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Research Article

Evaluating Indirect Effects of Hunting on Mule Deer Spatial Behavior

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ABSTRACT Mule deer (*Odocoileus hemionus*) are widely hunted throughout western North America and are experiencing population declines across much of their range. Consequently, understanding the direct and indirect effects of hunting is important for management of mule deer populations. Managers can influence deer mortality rates through changes in hunting season length or authorized tag numbers. Little is known, however, about how hunting can affect site fidelity patterns and subsequent habitat use and movement patterns of mule deer. Understanding these patterns is especially important for adult females because changes in behavior may influence their ability to acquire resources and ultimately affect their productivity. Between 2008 and 2013, we obtained global positioning system locations for 42 adult female deer at the Starkey Experimental Forest and Range in northeast Oregon, USA, during 5-day control and treatment periods in which hunters were absent (pre-hunt), present but not actively hunting (scout and post-hunt), and actively hunting male mule deer (hunt) on the landscape. We estimated summer home ranges and 5-day use areas during pre-hunt and hunt periods and calculated overlap metrics across home ranges and use areas to assess site fidelity within and across years. We used step selection functions to evaluate whether female mule deer responded to human hunters by adjusting fine-scale habitat selection and movement patterns during the hunting season compared to the pre-hunt period. Mule deer maintained site fidelity despite disturbance by hunters with 72 ± 4% (SE) within-year overlap between summer home ranges and hunt use areas and 54 ± 7% inter-annual overlap among pre-hunt use areas and 56 ± 7% among hunt use areas. Mule deer diurnal movement rates, when hunters are active on the landscape, were higher during the hunting period versus pre-hunt or scout periods. In contrast, nocturnal movement rates, when hunters are inactive on the landscape, were similar between hunting and non-hunting periods. Additionally, during the hunt, female mule deer hourly movements increased in areas with high greenness values, indicating that mule deer spent less time in areas with more vegetative productivity. Female mule deer maintained consistent habitat selection patterns before and during hunts, selecting areas that offered more forest canopy cover and high levels of vegetative productivity. Our results indicate that deer at Starkey are adopting behavioral strategies in response to hunters by increasing their movement rates and selecting habitat in well-established ranges. Therefore, considering site fidelity behavior in management planning could provide important information about the spatial behavior of animals and potential energetic costs incurred, especially by non-target animals during hunting season.

KEY WORDS animal movement, anti-predator behavior, human-wildlife interactions, hunting, mule deer, *Odocoileus hemionus*, site fidelity.

Successfully managing large herbivores requires an understanding of how increased human presence on the landscape, particularly during hunting seasons, can influence anti-predator strategies and behavior. Hunters can have direct effects (i.e., consumptive or density-mediated effects) on population dynamics of target animals through sex- and age-specific bag limits (Toïgo et al. 2008). Hunting can also elicit indirect effects (i.e., non-consumptive or trait-mediated effects) that include temporal and spatial changes in activity patterns (Cleveland et al. 2012, Ordiz et al. 2012), increased vigilance (Benhaiem et al. 2008, Reimers et al. 2009), altered foraging patterns (Hertel et al. 2016), and shifts in habitat use patterns (Grignolio et al. 2011, Bonnot et al. 2013, Spitz et al. 2019).

Indirect effects associated with predation risk can also concurrently influence many individuals within a population

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resulting in cumulative effects that can surpass those associated with direct effects (Preisser et al. 2007, Wirsing et al. 2008). Individual behavioral responses to predation risk are limited by nutritional thresholds that are directly associated with survival and reproduction (Lima and Dill 1990). At the core of this idea is the risk allocation hypothesis, which posits that prey species must trade time spent on antipredator behavior with other essential maintenance activities and the strength of prey responses will hinge on the energetic costs associated with that behavioral decision (Lima and Bednekoff 1999). Prey might respond less to prolonged risk than to risk that is high but less frequent (Creel et al. 2008). Over the short-term, prey perceive their surroundings based on the trade-off of food and security associated with foraging in available habitat (Bleicher 2017). As a result, prey may perceive a landscape of fear (Laundré et al. 2001) with areas of relatively high and relatively low predation risk.

The magnitude of behavioral responses to risk during hunting season can be tied to spatio-temporal variation in predation risk (Cromsigt et al. 2013). Thus, using an appropriate scale to quantify antipredator behaviors is necessary to successfully detect responses. For example, roe deer (*Capreolus capreolus*) changed their movement rates in response to various hunting regimes but did not change the overall size of their home ranges (Picardi et al. 2019). Although identifying changes in broad-scale spatial behavior (e.g., changes in home range size) during hunting seasons may be difficult, especially if the duration of risk varies at the scale of weeks or days, understanding these dynamics at multiple scales may provide a fuller characterization of spatial behavioral patterns than do those conducted at a single scale (Mayor et al. 2009). Indeed, home range dynamics such as familiarity (i.e., site fidelity) of an individual's previously established home range during hunting seasons could benefit individuals that might otherwise leave their respective ranges following the onset of hunter activity (Marantz et al. 2016).

