

Variation in the Nutritional Landscape Modulates Sublethal Effects of Competitors and
Predators on Herbivore Fitness

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Authorization to Submit Thesis

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Abstract

In heterogeneous landscapes large herbivores employ plastic behavioral strategies to cope with tradeoffs among environmental variables that influence fitness (e.g., forage availability, predation, and competition). Yet how individual responses to such tradeoffs scale up to influence population performance remains uncertain. Similarly, the degree to which sublethal effects of competitors and predators on herbivore fitness are modulated by variation in the nutritional landscape has not been addressed. Over the past several decades, mule deer (*Odocoileus hemionus*) populations have declined precipitously throughout their historic range in western North America. Competition with elk (*Cervus canadensis*) and predation by mountain lions (*Puma concolor*) are thought to have contributed both directly and indirectly to the decline of mule deer, but the mechanisms underpinning those effects have not been clearly established. We sought to understand (a) whether the risk of encountering competitors (elk) or predators (mountain lions) displaced mule deer from the most favorable parts of the nutritional landscape, (b) whether that displacement translated into effects on early winter body condition (and thus, ostensibly, fitness) of mule deer, and (c) whether the indirect effects of interference competition and predation risk on mule deer condition were modulated by plastic behavioral responses to those risks among individual deer. At the population level mule deer strongly avoided habitats with a high risk of predation, and this behavior was more pronounced during summer than spring. Avoidance of risky habitats also was coincident with either avoidance or indifference to the nutritional landscape during both seasons. Moreover, as risk of predation increased mule deer showed progressively stronger avoidance of the most favorable parts of the nutritional landscape, suggesting that they were forced to make tradeoffs between forage and predation risk. The

influence of competition on mule deer behavior was similar in nature but attenuated relative to the effect of predation risk. One apparent consequence of suboptimal use of the nutritional landscape by mule deer was that nutritional condition (measured as percent ingesta-free body fat) was below reported thresholds for maintaining positive population growth. At the individual level, stronger selection for the nutritional landscape during spring, when forage resources were more evenly distributed and the effects of predation risk on behavior were less pronounced, significantly improved nutritional condition in early winter. Our study is among the first to elucidate the nutritional mechanisms underpinning indirect effects of predation risk and competition on a large herbivore, and our results provide important insights into the drivers of mule deer declines in western North America.

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Dedication

I dedicate this work to the strong women in my family.

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Variation in the nutritional landscape modulates sublethal effects of competitors and predators on herbivore fitness

Introduction

Behavioral plasticity is a key mechanism by which animals buffer themselves against environmental variation, thereby enhancing fitness (Huey et al. 2003, Kearney et al. 2009). For example, by selecting favorable habitats or microclimates animals can regulate their exposure to temperature extremes or other environmental variables (Brandon 1988, Huey et al. 2003, Long et al. 2014). In heterogeneous landscapes, however, free-ranging animals often are forced to make complex tradeoffs (Berger 1991, Barten et al. 2001). For example, habitats that provide abundant, high-quality forage commonly support higher densities of competitors or predators (Berger 1991, Barten et al. 2001, Hurley et al. 2011). An increasing body of evidence suggests that individuals exhibit plastic behavioral strategies for coping with such tradeoffs that are conditioned upon endogenous traits such as age (Montgomery et al. 2013), nutritional condition (Monteith et al. 2011, 2013; Long et al. 2014), or personality (Dall et al. 2004, Stamps and Groothuis 2010). Yet, how responses of individuals to “risk” scale up to influence population performance is only beginning to be explored (MacLeod et al. 2014).

Interference competition, defined here as a direct negative interaction between species via physical, chemical, or behavioral mechanisms (Birch 1957, Park 1962, Case and Gilpin 1974, Keddy 1989), plays a fundamental role in structuring animal communities (Palomares and Caro 1999, Amarasekare 2002, Stewart et al. 2002, Caro and Stoner 2003). Indeed, interference competition often produces strong patterns of avoidance or displacement that can dictate species’ distributions, patterns of resource exploitation, and relative

abundances (Johnson et al. 2000, Linnell and Strand 2000, Amarasekare 2002, Stewart et al. 2002, Berger and Gese 2007, Allstadt et al. 2012). Despite the ubiquity of interference competition in nature, however, fitness consequences of sublethal competitive interactions (e.g., displacement of a subordinate competitor in space or time) are poorly understood. Similarly, the degree to which individuals of a subordinate species are able to mitigate negative consequences of interference competition by adjusting their behavior along a continuum of risk prone (i.e., weaker avoidance of the dominant competitor) to risk averse (i.e., stronger avoidance of the dominant competitor) has received almost no attention.

In contrast to interference competition, sublethal effects of predators on their prey (i.e., shifts in prey behavior, distribution, etc. in response to perceived risk of predation) have received considerable attention, in part because the ecological consequences of such effects are often more pronounced than the consequences of direct mortality from predation (Schmitz et al. 1997, 2004; Werner and Peacor 2003; Preisser et al. 2005; Pearson 2010; Kuijper et al. 2013). Tradeoffs between forage and predation risk can cause animals to avoid high-quality foraging habitats or to adopt inefficient foraging strategies (e.g., Hurley et al. 2011). Moreover, such alterations to herbivore behavior can, in turn, have important knock-on effects for plant and animal communities. For example, Schmitz et al. (1997) demonstrated that carnivores indirectly benefited plants (i.e., increased net productivity) by altering the foraging patterns of herbivores. Similarly, Ford et al. (2014) found that perceived risk of predation altered habitat selection by impala (*Aepyceros melampus*), which subsequently increased the prevalence of thorny trees in “safe” habitats and less-thorny trees in “risky” habitats. Despite ample evidence that herbivores modify their behavior in

response to predation risk, however, the fitness consequences of these adjustments, as well as the mechanisms that underpin them, remain mostly speculative.

In temperate and arctic environments, large terrestrial herbivores exhibit life-history strategies that revolve around seasonal changes in resource availability and the energetic demands imposed by key life-history events (Monteith et al. 2013). These long-lived, iteroparous mammals must accrue sufficient energy and protein reserves during summer to replenish reserves lost over winter, while also meeting the demands of lactation without endangering future survival and reproduction (Bårdsen et al. 2008, 2010; Therrien et al. 2008; Tollefson et al. 2010; Bårdsen and Tveraa 2012). Large herbivores utilize a variety of physiological and behavioral strategies for coping with these tradeoffs (Monteith et al. 2013), and maximizing energy intake during summer is among the most critical (Cook 2002; Cook et al. 2004; Monteith et al. 2013; Long et al. 2014, 2016). Small differences in the ratio of energy intake to expenditure during summer can have “multiplier effects” (White 1983, Cook et al. 2004) on early winter body mass and condition that directly influence survival and reproductive success (Festa-Bianchet et al. 1997, Gaillard et al. 2000, Côté and Festa-Bianchet 2001, Mysterud et al. 2001, Cook et al. 2004, Monteith et al. 2014). Nevertheless, a variety of factors, including interference competition and predation, may limit the ability of herbivores to optimize their use of the nutritional landscape. Under these conditions, differences among individuals in strength of selection for the nutritional landscape likely have important fitness consequences (van Beest and Milner 2013, Long et al. 2016). For example, in large herbivores, where direct competitive interactions are rarely lethal, individuals that procure access to more abundant or higher-quality forage by risking direct interactions with a competitor may enter winter in better condition, thereby increasing the

probability of survival and successful reproduction in the following year. Similarly, individuals that are older or in poor condition may increase energy intake from foraging as winter approaches by utilizing riskier habitats that also provide more abundant or higher-quality forage (e.g., Montgomery et al. 2013).

Over the past several decades, mule deer (*Odocoileus hemionus*) populations have declined precipitously throughout much of their historic range in western North America (Johnson et al. 2000, Manning et al. 2010, Bergman et al. 2015). At the same time, elk (*Cervus canadensis*) populations have remained stable or have increased (Manning et al. 2010). Accordingly, interference competition with elk has been hypothesized to be a leading cause of mule deer population declines. Numerous studies have shown that mule deer strongly avoid elk in space and time (Wisdom and Thomas 1996, Ager et al. 2003, Manning et al. 2010). For example, Johnson et al. (2000) reported that direct competition (i.e., active or passive social interactions) with elk influenced the distribution of mule deer in northeastern Oregon. Similarly, Stewart et al. (2002) reported strong patterns of dietary and habitat separation between mule deer and elk, and that elk movements negatively influenced habitat selection by mule deer. Those authors hypothesized that spatial separation of mule deer and elk was maintained largely by interference competition (Stewart et al. 2002). Nevertheless, neither the fitness consequences of displacement by elk nor the mechanisms that underpin them have been established.

Indirect effects of predators on mule deer behavior also may have contributed to the decline of this species (Salwasser 1979, Lindzey et al. 1997). Mountain lions (*Puma concolor*) are a primary predator of mule deer across much of their range in North America (Iriarte et al. 1990, Ballard et al. 2001, Forrester et al. 2013), and in many areas of the West

mountain lion populations have rebounded from near extirpation in the 19th and early 20th centuries (Lambert et al. 2006). Indeed, some of the highest densities of mountain lions observed in the West have been reported in recent years (Russell et al. 2012, Davidson et al. 2014). Mountain lions are a stalking predator (Hornocker 1970) that relies on concealment to successfully kill prey (Laundré et al. 2010). This hunting mode limits the ability of mule deer to directly detect mountain lions, thus increasing their reliance on indirect cues of predation risk (Preisser et al. 2007, Schmitz 2008). The result is a “landscape of fear” in which the perception of predation risk strongly influences patterns of space use (Laundré and Hernández 2003; Hurley et al. 2011; Laundré et al. 2014). Although this phenomenon has been amply demonstrated in mule deer, the degree to which behavioral responses to predation risk might negatively affect mule deer fitness by reducing energy intake from foraging is unknown.

