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Predators reduce niche overlap between sympatric prey

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Predators may alter niche overlap between prey species by eliciting divergent anti-predator behavior. Accordingly, we exploited heterogeneous gray wolf *Canis lupus* presence in Washington, USA, to contrast patterns of resource and dietary overlap between mule *Odocoileus hemionus* and white-tailed deer *O. virginianus* at sites with and without resident packs. Mule deer run (stot) in a way that is less effective as a means of fleeing from predators than the galloping gait of white-tailed deer. Consequently, mule deer manage risk from coursing predators like wolves by avoiding encounters, whereas white-tailed deer respond to such predators by exploiting areas where they are most likely to escape pursuit. Thus, under the 'refuge partitioning hypothesis' whereby predators reduce prey niche overlap by eliciting use of different refugia, we predicted wolf exposure to 1) decrease resource and dietary overlap between these ungulates, and 2) induce segregation consistent with each species using different parts of the landscape to reduce their wolf risk. At the home range scale, the ways in which resource overlap diminished in the wolf areas were consistent with the prey species reducing their respective risks, particularly with respect to slope, with mule deer separating from white-tailed deer by seeking steeper areas where wolf encounters are less likely. At the within-home range scale, the manner in which spatial overlap decreased in relation to forest cover was consistent with species-specific risk management, with mule deer avoiding wolf encounters by shifting toward this resource. Reduced resource overlap between the deer in areas occupied by wolves did not correspond with dietary divergence. Our findings suggest that wolf risk mediates spatial but not necessarily dietary overlap between sympatric ungulates, divergent anti-predator behavior is a non-consumptive pathway by which predators can reduce interspecific competition among prey, and use of disparate refugia by prey may not result in dietary divergence.

Keywords: anti-predator behavior, *Canis lupus*, competition, diet, gray wolf, mule deer, *Odocoileus hemionus*, *O. virginianus*, predation risk, refuge competition hypothesis, ungulates, white-tailed deer

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Introduction

Predators have the potential to shape communities by altering competition among co-occurring species at lower trophic levels (Connell 1961a, b, Murdoch 1969, Caswell 1978, Holt 1984). The dominant paradigm has been that predators promote coexistence by inhibiting competitive exclusion (Paine 1966). Although predators do commonly reduce the intensity of competition from the top down (Gurevitch et al. 2000), their effects may also be neutral or even exacerbate competitive interactions (Kotler and Holt 1989, Chase et al. 2002, Orrock et al. 2013, Sommers and Chesson 2019). Identifying the drivers of these different scenarios is therefore crucial to our understanding of the relationship between predation and competition (Sommers and Chesson 2019) and capacity to predict the effects of widespread and ongoing changes to predator abundance and distribution on community structure in the Anthropocene (Chase et al. 2002).

Avoidance behavior has emerged as a key non-consumptive mechanism that can determine how predators shape competition among their prey species. Under the 'refuge competition hypothesis', use of a shared refuge by prey species with a common predator (or predators) may heighten competition by forcing them to converge on a limited set of resources (Holt and Lawton 1994, Chase et al. 2002, Orrock et al. 2013, Pringle et al. 2019). Alternatively, under the 'refuge partitioning hypothesis', predators may reduce prey niche overlap by eliciting use of divergent refuge space by prey species that exploit the same foraging habitat (Jeffries and Lawton 1984, Holt and Lawton 1994, Kotler et al. 1994, Chase et al. 2002). Few studies to date have weighed support for these competing hypotheses in a field system with large vertebrates (see Lingle 2002 for an example). Accordingly, we tested them by examining patterns of resource and dietary overlap between co-occurring mule deer *Odocoileus hemionus* and white-tailed deer *O. virginianus* in areas of northeastern Washington, USA, with variable gray wolf *Canis lupus* presence.

Interactions between gray wolves and their prey in temperate regions of North America and Europe are well explored (Mech and Peterson 2003, Garrott et al. 2013, Winnie and Creel 2017). Few studies, however, have examined wolf effects on resource overlap between co-occurring prey, and most of these have taken place in systems where such effects are transmitted by selective predation (e.g. in Yellowstone National Park where diminished overlap between elk, *Cervus elaphus* and bison, *Bison bison*, has resulted from wolf predation on the former; Ripple et al. 2011). Accordingly, there remains need for investigation of the capacity of gray wolves to mediate resource overlap between sympatric prey species whose susceptibility to predation is more equivalent (e.g. species with more similar body size and defensive armament).

Mule and white-tailed deer can exhibit considerable spatial and dietary overlap where they co-occur (Krämer 1973, Whittaker and Lindzey 2004, Brunjes et al. 2006, Berry et al. 2019). However, mule deer tend to select for more open terrain at higher elevations whereas white-tailed deer are more strongly associated with lower elevation habitats that offer greater concealment (Brunjes et al. 2006). Thus, co-occurrence of the two species is thought to be promoted by a mosaic of open and dense cover (Brunjes et al. 2006). In regions where population sizes of the two deer species are asymmetrical, the more abundant species typically occurs in areas primarily used by the other (Whittaker and Lindzey 2004). Under these circumstances, the more abundant species might out compete the other because of exploitation of shared resources (Krämer 1973) and wolves could mediate this process by modifying the extent of prey resource overlap. To date, however, the impact of wolves on niche overlap between mule deer and white-tailed deer has not been addressed.

Gray wolves began naturally recolonizing Washington state, USA, from northern Idaho and southern British Columbia, Canada, in 2008. There are currently more than 20 confirmed packs that are distributed heterogeneously across eastern Washington (Washington Dept of Fish and Wildlife et al. 2020). Taking advantage of this quasi-experimental opportunity, we quantified patterns of resource overlap between adult mule and white-tailed deer in replicated areas occupied by and lacking established wolf packs. Notably, mule and white-tailed deer have different running gaits – stotting (bounding) and galloping, respectively (Lingle 1993). Whereas stotting by mule deer is ineffective as a means of fleeing from coursing or pursuit predators like coyotes *C. latrans* and wolves (Lingle 2002, Lingle and Pellis 2002), galloping allows white-tailed deer to flee effectively from coursing predators if there is gentle terrain to facilitate unobstructed movement (Kunkel and Pletscher 2001, Lingle and Wilson 2001, Kittle et al. 2008). Accordingly, Lingle (2002) showed that mule deer sought higher ground dominated by steep terrain to avoid attacks by coyotes, whereas white-tailed deer sought gentle terrain promoting their ability to flee from coyotes post-encounter. Similarly, in a study addressing the impact of wolf presence on intraspecific differences in habitat use, Dellinger et al. (2019) found that, relative to conspecifics in wolf-free areas, mule deer occupying pack territories in our study system increased their use of landscape features – notably areas close to forest cover and with steep slopes – that would be expected to decrease the likelihood of encountering wolves, whereas white-tailed deer at risk from wolves selected areas with gentler slopes that would be expected to facilitate rapid flight in the event of a wolf encounter. By implication, wolves may reduce interspecific niche overlap between these two deer species by inducing movement from jointly used space to disparate areas where predation risk is diminished, with reductions in overlap being greatest for landscape features that influence the danger posed by wolves to these two ungulates divergently. Under this refuge partitioning hypothesis, we predicted that 1) wolf exposure would decrease resource overlap between these two ungulates, 2) decreases in overlap would be most pronounced along gradients of slope and 3) use of distinct refugia would correspond with reduced dietary overlap (under the assumption that exposure to different resources would increase the likelihood of the deer species encountering different foods). It is also plausible, however, that wolves increase niche overlap between mule and white-tailed deer by inducing shared use of either resources not evaluated by Dellinger et al. (2019) or locations where wolf activity (i.e. pre-encounter risk) is depressed. This refuge competition hypothesis predicts increased resource and dietary overlap between the two deer species in areas where they are exposed to wolf packs.

