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Population Ecology and Summer Habitat Selection of Mule Deer in the White Mountains: Implications of Changing Landscapes and Variable Climate

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ABSTRACT

Changes in landscape composition have the potential to negatively influence animal populations through shifts in dominant plant communities, loss of important forage items, or changes in structural components of habitat. In the western United States, expansion of woodland vegetation into shrub dominated communities is of concern, particularly with regard to animal populations reliant on robust sagebrush and shrub vegetation. Once established, trees can out-compete shrubs and herbaceous plants resulting in declines in abundance and diversity of shrub-forb vegetation, which female mule deer are reliant on during summer months to meet nutritional demands and to provide hiding cover for young. As a result, shifts in the distribution of pinyon-juniper woodland and increases in tree densities could negatively affect mule deer population. The study had two primary objectives, (1) to determine summer habitat composition of female mule deer in the White Mountains of California and eastern Nevada, and assess implications of pinyon-juniper expansion on habitat availability, and (2) evaluate the status of the population relative to nutritional carrying capacity and determined the influence of habitat and precipitation on demographic rates.

I used mixed-effects logistic regression to model summer resource selection and demographic rates of female mule deer from 2005 to 2008. Summer resource selection was modeled at two spatial scales and among three behavioral periods, related to foraging, resting, and parturition. Summer habitat consisted of sites with high productivity, greater shrub abundance, and greater proximity to riparian areas. Deer avoided high levels of tree cover at all spatial and temporal scales, but they selected areas with low to intermediate tree cover during resting periods and during parturition. Moreover, mule deer avoided areas of productive shrub-forb vegetation (riparian and shrub NDVI), when surrounded by stands of high level pinyon-juniper cover, otherwise those vegetation types were strongly selected. During parturition female mule deer selected habitat that maximized hiding cover for newborns (greater shrub densities and structural cover), while still providing foraging opportunities (greater NDVI and shrub cover). Females underutilized certain areas that contained optimal forage such as riparian corridors, high AET sites, higher elevation shrub communities, and selected areas with low to moderate tree cover, suggesting some trade-off between minimizing predation risk for offspring, and maximizing foraging opportunities.

Demographic rates (body condition, survival, fetal rates, and index of recruitment) of female mule deer were sensitive to changes in resource availability resulting from variation in precipitation or habitat composition and suggestive of a population regulated to a greater degree by bottom-up processes, and likely nearing nutritional carrying capacity. Moreover, I identified a strong negative effect of pinyon-juniper cover on annual survival, only during periods of drought, otherwise individuals were able to maintain relatively high survival regardless of habitat composition. These results suggest that in productive years mule deer are able to inhabit areas of varying levels of pinyon-juniper cover with little effect on survival, and only during the drought years are negative effects evident.

Results from this study emphasize the importance of productive shrub and forb vegetation to mule deer inhabiting semi-arid regions. Maintaining areas with low-to-intermediate tree cover, where there is still abundant shrub understory and sufficient concealment cover, may be beneficial to mule deer populations. Nevertheless, the strong influence of resource availability on the population suggests that conversion of sagebrush-steppe communities into large stands of PJ dominated woodlands would likely reduce the quality and abundance of available habitat for mule deer in the Great Basin.

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INTRODUCTION

Understanding the complex relationships between animal species and their environment is a critical component to understanding their ecology. This information allows us to predict how populations might change through time, or how animal distributions might shift with changes in climate or landscape composition. Life history strategies for many large herbivores have been shaped by density-dependent feedbacks related to resource availability (McCullough 1999). These evolved life-history strategies influence how populations respond to environmental variation such as changes in climate, habitat composition, or predation pressure (Bowyer et al. 2005). Therefore, when assessing animal populations and their relationship to the environment it is important to consider both these intrinsic and extrinsic factors.

Most North American ungulates have experienced historic range contractions and population declines over the last 200 years (Laliberte and Ripple 2004). This is particularly evident in the western United States where mule deer (*Odocoileus hemionus*) populations have declined throughout much of their range since the late 1950s causing much ecological and management concern (Carpenter 1998, Gill 2001). Hypotheses regarding causes of these declines include land use change, competition with wild and domestic herbivores, predation, overharvest, fire suppression, vegetation change, extreme weather, and increased human disturbance (Clements and Young 1997, Gill 2001, Heffelfinger and Messmer 2003, Laliberte and Ripple 2004). Habitat loss and degradation resulting from anthropogenic disturbances such as mineral extraction, oil and natural gas exploration, and human development has been the focus of much research on ungulate declines in the Western United States (Sawyer et al. 2006, Markovchick-Nicholls et al. 2008, Beckmann et al. 2012, Lendrum et al. 2013). Moreover, long term shifts in plant communities, changing climate, and altered fire regimes, are also important factors which may contribute to population declines (Bender et al. 2013), and merit additional investigation.

Changes in landscape composition can negatively influence animal populations through shifts in dominant plant communities, loss of important forage items, or changes in structural components of habitat. 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 woody plant expansion (Archer et al. 1995, Romme et al. 2009). This expansion of woodland into shrub and grassland ecosystems has become an issue of concern worldwide (Bokdam and Gleichman 2000, Van Auken 2000, Buitenwef et al. 2012). The western United States has experienced a trend of increasing distribution and density of pinyon-juniper woodland over the past 120 years (Miller and Wigand 1994, Romme et al. 2009). In the Great Basin, single leaf pinyon pine (*Pinus monophylla*) and Utah juniper (*Juniperus osteosperma*) have extended their range from steeper mountain slopes to alluvial fans and grasslands (Tausch and West 1988). Since the late 19th century tree densities have increased, and there has been a shift of pinyon-juniper woodland from historically mid-elevations both upward and downward in elevation (Tausch et al. 1981). This trend often results in expansion into adjacent shrub steppe, grassland, aspen and riparian communities (Miller and Wigand 1994) with increased rates of infilling of more mesic sites (Weisberg et al. 2007, Jacobs 2011). Recently, tree die-offs have been identified at lower elevation sites likely the result of drought conditions due to a shifting climate (Van de Ven et al. 2007). This increase in distribution and density (infilling) of pinyon-juniper woodlands has been attributed to a combination of factors such as climactic shifts towards milder winters, and increased precipitation during the late 1800s and early 1900s, which promoted vigorous growth of pinyon and juniper (Romme et al. 2009). In addition, during that time there were high intensities of domestic livestock grazing that led to a reduction in fine fuels, reducing fire frequency, and helping to facilitate pinyon-juniper expansion (Miller and Wigand 1994, Jacobs 2011). Nevertheless, this process is, still not fully understood.

Given the scarcity of water in semi-arid ecosystems, 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). As expansion and infilling by pinyon-juniper woodland occurs, tree densities increase and understory biomass declines (Tausch et al. 1981, Everett and Ward 1984, Pieper 1990, Wrobleski and Kauffman 2003). This trend is most prevalent on south facing slopes, where canopy cover can range from 20-30%, with understory cover containing 5% shrubs, grasses, and forbs, and nearly 70% bare ground (Miller and Wigand 1994). Transition from plant communities dominated by shrubs and forbs to woodlands can have negative consequences for animal populations that rely on healthy 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). In addition, sites that become dominated by dense stands of PJ often reach a threshold where natural disturbance, such as fire, may be incapable of returning the system to an earlier successional stage (Twidwell et al. 2013).

Mule deer in the Great Basin are selective foragers, given their small body size, and require forage items with high protein and high digestible energy to meet nutritional demands during summer for lactation, and accumulation of energy stores for winter (Sadlier 1980, Barboza and Bowyer 2001, Tollefson et al. 2011). Resource acquisition, and ultimately nutritional condition, determine energy reserves available for maintenance and reproduction (Monteith et al. 2013), and as a result populations are sensitive to changes in resource availability, specifically the quality and quantity of forage (Parker et al. 2009). Resource availability is even more critical in arid ecosystems where annual fluctuations in precipitation can have strong effects on plant production, and nutritional quality for ungulate populations (Marshal et al. 2005, Stewart et al. 2005, Tollefson et al. 2010). Changes in patterns of precipitation along with shifts in landscape composition, or disturbance have the potential to negatively affect mule deer populations through reduction in forage availability or changes in structural components of the landscape.

Moreover, during parturition female mule deer often select habitat characteristics associated with low predator activity and increased concealment cover for young to enhance offspring survival and subsequently their own reproductive fitness (Main and Coblentz 1996, Shallow et al. 2015, Jacques et al. 2015). Mule deer neonates are most vulnerable to predation during the first month of life and mortality rates as high as 70% have been documented in some populations (Salwasser et al. 1978, Bleich et al 2006, Shallow et al. 2015). To minimize risk of predation on newborns, adult females often adopt one or more antipredator behaviors associated with parturition including isolation from conspecifics, and reduction of home range size or overlap (Fox and Krausman 1994, Schwede et al. 1993). Studies have shown that bed sites with higher shrub densities and steeper slopes can increase survival of young by reducing exposure to coursing predators, such a coyotes (Cook et al. 1971, Smith and Lecount 1979, Shallow et al. 2015). Because of their limited mobility neonates are especially vulnerable to predation and as a result, adequate birthing habitat is critical to neonate survival (Smith and Lecount 1979, Bangs and Krausman 2004). If increasing densities of pinyon-juniper lead to reductions in shrub cover and understory biomass this could also have negative effects on concealment cover for newborns and ultimately survival of young.

To assess the relationships between habitat composition, climatic variation and population demographics, I studied a population of mule deer in the White Mountains of eastern California and western Nevada, USA, from 2005 through 2008. I evaluated population regulation and summer habitat use in this semi-arid ecosystem with a focus on the influence of pinyon-juniper woodland. The White Mountains are a high elevation mountain range that fall within the rain shadow of the Sierra Nevada Mountains, resulting in very low rainfall for a mountain range of their size. Mule deer in the region tend to move up and down in elevation within the mountain range in response to seasonal availability of resources and use low elevation (1800 m) shrub habitat during the winter and spring, then transition to intermediate elevation, mesic-shrub communities and alpine habit during the summer months (2,900 m-4,000 m) (Hall 1991, Cox et al. 2009). Helicopter surveys from 2006, 2007, and 2008 identified very low mule deer densities in the White Mountains, in addition there is concern that the population is declining, based response from hunter postcard surveys and harvest data for the region (CA Department of Fish and Game, personal communication), however little baseline ecological data existed for this region. Lack of high-quality habitat was thought to be one factor contributing to low population density in the White Mountains. Expansion and infilling of pinyon-juniper woodland over the past decade has resulted in large stands of closed canopy pinyon-juniper habitat (Andre et al. 1965, Tausch et al. 1981, Cox et al. 2009). I was interested if this shift in plant community, from one dominated by palatable shrub species to unpalatable conifer species had the potential to decrease nutritional carrying capacity and cause declines in mule deer populations.

In Chapters 1 and 3, I characterized summer habitat selection of female mule deer in the White Mountains, with a focus on the influence of pinyon-juniper woodland. Chapter 1 focused on general summer habitat selection (July through September) where I evaluated selection at 2 spatial scales and 3 temporal scales. Chapter 3 focused on habitat selection during parturition, which is a critical life stage for survival of young. In evaluating habitat selection, I was particularly interested in accounting for variation in site productivity and animal behaviors that could obscure the true relationship between pinyon-juniper density and habitat use. Gradients in site productivity, which are driven largely by variation in elevation, precipitation, aspect, and soil composition, can influence forage abundance and quality even within plant communities, therefore it is important to account for this variation, particularly in heterogeneous landscapes with a great deal of spatial variability in soil moisture. Moreover, individuals may partition resources within their home range dependent on behaviors related to foraging or resting, which can obscure relationships between components of habitat.

I predicted that to maximize nutrient intake during foraging periods, mule deer would forage during cooler parts of the day, and select areas with greater site productivity, and robust forb-shrub vegetation, and avoid areas of moderate-to-high pinyon-juniper density. Conversely, I predicted that mule deer would rest during the hottest parts of the day and select habitat containing higher densities of pinyon-juniper during resting periods to aid in predator avoidance (Altendorf et al. 2001), or thermoregulation (Giotto et al 2013). I used generalized linear mixed models (GLMM) to estimate resource selection functions for female mule deer during summer (July-August) of 2005 to 2008 (Chapter 2). I calculated average hourly movement rates of females to identify periods of highest and lowest movement rates, which related to foraging and resting periods. I then modeled resource selection for each activity period separately to compare habitat use between foraging and resting (Chapter 2).

To evaluate patterns of resource selection during the time period surrounding parturition (Chapter 3) I used location data of female mule deer in the White Mountains, during June and July, from 2005 to 2008. Given that deer exhibit substantial reductions in movements surrounding parturition (Bertrand et al. 1996, Carstensen et al. 2003) I was able to estimate timing of birth using movement data from GPS-collared females and identified location clusters corresponding to habitat used during parturition (Long et al. 2009, Bush et al. 2015). I hypothesized that parturient females would select habitat that provided greater protection for neonates, such as increased understory cover, steeper slopes, and proximity to escape terrain, rather than solely focusing on prime foraging locations, during this period when neonates are most vulnerable to predation. I also hypothesized that pinyon- juniper woodlands would not contain characteristics, such as understory cover, necessary to conceal newborns and therefore would be avoided by parturient females. I evaluated these hypothesis at both a local and landscape scale to examine the influence of fine scale structural characteristics in addition to larger landscape scale processes related to topography and vegetation associations on resource selection of female mule deer during parturition.

In Chapter 2, I assessed population regulation in the White Mountains, to characterize the population status relative to ecological carrying capacity and assess the degree to which bottom-up or top-down processes are influencing this population. I was also interested in evaluating habitat quality and examine the influence of climate and habitat composition on demographic processes, particularly with respect to pinyon-juniper woodland. I considered hypothesized relationships between resource limitation and life-history characteristics (Bowyer et al. 2005) to assess the population status relative to ecological carrying capacity and to determine factors that contributed to regulation of this population (Pierce et al. 2012, Bowyer et al. 2014). Based on the hypothesized relationships identified by Bowyer et al. (2005), I predicted that if intraspecific competition for resources (bottom-up) was regulating this population, then fetal rates, body condition, and recruitment would be low relative to the reproductive potential of this species in highly productive environments. In addition, individuals would demonstrate later age at maturity, and greater variability in survival and recruitment, particularly for non-prime aged individuals (Festa-Bianchet et al. 1998). I also predicted that these metrics would be sensitive to annual fluctuations in resource availability driven by variation in habitat quality and precipitation. I used demographic data related to the productivity of the population (body condition, fetal rates, index of recruitment, adult survival) to evaluate this relationship to nutritional carrying capacity, and determine if these individual demographic rates were sensitive to fluctuation resource availability related to precipitation or summer home range composition. I predicted that vital rates would be negatively correlated with habitat characteristics that reduce forage availability or site productivity, such as greater overstory cover of pinyon-juniper. I also predicted that precipitation would moderate this relationship by mitigating negative effects of low quality habitat on vital rates or, conversely, that low-quality habitat might reduce benefits associated with periods of high precipitation (Blomberg et al. 2012, Owen-Smith 2014).

