulty *et al*. 2016; Kohl *et al*. 2018) were consistent with the hypothesis that selection for the vacant night-open and night-flat domains (Fig. 6a), which included preferred grassland foraging habitats, was sufficient to offset the effects of wolves and cougars on over-winter fat loss and pregnancy rate. This may explain how elk in other populations maintained access to grasslands, and why they too maintained high levels of over-winter nutrition and/or pregnancy rate despite the presence of wolves and cougars (Hamlin *et al.* 2009; White *et al.* 2009; Middleton *et al.* 2013a).

Third, selection for vacant domains, which permits prey to forage in risky places at safe times, limits the capacity for predators to trigger behaviourally mediated trophic cascades. In our system, numerous studies suggest that the growth increase of some palatable woody deciduous plants (e.g., aspen, *Populus tremuloides*; willow, *Salix spp.*) is, at least partly, attributable to reduced herbivory from elk avoiding risky places where they might be killed by wolves (reviewed by Peterson *et al.* 2014; Beschta & Ripple 2016). Our results suggest that this scenario is unlikely because wolves were not the main predator affecting elk habitat selection, and neither wolves nor cougars excluded elk from risky places. On the contrary, elk maintained regular access to risky places during daily lulls in wolf and cougar activity. This may help explain why many aspen and willow have not escaped herbivory (Kauffman *et al.* 2010; Marshall *et al.* 2014).

The overarching insight from our study is that prey habitat selection in nature, where almost all prey species are exposed to many predator species distributed unevenly in space and time, is unlikely affected by only one predator in one dimension. The classic single-predator, space-only paradigm of spatial predator–prey interactions (Fig. 1a) has provided tremendous insights. But given its limits for making sense of a wild, speciose system like northern Yellowstone National Park, we encourage ecologists to pursue a multi-predator, spatiotemporal understanding of spatial predator–prey interactions (e.g., Fig. 2). Such an approach may offer new clarity about the causes and consequences of prey spatial response to predation risk.

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AUTHORSHIP

M.T.K. and D.R.M. conducted the analyses and wrote the manuscript. T.K.R, M.C.M, D.R.S., P.J.W., and D.W.S assisted with data collection and field logistics. All authors contributed substantially to revisions.

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SUPPORTING INFORMATION

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

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