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Resource selection of mule deer in a shrub-steppe ecosystem: influence of woodland distribution and animal behavior

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Abstract. Ungulates inhabiting arid ecosystems are reliant on productive forb and shrub communities during summer months to meet nutritional demands for survival and reproduction. In the western United States, expansion of woodland vegetation into shrub-dominated communities and the potential loss of habitat are of concern with regard to animal populations reliant on robust sagebrush shrub and forb vegetation. We used mixed-effects logistic regression to model resource selection of female mule deer (*Odocoileus hemionus*) during the summers of 2005–2008. We considered selection at two spatial scales, and during three daily activity periods (night, crepuscular, and mid-day) corresponding to resting and foraging. We evaluated habitat variables related to vegetation type, site productivity, terrain attributes, and fine-scale abundance of pinyon–juniper cover. Those attributes allowed us to account for variation in site productivity and animal behaviors that could obscure the true relationship between density of pinyon–juniper woodland and habitat use by mule deer. We detected observable differences in habitat use by mule deer among the three activity periods with significant differences in movement rates. Deer were most active during crepuscular periods corresponding with foraging activity, and least active mid-day when temperatures were highest. Summer habitat consisted of sites with high potential productivity, greater shrub abundance, and greater proximity to riparian areas. Deer avoided high levels of tree cover (>40% coverage) at all spatial and temporal scales, and in general selection declined with increasing pinyon–juniper cover, particularly during foraging periods. Nonetheless, mule deer selected areas with low to intermediate tree cover (10% to 40%) during resting periods and avoided areas of productive shrub and forb vegetation and riparian areas, when surrounded by denser stands of pinyon–juniper cover. These results emphasize the importance of productive shrub and forb vegetation to mule deer inhabiting semi-arid regions and suggest that low levels of tree cover are beneficial, especially during resting periods. Nevertheless, dense pinyon–juniper cover was generally avoided even in areas of high site productivity. These relationships lend support to the concern that increases in large, dense stands of pinyon–juniper reduce availability of summer habitat and alter patterns of resource selection for mule deer, a shrub-dependent ungulate.

Key words: arid ecosystems; foraging; forest succession; Great Basin; mixed-effects models; movement rates; mule deer; *Odocoileus hemionus;* pinyon–juniper woodland; resource selection; ungulate; White Mountains.

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INTRODUCTION

Vegetation changes have the potential to influence animal populations through shifts in dominant plant communities, loss of important forage, or changes in structural components of habitat. Understanding the spatial ecology of animal populations can assist in prioritizing areas for habitat management or conservation and help to identify critical or limiting resources. Medium-bodied herbivores, such as mule deer (*Odocoileus hemionus*), are particularly sensitive to landscape structure and vegetation characteristics, particularly in semi-arid environments when resources are scarce and distribution of forage is highly variable (Bergman et al. 2014*b*, Monteith et al. 2014, Owen-Smith 2014). Additionally, resource availability and structural components of habitat—through their effects on individual body condition, survival, and reproduction—have direct consequences on population dynamics (Bender et al. 2007, Forrester and Wittmer 2013, Monteith et al. 2014, Shallow et al. 2015). Given the potential for habitat composition to influence population demographics, understanding how animals use landscape features in heterogeneous landscapes is critically important to identifying current resource use and predicting future effects of landscape change on species distributions.

Much research on the effects of successional dynamics and disturbance ecology on animals has focused on wildlife populations in forested environments (Kie and Czech 2000, Stephenson et al. 2006); however, semi-arid regions have also experienced shifts in vegetation coincident with the expansion of woody plants (Archer et al. 1995, Romme et al. 2009). Expansion of woodland into shrub and grassland ecosystems has become an issue of concern worldwide (Bokdam and Gleichman 2000, Van Auken 2000, Buitenwerf et al. 2012). Trees are able to out-compete shrubs and herbaceous plants for light, soil nutrients, and water, dramatically reducing vigor and productivity of shrub and forb communities and cause declines in understory biomass, particularly in semi-arid regions (Everett and Ward 1984, Pieper 1990, Wrobleski and Kauffman 2003). Over the past century, certain regions within the western United States have experienced an increase in the distribution and density of pinyon pine (*Pinus* spp.) and juniper (*Juniperus* spp.) woodlands (hereafter pinyon–juniper), with the greatest increases during the late 1800s and early 1900s (Miller and Wigand 1994, Romme et al. 2009). The result of this increase is evident today as those trees become larger and dominate the overstory with concomitant losses of herbaceous vegetation (Tausch et al. 1981).

Historically, pinyon–juniper woodlands occupied mid-elevations (2100–2300 m), but recent expansion and infilling has extended their distribution upward to steep mountain slopes, and downward onto alluvial fans and grasslands (Tausch et al. 1981, Tausch and West 1988, Weisberg et al. 2007). That expansion also has encroached into adjacent aspen, riparian, and shrub-steppe communities (Miller and Wigand 1994) with higher rates of infilling in more mesic sites (Weisberg et al. 2007, Jacobs 2011). Research in southwest Oregon identified an 80% decline in sagebrush cover with a 50% increase in juniper, and with additional loss of herbaceous species (Miller et al. 2000). Long lateral roots of pinyon and juniper allow those species to capitalize on water resources, and both may have a competitive advantage over species with shallow root systems such as forbs and grasses (Breshears et al. 1997). In arid environments, riparian and mesic sites that are dominated by forb and shrub communities tend to be the most productive and critically important to wildlife (Marshal et al. 2006, Atamian et al. 2010). Transition from plant communities dominated by broadleaved shrubs and forbs to conifer-dominated woodlands can have consequences for animal populations that rely on robust shrub communities to provide forage resources, thermal cover, and refuge from predators, among which are mule deer (*Odocoileus hemionus,* Bender et al. 2007), sage grouse (*Centrocercus urophasianus*, Blomberg et al. 2012), and pygmy rabbits (*Brachylagus idahoensis*, Larrucea and Brussard 2008).

Strong relationships exist for large herbivores among summer resource availability, nutritional condition of females, and recruitment of young, particularly in arid and semi-arid environments (Pettorelli et al. 2003, Stewart et al. 2005, Parker et al. 2009, Monteith et al. 2014). Adult females, in particular, are reliant on productive forb and shrub communities during summer months to meet the high energetic demands of lactation as well as for accumulating energy stores for winter (Parker et al. 2009, Tollefson et al. 2010). Declines in understory vegetation with increasing cover of conifer woodlands can negatively affect ungulates through reductions in nutritional condition thereby causing reductions in pregnancy rates, and survival of young (Verme and Ullrey 1984, Clements and Young 1997, Bender et al. 2007, Shallow et al. 2015). A study of mule deer in New Mexico identified a strong, negative correlation between body condition of females and amounts of pinyon–juniper woodland within an individual's home range, and estimated pinyon–juniper woodland to contain limited ground cover of preferred forbs and shrubs (Bender et al. 2007). Recent studies in Colorado have identified increases in both body condition (ingesta-free body fat) of adult mule deer and increased survival of young in areas with mechanical and chemical treatments to remove pinyon–juniper woodland (Bergman et al. 2014*a*, *b*). These studies indicate that pinyon–juniper woodland provides limited forage benefits to mule deer. Therefore, mule deer are likely a good indicator of changes in habitat quality and ecosystem health in arid and semi-arid environments (Loft and Bleich 2014), in part because they have sufficiently large home ranges to integrate spatial patterns across landscapes (Kie et al. 2003), making them sensitive to landscape-level processes such as conifer encroachment or loss of productive habitat.

Mule deer inhabiting the Great Basin are wide-ranging and dependent on healthy sagebrush shrub communities (Clements and Young 1997). We used a population of mule deer in the Great Basin ecosystem in the western United States as a model ecosystem to examine the relationship between woodland structure and resource selection by this shrub-dependent herbivore. We evaluated summer resource selection by female mule deer as a function of varying densities of pinyon–juniper cover. We were particularly interested in accounting for variation in site productivity and animal behaviors, related to resting or foraging activity periods that could obscure the true relationship between density of pinyon–juniper and habitat use. Gradients in site productivity, which are driven largely by variation in elevation, precipitation, aspect, and soil composition, influence forage abundance and quality within plant communities, and the ability to detect animal responses to pinyon–juniper cover may be influenced by this underlying variation. Thus, incorporating measures of site productivity and indices of forage abundance into models of resource selection are necessary to understand habitat relationships. Additionally, there may be some benefit of pinyon–juniper cover for predator avoidance or for thermal cover during summer. High ambient temperatures during summer can exert greater thermoregulatory stress on individuals and influence decisions on habitat use and movement patterns (Long et al. 2014). As a result, canopy cover can provide important microclimate conditions or thermal cover (Bleich et al. 1996, Giotto et al. 2013) that might be selected during resting periods, but avoided while foraging.