Site fidelity has been defined as an area-restricted, space-use behavior that could improve survival through familiarity with food distribution, escape cover, and predation risk (Switzer 1993, Börger et al. 2008). Strong site fidelity within a given year or season for prey species can be interpreted as a behavioral strategy to minimize encounter rates with predators (Forrester et al. 2015). For example, prey species that exhibit strong site fidelity during hunting seasons could reduce their risk by minimizing long-distance movements into novel areas. Additionally, if animals shift their foraging tactics during risky periods, deer that remain loyal to specific areas should have better access to known food resources. Thus, addressing site fidelity is especially important for studies that investigate associated effects of predation on habitat selection patterns. Maintaining site fidelity may also have fitness consequences if animals remain in poor quality habitat (e.g., patches yielding low energy intake rate; Merkle et al. 2015) or in areas with high levels of risk from predation (Tracz et al. 2010). Although mule deer (*Odocoileus hemionus*) exhibit site fidelity behavior that can vary between populations and seasons (Webb et al. 2013), we do not yet know how hunting, an annual disturbance event throughout most of the species' range, may affect fidelity and associated habitat selection and movement behaviors.

We investigated changes in spatial behavior of adult female mule deer in response to hunting of male (i.e., antlered) mule deer. Understanding the non-consumptive effects of hunting on females is important because indirect effects associated with predation risk have greater potential to affect reproductive success and survival from this segment of the population (DeCesare et al. 2014). This information is valuable for wildlife management in western North America as mule deer populations have experienced widespread declines across much of their range (Bishop et al. 2009, Bergman et al. 2015). Additionally, much of the hunting literature has focused research efforts on the targeted animals being pursued. Very little is known about the indirect effects of hunting on the behavior and life history of non-targeted species or age and sex classes (Grignolio et al. 2011). Given that hunting is likely a perceived risk by both target and non-target prey species as a disturbance, wildlife managers should carefully evaluate the behavioral effects of hunting on the entire population.

Because of the differential response to predation risk commonly recorded among sex and age classes in ungulates (Grignolio et al. 2007), we assumed that female mule deer would perceive the risk of predation from human hunters. We used 3 approaches to study how female deer modified their spatial behavior as a response to increased human presence and associated hunting pressure on the landscape. First, we investigated whether site fidelity varied across years or seasons; second, we used fine-scale locational data to assess female deer resource use before and during the hunting season; finally, we evaluated whether deer increased their daily movement rates during hunting season and identified habitat features that relate to increased hourly movement patterns before and during the hunting season. We hypothesized that deer would be unlikely to exhibit shifts in home ranges because movement into novel areas could expose deer to increases in either perceived predation risk from human hunters or realized predation risk from native predators. By contrast, we hypothesized deer would be more likely to alter diurnal habitat selection and movement patterns when human hunters were active on the landscape, especially if those behaviors are mitigated by changes in behavior (e.g., increased movement) during nocturnal periods when humans are not actively using the landscape. We predicted that site fidelity would be strongest during the hunting season; habitat selection during the hunt would be strongest for variables that provide security during the hunting season relative to non-hunt periods; and movement rates would be faster in risky habitat (e.g., open land cover types) relative to non-hunting periods.

STUDY AREA

We conducted this study at the Starkey Experimental Forest and Range (i.e., Starkey: Fig. 1), located in the Blue

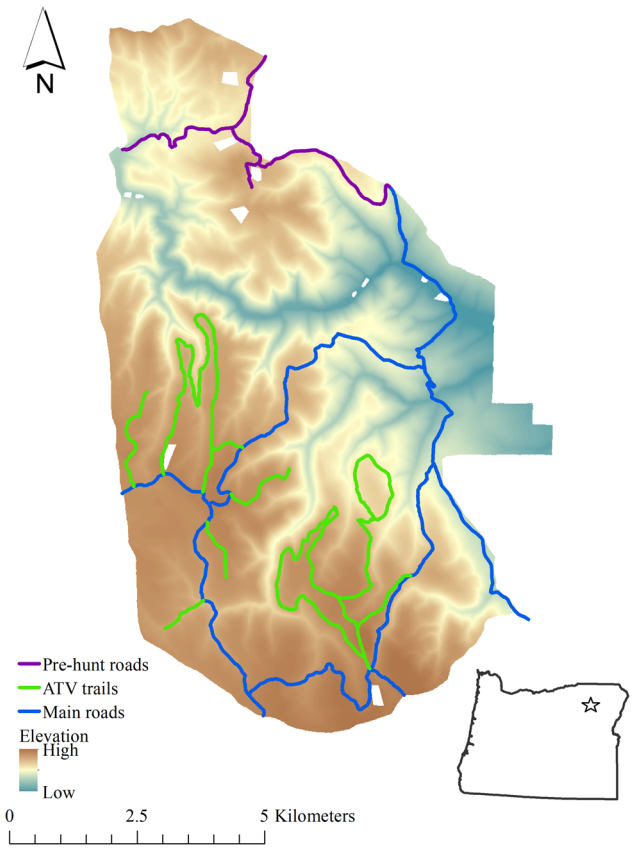

Figure 1. The main enclosure of Starkey Experimental Forest and Range, Oregon, USA, during hunts for male mule deer, 2008–2013. Lines denote the presence of main roads (blue) and all-terrain vehicle (ATV) trails (green). Pre-hunt roads (purple) were closed when hunters were present.