Resource availability and structural components of habitat—through their effects on body condition, survival, and reproduction—have direct fitness consequences on individuals and resulting demographics (Bender et al. 2007, Forrester and Wittmer 2013, Monteith et al. 2014, Shallow et al. 2015). Understanding how successional processes and climatic variation, influence habitat quality and population dynamics of animals, in dynamic ecosystems, is critically important to predicting how populations will change through time. This information is also important for understanding how populations will respond to future changes in landscape composition or shifts in climate.

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Chapter 1 - Woodland encroachment in a shrub-steppe ecosystem: effects on resource availability and behavior of a native ungulate

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ABSTRACT

Changes in landscape composition have the potential to negatively influence animal populations through changes in structural components of habitat, shifts in dominant plant communities, or loss of important forage items. In the western United States expansion of woodland vegetation into shrub dominated communities is of concern, particularly with regard to animal populations reliant on robust sagebrush and shrub vegetation. Once established, trees can out-compete shrubs and herbaceous vegetation for soil nutrients and water, leading to declines in understory biomass. Ungulates inhabiting semi-arid ecosystems are reliant on productive forb and shrub communities during summer months to meet the high energetic demands of lactation and for accumulating energy stores for winter. Declines in understory vegetation and forage availability have been shown to negatively affect body condition, pregnancy rates, and survival of young. Our objectives were to determine summer habitat composition of mule deer in the White Mountains, CA, and assess implications of pinyon-juniper expansion on habitat availability and resource use. We used mixed-effects logistic regression to model resource selection of female mule deer during summer from 2005 to 2008. We modeled summer resource selection at two spatial scales and among multiple activity periods to account for behavioral variation in habitat use. We included habitat variables related to vegetation type, site productivity, terrain attributes, and fine-scale abundance of pinyon-juniper to directly assess effects of tree cover on habitat selection. We detected significant differences in movement rates by mule deer among three activity periods (night, crepuscular and mid-day) with observable differences in habitat use. 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 at all spatial and temporal scales, but they selected areas with low to intermediate tree cover during resting periods and tended to use areas with smaller patches of trees (5m radius) slightly more frequently, then during foraging periods. Moreover, mule deer avoided areas of productive shrub-forb vegetation when it was surrounded by stands of high levels of pinyon-juniper cover. These results emphasize the importance of productive shrub and forb habitat to mule deer inhabiting arid and 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. These relationships lend support to the hypothesis that large, dense stands of pinyon-juniper cover reduce availability of summer habitat and alter patterns of resource selection for mule deer, a shrub-dependent ungulate.

INTRODUCTION

Landscape changes have the potential to negatively influence animal populations through shifts in dominant plant communities, loss of important forage items, or changes in structural components of habitat. 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 woody plant expansion (Archer et al. 1995, Romme et al. 2009). This expansion of woodland into shrub and grassland ecosystems has become an issue of concern worldwide (Bokdam and Gleichman 2000, Van Auken 2000, Buitenwef et al. 2012).

Trees can out-compete shrubs and herbaceous plants for light, soil nutrients, and water, dramatically reducing vigor and productivity of shrub-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, the certain regions within western United States has experienced an increase in the distribution and density of pinyon pine (*Pinus* spp.) and juniper (*Juniperus* spp.) woodlands (hereafter PJ), 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 (Tausch et al. 1981).

Historically, PJ woodlands occupied mid-elevations, but recent expansions have extended their distribution upward to steep mountain slopes and downward into alluvial fans and grasslands (Tausch et al. 1981, Tausch and West 1988) and often into adjacent aspen, riparian and shrub-steppe communities (Miller and Wigand 1994) with increased rates of infilling of more mesic sites (Weisberg et al. 2007, Jacobs 2011). Recently, tree die-offs have been identified at lower elevation sites being likely the result of drought conditions due to a shifting climate (Van de Ven et al. 2007). Given the scarcity of water in semi-arid ecosystems, 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 shrubs and forbs to woodlands can have negative consequences for animal populations that rely on healthy 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). In addition, sites that become dominated by dense stands of PJ often reach a threshold where natural disturbance, such as fire, may be incapable of returning the system to an earlier successional stage (Twidwell et al. 2013).

Type conversion of shrub communities to dense woodland can increase canopy fuel loads that result in high intensity fires (Holl et al. 2012), loss of understory vegetation or seed sources for native plants, invasion of non-native annuals that are fire adapted, or changes in soil hydrology, making reestablishment of native shrub communities difficult (Pierson et al. 2010, Miller et al. 2001). These interactions are more problematic in arid environments where nutrients are limited and plant growth occurs slowly and, as a result, disturbance and woody plant encroachment can have greater and more lasting impacts on plant and animal communities. Indeed, resource availability and structural components of habitat—through their effects on body condition, survival, and reproduction—have direct fitness consequences on individuals and resulting demographics (Bender et al. 2007, Forrester and Wittmer 2013, Monteith et al. 2014, Shallow et al. 2015). Understanding how these successional processes influence habitat quality and population dynamics of animals in heterogeneous landscapes is critically important to predicting future effects of landscape change on species persistence.

Mule deer populations in the Western US have declined across much of their range since the late 1950s (Carpenter 1998, Gill 2001, Heffelfinger and Messmer 2003). Habitat loss and degradation resulting from anthropogenic disturbances such as mineral extraction, oil and gas exploration, and other anthropogenic activities have been the focus of much research on mule deer declines (Tull et al. 2001, Sawyer et al. 2006, Markovchick-Nicholls et al. 2008, Beckmann et al. 2012, Lendrum et al. 2013); nonetheless, the potential effects of PJ expansion and other landscape change on mule deer populations remain uncertain.

Mule deer populations inhabiting the Great Basin are wide-ranging and dependent on healthy shrub communities. Strong relationships exist among summer resource availability, nutritional condition of females, and recruitment, particularly in semi-arid environments, for large herbivores (Pettorelli et al. 2003, Stewart et al. 2005, Parker et al. 2009, Montieth 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 and fawn rearing, as well as for accumulating energy stores for winter (Parker et al. 2009, Tollefson et al. 2010). Declines in understory vegetation can negatively affect demographics of ungulate species through reductions in body condition, pregnancy rates, and survival of young (Verme and Ullrey 1984, Clements and Young 1997, Bender et al. 2007, Shallow et al. 2015). Moreover, mule deer are likely a good indicator of changes in habitat quality and ecosystem health (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 PJ expansion or loss of productive habitat.

Species reliant on robust shrub communities may be especially sensitive to increases in densities and distribution of PJ woodlands. Given that increases in PJ densities lead to loss of understory biomass (Tausch et al. 1981), areas with moderate to high densities of PJ would likely be considered poor habitat for mule deer based on forage abundance and quality. If mule deer in fact avoid these areas, then a shift in plant community from one dominated by palatable shrub and forb species to unpalatable conifer species could decrease carrying capacity and alter animal distributions. Increases in tree cover may also influence predation pressures and predator avoidance behavior. Predicting species responses to shifts in plant communities is critically important, given the additional external threats to community stability introduced by anthropogenic sources such as climate change, establishment of invasive species, and changes in land-use.

We used a resident population of mule deer in the American Great Basin as a model system to examine the potential implications of changing PJ densities on habitat selection of this shrub-dependent herbivore. We evaluated summer resource selection by female mule deer as a function of varying levels of PJ density. Our goals were to identify key components of summer habitat and assess the potential effects of PJ expansion on resource use by those ungulates. We were particularly interested in accounting for variation in site productivity and animal behaviors that could obscure the true relationship between PJ density and habitat use. Gradients in site productivity, which are driven largely by variation in elevation, precipitation, aspect, and soil composition, can influence forage abundance and quality even within plant communities. The ability to detect animal responses to PJ densities can 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. Moreover, activity patterns related to time of day can also influence how animals respond to PJ densities. For example, 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). The shrub-like growth form of PJ, particularly in younger trees (Weisberg and Ko 2012) may also provide visual obstruction from predators during resting or foraging periods (Bender et al. 2007, White et al. 2010). To address these potentially confounding relationships in the context of PJ cover, we also examined diurnal patterns of habitat selection, which corresponded to resting and foraging periods during the summer months.

We compared summer resource selection at multiple spatial and temporal scales to determine how behavioral responses to PJ density changed relative to spatial scale and activity period. Because the importance of landscape covariates can differ over spatial scales (Boyce 2006), we evaluated selection at two levels: (1) placement of summer home ranges within the larger landscape; and, (2) selection of habitat attributes within individual home ranges. These scales correspond to 2nd and 3rd order resource selection (Johnson 1980). Given the negative relationship between overstory cover and understory biomass, we predicted that mule deer would avoid areas of high PJ density; however, low-to-moderate amounts of tree cover could be beneficial as concealment from predators or as thermal cover. As a result, we expected movement rates to decline mid-day, when temperatures were highest and correspond with resting periods, and that habitat selection would vary according to foraging or resting behaviors. We predicted that to maximize nutrient intake during foraging periods, deer would select areas with productive forb or shrub habitat and avoid areas of moderate-to-high PJ density. In contrast, we predicted deer would select habitat containing higher densities of PJ during resting periods.

STUDY AREA

The White Mountains are located in Inyo and Mono counties in California and Esmeralda County in Nevada, 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 rose in elevation over a distance of 20 km from their base in Fish Lake Valley at 1,400 m to their crest at elevations largely between 3,000 m and 4,000 m, reaching their maximum elevation of about 4,300 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 rainfall for their size and elevation. Average precipitation for this region was between 12.7 cm along lower elevations to 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 PJ woodland has resulted in large stands of closed canopy PJ habitat at mid elevations (Andre et al. 1965, Tausch et al. 1981, Van de Ven, et al. 2007).

The mule deer population on the east side of the White Mountains is generally non-migratory and remains within the range over both the summer and winter seasons. Our investigations yielded some evidence that individuals moved to the west side of the range during winter, but that occurred only rarely. Mule deer tended to use low elevation (1,800m) shrub habitat during the winter and spring, then transitioned to intermediate elevation and alpine habit during the summer months (2,900m-4,000m; Hall 1991) 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, Pierce et al. 2012) with greater contributions of forbs and grasses during the summer months (Hall 1991).

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 2,000 m and is dominated by sagebrush, ephedra (*Ephedra* spp.) and rabbitbrush (*Ericameria nauseosus*). Intermediate elevations from 2,000 m to 2,900 m are comprised predominantly of pinyon-juniper woodland. Single-leaf pinyon (*P. monophylla)* and Utah juniper (*J. osteosperma)* are the codominant tree species, with the understory dominated by sagebrush, bitterbrush, ephedra, and rabbitbrush. The Subalpine Zone extends from 2,900 m to 3,500 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 3,500 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.

The White Mountains contain a range of carnivore species generally occurring at low population densities including coyotes (*Canis latrans*), mountain lions (*Puma concolor*), bobcats (*Lynx rufus*), and black bears (*Ursus americanus*). Domestic livestock are actively grazed on 4 allotments, but grazing pressure has been greatly reduced from the historically high numbers of both 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.

METHODS

Animal capture and data collection

We captured mule deer during the winter and spring over 4 years using a net gun fired from a helicopter (Krausman et al. 1985). Once captured, 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 hours, and those collars also 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. A few collars were programmed to last for up to 2 years and were removed manually. We attempted to distribute capture efforts homogenously across the study area to avoid concentrating study animals and to maintain independent samples.

We used location data collected from July through September coincident with the period when mule deer nutritional demands and ambient temperatures in the study area were the highest and after females had transitioned onto summer ranges following parturition (generally mid-to-late June; Pojar and Bowden 2004, Bishop 2009, Monteith et al. 2011). All capture and handling of mule deer were compliant with procedures outlined by the California Department of Fish and Wildlife, were in keeping with protocols outlined by the American Society of Mammalogists for research involving mammals (Sikes et al. 2011), and were approved by the Institutional Animal Care and Use Committee at the University of Nevada Reno (IACUC: 00109).

Movement rate

We calculated an index of movement rates based on mean Euclidian distance between consecutive animal locations adjusted for the amount of time elapsed between points. Since this movement occurred over the time period between these two locations, we then 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 v2.12; R Development Core Team 2011) with individual as a random intercept term, and hour as a fixed effect. 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; given our long fix rate (3-7hr), however, we extended the sampling period to increase sample size during this activity period. Therefore, we defined the crepuscular periods as those within 3 hours surrounding sunrise or sunset and having the greatest rates of movement.

We used movement rates 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 activity period for the multiple combinations of time groupings (null, crepuscular only, mid-day only, all 3 separate) and evaluated model performance using the Akaike Information Criterion (AIC; Burnham and Anderson 2002).

We also modeled hourly movement rates using January locations to compare movements during hottest and coldest times of year to test the hypothesis that movement rate was related to daily temperatures and not just time of day. During summer months we expected peaks in movement during crepuscular hours and lower rates of movement mid-day when temperatures were warmest. During winter months we expected to see peaks in movement during crepuscular hours as well, but no decline in movement rates mid-day because individuals would be less constrained by high temperatures. During the summer season, the hottest times of day were between 1200 and 1600 based on averaged weather data from stations located within the study area at 1,500 m and 2,700 m, in Dyer, Nevada and the White Mountain Research Station, Crooked Creek facility, respectively (Western Regional Climate Center, www.wrcc.dri.edu).