We sought to understand (a) whether the risk of encountering competitors (elk) or predators (mountain lions) displaced mule deer from the most favorable parts of the nutritional landscape, (b) whether displacement translated into effects on early winter body condition (and thus, ostensibly, fitness) of mule deer, and (c) whether the indirect effects of interference competition and predation risk on mule deer condition were modulated by plastic behavioral responses to those risks among individual deer. To accomplish these objectives we utilized fine-scale data on the nutritional landscape and movements of sympatric mule deer, elk, and mountain lions from one of the longest-running ungulate enclosure experiments in the world, the Starkey Experimental Forest and Range. We hypothesized that mean nutritional condition of mule deer at Starkey during early winter would be below thresholds for maintaining positive population growth (~12.4% ingesta-free

body fat when $\lambda = 1$; Monteith et al. 2014) because (a) elk are excluding mule deer from the highest-quality portions of the nutritional landscape through interference competition, and (b) habitats that provide the most abundant forage often pose the highest risk of predation from mountain lions due to greater availability of concealment cover (Long et al. 2008, 2014), forcing mule deer to make tradeoffs between forage and predation risk. We also hypothesized that suboptimal use of the nutritional landscape by mule deer would be more pronounced during summer than spring because high-quality forage resources are more evenly dispersed, and therefore more easily accessible, during spring. Finally, we hypothesized that nutritional condition of individual deer in early winter would be positively correlated with consistency of selection for the nutritional landscape (i.e., deer that were consistently more “risk-prone” but survived the spring and summer would enter winter in better condition after controlling for the costs of reproduction).

Methods

Study Area

We conducted our study at the Starkey Experimental Forest and Range (hereafter Starkey), situated in the Blue Mountains of northeastern Oregon (45°12'N, 118°3'W), USA, during May–August of 2016 and 2017. Starkey encompasses 10,125 ha of the Wallowa-Whitman National Forest, with elevations ranging from 1,120m to 1,500m. A network of drainages and vegetation communities create a complex and varied foraging landscape at Starkey. Annual precipitation is 510 mm, falling primarily during winter as snow, and the site supports a mosaic of grasslands, wet meadows, shrublands, and coniferous forests (Fig. 1).

Animal capture and handling

We collected data on behavior of female mule deer during spring and summer, and on nutritional condition of a subset of those deer during early winter, using a combination of GPS collars, ultrasonography, and palpation scoring. During mid-November to mid-December, adult female mule deer were baited into wooden panel traps that were dispersed throughout the study area, or were chemically immobilized via darting (1-2 mL of the immobilization cocktail BAM: Butorphanol, Azaperone, and Medetomidine; Miller et al. 2009). Captured individuals were hobbled (unless immobilized, in which case deer were placed in sternal recumbency) and blindfolded to minimize stress. Immobilized deer were reversed with an intramuscular injection of 0.5 mL of Naltrexone and 2-4 mL of Atipamezole. During handling we removed GPS radio collars from the previous year (if necessary), replaced them with new collars (model 4400S and 4500S, or Lotek Wireless Inc., Newmarket, Ontario, Canada or VERTEX Plus, Vectronic Aerospace GmbH, Berlin, Germany; Wisdom et al. 1993), measured body mass with an electronic scale (± 1 kg), measured chest girth, and quantified nutritional condition using the methods of Cook et al. (2001, 2010). GPS collars were programmed to record a location once every 60 minutes throughout most of the following year. We used ultrasonography (E.I. Medical Imaging, Ibex, with a 5-MHz linear transducer) to measure subcutaneous rump fat thickness to the nearest 1 mm (MAXFAT), as well as thickness of the bicep and loin muscles (Bergman et al. 2014, Bishop et al. 2009, Monteith et al. 2011, Tollefson et al. 2011). In addition, a condition score was recorded via palpation of the sacrosciatic ligament (Cook et al. 2010). We combined condition data with data on body mass to estimate total percent ingesta-free body fat using the equations of Cook et al. (2010).

A subset of collared deer were recaptured between January and March, assessed for pregnancy via ultrasonography, and pregnant females were fitted with vaginal implant transmitters (VIT; M3930L, Advanced Telemetry Solutions [ATS], Isanti, MN) to monitor timing of parturition and aide in neonate capture (Monteith et al. 2014, Bishop et al. 2007). Neonates were captured the following spring and were fitted with an expandable very high frequency (VHF) radio collar with a mortality sensor (M4210; Advanced Telemetry Solution, Isanti, MN, USA). We monitored neonates daily for survival during the first two months of life, and weekly thereafter. If mortality occurred, we located the carcass immediately and attempted to identify the cause of death (Walsh 2016).

We captured adult female elk during early winter (December-January) of 2015-2016 by baiting them onto a winter feeding area where they could be manipulated into a squeeze chute. During winter elk were fed a maintenance diet of alfalfa hay until early spring (March-April), when 25-40 adult females were maneuvered into the squeeze chute for processing (Rowland et al. 1997). During processing we collected data on body mass using an electronic scale (± 1 kg) and fitted each individual with a GPS collar (model 4400M, 4500M, or 3300L, Lotek Wireless, Newmarket, Ontario, Canada) programmed to record a location every 30 minutes during the following year.

We captured mountain lions opportunistically during winter using trained hounds. Mountain lion captures were dependent on suitable tracking conditions (i.e., recent snowfall) and were thus restricted to winter months (Nov-Apr). During winter, we searched for fresh mountain lion tracks (i.e., <24 hours old) along roads within our study area. When fresh tracks were located we released trained dogs to track and pursue the mountain lion until it was treed. We did not selectively pursue mountain lions, and dogs were allowed to pursue

tracks made by any individual. Once treed, we chemically immobilized mountain lions via remote injection with a mixture of Ketamine (200mg/mL; Fort Dodge Animal Health, Fort Dodge, IA) and Xylazine (20mg/mL; Rompun®; Bayer, Inc., Shawnee Mission, KS) at a dosage of 0.4mL per 10kg of body mass. When data collection was complete we administered yohimbine (0.125 mg/kg; Yobine®; Lloyd Laboratories, Shenadoah, IA) as an antagonist for the xylazine. We weighed, aged, and sexed immobilized mountain lions, and when possible we extracted the first premolar of adult animals using a dental elevator to determine age via cementum annuli analysis (Trainer and Matson 1988). We also estimated age using evidence from pelage spotting progression (Shaw 1986), tooth wear (Ashman et al. 1983; Shaw 1986), and gum-line recession (Laundré et al. 2000). Mountain lions were classified as subadults (independent females <2 years and males <3 years of age) or adults (females ≥2 years and males ≥3 years of age). Adult mountain lions were fitted with a GPS collar (Lotek 4400S, Lotek IridiumTrack M, or Lotek IridiumTrack M Basic; Lotek Engineering, Newmarket, ON Canada) programmed to record a location every three hours, and we attached a numbered ear tag to uniquely identify each study animal. We monitored individuals continuously until their collar failed, mortality occurred, or the study ended. All animal handling was performed in accordance with protocols approved by the Institutional Animal Care and Use Committees at the University of Idaho (protocol #IACUC-2015-42), University of Nevada-Reno (protocol #IACUC-00565), and the USDA Forest Service, Starkey Experimental Forest (IACUC No. 92-F-0004; protocol #STKY-16-01), and followed the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes and Gannon 2011).

Mapping the nutritional landscape

During spring (May 13-June 30) and summer (July 1-August 15) of 2016–2017, we conducted intensive vegetation sampling to map the nutritional landscape available to mule deer at Starkey. We used the Integrated Landscape Assessment Project (ILAP) potential vegetation layer to stratify Starkey into the following potential vegetation types (PVTs): grassland, ponderosa-pine forest, grand-fir forest, Douglas-fir forest, and grand/subalpine-fir forest. We then selected transect locations for sampling mule deer forage using a stratified random design, wherein the number of transects within each PVT was proportional to the relative area of the PVT within Starkey. We also stratified our sampling by season (spring vs. summer) in each year, and transects did not overlap between seasons or years (i.e., sampling was without replacement). Transects were 100 m long and included five 4x10 m plots centered on the transect line and spaced at 10-m intervals. Each plot contained two 1-m² quadrats, located in opposite corners. We sampled quadrats to quantify forage biomass and plots to quantify nutritional quality of key forage species for mule deer along each transect. We used both published (Damiran 2006; Stewart et al. 2011) and unpublished (provided by R. Cook, L. Shipley and S. Berry) data on mule deer diets in similar ecosystems to identify key forage species for mule deer at Starkey (Appendix A). We then used information on the level of selection of those species in mule deer diets (selected, neutral, or avoided) and in “wet” (grand-fir forest, Douglas-fir forest and grand/subalpine-fir forests) versus “dry” (grassland and ponderosa-pine forests) PVTs to arrive at a final species sampling list for each PVT at Starkey.

We estimated biomass of forage species along each transect using the clip-and-weigh (CW) method (Butler and Wayne 2007) and a double sampling scheme. We started by visually estimating percent cover of each forage species within each 1-m² quadrat along the

transect. We then selected the two most species-rich quadrats for biomass clipping. We clipped all forage species in those two quadrats at ground level, separated them by plant part (e.g., leaves and inflorescences for graminoids and forbs, and leaves and current annual growth for shrubs) and placed them into paper bags for drying. At the end of each day, we placed biomass samples into a forced convection oven to dry at 100°C for 24 hours. At the end of each drying period we removed samples and weighed them using a Mettler platform scale (± 0.1 g). We tallied biomass samples at the end of each season and conducted additional sampling when necessary to ensure that species-specific sample sizes were sufficient ($n \geq 10$) for predicting biomass from cover estimates using simple linear regression. When field sampling was completed, we estimated biomass of forage species in all unclipped quadrats using fitted, species-specific regressions of biomass against percent cover (Bonham 1989).

We quantified nutritional quality of forage along each transect by clipping additional samples within the 4x10 m plots. We used cover estimates from each transect to identify the 10 most abundant selected species and the 10 most abundant neutral species, and we combined all the most abundant avoided species by life form (shrubs, graminoids, forbs). When necessary, species also were separated by plant parts. We placed nutrition samples into paper bags and dried them at 40°C in a forced convection oven for 24 hours; all samples were dried within 24 hours of collection to minimize effects of respiration and fermentation. We aggregated nutrition samples at the PVT level within seasons by combining samples across transects for each species. We then ground composited samples in a Wiley Mill (1-mm screen) and analyzed them for crude protein (CP), neutral detergent fiber (NDF), and acid detergent lignins (ADL; Dairy One Forage Lab, Ithaca, New York).