Mountains, northeastern Oregon, USA (45°13′N, 118°31′W). Since 1987, the United States Forest Service (USFS) maintained a 2.4-m high fence around Starkey, which prevented ungulate movement in and out of the adjacent area (Rowland et al. 1997, Kie et al. 2005). Starkey was divided into multiple study areas of approximately 10,125 ha. Elevations ranged from 1,116 m to 1,502 m. Starkey was subject to a dry continental climate; highest and lowest seasonal mean monthly temperatures were 18°C in July and −4°C in January. Mean total precipitation was 18.4 cm during spring, 6.9 cm during summer, and 6.8 cm during fall. The main study area (7,768 ha), where this research was conducted, contained conifer forests, shrublands, grasslands, and moderately sloping uplands dissected by drainages (Rowland et al. 1997). Mule deer, white-tailed deer (*O. virginianus*), and Rocky Mountain elk (*Cervus canadensis*) were present, along with several potential predator species including mountain lions (*Puma concolor*), black bears (*Ursus americanus*), coyotes (*Canis latrans*), and bobcats (*Lynx rufus*).

METHODS

Experimental Design and Deer Capture

From 2008–2013 rifle hunts were held annually at Starkey for male deer with visible antlers. The number of tags issued for each hunt was consistent across years (25 tags/hunt), and hunter densities ranged between 0.24 and 0.33 hunter/km^2 (Table S1, available online in Supporting Information). We defined a 20-day period surrounding each hunt and divided it into 4 consecutive 5-day periods with varying levels of human disturbance: a pre-hunt period that preceded the arrival of hunters and served as our control, a scout period during which hunters were present and could travel throughout Starkey but could not harvest animals, a hunt period (permitted hunting season) when hunters were allowed to harvest male deer, and a post-hunt period in which hunters were absent or inactive. We interpret the pre-hunt period as representing baseline levels of anthropogenic disturbance (i.e., low levels of human activity unrelated to hunting). In addition to the rifle season for male deer, archery and rifle hunts for male elk were held annually before and after the deer hunt, respectively. The elk archery and rifle hunts consisted of the same number of days as the deer hunt. The last day of the elk archery hunt and the deer rifle pre-hunt periods were separated by 20 days, and the deer rifle post-hunt and elk rifle hunt periods were separated by 15 days (Fig. 2A; Table S2, available online in Supporting Information). Hunters could legally harvest males from 30 minutes before sunrise to 30 minutes after sunset. Additionally, harvest was prohibited inside a 400-m buffer along the perimeter fence.

We captured female mule deer (adults ≥2 yrs of age) at Starkey during winters 2007–2012 with baited panel traps (Rowland et al. 1997). We fitted deer with global positioning system (GPS) radio-collars (models 4400 and 4500 Lotek, Newmarket, Ontario, Canada) in accordance with USFS Institutional Animal Care and Use Committee (number 92-F-0004; Wisdom et al. 1993). All collars were programmed to collect locations at a 30-minute or higher frequency during the fall hunting season (15 Aug–30 Oct). Outside of the hunting season, collars generated 2 locations/day because of limitations on battery life. We then excluded data from collars with an acquisition rate lower than 0.85, which resulted in 53 animal-years of location data from 42 unique individuals. Prior to analyses, we checked data for duplicates and outlier movements (i.e., movement rates that were unlikely for a deer to reach over the given fix schedule; Bjørneraas et al. 2010).

Deer Site Fidelity

We assessed site fidelity using 2 temporal indices: concentrated activity in a given area within a year (within-year site fidelity) and reuse of the same area across consecutive years (inter-annual site fidelity; White and Garrott 1990, Wittmer et al. 2006). We assessed within-year site fidelity for each deer by measuring overlap between summer home ranges and the area occupied during the pre-hunt and hunt periods and by measuring the overlap between the pre-hunt and hunt use areas used within a given year. For each individual deer, we used all available telemetry locations to estimate separate summer home ranges (15 Jun–15 Aug) and pre-hunt and hunt use areas by fixed-kernel density estimation (Worton 1989). We implemented this approach in the adehabitatHR R package (Calenge 2006) with a