Material and methods

Study area

This study took place from 2013 to 2016 in a region spanning Okanogan and Ferry Counties of northeastern Washington that included portions of the Okanogan-Wenatchee and Colville National Forests and the Colville Indian Reservation. Our study area consisted of four distinct sites (400–735 km^2), two occupied by gray wolf packs ('Strawberry' and 'Nc'icn') and two that had yet to be colonized. Patterns of habitat composition, human activity and plant and wildlife species assemblages within the study area were similar across the four sites and are described in detail by Dellinger et al. (2019). Thus, we used sites within each wolf treatment category (present or absent) as replicates.

Field data collection

We monitored gray wolf activity intensively in all four sites as described by Dellinger et al. (2019). Briefly, we surveyed roads and game trails for animal sign (e.g. tracks) on a weekly basis during the winter, deployed motion-activated camera grids across the landscape (16 cameras per 4 × 4 km site), and took advantage of positional data from GPS radio-collars deployed on individuals within each of the two focal wolf packs by the Colville Indian Reservation Fish and Wildlife Department. None of these monitoring methods revealed gray wolf pack activity in either wolf-absent site during the study, though we did detect lone wolves intermittently on our remote game cameras (n = 5 individual detections) that were likely either dispersing or exhibiting extraterritorial movement. By contrast, all three yielded strong and consistent evidence of wolf pack activity in the sites we designated as wolf occupied: the cameras detected wolves on more than 300 occasions in the two wolf-occupied sites over the three years of the investigation, and GPS data from radio-collars on at least two members of each pack revealed that both packs ranged between 3 and 8 members (mean = 5) and consistently used the two wolf-impacted sites as their respective home ranges in each of the three years of the investigation. Accordingly, we are confident in our categorization of the four sites as either wolf free and wolf occupied for the purposes of this study.

As a basis for contrasting coarse- (i.e. home range level) and fine-scale (i.e. within home range) resource partitioning between mule and white-tailed deer, we captured individuals of both species during winter using a combination of aerial net gunning and baited clover traps (Haulton et al. 2001) and then outfitted them with GPS radio-collars as described in Dellinger et al. (2019). Over the course of three years, we equipped 120 adult deer (n = 40 female and 21 male mule deer, n = 40 female and 19 male white-tailed deer) with GPS collars. All GPS data were stratified into temporal bins for winter (October–March; i.e. months with snow cover) and summer (April–September) and spatial bins representing areas where wolf packs were either present or absent. Mule deer collar deployments averaged 436 (± 306 SD) days and yielded an average of 744 (± 507 SD) GPS locations in the non-wolf areas, and averaged 552 (± 221 SD) days and yielded an average of 975 (± 379 SD) GPS locations in the wolf-affected areas; white-tailed deer collar deployments averaged 335 (± 278 SD) days and yielded an average of 589 (± 493 SD) GPS locations in the non-wolf areas, and averaged 493 (± 373 SD) days and yielded an average of 721 (± 561 SD) GPS locations in the wolf-affected areas.

To assess deer diets, 44 captured individuals were instead equipped with animal-borne video camera collars (Exeye LLC, Bristow, VA; model ABC01). The systems, which were deployed on deer occupying all four study sites, were positioned such that the instrumented deer's chin and mouth were visible in the foreground, with a view of the animal's surroundings in the background, so that all items targeted (i.e. bitten) during foraging bouts could be viewed and documented (Supporting information). The video cameras collected data on SD cards for two weeks, turning on for 10 min out of every 30 min during daylight hours (08:00–16:00), and then dropped off using a timed release. Animal captures and collar deployments were conducted under University of Washington Institutional Animal Care and Use Committee (IACUC) protocol 4226-01 and wildlife collection permits from the Washington Department of Fish and Wildlife and the Colville Tribes Fish and Wildlife Department.

Resource covariates

Many studies have used resource overlap as a proxy to examine interspecific competition (MacArthur 1958, Colwell and Futuyama 1971, Pianka 1974, Abrams 1980, Jenkins and Wright 1988, Smith et al. 2018). Accordingly, we estimated the degree to which mule and white-tailed deer overlapped along gradients of a set of resources (habitat features) selected based on previous studies of these species (Whittaker and Lindzey 2004, Brunjes et al. 2006). Habitat covariates included elevation (in meters, m), slope (in degrees) and distance to vegetation type (m; forest or shrub steppe). We obtained raw data for vegetation types from the Washington GAP (Geospatial Analysis Project) raster habitat layer (United States Geological Survey 2011), and for secondary roads and landscape attributes from the Washington State GIS data clearinghouse (<https://wagda.lib.washington.edu/data/geography/wa_state/>; accessed 15 November 2016). No major events (e.g. forest fires) occurred in our study areas between 2011 and the culmination of our data collection interval that would have compromised the applicability of the raw vegetation data we used. We originally compiled all resource data at a 30 × 30 m resolution (the finest resolution we could obtain for all pertinent GIS layers). We assessed habitat type using a Euclidean distance analysis (EDA) framework (Benson 2013). We estimated the straight-line distance from each pixel (30 × 30 m resolution) to the nearest forest cover or shrub steppe vegetation cover cell. We then standardized these distance values, as well as elevation and slope, by subtracting each value by the mean and then dividing by the standard deviation to render coefficient estimates derived from these variables easier to interpret (Benson 2013).

Dietary analysis

Trained observers reviewed a total of five minutes of randomly chosen 10-s videos from the morning (07:30–07:35), midday (12:00–12:05) and evening (15:30–15:35), respectively, for each day of video recorded per deer. For each 10-s video, observers recorded the amount of time in seconds that the focal deer devoted to actively feeding on (i.e. biting or chewing tissue removed from) different plant types. Plants could not always be reliably discriminated to species, so we instead categorized them broadly as coniferous tree, deciduous tree, ground cover (sprawling or creeping live plants), shrub, lichen, ground litter (dead, detached plant matter) or other. Because the number of videos per deer varied (Supporting information), we pooled data for each deer, thus creating an overall winter diet composition matrix (i.e. proportion of time individual deer devoted to foraging on each dietary category during winter over the course of each deployment).

Statistical analyses

We anticipated that wolves might mediate patterns of resource overlap between the deer species at multiple spatial scales because a companion study found that wolves influenced their resource selection at multiple scales (Dellinger et al. 2019). Thus, we first examined resource overlap between mule deer and white-tailed deer in wolf and non-wolf areas at a coarse spatial scale (i.e. 1-km^2 cells; Peters et al. 2013). We examined large-scale overlap, corresponding to habitat use patterns at the second order scale of home range positioning on the landscape (Johnson 1980), as a function of a suite of resource covariates using the ordination method of redundancy analysis (RDA; Bowman et al. 2010, Peters et al. 2013). We subsetted the GPS data according to season (summer/winter) and wolf presence/absence, so there were four separate RDA analyses. We classified winter as October–March (i.e. months with snow cover) and summer as April–September (see the Supporting information for how this seasonal classification may have affected the results). In RDA, the ordination axes for the species matrices are constrained linear combinations of the independent variable matrices that result in the best linear combination of resource covariates that minimize resource overlap between the species (ter Braak 1995). Thus, in our case RDA revealed where the two deer species occurred along gradients of the resource covariates under investigation and attempted to define a niche space for each within the study area. Each RDA analysis resulted in two ordination axes, the first representing resource covariates explaining separation between species and the second resource covariates explaining association between species (Bowman et al. 2010, Peters et al. 2013). Negative coefficient estimates on either ordination axis were interpreted such that increasing values were associated with mule deer. Conversely, positive coefficient estimates on either ordination axis were interpreted such that increasing values were associated with white-tailed deer (Peters et al. 2013). Thus, within each treatment subset the deer species with the smallest difference between their own species score and the coefficient estimates for any particular resource covariate (Table 1) primarily used that resource compared to the other deer species (Peters et al. 2013). A resource covariate derived using EDA was interpreted such that a higher value meant increasing distance to that resource (Benson 2013). Therefore, the deer species with the largest difference between their own species score and an EDA-derived coefficient estimate for a resource covariate was positioning itself closer to the resource.