Habitat variables

To capture local variation in plant communities resulting from variation 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 U.S. Forest Service 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 Forest Service 1981). We reclassified this layer into 13 vegetation associations based on dominant plant species we thought to be of importance to mule deer: (1) grasses and forbs; (2) bare ground; (3) bristlecone pine; (4) Great Basin mixed shrub (mesic shrub community); (5) sagebrush (mid-elevation shrub, most dominant); (6) bitterbrush (lower elevation shrub, major component of winter diet) ; (7) mountain mahogany; (8) pinyon- juniper woodland; (9) Limber pine (upper montane pine); (10) willow; (11)aspen; (12) alpine shrub (13) desert mixed scrub (low elevation and valley, shrub communities).

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 Farm Service Agency 2008) collected during August of 2008. The classification model incorporated the 4 spectral bands from the orthophoto (blue, green, red, and color-infrared), a fifth band containing the Normalized Difference Vegetation Index (NDVI; Pettorelli et al. 2005), and 750 photo-interpreted training 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.

Using NAIP orthophoto imagery, we characterized tree cover at a 1-m resolution, which allowed for more precise estimates of non-riparian tree cover. The classification procedure could not distinguish among conifer species (pinyon, juniper, limber pine, lodge pole pine, bristlecone pine) or mountain mahogany. Using information on vegetation associations from the US Forest Service classification layer for the study area, however, we determined that the majority of non-riparian tree cover was comprised of PJ (70%), with 20% mountain mahogany, 5% bristlecone pine, and 5% limber-lodge pole pine. As a result, we included vegetation associations in our analysis to account for additive effects of plant community, but did not investigate interactions between tree cover and species because the vast majority of tree cover was attributed to PJ. It is possible that deer may respond differently to mountain mahogany than PJ given its potential value as forage and differing understory characteristics and is why we included vegetation associations in our analysis. Nevertheless we generally expected similar successional relationships among forest associations, where increasing overstory cover leads to declines in understory vegetation and results in similar structural characteristics among forest types (Altendorf et al. 2001).

Using the fine resolution classification, we estimated the percent of tree and riparian pixels within a 200-m, 100-m, 30-m, and 5-m radius buffer surrounding the focal cell (Spatial Analyst, ArcGIS 10.0 ESRI, Redlands, California, USA) which allowed us to investigate the influence of habitat composition at the multiple scales relating to patch size; larger stands (100-m or 200-m radius),smaller foraging patches (30-m radius) individual feeding or resting points on the landscape (5 m), which were based on daily movement rates (Hobbs 2003, Boyce 2006). We calculated the distance to the nearest riparian area for each focal pixel (5 m) in the study area. We also calculated an index of greenness using NDVI (Pettorelli et al. 2005) at the patch scale for all non-tree, non-riparian pixels to differentiate between shrub dominated areas with robust shrub cover versus 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 5-m resolution and next 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; United States Geological Survey 2010). Topographic position index is a measure of the relative difference in mean elevation between the focal cell and the surrounding 10-m or 200-m neighborhood, where lower values represent lower hill slope positions and higher values indicate ridge tops.

To account for underlying variation in site productivity in relation 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. 2014). Our model incorporated the 30-year average PRISM climate data (PRISM Group, 2010) to identify relative productivity. To do so, 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: resource selection function

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). To assess 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 650 random points per individual adequately characterized availability at the landscape scale.

To determine available habitat for analysis of within home range selection (third order selection) we created a minimum convex polygon (MCP) for each individual with a 500 m buffer (Geospatial Modelling Environment; Beyer 2012). One available point was generated for every 200 m^2 of home range area (MCP), with a minimum of 350 and maximum of 1,500 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 potential multicollinearities between resource covariates using Pearson correlation (Rcmdr package in R; R Core Team 2013); we classified variables as collinear if the Pearson correlation >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 Core Team 2013). Response variables were coded as used (1) or available (0) locations with habitat covariates included as fixed effects and individuals 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-m, 35-m, 100-m, 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. 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 then identified which of the local scales (5-m, 30-m, 100-m, 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. These interactions allowed us to investigate the influence of tree cover on use of preferred habitat, as well as interactions between site productivity (AET) and habitat covariates, on use. Once we identified our top model using this multistep approach, we used the model dredge command in R (MuMIn package R; R Core Team 2013) to evaluate covariate combinations related to tree cover and its interactions and contained within the top model to confirm that we had identified the most parsimonious structure based on AIC scores. This same iterative process was performed for the landscape and home range scales of selection separately; see Appendix S1 for the list of model results. We then identified the top model for each analysis which was used to investigate covariate effects.

Using the top model from the within home range analysis (3rd order selection), we tested the hypothesis of differential selection in relation to daily activity patterns. Locations from the within home range analysis were grouped based on results from the 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 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/mid-day. The second grouping contained 3 categories for time, either crepuscular, night, or mid-day. Differential selection among the 3 time periods was supported by the analysis. Because we were interested in comparing selection coefficients during each period, we divided the data into 3 separate datasets corresponding to each time period. 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 ($\mu = 0$, SD >1) to allow for direct comparison 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 indicate 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 on habitat use.

RESULTS

RSF Spatial analysis

We monitored a total of 48 adult female mule deer over a period of 4 years (5 in 2005, 15 in 2006, 12 in 2007, and 16 in 2008). We collected between 150 to 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 A). At the landscape scale female mule deer selected areas closer to riparian vegetation, with greater NDVI and riparian cover; we also identified a moderating effects of site productivity (AET) and tree cover (200m) on selection of these habitat variable (see Appendix B for full list of parameter estimates, and Figs. 2, 3). Mule deer selected areas closer to riparian vegetation when site productivity was low, and were less constrained to be near 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 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 of high tree cover at the larger patch size (200-m) at both the landscape and home range scale (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 (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). At sites with high AET, however, mule deer more strongly avoided areas of high 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 tree cover (Fig. 4). Additionally, we observed a negative interaction between tree cover (200-m) and productive habitat (NDVI and riparian; Fig. 3), suggesting 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 identified greater use of areas identified as willow, grasses and forbs, and low elevation shrub communities (bitterbrush, great basin mixed scrub, and desert scrub), and 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. However, estimates for some vegetation associations may be inflated, due to their being rare in the sample (Boyce 2002).

Movement analysis

We Identified peaks in movement rates during crepuscular hours crepuscular (04:00 to 08:59 or 17:00 to 20:59), with deer becoming more sedentary during night (21:00 to 03:59) and even more so during mid-day (09:00 to 16:59;Fig. 6). In contrast, winter movement rates were similar between crepuscular and mid-day hours, but were lowest at night (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 15 ΔAICc over models containing only two groups (crepuscular/night and mid-day; or crepuscular and night/mid-day; Table1). We then used these 3 distinct time groupings to further test hypotheses related to temporal variance in resource selection.

RSF Temporal analysis

We identified support for differential section of habitat covariates based on activity periods (crepuscular, mid-day, night). Inclusion of an interaction between activity period and habitat covariates significantly improved model fit (ΔAIC =268) over the base model 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-liner relationships and interactions with tree cover, that were identified as important components of resource selection from the spatial analyses (see Appendix C for parameter estimates).

In general mule deer showed patterns in resource selection that reflected those identified during our home range analysis, with night and crepuscular periods being most similar and mid-day period being more disparate. Furthermore, parameter estimates from each temporal model indicated similar relationships in selection among all 3 time periods for riparian habitat (35-m), NDVI, and associated interactions with tree cover (200-m; Appendix C), 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 did, however, vary among time periods. Mule deer selected mid-slope positions during crepuscular and night time periods, but used lower hill-slope positions 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 C). Deer tended to select vegetation associations that contained greater cover (such as willow, aspen, pinyon-juniper, mountain mahogany, limber pine, bristlecone) during mid-day when compared with nighttime or crepuscular (Figure 9). Mule deer also avoided vegetation associations that occurred at higher elevations, and selected vegetation association comprised of more open areas during nighttime periods (Figure 9). Overall, vegetation associations used during crepuscular periods were most similar to those used during mid-day, indicating that mule deer select vegetation associations that provide both foraging and resting opportunities at this coarse level of analysis; nonetheless, we did identify differences in selection of tree cover during mid-day periods using finer resolution data (Figure 8). 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 similar to our finding in the home range analysis. Conversely, we did identify a strong negative relationship with tree cover (200-m) during night and crepuscular periods in areas with high levels of AET. This relationship was weak, however, during mid-day periods, with use declining only at very high levels of tree cover (200-m; Figure 9). At the fine scale (5-m), deer tended to select areas that contained trees during mid-day, with no influence of tree cover during crepuscular and night time periods (Figure 9).

DISCUSSION

Mule deer appeared to make decisions about selection of habitat features based on both placement of home range on the landscape, and then subsequent use of habitat patches within that home range. Moreover, we identified noticeable differences in movement rates among the three activity periods (night, crepuscular and mid-day), with corresponding differences in habitat use (Table 1). Significant increase in movement rates during crepuscular and night periods relative to mid-day suggest activity patterns that correspond with foraging and resting behaviors, respectively. 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, Long et al 2014, Giotto et al 2013). This variation in both scale of selection and activity pattern highlight the importance of evaluating selection at multiple spatial and temporal scales to fully understand the dynamics of resource use (Boyce 2006).

In general, preferred summer habitat for mule deer in this semi-arid region consisted of sites close to riparian areas, high site productivity (AET), and greater shrub abundance and greenness (NDVI) in addition to flat or intermediate slopes and low hillslope position. Mule deer inhabiting this Great Basin environment also consistently used vegetation associations that occurred at mid-elevations and contained foraging opportunities such as willow, bitterbrush, mesic shrub (great basin mixed scrub) and grass-forb vegetation, particularly for placement of home ranges at the landscape scale. It is likely that strong selection for proximity to riparian areas and access to riparian vegetation influenced placement of summer home ranges at the landscape scale.

In contrast, resource selection within home range was driven primarily by site productivity (AET) and productive shrub vegetation (NDVI), with riparian areas having a weaker influence on use at this scale (Fig. 2 and Appendix B). These results are consistent with our hypothesis that habitat selection was driven by forage availability and water resources in this semi-arid ecosystem. Reliable water and productive forb and shrub communities have been identified as important components of ungulate summer habitat (Marshal et al. 2006), and concentrated use of areas close to 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 to 50 % increase in energetic demands associated with costs of gestation and lactation (Barboza and Bowyer 2001). Moreover digestive constraints during this period reinforce selection for forages that are highly digestible, with high protein, high energy, and low fiber (Tollefson et al. 2011, Parker et al. 2009). As a result, animals will often concentrate foraging in highly productive areas and the ready availability of resources likely precludes animals from feeding in areas with low forage abundance or low nutritive value (Festa-Bianchet et al. 1988, Parker et al. 2009).

We also identified support for an interaction between site productivity (AET) and distance to riparian areas (Appendix A), wherein areas with relatively low AET, generally drier, hotter, and less productive sites the importance of riparian vegetation increased with mule deer remaining more closely associated with riparian areas. Conversely, in areas with greater AET, generally wetter, cooler, and more productive sites, 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 adequate forage is available (Delgiudice, et al. 1984, Gedir et al. 2016). Within the White Mountains water is scarce and riparian corridors along with wet meadows and seeps provided not only access to free water and generally are associated with productive forb, shrub, and willow communities (Hall, 1991).

We identified multiple lines of evidence that supported our hypothesis of a decrease in habitat suitability as tree cover increased, particularly during summer months when nutritional constraints for female mule deer were highest. High densities of tree cover (200-m) were generally avoided at each spatial and temporal scale (Fig. 9). Mule deer did select low to intermediate levels of tree cover during mid-day periods, presumably while resting; however, deer continued to avoid areas of high tree cover even during that period. 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 tree cover (200-m). Investigators have determined that as PJ overstory cover increases understory biomass declines, resulting in a loss of forb and shrub abundance in addition to species diversity (St Andre et al. 1965, Tausch et al. 1981, Tausch and Tueller 1990, Pierson et al. 2010). 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). Loss of understory vegetation has been linked to increased runoff and erosion, each of which further reduces soil water infiltration (Pierson et al 2010) and are especially problematic in arid environments with limited rainfall.

In a controlled study Bates et al. (2000) reported that removal of juniper reduced below-ground interference for soil water and nitrogen in southeastern Oregon and resulted in a 9-fold increase in nitrogen uptake and understory biomass. This loss in understory biomass has direct implications for forage availability for mule deer in arid ecosystems. Moreover, researchers in northern New Mexico determined that PJ provided 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). Our results suggest that landscape patches dominated by dense stands of PJ would provide less suitable habitat for female mule deer during summer months and, when coupled with previous research, suggest that a transition from shrub-forb communities into PJ dominated woodland has negative implication for forage abundance and habitat availability 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 PJ cover to promote robust shrub-forb vegetation communities (Taylor 1997, Cox et al. 2009).

Although larger stands of dense tree cover were generally avoided, mule deer did select areas that contained trees at a fine spatial scale (5-m), and areas of moroderate tree cover (200-m) during resting periods. These results further support our hypothesis that tree cover may provide some beneficial structural components for either predator avoidance or thermal cover (Giotto et al. 2013, Altendorf et al. 2001). Prior investigations have indicated that mule deer spend a greater 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 forest habitat, 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. These results are consistent with our observations of fine-scale selection for individual trees and negative effects of tree cover on selection occurring mainly at high densities.

Smaller bodied ungulates often select resting sites with greater tree canopy cover during times of year where 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 (TNZ) for adult mule deer ranges from 20 to 30 degrees Celsius 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 degrees Celsius. Ambient temperatures above the TNZ 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 TNZ, 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 in New Mexico foraged in shrub-dominated sites, but that bed-sites were located in areas of greater overstory cover, generally under pinyon or juniper trees, and that activity mid-day was avoided when temperatures exceeded thermal tolerance. In the Great Basin, ambient temperatures mid-day often exceed 30 degrees Celsius and our observations of decreased movement of mule deer mid-day—when temperatures were the hottest (Fig. 6), in addition to greater use of tree cover (Fig. 9), are consistent with behaviors aimed at minimizing costs associated with thermoregulation. Alternatively, mule deer selection for riparian habitat and areas with high NDVI interacted with tree cover similarly among activity periods (Appendix C). These results suggest that riparian vegetation and robust shrub communities provide adequate structural cover during resting periods that aid in predator avoidance and thermoregulation while also providing enhanced foraging opportunities. As such, deer using these plant communities were not forced to make tradeoffs between foraging and resting sites and to not rely on low-density PJ for daytime thermal cover. 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.