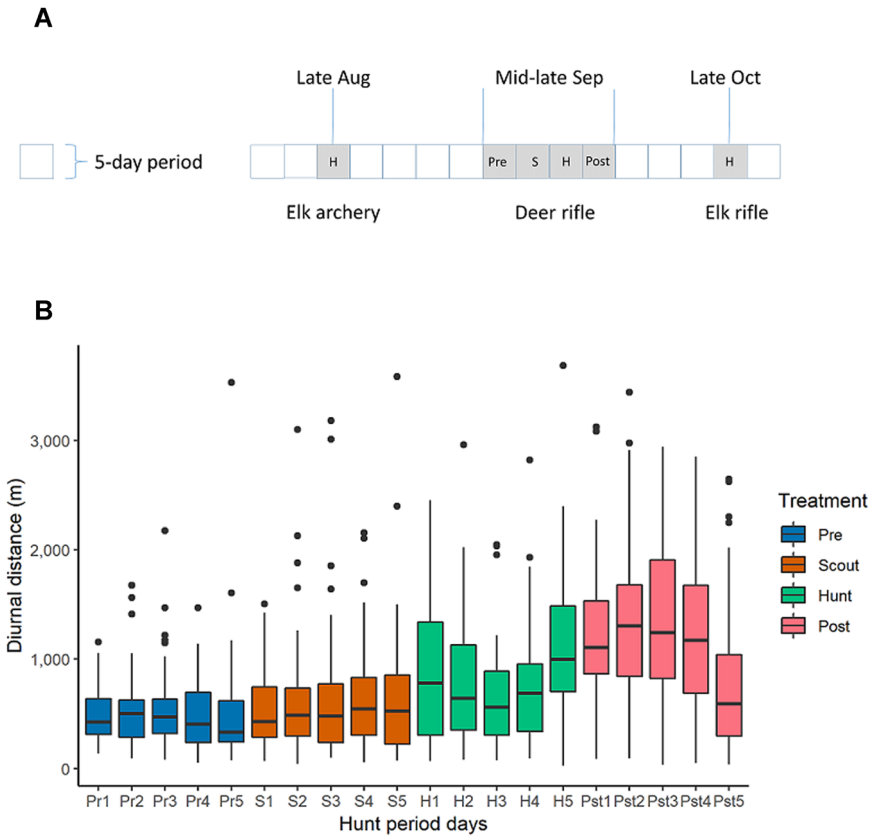

Figure 2. Our study focused on female deer behavior across the male deer rifle season, which consisted of 4 5-day periods (A) in the Starkey Experimental Forest and Range, Oregon, USA, 2008–2013. During these periods, hunters were absent during the pre-hunt period (Pre), present but not hunting during scout period (S), actively hunting during the deer rifle season (H), and absent or leaving the area during the post-hunt period (Post). Average daily diurnal movements of female deer for each period (B) were defined as pre-hunt (Pr1–Pr5), scout (S1–S5), hunt (H1–H5), and post-hunt (Pst1–Pst5). Box plots show median values (solid horizontal line), 25% and 75% quantile values (lower and upper hinges); whiskers represent 1.5 × interquartile range extending no further than maximum or minimum values; outliers are shown as solid black circles (•).

bivariate Gaussian kernel and determined the utilization distributions (UDs) of the tracked deer. We set grid resolution to 100 m × 100 m and used the reference method to calculate the smoothing factor (h) for each individual. We defined hunt use areas as the 95% isopleth value during the 5-day pre-hunt and hunt periods. We evaluated inter-annual site fidelity for each deer that we monitored for ≥2 consecutive years ($n = 18$) by measuring overlap between pre-hunt and hunt use areas among years, resulting in 128 across year comparisons.

We calculated within-year and inter-annual site fidelity using 2 methods to quantify spatial intersection. We first investigated the proportion of the home range of time period i covered by the home range of time period j.

$$\text{Percent overlap} = \frac{\text{A}[i,j]}{\text{A}[i]} \times 100,$$

where $\text{A}[i,j]$ is the area of the intersection between home ranges occupied during time periods i and j, respectively, and $\text{A}[i]$ is the area of home range at time period i (Fieberg and Kochanny 2005). Additionally, we calculated the utilization distribution overlap index (UDOI):

$$\text{UDOI} = A_{i,j} \int_{\infty}^{\infty} \int_{\infty}^{\infty} \widehat{UD_i}(x,y) \times \widehat{UD_j}(x,y)\,dxdy$$

where $A_{i,j}$ is the area of overlap between the 2 home ranges and $\widehat{UD_i}$ and $\widehat{UD_j}$ are the utilization distributions for time periods i and j, respectively (Fieberg and Kochanny 2005). Values usually range between zero (no overlap) and 1 (uniformly distributed and 100% overlap) but can be >1 and are thought to be the most appropriate metric of space-use overlap (Fieberg and Kochanny 2005). The UDOI provides a measurement of the amount of overlap relative to 2 individuals or the same individual in consecutive years using the same space uniformly. We performed calculations of percentage overlap and UDOI in the adehabitatHRF package (Calenge 2006) in Program R version 3.5.3. We used linear mixed-effects models (LMEs) with hunting period, year, and animal identification (ID) nested within year to investigate how our site fidelity indices (% overlap and UDOI) varied between hunting periods. We calculated 95% confidence intervals of each model's fixed effects factors and P-values for pairwise comparisons of all contrast combinations adjusted with the Tukey method with the multcomp (Hothorn et al. 2016) and lsmeans (Lenth 2017) packages.

Deer Resource Use

To fit step selection functions (SSF) to locational data, we subset GPS location data for individual deer to a consistent half-hour schedule and analyzed all locations collected during the pre-hunt (control) and deer hunt (treatment) periods only. We matched each observed location with 5 available points generated by resampling step lengths and turning angles from their empirical distribution (Fortin et al. 2005) in the amt package in Program R (Signer et al. 2019). When using conditional regression approaches, the number of available points can remain low with no effect on parameter estimation (Thurfjell et al. 2014). This resulted in each step including a stratum of 6 locations (1 used, 5 available). The data set contained 17,035 telemetry locations with 85,175 associated available locations. We extracted habitat covariate values for the end-point of each step; they consisted of environmental and anthropogenic variables related to hunter activity. We used normalized difference vegetation index (NDVI) amplitude to represent the annual peak increase in photosynthetic activity above the baseline at the start of the growing season. We acquired all 250-m resolution Moderate Resolution Imaging Spectroradiometer (MODIS) NDVI images from 2008–2013. This metric captures spatial variation in greenness across the growing season relative to non-growing season conditions and has been used as a proxy of ungulate forage biomass production (0–100%; Pettorelli et al. 2011). We used overstory forest canopy cover (0–100%), slope (degrees), and distance to forest edge (distance to nearest pixel with ≥40% canopy cover; m) as surrogates for perceived security by female mule deer; these variables have explained habitat use of mule deer in other portions of Oregon (Eckrich et al. 2020). We used distance to roads (km) and trails (km) open to motorized vehicle use during the hunt as an index of hunter access. We obtained canopy cover, slope, distance to forest edge, and distance to roads values at a 30-m resolution. The effect of roads and all-terrain vehicles (ATV) was limited to 1.5 km based on maximum hourly deer movements during the hunting period.

