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Habitat use of sympatric prey suggests divergent anti-predator responses to recolonizing gray wolves

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Abstract

The non-consumptive effects of predators on prey are now widely recognized, but the need remains for studies identifying the factors that determine how particular prey species respond behaviorally when threatened with predation. We took advantage of ongoing gray wolf (*Canis lupus*) recolonization in eastern Washington, USA, to contrast habitat use of two sympatric prey species—mule (*Odocoileus hemionus*) and white-tailed (*O. virginianus*) deer—at sites with and without established wolf packs. Under the hypothesis that the nature and scale of responses by these ungulates to wolf predation risk depend on their divergent flight tactics (i.e., modes of fleeing from an approaching predator), we predicted that (1) mule deer would respond to wolves with coarse-scale spatial shifts to rugged terrain favoring their stotting tactic; (2) white-tailed deer would manage wolf risk with fine-scale shifts toward gentle terrain facilitating their galloping tactic within their current home range. Resource selection functions based on 61 mule deer and 59 white-tailed deer equipped with GPS radio-collars from 2013 to 2016 revealed that habitat use for each species was altered by wolf presence, but in divergent ways that supported our predictions. Our findings add to a growing literature highlighting flight behavior as a viable predictor of prey responses to predation risk across multiple ecosystem types. Consequently, they suggest that predators could initiate multiple indirect non-consumptive effects in the same ecosystem that are transmitted by divergent responses of sympatric prey with different flight tactics.

Keywords *Canis lupus* · Galloping · Mule deer · Non-consumptive effects · *Odocoileus hemionus* · *O. virginianus* · Predation risk · Stotting · White-tailed deer

Introduction

Behavioral responses of prey to predators often take the form of shifts in habitat use, which in turn may influence how prey exploit resources and interact with co-occurring species (Lima and Dill 1990; Fortin et al. 2005; Thaker et al. 2011; Latombe et al. 2014). Prey individuals are typically assumed to avoid their predators (Laundré et al. 2010), diminishing their ecological effects (e.g., foraging pressure) where predators are more numerous, while increasing their impacts where predators are relatively scarce (Ripple and Beschta 2012). A growing literature, however, suggests that prey responses to predators hinge on key features of the interaction such as predator hunting mode and landscape context and, as a result, that anti-predator habitat shifts and their consequences will not always follow this pattern (Schmitz 2008; Heithaus et al. 2009; Wirsing et al. 2010). For example, Schmitz (2008) found that the hunting mode of sympatric spider predators

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(sit-and-wait versus active) dictated whether herbivorous grasshoppers (Melanoplus *femurrubrum*) foraged in refuge or exposed grassland habitat and, as a result, promoted either increased or reduced plant diversity. Working in a coral reef ecosystem, Catano et al. (2016) observed that landscape heterogeneity mediated avoidance of a predator decoy by herbivorous fishes, with reef complexity apparently enhancing avoidance, because it impedes predator detection and facilitates prey escape. By implication, efforts to identify the factors that determine how prey use space when threatened with predation are crucial to the development of a general framework for predicting the effects of predators on their prey and, ultimately, ecosystems.

Flight behavior, or the means by which prey flee from approaching predators (Ydenberg and Dill 1986), has been highlighted as an important driver of context dependence in predator–prey relationships that can interact with predator hunting mode and landscape features to determine prey spatial responses to predation risk (Lingle 2002; Heithaus et al. 2009; Wirsing et al. 2010). Overall predation risk can be deconstructed into the probability of encountering a predator (pre-encounter risk) and the probability of death as a result of the encounter (post-encounter risk) (Lima and Dill 1990; Hebblewhite et al. 2005). Thus, prey individuals with certain flight tactics might actually benefit from minimizing post-encounter risk using space where predators are relatively abundant but less lethal, whereas prey species with flight tactics that do not facilitate surviving an encounter with a predator should seek to minimize pre-encounter risk by avoiding the predator altogether (Heithaus et al. 2009; Wirsing et al. 2010). In a given ecosystem, the hunting mode of the predator and the structure of the landscape will determine the spatial pattern of predator lethality experienced by each prey species and, consequently, which prey species might benefit from managing pre- versus post-encounter risk (Heithaus et al. 2009; Wirsing et al. 2010). This framework has implications for the spatial scale at which prey species should respond to the risk of predation. Namely, prey species whose flight behavior confers a high likelihood of surviving an encounter should be better able to manage risk through fine-scale (i.e., within home range) habitat shifts when exposed to the threat of predation, whereas those less able to survive an attack should be more likely to manage pre-encounter risk via coarse-scale shifts in habitat use (i.e., changes to home range location; Kauffman et al. 2007). To date, a few studies have assessed the relationship between flight behavior and habitat use patterns of multiple prey species at multiple spatial scales in response to predation risk from a shared predator. Accordingly, we examined the possibility that recolonizing gray wolves (*Canis lupus*) in eastern Washington, USA, elicits divergent habitat shifts by two sympatric herbivores—mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*)—with different flight tactics.

In 2008, gray wolves began naturally recolonizing Washington from southern British Columbia, Canada, and northern Idaho, and there are now 20 confirmed packs in the state (Jimenez and Becker 2016). At present, these packs are distributed heterogeneously across eastern Washington, setting the stage for natural experiments examining the effects of gray wolf recolonization on prey populations, including habitat use patterns, by contrasting areas with and without resident wolves. In this region, mule deer and white-tailed deer dominate the ungulate guild (Robinson et al. 2002), and gray wolves are known to primarily consume both species (making up $\geq 50\%$ of wolf diet depending on the pack) locally (Spence 2017). Mule deer and white-tailed deer may differ in their responses to the presence of wolves, however, because their respective flight behaviors are believed to be most effective in different habitat types (Lingle and Pellis 2002). Specifically, mule deer stot (i.e., bound in a forward direction with all four legs touching the ground simultaneously) when approached by canid predators, and the efficacy of this running gait as a means of escaping an attack is thought to be facilitated by uneven terrain (Geist 1981; Lingle 2002). White-tailed deer, by contrast, are believed to be better equipped to evade canids on relatively gentle terrain, because they sprint away from predators and rely on the early detection (Kunkel and Pletscher 2001; Lingle and Pellis 2002; Kittle et al. 2008). As coursing predators, gray wolves tend to select for relatively gentle terrain while hunting (see ESM 1; Mech and Peterson 2003; Oakleaf et al. 2006). Thus, we might expect mule deer to exhibit coarse-scale habitat shifts from gentle to rugged terrain that reduce the likelihood of encounters with gray wolves (i.e., pre-encounter risk) and avoid substrates that hinder the effectiveness of stotting in the event of an attack. Conversely, white-tailed deer exposed to wolves should be more likely to remain in areas dominated by gentle terrain, given that their running gait is not well suited to rugged areas, and exhibit finer-scale shifts in habitat use that facilitate sprinting in the event of a predator encounter.