We also identified intermediate movement rates at night during summer months, which likely reflected a combination of foraging and resting behavior. Habitat selection was more similar between night and crepuscular periods, which lent support to the hypothesis of nighttime foraging by mule deer in this population. Nevertheless, relatively low movement rates suggest that deer were also resting at night, or did not travel to the same extent that they did during crepuscular hours. Deer in arid ecosystems may forage during night time periods 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 at mid-day, and may use different strategies to avoid nocturnal predators (Lynch et al. 2015). Moreover, our comparison of summer and winter movement rates identified periods of resting concentrated at mid-day during summer months when temperatures were high, a behavior we did not detect during winter when thermoregulatory costs occur mostly at night.

Our research demonstrates 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, and nutrient intake. 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 due to 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, alternatively, 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 PJ cover on habitat selection and to provide insight on how historic changes in distribution and abundance might have influenced mule deer populations 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, among which are habitat loss associated with human development, inappropriate grazing practices, land-use changes, and changing climate condition. Moreover, loss of productive sagebrush-steppe habitat due to expansion and infilling of pinyon-juniper woodland can negatively influence understory composition and forage resources for mule deer and further reduce habitat quality (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, these negative effects are likely pronounced. Moreover, increased rates of PJ expansion on mesic sites have been identified (Weisberg et al. 2007, Jacobs 2011); such sites are more productive and highly selected by mule deer, and PJ woodland is predicted to shift upward into higher elevation shrub communities with increasing temperatures (Van deVen et al. 2007). Conversion of these preferred sites to PJ woodland will undoubtedly intensify negative effects of tree cover on availability of preferred habitat and lead to declines in forage abundance. 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 that may aid in thermoregulation during periods of high temperatures (Giotto et al. 2013). Nevertheless, we expect those benefits to decline as tree densities increase to a level where understory biomass is impacted (Altendorf et al. 2001). Managing for a mosaic of habitat types, with low tree cover, while protecting riparian areas and mesic shrub communities from PJ expansion will likely promote high quality mule deer habitat in these semi-arid ecosystems.

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TABLES

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 to 2008.

Model	*k*	AIC	ΔAIC
Movement Analysis			
Night + Crepuscular + Mid-Day	5	62581	0.0
Crepuscular + (Night & Mid-Day)	4	62598	16.6
(Night & Crepuscular) + Mid-Day	4	63051	469.8
Habitat Selection			
Base +Time(3 periods) * Covariates	36	55307	0.0
Base	23	55574	267.2

Notes: Abbreviations are: k, the number of parameters; AIC, Akaike information criterion value; ΔAIC, difference from model with lowest AIC value.

FIGURES

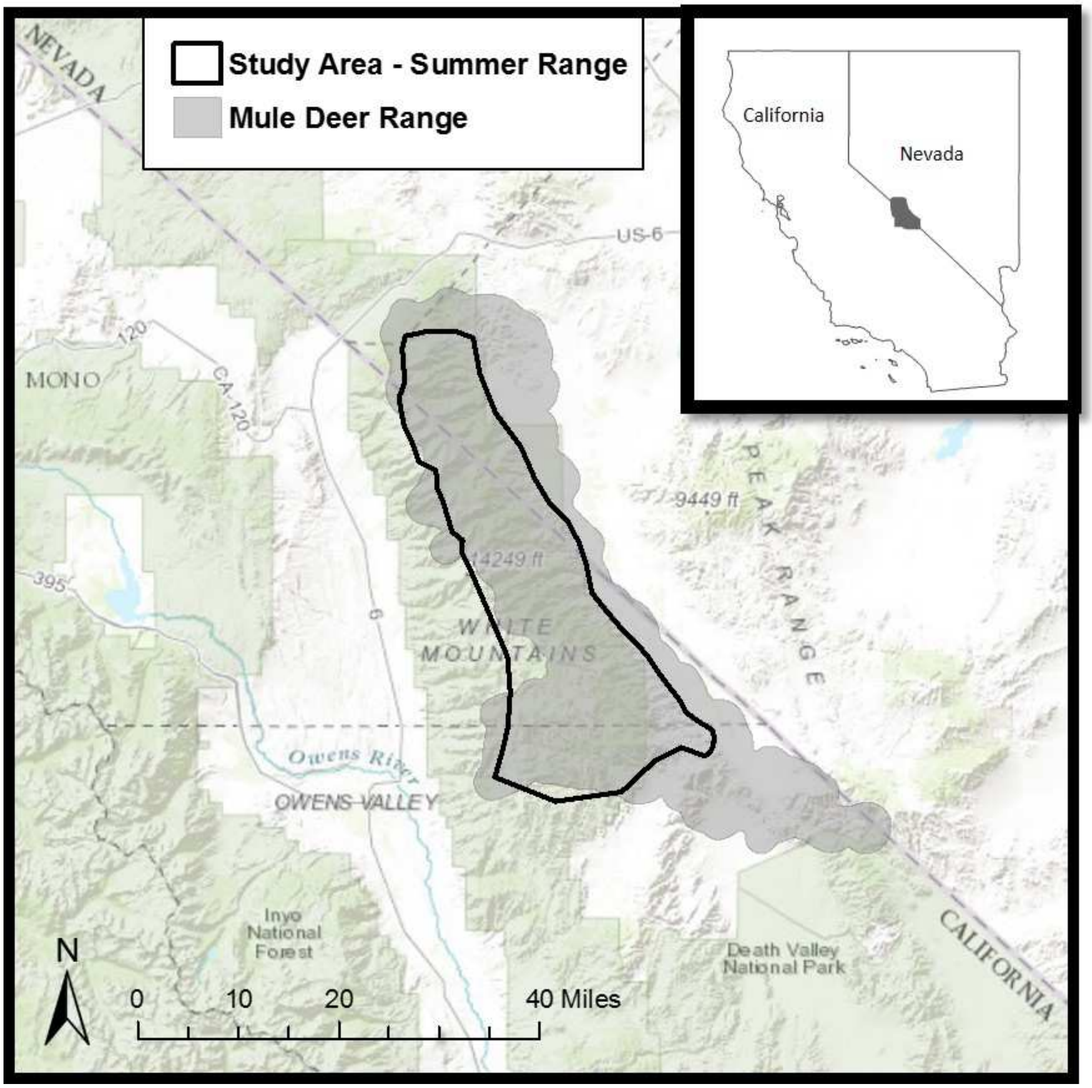

Fig 1. Study area in White Mountains of eastern California and western Nevada, USA. Mule deer range occurred primarily on the eastern side of the mountains with summer range extending between 2,900 m-4,000 m and deer using lower elevations during the winter months.

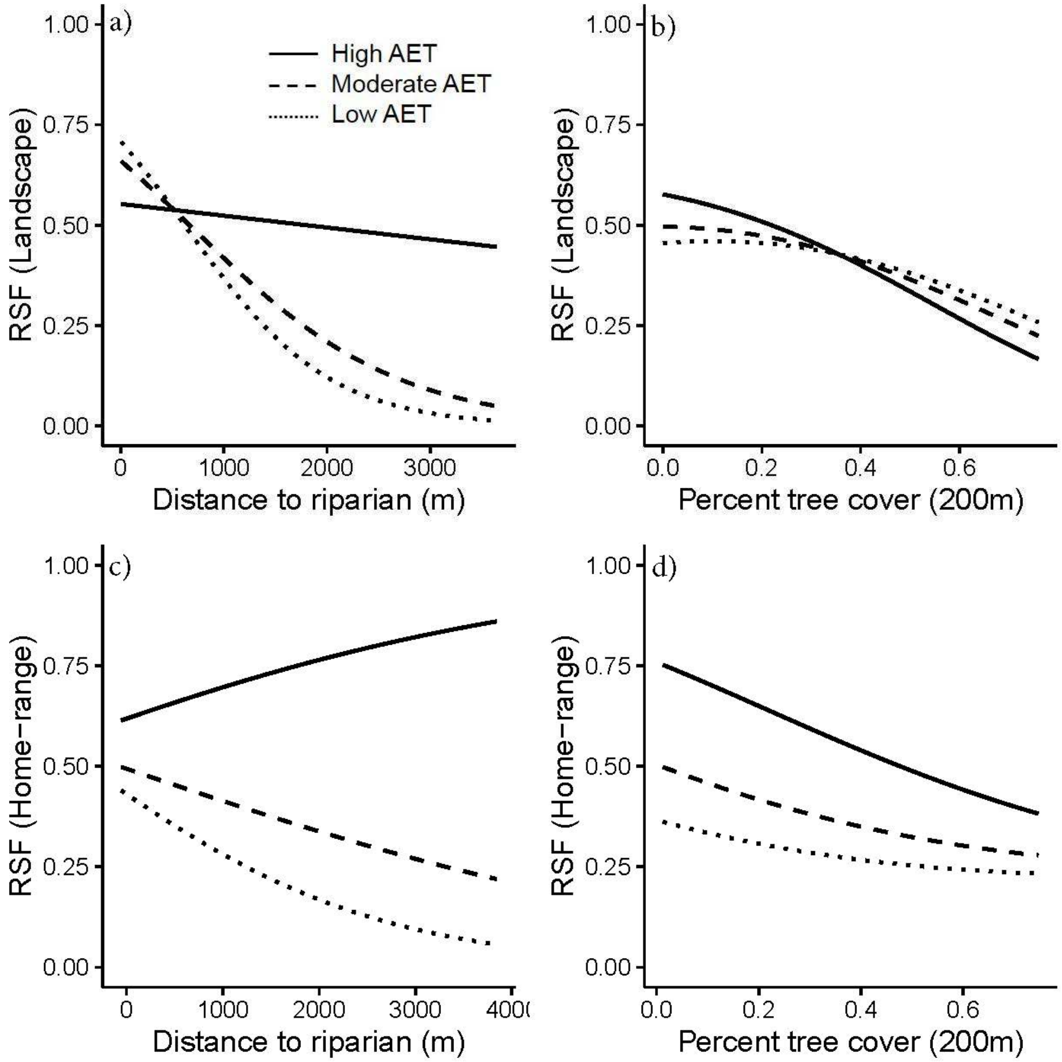

Fig. 2 The influence of distance to riparian vegetation or percent tree cover and interactions with site productivity (AET), on summer resource selection of female mule deer in the White Mountains, California and Nevada, USA from 2005 to 2008. Predicted values were estimated from best generalized linear mixed models for spatial scale. Landscape and home range 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, black) site productivity (AET) based on the range of values in the data. Sites with high AET are generally are wetter, cooler and have more productive plant growth.

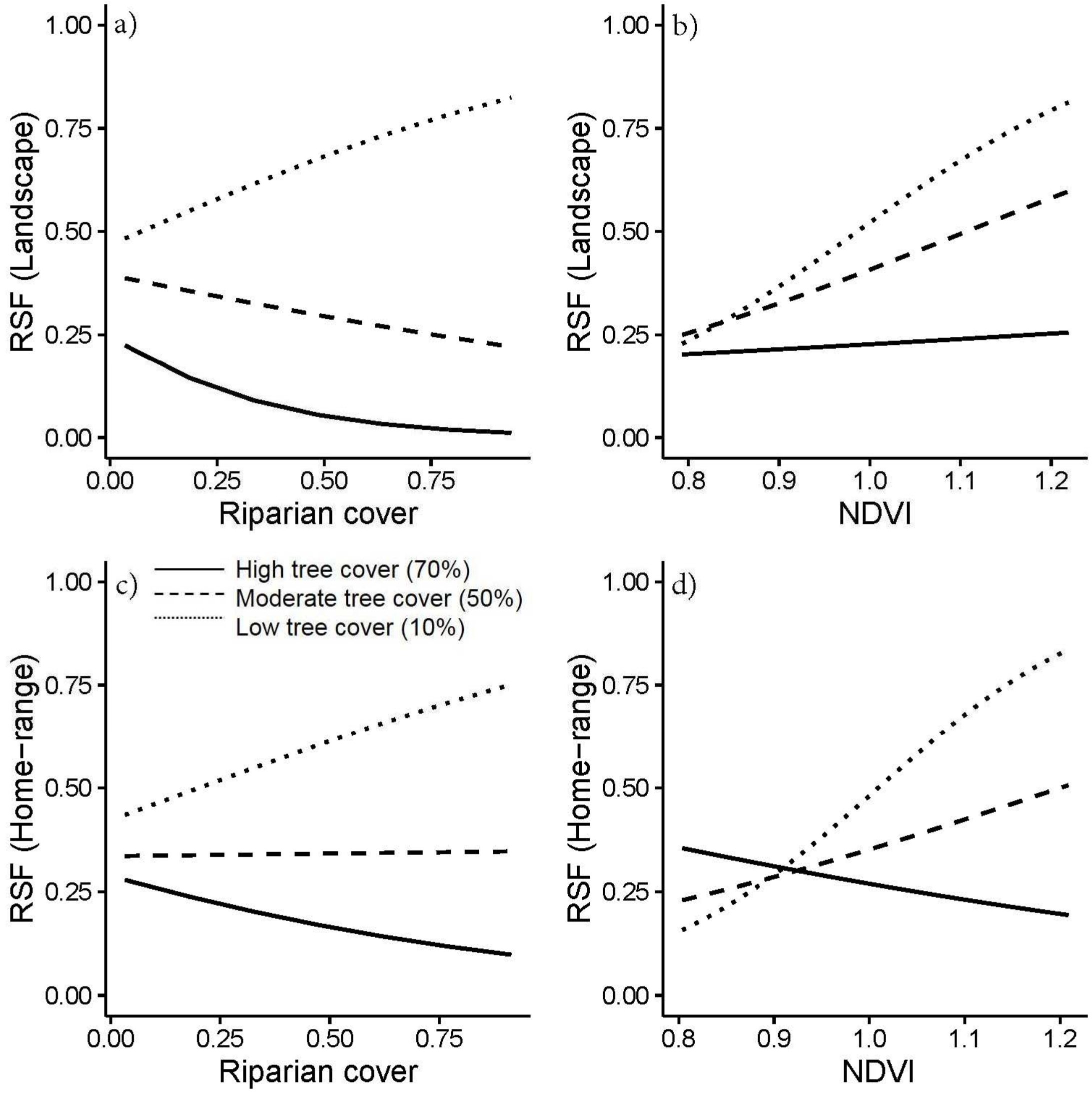

Fig. 3. The influence of riparian cover or shrub NDVI and interactions with tree cover on summer resource selection of female mule deer in the White Mountains, California and Nevada, USA from 2005 to 2008. Predicted values were estimated from best generalized linear mixed models for spatial scale. Landscape and home range 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%, black) tree cover, based on the range of values in the data.