We hypothesized that site productivity and vegetation composition influence selection of resources by mule deer and that those relationships would vary relative to activity periods, coincident with foraging, or for resting. Accordingly, we predicted that mule deer would maximize nutrient intake by avoiding areas of low site productivity (as measured by potential for plant growth irrespective of the plant community) and that site productivity would interact with vegetation composition to influence selection. Additionally, given the inverse relationship between overstory cover of pinyon–juniper woodlands and understory biomass, we predicted that mule deer would avoid areas of high pinyon–juniper cover. Moreover, we predicted that the presence of high pinyon–juniper cover would make areas with otherwise preferred vegetation types less desirable. Further, we hypothesized that use of pinyon–juniper woodland by mule deer would vary by activity, foraging or resting. Consistent with our first hypothesis, we predicted that mule deer would more strongly avoid pinyon–juniper during foraging periods. Conversely, we predicted that during resting periods mule deer would select areas of low-to-moderate amounts of pinyon–juniper woodland, possibly for thermal cover to reduce heat stress mid-day or to avoid predators.

METHODS

Study area

The White Mountains are located in Esmeralda County in Nevada, and Inyo and Mono counties in California, northeast of Bishop, California (37.4°N, 118.5°W). Our study area extended approximately 80 km along the eastern side of the mountain range from Deep Springs Valley north to Montgomery Pass (Fig. 1). The White Mountains rise in elevation over a distance of 20 km from their base in Fish Lake Valley at 1400 m to their crest at elevations largely between 3000 and 4000 m, reaching their maximum elevation of about 4300 m at White Mountain Peak, the highest point in the range (Hall 1991). The White Mountains are strongly influenced by the rain shadow of the Sierra Nevada, resulting in low precipitation for their size and elevation. Average precipitation for this region was between 12.7 cm along lower elevations and 50.8 cm at highest elevations (Hall 1991) with the majority of precipitation falling during the winter months, making the White Mountains representative of the many semi-arid mountain ranges within the Great Basin. Within the Great Basin, expansion and infilling by pinyon–juniper woodland has resulted in large stands of closed canopy pinyon–juniper habitat at mid-elevations

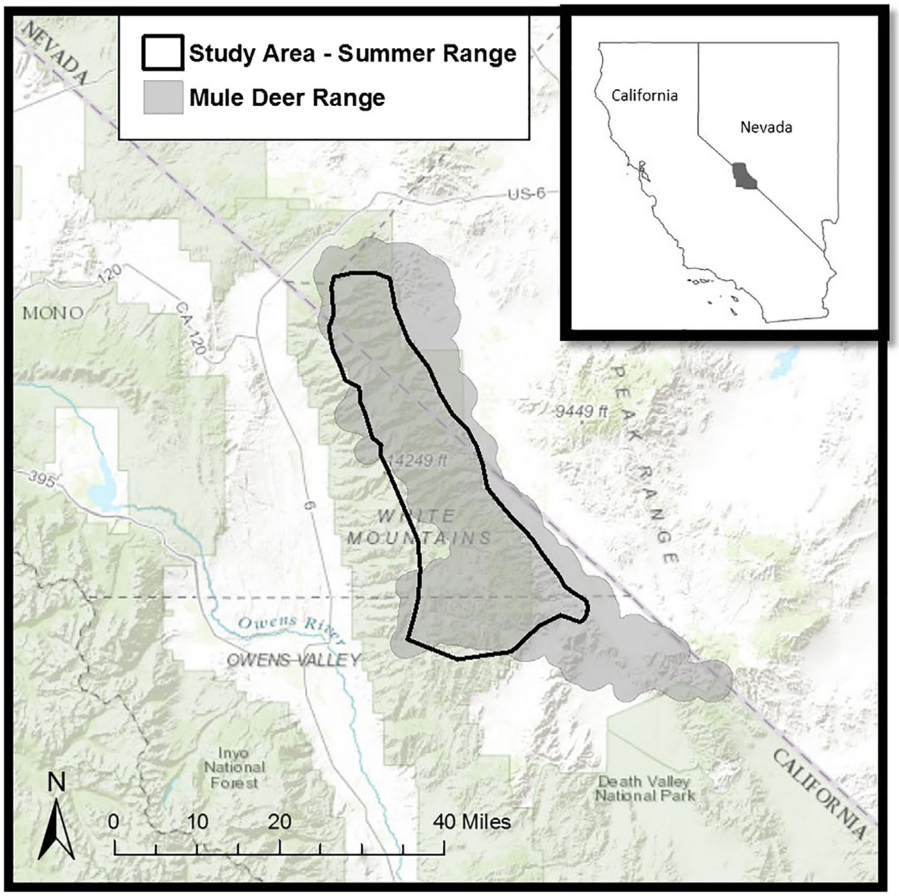

Fig. 1. Study area in White Mountains of eastern California and western Nevada, USA. Mule deer range occurred primarily on the eastern side of the mountains with summer range extending between 2900 and 4000 m and deer using lower elevations during the winter months. Seasonal ranges were delineated from home range information from GPS-collared individuals, VHF locations, and aerial survey data collected between 2005 and 2008.

(St. Andre et al. 1965, Tausch et al. 1981, Van de Ven et al. 2007).

The study area included various vegetative communities that changed along an elevational gradient (Hall 1991). The sagebrush-steppe zone extends from the valley floor to approximately 2000 m and is dominated by sagebrush, ephedra (*Ephedra* spp.) and rabbitbrush (*Ericameria nauseosus*). Intermediate elevations from 2000 to 2900 m are vegetated predominantly by pinyon–juniper woodland. Single-leaf pinyon (*P. monophylla)* and Utah juniper (*J. osteosperma)* are the codominant tree species at this elevation and tend to maintain a shrub-like growth form, particularly as younger trees (Weisberg and Ko 2012). They will co-occur with sagebrush, bitterbrush, ephedra, and rabbitbrush, until trees become larger where they tend to become the dominant plant species with less understory structure. The Subalpine Zone extends from 2900 to 3500 m and consists of a patchy mosaic of sagebrush and open forest dominated by stands of bristlecone pine (*P. longaeva*), lodgepole pine (*P. contorta*), and limber pine (*P. flexilis*), with quaking aspen (*Populus tremuloides*) occurring in moist areas, and dense stands of curl-leaf mountain mahogany (*Cercocarpus ledifolius*) along dry slopes at lower elevations. Subalpine meadows are scattered throughout the landscape. The Alpine Zone occurs at elevations above 3500 m and is characterized by dolomite or granite fields with sparse, dwarfed vegetation of which the most common species are phlox (*Phlox* spp.), buckwheat (*Eriogonum* spp.), and dwarf sagebrush (*A. arbuscula*). The region relies heavily on snowmelt for water recharge and plant growth (Comstock and Ehleringer 1992, Fan et al. 2014). Several drainages contain perennial water, with riparian areas at lower elevations dominated by willow (*Salix* spp.) and higher elevations by quaking aspen. Seeps, wet meadows, and intermittent streams also occur throughout the landscape from spring to late summer.

Mule deer occupying the east side of the White Mountains undertake seasonal movements in elevation but remain within that range year-round (Blankinship 1986; this study). Mule deer tended to use low-elevation (1800 m) shrub habitat during the winter and spring, and then transitioned to intermediate elevation and alpine habit during the summer months (2900–4000 m), with substantial overlap between summer and winter home ranges at intermediate elevations. Sagebrush (*Artemisia* spp.) and bitterbrush (*Purshia* spp.) are fundamental components in diets of mule deer, especially during winter (Kucera 1997, Pierce et al. 2004, 2012) with greater contributions of forbs and grasses during the summer months (Hall 1991).

Carnivores occur at low densities in the White Mountains and include coyotes (*Canis latrans*), mountain lions (*Puma concolor*), bobcats (*Lynx rufus*), and black bears (*Ursus americanus*). Domestic livestock are actively grazed on four allotments, but grazing pressure has been greatly reduced from the historically high numbers of sheep and cattle that occurred in the early 1900s. The area also supports other large herbivores including bighorn sheep (*Ovis canadensis*), feral horses (*Equus caballus*), and pronghorn (*Antilocapra americana*), most of which occurred infrequently on summer ranges used by mule deer.

Animal capture and data acquisition

We captured mule deer during the winter and spring over 4 yr using a net gun fired from a helicopter (Krausman et al. 1985). Upon capture, animals were transported to a central processing area where biological samples were collected and standard global positioning system (GPS) telemetry collars (Advanced Telemetry Systems, Isanti, Minnesota, USA) were deployed. We programmed collars to gather location data every 3 or 7 h. Collars were equipped with a release mechanism programmed to drop the collar from the individual after approximately one year, at which time they would be collected and the data acquired. We attempted to distribute capture efforts evenly across the study area to avoid concentrating study animals and to maintain independent samples.

We used location data collected from July through September, when mule deer nutritional demands were greatest and ambient temperatures in the study area were the highest, following parturition (generally mid-to-late June; Kucera 1992, Taylor 1996, Monteith et al. 2014) and after females had transitioned to summer ranges. All capture and handling of mule deer were compliant with procedures outlined by the California Department of Fish and Wildlife (Jessop et al. 2001), were in keeping with protocols outlined by the American Society of Mammalogists for research involving mammals (Sikes and Gannon 2011), and were approved by the Institutional Animal Care and Use Committee at the University of Nevada Reno (IACUC: 00109).