Here, taking advantage of spatial heterogeneity in wolf presence, we contrasted both coarse- and fine-scale habitat use patterns of adult mule deer and white-tailed deer in areas with and without established packs. We hypothesized that the nature and scale of anti-predator responses of these two deer species to wolves are mediated by flight behavior. Under this hypothesis, we expected mule deer to seek to avoid wolf encounters by increasing their use of rugged terrain and, consequently, that differences in habitat use patterns of this prey species in wolf-present and wolf-absent areas would be greatest at a relatively coarse spatial scale (Wirsing et al. 2010). Specifically, we predicted that, relative to conspecifics in wolf-absent areas, mule deer in wolf-present areas would exhibit increased use of space: (1) with greater slope (Lingle and Pellis 2002); (2) farther from roads (due to roads being graded/flatter surfaces that facilitate coursing movements, Whittington et al. 2011); (3) closer to cover (i.e., more forested habitat to avoid detection, Hernandez and Laundre 2005) (Table 1). By contrast, because the running gait of white-tailed deer is thought to be best suited for terrain that is typically hunted by wolves, we predicted that differences in habitat use patterns of this prey species in wolf-present and wolf-absent areas would be greatest at relatively fine spatial scales (Heithaus et al. 2009; Wirsing et al. 2010). Specifically, we predicted that, relative to conspecifics in wolf-absent areas, white-tailed deer in wolf-present areas would show increased use of space: (1) with reduced slope (Lingle and Pellis 2002); (2) closer to roads (fewer obstacles on roads to inhibit fleeing; Kunkel and Pletscher 2001); (3) farther from cover (i.e., more open shrub habitat to aid in the early detection; Kittle et al. 2008) (Table 1).

Table 1 Predicted and observed relationships between gray wolves and patterns of habitat selection by mule and white-tailed deer across multiple spatial scales (coarse and fine) and seasons (winter and summer)

Species	Scale	Variable	Season	Predicted	Observed
Mule deer	Coarse	Distance to road	Winter	–	–
			Summer	–	–
		Slope	Winter	+	+
			Summer	+	+
		Distance to forest	Winter	+	+
			Summer	+	+
		Distance to shrub	Winter	–	+
			Summer	–	–
Mule deer	Fine	Distance to road	Winter	↔	+
			Summer	↔	↔
		Slope	Winter	↔	+
			Summer	↔	↔
		Distance to forest	Winter	↔	+
			Summer	↔	↔
		Distance to shrub	Winter	↔	+
			Summer	↔	↔
White-tailed deer	Coarse	Distance to road	Winter	↔	↔
			Summer	↔	↔
		Slope	Winter	↔	–
			Summer	↔	↔
		Distance to forest	Winter	↔	↔
			Summer	↔	↔
		Distance to shrub	Winter	↔	+
			Summer	↔	↔
White-tailed deer	Fine	Distance to road	Winter	+	+
			Summer	+	+
		Slope	Winter	–	–
			Summer	–	–
		Distance to forest	Winter	–	–
			Summer	–	–
		Distance to shrub	Winter	+	+
			Summer	+	+

Negative symbols signify either (1) an increasing relationship between selection and a distance variable or (2) an inverse relationship between selection and slope for deer in wolf-present areas relative to deer in wolf-absent areas. Positive symbols signify either (1) an inverse relationship between selection and a distance variable or (2) an increasing relationship between selection and slope for deer in wolf-present areas relative to deer in wolf-absent areas. Double arrows indicate no significant difference in selection for a specified habitat variable by deer in wolf-present areas relative to those in wolf-absent areas. The distance to road variable represents distance in meters to the nearest secondary road. The slope variable represents slope in degrees. Distances to forest and shrub represent distance in meters to nearest forest and shrub-steppe habitat, respectively

Materials and methods

Study area

This study took place from 2013 to 2016 in an area of eastern Washington spanning Okanogan and Ferry Counties and including portions of the Okanogan-Wenatchee and Colville National Forests and the Colville Reservation (Fig. 1). The study area contains the Okanogan Highlands and Kettle River Range. These areas are composed of similar topography with predominantly moderate slopes on mountainous and hilly terrain (see ESM 2). The Sanpoil River is the main drainage that bisects the Okanogan Highlands and Kettle River Range. Elevation in the area ranges from 300 to 2065 m. Shrub-steppe habitats composed primarily of sagebrush (*Artemisia tridentata*) and bitterbrush (*Purshia tridentata*) makeup most of the habitat at lower