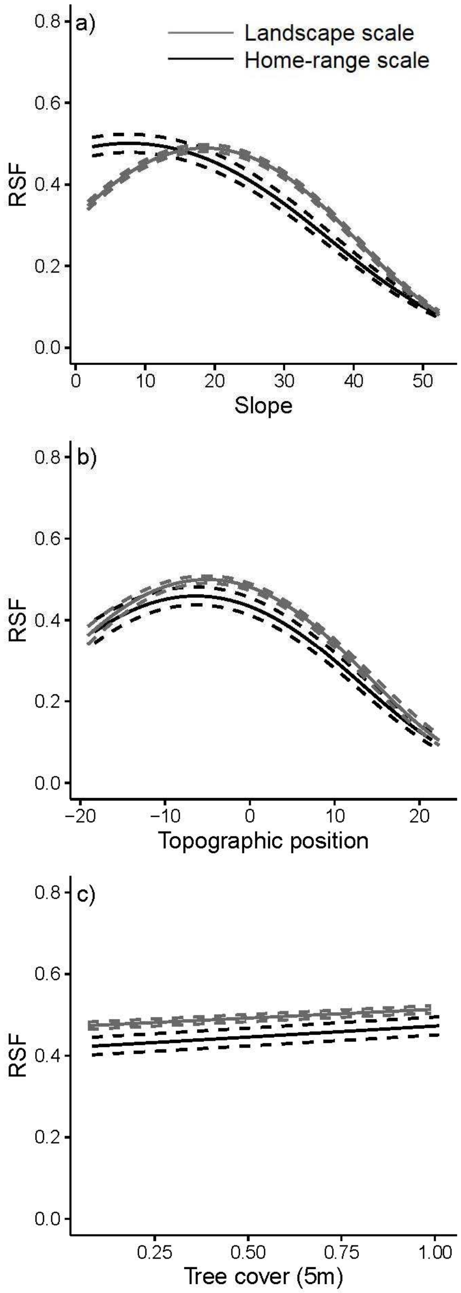

Fig. 4. The influence of slope (a) topographic position (b) and tree cover 5m (c) on summer resource selection of female mule deer in the White Mountains, California and Nevada, USA from 2005 to 2008. Predicted values and 95%confidence intervals were estimated from best generalized linear mixed models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

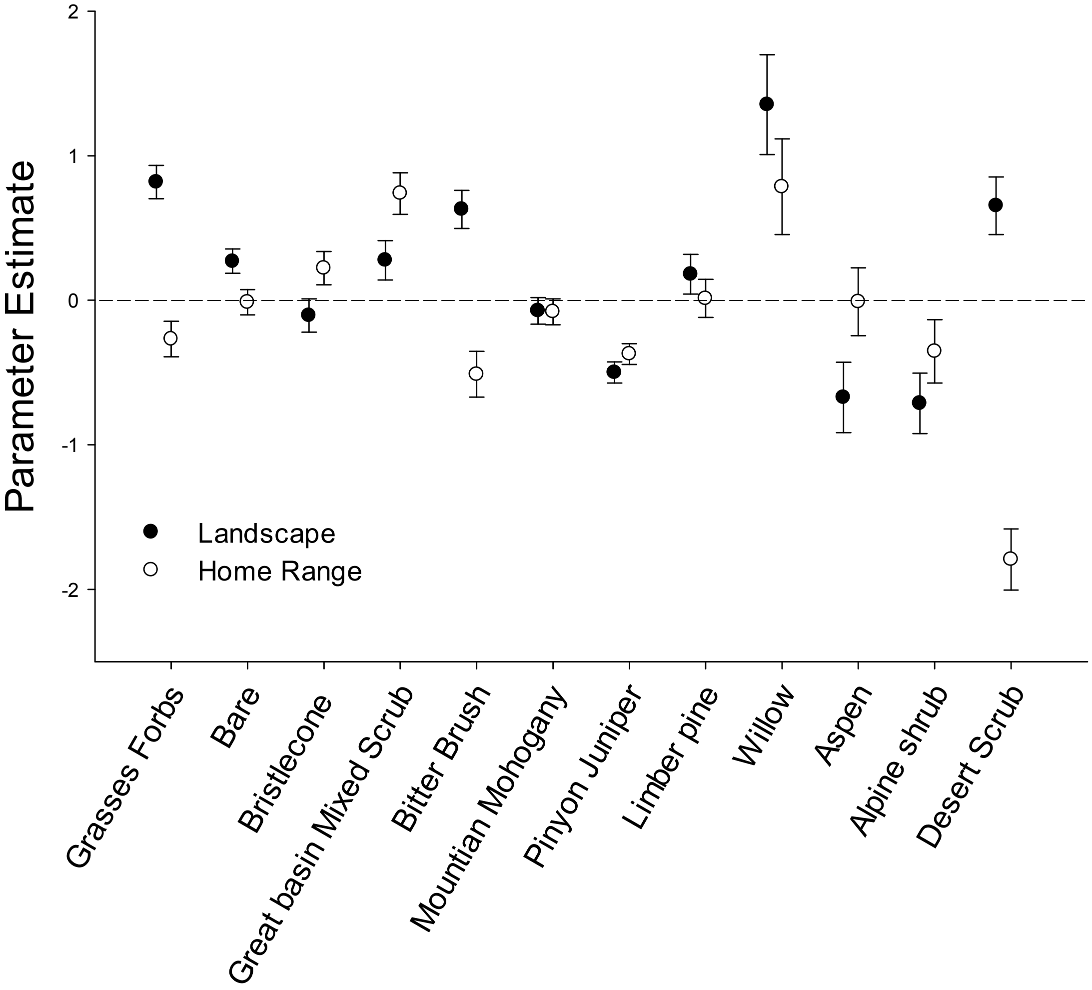

Fig. 5. Parameter estimates ± 95% confidence intervals from best spatial models of summer resource selection (GLMM) for mule deer in the White Mountains, California and Nevada, USA from 2005 to 2008. Landscape and home range refer to spatial scale associated with second or third order selection, respectively.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

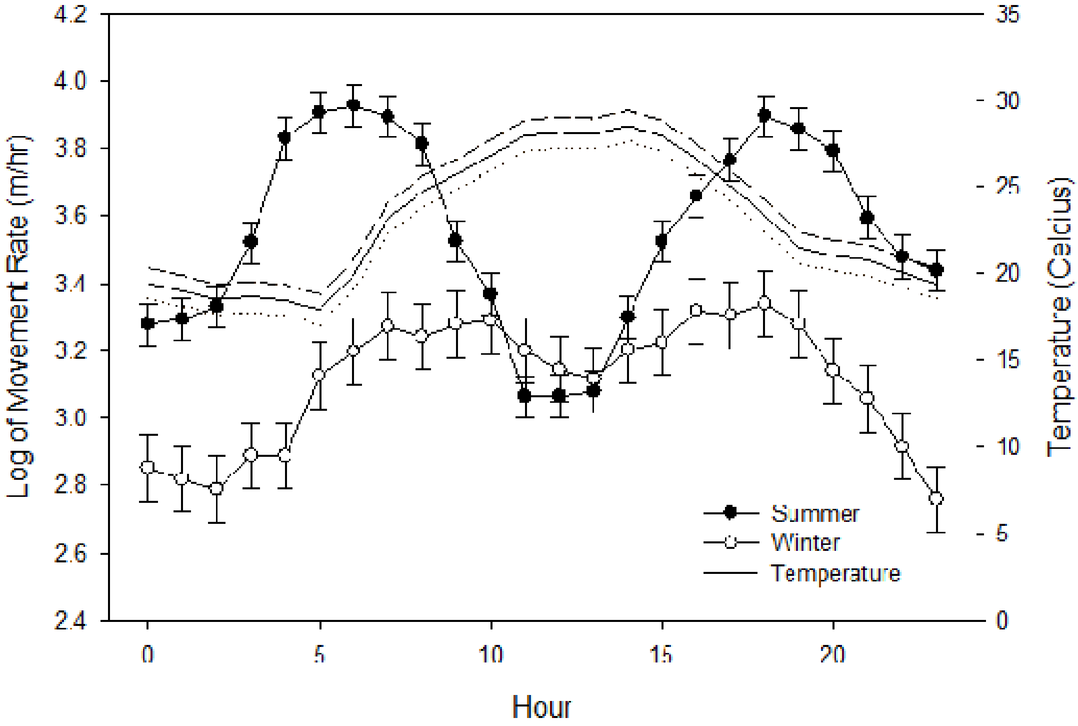

Fig. 6. . Model derived estimates (GLMM) ± 95% confidence intervals for hourly movement rates of mule deer and summer temperature in the White Mountains, California and Nevada, USA based on data collected from GPS collars during the summer or winter 2005–2008. Temperature data were obtained from temperature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

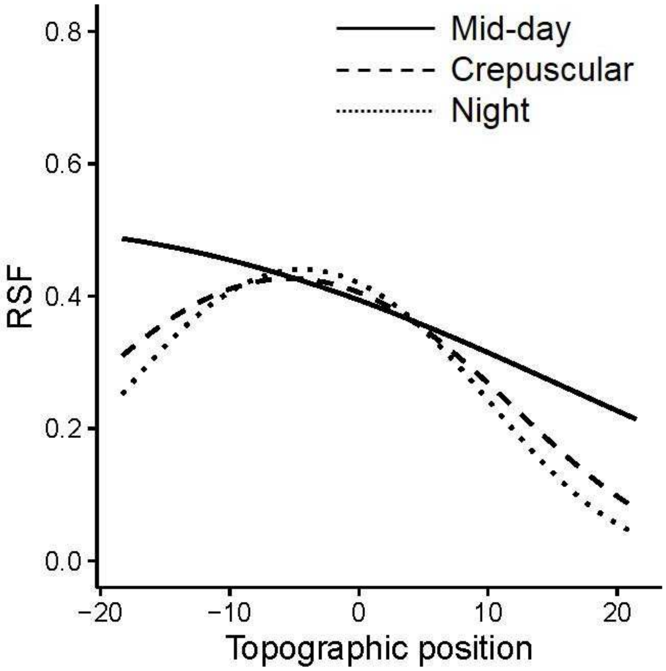

Fig. 7. Relative probability resource selection given varying topographic position of habitat selection for mule deer under varying levels of actual evapotranspiration (AET). Probabilities generated from best temporal model of summer resource selection for mule deer in the White Mountains, California 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 (black) periods.

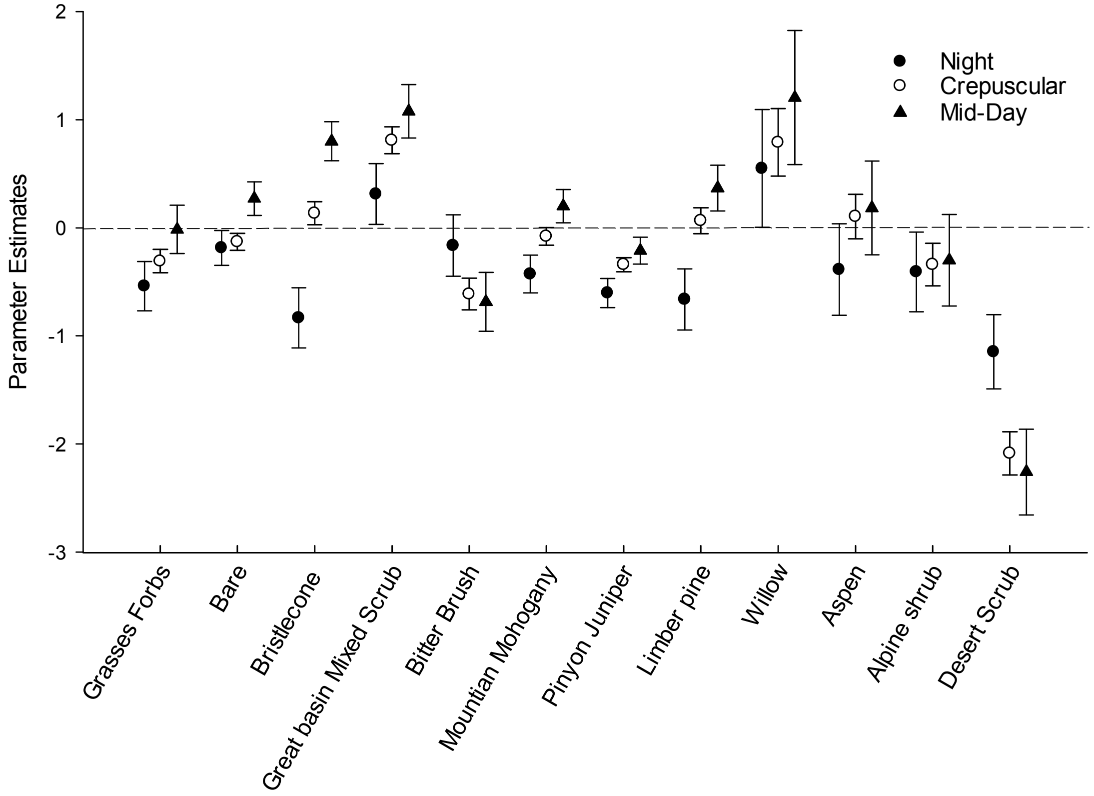

Fig. 8. Parameter estimates ± 95% confidence intervals from best temporal models of summer resource selection (GLMM) for mule deer in the White Mountains, California and Nevada, USA from 2005 to 2008. Resource selection was modeled separately for each time of day (night, crepuscular and mid-day), which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

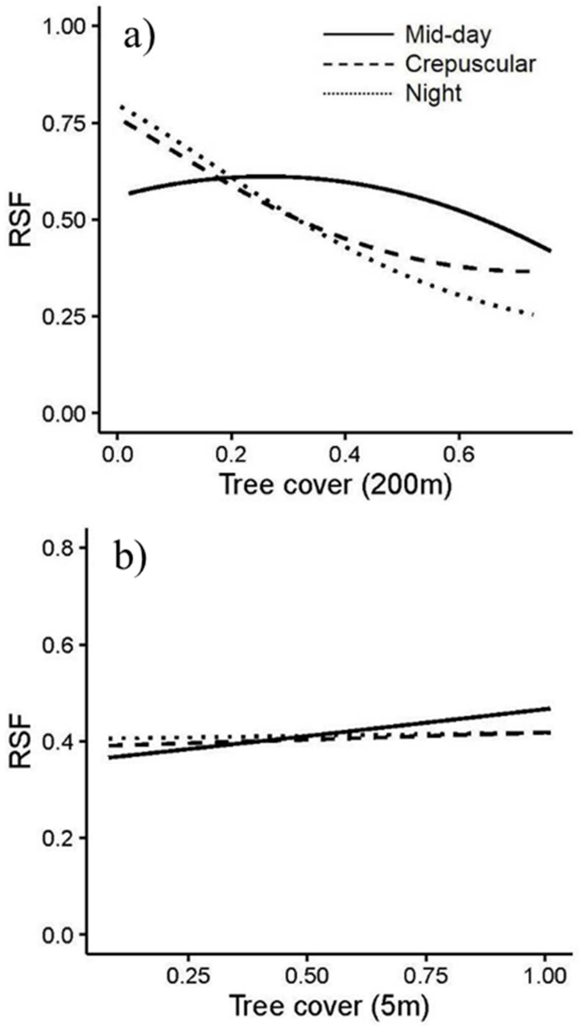

Fig. 9. Influence of tree cover on summer resource selection of mule deer in the White Mountains, California and Nevada, USA from 2005 to 2008. Tree cover 200-m (a) also contains an interaction with site productivity (AET) and results are shown for areas of high AET only, generally wetter, cooler, more productive sites, as 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 time period.