Table 1. Summary of redundancy analyses (RDA) addressing coarse-scale (home range level) spatial overlap with respect to a suite of resource covariates between mule deer and white-tailed deer. The analyses were stratified by season (winter: October–March; summer: April–September) and wolf presence/absence. RDA 1 represents resource covariates that explain separation between the deer species, whereas RDA 2 represents resource covariates that explain association between the species. Resource covariate values represent mule deer responses relative to white-tailed deer and vice versa.

	Non-wolf winter		Wolf winter		Non-wolf summer		Wolf summer	
	RDA 1	RDA 2	RDA 1	RDA 2	RDA 1	RDA 2	RDA 1	RDA 2
Eigenvalues	0.235	0.012	0.135	0.052	0.116	0.023	0.110	0.021
% Total variance explained by constrained variance	0.118	0.006	0.068	0.026	0.058	0.011	0.055	0.011
% Constrained variance explained by axis	0.951	0.049	0.722	0.278	0.835	0.165	0.837	0.163
Mule deer scores	−1.789	0.365	−0.481	1.045	−1.261	0.543	−1.013	0.568
White-tailed deer scores	1.613	0.405	1.685	0.298	1.221	0.561	1.288	0.447
Resource covariates	Covariate coefficient estimates							
Elevation (m)	−0.673	0.563	−0.624	−0.098	−0.554	0.416	−0.227	−0.413
Slope (°)	−0.331	0.244	−0.489	0.357	−0.388	−0.279	−0.923	0.112
Distance to forest cover (m)	−0.112	−0.767	0.514	0.011	−0.093	−0.426	0.021	0.532
Distance to shrub habitat (m)	0.256	0.568	−0.124	−0.661	0.379	0.499	0.074	−0.920

We conducted RDA analyses by overlaying a 1 × 1 km sampling grid onto our study region and determining presence and number of GPS locations of each deer species in each grid cell for each season and wolf treatment. We first excluded null values resulting from grid cells that did not contain any GPS locations (i.e. empty grid cells) and then used numbers of GPS locations for each deer species in each cell as the basis for these analyses. Because all resource covariates were continuous, we averaged values for each resource variable within each grid cell. We then used Monte Carlo permutation tests to assess the significance of each deer species being constrained to a linear combination of the resource covariates (999 permutations, $\alpha = 0.05$; ter Braak 1995). We report the coefficient estimate of each resource covariate as it relates to each deer species and the scores for each species (Bowman et al. 2010, Peters et al. 2013). Lastly, we calculated the graphical distance between scores for each deer species and coefficient estimates for each resource covariate, respectively. We compared these differences between the two deer species numerically to determine whether they increased or decreased in magnitude along coarse-scale resource gradients as a function of wolf treatment within each season (Ramette 2007). For example, an increased difference in absolute value between each species' score for distance to forest cover in wolf versus non-wolf areas during a given season would indicate increased partitioning of forest cover in the wolf-occupied areas.

We next examined fine-scale resource overlap between mule and white-tailed deer in wolf and non-wolf areas by using logistic regression (Hosmer and Lemeshow 2000) to estimate coefficients for latent selection difference (LSD) functions (Latham et al. 2011, Peters et al. 2013). Examination of fine-scale resource overlap with LSD functions corresponds to exploring differences in overlap at the third-order scale (i.e. selection of resources within the home range; Johnson 1980). We coded locations selected by mule deer as 1 and those of white-tailed deer as 0 (Latham et al. 2011) and intersected locations with spatial data on habitat covariates at the 30 × 30 m resolution. We subsetted the data according to season (summer/winter) and wolf presence/absence to examine impacts of wolf presence on seasonal resource overlap, so there were four separate LSD functions modeled. We estimated the degree of resource overlap using β coefficients from LSD functions. Negative coefficients indicated greater selection by white-tailed deer compared to mule deer and positive coefficients indicated greater resource selection by mule deer compared to white-tailed deer (Latham et al. 2011). For example, a positive coefficient estimate for elevation would indicate greater selection of higher elevations by mule deer relative to white-tailed deer. However, EDA derived coefficients had to be interpreted differently. Namely, a negative coefficient estimate for distance to forest cover would indicate greater selection of areas farther from forest cover by white-tailed deer relative to mule deer. Once coefficient estimates were derived, the resulting value of e^{β} for each positive coefficient estimate indicated that with every unit increase in the value of, or distance to, a given resource, the amount of overlap with respect to that resource between mule deer and white-tailed deer increased or decreased by x%. Conversely, negative coefficient estimates were transformed using $-[1 - e^{\beta}] \times 100$ and quantified the extent of overlap of resources between white-tailed deer and mule deer (Czetwertynski 2007). We plotted these χ% relative resource partitioning differences to visually assess seasonal differences in fine-scale resource overlap between mule and white-tailed deer as a function of wolf presence.

Using 80% of the GPS locations, we built global LSD functions for each of the four data subsets according to season and wolf treatment using all resource covariates mentioned above at a 30 × 30 m resolution (i.e. the finest resolution possible). We screened resource covariates for collinearity using the Pearson's correlation coefficient threshold of $r > 0.5$, retaining the collinear variable with the higher log-likelihood and lowest p-value as determined using univariate logistic regression analysis. We then used Akaike's information criteria corrected for small sample size (AICc) to determine the most parsimonious LSD models (Anderson and Burnham 2002). We used the remaining 20% of the GPS locations to test the predictive capabilities of LSD models for mule and white-tailed deer resource overlap (Boyce et al. 2002, Johnson et al. 2006, Benson 2013, Dellinger et al. 2013). To complete this step, we translated coefficient estimates of our most parsimonious LSD models predicting mule and white-tailed deer fine-scale resource overlap into spatial predictive maps (Hirzel and Le Lay 2008). We used the raster layers of resource covariates mentioned above to aid in deriving the spatial predictive maps of resource overlap. The resulting maps contained pixels with values ranging from 0 to 1; values closer to 1 indicated decreased resource overlap with mule deer primarily using the resources at the given location and values closer to 0 indicated decreased resource overlap with white-tailed deer primarily using the resources at the given location. Thus, extreme values (i.e. near 1 or 0) indicated areas of little resource overlap between the two deer species whereas intermediate values (e.g. 0.3–0.7) indicated areas of increased resource overlap (Peters et al. 2013). We then classified the predicted probabilities of mule and white-tailed deer selection across the study area into 10 equal-sized and area-weighted bins (0–0.1, 0.1–0.2, etc.; per Johnson et al. 2006) and used Spearman's rank-order correlations to assess relationships between expected and observed numbers of GPS locations of each deer species in each category (Johnson et al. 2006). Lastly, we counted the frequency of GPS locations for each species in each category. High predictive ability of the most parsimonious models should result in: 1) strong correlation between expected and observed numbers of GPS locations of each deer species in each category; 2) a high proportion of mule deer GPS locations in the higher probability categories (i.e. 8–10); and 3) a high proportion of white-tailed deer GPS locations in the lower probability categories (i.e. 1–3).

We used program R ver. 3.1.2 (<www.r-project.org>), coupled with ArcView GIS ver. 10.2 Geographic Information System (GIS; ESRI, Redlands, California) and Geospatial Modeling Environment ver. 0.7.4.0 (Beyer 2015), for these overlap analyses. At both spatial scales, we initially included sex as a fixed effect for each deer species, but preliminary analyses revealed no effects of this factor on patterns of overlap. Hence, to maximize sample size, we pooled the sexes in the analyses presented here. For ordination approaches such as RDA, the inclusion of random effects is not possible. Thus, for our coarse-scale analysis, we were unable to include such a variable to test for site-specific differences for which our resource covariates could not account. Instead, we ran separate coarse-scale RDA analyses for each unique site, treatment and season combination. The individual RDA analyses closely matched our combined analysis, indicating that the two sites within each treatment category served as replicates and that our findings were not confounded by unmeasured site-specific variables (Supporting information). Hence, to ease interpretation, we present results from the RDA analysis for which data from the two sites within each treatment (wolf versus non-wolf) were pooled. Our fine-scale (LSD) analysis included a random variable for site to account for the effects of unmeasured differences between our study areas. We also note separate LSD analyses for each unique site, treatment and season combination, but lacking a random site effect, produced results closely matching those presented below (Supporting information).