Movement analysis and activity periods

We used GPS locations of our collared individuals to calculate movement rates of mule deer during summer. This information allowed us to identify periods of high and low movement, likely related to foraging and resting periods. We then used those clustered periods of activity to assess whether there was variation in habitat selection during foraging or resting periods. We calculated an index of movement rates based on mean Euclidian distance between consecutive animal locations adjusted for time elapsed between points. Since this movement occurred over the length of time between these two locations, we ascribed each movement value to the hour that corresponded with the mid-point between the two consecutive locations. First, we modeled movement rate as a function of hour for the entire population using a linear mixed-effects model (lme4 package in program R v 2.12; R Development Core Team 2013) with individual as a random intercept term and hour as a fixed effect. Movement rates were log-transformed to meet normality. Using the model-derived parameter estimates for hour, we calculated hourly movement rates for the population and then visually grouped time periods where movement rates were similar and most consistent with foraging or resting (crepuscular, mid-day, night). Deer generally forage during crepuscular hours (Eberhardt et al. 1984); given our long fix rate (3–7 h), however, we extended the sampling period to increase sample size during this activity period. Therefore, we defined crepuscular periods as those within 3 h surrounding sunrise or sunset and having the greatest rates of movement.

We used the grouped movement rates from our previous analysis to define our activity periods as night (21:00 to 03:59), crepuscular (04:00 to 08:59 or 17:00 to 20:59), or mid-day (09:00 to 16:59). We then modeled movement rates as a function of iterative combinations of these three activity periods (null, crepuscular only, mid-day only, all three separate) and evaluated model performance using the Akaike information criterion adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002). This allowed us to assess model support for differences in movement rates among these three time periods and determine whether they should be considered separately or grouped together for the further analysis of habitat use. Once we identified the appropriate activity periods, we then assessed whether habitat selection differed among those periods, presumably resulting from differences in foraging or resting behavior. Further description of those model selection procedures is presented below in the statistical analysis of habitat selection subsection.

Habitat variables

To capture local variation in plant communities resulting from differences in site characteristics such as topography and soil moisture, we included remotely sensed measurements of vegetation composition, tree density, and resource abundance at a fine (1 m) resolution in addition to coarse (30 m) measures of site productivity, terrain characteristics (10 m), and general vegetation associations (100 m). We delineated land cover types based on the USDA Forest Service (USFS) existing vegetation mid-level map for the Great Basin Region, which uses the CALVEG classification system, to identify dominant vegetation associations at 100 m resolution (USDA, FS 1981). We reclassified this layer into 13 vegetation associations based on dominant plant species, which were most common throughout the study area and likely to influence selection: (1) grasses and forbs (generally occur at mid- to upper elevation—component of summer diet); (2) bare ground; (3) bristlecone pine (high elevation, rocky, acidic soils); (4) Great Basin mixed shrub (higher elevation mesic shrub community; contains some sagebrush and bitterbrush—components of summer diet); (5) sagebrush (mid-elevation shrub, most dominant); (6) bitterbrush (lower elevation bitterbrush and desert mixed shrub, major component of winter diet); (7) mountain mahogany; (8) pinyon–juniper woodland; (9) limber pine (upper montane pine); (10) willow (mid- to upper elevation, often associated with riparian vegetation—component of summer diet); (11) aspen (generally occur in mid- to upper elevations often associated with riparian vegetation); and (12) alpine shrub (13) desert mixed scrub (low elevation and valley, shrub communities). In general, mid- to upper elevation vegetation association and mesic shrub communities tend to provide important forage items (forbs, sedges, grasses, and current year shrub growth) for mule deer during summer months when the lower elevation plants tend to senesce. It is also likely that areas with robust horizontal cover (dense shrub communities, low-density pinyon–juniper and mahogany stands) may provide hiding cover for young, whereas areas with greater overstory cover (tall shrubs, trees) may provide thermal cover during the hottest parts of the day.

In addition to the coarse vegetation associations from the USFS vegetation layer, we were interested in generating more precise estimates of tree density, distance to riparian areas, and shrub abundance. Thus, we created a fine-resolution (1 m) vegetation layer with 4 broad categories—tree, riparian (willow, aspen, and cottonwood), shrub, and bare ground—and from those calculated a suite of landscape metrics (discussed later). The broad vegetation classes were created using maximum likelihood classification in ArcGIS 10.0 (ESRI, Redlands, California, USA) and 1-m resolution orthophoto imagery from the National Agriculture Imagery Program (NAIP; USDA FSA 2008) collected during August of 2008. The classification model incorporated the four spectral bands from the orthophoto (blue, green, red, and near-infrared), a fifth band containing the normalized difference vegetation index (NDVI); Tucker 1979, Pettorelli et al. 2005) and was trained on 750 photo-interpreted points. The overall classification accuracy for the vegetation layer was 0.66 based on 600 photo-interpreted validation points, and 0.74 and 0.96 for the tree and riparian classes, respectively. These values are within the range of overall accuracy achieved in similar studies in this region (0.62–0.79; Greenwood and Weisberg 2009). The majority of misclassification in the tree layer was a result of tree shadows in the image which tend to overestimate tree cover in areas with already dense trees. Moreover, we only used information from the tree and riparian vegetation classes for further analysis.

Using NAIP orthophoto imagery, we classified tree cover at a 1-m resolution, which allowed for more precise estimates of non-riparian tree cover. The classification procedure did not distinguish among conifer species, pinyon pine, juniper, limber pine, lodgepole pine, and bristlecone pine or between conifers and mountain mahogany. Using information on vegetation associations from the USFS classification layer for the study area, however, we determined that the majority of non-riparian tree cover was comprised of pinyon pine and juniper (70%), with 20% mountain mahogany, 5% bristlecone pine, and 5% limber-lodgepole pine.

Using this fine-resolution vegetation classification, we estimated the percent of tree and riparian pixels within a 200, 100, 30, and 5 m radius buffer surrounding a center pixel (1 m; Spatial Analyst, ArcGIS 10.0 ESRI, Redlands, California, USA). This process allowed us to investigate the influence of habitat composition at multiple spatial scales (Hobbs 2003, Boyce 2006). Patch sizes included: large stands (100 or 200 m radius), smaller foraging patches (30 m radius), and individual feeding or resting points on the landscape (5 m). Given that riparian areas are often associated with sources of free-standing water in addition to forage resources, we calculated the distance to the nearest riparian area for each focal pixel in the study area to evaluate the influence of these corridors on habitat selections. Using the red and near-infrared bands (NIR), from the NAIP imagery, we also calculated the normalized difference vegetation index (NDVI= (NIR−red)/(NIR +red; Tucker 1979, Pettorelli et al. 2005). NDVI was calculated at the patch scale for all non-tree, non-riparian pixels to differentiate between areas that were to a greater extent shrub-dominated and areas with little plant growth and greater amounts of bare ground.

Shrub NDVI was generated using the August 2008 NAIP imagery. First, we removed all riparian and tree pixels at a 1-m resolution and then calculated NDVI for the remaining pixels, and averaged them for all pixels within 30 m from focal cell. We calculated slope and topographic position index (TPI) using a 10 m digital elevation model (DEM; U.S. Geological Survey 2010). Topographic position index is a measure of the relative difference in mean elevation between the focal cell and the surrounding 100 m or 200 m neighborhood, where lower values represent lower hill-slope positions and higher values indicate ridge tops (Weiss 2001). This allowed us to vary the spatial scale of the measure to include more of the surrounding landscape.

To account for underlying variation in site productivity relative to abiotic characteristics, we calculated a site-based measure of actual evapotranspiration (Stephenson 1998). Actual evapotranspiration (AET) estimates potential plant growth for a given pixel based on elevation, solar radiation, temperature, soil, water, slope, and aspect, and is calculated from a Thornthwaite water balance model (Stephenson 1998, Dilts et al. 2015). Our model incorporated the 30-yr average climate data from a Precipitation–elevation Regressions on Independent Slopes Model (PRISM) to identify relative productivity (PRISM Group 2010). We used AET values from July and August, when the majority of the mid- to high-elevation plant growth occurs, to characterize a gradient between sites that were hot or dry and generally less productive, to sites that were cooler, wetter, and more productive.

Statistical analysis for habitat selection

We modeled resource selection functions following a use–availability design, where used locations were obtained from GPS collar locations and available points were randomly generated to coincide with second- and third-order selection (Johnson 1980). We combined data over the study periods (2005–2008) to allow for a more robust sample size. To assess the placement of home ranges within the landscape (second-order selection), we defined available habitat as the eastern side of the mountain range between the foothills and the crest, an area that encompassed all mule deer summer locations and the majority of fall and winter locations. To determine the number of random points required to adequately characterize resource availability for each individual, we randomly generated 250 points, and then increased that number by 200 points, repeating the process until the addition of points did not appreciably change the mean values for available habitat (Gillies et al. 2006). We determined that roughly 400 random points per individual adequately characterized availability at the landscape scale (Appendix S1: Fig. S1).