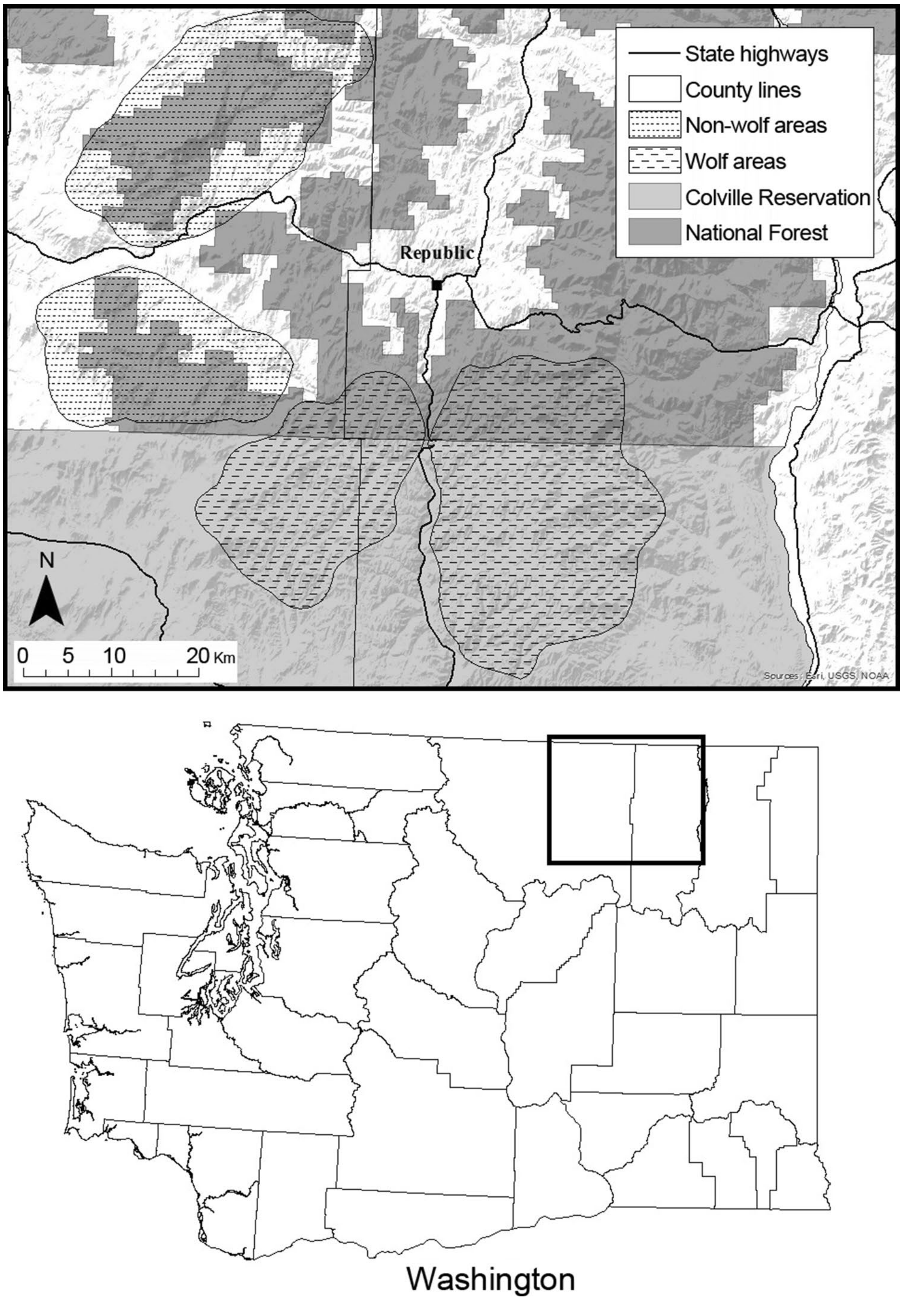

Fig. 1 Location of the study area in Washington, USA (UTM 11 N 372231E 5589670), which included the two study sites occupied by gray wolf packs primarily within the Colville Reservation (Nc'icn and Strawberry) and two nearby wolf-free areas in the Okanogan-Wenatchee National Forest (Aeneas and Bonaparte)

elevations, whereas ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), and subalpine fir (*Abies lasiocarpa*) forest dominate at higher elevations. Riparian areas, composed primarily of poplars (*Populus* spp.), are regularly dispersed along drainages (Clausnitzer and Zamora 1987). Mule deer, white-tailed deer, elk (*Cervus elaphus*), and moose (*Alces alces*) comprise the resident ungulate community, though each deer species is 20 and 50 times more abundant than moose and elk, respectively (Spence 2017). Coyotes (*Canis latrans*), bobcats (*Lynx rufus*), American black bears (*Ursus americanus*), and cougars (*Puma concolor*) represent the larger mammalian predators present throughout the study area.

We broke the study area into four separate sites, two occupied by gray wolf packs and two lacking wolves. The four sites encompassed an average of 613 km^2 (range = 550–680 km^2). In areas of Washington that have been recolonized by gray wolves, average home range size, average pack size, and pack density are similar to those documented in the other managed landscapes in neighboring states (Jimenez and Becker 2016), but pack size and pack density in all of these managed areas are low relative to protected areas (Jimenez and Becker 2016). Wolf packs were first detected in the region in the summer of 2010 and, over the course of the investigation, were found to occupy the Colville National Forest and Colville Reservation but not the adjacent Okanogan-Wenatchee National Forest (Fig. 1). Specifically, wolf-present areas were situated immediately east (Nc'icn Pack) and west (Strawberry Pack) of the Sanpoil River and State Highway 21. One wolf-absent site, named 'Aeneas', was immediately south of Aeneas Valley and State Highway 20, and north of the Colville Reservation. The other wolf-absent site, named 'Bonaparte', was located near Bonaparte Lake and north of State Highway 20 (Fig. 1). No site was more than 30 km from the three other sites. All four sites experience similar levels of human use in the form of cattle ranching, logging, and hunting. Human density was low throughout the study area and averaged 2.25 persons/km^2 (range: 0–179/km^2; United States Census Bureau 2016). Cattle grazed freely on the landscape in each year of the investigation from approximately mid-June to mid-October. Logging occurred year round with variable harvest intensity and cut block size. Hunting of both deer species on the National Forests occurs in autumn and length of season varies depending on Game Management Unit (GMU) and weapon type. In general, no GMU is hunted more than 2 full months in a year during autumn. Both wolf-absent areas primarily occurred in GMU 204. Hunting of both species on the Colville Reservation primarily occurs during the autumn months. There are no data on the population status of the other large-bodied predators in our study area, but game cameras deployed on each site (see below) yielded similar detection rates for coyotes, black bears, and cougars across the four study sites (C. Shores *unpublished data*).

Field data collection

We monitored gray wolf activity in all four sites within the study area in three ways. First, we deployed 16 motion-activated game cameras (M880 by Moultrie®, Calera, AL, USA) year round as a grid (1 per 5 km^2) along logging roads and game trails at each site, and checked the cameras every 3 months. Second, we conducted weekly track surveys at each study site along logging roads and game trails during winter months (mid-December to mid-March) using snowmobiles. Third, radio-collars deployed on at least two members of each wolf pack occupying the designated wolf areas by the Colville Confederated Tribes Fish and Wildlife Department aided in monitoring wolf presence, movements, and pack size. Combined, these three methods enabled continuous and intensive monitoring of occupancy and overall number of wolves present in each site. Neither wolf-absent site had any documented wolf pack activity during the course of this study, though we did detect lone individuals occasionally on our remote game cameras ($n = 5$ detections) that were likely dispersing. By contrast, both of the wolf-present sites were occupied continuously over the course of the investigation by packs ranging in size from 3 to 8 individuals (mean of 5 individuals for each pack) with annual pack home ranges of 550 and 680 km^2, respectively.

To determine habitat use patterns of mule and white-tailed deer, we captured individuals of each species in each of the four study sites over three consecutive winters (December–March) using aerial net gunning and baited clover trapping (Haulton et al. 2001). In the wolf areas, we focused deer capture efforts on core areas within each wolf pack home range. We outfitted clover traps with trap transmitters to alert us to captures. Trap transmitter signals were checked daily in the early morning and late afternoon. Captured deer were equipped with Global Positioning System (GPS) radio-collars (Globalstar Survey Collars, Vectronic Aerospace Gmbh, Berlin, Germany), ear tagged, aged, sexed, and weighed. To ensure that only adults were collared, we did not instrument any individual weighing < 30 kg (Haulton et al. 2001). The GPS collars were programmed to obtain a location every 12 h and 5 min, in the interest of obtaining an even distribution of locations throughout the day, and to switch to mortality mode if the instrumented deer exhibited no movement for a 24-h period. Concurrent research leveraging the mortality data provided by these collars revealed that cougars were the primary predator of both deer species, followed by coyotes and then gray wolves (Dellinger et al. 2018). All animal captures and collar deployments were conducted under University of Washington

Institutional Animal Care and Use Committee (IACUC) protocol number 4226-01 and wildlife collection permits from the Washington Department of Fish and Wildlife and the Colville Tribes Fish and Wildlife Department.