We obtained additional forage samples for analysis of tannin content at the junction of the spring and summer seasons in 2017. We collected tannin samples opportunistically from each PVT and stored them in a freezer at -18°C. We subsequently freeze-dried those samples for 24 hours, ground them in a Wiley Mill (1-mm screen), and analyzed them for tannin precipitation at the Wildlife Habitat Nutrition Laboratory at Washington State University. We were not able to obtain samples of all forage species for tannin analysis, and thus we utilized published values (Ulappa, 2015, Wagoner 2011, Lopez-Perez 2006) to estimate tannin precipitation for species not sampled in 2017.

We estimated digestible energy (DE) and crude protein (CP) content of each composited forage sample using the summative equations of Robbins et al. (1987 a,b), which integrated our measurements of NDF, ADL, CP and tannins. We combined species-specific estimates of biomass with values of DE and CP from composited forage samples that contained those species to estimate useable forage biomass (relative to critical nutritional thresholds for female mule deer post peak lactation; Wagoner 2011, Parker et al. 1999) at each transect location using the FRESH-Deer model of Hanley et al. (2012). These spatiotemporally explicit estimates of useable biomass (kg/ha) for mule deer served as the basis for our subsequent mapping of the nutritional landscape within seasons and years. We used spatial interpolation in the Geostatistical Analyst extension of ArcGIS to model useable biomass as a continuous response surface (Fig. 3). Ordinary kriging with an exponential correlation structure produced the best-fit model during all four combinations of year and season (best-fit models were based on minimizing the mean and root mean square prediction error; Cressie 1988).

Modeling the probability of use by elk

Numerous studies have quantified patterns of resource selection by elk at Starkey (e.g., Johnson et al. 2000; Coe et al. 2001, 2011; Stewart et al. 2002, Long et al. 2014). Therefore, we selected six variables that were consistently identified as important predictors of elk space use in those studies for inclusion in seasonal resource selection functions (RSFs) for elk: 1) slope; 2) canopy cover; 3) distance to open roads; 4) aspect; 5) distance to cover ($\geq 40\%$ canopy cover); and 6) distance to streams. We employed a use-availability design wherein GPS locations from individual elk represented used locations (coded 1 in our analyses), and randomly generated locations (coded 0 in our analyses; 750 total random locations) were used as an index to habitat availability at the landscape scale (i.e., within the Starkey enclosure). To estimate RSFs we fit generalized linear mixed models with a logit link function and binomial error distribution to the used and random locations for elk (Gillies et al. 2006, Long et al. 2014). We included a random intercept grouped by individual animal to account for autocorrelation among GPS locations within animals (Zuur et al. 2009). We fit separate models for each year and season (four models total), and each model included the six variables demonstrated to be important predictors of elk space use in previous studies at Starkey (Appendix B; Table B1). We then applied those models to the Starkey landscape (after removing variables with $P > 0.15$) to generate maps of predicted probability of use by elk in each year and season (Fig. 3).

Modeling risk of predation

We modeled risk of predation by mountain lions using the methods of Kauffman et al. (2007). We had limited information on locations where mountain lions killed mule deer within Starkey. Consequently, we utilized a larger dataset on mule deer kill sites (i.e., locations where mule deer were killed by mountain lions) collected by Clark et al. (2014) in

the National Forest adjacent to Starkey from 2009–2012 to develop our model of predation risk. Clark et al. (2014) used an algorithm developed by Knopff et al. (2009) to identify potential kill sites from clusters of GPS locations from 25 mountain lions. Potential kills sites were systematically searched for mountain lion kills, and clear evidence of mountain lion predation (e.g., claw or bite marks on hide, puncture marks on skull or neck) or presence in the immediate vicinity (e.g., bed sites, scat, tracks or a cached or covered carcass; Shaw 1977) was required to conclude that a carcass was a mountain lion kill. Prey species was determined by using skeletal, anatomical, and pelage characteristics, and date of the predation event was determined using the date of the first GPS location included in the cluster. We only included mule deer kills sites from spring ($n = 89$) and summer ($n = 91$) in our models of predation risk.

We used conditional logistic regression (Hosmer and Lemeshow 2000) to estimate the relative probability of a mule deer being killed by a mountain lion at any location in the landscape as a function of spatial covariates that ostensibly influenced that probability (Kauffman et al. 2007). We used a matched case-control design in which kill sites (strata) were matched with 100 random control points cast within the boundary of the wildlife management unit that included Starkey, excluding agricultural fields along the boundary where no kill sites were observed. A conditional likelihood function (Kauffman et al. 2007, Eqn. 1) was fit for each stratum (i.e., kill site) to estimate coefficients for the covariates. The resulting model predicted the probability that a location was, in fact, a kill site relative to the control locations. We interpreted fitted coefficients as odds ratios, and the relative probability of a predation event occurring at any location on the landscape was calculated using equation 2 of Kauffman et al. (2007; following Keating and Cherry 2004). We standardized all

covariates (Cade 2015), fit all possible additive combinations of those variables, and used model-averaging to calculate final parameter estimates for each variable from the 90% confidence set of models (Burnham and Anderson 2002). Model-averaged parameter estimates were weighted based on the Akaike weights (w_i) associated with each model (Burnham and Anderson 2002). We also calculated unconditional standard errors (SE ; Burnham and Anderson 2002) for each parameter estimate and concluded that the estimate differed from 0 if its 90% confidence interval (based on the unconditional SE) did not contain 0 (Appendix B; Table B2; Long et al. 2009, 2014). We developed separate models of predation risk for spring and summer using kill site data from each of those two seasons. We evaluated the predictive strength of each seasonal model using k -fold cross-validation (Boyce et al. 2002).

We considered a variety of different covariates in models of predation risk by mountain lions, including patterns of space use by mountain lions themselves, as well as by their two primary prey species (mule deer and elk; Appendix B; Table B2). We quantified patterns of space use by using GPS collar data from mule deer, elk, and mountain lions at Starkey to estimate RSFs for each combination of species and season in 2017, when we had overlapping GPS location data for all three species. Our approach to estimating RSFs for mountain lions and mule deer was identical to the approach described previously for elk (see “Modeling probability of use by elk”), with the exception that RSFs for mountain lions were based only on nighttime GPS locations when lions were most likely to be hunting (Appendix B; Table B2). Predictor variables considered in RSFs for mule deer were: 1) PVT; 2) aspect; 3) slope; 4) elevation 5) distance to roads; and 6) distance to streams. Predictor variables included in RSFs for mountain lions were: 1) aspect; 2) slope; 3) cover of down wood; 4)

canopy cover; 5) distance to streams; and 6) elevation. We applied final RSFs (after back-calculating unstandardized coefficients for each predictor variable with $P < 0.15$) for each species and season to the larger landscape from which our kill site data were obtained to generate spatiotemporally explicit maps of predicted probability of use by mountain lions, mule deer, and elk for inclusion as predictor variables in the predation risk model (Fig. 3; Kauffman et al. 2007).

Use of the nutritional landscape by mule deer

We used RSFs to quantify how strength of selection for the nutritional landscape by mule deer was influenced by the risk of encountering competitors or predators. We used the approach described previously for estimating RSFs for other species (e.g., generalized linear mixed effects model, use-availability design, etc.), but focused this analysis on the following specific predictor variables: 1) the nutritional landscape (i.e., spatiotemporally explicit estimates of usable forage biomass); 2) the “elk use” landscape (i.e., the predicted relative probability of use by elk from the elk RSF); 3) the “predation risk” landscape (i.e., the predicted relative probability that a mountain lion kill would occur at a given location, estimated from the kill-site model); and 4) interactions between the nutritional landscape and the competition and predation risk variables (to quantify whether selection for the nutritional landscape changed as a function of changing risk of encountering competitors or predators). We also included a random slope for the nutritional landscape variable to facilitate subsequent analysis of selection at the individual level (see next paragraph). We standardized all predictor variables prior to model fitting to facilitate direct comparison of model coefficients and to simplify interpretation of interaction terms. Statistical significance was inferred based on $\alpha \leq 0.15$. Prior to model fitting we evaluated each dataset for

collinearity among predictor variables; no variables were removed due to collinearity (all $|r| < 0.45$).

We evaluated how patterns of selection for the nutritional landscape by individual mule deer influenced their condition in early winter using multiple linear regression (Neter et al. 1996). We extracted the conditional, or individual-level, parameter estimates generated by including an uncorrelated random slope for the nutritional landscape (grouped by individual deer) in the generalized linear mixed model used to estimate the population-level RSF. Those conditional slopes represented, for each individual deer, relative strength of selection for the nutritional landscape at mean values of the competition and predation risk landscapes (due to the inclusion of interactions between those variables and the nutritional landscape; Gillies et al. 2006, Wagner et al. 2011, Long et al. 2014). We included the difference in conditional estimates for each deer between spring and summer as a predictor variable in the multiple regression model. This variable quantified consistency of selection for the nutritional landscape by deer throughout the spring and summer; negative values indicated stronger selection during summer than during spring, positive values indicated stronger selection during spring, and values close to 0 indicated that selection was consistent across both seasons. We also included duration of lactation (estimated as the number of days between parturition and either the death of the fawn(s) or the day of capture in early winter if the fawn was still living) as a predictor variable in the model to account for the costs of reproduction. Low recapture success in early winter of both years resulted in a small sample size of individuals that could be included in this analysis ($n = 9$), so we interpret these modeling results with caution.

Results

Estimates of useable forage biomass (kg/ha) were consistently higher in spring than in summer across PVTs, but were highly variable within PVTs (Fig. 2). As a result, differences in usable biomass among PVTs rarely were significant within a season and year (based on overlap of 90% CIs; Fig. 2). Usable forage also was more evenly distributed across the landscape during spring (Fig. 3), suggesting that tradeoffs between forage and competition or predation risk were less likely to occur in that season.