To quantify overall resource (niche) overlap between mule and white-tailed deer as a function of wolf presence at the landscape scale, we calculated Levin's niche overlap index values for each deer species as a function of season and wolf treatment using the coarse-scale sample grids created for RDA analyses. Levin's index values were calculated using the Species Association Analysis (SPAA) package in R (ver. 0.2.2. <https://cran.r-project.org/package=spaa>).

For the dietary overlap analysis, we used the R package 'vegan' to perform a permutational multivariate analysis of variance (McArdle and Anderson 2001) on the Bray–Curtis distance matrix (Faith et al. 1987) of the proportion of time spent by each individual deer foraging on each of the six food categories (weighted by the individual's total foraging time; the 'other' category was excluded from analysis) testing for relationships between diet composition and deer species, wolf presence (i.e. sites where wolves were present versus those from which wolves were absent), and a species by wolf presence interaction. We visualized these relationships using nonmetric multidimensional scaling (NMDS, Minchin 1987).

For analyses furnishing p values (all save the process to determine the most parsimonious LSD models), we considered $p \leq 0.05$ to be statistically significant.

Results

Resource overlap

Raw values of use of the landscape covariates we evaluated by both deer species as a function of scale, season and wolf presence are shown in the Supporting information.

The RDA analysis revealed significant relationships between coarse-scale overlap of mule deer and white-tailed deer and the resource covariates for all season by wolf treatment combinations (wolf winter: $F_{8,1031} = 12.22$, $p < 0.01$; non-wolf winter: $F_{7,1217} = 7.84$, $p < 0.01$; wolf summer: $F_{8,1203} = 9.59$, $p < 0.01$; non-wolf summer: $F_{7,1424} = 14.38$, $p < 0.01$). The first RDA ordination axis accounted for most of the variance in species–resource covariate relationships for each season by wolf treatment combination (Table 1), whereas the second RDA ordination axis accounted for relatively little of this variance. Thus, the resource covariates better explained resource segregation between the two species than resource association.

For each season by wolf treatment subset, relative species scores for their first ordination axes were largely opposite one another, indicating resource separation (Table 1). Coefficient estimates for elevation and slope were negative for all subsets, meaning mule deer primarily used both higher elevations and steeper slopes relative to white-tailed deer. Coefficient estimates on the first ordination axis for proximity to forest cover and shrub steppe habitat varied between deer species, wolf treatment and season. For example, negative coefficient estimates for proximity to forest cover on the first ordination axis for mule deer in non-wolf areas showed that this species distanced itself from tree cover when not in the presence of wolves.

Increased elevation and steeper slope were most closely associated with mule deer in all RDA analyses, whereas lower elevation and gentler slope were most closely associated with white-tailed deer (Table 2). Resource segregation was greatest along a gradient of slope in the wolf areas during both seasons. Decreased overlap with respect to distance to forest cover was also marked in wolf relative to non-wolf areas in both seasons. However, overlap between deer species was not always lower in wolf areas for a given resource covariate. For example, mule and white-tailed deer niches overlapped more with respect to proximity to shrub steppe in non-wolf versus wolf areas in both seasons (Table 2). Differences between mule and white-tailed deer species scores, respectively, and coefficient estimates for resource covariates revealed that there was less overall coarse-scale niche overlap between the two species in wolf versus non-wolf areas in winter as compared to summer (Table 2).

Using LSD analysis, we found that the suite of resource covariates significantly predicted patterns of fine-scale resource overlap between mule and white-tailed deer. All resource covariates were included in the most parsimonious models for all wolf presence by season treatments. Mule deer tended to select higher elevations, steeper slopes and areas closer to shrub steppe habitat than white-tailed deer. Resource overlap between the deer species varied with wolf treatment and season (Fig. 1). In the non-wolf areas, mule deer tended to select areas farther from forest cover relative to white-tailed deer. This pattern was reversed in the wolf areas in both seasons, with mule deer selecting for areas close to forest cover relative to white-tailed deer, leading to increased partitioning of this resource (Table 3). Fine-scale segregation along gradients of slope revealed that mule deer selected

Table 2. Species-specific standardized coefficient estimates for each resource covariate under each season × wolf treatment combination and graphical distances ('Difference') between species scores for mule deer (MD) and white-tailed deer (WTD), respectively. Graphical distances were determined from redundancy analysis (RDA) of mule deer and white-tailed deer presence using GPS locations of each deer species collected from 2013 to 2016 in northeastern Washington. Data were broken down by season (winter: October–March; summer: April–September) and wolf presence/absence. Bold values indicate greater difference between each deer species score for the given resource covariate relative to the opposing treatment (i.e. non-wolf is the opposing treatment for wolf areas) within the same season. For example, there was greater resource partitioning between mule deer and white-tailed in wolf areas relative to non-wolf areas in winter with respect to elevation and slope.

	Non-wolf summer			Wolf summer			Non-wolf winter			Wolf winter		
Resource covariates	MD	WTD	Difference	MD	WTD	Difference	MD	WTD	Difference	MD	WTD	Difference
Elevation (m)	0.718	1.781	**1.063**	1.257	1.743	0.485	1.133	2.291	1.158	1.152	2.343	**1.191**
Slope (°)	1.199	1.815	0.616	0.465	2.236	**1.772**	1.463	1.951	0.488	0.688	2.175	**1.487**
Distance to forest cover (m)	1.518	1.643	0.126	1.035	1.270	**0.235**	2.023	2.085	0.062	1.435	1.206	**0.229**
Distance to shrub habitat (m)	1.641	0.844	**0.796**	1.843	1.828	0.015	2.055	1.367	**0.688**	1.743	2.047	0.305
		Total	**2.601**		Total	2.507		Total	2.396		Total	**3.212**

steeper slopes relative to white-tailed deer in all treatments and seasons. Increased partitioning of slope in wolf relative to non-wolf areas only occurred in summer and the difference in overlap during this season was modest (i.e. it increased from 2.90% to 4.29% as a function of wolf presence; Fig. 2, Table 3). In both seasons, overall fine-scale resource overlap between mule deer and white-tailed deer was reduced in wolf versus non-wolf sites (Fig. 2, Table 3).

The most-parsimonious LSD models for each data subset had good predictive ability. All of the most-parsimonious LSD models had high Spearman correlation coefficients (wolf winter: average $r_s = 0.97$, $p < 0.01$; non-wolf winter: average $r_s = 0.99$, $p < 0.01$; wolf summer: average $r_s = 0.99$, $p < 0.01$; non-wolf summer: average $r_s = 0.98$, $p < 0.01$). Thus, withheld GPS location data agreed with expected numbers of GPS locations in each probability of selection category derived from the most parsimonious LSD models. Furthermore, high proportions of mule and white-tailed deer GPS locations from the test data were contained within the higher and lower probability categories (Fig. 3), demonstrating strong ability to predict resource overlap between the two deer species in wolf present/absent areas and across seasons.

Overall resource (niche) overlap

The two deer species exhibited reduced overall niche overlap across the landscape, with respect to the resources we assessed, in the wolf-occupied relative to the non-wolf areas (on a scale of 0–1 as quantified by the Levin's index). Specifically, niche overlap index values were 0.002 for the wolf-affected areas in summer, 0.02 for the non-wolf areas in summer, 0.009 for the wolf-affected areas in winter and 0.03 for the non-wolf areas in winter.

Dietary overlap

We equipped 44 adult deer (n = 23 mule deer, n = 21 white-tailed deer) with animal-borne video camera collars over the course of the investigation. Permutational multivariate analysis of variance revealed that mule and white-tailed deer diets in the wolf sites differed significantly from those of conspecifics in the wolf-free areas (p = 0.003; Fig. 4, Table 4). Dissimilarities between the two deer species overall (p = 0.07) and as function of wolf presence (p = 0.09) were not significant, however (Fig. 4, Table 4).