We compared matched sets of used and available locations using Poisson regression, where stratum-specific intercepts are modeled as a random effect (Muff et al. 2019). We manually fixed the variance to a large value to ensure that stratum-specific intercepts did not shrink towards their overall mean. We used the glmmTMB package in Program R (Brooks et al. 2017) to perform statistical analyses. We included independent individual-specific slopes for all vegetative cover, landscape, and road covariates to account for individual variation in response to available conditions. We found no highly correlated variables (i.e., $|r| \geq 0.6$) and all potential variables could be included in the same model.

We developed an *a priori* set of 8 models based on combinations of biological and management relevance from past mule deer research. We grouped variables into 2 categories to assess habitat use by mule deer during hunting season: 1) topographic and vegetation structure and 2) hunter road access. We then developed models to distinguish between those variables that could seasonally be influenced by land managers during hunting season (hunter road access) versus those could not easily be managed but have been identified by previous work as important landscape features that explained resource use by mule deer (landscape feature model). Our final model set consisted of 8 models including 1) landscape feature model (i.e., slope, canopy, NDVI amplitude, distance to forest edge), 2) landscape feature model with distance to ATV trails, 3) landscape feature model with distance to road open to motorized vehicle use, 4) landscape feature model and distance to ATV trails and roads open to motorized vehicle use, and 5–8) landscape feature model and distance to ATV trails and roads models with a hunt interaction.

We fit separate models for diurnal and nocturnal time periods during both the pre-hunt and hunt periods. We took this approach because hunters are unlikely to be active during nocturnal periods and thus unlikely to influence deer movements during non-shooting hours. When ranking models, we used Akaike's Information Criterion corrected for small sample size (AIC_c) to assess the relative support of candidate models (Burnham and Anderson 2002). We assessed the predictive performance of models using a 5-fold cross validation based on individual blocking (Roberts et al. 2017). Here, we split data by randomly selecting individuals, in which each deer contributed all GPS fixes to a single fold.

Deer Movement

Because energy expenditure for mule deer increases linearly with velocity of motion (Parker et al. 1984), we presume that an increase in diurnal movement during hunting seasons can have energetic costs. To examine deer movement rates in relation to habitat features, we calculated the distance between 2 successive GPS locations (step length) for each individual and divided this distance by the time between locations (m/hr). For this analysis, we used steps between 30-minute fixes to maintain consistent frequency, and log-transformed movement rate to achieve normally distributed residuals. We modeled generalized linear mixed models of hourly movement rate as a function of environmental variables and road variables at the beginning of each step with the lme4 package (Bates et al. 2015). We used the same set of *a priori* models as our step selection analyses and the interaction between pre-hunt and hunt periods to evaluate differences in movement rates. We fit separate models of movement rates for diurnal and nocturnal periods during both the pre-hunt and hunt periods. We used AIC_c to assess the relative support for models.

Changes in hourly movement may not translate to an increase or decrease in overall daily movement if the perceived risk deer face is temporally predictable and they adjust their movement around spikes in hunter activity. Therefore, we also evaluated whether daily deer movements varied across all 4 consecutive periods (i.e., pre, scout, hunt, post). We calculated net daily movements during the 4 periods and presented results as means ± standard errors (SE).

RESULTS

Mule deer use areas averaged $2.9 \pm 0.22\ km^2$ during the pre-hunt, and $3.2 \pm 0.25\ km^2$ during the hunt. Summer mule deer home ranges averaged $6.0 \pm 0.71\ km^2$. Percent overlap was highest when comparing within-year site fidelity between summer home ranges and pre-hunt use areas ($\bar{x} = 74 \pm 4\%$) and between summer home ranges and hunt use areas ($\bar{x} = 72 \pm 4\%$). Percent overlap was also high between the pre-hunt and hunt use areas within a year ($\bar{x} = 69 \pm 3\%$). Inter-annual percent overlap was considerably lower than within-year comparisons; however, spatial overlap was still >50% for both pre-hunt use areas ($\bar{x} = 54 \pm 7\%$) and hunt use areas ($\bar{x} = 56 \pm 7\%$). Based on the UDOI, overlap was again higher for within-year metrics of pre-hunt and hunt periods (0.47 ± 0.03) and between summer range and hunt use areas (pre-hunt: $\bar{x} = 0.41 \pm 0.04$; hunt: $\bar{x} = 0.44 \pm 0.03$) compared to inter-annual overlap metrics (pre-hunt: $\bar{x} = 0.32 \pm 0.05$; hunt: $\bar{x} = 0.38 \pm 0.06$). Within-year site fidelity, assessed using UDOI and percent overlap, indicated pre-hunt and hunt site fidelity did not differ in either UDOI ($F_{1,42} = 0.013$, $P = 0.91$) or percent overlap ($F_{1,128} = 0.19$, $P = 0.64$). Inter-annual site fidelity metrics also did not differ between pre-hunt and hunt periods using UDOI ($F_{1,42} = 0.44$, $P = 0.50$) or percent overlap ($F_{1,42} = 0.94$, $P = 0.83$).