To determine available habitat for analysis of within home range selection (third-order selection), we created a minimum convex polygon (MCP; Geospatial Modelling Environment; Beyer 2012) for each individual. We included a 500 m buffer around each MCP which corresponding to the average distance moved between GPS locations within a day. This approach allowed the extent of availability to be determined by the movement metrics of the study animals. One available point was generated for every 200 m^2 of home range, with a minimum of 350 and maximum of 1500 points (Hebblewhite and Merrill 2008). This allowed for equal categorization of availability even though home ranges differed in size. We attributed values for each covariate of interest to the used and random location data and randomly assigned hour values to the available points. We identified collinearity between resource covariates using Pearson correlation (R Core Team 2013) and removed variables with correlation coefficients $|r| > 0.6$ (Zar 2010). In cases where pairs of variables were collinear, we selected the covariates to retain in the models based on their relevance to our biological hypotheses of interest and model support.

We estimated resource selection functions (RSF) using a generalized linear mixed model (GLMM) with a logit-link function and a binomial error distribution (lme4 package in Program R; R Development Core Team 2013). Response variables were coded as used (1) or available (0) locations with habitat covariates included as fixed effects and individual as a random intercept term (Manly et al. 2002, Hebblewhite and Merrill 2008, Zuur et al. 2009). We used an information theoretic approach to evaluate model performance. We retained variables if addition of the variable reduced AIC > 2.0 (Burnham and Anderson 2002).

Because the number of covariates we considered was large, we modeled resource selection in an iterative process. First, we identified the most appropriate local scale (5, 30, 100, or 200 m neighborhood) for the tree and riparian covariates while holding the other model parameters constant, and then included non-linear relationships and interactions. To evaluate the appropriate local scale, we began with a base model that contained all uncorrelated covariates of interest: vegetation associations, AET, NDVI, distance to riparian vegetation, tree cover, riparian vegetation, slope, and TPI. We then identified which of the local scales (5, 30, 100, 200 m) had the greatest model support for each variable of interest.

Once we identified the best additive model structure and appropriate local scale, we then considered non-linear relationships and hypothesized interactions between covariates: tree cover, site productivity, and robust shrub and riparian communities. These interactions allowed us to investigate the influence of tree cover on selection of productive habitat (riparian vegetation and shrub NDVI), as well as interactions between site productivity (AET) and habitat covariates (distance to riparian vegetation and tree cover), on selection by mule deer. Once we identified our top model using this multistep approach, we used the model dredge command in R (MuMIn package R; R Development Core Team 2013) on our top model to confirm that we had identified the most parsimonious model structure given the suite of covariates and their interactions, based on $\mathrm{AIC_c}$ scores. This same iterative process was performed for the landscape and home range scales of selection separately; see Appendix S1: Table S1 for the list of model results. We then identified the top model for each analysis, which was then used to investigate covariate effects.

Using the top model from the within home range analysis (third-order selection), we tested the hypothesis of differential selection relative to daily activity patterns. Locations from within home range analysis were grouped based on results from movement analysis into night, crepuscular, and mid-day periods, which we used to explore whether habitat selection differed during these three periods possibly as a result of foraging behavior, predator avoidance, or thermal tolerance. We generated a base model from the top model of our within home range analysis. This base model contained the full suite of covariates identified as influencing selection in the previous analysis. To avoid the need for a three-way interaction, we only retained the additive covariate effects allowing us to compare this base model to models that contained an interaction between habitat composition and time of day. To test our hypothesis of differential selection, we compared the model that contained interactions between habitat variables and two alternative groupings of time. The first grouping included two categories for time, either crepuscular, or night and mid-day combined. The second grouping contained three categories for time, either crepuscular, night, or mid-day. Differential selection among the three periods was supported by the analysis, and we retained three periods for subsequent analyses. We modeled resource selection for each time period (crepuscular, mid-day, night) following the same procedure used in the spatial scale analysis.

For each analysis, we were interested primarily in estimates of effects rather than prediction, so covariates were converted to standard normal values ($\mu = 0$, $\mathrm{SD} > 1$) to allow for direct comparisons of covariate effects (Zar 2010). We assessed the extent to which parameters influenced selection by comparing the magnitude of the effect and whether 95% confidence intervals overlapped zero. Standardized parameter estimates greater than zero indicated use was greater than expected based on availability and estimates less than zero indicated use was lower than expected. We compared differences in model parameter estimates, standard errors, and magnitude of effects between the two spatial models and among the three temporal models separately in order to examine hypothesized relationships between scale and time of day (activity period—foraging, resting) on habitat use.

Models were validated using fivefold cross-validation (Roberts et al. 2017). Each fold was a subset (20%) of the data blocked by individuals. The data were split randomly where multiple individuals contributed all their GPS locations to one fold. Predicted values were fit to data points based on each model of interest. RSF values from used locations were binned into 10 equal area sets, and the Spearman rank test was used to evaluate the correlation between frequency of occurrence and relative RSF score for each data fold (Boyce et al. 2002).

RESULTS

RSF spatial analysis

We monitored a total of 48 adult female mule deer over a period of 4 yr (5 in 2005, 15 in 2006, 12 in 2007, and 16 in 2008). Data were combined for the entire study period. We collected between150 and 700 locations per individual ($\bar{X}$ = 400, SD = 141). The best RSF model for both the landscape and home range scale contained the full suite of habitat covariates (Appendix S1: Table S1). At the landscape scale, female mule deer selected areas closer to riparian vegetation, with greater NDVI and riparian cover; however, we also identified an influence of site productivity (AET) and tree cover (200 m) on selection of those habitat variables (Figs. 2, 3 and see Appendix S1: Tables S2, S3 for full list of parameter estimates). Mule deer selected areas closer to riparian vegetation when site productivity was low and were less constrained by proximity to riparian zones when site productivity was high (Fig. 2). Mule deer also avoided low AET sites that were farther from riparian vegetation (Fig. 2). This relationship between riparian distance and AET was stronger at the home range scale, with individuals selecting sites farther from riparian zones in highly productive areas (Fig. 2). Mule deer also selected areas of

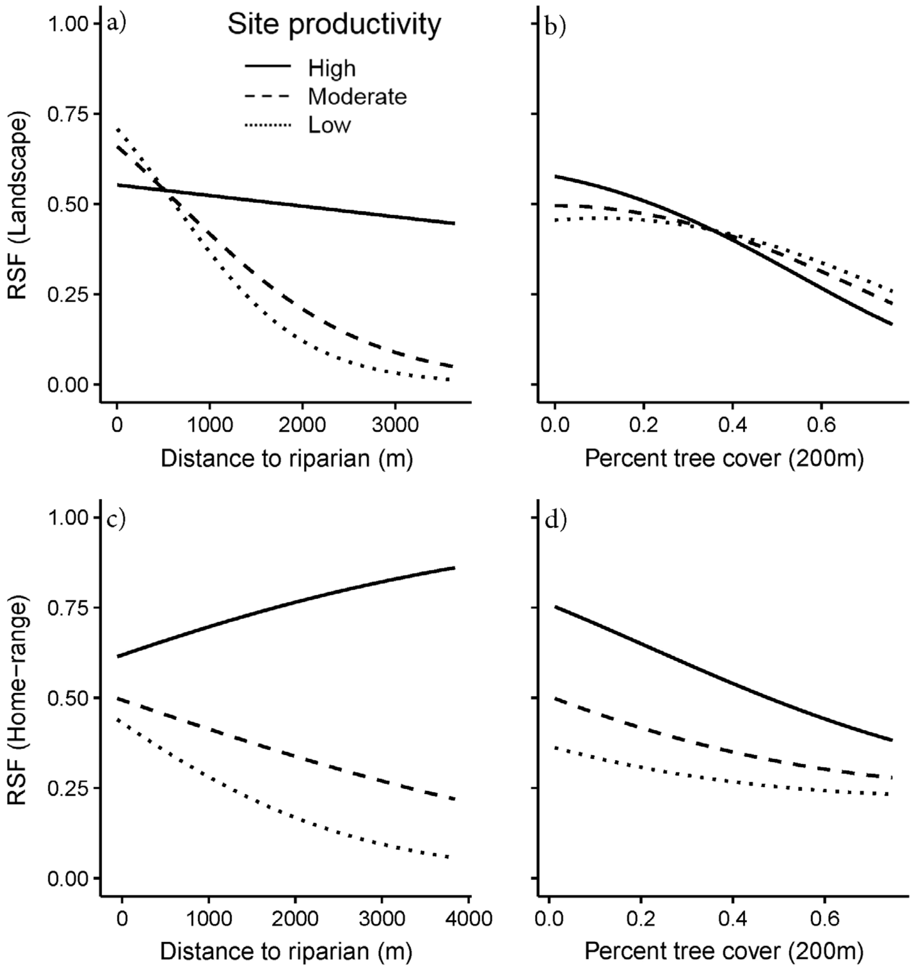

Fig. 2. The influence of distance to riparian vegetation or percent tree cover and interactions with site productivity actual evapotranspiration (AET), on summer resource selection of female mule deer in the White Mountains, California and Nevada, USA, from 2005 to 2008. Predicted values were estimated from best generalized linear mixed models for spatial scale. Landscape (a, b) and home range (c, d) refer to spatial scale associated with second- or third-order selection, respectively. Lines represent values of low (40; dotted), moderate (70; dashed), and high (133; solid) site productivity (AET) based on the range of values in the data. Sites with high AET generally are wetter, cooler and have more productive plant growth.