Discussion

Taking advantage of the return of gray wolves to a multi-prey landscape in the American west as the basis for a natural experiment, we found support for the idea that wolves mediate patterns of resource overlap between sympatric ungulate prey species. Specifically, during winter, coarse-scale overlap of mule deer and white-tailed deer was lower in areas with wolves than in wolf-free sites for all resources except distance to shrub steppe, and fine-scale overlap was reduced in the presence of wolves for all resources save slope. Furthermore,

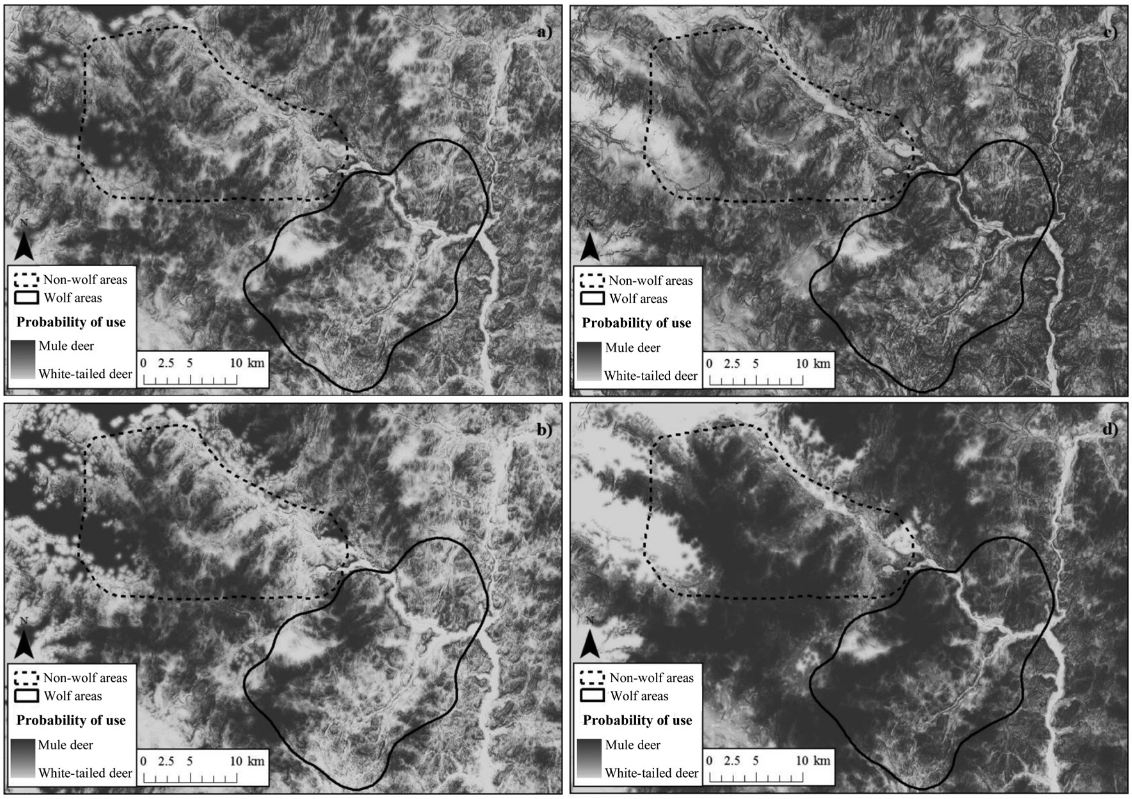

Figure 1. Spatial representation of latent selection difference (LSD) models for understanding differences in the relative probability of selection of habitat between mule deer and white-tailed deer at a fine spatial scale (30 × 30 m). Spatial representations of LSD models are broken down by season (winter: October–March; summer: April–September) and gray wolf presence/absence: (a) non-wolf summer; (b) non-wolf winter; (c) wolf summer and (d) wolf winter. Darker shading represents areas most likely to be selected by mule deer, whereas lighter shading represents areas most likely to be selected by white-tailed deer according to LSD models. For each season, comparison of wolf (solid polygon) and non-wolf (dashed polygon) areas provides a visual prediction of how deer overlap might change were they to be colonized by wolves. The inset shows where the study area falls within Washington, USA.

overall resource niche overlap between the two deer species across the landscape was an order of magnitude lower in the wolf-impacted relative to the wolf-free areas in both seasons. Accordingly, our results suggest that wolves may reduce niche overlap in large mammal communities when targeting co-occurring prey species with spatially divergent anti-predator responses. Moreover, the direction of spatial segregation with respect to some resources in the wolf-impacted areas, notably

Table 3. Standardized coefficient estimates (CE), standard errors (SE) and resource partitioning (RP) difference from the most parsimonious latent selection difference (LSD) models comparing fine-scale resource partitioning between mule deer and white-tailed deer in northeastern Washington, 2013–2016. GPS location data for LSD models were stratified by season (winter: October–March; summer: April–September) and wolf presence/absence. Resource covariates included elevation (Elev), slope, distance to forest cover (D2F) and distance to shrub habitat (D2S); the analysis also included a random effect for study site. Coefficient estimates > 0 should be interpreted as the percent change in partitioning of a resource (RP) between mule and white-tailed deer with every unit increase in the resource or for every unit increase in distance to the resource. Coefficient estimates < 0 should be interpreted as the percent decrease in partitioning of a resource (RP) between mule and white-tailed deer with every unit increase in the resource or for every unit increase in distance to the resource. Bold values indicate increased resource partitioning between the two deer species relative to the opposing treatment within the same season. For example, there was greater resource partitioning between mule deer and white-tailed in wolf areas relative to non-wolf areas in both seasons with respect to distance to forest cover.

	Treatment											
	Non-wolf summer			Wolf summer			Non-wolf winter			Wolf winter		
Covariates	CE	SE	RP %	CE	SE	RP %	CE	SE	RP %	CE	SE	RP %
Elev	1.76	0.03	**5.83**	0.86	0.03	2.36	2.68	0.04	14.57	2.71	0.05	**15.07**
Slope	1.05	0.03	2.87	1.53	0.03	**4.60**	0.92	0.03	**2.51**	0.82	0.03	2.28
D2F	1.48	0.05	4.38	−0.51	0.09	**40.01**	2.69	0.09	14.76	−2.09	0.20	**87.58**
D2S	−1.04	0.04	**64.48**	−1.12	0.04	67.24	−0.85	0.04	57.17	−1.00	0.06	**63.14**
		Total	77.55		Total	**114.21**		Total	89.01		Total	**168.07**