SUPPLEMENTAL MATERIAL

Appendix A

Table S.1. List of model results from assessment of tree effects at the landscape and home range scales. All model combinations for tree density and its interactions were evaluated using AIC values generated from GLMM of resource selection. Models containing a quadratic term or interaction also contained the single variable term.

Veg Type	Slope^2	TPI^2	AET*Dis to Rip	Tree density (5m)	Tree density (200m)	Tree density^2 (200m)	AET* Tree density (200m)	NDVI* Tree density (200m)	Rip*Tree density (200m)	*k*	AIC	ΔAIC
Landscape Scale Models												
+	-	-	+	+	-	-	-	-	-	29	51851	0.0
+	-	-	+	NA	-	-	-	-	-	28	51887	36.2
+	-	-	+	NA	-	-	NA	-	-	27	51905	53.8
+	-	-	+	NA	-	-	-	NA	-	27	51926	74.8
+	-	-	+	NA	-	-	NA	NA	-	26	51950	98.8
+	-	-	+	NA	-	-	-	-	NA	27	52014	163.4
+	-	-	+	+	-	-	NA	NA	NA	26	52028	177.0
+	-	-	+	NA	-	-	NA	-	NA	26	52036	185.4
+	-	-	+	+	NA	-	NA	NA	NA	25	52043	191.9
+	-	-	+	NA	-	-	-	NA	NA	26	52045	194.3
+	-	-	+	NA	-	-	NA	NA	NA	25	52073	222.3
+	-	-	+	NA	-	-	NA	NA	NA	25	52073	222.3
+	-	-	+	NA	NA	-	NA	NA	NA	24	52077	225.5
+	-	-	+	+	-	NA	NA	NA	NA	25	52099	248.4
+	-	-	+	NA	-	NA	NA	NA	NA	24	52157	305.7
+	-	-	+	+	NA	NA	NA	NA	NA	24	52290	438.9

+	-	-	+	NA	NA	NA	NA	NA	NA	23	52301	450.3
Home Range Scale Models												
+	-	-	+	+	-	+	-	-	-	29	54952	0.0
+	-	-	+	NA	-	+	-	-	-	28	55013	61.2
+	-	-	+	NA	-	+	NA	-	-	27	55028	76.7
+	-	-	+	NA	-	+	-	-	NA	27	55063	111.1
+	-	-	+	NA	-	+	NA	-	NA	26	55078	126.1
+	-	-	+	+	-	-	NA	NA	NA	26	55142	190.4
+	-	-	+	+	-	NA	NA	NA	NA	25	55150	198.4
+	-	-	+	NA	-	-	-	NA	-	27	55154	202.5
+	-	-	+	NA	-	-	NA	NA	-	26	55169	217.6
+	-	-	+	NA	-	-	-	NA	NA	26	55193	241.9
+	-	-	+	NA	-	-	NA	NA	NA	25	55208	256.6
+	-	-	+	NA	-	-	NA	NA	NA	25	55208	256.6
+	-	-	+	NA	-	NA	NA	NA	NA	24	55221	269.0
+	-	-	+	+	NA	-	NA	NA	NA	25	55275	323.5
+	-	-	+	NA	NA	-	NA	NA	NA	24	55304	352.1
+	-	-	+	+	NA	NA	NA	NA	NA	24	55486	534.8
+	-	-	+	NA	NA	NA	NA	NA	NA	23	55498	546.4

Notes: Abbreviations are: k, the number of parameters; AIC, Akaike information criterion value; ΔAIC, difference from model with lowest AIC value, NA indicates term was not included in model, +/- refer to whether the estimate for a given parameter was positive or negative.

Appendix B

Table S.1. List of model beta estimates and standard errors, from the best model for both landscape-level and home range-level analysis of summer resource selection of female mule deer in the White Mountains of California and Nevada, during 2005 to 2008. Models containing a quadratic term or interaction also contained the single variable term.

	Landscape		Home Range	
Model parameter	Estimate	SE	Estimate	SE
Intercept	-0.04	0.06	-0.10	0.15
Vegetation Associations:				
Bare	0.27	0.04	-0.01	0.04
Bristlecone	-0.11	0.06	0.22	0.06
Great Basin mixed scrub	0.28	0.07	0.74	0.07
Grasses and forbs	0.82	0.06	-0.27	0.06
Bitterbrush	0.63	0.07	-0.51	0.08
Mahogany	-0.07	0.05	-0.08	0.05
Pinyon-juniper	-0.50	0.04	-0.37	0.04
Limber pine	0.18	0.07	0.01	0.07
Willow	1.35	0.18	0.78	0.17
Aspen	-0.67	0.12	-0.01	0.12
Alpine shrub	-0.71	0.11	-0.35	0.11
Desert scrub	0.65	0.10	-1.79	0.11
Dist to riparian	-0.73	0.02	-0.25	0.02
AET	0.10	0.01	0.50	0.02
Tree^2	-0.05	0.01	0.02	0.01
Slope	-0.14	0.01	-0.36	0.01
Slope^2	-0.21	0.01	-0.12	0.01
TPI	-0.10	0.01	-0.11	0.01
TPI2	-0.04	0.01	-0.03	0.01
Tree (5m)	0.08	0.01	0.10	0.01
Tree (200m)	-0.10	0.02	-0.25	0.02
Shrub NDVI	0.38	0.02	0.47	0.02
Riparian	0.27	0.02	0.23	0.02
Dist to riparian *AET	0.32	0.01	0.26	0.01
AET*Tree (200m)	-0.07	0.02	-0.07	0.02
Shrub NDVI*tree (200m)	-0.09	0.01	-0.15	0.01
Riparian*tree (200m)	-0.20	0.02	-0.11	0.02

Appendix C

Table S.1. List of model beta estimates and standard errors, from the best model of summer resource selection of female mule deer during three time periods (night, crepuscular, and mid-day) in the White Mountains of California and Nevada, during 2005 to 2008. Time periods correspond with activity periods associated with foraging (crepuscular), resting (mid-day) and mixed (night). Models containing a quadratic term or interaction also contained the single variable term.

	Night		Crepuscular		Mid-Day	
Model parameter	Estimate	SE	Estimate	SE	Estimate	SE
Intercept	-0.50	0.19	-0.46	0.18	-0.23	0.18
Vegetation Associations:						
Bare	0.35	0.12	0.18	0.10	0.29	0.12
Bristlecone	-0.29	0.18	0.44	0.14	0.82	0.14
Great Basin mixed scrub	0.85	0.18	1.11	0.15	1.09	0.16
Sagebrush	0.54	0.12	0.29	0.10	0.01	0.11
Bitterbrush	0.37	0.18	-0.30	0.17	-0.67	0.18
Mahogany	0.11	0.14	0.23	0.12	0.22	0.13
Pinyon-juniper	-0.06	0.14	-0.03	0.12	-0.20	0.13
Limber pine	-0.12	0.18	0.37	0.15	0.38	0.15
Willow	1.09	0.30	1.10	0.31	1.22	0.33
Aspen	0.15	0.24	0.41	0.21	0.20	0.24
Alpine shrub	0.13	0.21	-0.03	0.20	-0.29	0.23
Desert scrub	-0.61	0.21	-1.77	0.21	-2.24	0.23
Dist to riparian	-0.32	0.03	-0.28	0.03	-0.18	0.03
AET	0.57	0.03	0.51	0.03	0.38	0.03
Tree^2	0.05	0.02	0.07	0.02	-0.07	0.02
Slope	-0.37	0.02	-0.30	0.02	-0.41	0.02
Slope^2	-0.11	0.02	-0.11	0.02	-0.15	0.02
TPI	-0.13	0.02	-0.11	0.02	-0.11	0.02
TPI2	-0.06	0.01	-0.04	0.01	-0.01	0.01
Tree (5m)	0.03	0.02	0.06	0.02	0.21	0.02
Tree (200m)	-0.31	0.04	-0.36	0.04	-0.05	0.04
Shrub NDVI	0.47	0.03	0.47	0.03	0.43	0.03
Riparian	0.21	0.03	0.21	0.03	0.26	0.03
Dist to riparian *AET	0.29	0.03	0.28	0.02	0.19	0.02
AET*Tree (200m)	-0.17	0.03	-0.09	0.02	0.07	0.03
Shrub NDVI*tree (200m)	-0.17	0.02	-0.15	0.02	-0.13	0.02
Riparian*Tree (200m)	-0.13	0.03	-0.11	0.03	-0.10	0.03

Chapter 2 - Evidence for density-dependent population regulation of a native ungulate: influence of age, climate, and habitat composition

Sabrina Morano, Kelley M. Stewart, Alisa Ellsworth, Vernon C. Bleich

ABSTRACT

Many populations of large herbivores are regulated by density-dependent feedbacks related to nutritional condition. Populations that reach their nutritional carrying capacity often exhibit declines in body condition, declines in pregnancy rates, increase in reproductive pause, and later age at sexual maturity. Resource limitation and density dependence can regulate populations in concert with other extrinsic factors, such as environmental conditions, predation, or changes in habitat composition. In arid ecosystems precipitation has a strong effect on plant production that, when combined with habitat composition, has direct influences on herbivore populations through shifts in availability of resources for maintenance and reproduction. We studied a low density population of mule deer in the White Mountains of California from 2005-2008 to assess the status of the population with respect to nutritional carrying capacity, and examined the degree to which top-down versus bottom-up factors regulated the population. We also assessed the influence of habitat composition on demographic rates. We used generalized linear mixed models to estimate the relationships between age, precipitation and habitat composition of home range, on body condition, fetal rates, survival, and recruitment.

We identified relationships among age, reproductive traits, body condition, survival, and climatic variables that are consistent with a population at or near ecological carrying capacity. Body condition and fetal rates of prime-aged individuals were generally low; adult females consistently carried fewer than two offspring, yearlings had low fetal rates (≤1 fetus), and individuals did not reach maximum reproductive output until >4 years-of-age. Adult survival was high and relatively stable over the study period, with declines only evident at ages >5 years and very low levels of precipitation. Moreover, precipitation, presumably through its effect on plant growth, had a positive effect on body condition, fetal rate, and recruitment, lending further support to the hypothesis that the population was regulated to a greater degree by resource availability. We also identified a modifying effect of precipitation on relationships between habitat composition and individual demographic rates. In years with low precipitation most individuals were in such poor condition that we were unable to detect an effect of habitat composition on body condition. Conversely, habitat effects on survival were evident only during periods of low precipitation; otherwise, individuals were able to maintain relatively high survival regardless of habitat composition. These results highlight the importance of considering climatic processes when attempting to understand nutritional carrying capacity, especially in arid ecosystems, because precipitation can cause major shifts in the nutritional carrying capacity of a region over short periods of time. This research demonstrates that we were able to use demographic data from mule deer in the White Mountains to evaluate population status in relation to nutritional carrying capacity and observed support for regulation, to a greater degree, by bottom-up processes rather than predation.

INTRODUCTION

Life-history strategies for many large herbivores have been shaped by density-dependent feedbacks related to intraspecific competition for resources (van Noordwijk and de Jong 1986, Clutton-Brock et al. 1983, McCullough 1999). These life-history strategies evolved over millennia and influence how animal populations respond to environmental variation, such as habitat loss, resource scarcity, and changes in predation pressure. Therefore, when assessing population status, it is important to consider both intrinsic and extrinsic factors, and how they interact to regulate animal populations (Choquenot 1998). Long-lived species exhibit life-history strategies that feature conservative reproductive tactics (Stearns 1992, Gaillard et al. 1998) and risk-sensitive resource allocation, whereby fitness is maximized by favoring high and stable adult survival and variable reproductive output (Gaillard et al 1998, Hamel et al. 2010, Bardsen et al. 2011, Morano et al. 2013). Resource acquisition, and ultimately nutritional condition, determine energy reserves available for maintenance and reproduction (Monteith et al. 2013), and as a result herbivore populations are sensitive to changes in resource availability, specifically the quality and quantity of forage (Parker et al. 2009). As animal numbers increase and populations approach nutritional carrying capacity, density-dependent regulation of demographic parameters, such as survival and recruitment, becomes more prevalent (Clutton-Brock et al. 1983, McCullough 1999, Stewart et al. 2005). Similarly, regulation also may occur when carrying capacity is reduced by changes in climate or loss of habitat (McCullough 1999).

Ungulates living in arid environments are particularly sensitive to fluctuations in resource availability, often with direct effects on demographics (Cook et al. 2004, Parker et al. 2009). These large-bodied herbivores are reliant on a relatively low quality and seasonally abundant forage resource to meet the high metabolic requirements for survival and reproduction (Barboza et al. 2009). Animals will often increase the size of their home range to obtain adequate resources for survival and reproduction, particularly in areas of low quality habitat (Bender et al. 2013). In arid ecosystems, precipitation is a strong driver of plant productivity and nutritional quality of forage, which has a direct influence on availability of resources to ungulate populations (Marshal et al. 2005b, Stewart et al. 2005, Tollefson et al. 2010). Adequate nutrition during summer to accommodate energetic demands for lactation and building of body reserves to sustain animals during winter, when plants have senesced, is critically important (Mautz 1978, Cook et al. 2004, Monteith et al. 2013). Given the importance of resource acquisition during summer, habitat composition in summer home ranges can have direct influences on annual survival and recruitment (Bender et al. 2007b, Monteith et al. 2013).