Across diurnal and nocturnal periods, deer were more likely to select steps associated with our environmental model set that included canopy cover, distance to edge, NDVI amplitude, and slope (Table 1). The hunt interaction term was not retained in the best-ranked models in the diurnal or nocturnal model sets (Table 1), which suggested patterns of deer habitat selection were similar regardless of hunter presence on the landscape. Deer were more likely to select steps in areas with greater forest canopy cover and with higher vegetative productivity (Table S3, available online in Supporting Information). During diurnal periods, deer were more likely to select steps that were closer to forest edges ($\widehat{\beta} = -0.2$, SE = 0.01) but began moving into areas farther from edge during nocturnal periods ($\widehat{\beta} = 0.06$, SE = 0.02). Additionally, deer selected steeper areas ($\widehat{\beta} = 0.1$, SE = 0.07) during diurnal periods and moved into flatter terrain during nocturnal periods ($\widehat{\beta} = -0.2$, SE = 0.08). Diurnal and nocturnal model 5-fold cross validation r_s values were 0.83 and 0.86, respectively.

Diurnal movement, assessed using net daily movements, varied between the 4 hunt periods (Fig. 2B). On average, daily diurnal deer movements were greater during the hunt period ($\bar{x} = 992 \pm 48$ m) and post-hunt periods ($\bar{x} = 1{,}252 \pm 64$ m) compared to the pre-hunt ($\bar{x} = 544 \pm 31$ m) and scout ($\bar{x} = 642 \pm 40$ m) periods. On average, deer nocturnal movements were slightly higher during the pre-hunt period ($\bar{x} = 1{,}040\ m \pm 50$ m), and remained relatively consistent across the scout ($\bar{x} = 862\ m \pm 37$ m), hunt ($\bar{x} = 895\ m \pm 40$ m), and post-hunt ($\bar{x} = 880\ m \pm 40$ m) periods (Fig. S1, available online in Supporting Information).

The model with highest empirical support predicting hourly movement rate during both diurnal and nocturnal periods included forest canopy cover, distance to edge, NDVI amplitude, slope and the hunt interaction term (Table 1). During diurnal periods, deer movement was greater during the hunt period than during the pre-hunt period (Fig. 3). Deer moved faster in areas that were farther from forest edges, with more open forest canopy, and on flatter slopes during both seasons. Additionally, deer movement during hunting seasons was greater in areas of increased vegetation productivity, whereas deer movement decreased with increasing NDVI during the pre-hunt period (Fig. 3). For the nocturnal period, deer movement during the hunting season was greater in areas with increased

Table 1. Comparison of model selection of mule deer resource selection and hourly movement (m/hr) using generalized linear mixed models in the Starkey Experimental Forest and Range, Oregon, USA, 2008–2013. The fixed effects and interaction terms were constant across all model sets. We present the difference in corrected Akaike's Information Criterion (AIC_c) values between each model (ΔAIC_c). Model 1 denotes the top-ranked model for diurnal and nocturnal habitat selection. Model 5 denotes the top ranked model for diurnal and nocturnal movement.

	Habitat selection[a]		Movement[b]	
Model	Diurnal ΔAIC_c	Nocturnal ΔAIC_c	Diurnal ΔAIC_c	Nocturnal ΔAIC_c
1. Canopy + slope + distance forest edge + NDVI amplitude	0	0	141	16
2. Canopy + slope + distance forest edge + NDVI amplitude + distance road + distance road^2	8	3	152	24
3. Canopy + slope + distance forest edge + NDVI amplitude + distance ATV trail + distance to ATV trail^2	9	8	137	35
4. Canopy + slope + distance forest edge + NDVI amplitude + distance road + distance road^2 + distance ATV trail + distance to ATV trail^2	16	10	153	43
5. Canopy + slope + distance forest edge + NDVI amplitude × hunt	7	9	0	0
6. Canopy + slope + distance forest edge + NDVI amplitude + distance road + distance road^2 × hunt	19	16	301	17
7. Canopy + slope + distance to forest edge + NDVI amplitude + distance ATV trail + distance to ATV trail^2 × hunt	20	21	25	233
8. Canopy + slope + distance forest edge + NDVI amplitude + distance road + distance road^2 + distance ATV trail + distance to ATV trail^2 × hunt	31	37	56	54

[a] Diurnal and nocturnal resource selection as a function of environmental variables (e.g., normalized difference vegetation index [NDVI] amplitude), road variables (e.g., distance to all-terrain vehicle [ATV] trails), and hunt period interaction.
[b] Diurnal and nocturnal movement as a function of environmental variables, road variables, and hunt period interaction.