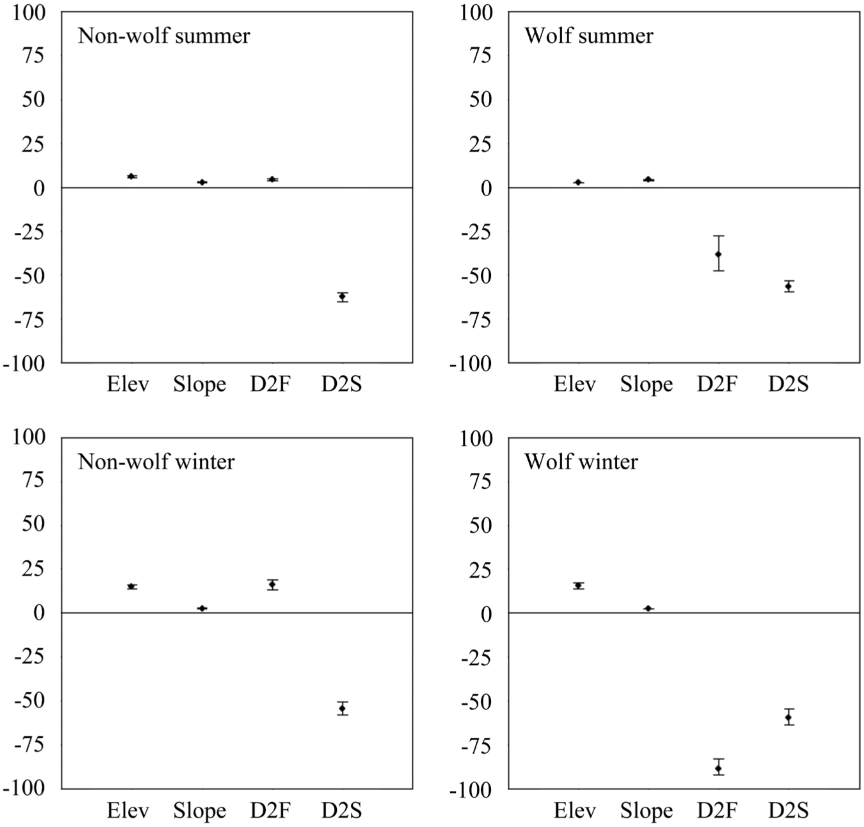

Figure 2. Resource separation plots resulting from latent selection difference (LSD) models for understanding relative differences in resource selection between mule deer and white-tailed deer at a fine spatial scale (30 × 30 m). Resource separation plots are subsetted by season (winter: October–March; summer: April–September) and gray wolf presence/absence. Resources include: elevation (m; elev); slope (°); distance to forest cover (D2F); and distance to shrub steppe habitat (D2S). Y-axis values 0–100 represent relative percent probability of selection of a resource being utilized by mule deer over white-tailed deer. Y-axis values −100 to 0 represent relative percent probability of selection of a resource being utilized by white-tailed deer over mule deer.

slope at the coarse spatial scale, putatively facilitated the respective defensive tactics of the two deer species, suggesting that anti-predator behavior as mediated by running mechanics could play an important role in shaping how wolves alter patterns of niche overlap among their ungulate prey. Yet, in summer, coarse- and fine-scale resource overlap between the prey species did not change markedly in response to wolf presence, and the magnitude and direction of differences in resource segregation between the wolf-occupied and wolf-free areas varied with spatial scale. Indeed, overlap with respect to shrub-steppe habitat was actually reduced in the presence of wolves at the coarse-scale. Moreover, exposure to wolf packs did not correspond with significantly increased disparity between the winter diets of the two ungulates. By implication, changes to prey overlap in response to predation risk are resource-specific, hinge on spatiotemporal context and may not always lead to dietary divergence.

Predators are typically thought to promote coexistence within prey guilds by consuming competitive dominants (Chase et al. 2002). Yet, there is growing evidence from both theory (Kotler and Holt 1989) and a variety of taxa that, in heterogeneous environments where sympatric prey use different refugia, predation risk can also promote spatial segregation and, perhaps, reduce interspecific competition (e.g. amphibians: Werner 1991; crustaceans: Hill and Lodge 1994; fishes: Mittelbach 1986, 1988, Persson 1993; small mammals: Kotler 1984, Hughes et al. 1994, Bouskila 1995; large mammals: Lingle 2002). Coupled with Lingle (2002), who found similar effects of coyotes on the deer species addressed here, our findings broaden support for the refuge partitioning hypothesis by providing an example of spatially divergent refuge use in response to a shared predator by sympatric large mammals. Exposure to wolf risk led mule deer to select steeper slopes and greater proximity to forest cover relative to white-tailed deer, markedly reducing coarse- and fine-scale niche overlap between the two ungulates. By implication, prey-specific refuge use is likely a pervasive non-consumptive mechanism by which predators ameliorate interspecific competition and promote biodiversity within communities.

Under the refuge partitioning hypothesis, we predicted that mule and white-tailed deer in areas occupied by wolves would be especially likely to segregate spatially along gradients of landscape features with divergent effects on their capacities to manage risk from coursing predators. Accordingly, mule deer in the wolf areas associated with steeper terrain characterized by reduced probability of wolf encounters, whereas

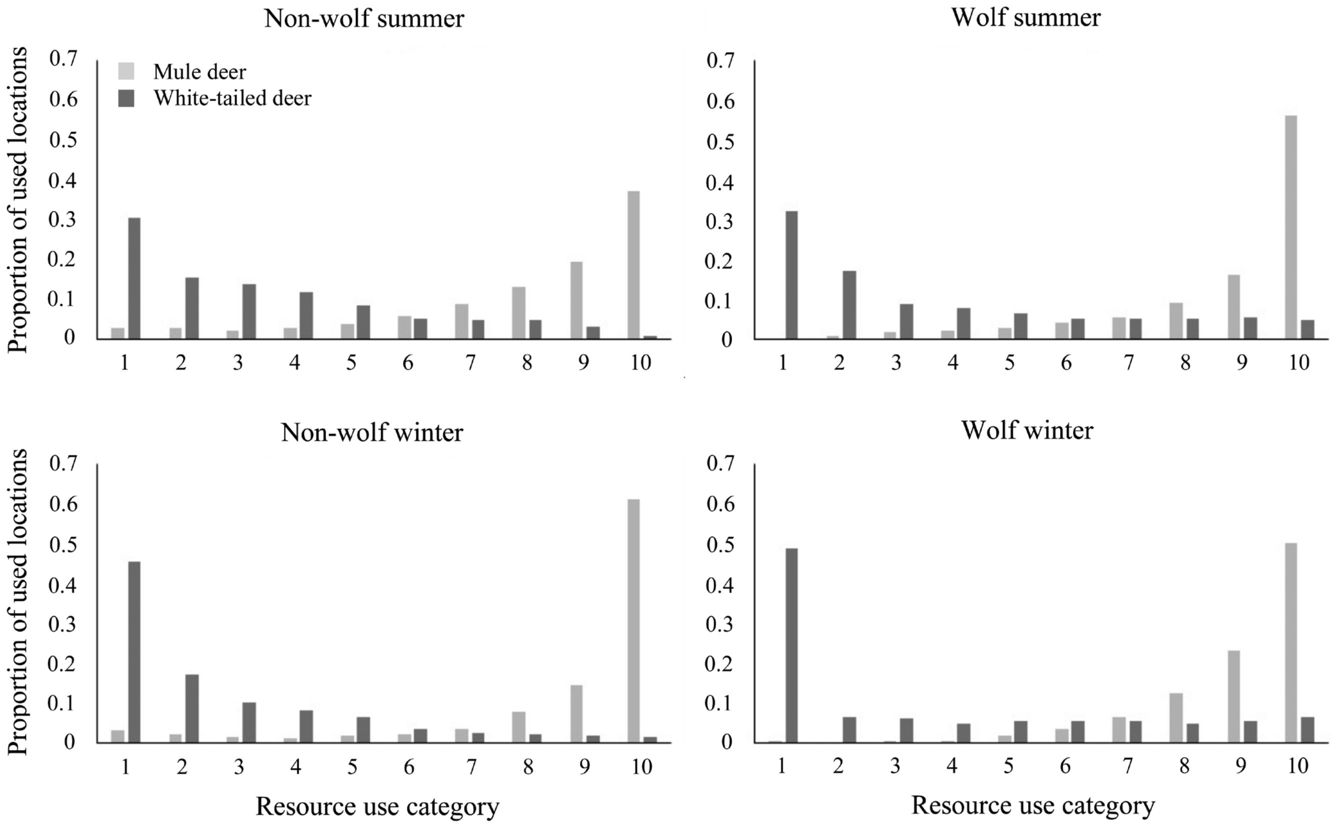

Figure 3. Frequency of occurrence of mule deer and white-tailed deer GPS location data in 10 equal-sized categories of resource selection predicted from the most parsimonious LSD models for understanding relative differences in resource selection between the two species in northeastern Washington from 2013 to 2016. Frequency of occurrence values were generated from GPS location data (25% of overall data) withheld from the model building process and thereby serve as a cross-validation of model performance. Categories closer to 10 indicate that the single most parsimonious LSD model predicted high relative probability of selection by mule deer, whereas categories closer to 1 indicate that the single most parsimonious LSD model predicted high relative probability of selection by white-tailed deer. Frequency of occurrence plots are subsetted by season (winter: October–March; summer: April–September) and gray wolf presence/absence. The proportion of observed white-tailed deer and mule deer locations in low (1–3) and high (8–10) resource categories, respectively, demonstrate good model performance.