Extrinsic factors such as predation, extreme weather, and spatiotemporal heterogeneity of resources can mask the extent to which density-dependent mechanisms regulate populations (Choquenot 1998, Wang et al. 2006). If resources vary in time and space, their regulating effect on a population may be difficult to detect without explicitly considering this temporal and spatial variation. Additionally, individual variation in habitat use, social status or competitive abilities may provide certain individuals access to higher quality or more abundant resources, allowing them to obtain higher energy reserves, and thereby buffering them against annual or seasonal variation in resource availability or precipitation. Thus, identifying what constitutes high-quality habitat (having a positive effect on demographic rates) has direct implications for understanding individual variation in demographic rates. In addition, populations held below carrying capacity, whether by predation or other limiting factors, may exhibit only weak evidence of density-dependence under average environmental conditions (Wang et al. 2009).

Determining the degree to which density-dependent regulation influences demographics relative to other limiting factors, such as extreme weather events or predation, is necessary for species conservation. Populations near ecological carrying capacity are more sensitive to environmental fluctuations or habitat alterations that modify resource availability, because of high interspecific competition for resources and a greater proportion of individuals in less than optimum condition (McCullough 1999). Thus, understanding how internal forcing from density dependence is modified by climatic effects on plant productivity, as well as habitat composition and variation among individuals, will ultimately help to predict the future response of a population to environmental and landscape changes.

When attempting to understand population dynamics of large herbivores, predation is often cited as causing population declines, primarily because predation is easily observed and is often the proximate cause of mortality (Bowyer et al. 2013). In semi-arid ecosystems, lack of high-quality habitat is thought to be one factor that has contributed to low ungulate densities in certain regions. Despite the apparent impacts of predation, changes in quality or quantity of forage resources are, nevertheless, often the ultimate cause of mortality (Bishop et al. 2009).

We studied a population of mule deer (*Odocoileus hemionus*) in the White Mountains of eastern California and western Nevada, USA, from 2003 through 2008, to understand population regulation in a semi-arid ecosystem. Aerial surveys conducted in the region identified this range as having low densities relative to populations in more productive areas and resource limitations were thought to be a factor. Given this baseline information, our objectives were (1) to characterize the population status relative to ecological carrying capacity and assess to what degree intrinsic versus extrinsic factors regulated the population; and (2) to assess habitat quality and examine the influence of climate and habitat composition on demographic processes, with an emphasis on the influence of pinyon-juniper woodland. Loss of productive sagebrush-steppe habitat resulting from expansion and infilling of pinyon-juniper woodland (also referred to as PJ) may alter understory composition and forage resources (Tausch et al. 1981, Tausch and Tueller 1990), which can reduce habitat quality (Bender et al. 2007b, 2013) and lead to declines in carrying capacity. Alternatively, at a fine scale, tree cover may provide beneficial attributes, such as structural cover for predator avoidance or overstory cover that may aid in thermoregulation during periods of high temperatures (Giotto et al. 2013), however we expect those benefits to decline as densities increase and understory biomass declines (Altendorf et al. 2001, and see Chapter 1).

We considered hypothesized relationships between resource limitation and life-history characteristics (Table 1; Bowyer et al. 2005) to assess the population status of mule deer relative to ecological carrying capacity and to determine factors that contributed to regulation of this population (Pierce et al. 2012, Bowyer et al. 2014). We predicted that if intraspecific competition for resources was regulating this population, then fetal rates, body condition, and recruitment would be low relative to the reproductive potential of this species in highly productive environments. In addition, we expected later age at maturity, and greater variability in survival and recruitment, particularly for young and old individuals (Festa-Bianchet et al. 1998). We also predicted that these metrics would be sensitive to annual fluctuations in resource availability driven by variation in habitat quality and precipitation.

To assess habitat quality and to determine the influence of habitat use and climate on demographic rates of mule deer in this population, we evaluated the relationship between habitat composition within summer home range and precipitation, on both individual vital rates (i.e. survival, body condition, fetal rates) and home range size. We predicted that vital rates would be negatively correlated with habitat characteristics that reduce forage availability or site productivity. We also predicted that precipitation would moderate this relationship by mitigating negative effects of low quality habitat on vital rates or, conversely, that low-quality habitat might reduce benefits associated with periods of high precipitation (Blomberg et al. 2012, Owen-Smith 2014). We also investigated the influence of tree cover on vital rates to assess potential impacts of pinyon-juniper expansion in the Great Basin (Romme et al. 2009) on mule deer populations given the negative relationship between overstory cover and understory biomass (Tausch et al. 1981, Tausch and Tueller 1990).

STUDY AREA AND METHODS

Our study was conducted in the White Mountains near Bishop, California (37.4° N, 118.5° W) in Inyo and Mono counties, California and Esmeralda County, Nevada. The study area extended approximately 80 km along the eastern side of the mountain range from Deep Springs Valley north to Montgomery Pass (Fig. 1), and rose in elevation from 1,400 to 4,300 meters. Landscape characteristics and vegetation were representative of semi-arid mountains within the Great Basin Ecoregion of the United States (Hall 1991, see Chapter 1). This region is characterized by low rainfall coupled with high summer temperatures and is dominated by sagebrush steppe and pinyon-juniper vegetation associations (Hall 1991). The basin and range topography allows for variation in precipitation and temperature along elevational gradients, resulting in a heterogeneous landscape. Lower elevations (< 2000 m) are dominated by sagebrush (*Artemisia* spp.), ephedra (*Ephedra* spp.) and rabbitbrush (*Ericameria nauseosus*) communities. Intermediate elevations (>2000 m) support single-leaf pinyon pine (*P. monophylla)* and Utah juniper (*J. osteosperma)* woodlands with an understory comprised of bitterbrush (*Purshia spp*.), forbs (*Astragalus* spp., *Lupinus* spp., *Phlox* spp., *Eriogonum* spp.), bunch grasses (*Poa* spp., *Stipa comata*), and sagebrush-steppe communities. Sub-alpine (>2900m) and alpine zones (>3500m) contain open forest dominated by stands of bristlecone pine (*P. longaeva*), lodgepole pine (*P. contorta*), limber pine (*P. flexilis*), or mountain mahogany (*Cercocarpus ledifolius*), with quaking aspen (*Populus tremuloides*) and willow (*Salix* spp.) occurring in riparian areas (see Chapter 1). The understory within these stands was comprised of robust sagebrush communities with dwarfed vegetation at higher elevations (see Chapter 1). Carnivore populations generally occurred at low densities throughout the range, and included coyotes (*Canis latrans*), mountain lions (*Puma concolor*), bobcats (*Lynx rufus*), and black bears (*Ursus americana*).

Mule deer within our study were generally non-migratory, but moved up and down in elevation in response to seasonal availability of resources, with overlap between summer and winter home range at intermediate elevations. Mule deer tended to use low elevation (≤1,800 m) shrub habitat during the winter and spring, then transitioned to intermediate elevation and alpine habit during the summer months (2,900m-4,000m; Hall 1991).

Animal capture and monitoring

We captured adult (>1 yr old) female mule deer in November and March of 2005 – 2008, using a net gun fired from a helicopter (Krausman et al. 1985). Once captured, animals were transported to a base camp where biological samples were collected. An incisiform canine was extracted (Swift et al. 2002, Bleich et al. 2003) from adult deer to determine age using cementum annuli (Gilbert 1966, Matson's Laboratory, Milltown, MT). Individuals that had not yet replaced their fourth incisor were classified as fawns. Body mass and morphological measurements were collected in addition to body condition information. We used ultrasonography to measure subcutaneous fat on the rump and withers to the nearest 0.1 cm (Stephenson et al. 2002) and calculated a body condition score validated for mule deer by palpating the wither, ribs and rump (Cook et al. 2007) to aid in estimating condition when subcutaneous fat levels are very low. This information was combined to estimate ingesta-free body fat (IFBFat) using the equations (live index unscaled) provided by Cook et al. (2010). To determine pregnancy and fetal rates, we performed transabdominal scanning using ultrasonography on the left-caudal portion of the abdomen. We were only able to measure fetal rates for individuals captured in the spring, because autumn captures occurred too early to detect fetal development. We included demographic data (fetal rates and nutritional condition) collected during the spring capture period in our analysis, because that was the period for which we had the most complete data. Body condition in late spring also accounts for depletion of summer-autumn resource acquisition and environmental conditions over winter, and is indicative of endogenous resources available to the individual during the reproductive season (Parker et al. 2009, Monteith et al. 2013).

Each individual was fitted with a standard global positioning system (GPS) or VHF telemetry collar (Advanced Telemetry Systems, Isanti, Minnesota, USA). Aerial telemetry flights were conducted monthly to monitor radio-tagged individuals for mortalities and to determine animal locations. GPS collars were programmed to gather location data for approximately 300 days, at which time the collar dropped off the individual and data were collected. VHF collars generally remained on the individual for the duration of the study, unless it was replaced with a GPS collar or an individual died. This method allowed us to monitor fine scale summer movements in addition to survival.

New individuals were captured each season to replace animals lost to mortality or removed from the study when the collars detached. We attempted to distribute capture efforts equally across the study area to gather a representative sample of individuals and avoid concentrating collars in any one area. All capture and handling of mule deer were compliant with procedures outlined by the California Department of Fish and Wildlife, were in keeping with guidelines established by the American Society of Mammalogists for research involving mammals (Sikes et al. 2011), and were approved by the Institutional Animal Care and Use Committee at the University of Nevada Reno (IACUC: 00109).

California Department of Fish and Wildlife conducted spring helicopter surveys to estimate population size in addition to sex and age composition of the population. Transects were flown throughout the range in areas with high and low densities of mule deer. Surveys of the full study area were not completed most years due to weather constraints; however, composition counts for a subset of groups encountered during those surveys were recorded. Surveys were conducted in early spring after males had shed their antlers, making it difficult to distinguish sex from the helicopter; therefore, composition of groups was recorded as the number of adult deer relative to young. This information was used as an index to recruitment of young that were born the previous summer and survived until spring.

Environmental variables

The region experienced substantial variation in precipitation over the course of this study, which allowed us to assess the effects of weather-induced changes in resource availability, interactions with habitat composition, and influences on population regulation. We identified a set of climatic and habitat variables to test our predicted relationships of density dependence, precipitation, and habitat quality on demographic rates. Seasonal precipitation and snowpack have been linked to plant growth and ultimately body condition of mule deer in semi-arid ecosystems (Monteith et al. 2013). Water content of the snowpack in late spring has been shown to influence leader growth in bitterbrush, a primary winter forage for mule deer (Kucera 1997, Pierce et al. 2004). We obtained snowpack data from a nearby mountain range at an elevation of 3,000 m (http://cdec.water.ca.gov). The majority of precipitation in the White Mountains occurs during the autumn, winter, and spring (Fig. 2). We used PRISM climate data (PRISM Group 2010) averaged over 3 representative elevations throughout the White Mountains to calculate annual precipitation (January – December) and winter precipitation (Nov – March). Annual precipitation is a cumulative estimate of precipitation, which considers both the previous and current winter conditions. In contrast, winter precipitation measures only late season precipitation; both have been shown to influence pregnancy rates, recruitment, and survival of mule deer (Monteith et al. 2013).

Variables related to vegetation type were generated from GIS layers to characterize summer home range composition (see Chapter 1). We delineated land cover types based on the U.S. Forest Service existing vegetation mid-level map for the Great

Basin Region, which uses the CALVEG classification system to identify dominant vegetation communities at 100 m resolution (USDA Forest Service 1981). We reclassified the map into 13 broad vegetation associations based on dominant plant species: (1) high elevation wet meadow, grasses and forbs; (2) bare ground; (3) bristlecone pine; (4) sub-alpine shrub; (5) sagebrush; (6) bitterbrush; (7) mountain mahogany; (8) pinyon- juniper woodland (PJ); (9) upper montane pine; (10) riparian shrub; (11) riparian tree (aspen, cottonwood); (12) alpine shrub (13) desert mixed shrub. We also employed maximum likelihood classification in ArcGIS 10.0 (ESRI, Redlands, California, USA) to derive fine resolution vegetation classes related to bare ground, tree, shrub, and riparian cover (willows, aspen, cottonwood) using 1-m resolution color-infrared orthophoto imagery from the National Agriculture Imagery Program (NAIP, USDA Farm Service Agency 2008) collected during August, 2008. From those data we generated estimates for percent tree cover, riparian cover, and distance to riparian zones. We also calculated shrub-NDVI (Normalized Difference Vegetation Index), an index of greenness using NDVI (Pettorelli et al. 2005) for all non-tree, non-riparian pixels to differentiate between shrub areas with robust plant cover and areas with greater proportions of bare ground.

We calculated a site-based measure of actual evapotranspiration (AET) to estimate potential plant growth for a given pixel based on elevation, solar radiation, temperature, soil, water, slope, and aspect with a Thornthwaite water balance model (Stephenson 1998, Dilts et al. 2015). We used the 30-year average PRISM climate data (PRISM Group 2010) to calculate AET, which allowed us to identify an index of relative site productivity irrespective of plant composition. AET was calculated using values from July and August, the period of greatest productivity at mid to high elevations, to characterize sites along a gradient from hot, dry and generally less productive, to areas that were cooler, wetter and more productive (see Chapter 1).

Home range

Home range was calculated for summer GPS locations using the 95% kernel density estimator (KDE) calculated with a smoothed-cross-validation bandwidth algorithm (Geospatial Modeling environment vs 0.7.2.1; Beyer 2012). Summer locations were recorded for July through September coincident with the period when nutritional demands of mule deer were high and after females had transitioned onto the summer range following parturition (generally mid to late June; Pojar and Bowden 2004, Bishop et al. 2009, Monteith et al. 2011). Aerial telemetry locations were gathered for individuals with VHF collars during summer, and were used to create minimum convex polygons (MCP) for each individual. To keep home range size consistent with our KDE analysis, we then took the centroid of the MCP and buffered it by the mean KDE area of the population + 1 SD (1800 m), for our use in the analysis of habitat composition for VHF-collared individuals. We only included GPS collared individuals in our analysis of home range size, since KDE provides a more accurate estimate of the exact size and shape of an individual's home range in comparison to MCPs, however all individuals were used in our analysis of habitat composition. We also calculated an index to local population density for each individual as the amount of home range overlap with other radio collared individuals in the population. The percent cover of each vegetation type was calculated within each individual's summer home range and was log-transformed to meet assumptions of normality (Zar 2010). AET, shrub-NDVI, and distance to riparian areas were calculated as the mean value of all pixels within an individual's summer home range.