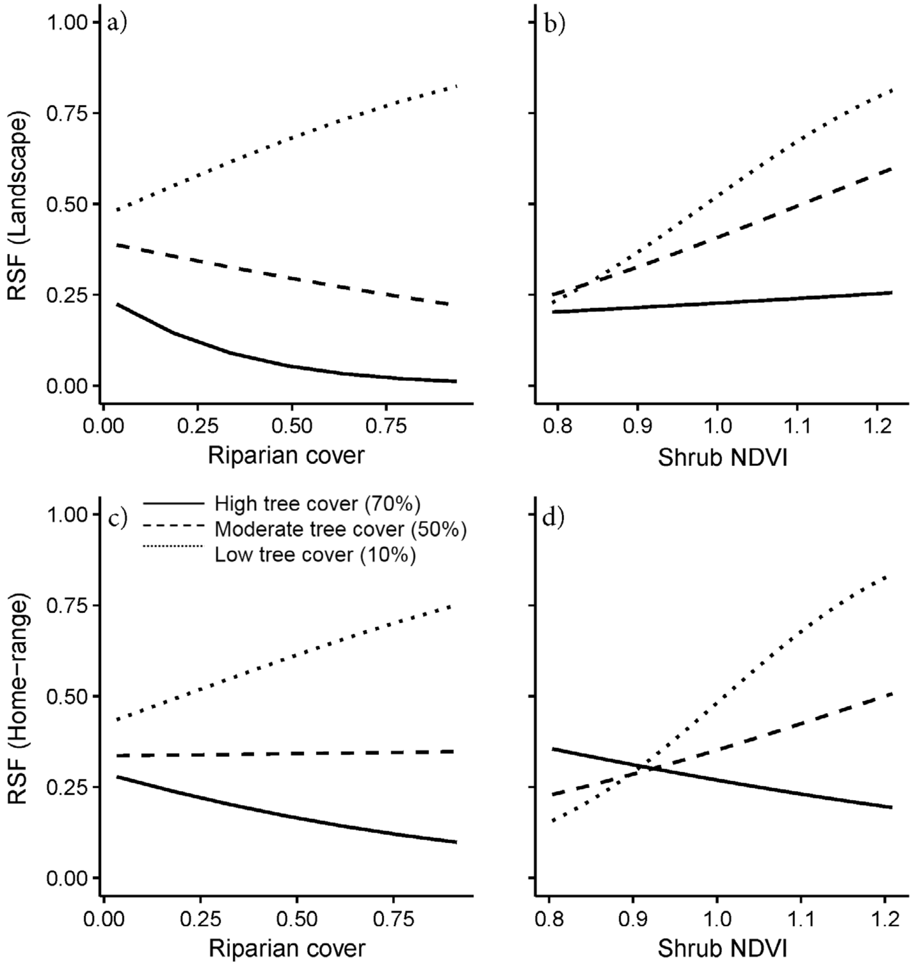

Fig. 3. The influence of riparian cover or shrub NDVI and interactions with tree cover on summer resource selection of female mule deer in the White Mountains, California and Nevada, USA, from 2005 to 2008. Predicted values were estimated from best generalized linear mixed models for spatial scale. Landscape (a, b) and home range (c, d) refer to spatial scale associated with second- or third-order selection, respectively. Lines represent values of low (10%; dotted), medium (50%; dashed), and high (70%; solid) tree cover, based on the range of values in the data.

mid hill-slope position (TPI) and moderate slopes at the landscape scale (Fig. 4), with selection for flatter slopes at the home range scale (Fig. 4) but avoided steep slopes at both the landscape and home range scales.

In general, female mule deer avoided areas with >35% tree cover as estimated by NAIP imagery at the large (200 m) patch size at both the landscape and home range scales (Fig. 2). Additionally, we identified an interaction between tree cover and AET at the home range scale, where the negative effect of tree cover (200 m) was moderated for sites with low AET (AET value = 40; Fig. 2). At this finer spatial scale within home range, mule deer were less likely to select low AET sites, but within those low AET sites were not as influenced by tree cover (200 m). However, at sites with high AET (average value = 133), mule deer showed strong avoidance of areas with greater tree cover (Fig. 2). Alternatively, female mule deer did not avoid tree cover at the smaller patch size (5 m) and showed slight selection for areas containing trees (Fig. 4). Additionally, we observed a negative interaction between tree cover (200 m) and productive habitat as characterized by having

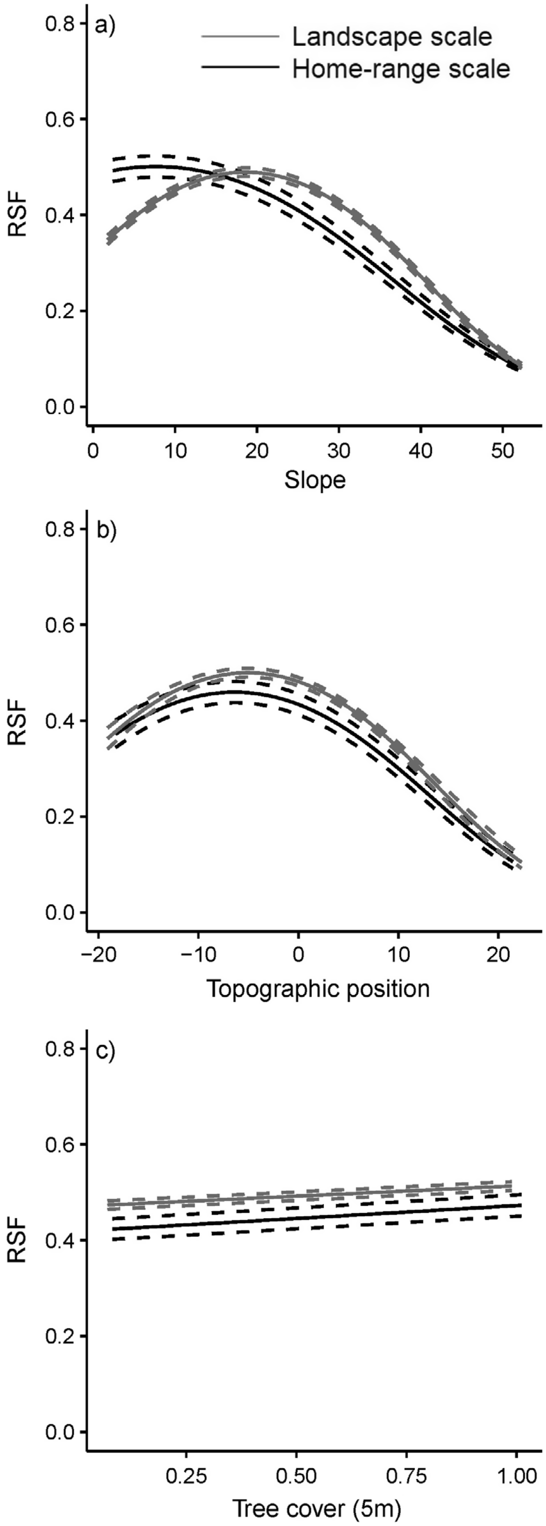

Fig. 4. The influence of slope (a) topographic position (b) and tree cover 5 m (c) on summer resource selection of female mule deer in the White Mountains, California and Nevada, USA, from 2005 to 2008. Predicted values and 95% confidence intervals were estimated from best generalized linear mixed models for spatial scale. Landscape (black line) and home range (gray line) refer to spatial scale associated with second- or third-order selection, respectively.

higher shrub NDVI values (for non-tree, non-riparian areas) and greater riparian vegetation (Fig. 3). These results suggest that productive habitat that occurred within dense stands of trees was avoided or underutilized.

Summary analysis of vegetation associations indicated that available habitat was comprised of sagebrush (33%), pinyon–juniper (25%), bare ground (10%), mountain mahogany (8%), bitterbrush (5%), and bristlecone pine (5%), with the remaining categories each contributing less than 5% to overall composition. Sagebrush had the greatest availability and was used in proportion to availability at both spatial scales; therefore, we used sagebrush as the reference category in our analyses. Estimates for selection of vegetation type differed between each spatial scale (Fig. 5). Landscape-level analysis indicated greater use of areas identified as willow, grasses and forbs, and low-elevation shrub communities (bitterbrush, Great Basin mixed-scrub, and desert scrub). Landscape-level analyses also indicated lower use of aspen, high-elevation shrub, and pinyon–juniper associations. At the home range scale, selection was greatest for willow and Great Basin mixed-scrub associations; and lowest for alpine shrub and low-elevation shrub associations, such as desert scrub and bitterbrush. Bitterbrush tends to be a more major component of winter diets (Kucera 1997, Pierce et al. 2004, 2012) and the bitterbrush vegetation association tends to be found at lower elevations consistent with winter range, which might contribute to its lack of selection within home range during summer. We would expect to see strong selection for bitterbrush during winter when deer are foraging on bitterbrush and reside at similar elevations. Additionally, estimates for some vegetation associations may be inflated, because they were rare in the sample (Boyce et al. 2002).