Effects of forage, competition, and risk of predation on mule deer behavior and condition

The interaction between predation risk and the nutritional landscape was negative and significant across all seasons and years (Table 2), indicating that as predation risk increased mule deer showed stronger avoidance of high-quality portions of the nutritional landscape. This suggests that mule deer were, in fact, forced to make a tradeoff between forage and predation risk at Starkey during both spring and summer. Standardized coefficients for the predation \times nutrition interaction term also were considerably higher in summer than spring during both years (Table 2), indicating that the tradeoff between forage and predation risk was more pronounced during summer. In contrast to risk of predation, the interaction between competition and the nutritional landscape was more variable in both sign and significance across seasons and years (Table 2), suggesting that risk of predation had a more marked effect than the risk of encountering elk on use of the nutritional landscape by mule deer. Indeed, during 2017 the competition \times nutrition interaction was positive and significant (the opposite of what we observed for the predation \times nutrition interaction), indicating that in areas with a higher risk of encountering an elk mule deer showed stronger selection for high-quality portions of the nutritional landscape (Table 2).

Similar patterns were evident in the main effects of our model of space use by mule deer (Table 2). The coefficient for predation risk was negative and significant in all seasons and years other than spring, 2017 (Table 2), indicating that at average levels of useable forage biomass mule deer strongly avoided areas with a high risk of predation. Moreover, as further evidence of a tradeoff between forage and predation risk the main effect (i.e., coefficient) for the nutritional landscape was either negative and significant or non-significant across seasons and years. This indicates that at average levels of predation risk and potential competition with elk mule deer did not select the highest-quality portions of the nutritional landscape at any time during our study. The main effect for competition was not significant in spring of either 2016 or 2017, but was positive and significant in both summers, indicating that at average levels of useable forage biomass mule deer were indifferent to elk in spring but selected areas where they had a higher probability of encountering an elk during summer.

Mean (\pm SE) nutritional condition (% ingesta-free body fat) of female mule deer recaptured in early winter was $8.48\% \pm 0.52$. Although our sample size for quantifying early winter condition of deer was small ($n = 9$), this estimate of condition was significantly below the threshold for maintaining positive population growth (i.e., $\lambda > 1$) in mule deer reported by Monteith et al. (2014). Among individual deer in this sample, those that showed stronger selection for the nutritional landscape during spring, when forage resources were more evenly distributed and the effects of predation risk on behavior were less pronounced, significantly improved their condition in early winter (Fig. 4). The effect of lactation on early winter condition was not significant in our multiple regression model ($P = 0.844$), likely

because all but three of the female deer in our early winter sample lost their fawns within 4 weeks of parturition.

Discussion

Many environmental factors with potential to influence fitness of large herbivores are highly variable across space and time, and herbivores often exhibit plastic behavioral strategies for coping with such variation (e.g., Long et al. 2014, 2016). A defining feature of those strategies is the need for females to balance energy invested in current offspring against the probability of surviving to reproduce again (Trivers 1974, Stearns 1992). When faced with a tradeoff between forage acquisition and risk of mortality from predation, long-lived, iteroparous ungulates generally favor their own survival over their ability to store energy reserves for allocation to reproduction (Martin and Festa-Bianchet 2010, Monteith et al. 2013). Thus, the “landscape of fear” (Kauffman et al. 2007, Laundré et al. 2014) can indirectly reduce fitness of large herbivores by limiting their access to high-quality forage and their concomitant ability devote endogenous energy reserves to offspring. Indeed, numerous studies have demonstrated that in ungulates, offspring that are born small have a higher probability of mortality than larger individuals (Festa-Bianchet et al. 1997, Keech et al. 2000, Monteith et al. 2014, Long et al. 2016), highlighting the potential fitness consequences of poor nutrition among maternal females. Our study is among the first, however, to directly link the avoidance of predation risk to sub-optimal use of the nutritional landscape by a large herbivore. Moreover, this indirect effect of predators had important consequences for a declining herbivore population, providing support for our first hypothesis; mean nutritional condition of mule deer in early winter was below the estimated threshold for maintaining positive population growth (Monteith et al. 2014), and only 22% of individuals

in that sample successfully reared a fawn to the time of recapture in early winter (Table 1). Although our sample size for this inference was small, the mule deer population at Starkey was similarly small (estimated at <100 individuals), and assuming a 50:50 sex ratio (harvest is tightly regulated at Starkey and limited to a few male deer each year) our sample likely represented $\geq 20\%$ of the adult female population.

The influence of predation risk on use of the nutritional landscape by mule deer consistently was more pronounced than the influence of competition, suggesting that predators had stronger indirect effects on mule deer than competitors. This observation provides more nuanced support for our first hypothesis in that exclusion of mule deer from the most favorable parts of the nutritional landscape was not equally driven by both competitors and predators. A likely explanation for this result stems from the fact that competition and predation are not equally likely to directly affect fitness. Although mule deer have been shown to strongly avoid elk in space and time (Wisdom and Thomas 1996, Ager et al. 2003, Manning et al. 2010), direct competitive interactions with elk rarely are lethal. Thus, selective pressure to avoid habitats that are used by elk likely is attenuated by the lower probability of a negative fitness consequence (relative to the risk of encountering a mountain lion). Furthermore, in contrast to predation risk, our results suggest that mule deer were not always faced with a tradeoff between forage selection and the probability of encountering an elk, but when a tradeoff did exist (i.e., during summer) mule deer selected habitats that simultaneously provided high-quality forage and had a high probability of use by elk. In other words, mule deer were “risk averse” in response to tradeoffs between forage and predation, but “risk prone” when faced with tradeoffs between forage and competition. These results align with past research by Stewart et al. (2002), who reported significant

overlap in space use between mule deer and elk during summer, and hypothesized that this likely increased the magnitude of both exploitive and interference competition.

Our second hypothesis, that selection for suboptimal habitats by mule deer would be more pronounced in summer than in spring, also was supported. The negative effect of predation risk on space use by mule deer (at average levels of usable forage biomass) was roughly twice as large in summer than spring during 2016, and roughly six times as large in summer than spring during 2017. Similarly, the effect of competition on space use by mule deer (at average levels of usable forage biomass) was statistically significant during summer, but not during spring. As previously discussed, however, this effect was positive in both summers, indicating that mule deer were selecting habitats that also were being used by elk. This seasonal change in behavior was most likely a result of 1) a lower probability that competitive interactions with elk would negatively impact fitness (relative to interactions with predators), and 2) significantly lower availability, and a more clumped distribution, of high-quality forage during summer. Summer is a critical period for capital-breeding large herbivores (Bårdsen et al. 2008, 2010; Therrien et al. 2008; Bårdsen and Tveraa 2012), and small reductions in energy intake can significantly impact early winter body mass and condition (Gaillard et al. 2000, Côté and Festa-Bianchet 2001, Cook et al. 2004, Monteith et al. 2014). Consequently, mule deer likely were more willing to incur the risk of encountering an elk in order to secure access to better forage during summer. This response may have been further amplified by the stronger avoidance of predation risk we observed during summer.

Our analysis of how individual-level responses to the nutritional landscape translated into effects on early winter condition of mule deer suffered from a low sample size, and thus low statistical power. Nevertheless, we detected a significant relationship between

consistency of selection for the nutritional landscape during spring and summer and nutritional condition of mule deer at the onset of winter. The nature of that relationship, however, did not support our third hypothesis. Our results indicated that female mule deer that showed stronger selection for the nutritional landscape during spring, relative to summer, entered winter in better condition. This contrasts not only with our hypothesis, but also with the expectation that if selection during only one season was driving variation in early winter condition, that season should be summer due the increased nutritional limitation typically experienced by temperate large herbivores in summer (Cook et al. 2004). Increased magnitude of the tradeoff between forage and predation risk during summer may provide a plausible explanation for this result. Given that the negative effect of predation risk on use of the nutritional landscape by mule deer was considerably stronger during summer than during spring, individuals that more effectively optimized their use of the nutritional landscape in spring, when high-quality forage resources were abundant and evenly distributed, may have more effectively compensated for the stronger indirect effect of predators during summer. Variation in behavior among individuals also was reduced during summer, when all collared mule deer were strongly avoiding habitats with a high risk of predation. The non-significant effect of lactation also was an unexpected result of this analysis. However, this can likely be explained by the fact that only 3 out of 9 deer in our early winter sample had fawns that survived for >4 weeks, and thus our data encompassed minimal variation in lactation.

An alternative hypothesis for explaining poor condition of female mule deer in early winter is that even the highest-quality forage available at Starkey is insufficient for supporting positive population growth. Critical thresholds of CP and DE for a female mule deer at peak lactation (with one fawn) are 12% CP and 11.5% DE (Wagoner 2011). After

peak lactation those thresholds drop to 8% CP and 9.5% DE (Wagoner 2011). Maximum mean values of CP and DE available in PVTs at Starkey during spring were 12.77% and 11.51%, respectively. During summer, maximum mean CP and DE were 11.77% and 10.98%, respectively, suggesting that at peak lactation mule deer could be limited by both CP and DE. However, mule deer not at peak lactation were unlikely to be limited by either macronutrient in either season. Thus, given that the majority of deer in our early winter sample lost their fawns after only a few weeks, our results are more consistent with the hypothesis that effects of nutrition on early winter condition of mule deer in our study were behaviorally mediated.

Quality, abundance, and distribution of forage resources, which together make up the nutritional landscape, play a critical role in determining the trajectory of populations (Bishop et al. 2009). Previous researchers have hypothesized that inadequate nutrition may be directly (e.g., via habitat change or loss) or indirectly (e.g., via avoidance of competitors or predators) responsible for the decline of many mule deer populations (Cook et al. 2007). Our study sheds important light on the nutritional mechanisms by which competitors and predators can influence condition, and thus fitness, of large herbivores. Our results suggest that indirect (i.e., mediated by changes in how individuals utilized the nutritional landscape) effects of mountain lions on nutritional condition of mule deer have likely contributed to the decline of that species in our study area. More broadly, our work highlights the value of integrating the mechanistic principles of nutritional ecology with the theory and concepts that currently define our understanding of trophic interactions. We propose that an increased focus on understanding the nutritional consequences of individual behaviors could motivate new lines

of inquiry and provide important and novel insights in future studies of the sublethal effects of competitors and predators on herbivores.

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Tables

Table 1. Body mass and condition metrics for female mule deer (*Odocoileus hemionus*) recaptured in early winter 2016 (Nov 22 - Dec 18; n = 5) and 2017 (Dec 1 - Dec 6; n = 4) at the Starkey Experimental Forest and Range, Oregon, USA. Weight, MAXFAT, and rBCS measurements were obtained at the time of capture, and IFBF was calculated using the methods of Cook et al. (2010). The number of fawns was recorded at parturition and again at the time of winter capture (via radio collars affixed to fawns). Duration of lactation was estimated as the number of days between parturition and either the death of the fawn(s) or the day of capture in early winter.