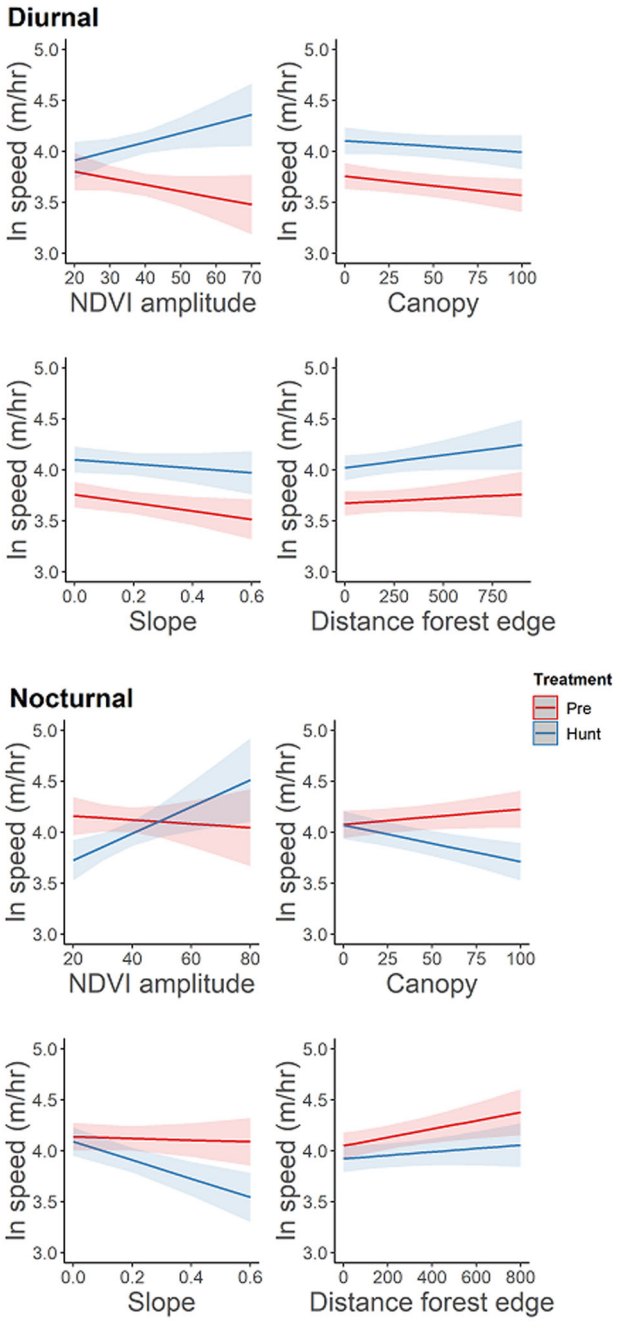

Figure 3. Predicted values of diurnal and nocturnal hourly movements during pre-hunt (red) and hunt (blue) periods for female mule deer in the Starkey Experimental Forest and Range, Oregon, USA, 2008–2013. Predictions are shown with 95% confidence intervals and were generated for each focal variable retained in the top model. Distance forest edge = distance (m) to nearest pixel with ≥40% forest canopy cover; NDVI amplitude = normalized difference vegetation index amplitude; canopy = overstory forest canopy cover (0–100%); slope = topographic slope (degrees).

vegetation productivity and open canopy, but these trends were not apparent in the pre-hunt period. Likewise, as slope increased, deer movement decreased during the hunt, but this trend was not apparent in the pre-hunt period. Deer increased nocturnal movement in areas farther from forest edge in both the hunt and pre-hunt periods.

DISCUSSION

The hypothesis that deer would not shift home range patterns, but would alter habitat selection and movement patterns, when human hunters were active was partially supported by our data. We found evidence that female mule deer increased their movements in response to perceived hunting risk, whereas deer site fidelity and habitat selection remained consistent before and during the hunting season. Modifications in movements, but not home range location, suggest that female mule deer movements increased only in areas familiar to deer, and were the primary anti-predator strategies deployed by deer in our system. Our results align with other studies that have found that large ungulates, including non-target animals, increase their movements during the hunting season (Proffitt et al. 2009, Brown et al. 2018). Our results, however, differ from researchers that have reported ungulates will shift their distributions after the onset of hunting (Bonnot et al. 2013, Spitz et al. 2019). Studying movement allows researchers to recognize the underlying behavior by which animals mediate trade-offs in life-history requirements arising from heterogeneous and dynamic habitats (Johnson et al. 1992). Movement rates during hunting season are a suitable metric to quantify responses to risk because they allow for direct fine-scale measurements of distance traveled (Picardi et al. 2019). Greater movement rates can lower predation risk by reducing the probability of encounter, as shown by animals leaving habitat patches when they become risky (Hammond et al. 2007). Alternatively, other researchers reported that lower movement rates can decrease the chance of detection by predators in risky landscapes (Marantz et al. 2016), and less movement can increase chances of survival (Ciuti et al. 2012).

One possible explanation for the discrepancy in results across studies is that the temporal scale of risk during hunting season varies across systems. The length of the hunting season in our study (5 days) exposed deer to a relatively short pulse of perceived risk. The risk allocation hypothesis predicts that the magnitude of indirect effects (per unit time) should decline as exposure to risk is prolonged (Lima and Bednekoff 1999). Thus, deer may be responding to hunters initially by increasing movements during short windows of disturbance but may dampen their response when energetic costs of increased movements begin outweighing the benefits during longer, sustained hunts. Additionally, the increase in movement in areas with higher vegetative productivity suggests that deer might be relinquishing forage opportunities to avoid human disturbance. We also found that daily diurnal movements did not immediately decrease during the post-hunt period, which could signify carry-over effects from the hunting season. Other researchers reported that hunted species will maintain heightened spatial responses during post-hunt periods (Scillitani et al. 2010, Proffitt et al. 2013). If deer maintain high levels of movement activity during longer hunting periods, the added energetic costs have the potential to reduce body fat at a time of year when nutritional

resources are increasingly limited. Inadequate body fat in adult female mule deer can result in reduced reproduction (i.e., pregnancy or fecundity) and increased mortality for animals in poor nutritional condition (Monteith et al. 2013, 2014). Body fat of adult female mule deer at Starkey was low in response to inadequate biomass of important forage species during spring and summer (Merems et al. 2020), which in turn may increase their vulnerability to predation and seasonal stressors such as severe winter conditions (Johnson et al. 2004). Additive loss of body fat during hunting seasons may further magnify this cascading set of problems for the species.