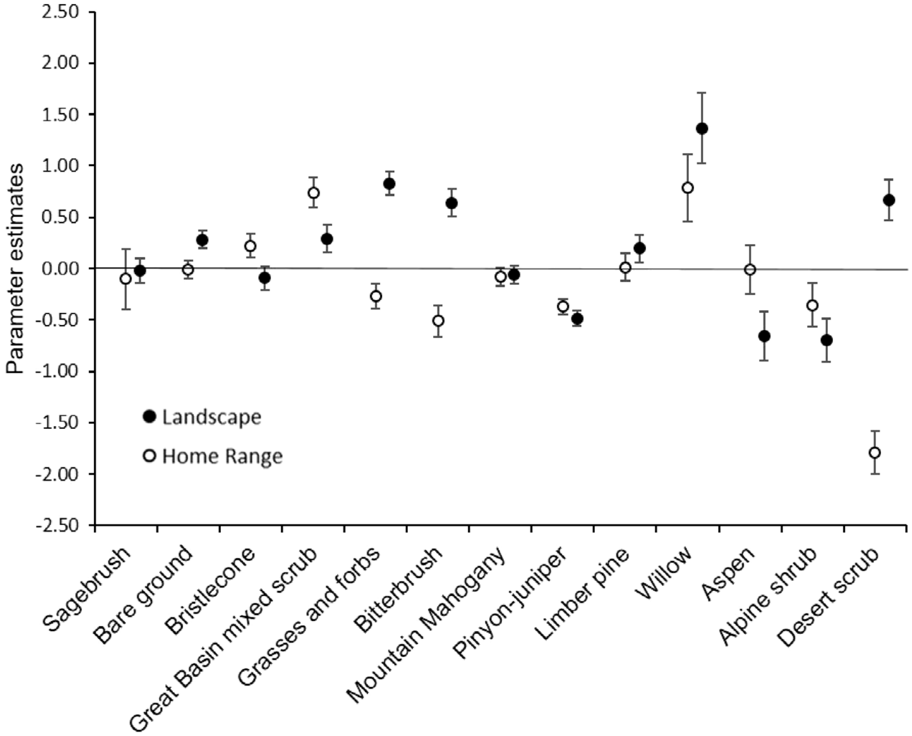

Fig. 5. Parameter estimates ± 95% confidence intervals from best spatial models of summer resource selection (GLMM) for mule deer in the White Mountains, California and Nevada, USA, from 2005 to 2008. Landscape and home range refer to spatial scale associated with second- or third-order selection, respectively. Estimates refer to strength of selection for categorical vegetation associations. The sagebrush shrub vegetation association was used as reference value because it was abundant on the landscape and used in relative proportion to availability. Confidence intervals that overlap zero indicate selection for particular vegetation type was similar to reference.

Movement analysis and activity periods

During summer, we identified peaks in movement rates during crepuscular hours (04:00 to 08:59 or 17:00 to 20:59), with deer becoming more sedentary at night (21:00 to 03:59) and during mid-day (09:00 to 16:59; Fig. 6). Model results further supported a difference in movement rate corresponding to the three activity periods. The best model contained activity period (3 time periods) as a fixed effect and a random intercept for individual. This model also contained the full model weight and improved fit by >16 ΔAIC_c over models containing only two groups (i.e., crepuscular, and night and mid-day combined; or mid-day, and crepuscular and night combined; Table 1). We then used these three distinct time groupings to further test hypotheses related to temporal variance in resource selection.

RSF temporal analysis

We identified support for differential selection of habitat covariates based on activity periods (crepuscular, mid-day, night). Inclusion of an interaction between activity period and habitat covariates substantially improved model fit over the base model ($\Delta AIC = 267.2$) generated from our home range-level analysis of resource selection (Table 1). To further examine the influence of activity period on selection, we analyzed each time period independently. The best supported models for each temporal dataset contained the full suite of covariates, including non-linear relationships and interactions with tree cover, that were identified as important components of resource selection from the spatial analyses (see Appendix S2: Table S3 for parameter estimates).

In general, mule deer showed patterns in resource selection that reflected those identified

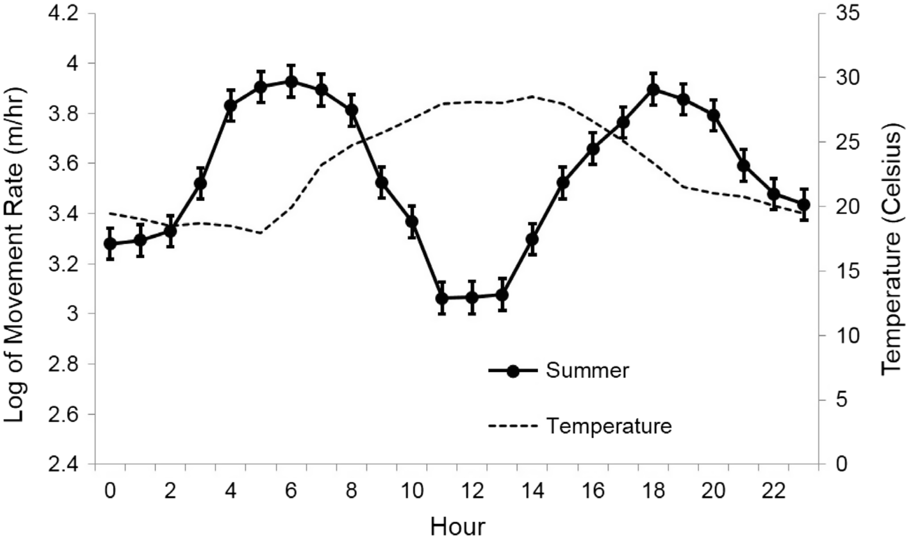

Fig. 6. Model-derived estimates (GLMM) ± 95% confidence intervals for hourly movement rates of mule deer and summer temperature in the White Mountains, California and Nevada, USA, based on data collected from GPS collars during the summer or winter 2005–2008. Temperature data were obtained from temperature loggers on GPS collars for corresponding summer locations.

Table 1. Model results from GLMM of movement rates for various time periods (top); and interaction between base model generated from home range scale RSF and activity periods (bottom) for mule deer in the White Mountains, California and Nevada, USA, during summer of 2005–2008.

Model	*k*	AIC_c	ΔAIC
Movement analysis			
Night + Crepuscular + Mid-day	5	62,581	0.0
Crepuscular + (Night and Mid-day)	4	62,598	16.6
(Night and Crepuscular) + Mid-day	4	63,051	469.8
Habitat selection			
Base + Time (3 periods) × Covariates	36	55,307	0.0
Base	23	55,574	267.2

Notes: *k*, the number of parameters; AIC_c, Akaike information criterion adjusted for small sample sizes, ΔAIC, difference from model with lowest AIC_c value.

during our home range analysis, with night and crepuscular periods being similar and mid-day period being disparate. Furthermore, parameter estimates from each temporal model indicated similar relationships in selection among all three time periods for riparian habitat (30 m), NDVI, and associated interactions with tree cover (200 m; Appendix S2: Table S3), in addition to slope, with some variability in magnitude of the effects. Selection for topographic position, vegetation association, and interactions between distance to riparian vegetation or tree cover and AET also varied among time periods. Mule deer selected mid-slope positions during crepuscular and night time periods but used positions lower on hillsides during mid-day (Fig. 7). Mule deer also selected areas that were closer to riparian habitat more strongly during night and crepuscular periods than during mid-day (Appendix S2: Table S3). Deer tended to select vegetation associations that contained greater overstory cover (i.e., willow, aspen, pinyon–juniper, mountain mahogany, limber pine, bristlecone) during mid-day when compared with use at night or during crepuscular periods (Fig. 8). Mule deer also avoided vegetation associations that tended to occur at higher elevations, such as bristlecone and limber pine, or grass/forb associations, and selected vegetation associations comprised of more open shrublands, such as sagebrush and bitterbrush, at night (Fig. 8). Overall, vegetation associations used during crepuscular periods were most similar to those used during mid-day, indicating that mule deer selected vegetation associations that provided both foraging and resting opportunities at this coarse level of analysis; nonetheless, we identified differences in selection of tree cover