Statistical analyses

We used GPS data from radio-collared mule deer and white-tailed deer to examine patterns of resource use with a use-availability framework that compared landscape attributes associated with used locations to those at regularly generated available locations (Benson 2013). We analyzed resource use at two spatial scales: coarse (i.e., home range positioning relative to the surrounding landscape) and fine (i.e., within the home range). First, we created a 95% minimum convex polygon (MCP) home range estimate for each radio-collared deer. Regularly spaced points occurring every 30 m (minimum pixel size of spatial data used in analyses) within each 95% MCP home range served as used locations. Then, we created a 95% MCP encompassing all deer GPS locations at a site to represent available habitat for a second-order resource use analysis examining the drivers of home range establishment across the landscape by mule and white-tailed (Johnson 1980). Regularly spaced points occurring every 30 m within the study area, but not within individual deer home ranges, served as available locations for this coarse-scale analysis (Johnson 1980; Benson 2013). We then compared regularly spaced points within individual deer home ranges to regularly spaced points within the study area to quantify any differences in coarse-scale habitat use (i.e., home range establishment) for both deer species in wolf-present and wolf-absent areas. Second, we used the 95% MCP home range estimates for each radio-collared deer above as the basis for a third-order resource use analysis that explored the drivers of space use within the home range (Johnson 1980). Regularly spaced points occurring every 30 m within each individual deer home range served as available locations for this relatively fine-scale habitat use analysis (Johnson 1980; Benson 2013). We then compared GPS fix locations to available locations within each individual home range to determine differences in fine-scale habitat use (i.e., within home range) patterns of both deer species in wolf-present and wolf-absent areas. We developed resource selection functions (RSFs) for both deer species, at both spatial scales, by estimating coefficients for landscape attributes from a binomial logistic regression of used versus available locations (Manly et al. 2002; Johnson et al. 2006). We accounted for the influence of GPS fix success on RSF estimates by including weights for detection depending on habitat type (Nielson et al. 2009). We included a random effect for individual in the model building process to account for among-individual variance in habitat use patterns that we could not specifically address with fixed effects. RSFs resulting from this approach yield coefficient estimates that can be used to understand relative probability of use of areas along a gradient of habitat attributes for species of interest (Boyce et al. 2002).

We included the following landscape attributes as explanatory variables in the global RSFs (i.e., the base models from which the above predictions were tested) for each deer species and spatial scale combination (four total): (1) distance to habitat type in meters (forest and shrub); (2) landscape attributes (slope and distance to nearest road); (3) wolf presence/absence; (4) season. We classified season by noting the date of each GPS location and then using binary coding (0/1), with winter (October–March) set as the reference season (0). Binary classification of season allowed for simplistic representation of snow presence (present versus absent) on the landscape. Wolf presence was also expressed as a binary effect (0/1), whereby radio-collared deer in areas without wolves present served as the reference treatment. We included a two-way interaction between wolf and season to investigate differences in deer behavior among various combinations of treatment (wolf-present and wolf-absent) and season (summer and winter). We also included two-way interactions between wolf and season, respectively, and each other variable (habitat types and landscape attributes). If deer in wolf-present and wolf-absent areas behaved divergently, then both the binary wolf presence/absence variable and at least one of the two-way interactions including the wolf variable would be significant. Furthermore, we included three-way interactions involving wolf presence/absence, season, and each other variable. These three-way interactions allowed for discerning potential differences in habitat use between mule deer and white-tailed deer as a function of various combinations of treatment (wolf-present and wolf-absent) and season (summer and winter). We obtained raw data for habitat 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 11/15/2016). We analyzed all spatial data at a 30 × 30 m resolution. We assessed habitat type and landscape attributes using a Euclidean Distance Analysis (EDA) framework (Benson 2013). Briefly, we estimated the straight-line distance from each pixel (at 30 × 30 m resolution) to the nearest secondary road, forest cover, or shrub habitat. We then standardized these EDA distance values 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). Initially, we also included deer sex for both ungulate species as a fixed effect in our RSFs. However, preliminary analyses revealed a little effect of sex on differences in habitat use patterns between deer of either species in wolf-present and wolf-absent areas and between seasons at either spatial scale. Accordingly, to maximize sample size, we pooled the sexes in subsequent models (Table 2). We assessed performance of RSFs using cross-validation procedures (see ESM 3; Johnson et al. 2006; Benson 2013; Dellinger et al. 2013).

We used Program R version 3.1.2 (R Core Team 2016) for all statistical analyses, and ArcView GIS version 10.2 Geographic Information System (GIS; ESRI, Redlands, California) and Geospatial Modeling Environment version 0.7.4.0 (Beyer 2015) for spatial analyses. In all analyses, we considered $P \leq 0.05$ to be statistically significant.

Results

Across our four study sites over the course of 3 years, we collared 120 adult deer ($n = 61$ mule deer, $n = 59$ white-tailed deer; Table 2). We collected an average of 700 locations (± 562 sd) per radio-collared individual, with an average successful GPS fix rate of 81% (range 75–88%). Individuals were monitored for an average of 433 days (± 275 sd). Distributions of mule deer and white-tailed deer GPS fixes in the wolf-occupied sites largely overlapped with the core areas of each wolf pack's home range (Fig. 2).

Overall, model-averaged coefficient estimates for mule deer demonstrated greater disparity in resource use patterns as a function of wolf presence at a coarse spatial scale (i.e., with respect to the second-order resource use; Table 3, Fig. 3). Furthermore, differences in use of particular resources by mule deer in wolf-present and wolf-absent areas generally supported the prediction that this species would manage wolf predation risk with coarse-scale habitat shifts (Tables 1, 3). Specifically, relative to conspecifics in wolf-absent areas, mule deer in wolf-present areas exhibited (1) a lower probability of using areas close to secondary roads at the coarse scale of analysis (Fig. 3a); (2) a lower probability of using areas with low slope at the coarse scale (Fig. 3b); (3) a higher probability of using areas close to forested habitat at the coarse scale (Fig. 3c). Mule deer in wolf-present and wolf-absent areas selected shrub habitat in a similar manner at both coarse and fine spatial scales (Fig. 3d and h). Mule deer exhibited some seasonality in habitat use patterns at the coarse scale. Namely, the use of space relative to roads varied between seasons, with mule deer manifesting increased use of areas close to roads in wolf-absent areas during winter and the opposite pattern in the wolf-present areas (Fig. 3a). Furthermore, at the coarse scale, mule deer in wolf-present areas selected for forest more in winter compared to summer (Fig. 3c). Fine-scale habitat use patterns of mule deer in wolf-present versus wolf-absent areas were more similar in summer than in winter Fig. 3e–h). For example, mule deer in wolf-present areas more readily avoided areas as distance to forest and shrub cover increased, respectively, compared to mule deer in wolf-absent areas during winter (Fig. 3g, h).