white-tailed deer chose flatter ground where high-speed sprinting is facilitated, save during winter at the fine spatial scale (Table 2, 3). This result highlights slope as a feature of the environment that mule and white-tailed deer appear to use differently to manage predation risk, at least from coyotes (Lingle 2002) and wolves. Building on earlier work by Heithaus et al. (2009), it also suggests that a framework incorporating the relationship between prey anti-predator behavior and landscape features should aid in predicting how patterns of prey niche overlap are likely to be shaped by spatiotemporal variation in predation risk. In a concurrent analysis, Dellinger et al. (2019) found that only mule deer altered their use of forest cover when at risk from wolves relative to conspecifics in wolf-free areas. Consequently, we did not expect strong changes to overlap with respect to forest cover between the deer species in wolf-occupied versus non-wolf areas. Yet, where wolves were present we also observed reduced overlap with respect to distance to forest cover at both scales and in all seasons, with mule deer moving into cover relative to white-tailed deer (Table 2, 3). This result may indicate that, to avoid encounters with wolves, mule deer push closer to a resource (forest cover) that allows for concealment. It also underscores the value of explicitly examining interspecific resource overlap in response to predators and other drivers, in addition to intraspecific patterns of resource use/selection, in multi-species systems, given that divergent shifts by sympatric populations in response to any factor could increase interspecific overlap, decrease interspecific overlap or leave overlap unchanged along any landscape gradient depending on starting positions with respect to the covariate in question and the relative magnitude of the shifts by both species. Furthermore, across their respective ranges, mule deer are often more associated with open areas than are white-tailed deer (Brunjes 2006). Thus, the presence of wolves may in some cases modify the pattern of forest segregation that has typically been observed between these two ungulates.

In some cases we found increased resource overlap between the deer species in wolf-occupied versus non-wolf areas. In support of the refuge competition hypothesis, for example,

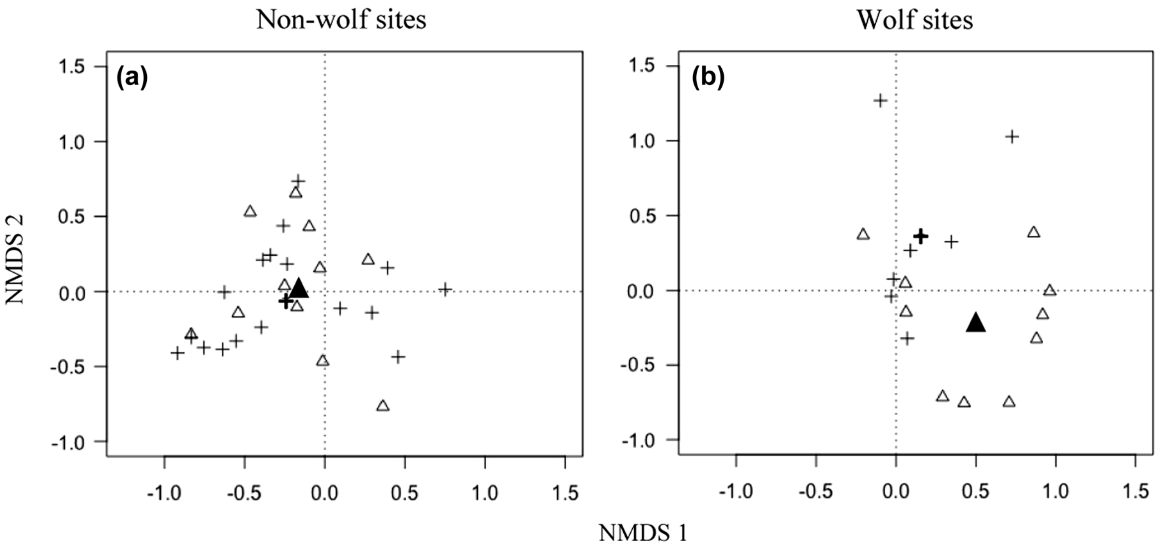

Figure 4. Nonmetric multidimensional scaling (NMDS) plot of inter- and intra-specific dietary similarity in mule deer (+, n = 24) and white-tailed deer (Δ, n = 21) diets in areas lacking (a) and occupied by (b) wolf packs. Each symbol represents one individual deer. The NMDS analysis was based on estimates of the relative use of six broad dietary categories (coniferous tree, deciduous tree, live ground vegetation, shrub, lichen, dead ground litter, other) generated using footage from two-week animal-borne video camera deployments on the two deer species achieved over the course of three winters. Population centroids are given in each panel for mule deer (bolded +) and white-tailed deer (filled triangle).

the presence of wolves corresponded with increased overlap along gradients of shrub steppe habitat at the coarse spatial scale in both seasons (Table 2). The nature of this increase in overlap from non-wolf to wolf-occupied areas was such that mule deer in the wolf-affected areas used shrub-steppe more similarly to conspecifics in non-wolf areas compared to white-tailed deer. In other words, mule deer seemed to use shrub-steppe similarly across wolf treatments, whereas white-tailed deer in the wolf areas shifted to using more shrub-steppe habitat relative to conspecifics in non-wolf areas. This coarse-scale pattern could reflect mule deer needing to use shrub steppe habitat for foraging and consequently having limited scope for altering their use of this resource in response to predation risk (Whittaker and Lindzey 2004) and white-tailed deer increasing their use of this open (relatively obstacle free) habitat type to aid in being able to escape pursuit. If so, then by implication the extent to which gray wolves mediate overlap along gradients of any given resource among deer species could depend on how the resource in question is used for risk management versus other purposes (Haswell et al. 2017). More broadly, this result suggests that non-consumptive effects of predators on the nature of competition among their prey species can be resource-specific (i.e. contingent; Wirsing et al. 2021) rather than unidirectional.

Table 4. Results of a permutational multivariate analysis of variance (PERMANOVA) on the Bray–Curtis distance matrix of the proportion of time spent by individual mule and white-tailed deer foraging on each of the six food categories (coniferous tree, deciduous tree, live ground vegetation, shrub, lichen, dead ground litter, other) testing for relationships between diet composition and deer species (mule versus white-tailed, sexes pooled), wolf presence (wolf-free versus wolf-occupied sites) and a species by wolf presence interaction. Significant covariate effects are bolded (α = 0.05).

Covariates	F	p	r^2
Deer species	2.081	0.065	0.041
Wolf	5.313	**0.003**	0.105
Deer species: wolf	2.052	0.085	0.041

Previous studies demonstrate variable patterns of resource overlap between co-occurring ungulates as a function of spatial scale (Whittaker and Lindzey 2004, Peters et al. 2013). We also found that overlap with respect to particular resources between mule and white-tailed deer in wolf versus non-wolf sites was inconsistent across the two scales of analysis. For example, at the coarse-scale, decreased resource overlap between the deer species in the wolf areas occurred along gradients of slope and forest cover in all seasons (Table 2). However, at the finer scale, decreased resource overlap in wolf areas only occurred for distance to forest cover in all seasons (Fig. 2, Table 3). This disparity could owe to the different scales at which the two deer species make resource selection and anti-predator decisions. Mule deer have been shown to prioritize foraging needs over predation risk avoidance (Pierce et al. 2004). Like other ungulates, mule deer feeding decisions are normally made at fine spatial scales because energetic benefit and palatability vary from plant to plant (Whittaker and Lindzey 2004). Furthermore, in our study system, mule deer appear to manage predation risk from wolves at the coarse scale (Dellinger et al. 2019). Conversely, white-tailed deer are thought to prioritize predation risk over foraging needs (Whittaker and Lindzey 2004) and, in our system, appear to account for predation risk by wolves at a fine scale (Dellinger et al. 2019). Thus, we might expect wolf-mediated patterns of resource overlap at the coarse scale to reflect mule deer anti-predator adjustments and overlap patterns at the finer scale to be more a product of the interplay between mule deer feeding choices and white-tailed deer risk management. More broadly, because many sympatric prey species likely prioritize foraging needs differently and respond to predation risk at differing spatial scales, our findings suggest that studies addressing a single spatial scale may miss key predator (and bottom–up) effects on prey niche overlap.