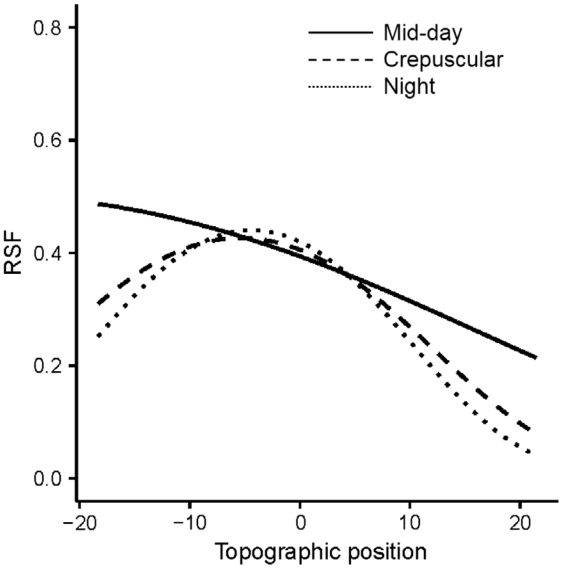

Fig. 7. Relative probability of selection given varying topographic position of habitat selection for mule deer. Probabilities generated from best temporal model of summer resource selection for mule deer in the White Mountains, California and Nevada, USA, from 2005 to 2008. Resource selection was modeled separately for each time of day (night, crepuscular, and mid-day), which corresponded to foraging and resting periods. Lines indicate night (dotted), crepuscular (dashed), and mid-day (solid) periods.

during mid-day periods using finer resolution data (Fig. 9). When we accounted for an interaction between AET and tree cover, parameter estimates indicated avoidance of areas with low AET and little influence of tree cover on use, and were similar to our finding in the home range analysis. Conversely, we also identified a strong negative relationship with tree cover (200 m) during night or crepuscular periods in areas with high levels of AET. This relationship was weak, however, during mid-day, with use declining only at very high levels of tree cover (200 m; Fig. 9). At the fine scale (5 m), deer tended to select areas that contained trees during mid-day, but there was no influence of tree cover during crepuscular and night time periods (Fig. 9).

Model validation

The fivefold cross-validation identified strong correlations between RSF bins and area-adjusted frequencies across all of the data folds (Table 2). Average Spearman rank correlations for the best models in the landscape level and the home range analysis were $r_s = 0.93$ and $r_s = 0.96$, respectively. These results indicate a strong correlation between area-adjusted frequencies and the relative RSF in summer.

DISCUSSION

In general, mule deer selected productive areas on the landscape that would likely contain robust shrub and forb communities and increased foraging opportunities, and avoided areas with dense pinyon–juniper cover; however, this relationship varied across spatial scales and among activity periods. This variation highlights the importance of evaluating selection at multiple spatial and temporal scales to fully understand the dynamics of resource use (Boyce 2006). Mule deer in this region exhibited noticeable differences in movement rates throughout a 24-h period which were then grouped into three distinct activity periods (night, crepuscular, and mid-day). Significant increase in movement rates during crepuscular and night periods relative to mid-day suggested activity patterns that correspond with foraging and resting behaviors, respectively, and selection of resources varied in accordance with these activities. Studies of ungulate behavior in arid environments have identified diurnal patterns in activity during summer months consistent with resting during mid-day, when ambient temperatures are highest, and foraging during crepuscular hours and at night (Tull and Krausman 2001, Giotto et al. 2013, Long et al. 2014).

Mule deer inhabiting this Great Basin environment placed home ranges in vegetation associations that occurred at mid-elevations and near riparian areas that provided forage, and within their home range selected sites and vegetation types with high productivity, both AET and NDVI, likely indicating that those sites may have had higher quality forage available. These results support our hypothesis that habitat selection was driven by forage availability and water resources in this semi-arid ecosystem. In many ecosystems, reliable water and productive forb and shrub communities have been identified as important components of ungulate summer habitat (Marshal

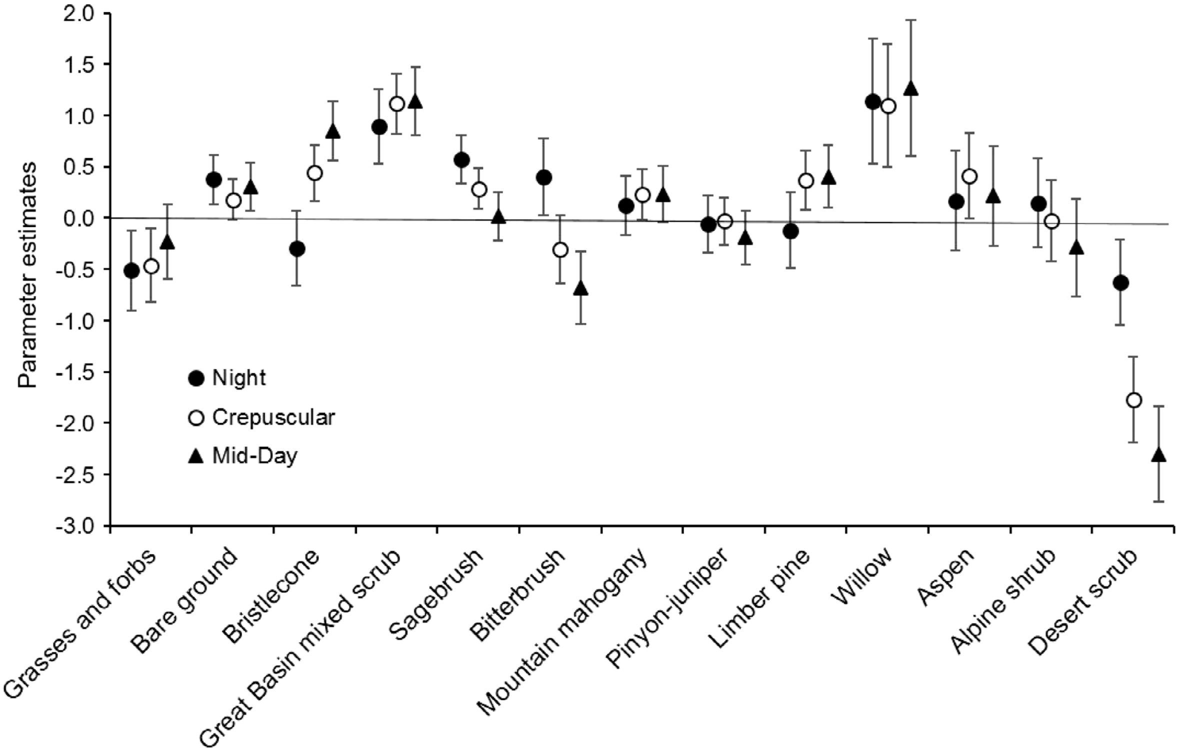

Fig. 8. Parameter estimates ± 95% confidence intervals from best temporal models of summer resource selection (GLMM) for mule deer in the White Mountains, California and Nevada, USA, from 2005 to 2008. Resource selection was modeled separately for each time of day (night, crepuscular, and mid-day), which corresponded to foraging and resting periods. Estimates refer to strength of selection for categorical vegetation associations. The sagebrush shrub vegetation association was used as the reference value because it was abundant on the landscape and used in proportion to availability. Confidence intervals that overlap zero indicate selection for particular vegetation type was similar to the reference vegetation category.

et al. 2006, McKee et al. 2015), and concentrated use of areas close to water or riparian zones is common (Bleich et al. 2010, Horncastle et al. 2013, and review by Simpson et al. 2011). During late spring and summer, female mule deer may experience a 30–50% increase in energetic and water demands associated with gestation and lactation (Barboza and Bowyer 2001). In addition, digestive constraints during this period reinforce selection for forages that are highly digestible, with high protein, high energy, and low fiber (Parker et al. 2009, Tollefson et al. 2011). As a result, animals often concentrate foraging in highly productive areas, which usually consists of vegetation of high quality compared with less productive areas (Festa-Bianchet 1988, Parker et al. 2009).

We also identified an interaction between site productivity (AET) and distance to riparian areas. In areas with relatively low AET that generally were drier, hotter, and less productive, the importance of riparian vegetation increased with mule deer remaining more closely associated with riparian areas. Conversely, in areas with greater AET that generally were wetter, cooler, and more productive, mule deer were less constrained by proximity to riparian zones, and tended to select habitat farther from those areas. Ungulates may be able to obtain some water from forage, allowing them to range farther from free water sources when high-quality forage is available (DelGiudice and Rodiek 1984, Gedir et al. 2016). Within the White Mountains, water is limited and riparian corridors, along with wet meadows and seeps, provided not only access to free water, but generally are associated with more productive forb, shrub, and willow communities (Hall 1991).

We identified multiple lines of evidence that supported our hypothesis that areas of dense pinyon–juniper woodland are of low value to mule deer and may deter use of more productive habitat, particularly during summer when nutritional constraints for females are highest. Mule deer avoided areas with high tree cover at both spatial scales and among the three activity periods. In addition, mule deer were less likely to select patches of otherwise preferred habitats including areas of high site productivity (AET), riparian vegetation, or productive shrub communities (NDVI) if they were located within stands of high conifer cover. Investigators also have determined that as overstory cover of conifers increases in arid environments, understory biomass declines, resulting in a decline of forb and shrub abundance and reduction in species diversity (St. Andre et al. 1965, Tausch et al. 1981, Tausch and Tueller 1990, Pierson et al. 2010). This loss in understory biomass has direct implications for forage availability and population productivity of mule deer in arid ecosystems.