Table 2 Adult deer sample sizes and numbers of GPS locations by wolf presence/absence, sex, and species

Treatment	Species	Sex	Collared	#GPS locations
Wolf-present	White-tailed deer	Male	6	2081
Wolf-present	White-tailed deer	Female	19	12,339
Wolf-present	Mule deer	Male	9	5825
Wolf-present	Mule deer	Female	18	20,740
Wolf-absent	White-tailed deer	Male	13	6436
Wolf-absent	White-tailed deer	Female	21	11,969
Wolf-absent	Mule deer	Male	12	10,403
Wolf-absent	Mule deer	Female	22	14,197
		Total	120	83,990

- Number

Overall, model-averaged coefficient estimates of white-tailed deer demonstrated greater disparity in resource use patterns as a function of wolf presence at a relatively fine spatial scale (i.e., with respect to the third-order resource use; Table 3, Fig. 4). Moreover, differences in use of particular resources by white-tailed deer in wolf-present and wolf-absent areas generally supported the prediction that this species would manage predation risk from wolves with fine-scale habitat shifts (Tables 1, 3). Specifically, relative to conspecifics in wolf-absent areas, white-tailed deer in wolf-present areas exhibited (1) a higher probability of using areas close to secondary roads at the fine spatial scale of analysis (Fig. 4e); (2) a higher probability of using areas with low slope at the fine spatial scale (Fig. 4f); (3) a higher probability of using areas close to shrub habitat at the fine spatial scale in winter (Fig. 4h). White-tailed deer in wolf-present and wolf-absent areas selected forested habitat similarly at both the coarse and fine spatial scales of analysis (Fig. 4c and g). White-tailed deer exhibited some seasonality in habitat use patterns. Namely, in all study areas, white-tailed deer selected areas with lower slope in summer compared to winter at the fine spatial scale (Fig. 4f). Coarse-scale habitat use patterns of white-tailed deer in wolf-present areas versus white-tailed deer in wolf-absent areas were more similar in summer than in winter (Fig. 4a–d). For example, at the coarse spatial scale, white-tailed deer in wolf-present areas responded more to increasing distance from shrub cover during winter relative to summer compared to conspecifics in wolf-absent areas (Fig. 4d). Cross validation of model-averaged coefficient estimates revealed good predictive ability

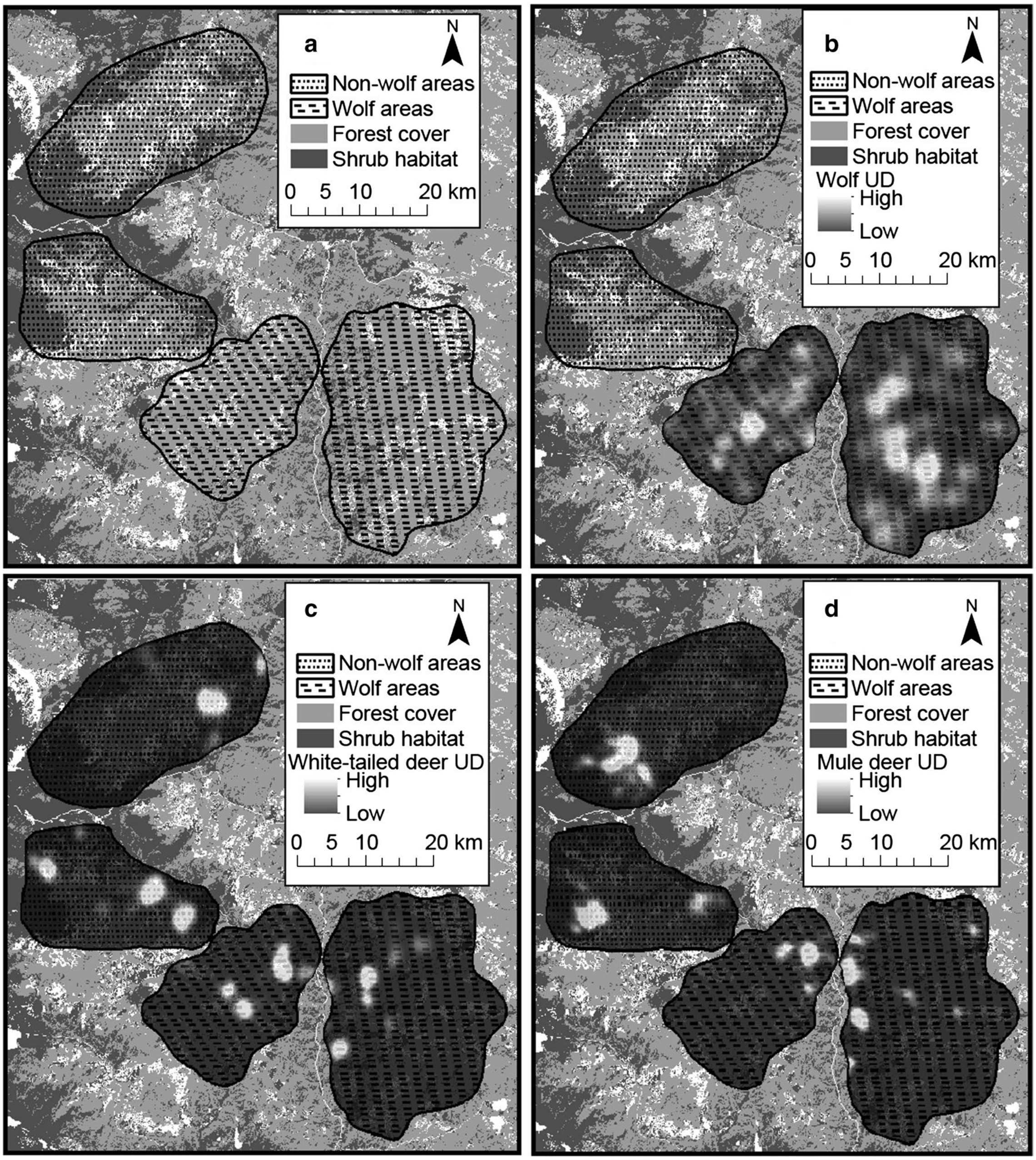

Fig. 2 **a** Land cover by forest and shrub habitat across the four study sites; **b** gray wolf utilization distribution calculated using data from two radio-collared animals per pack and representing years 2013–2016; **c** white-tailed deer utilization distributions calculated using data from 59 radio-collared animals representing years 2013–2016; **d** mule deer utilization distributions calculated using data from 61 radio-collared animals representing years 2013–2016

of resource use by mule and white-tailed deer at both coarse and fine spatial scales (see ESM 3).

Discussion

There is now broad agreement that predators can influence prey populations and community dynamics by eliciting anti-predator behavior (Lima 2002; Hernandez and Laundre 2005; Creel and Christianson 2008). Yet, predicting the responses of prey to particular predators, and by extension the nature of non-consumptive predator indirect effects in communities, remains a challenge (Heithaus et al. 2009). Predator recolonization events set the stage for natural experiments that contrast the responses of sympatric prey in areas with and without the returning predator and thereby allow examination of the factors driving divergent anti-predator responses both within and among prey species (Wirsing

Table 3 Model-averaged fixed effect coefficient estimates and standard errors for each set of models grouped by deer species and spatial scale