Year	Animal ID	Weight (kg)	MAXFAT (cm)	rBCS	IFBF (%)	Number of fawns at parturition capture	Duration of lactation
2016	060104D01	71.89	0.4	3.50	7.71	2 0	53
2016	110104D01	68.49	0.8	3.50	10.03	1 1	180
2016	141125D01	59.42	0.0	3.00	8.83	1 0	17
2016	131218D01	66.18	0.1	2.25	6.10	1 0	10
2016	131216D02	64.18	0.3	2.50	7.29	1 0	25
2017	060104D01	73.66	1.1	2.00	11.44	2 0	3
2017	120124D01	67.99	0.4	1.75	7.79	2 1	200
2017	141125D01	60.96	0.5	3.00	8.56	1 0	4
2017	131216D03	61.69	0.5	1.60	8.53	1 0	8

rBCS = Body condition score

IFBF = Ingesta-free body fat

Table 2. Standardized parameter estimates (β) and associated standard errors (SE) and P -values from resource selection functions that quantified the influence of usable forage biomass (Nutrition) and the probability of encountering elk (Competition) or being killed by a mountain lion (Predation risk) on space use by female mule deer (*Odocoileus hemionus*) during spring (May 13 – June 30) and summer (July 1 – August 11) of 2016 ($n = 18$) and 2017 ($n = 13$) at the Starkey Experimental Forest and Range, Oregon, USA.

Variable	Spring 2016			Spring 2017			Summer 2016			Summer 2017		
	β	SE	P-value	β	SE	P-value	β	SE	P-value	β	SE	P-value
Intercept	-0.136	0.107	NS	-0.541	0.150	<0.001	-1.065	0.269	< 0.001	-0.570	0.108	< 0.001
Nutrition	-0.036	0.255	NS	-0.499	0.296	0.092	-1.159	0.542	0.033	0.181	0.292	NS
Competition	-0.110	0.100	NS	-0.050	0.115	NS	0.251	0.042	< 0.001	0.153	0.063	0.016
Predation risk	-0.279	0.108	0.010	-0.086	0.073	NS	-0.555	0.109	< 0.001	-0.491	0.218	0.024
Competition x Nutrition	-0.333	0.020	< 0.001	0.089	0.022	<0.001	-0.015	0.023	NS	0.122	0.027	< 0.001
Predation risk x Nutrition	-0.146	0.019	< 0.001	-0.062	0.022	0.005	-0.229	0.030	< 0.001	-0.833	0.054	< 0.001

NS, not significant ($P \geq 0.15$).

Figures

Figure 1. Location of the study area and potential vegetation types at Starkey Experimental Forest and Range, Oregon, USA.

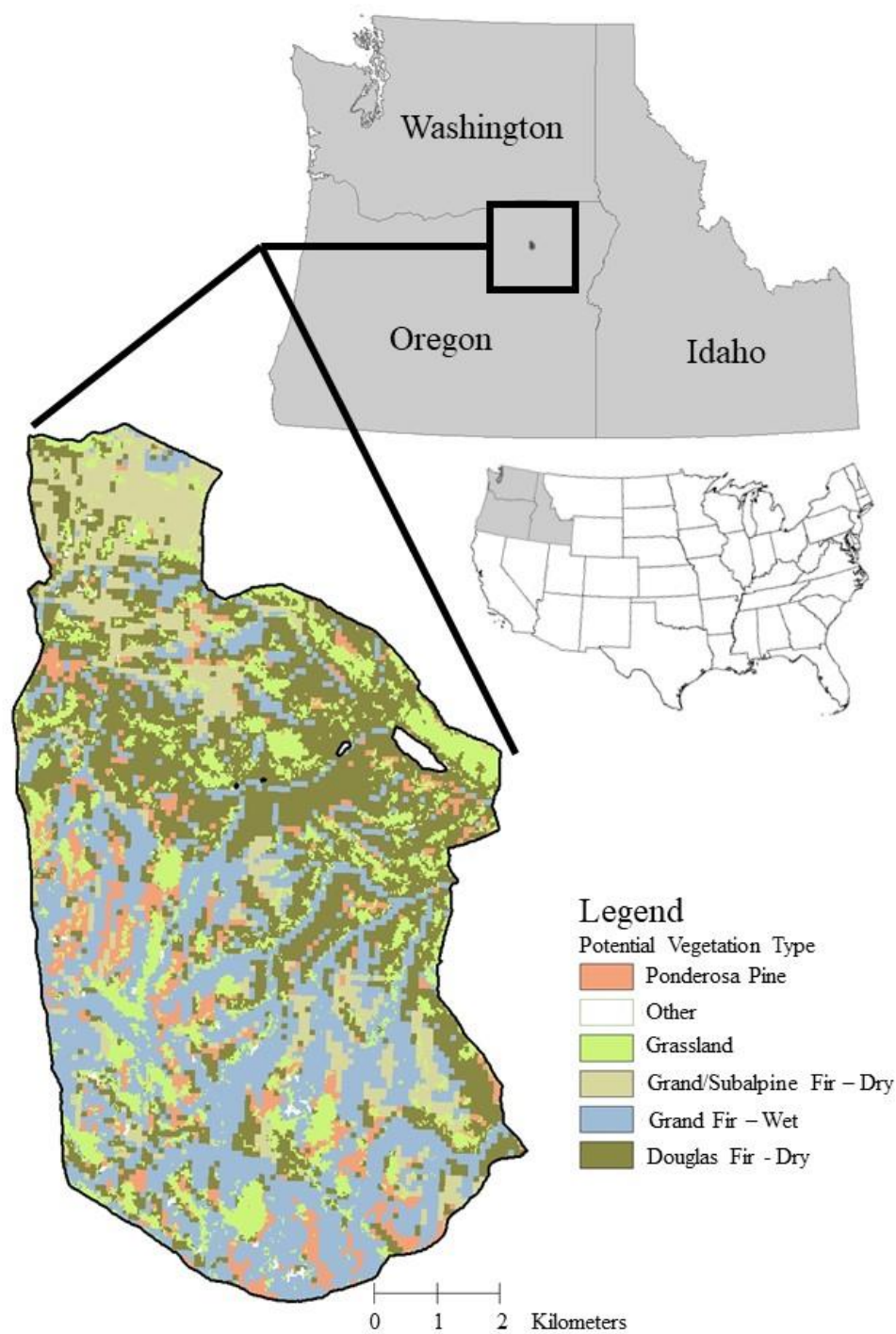


Figure 2. Mean useable biomass (kg/ha) \pm 90% CI for all transects within each potential vegetation type during spring (May 13 – June 30) and summer (July 1 – August 11) of 2016 and 2017 at the Starkey Experimental Forest and Range, Oregon, USA.

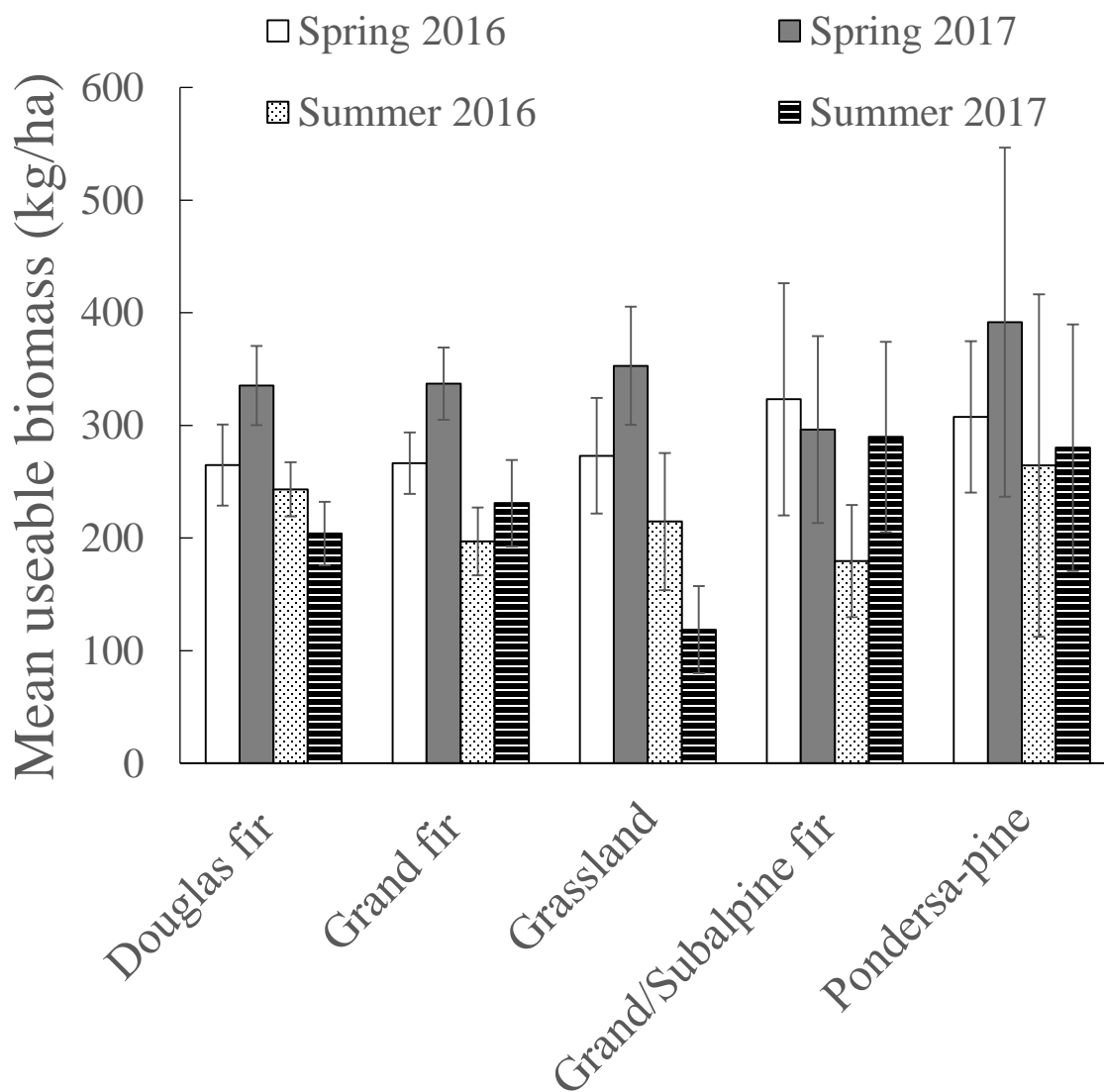


Figure 3. Spatiotemporal variation in the nutritional landscape (usable forage biomass), the competition landscape (predicted probability of use by elk), and the predation risk landscape (predicted probability of being killed by a mountain lion) during spring (May 13 – June 30) and summer (July 1 – August 11) of 2016 and 2017 at the Starkey Experimental Forest and Range, Oregon, USA.