In a controlled study, Bates et al. (2000) reported that in southeastern Oregon removal of juniper reduced below-ground interference for soil water and nitrogen and resulted in a ninefold increase in understory biomass and nitrogen uptake by those plants. Researchers in northern New Mexico determined that conifer woodland had little combined ground cover of preferred forb and shrub vegetation, and was negatively associated with body condition of mule deer (Bender et al. 2007, 2013). Moreover, pinyon–juniper removal studies in Colorado have also identified increases in body condition of adult females and increased survival in young with woodland removal (Bergman et al. 2014*a*, *b*). Our results also suggest that landscape patches dominated by dense stands of pinyon–juniper woodlands would provide less suitable habitat for female mule deer during summer months. Additionally, when coupled with previous research, our results also suggest that succession of shrub–forb communities to conifer-dominated woodland has negative implications for forage abundance and habitat for mule deer and probably other sagebrush obligate species in this region. Our results are consistent with and strongly support guidelines for habitat management of mule deer in the intermountain west ecoregion, which recommend reducing pinyon–juniper cover to promote robust shrub and forb vegetation communities (Taylor 1997, Cox et al. 2009).

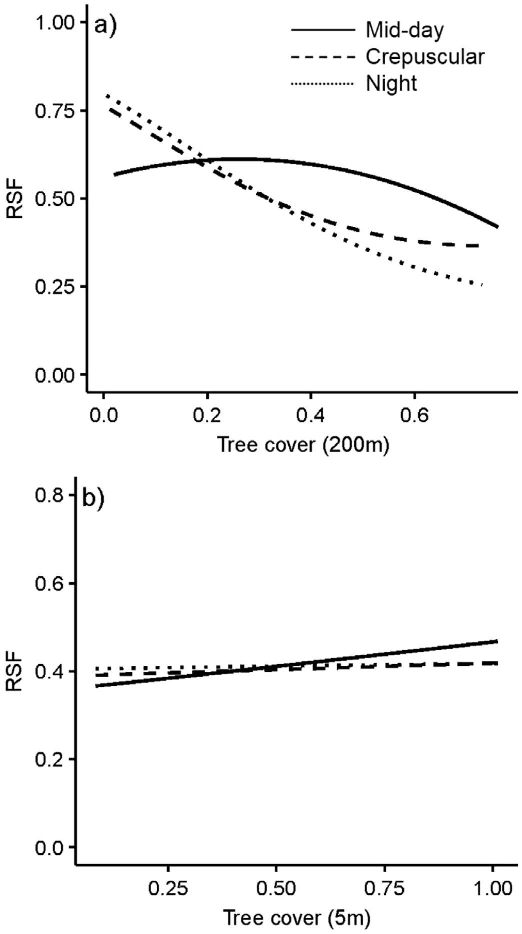

Fig. 9. Influence of tree cover on summer resource selection of mule deer in the White Mountains, California and Nevada, USA, from 2005 to 2008. Tree cover 200 m (a) also contains an interaction with site productivity (AET) and results are shown for areas of high AET only, generally wetter, cooler, more productive sites, because low AET sites were generally avoided and similar among time periods. Tree cover 5 m (b) indicates a smaller patch size and does not contain any interaction term. Resource selection was modeled separately for time of day (night, crepuscular, and mid-day), which corresponded to foraging and resting periods and resource selection functions were generated from the best temporal model and contained the same model structure for each period.

Table 2. Cross-validation results evaluating the performance of landscape level and home range, resource selection functions (RSF) models.

RSF model	Fold 1	Fold 2	Fold 3	Fold 4	Fold 5	Average
Landscape	0.98	0.93	0.91	0.94	0.91	0.93
Home range	0.99	0.99	0.96	0.95	0.89	0.96

Notes: The Spearman rank correlations (r_s) between binned RSF values and area-adjusted frequencies are reported for each fold (P-values for all estimates were <0.001). Folds comprise 20% of the original data withheld, blocked by individuals.

Although larger stands of dense tree cover generally were avoided, mule deer selected areas that contained trees at a fine spatial scale (5 m), and areas of low to moderate tree cover at larger spatial scale (200 m) during resting periods. These results further support our hypothesis that conifer woodland provides some beneficial structural components likely for either predator avoidance or thermal cover (Altendorf et al. 2001, Giotto et al. 2013). Prior investigations have indicated that mule deer spend an increased amount of time in forested habitat during resting periods (Collins and Urness 1983, Altendorf et al. 2001) and exhibited lower rates of vigilance behavior in forested areas, which was interpreted as lower perceived risk of predation. Altendorf et al. (2001) further observed that mule deer spent a greater amount of time in edge habitat, which contained a mixture of tree and shrub vegetation, than in either forested or open areas, and were most likely to forage in areas containing mixed vegetation. Those results are consistent with our observations of fine-scale selection for individual trees and avoidance of larger areas characterized by high tree cover.

Small ungulates often select resting sites with greater canopy cover during times of year when ambient temperatures are highest and less so during cooler parts of the year (Tull and Krausman 2001, Giotto et al. 2013). Parker and Gillingham (1990) estimated that under optimal conditions of wind and solar radiation, the upper limit of the thermal neutral zone for adult mule deer ranges from 20°C to 30°C during summer. They also reported that with calm winds and high solar radiation, the upper critical limit could occur with temperatures as low as 10°C. Ambient temperatures above the thermal neutral zone cause metabolic rates to increase and force individuals to expend energy for thermoregulation (Parker and Gillingham 1990).

Alternative strategies to offset costs associated with thermoregulation and to increase nutrient intake during summer months include foraging at night when temperatures are within the thermal neutral zone, resting during the hottest part of the day, or preferentially selecting habitat to minimize thermal costs (Long et al. 2014). Bender et al. (2012) reported that elk (*Cervus canadensis*) in New Mexico foraged in shrub-dominated sites, but that bed sites generally were under conifer trees in areas of greater overstory cover, and daytime that activity was avoided when temperatures exceeded thermal tolerance. In the Great Basin, ambient mid-day temperatures often exceed 30°C and decreased movement of mule deer mid-day—when temperatures were the hottest, in addition to greater use of tree cover—are consistent with behaviors that minimize costs associated with thermoregulation.

Medium-bodied ungulates, in arid ecosystems, may forage at night to reduce heat stress during summer months (Hayes and Krausman 1993). In addition, mule deer likely selected resting sites differently at night because they were not constrained by the same thermal environments as daytime and may also use different strategies to avoid nocturnal predators (Lynch et al. 2015).

Our results suggest that riparian vegetation and robust shrub communities both provide structural cover during resting periods that may aid in predator avoidance and thermoregulation while also providing enhanced foraging opportunities. As such, mule deer using these plant communities did not need to make tradeoffs between foraging and resting sites. Similar to this result, Pierce et al. (2004) reported no trade-off between predation risk and acquisition of high-quality forage in robust shrub communities on mule deer winter range.

Our research demonstrated the importance of considering behavioral mechanisms when assessing resource selection, as animals likely make decisions about resource use to balance confounding processes such as predator avoidance, thermoregulatory needs, nutrient intake, and provisioning young. We also identified the importance of accounting for underlying differences in site productivity when assessing the influence of tree cover. In semi-arid ecosystems, resources are often patchily distributed resulting from gradients in site productivity related to soil composition, moisture, and climate patterns (Stephenson 1998). Less productive sites may be affected at lower pinyon–juniper densities because soil water and nutrients are already limited, or they may be avoided all together, regardless of tree densities. By including a high-resolution layer of tree cover, we were able to directly assess effects of tree cover on habitat selection relative to other components of site productivity in the White Mountains and in the Great Basin in general.

There are multiple threats to persistence of sagebrush-dependent species in semi-arid ecosystems, and loss of productive sagebrush-steppe habitat resulting from expansion and infilling of conifer woodland can negatively influence understory composition and forage resources. In some areas, this has resulted in dramatic declines in habitat quality for mule deer and likely other sagebrush obligate species (Tausch et al. 1981, Tausch and Tueller 1990, Miller et al. 2000, Bender et al. 2007, 2013). In arid ecosystems, where forage is already scarce and often patchily distributed, negative effects of woodland expansion are likely more pronounced (Bleich et al. 1994). Moreover, increased rates of conifer expansion on mesic sites have been well documented (Weisberg et al. 2007, Jacobs 2011). Those mesic sites are productive and highly selected by mule deer, and conifer woodland is predicted to shift upward into higher elevation shrub communities with increasing temperatures (Van de Ven et al. 2007).

Our results indicate that, at a fine scale, tree cover may provide beneficial attributes such as structural cover for predator avoidance (Altendorf et al. 2001) or overstory cover aiding thermoregulation during high temperatures (Giotto et al. 2013). Nevertheless, the benefit of increased overstory cover appears to decline as tree densities increase to a level where understory biomass is reduced or lost (Altendorf et al. 2001). Managing for a mosaic of habitat types with low tree cover, protecting riparian areas, and ensuring that mesic shrub communities do not succeed to conifer woodlands will likely promote high-quality habitat for mule deer in these semi-arid ecosystems.

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