Fixed effects	Species							
	Mule deer				White-tailed deer			
	Coarse scale		Fine scale		Coarse scale		Fine scale	
	β	SE	β	SE	β	SE	β	SE
Intercept	−2.050	0.013	−1.709	0.013	−2.353	0.023	−2.090	0.025
Wolf	−1.756	0.049	−1.020	0.052	−0.218	0.037	0.208	0.038
Season	−0.163	0.019	0.325	0.020	−0.116	0.029	−0.158	0.033
Dist to road	−0.039	0.006	0.092	0.009	−0.302	0.014	0.032	0.015
Slope	0.174	0.011	0.471	0.013	−0.483	0.018	−0.349	0.017
Dist to forest	−0.049	0.020	−0.418	0.023	−1.158	0.052	−0.611	0.061
Dist to shrub	−0.266	0.018	−0.368	0.018	0.266	0.014	0.173	0.014
Wolf: season	1.280	0.055	0.916	0.059	0.085*	0.049	0.330	0.051
Wolf: dist to road	0.046	0.009	0.054	0.013	−0.176	0.024	−0.650	0.027
Wolf: slope	0.290	0.016	−0.229	0.017	0.263	0.024	−0.133	0.023
Wolf: dist to forest	−2.452	0.109	−0.737	0.119	−0.047*	0.078	0.739	0.078
Wolf: dist to shrub	−1.155	0.038	−0.965	0.038	−0.895	0.034	−0.720	0.037
Season: dist to road	−0.028	0.010	−0.093	0.015	−0.046	0.020	−0.162	0.024
Season: slope	−0.259	0.016	−0.218	0.019	−0.474	0.026	−0.416	0.025
Season: dist to forest	0.199	0.026	0.129	0.030	0.496	0.061	0.856	0.073
Season: dist to shrub	−0.504	0.029	−0.151	0.029	−0.093	0.021	0.021*	0.019
Wolf: season: dist to road	0.084	0.013	0.119	0.019	−0.052*	0.035	0.102	0.038
Wolf: season: slope	0.277	0.022	0.241	0.024	0.002*	0.036	−0.069	0.035
Wolf: season: dist to forest	1.163	0.121	0.982	0.131	−0.299	0.097	−0.377	0.102
Wolf: season: dist to shrub	1.141	0.049	0.910	0.049	0.661	0.044	0.647	0.047
Random effects	Variance	SD	Variance	SD	Variance	SD	Variance	SD
Individual	< 0.001	0.024	0.682	0.826	< 0.001	< 0.001	0.845	0.919

Also included are model-averaged random-effect variance and standard deviations for each set of models grouped by deer species and spatial scale. Coefficient estimates were derived from resource selection functions in a use/available framework. Asterisks (*) indicate that 95% confidence intervals include zero

et al. 2010; Dorresteijn et al. 2015). Taking advantage of the return of gray wolves to a multi-prey landscape in eastern Washington, USA, we found support for the hypothesis that the nature and scale of prey responses to predation risk are mediated by flight behavior. Specifically, mule deer at risk from wolves exhibited coarse-scale spatial shifts that putatively suited their running gait (stotting) and resulted in wolf avoidance, whereas white-tailed deer manifested fine-scale shifts that facilitated their gait (sprinting) but resulted in spatial overlap with wolves. Our results offer new insights into the way that these ungulates manage their risk of predation from wolves both spatially and temporally. More broadly, they suggest that consideration of flight tactics, in conjunction with predator hunting mode and landscape structure, could aid in predicting prey responses to predation risk (Heithaus et al. 2009; Wirsing et al. 2010) and that predators with the certain hunting modes could trigger multiple indirect non-consumptive effects in the same ecosystem owing to divergent spatial shifts of sympatric prey in response to predation risk (Thaker et al. 2011; Catano et al. 2016; Makin et al. 2017).

Mule deer flee from canid predators with a stotting gait (Lingle 2002; Bonar et al. 2016) that is thought to be favored by uneven terrain with obstacles (Geist 1981; Lingle and Pellis 2002). Namely, though slower than sprinting on flat ground, a bounding gait can facilitate the avoidance of impediments and thereby allow for rapid movement over broken terrain (Geist 1981; Lingle 2002; Bonar et al. 2016). Given that the running gait of mule deer putatively inhibits escaping wolves in areas that these canids frequent (i.e., areas with gentle and rolling terrain), we predicted that this prey species would avoid encounters with and reduce the probability of being detected by wolves (Atwood et al. 2009; Wirsing and Ripple 2011) by manifesting coarse-scale shifts toward more rugged uplands with increased slopes (i.e., uneven ground; Wirsing et al. 2010; Whittington et al. 2011) (Table 1). In accord with this prediction, differences in resource use by mule deer were best captured by the

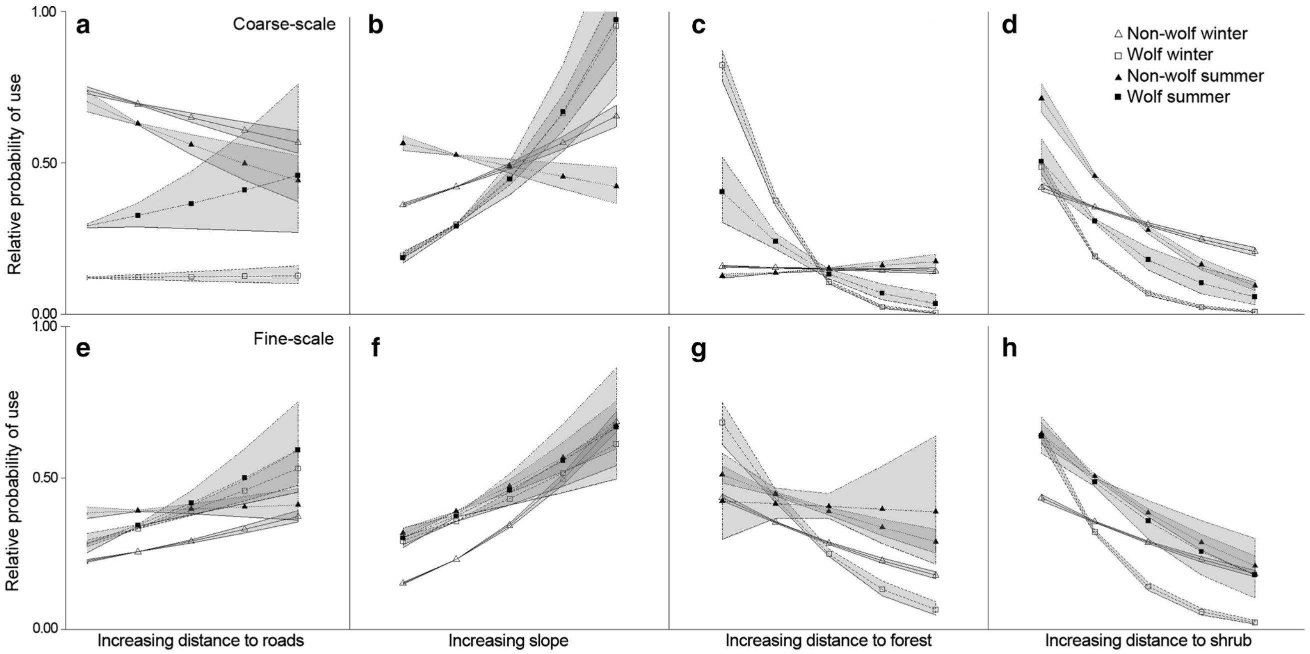

Fig. 3 Mule deer relative probability of use (symbols connected by lines) and associated 95% confidence intervals (gray shading bounded by lines) of landscape and habitat variables. Relative probabilities of use of landscape and habitat variables are broken down by wolf presence/absence and season, respectively, for coarse-scale (**a**–**d**) and fine-scale (**f**–**h**) habitat use patterns. Relative probabilities were derived from coefficient estimates from resource selection functions in a use/available framework. Distance to road variable represents distance in meters to nearest secondary road. Slope variable represents slope in degrees. Distances to forest and shrub represent distance in meters to nearest forest and shrub-steppe habitat, respectively. *X*-axes are the scaled values of respective variables. Scaled values were derived by subtracting the mean from all values and then diving by the standard deviation