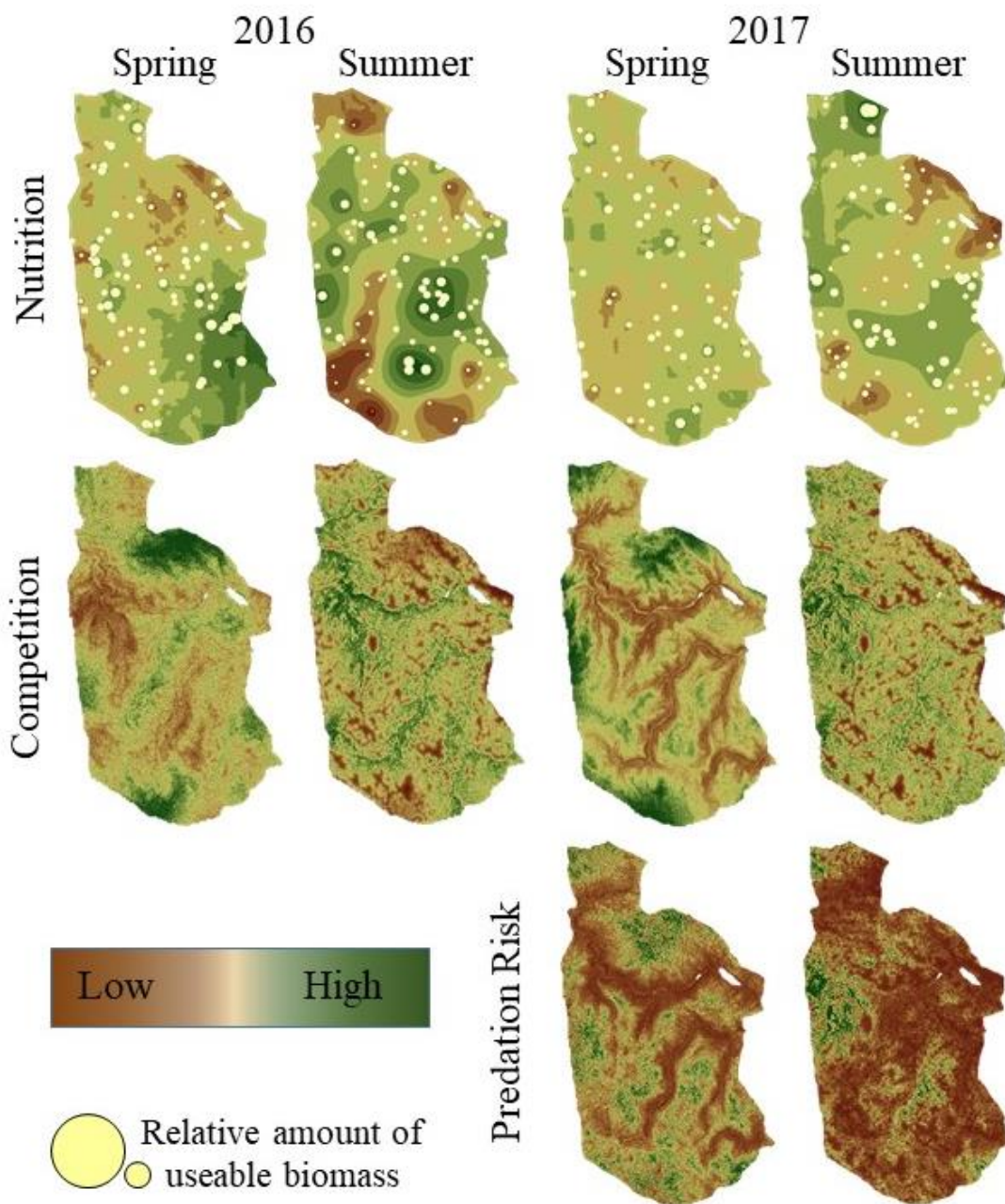
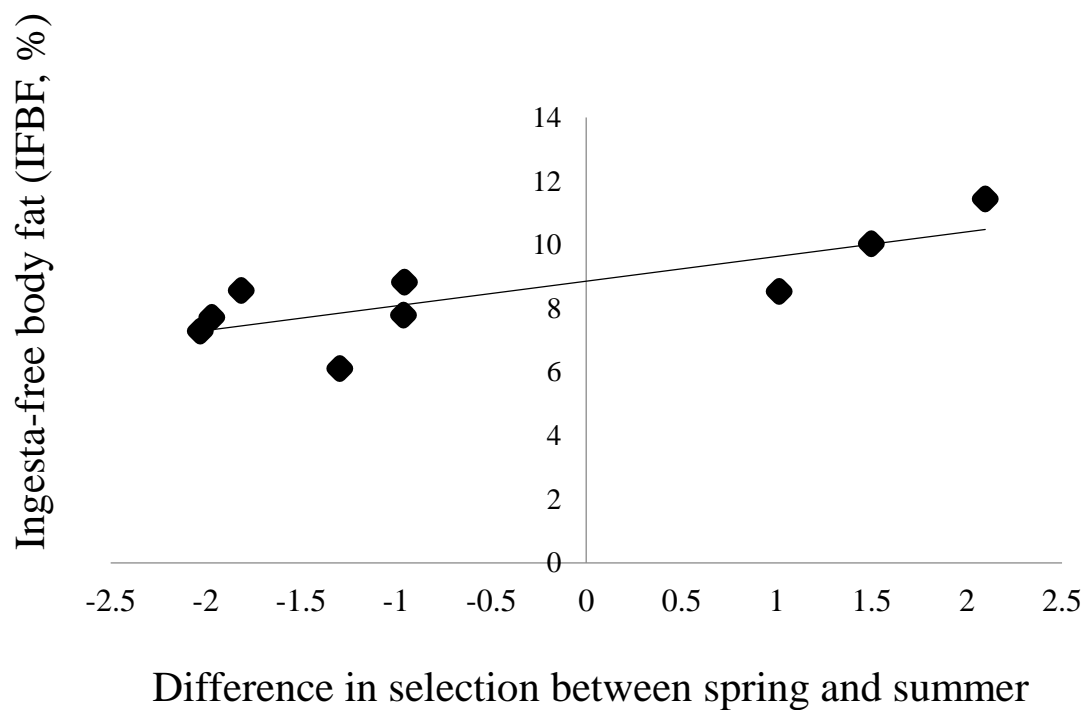


Figure 4. Influence of consistency of selection for the nutritional landscape by female mule deer (*Odocoileus hemionus*; $n = 9$) during spring and summer on nutritional condition (% ingesta-free body fat) in early winter at the Starkey Experimental Forest and Range, Oregon, USA. Negative x-values indicate weaker selection of the nutritional landscape in spring relative to summer, whereas positive x-values indicate stronger selection during summer; an x value of 0 indicates consistent selection across seasons ($R^2 = 0.6304$).



Appendices

Appendix A. List of plant species consumed by mule deer and associated level of selection in various potential vegetation types at the Starkey Experimental Forest and Range, Oregon, USA. Wet habitats included grand-fir forests, Douglas-fir forests and grand/subalpine-fir forests. Dry habitats included grassland and ponderosa-pine forests. Level of selection was based on unpublished data provided by R. Cook, L. Shipley and S. Berry. Taxonomy: The PLANTS Database, USDA, NRCS, 2016 (<http://plants.usda.gov>, accessed 4/1/2016)

Plant code	Family	Scientific name	Common name	Level of selection	
				Wet	Dry
ACGLD4	Aceraceae	<i>Acer glabrum</i>	Douglas Maple	Neutral	-
ACMI2	Asteraceae	<i>Achillea millefolium</i>	Common Yarrow	Avoided	Selected
ADBI	Asteraceae	<i>Adenocaulon bicolor</i>	American trailplant	Selected	-
AGHE2	Asteraceae	<i>Agoseris heterophylla</i>	Annual Agoseris	-	Avoided
AGROSE	Poaceae	<i>Agrostis spp.</i>	Bentgrass	Avoided	-
ALFI	Liliaceae	<i>Allium fibrillum</i>	Cuddy Mountain Onion	Neutral	Avoided
AMAL2	Rosaceae	<i>Amelanchier alnifolia</i>	Saskatoon serviceberry	Selected	Selected
ANAN2	Asteraceae	<i>Antennaria anaphaloides</i>	Pearly pussytoes	Neutral	-
ANLU2	Asteraceae	<i>Antennaria luzuloides</i>	Rush pussytoes	Neutral	Avoided
ANMI3	Asteraceae	<i>Antennaria microphylla</i>	Littleleaf pussytoes	Avoided	-
APAN2	Apocynaceae	<i>Apocynum androsaemifolium</i>	Spreading dogbane	Neutral	Selected
AQFO	Ranunculaceae	<i>Aquilegia formosa</i>	Western columbine	Neutral	-
ARCO9	Asteraceae	<i>Arnica cordifolia</i>	Heartleaf arnica	Selected	Neutral
ARSO2	Asteraceae	<i>Arnica sororia</i>	Twin arnica	Neutral	Neutral
ARUV	Ericaceae	<i>Arctostaphylos uva-ursi</i>	Kinnikinnick	Neutral	-
ASCA11	Fabaceae	<i>Astragalus canadensis</i>	Canadian milkvetch	Neutral	-
ASTER	Asteraceae	<i>Aster spp.</i>	Aster	Neutral	Neutral
BAIN	Asteraceae	<i>Balsamorhiza incana</i>	Hoary balsamroot	-	Neutral
BASA3	Asteraceae	<i>Balsamorhiza sagittata</i>	Arrowleaf balsamroot	-	Neutral
BERU	Scrophulariaceae	<i>Besseyia rubra</i>	Red besseyia	Neutral	Neutral
BRAR5	Poaceae	<i>Bromus arvensis</i>	fied brome	Avoided	Avoided
BRCA5	Poaceae	<i>Bromus carinatus</i>	California brome	Avoided	Neutral
BRIN2	Poaceae	<i>Bromus inermis</i>	Smooth brome	Avoided	-
BRTE	Poaceae	<i>Bromus tectorum</i>	Cheatgrass	Avoided	Avoided
BRVU	Poaceae	<i>Bromus vulgaris</i>	Columbia brome	Neutral	-