The energetic costs of eluding hunters are likely compounded in scenarios with higher hunter densities and longer hunting seasons than those during our hunts at Starkey. Although hunter densities in our study area were on average similar to those from other deer hunts conducted in the Blue Mountains (0.33 hunters/km^2), some areas have experienced hunter densities >0.50 hunters/km^2 (Oregon Department of Fish and Wildlife 2019). Johnson et al. (2004) reported that elk velocities increased as rifle hunter density increased, and resulted in a 4–10% increase in the normal daily energy budget. In this scenario, hunter densities were substantially higher (0.91 hunters/km^2) than the densities from this study (0.29 hunter/km^2; Table S1), which could be 1 factor influencing the strength of the response. Landscape of fear theory predicts that the level of perceived predation risk is influenced by predator intensity (Bleicher 2017). Thus, we predict that an increase in hunter densities is needed to push female deer to further increase movements and additional hunter densities are required for deer to abandon their ranges.

Although diurnal deer movement rates were generally higher during the hunting season than prior to hunting seasons, they appear to be contained within established use areas. We predicted that deer would exhibit high site fidelity during the hunt versus during pre-hunt periods to avoid interactions with hunters. Although female deer were not under direct predation risk from hunters in our study, based on our indices, it appears they were making the trade-off that remaining within a familiar range was a more efficient strategy to reduce perceived risk than moving to a novel area. The risk allocation hypothesis predicts that individuals in better nutritional condition can afford to be more risk averse, spending energetic reserves to avoid perceived threats. It is possible that the nutritionally limited deer in our study area (Merems et al. 2020) were unable to afford costly movements into novel habitat. Further, abandonment of established home ranges may have additional fitness consequences; survival is lower for deer when they leave their home ranges (Forrester et al. 2015).

One of the assumed benefits of site fidelity is an improved knowledge of the spatial distribution of forage and cover resources (Wolf et al. 2009) and predation risk (Gehr et al. 2020). In our system, maintaining strong site fidelity may not only reduce encounter probabilities with hunters but also from natural predators (e.g., mountain lions). If deer are to take advantage of known habitat, we are more likely to see consistent habitat selection patterns over time. The small size of use areas ($\bar{x} = 3.2$ km^2) that we observed during hunting seasons in our study indicates that deer were acquainted with the seasonal distribution of forage and cover. Deer consistently selected for areas with more cover and higher vegetative productivity during both diurnal and nocturnal periods across pre-hunt and hunt periods. Forest canopy cover is an important habitat component for mule deer during summer (Ager et al. 2003, Eckrich et al. 2020), and other studies have found that ungulates use habitat that provides cover opportunities, such as closed-canopy forests, during the hunting season (Bjørneraas et al. 2011, Bonnot et al. 2013, Lowrey et al. 2020). The lack of change in site fidelity, in conjunction with consistent habitat selection patterns before and during the hunt, suggests that deer are taking advantage of familiar surroundings, including food and cover resources. Thus, including site fidelity metrics has allowed for additional insight into potential risk avoidance strategies. Future work should consider whether this response is being influenced by the nutritional condition of deer going into the hunt in conjunction with fluctuations in hunter densities.

Another important consideration is that the strategies employed by non-target individuals to navigate a risky landscape may differ from individuals that were targeted (Grignolio et al. 2011). Our study evaluated the relative importance of indirect disturbance from hunting on the spatial behavior of female mule deer, a group of animals that have not been legally harvested since 1989 in our study area (Rowland et al. 1997). Female mule deer in other systems have displayed rapid movements in response to anthropogenic disturbance (Lendrum et al. 2013), and human hunters are likely eliciting changes to both hourly and daily movements of deer. Nonetheless, behavioral effects associated with hunting are not limited to target species (Spitz et al. 2019), and little information exists regarding effects of widespread hunting activities on non-target species using the same landscape. Many analyses used to set hunting regulations (e.g., tag limits) still consider only direct effects, whereas indirect effects do not play a prominent role when setting management objectives or goals.

MANAGEMENT IMPLICATIONS

Our work highlights the importance of evaluating effects of hunting on non-target animals, and of considering multiple temporal and spatial scales when studying anti-predator strategies of ungulates. Wildlife management can benefit by considering that movement patterns and habitat selection may be constrained by behavioral traits, such as site fidelity. Wildlife managers should consider altering the number of tags or duration of hunts in areas with high levels of hunter access to minimize indirect effects on mule deer populations, especially in areas where mule deer populations may be nutritionally limited and increased human disturbance could affect population productivity. In areas with high road densities, wildlife managers should work with land managers to implement seasonal restrictions on motorized vehicle use, which should reduce intensity of human

use of these areas and minimize disturbance to mule deer. If responses are consistent across hunts targeting other species (e.g., elk), non-target animals may be subjected to prolonged reduced foraging opportunities and increased movement rates for a substantial portion of the year in some systems. For example, in areas where elk and mule deer co-occur in Oregon, authorized hunting occurs from beginning in late August through mid-November, with minimal breaks between hunts. These sustained levels of human disturbance could have population-level consequences for mule deer and managers should consider these effects when they design and implement hunting seasons.

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