coarse-scale analysis, and individuals exhibited the patterns of use that are consistent with encounter avoidance. Specifically, in areas with wolves, mule deer exhibited greater use of areas with forest cover where detection by cursorial predators like wolves is generally less likely (Fortin et al. 2005). Mule deer at risk from wolves also avoided areas with gentle terrain, which wolves use heavily for hunting (Mech and Peterson 2003; Oakleaf et al. 2006), and roads and trails, which wolves often use as travel routes (see ESM 1; Kunkel and Pletscher 2001). We also predicted that, at the coarse scale, mule deer in wolf-present areas would avoid areas close to shrub habitat to a greater extent than conspecifics in wolf-absent areas, because these open areas likely facilitate being detected by wolves. We found, however, that mule deer in wolf-present areas showed no significant difference in use of areas close to shrub habitat compared to mule deer in wolf-absent areas, perhaps, indicating the foraging benefits of shrub habitat for mule deer (Pierce et al. 2004). Nevertheless, our results are generally consistent with the idea that mule deer habitat use responses to wolves are potentially governed at least in part by their flight tactic. In accord with our study, Bowyer (1987) suggested that mule deer fawns select steeper slopes to avoid coyotes, and Lingle (2002) found that mule deer at risk from coyotes on the Alberta prairie responded by shifting to rugged terrain. Notably, however, these studies did not address mule deer responses to wolves, which may differ from those to coyotes. Moreover, along with the present study, these investigations were conducted in areas characterized by topographical complexity. Accordingly, the manner in which mule deer respond to the threat of predation from coursing canids in areas with less topographical variation remains to be determined. We also recognize that mule deer use of more gentle terrain and areas closer to roads in the non-wolf areas relative to the wolf areas may be an attempt to decrease predation risk from cougars (Pierce et al. 2004), whereas the habitat use pattern that we observed in the wolf areas could reflect risk from both predators (Atwood et al. 2009). We were unable to explore these possibilities, underscoring the value of future studies capable of discriminating between the effects of these two predators on mule deer.

White-tailed deer use flight and early detection as anti-predator tactics (Lingle 2002; Bonar et al. 2016), and both of these countermeasures are thought to be aided by gentle, open terrain with good visibility and a few obstacles (Kunkel and Pletscher 2001; Lingle and Pellis 2002; Kittle et al. 2008). Given that the anti-predator behaviors of white-tailed deer may actually promote eluding wolves in areas where wolves hunt, we predicted that this species would not avoid wolves but rather exhibit fine-scale shifts facilitating

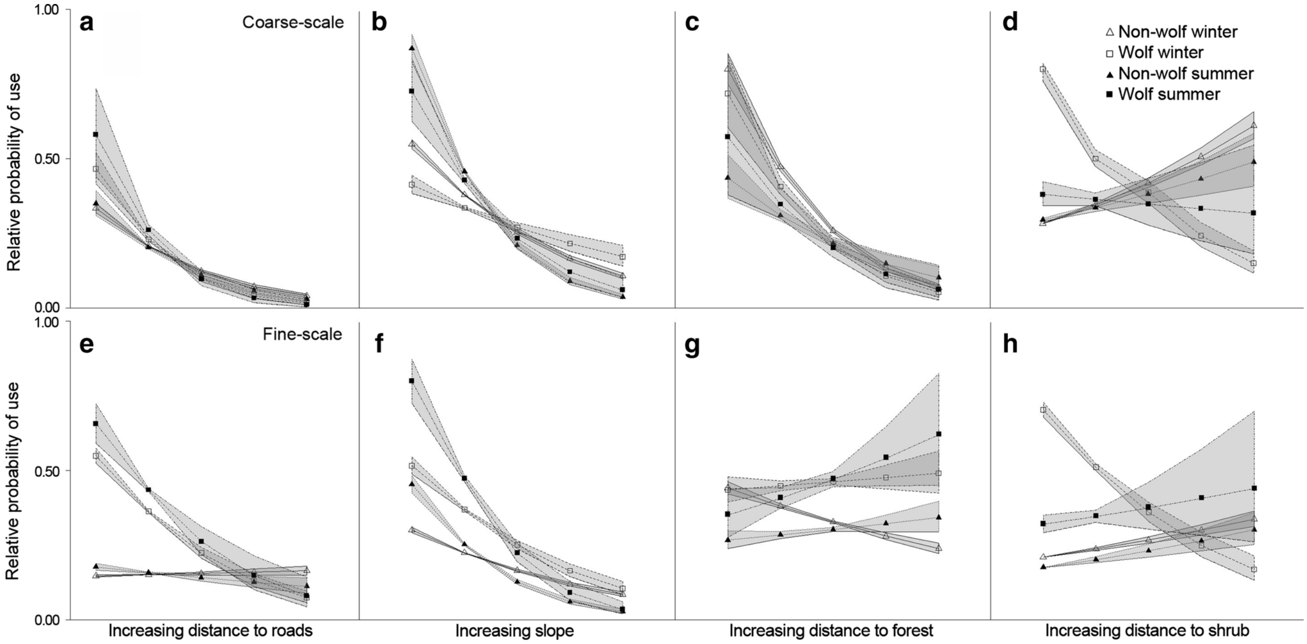

Fig. 4 White-tailed deer relative probability of use (symbols connected by lines) and associated 95% confidence intervals (gray shading bounded by lines) of landscape and habitat variables. Relative probabilities of use of landscape and habitat variables are broken down by wolf presence/absence and season, respectively, for coarse-scale (**a**–**d**) and fine-scale (**f**–**h**) habitat use patterns. Relative probabilities were derived from coefficient estimates from resource selection functions in a use/available framework. Distance to road variable represents distance in meters to nearest secondary road. Slope variable represents slope in degrees. Distance to forest and shrub represent distance in meters to nearest forest and shrub-steppe habitat, respectively. *X*-axes are the scaled values of respective variables. Scaled values were derived by subtracting the mean from all values and then dividing by the standard deviation

running and vigilance (Wirsing et al. 2010; Wirsing and Ripple 2011) (Table 1). In accord with this prediction, differences in resource use by white-tailed deer were best captured by the fine-scale analysis (Kuijper et al. 2015), and individuals exhibited the patterns of use that are consistent with facilitating post-encounter escape (Lingle 2002). Namely, white-tailed deer at risk from wolves selected areas close to roads, which, in our study area, bisect relatively flat areas with a few obstacles to hinder escape, areas with little-to-no slopes (i.e., areas characterized by level ground that facilitate sprinting), and more open habitats offering greater visibility. (Kunkel and Pletscher 2001; Lingle and Pellis 2002). Our results for white-tailed deer habitat use patterns in areas with and without wolves agree with the previous research and suggest that white-tailed deer minimize predation risk from coursing predators by relying on the early detection, which is facilitated by the use of open habitats and avoidance of dense cover (e.g., Kunkel and Pletscher 2001). They are also consistent with work by Kittle et al. (2008), who found that white-tailed deer in Ontario, Canada, selected for sheltered deer yards with low snowfall in winter that placed them in close proximity to hunting wolves, and with the previous studies demonstrating that, following detection, white-tailed deer are more vulnerable to coursing predators where escape is impeded by obstacles (e.g., deep snow) or not facilitated via the use of roads or established trails (Nelson and Mech 1991). Collectively, these investigations support the notion that, rather than avoiding canids like mule deer, white-tailed deer at risk from these coursing predators select resources that promote the effectiveness of their sprinting gait.