Past research has revealed seasonal variability in resource overlap between mule deer and white-tailed deer. For example, overlap in densely-vegetated areas between females of both species increased in summer, for fawning purposes, but decreased in winter (Brunjes et al. 2006). Moreover, there is evidence that many ungulate species may commonly select steep terrain to avoid or deter predators during the parturition period (Bonar et al. 2016). Similarly, we found that the degree and nature of resource overlap between mule deer and white-tailed deer in wolf versus non-wolf areas were season-dependent at both spatial scales. In particular, overall resource overlap between the deer species was lowest in wolf areas in winter at both scales (Table 2, 3). Reduced resource overlap in winter at multiple scales in our study could owe to a general increase in vulnerability of prey during this season because of increased relative wolf mobility owing to snow presence and/or depressed physical condition (Latombe et al. 2014). Accordingly, future research should consider seasonality when seeking to understand how predators might mediate competitive interactions between multiple co-occurring prey species.

Increased refuge use by prey will not necessarily coincide with dietary modification. Food availability between refuge and exposed space may be similar, for example, or prey may be able to maintain dietary consistency through changes to other traits (e.g. increased foraging time; Preisser and Bolnick 2008). Accordingly, significantly elevated inter-specific dietary disparity between mule and white-tailed deer failed to emerge where wolves were present. This result is somewhat surprising given that plant communities vary between steeper and low-lying (and especially riparian) areas in our system (A. Craig unpubl.) and, consequently, dietary divergence might be expected to accompany the opposing shifts to steeper terrain for mule deer and gentler terrain for white-tailed deer, respectively. Our finding may owe to reduced opportunity for interspecific dietary divergence between the deer species in the wolf-occupied sites (e.g. stemming from lower plant community diversity). Rigorously addressing this explanation is beyond the scope of the present study, but the observed intra-specific differences in mule and white-tailed deer diets as a function of wolf pack presence are consistent with the idea that plant communities in the wolf-occupied and non-wolf sites were not identical. It is also possible that the divergent ungulate spatial shifts were insufficient to trigger dietary modification (i.e. plant communities inside and outside refugia were similar), or that one or both deer species were able to compensate for differences in plant availability in their respective refugia via behavioral adjustments. To address these scenarios, there remains need for investigation of spatial variation in plant communities and foraging decisions by these ungulates along gradients of wolf risk. Irrespective of the mechanism, our results suggest that wolves in our system are more likely to indirectly affect plant communities by altering spatial patterns of mule and white-tailed deer herbivory than by altering their diets, and more broadly that spatial segregation among prey species can occur without marked dietary partitioning.

Notably, the non-significant trend toward increased dietary disparity in the wolf areas (Fig. 4) is consistent with the refuge partitioning hypothesis. Moreover, our dietary analysis was coarse and based on a relatively small sample of mule and white-tailed deer. Hence, a more detailed (e.g. plant species-specific) analysis of a larger sample of deer may have revealed marked dietary divergence in the wolf areas. Indeed, a recent study in a nearby region of eastern Washington found that, during summer, dietary similarity between these two ungulates was greater when considering plant functional groups as opposed to individual plant species (Berry et al. 2019).

Previous research in eastern Washington revealed that white-tailed deer exhibit higher survival and population growth rates than sympatric mule deer (Robinson et al. 2002). Moreover, in a case of apparent competition, increasing spatial overlap between mule and white-tailed deer with expansion of the latter species has apparently led to elevated cougar *Puma concolor* predation on mule deer (Robinson et al. 2002). Thus, high resource overlap between the two species could negatively affect mule deer populations in Washington. Insofar as wolves drive changes to spatial overlap between mule and white-tailed deer, then, continued expansion of this top predator in Washington could not only alter resource overlap between these two deer species but also reduce cougar predation on mule deer stemming from apparent competition. It is also possible, however, that mule deer shifts away from low-lying areas hunted by wolves could place them at greater risk of predation by cougars, which tend to target prey in areas offering stalking cover and rugged terrain (Atwood et al. 2009) and perhaps from human hunters, who achieve greater success when targeting ungulates on steeper slopes (Lone et al. 2014).

A number of studies have demonstrated the potential for bottom–up and abiotic processes like seral stage and fire to mediate resource overlap between ungulates (Brunjes et al. 2006, Sittler et al. 2015). Our findings build on Lingle (2002) to suggest that top–down processes can also mediate spatial niche overlap between co-occurring ungulate prey, at least spatially, while also revealing that these top–down effects can persist over longer time scales (i.e. not just when canid predators are nearby). Notably, wolves in our study system existed at densities that are comparable to other human-modified ecosystems and lower than those more typical of protected areas (Jimenez and Becker 2016). Yet, we detected a relationship between wolf predation risk and resource overlap between mule and white-tailed deer, hinting at the potential for even stronger wolf impacts on prey niche overlap where their numbers and distribution are not constrained by humans (Kuijper et al. 2015). We acknowledge, however, that our results are correlative, preventing us from controlling for other possible environmental drivers of overlap between the prey species. Several lines of evidence weaken support for these alternative explanations (Supporting information). Nevertheless, there remains need for manipulative research capable of simultaneously examining bottom–up and top–down forcing of prey niche overlap and, by extension, competition (Ford and Goheen 2015).

A growing literature has refined our understanding of prey responses to predators by highlighting how the context of predator–prey interactions can help predict their outcome (Preisser and Bolnick 2008, Schmitz 2008, Heithaus et al. 2009, Creel 2011, Haswell et al. 2017, Wirsing et al. 2021). This emerging framework highlights how a single predator species can have different non-consumptive effects on multiple prey species (Heithaus et al. 2012, Latombe et al. 2014). Our findings suggest that it could be extended beyond bilateral predator–prey relationships to include more complex non-consumptive interactions between multiple prey species responding to shared predators. For example, niche overlap between two sympatric prey species with a shared predator is likely to depend on similarity in their running mechanics, and more broadly traits influencing the likelihood of escaping an attack, which dictate how prey position themselves spatially to reduce predation risk (Laundre et al. 2014, Wirsing et al. 2021). Where co-occurring prey responding to predation risk segregate spatially along resource gradients, the predator may trigger multiple trophic cascades, each transmitted by a different prey species, with spatially variable consequences for plant communities (Wirsing and Ripple 2011). Scaling up to complex communities, the presence of multiple shared predators with different hunting modes could influence resource overlap among sympatric prey species, and cascading effects on primary producers, to the extent that different landscapes promote prey safety and predator success. Accordingly, we encourage further work that explores patterns of prey resource overlap under predation risk while accounting for drivers of contingency in predator–prey relationships including how specific resources relate to prey anti-predator behavior, predator hunting mode, scale and temporal heterogeneity (Wirsing et al. 2021).

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Author contributions

Justin A. Dellinger: Conceptualization (supporting); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Resources (supporting); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Carolyn R. Shores**: Conceptualization (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Apryle D. Craig**: Conceptualization (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Resources (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Shannon M. Kachel**: Data curation (supporting); Formal analysis (equal); Validation (supporting); Visualization (supporting); Writing – review and editing (supporting). **Michael R. Heithaus**: Conceptualization (equal); Methodology (supporting); Project administration (supporting); Resources (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Bill J. Ripple**: Conceptualization (supporting); Funding acquisition (supporting); Methodology (supporting); Project administration (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Aaron J. Wirsing**: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Investigation (supporting); Methodology (supporting); Project administration (lead); Resources (lead); Supervision (lead); Validation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.9p8cz8whc> (Wirsing 2021).

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