CAGE2	Cyperaceae	<i>Carex geyeri</i>	Geye's sedge	Avoided	Neutral
CALOC	Liliaceae	<i>Calochortus</i>	Mariposa lily	Avoided	Avoided
CAQU2	Liliaceae	<i>Camassia quamash</i>	Small camas	Neutral	Neutral
CAREX	Cyperaceae	<i>Carex</i> spp.	Sedge	Avoided	Neutral
CARU	Poaceae	<i>Calamagrostis rubescens</i>	Pinegrass	Avoided	Avoided
CASTI2	Scrophulariaceae	<i>Castilleja</i> spp.	Indian paintbrush	Neutral	-
CEVE	Rhamnaceae	<i>Ceanothus velutinus</i>	Snowbrush ceanothus	Selected	-
CHAN9	Onagraceae	<i>Chamerion angustifolium</i>	Fireweed	Selected	-
CHUM	Pyrolaceae	<i>Chimaphila umbellata</i>	Pipsissewa	Avoided	-
CIRSI	Asteraceae	<i>Cirsium</i> spp.	Thistle	Neutral	-
CLLA2	Portulacaceae	<i>Claytonia lanceolata</i>	Lanceleaf springbeauty	Avoided	Avoided
CLPEP	Portulacaceae	<i>Claytonia perfoliata</i>	Miner's lettuce	Avoided	Neutral
CLPU	Onagraceae	<i>Clarkia pulchella</i>	Pinkfairies	-	Neutral
COLI2	Polemoniaceae	<i>Collomia linearis</i>	Tiny Trumpet	Avoided	Avoided
COPA3	Scrophulariaceae	<i>Collinsia parviflora</i>	Maiden blue eyed Mary	Avoided	Avoided
CYMO2	Orchidaceae	<i>Cypripedium montanum</i>	Mountain lady's slipper	Neutral	-
CYOF	Boraginaceae	<i>Cynoglossum officinale</i>	Gypsyflower	Avoided	-
DAGL	Poaceae	<i>Dactylis glomerata</i>	Orchardgrass	Neutral	-
DAUN	Poaceae	<i>Danthonia unispicata</i>	Onespike danthonia	Selected	Selected
DEEL	Poaceae	<i>Deschampsia elongata</i>	Slender hairgrass	Avoided	-
DELPH	Ranunculaceae	<i>Delphinium</i> spp.	Larkspur	Avoided	Avoided
DIDE	Caryophyllaceae	<i>Dianthus deltoides</i>	Maiden pink	Neutral	Neutral
DODEC	Primulaceae	<i>Dodecatheon</i>	Shootingstar	Avoided	Selected
ELYMU	Poaceae	<i>Elymus</i> spp.	Wildrye	Neutral	-
EPBR3	Onagraceae	<i>Epilobium brachycarpum</i>	Tall annual willowherb	Avoided	Avoided
EPCIG	Onagraceae	<i>Epilobium ciliatum glandulosum</i>	Fringed willowherb	Avoided	-
ERHE2	Polygonaceae	<i>Eriogonum heracleoides</i>	Parsnipflower buckwheat	Selected	Selected
EUCO36	Asteraceae	<i>Eurybia conspicua</i>	Western showy aster	Selected	-
FEID	Poaceae	<i>Festuca idahoensis</i>	Idaho fescue	Selected	Neutral
FEOC	Poaceae	<i>Festuca occidentalis</i>	Western fescue	Avoided	Avoided
FRSP	Gentianaceae	<i>Frasera speciosa</i>	Elkweed	Neutral	-
FRVE	Rosaceae	<i>Fragaria vesca</i>	Woodland strawberry	Avoided	-
FRVI	Rosaceae	<i>Fragaria virginiana</i>	Virginia strawberry	Neutral	Neutral
GAAP2	Rubiaceae	<i>Galium aparine</i>	Stickywilly	Neutral	Avoided
GABO2	Rubiaceae	<i>Galium boreale</i>	Northern bedstraw	Neutral	-
GATR3	Rubiaceae	<i>Galium triflorum</i>	Fragrant bedstraw	Selected	-
GEAF	Gentianaceae	<i>Gentiana affinis</i>	Pleated gentian	Avoided	-
GEMA4	Rosaceae	<i>Geum macrophyllum</i>	Largeleaf avens	Neutral	-
GETR	Rosaceae	<i>Geum triflorum</i>	Old man's whiskers	Selected	Neutral
GEVI2	Geraniaceae	<i>Geranium viscosissimum</i>	Sticky purple geranium	Neutral	-

GOOB2	Orchidaceae	<i>Goodyera oblongifloia</i>	Wester rattlesnake plantain	Selected	-
HEPU6	Hydrophyllaceae	<i>Hesperochiron pumilus</i>	Dwarf hesperochiron	-	Avoided
HEUN	Asteraceae	<i>Helianthella uniflora</i>	Oneflower helianthella	-	Neutral
HIAL	Asteraceae	<i>Hieracium</i> spp.	Hawkweed	Neutral	Selected
HODI	Rosaceae	<i>Holodiscus discolor</i>	Oceanspray	Avoided	Avoided
HYCA4	Hydrophyllaceae	<i>Hydrophyllum capitatum</i>	Ballhead waterleaf	-	Avoided
HYPE	Clusiaceae	<i>Hypericum perforatum</i>	Common St. Johnswort	Neutral	Neutral
JUNCU	Juncaceae	<i>Juncus</i> spp.	Rush	Neutral	Avoided
JURB3	Juncaceae	<i>Juncus brachyphyllus</i>	Tuftedstem rush	-	Neutral
KOMA	Poaceae	<i>Koeleria macrantha</i>	Prairie Junegrass	Neutral	Avoided
LASE	Asteraceae	<i>Lactuca serriola</i>	Prickly lettuce	Avoided	Neutral
LEPID	Brassicaceae	<i>Lepidium</i> spp.	Pepperweed	-	Neutral
LIBO3	Caprifoliaceae	<i>Linnaea borealis</i>	Twinflower	Avoided	-
LIGL2	Saxifragaceae	<i>Lithophragma glabrum</i>	Bulbous woodland-star	Avoided	Avoided
LOAM	Apiaceae	<i>Lomatium ambiguum</i>	Wyeth biscuitroot	-	Selected
LOCI3	Caprifoliaceae	<i>Lonicera ciliosa</i>	Orange honeysuckle	Selected	-
LOMA3	Apiaceae	<i>Lomatium macrocarpum</i>	Bigseed biscuitroot	-	Neutral
LOMAT	Apiaceae	<i>Lomatium</i>	Desertparsley	-	Avoided
LOUT2	Caprifoliaceae	<i>Lonicera utahensis</i>	Utah honeysuckle	Selected	-
LUPIN	Fabaceae	<i>Lupinus</i> spp.	Lupine	Neutral	Neutral
LUZUL	Juncaceae	<i>Luzula</i> spp.	woodrush	Neutral	-
MAGL2	Asteraceae	<i>Madia glomerata</i>	Mountain tarweed	Avoided	Avoided
MARA7	Liliaceae	<i>Maianthemum racemosum</i>	Feathery false lily of the valley	Selected	-
MARE11	Berberidaceae	<i>Mahonia repens</i>	Creeping barberry	Neutral	Neutral
MAST4	Liliaceae	<i>Maianthemum stellatum</i>	Starry false lily of the valley	Selected	-
MICRO6	Asteraceae	<i>Microseris</i> spp.	Silverpuffs	Avoided	Avoided
MIST3	Saxifragaceae	<i>Mitella stauropetala</i>	Smallflower miterwort	Neutral	-
MOMA3	Caryophyllaceae	<i>Moehringia macrophylla</i>	Largeleaf sandwort	Avoided	-
OLDOD	Iridaceae	<i>Olsynium douglasii</i>	Douglas' grasswidow	Neutral	-
ORSE	Pyrolaceae	<i>Orthilia secunda</i>	Sidebells wintergreen	Avoided	Avoided
ORTH	Asteraceae	<i>Orochaenactis thysanocarpa</i>	California mountainpincushion	-	Avoided
OSBE	Apiaceae	<i>Osmorhiza berteroi</i>	Sweetcicely	Avoided	-
PAMY	Celastraceae	<i>Paxistima myrsinites</i>	Oregon boxleaf	Neutral	-
PEGA	Scrophulariaceae	<i>Penstemon gairdneri</i>	Gairdner's beardtongue	Avoided	Avoided
PENST	Scrophulariaceae	<i>Penstemon</i> spp.	Beardtongue	Neutral	-
PHMA5	Rosaceae	<i>Physocarpus malvaceus</i>	Mallow ninebark	Avoided	-
PHPR3	Poaceae	<i>Phleum pratense</i>	Timothy	Neutral	Neutral
POA	Poaceae	<i>Poa</i> spp.	Bluegrass	Avoided	-
POBU	Poaceae	<i>Poa bulbosa</i>	Bulbous bluegrass	Neutral	Neutral