Mule deer and white-tailed deer in areas with wolves exhibited greater seasonality in resource use patterns at the predicted spatial scales of their responses to wolves than conspecifics in areas without wolves. Specifically, at the coarse scale, mule deer in wolf-present areas had a higher probability of selecting areas close to forest cover in winter versus summer (Table 1; Fig. 3). This pattern might be the result of adult mule deer making more of an effort to avoid encounters with wolves in winter, the season during which cervid vulnerability to predation tends to be greatest (Nelson and Mech 1991). At the fine scale, white-tailed deer in wolf areas showed a higher probability of selecting areas close to open shrub in winter versus summer, possibly as a means of more efficiently detecting and escaping wolves during the most dangerous time of year. Adult white-tailed deer and mule deer in other systems have been found to exhibit seasonal differences in habitat use patterns in relation to predation risk, most notably in response to hunting whereby both deer species selected for cover to decrease detection by human hunters (Swenson 1982; Kilgo et al.

1998). To date, however, seasonal differences in habitat use patterns of either species in relation to non-human predation risk remain largely unexplored. Our results highlight the seasonality that can characterize mule and white-tailed deer responses to wolves and, by extension, imply that studies with limited temporal scope may underestimate or miss the effects of predators on these ungulates. More broadly, they suggest that consideration of spatiotemporal patterning can strengthen insights into predator–prey interactions by revealing context specific processes that influence how prey behaviorally manage predation risk (Padie et al. 2015).

The conceptual framework underlying this study derived from cross fertilization of research in aquatic and terrestrial environments (Lima 2002; Heithaus et al. 2009; Wirsing et al. 2010) and was then invoked in a marine ecosystem (Heithaus et al. 2012; Catano et al. 2016). Our findings add to a growing literature (e.g., Crowell et al. 2016; Martin and Owen-Smith 2016), suggesting that it also applies in terrestrial settings. Accordingly, they underscore the value of considering the interaction between prey flight behavior, predator hunting mode, and landscape structure when predicting prey responses to predation risk. For example, large roving predators such as gray wolves (Middleton et al. 2013) and African wild dogs (*Lycaon pictus*, Thaker et al. 2011) have been posited as having weak non-consumptive impacts on prey relative to ambush predators, because their spatially diffuse risk signature minimizes the effectiveness of anti-predator habitat shifts. Other studies, however, have found that roving predators can influence prey behavior (e.g., Creel et al. 2014). This disparity may owe to context dependence. Rather than exerting uniformly weak non-consumptive effects, roving predators like wolves may elicit marked behavioral changes when and where the setting allows prey with certain flight tactics (or other defenses) the scope to manage risk.

A growing literature suggests that the effects of top predators can be attenuated in human-dominated ecosystems (Hebblewhite et al. 2005; Gervasi et al. 2013; Ripple et al. 2014; Kuijper et al. 2016). In a companion study, we found that wolves in our study system, where human activity is pervasive, had weak effects on survival of adult mule and white-tailed deer (Dellinger et al. 2018). Here, we detected marked behavioral differences in both deer species that were spatially consistent with the presence or absence of recolonizing wolves. By implication, wolves in our human-managed system might not be numerous enough to kill many prey individuals (Jimenez and Becker 2016), but their presence may still be sufficient to cause prey to invest in defensive behavior. Microcosm experiments with have demonstrated that even when the ability of invertebrate predators to consume prey is removed, prey may maintain defensive countermeasures similar those exhibited by conspecifics exposed to lethal predators (Schmitz et al. 1997; Nelson et al. 2004). Our findings add support to the idea that non-consumptive predator effects can operate even when direct predation is negligible (Schmitz et al. 1997; Nelson et al. 2004; Creel and Christianson 2008). Insofar as they were reacting to wolf predation risk, the mule and white-tailed deer spatial shifts which we observed also suggest that wolves have the potential to exert behavior-mediated indirect effects on plant communities. There remains need, however, for studies asking whether the behavioral responses which we observed are strong enough to affect lower trophic levels and examining the possibility that the effects of wolves on deer in managed landscapes could be superseded in some circumstances by risk effects imposed by humans (Lone et al. 2014; Dorresteijn et al. 2015).

Although our results implicate flight behavior as being at least partially responsible for the observed patterns of mule and white-tailed deer habitat use in relation to wolf presence, the correlative nature of our study leaves opens the possibility of alternative explanations. It is possible, for example, that differences in food supply or quality across the four sites led mule and/or white-tailed deer in the wolf-occupied sites to use space differently than conspecifics in sites without wolves. A similar scenario might arise from spatial differences in the impacts of other deer predators in the study system (e.g., cougars). A fully experimental approach, with replication of wolf impacts and true controls, would be needed to rule out these alternatives (Ford and Goheen 2015). Yet, in our view, several aspects of our study design render them unlikely. First, patterns of topography, land cover, and the activity of other predators were broadly similar across the four sites, whereas wolves only occupied two. As a natural experiment, therefore, our investigation did provide a reasonably strong basis for attributing any observed differences in deer behavior to wolves. Second, we replicated our wolf and non-wolf areas, meaning that any non-wolf factor responsible for the observed patterns of deer behavior would also need to differ systematically as a function of wolf presence. Third, the patterns of deer habitat use which we observed at both spatial scales were largely consistent with a priori predictions stemming from the hypothesis of a wolf effect.

Our results highlight the potential for top predators to non-consumptively impact multiple sympatric prey species in different ways and at varying spatial scales (Padie et al. 2015; Makin et al. 2017). Thus, we encourage further exploration of direct and indirect effects of predators with shared prey that exhibit divergent flight tactics in the interest of better understanding the non-consumptive pathways by which top–down forcing can occur in ecosystems. Given that prey flight responses can depend on predator hunting mode and landscape context (Lingle 2002; Heithaus et al. 2009; Wirsing et al. 2010; Latombe et al. 2014), studies in systems with multiple predator and prey species interacting across heterogeneous landscapes are likely to be especially revealing. Finally, from a conservation standpoint, our findings emphasize the important roles played by predators in all landscapes rather than the just protected areas (Heithaus et al. 2012; Dorresteijn et al. 2015; Kuijper et al. 2016). In particular, they suggest that even if predators do not inflict much mortality in human-modified ecosystems, their recovery might at least partly restore key processes such as prey-defensive investment (Kuijper et al. 2016).

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Author contribution statement AJW, MRH, and WJR originally conceptualized the study. JAD, CRS, and AC contributed to fieldwork. JAD analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed.

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