PODO4	Polygonaceae	<i>Polygonum douglasii</i>	Douglas' knotweed	Avoided	Avoided
POGL9	Rosaceae	<i>Potentilla glandulosa</i>	Sticky cinquefoil	Neutral	Selected
POGR9	Rosaceae	<i>Potentilla gracilis</i>	Slender cinquefoil	Neutral	Selected
POPA2	Poaceae	<i>Poa palustris</i>	Fowl bluegrass	Avoided	-
POPR	Poaceae	<i>Poa pratensis</i>	Kentucky bluegrass	Avoided	Neutral
PORE5	Rosaceae	<i>Potentilla recta</i>	Sulphur cinquefoil	-	Neutral
POSE	Poaceae	<i>Poa secunda</i>	Sandberg bluegrass	Neutral	Neutral
PRHOH	Liliaceae	<i>Prosartes hookeri</i>	Drops-of-gold	Selected	-
PRVU	Lamiaceae	<i>Prunella vulgaris</i>	Common selfheal	Neutral	-
PSSPS	Poaceae	<i>Pseudoroegneria spicata</i>	Bluebunch wheatgrass	Selected	Avoided
RAGL	Ranunculaceae	<i>Panunculus glaberrimus</i>	Sagebrush buttercup	Avoided	Avoided
RICEC2	Grossulariaceae	<i>Ribes cereum</i>	Wax currant	Avoided	-
RILA	Grossulariaceae	<i>Ribes lacustre</i>	Prickly currant	Neutral	-
RIVI3	Grossulariaceae	<i>Ribes viscosissimum</i>	Sticky currant	Selected	-
ROGY	Rosaceae	<i>Rosa gymnocarpa</i>	Dwarf rose	Selected	Selected
RUAC3	Polygonaceae	<i>Rumex acetosella</i>	Common sheep sorrel	Avoided	Neutral
RUPA	Rosaceae	<i>Rubus parviflorus</i>	Thimbleberry	Selected	-
SAAN2	Rosaceae	<i>Sanguisorba annua</i>	Prairie burnet	Neutral	Neutral
SARH2	Saxifragaceae	<i>Saxifraga rhomboidea</i>	Diamondleaf saxifrage	-	Avoided
SEDUM	Crassulaceae	<i>Sedum spp.</i>	Stonecrop	Avoided	Avoided
SEIN2	Asteraceae	<i>Senecio integerrimus</i>	Lambstongue ragwort	Selected	Neutral
SIOR	Malvaceae	<i>Sidalcea oregana</i>	Oregon checkerbloom	Neutral	Neutral
SOMI2	Asteraceae	<i>Solidago missouriensis</i>	Missouri goldenrod	Neutral	-
SOSC2	Rosaceae	<i>Sorbus scopulina</i>	Greene's mountain ash	Selected	-
SPBEL	Rosaceae	<i>Spiraea lucida</i>	Shinyleaf spirea	Selected	Selected
STIPA	Poaceae	<i>Stipa spp.</i>	Stipa	Avoided	Neutral
SYAL	Caprifoliaceae	<i>Symphoricarpos albus</i>	Common snowberry	Selected	Neutral
TAOF	Asteraceae	<i>Taraxacum officinale</i>	Common dandelion	Selected	Neutral
THMO6	Fabaceae	<i>Thermopsis montana</i>	Mountain goldenbanner	Avoided	-
THOC	Ranunculaceae	<i>Thalictrum occidentale</i>	Western meadow-rue	Neutral	-
TRCA21	Poaceae	<i>Trisetum canescens</i>	Tall trisetum	Neutral	-
TRGR7	Liliaceae	<i>Triteleia grandiflora</i>	Largeflower triteleia	Avoided	Avoided
TRIFO	Fabaceae	<i>Trifolium spp.</i>	Clover	Selected	-
VAMEGL	Ericaceae	<i>Vaccinium spp.</i>	Huckleberry	Neutral	-
VECA2	Liliaceae	<i>Veratrum californicum</i>	California false hellebore	Neutral	-
VEDU	Poaceae	<i>Ventenata dubia</i>	North Africa grass	-	Avoided
VESEH2	Scrophulariaceae	<i>Veronica serpyllifolia</i>	Brightblue speedwell	Avoided	-
VIOLA	Violaceae	<i>Viola spp.</i>	Violet	Selected	-
ZIGAD	Liliaceae	<i>Zigadenus spp.</i>	Deathcamas	-	Neutral

Appendix B. Detailed results of models used to predict the relative probability of use by elk (competition landscape) and the relative probability of a mule deer being killed by a mountain lion (predation risk landscape) at each pixel within the Starkey Experimental Forest and Range, Oregon, USA

Patterns of space use by elk varied across seasons and years with much of the variation occurring in spring (Table B1). Across all models, the parameter estimates indicated selection for moderate to steep slopes with north to northeasterly aspects away from open roads, with the exception of spring 2016, where gentler slopes close to open roads were selected. Elk selected habitats that provided a moderate to high degree of cover and that were closer to areas with $\geq 40\%$ cover with one exception (spring 2017), where the opposite pattern was observed. Elk consistently selected habitats further from streams in spring when water was more readily available on the landscape, and habitats closer to streams in summer when water was more limiting (Table B1).

In spring, mountain lions selected habitats with moderate to steep slopes and moderate to high cover of the tree canopy and of down wood, in contrast to summer, when they selected lower elevation habitats close to streams. We used modeling averaging to produce the best fit model, which included the three species-specific (elk, mule deer, and mountain lions; Table B2) RSFs as predictor variables. In spring, the predicted relative probability of a kill increased in habitats that were less likely to be selected by mule deer or elk, and on gentle to moderate slopes with northeasterly aspects. However, in summer the predicted relative probability of a kill increased in habitats that were more likely to be selected by elk but avoided by mule deer (Table B2). During both seasons, the predicted

relative probability of a kill increased further from streams and higher densities roads, and with low to moderate cover of down wood (Table B2).

Table B1. Standardized parameter estimates (β) and associated standard errors (SE) and P -values from models of resource selection by elk (*Cervus canadensis*) at the Starkey Experimental Forest and Range, Oregon, USA during spring (May 13 – June 30) and summer (July 1 – August 11) of 2016 ($n = 34$) and 2017 ($n = 27$).

Variable	Spring 2016			Summer 2016			Spring 2017			Summer 2017		
	β	SE	P-value	β	SE	P-value	β	SE	P-value	β	SE	P-value
Intercept	1.041	0.033	< 0.001	0.912	0.030	< 0.001	0.866	0.128	< 0.001	0.864	0.034	< 0.001
Sin aspect	0.047	0.007	< 0.001	0.043	0.008	< 0.001	0.052	0.008	< 0.001	0.050	0.009	< 0.001
Cos aspect	0.053	0.007	< 0.001	0.044	0.008	< 0.001	0.053	0.009	< 0.001	0.058	0.009	< 0.001
Slope	0.057	0.008	< 0.001	-0.034	0.009	< 0.001	-0.164	0.009	< 0.001	-0.110	0.010	< 0.001
Canopy cover	0.034	0.009	< 0.001	0.087	0.009	< 0.001	-0.001	0.010	NS	0.055	0.011	< 0.001
Distance to open roads	-0.100	0.008	< 0.001	0.072	0.009	< 0.001	0.055	0.009	< 0.001	0.120	0.010	< 0.001
Distance to streams	0.139	0.008	< 0.001	-0.179	0.008	< 0.001	0.197	0.010	< 0.001	-0.060	0.009	< 0.001
Distance to cover ($\geq 40\%$)	-0.024	0.008	0.004	-0.254	0.009	< 0.001	0.034	0.009	< 0.001	-0.357	0.010	< 0.001

NS, not significant ($P \geq 0.15$)

Table B2. Model-averaged standardized parameter estimates and 90% confidence intervals from models used to estimate the probability of occurrence of mountain lion-killed mule deer at the Starkey Experimental Forest and Range, Oregon, USA.

Variable	Spring				Summer			
	β	SE	90% CI		β	SE	90% CI	
			Low	High			Low	High
Elevation	-0.036	0.157	-0.295	0.222	-0.046	0.172	-0.33	0.237
Sine Aspect	0.271	0.135	0.049	0.492	-0.097	0.112	-0.282	0.088
Cosine Aspect	0.142	0.135	-0.081	0.364	3E-05	0.124	-0.203	0.204
Road density (m/km ²)	0.243	0.135	0.021	0.465	0.367	0.075	0.244	0.491
Distance to streams	1.190	0.387	0.553	1.826	0.398	0.163	0.131	0.666
Cover of down wood	-0.331	0.211	-0.678	0.016	-0.321	0.175	-0.608	-0.034
Slope	-1.012	0.421	-1.705	-0.320	0.423	0.314	-0.094	0.939
Deer RSF ^{a,b}	-0.435	0.192	-0.751	-0.119	-0.330	0.228	-0.705	0.045
Elk RSF ^{c,d}	-1.305	0.489	-2.109	-0.500	0.912	0.255	0.493	1.332
Mt. Lion RSF ^{e,f}	0.246	0.382	-0.383	0.874	0.316	0.221	-0.047	0.678

NS, not significant ($P \geq 0.15$).

^aDeer RSF (spring) = $\exp(-0.0126\text{slope} - 0.0009\text{distance to open roads} + 0.0002\text{distance to streams} - 0.0012\text{elevation} - 0.3138\text{Grand} - 0.4556\text{Grand/Sub} - 0.5686\text{Grass} + 0.0000\text{Douglas} + 0.1390\text{Ponderosa})$.

^bDeer RSF (summer) = $\exp(0.0563\text{cosine aspect} - 0.0273\text{slope} - 0.0005\text{distance to open roads} - 0.0006\text{distance to streams} + 0.0065\text{Grand} + 0.2237\text{Grand/Sub} - 1.0120\text{Grass} + 0.0000\text{Douglas} + 0.0895\text{Ponderosa})$.

^cElk RSF (spring) = $\exp(0.074\text{sine aspect} + 0.076\text{cose aspect} - 0.023\text{slope} + 0.000\text{distance to open roads} + 0.000\text{distance to streams} + 0.000\text{distance to cover})$.

^dElk RSF (summer) = $\exp(0.0710\text{sine aspect} + 0.0822\text{cosine aspect} - 0.0149\text{slope} + 0.0002\text{distance to open roads} - 0.0001\text{distance to streams} - 0.0108\text{distance to cover} + 0.0028\text{canopy cover})$.

^eMt. Lion RSF (spring) = $\exp(0.0642\text{slope} + 0.0068\text{canopy cover} + 0.0923\text{cover of down wood})$.

^fMt. Lion RSF (summer) = $\exp(0.0442\text{slope} - 0.0016\text{elevation} - 0.0006\text{distance to streams} + 0.0163\text{canopy cover} + 0.1080\text{cover of down wood})$.