Statistical Analysis

Demographic Parameters - We modeled nutritional condition, number of fetuses (1or 2), survival, recruitment, and home range size for mule deer as a function of predictor variables that were representative of both population processes, such as annual variation in climatic conditions, and individual variation related to age and habitat composition, when available. Each demographic parameter was analyzed independently using a variety of modeling approaches; however, all analyses contained a variation of a generalized linear model, with either a binomial or Gaussian error distribution. In each instance, we followed a similar process for model creation and assessment, but not all explanatory variables were considered for each demographic parameter (e.g. habitat information was not available for recruitment data).

We used generalized linear mixed models (package lme4 in R2.15.3; R Development Core Team 2013), with year as a random term, to estimate the effect of the explanatory variables on IFBFat, fetal rate, and recruitment (Zurr et al. 2009, Simard et al. 2014). Fetal rate was translated to a binomial response variable, (0) none or one fetus, and (1) two fetuses. IFBFat and recruitment (fawn-adult ratios) were analyzed as continuous variables using a Gaussian distribution. We considered the full suite of environmental variables in our analysis of IFBFat and fetal rates; however, we only considered weather variables in our analysis of recruitment because it was a population-level metric, and we did not have information regarding habitat composition; therefore, we could only assess annual variation in precipitation.

Monthly survival was estimated using known-fate analysis in program MARK (White and Burnham 1999), which employs maximum likelihood estimation to determine survival probability using a binary response variable (alive or dead). We considered the full suite of explanatory variables to determine factors that influenced survival at both the population and individual levels. Home range size was log-transformed to meet assumptions of normality, and analyzed using a generalized linear model with no random effects. We considered summer home range to be representative of general summer habitat use given the high level of philopatry observed in female deer (Lesage et al. 2000). We did not consider annual variation in home range in our analysis, only variables representative of habitat composition, age, nutritional condition, number of fetuses, and density.

Model structures were derived from hypothesized relationships of demographic rates to precipitation, age, and habitat composition. Model selection was performed in an iterative process, whereby we identified the best model from each stage and retained that structure in the subsequent step. All habitat and environmental variables were converted to standard normal values ($\mu = 0$, SD >1) to allow for direct comparison of covariate effects (Zar 2010, McKee et al. 2015). Models were ranked using Akaike information criterion corrected for small sample size (AICc), which identifies the most parsimonious model by balancing model complexity with the amount of variance explained, where the best model had the lowest AICc value (Burnham and Anderson 2002).

We first assessed the effect of age or a quadratic relationship of age on demographic rates. Then assessed population-level metrics such as period (seasonal or annual) or weather-driven influences on demographic rates. The best model from this process became our base model, typically containing age and precipitation. From that model we evaluated our suite of habitat variables, density and recruitment indexes, and interactions with precipitation. Because of small sample sizes and large number of variables describing habitat composition, we assessed habitat effects by comparing models containing both the additive effect of habitat composition and an interaction between habitat and precipitation, to the base model. For the recruitment and home range models our base model was simply the null, or intercept-only model. We considered the covariate effect supported if inclusion of the parameter improved model fit, over the base model and if the 85% confidence intervals did not overlap zero (Arnold et al. 2010). This iterative method allowed us to identify which variables influenced variation in life history traits and directly compared strength of support for those effects. Comparison of standardized parameter estimates and standard errors within the top suite of models (AICc > base model) allowed us to assess the relative strength of effect for each covariate of interest.

Density Dependence - Density dependence is often assessed in the context of animals per unit resource. Nonetheless, obtaining exact animal counts and quantifying forage resources for large, heterogenous areas can be challenging. It is often more feasible and accurate to use population metrics such as survival, reproduction, and body condition to determine the population status relative to nutritional carrying capacity (Pierce et al. 2012, Bowyer et al. 2014). We used results from our modeled population-level demographic rates to assess population regulation and evaluate the status of the population relative to nutritional carrying capacity based on the hypothesized relationships between resource limitation, age, and weather variables on fetal rate, survival, nutritional condition, and recruitment (Table 1; Bowyer et al. 2005).

RESULTS

We collected demographic data and habitat composition for 70 adult females during spring and summer 2005–2008 (*n* =13, 14, 16, and 27 individuals per year, respectively). We targeted adult female mule deer for this study and the age distribution of our sample was generally skewed towards prime-aged individuals (3-5 years, based on maximum fetal rates and body condition), with approximately 20% of individuals 2 years-of-age or younger, and 20% of individuals between 6 and 11 years of age. GPS collars were deployed on 55 individuals; VHF collars were deployed on 15 individuals and several individuals received both collar types. We also identified the composition of 134 groups of mule deer as an index to population-level recruitment during spring helicopter surveys in 2003, and 2005–2008 (*n* = 7, 22, 18, 28, 59 groups per year, respectively). The region experienced substantial variation in precipitation during the study period, with very low precipitation in 2003 and 2007, average to slightly below average precipitation in 2008 and 2009 and high levels of precipitation during 2005 and 2006, when compared with the 10-year mean (Fig. 2).

Body condition

Mean IFBFat of female mule deer captured during March was 5.0% ± 0.98 SD. Mean annual values ranged from a low of 4.3% ± 0.60 SD in 2007, a drought period, to a high of 5.7% ± 2.43 SD in 2006, a year with above-average precipitation and the greatest precipitation recorded during this study period (Fig. 2). Individual values of IFBFat ranged from 1.7% to 10.1% and varied as a function of age, precipitation, and habitat composition (Table 2). We observed support for a quadratic relationship between age and IFBFat, where body condition was greatest for young individuals and experienced a rapid decline after 5 years-of-age (Fig. 3).

Winter precipitation had a positive influence on IFBFat, and models containing this variable received greater support than models containing other covariates designed to reflect annual variation (e.g. annual precipitation, snow water content during the previous spring, density, or annual recruitment; Appendix A). Winter precipitation alone, however, was not a strong predictor of March condition, with only a 1% change in IFBFat between years with highest and lowest rainfall, and only a slight decrease in AICc when compared to the less parameterized model (Appendix A). We retained the variable in our base model to maintain consistency among analyses for our other demographic parameters, and because the beta coefficient for winter precipitation was supported based on the 85% confidence interval. Thus, our base model contained additive effects of age (quadratic) and winter precipitation on IFBFat (Table 2).

Our additive habitat models identified support for a negative effect of percent cover of pinyon-juniper woodland (β= -0.32, ± 0.16 SE), and a positive effect of percent cover of alpine meadows (β= 0.31, ± 0.16 SE) on IFBFat. Models that contained an interaction between precipitation and either PJ, aspen, or sagebrush cover had significant support over the additive habitat models (Table 2). Models containing an interaction between precipitation and either sub-alpine shrub, bristlecone, or riparian vegetation associations were supported over the base model, but fell within 2 ΔAICc, indicating only marginal support for the additional terms (Table 2).

The top models identified interactions between precipitation and multiple habitat metrics (Table 2), where individuals whose home range contained greater amounts of PJ, aspen, or sagebrush vegetation associations had lower IFBFat in wet years than individuals containing less of those vegetation types (Fig. 4). During dry years, however, those habitat variables had less influence on body condition, and IFBFat either remained constant or increased slightly with percent cover (Fig. 4). We also identified support for a positive effect of greater proportion of alpine meadows on IFBFat, in addition to interactions between precipitation and both sub-alpine shrub and bristlecone communities. Deer whose home range contained greater proportion of these high-elevation vegetation associations obtained greater IFBFat during years with high precipitation. The influence of alpine meadows remained positive over the range of climatic conditions; however, sub-alpine shrub or bristlecone vegetation associations had little influence on condition during dry years.

Fetal rate

Mean fetal rate for the population was 1.4 (± 0.49 SD) and varied annually over the study period. The highest fetal rate occurred in 2006 (1.57 ± 0.51 SD), and the lowest occurred in 2007 (1.06 ± 0.44 SD), concurrent with the years of highest and lowest winter precipitation, respectively. The maximum number of fetuses observed for a single individual was 2, and we observed only a single individual, a yearling, that was not pregnant. Mean fetal rates also varied with age in adult females, where fetal rates were lowest for individuals < 3 years-of-age (0.90 ± 0.47 SD), reached a maximum at age 5 (1.6 ± 0.51 SD), and then declined slightly for ages greater than 7 years (1.3 ± 0.57 SD). This quadratic relationship between age and fetal rate was also supported by model selection (Table 2, and see Appendix B for full model selection results). Because we only identified one non-pregnant individual, fetal rate as a response variable in our analysis reflected the probability of a female carrying twins during late spring. Our base model contained a quadratic effect of age and a positive effect of winter precipitation on fetal rates (Fig. 3), which was comparable with model results from our analysis of body condition.

The inclusion of an additive effect of habitat composition, density, or recruitment failed to improve model fit over the base model. We observed support for a positive effect of IFBFat (β=0.47 ± 0.35 SE), where individuals with higher fat levels during early spring were more likely to be carrying twins compared to females with lower fat levels. Support for that covariate effect was weak, likely because much of the variation in IFBFat was related to winter precipitation and age, which were also contained in the base model. We identified support for an interaction between winter precipitation the amount of alpine shrub, riparian vegetation, or productive shrub habitat (NDVI), within an individual's home range, where in each case the influence of habitat changed depending on winter precipitation (Table 2). High elevation shrub communities were positively associated with fetal rates during years with average to above average precipitation, and negatively associated with fetal rates during dry years (Fig. 5). Individuals with higher shrub NDVI (non-riparian, non-tree) values had increased fetal rates during years with average to above average precipitation (Fig. 5). In addition, individuals with low shrub NDVI had generally low fetal rates, and were less sensitive to the influence of precipitation (Fig. 5). In years with below average precipitation fetal rates increased with greater amounts of riparian vegetation within an individual's home range (Fig. 5). In years with above average precipitation, however, fetal rates declined with increasing riparian vegetation (Fig. 5), suggesting that the benefits of riparian vegetation were only realized during dry years.

Recruitment

Our index of recruitment reflected population-level demographic processes, and we assessed annual variation as a function of climatic variables and did not incorporate habitat composition into that analysis. Results from our generalized linear mixed models identified annual precipitation as a strong predictor of recruitment during spring (Table 2). The top model contained an effect of annual precipitation (Jan–Dec), and significantly improved model fit over the intercept only model (Null) and the base model containing full annual variation in recruitment. Differences in precipitation between the driest and wettest years were correlated with a change in ratios of young to adult from 0.20 (± 0.06 SE) to 0.40 (± 0.07 SE). We did not find significant support for an effect of winter precipitation (Nov-March), or snow water content (t-1) on spring recruitment (Table 2).

Survival

Annual survival rates varied during the study, with the highest rate occurring in 2005 and 2006 (0.93 ± 0.025 SE) and lowest rates in 2007 (0.77 ± 0.06 SE) and 2008 (0.87 ± 0.029 SE). Model results identified a linear decline in survival with age, where survival was highest for prime age individuals and declined significantly at later ages (Fig. 3). We did not find support for a quadratic relationship of age (Table 3) as observed with the other demographic rates. Individual survival was also influenced by both precipitation and habitat composition, with support for interactions between the suites of variables (Table 3). Annual precipitation was positively associated with survival and was better supported than models which included annual variation or seasonal variation in survival. Annual precipitation was also better supported than other environmental variables, such as snow water content or winter precipitation (Appendix C). Thus our base model contained an additive effect of annual precipitation and age on survival.

The suite of top models contained interactions between habitat variables and annual precipitation, which improved model fit over the base model (Table 3). We found the greatest support for an interaction between annual precipitation and either percent tree cover, AET, shrub NDVI, or mountain mahogany vegetation association. The top model contained a quadratic relationship between tree cover and survival, which was improved by including an interaction with annual precipitation. As tree cover increased survival declined during dry years, but during years with above average precipitation the effect was not apparent (Fig. 6). Model results identified a positive relationship between AET and survival during years with greater precipitation, but a negative effect in years with low precipitation (Fig. 6). Productive shrub habitat (shrub NDVI) was positively correlated with survival during dry years, and had little influence on survival during wet years (Fig. 6). In general, the relationship between habitat composition and survival changed in dry versus wet years, where habitat composition had the greatest influence during years with below average precipitation, and small to no effect during years of above average precipitation (Fig. 6).

Home Range

We calculated the size of summer home ranges for 48 female mule deer between 2005 and 2008. Summer home range varied in size between 1.3 km^2 and 19.5 km^2 with a mean of 5.8 km^2 (SD=3.9km^2). Average distance to the nearest riparian area, and the amount of riparian vegetation, within an individual's home rage were the strongest predictors of home range size (Table 4; see Appendix D for full model selection results).

Also, the size of an individual's home range was positively correlated with the distance to riparian areas, averaged among all the pixels within and individual's home range. Individuals who were on average farther from riparian areas tended to have larger home ranges ($\beta = 0.45 \pm 0.07$ SE). In contrast, individuals with greater amounts of riparian or Aspen vegetation had smaller home ranges ($\beta = -0.34 \pm 0.08$ SE and $\beta = -0.29 \pm 0.09$ SE, respectively). Greater amounts of both alpine shrub and desert shrub vegetation were correlated with larger home range sizes ($\beta = 0.23 \pm 0.09$ SE and $\beta = 0.19 \pm 0.09$ SE respectively). Fetal rate, IFBfat, and snow water content were also negatively correlated with home range size but support for this relationship was weak; 85% confidence intervals of beta estimates overlapped 0 and AICc values within 2 ΔAICc of the null model.

DISCUSSION

We identified relationships among age, reproductive traits, body condition, survival, and precipitation that are consistent with a population at or near ecological carrying capacity (Table1; Bowyer et al 2005); body condition and fetal rates of prime-aged individuals were generally low, females consistently carried fewer than 2 offspring, yearlings had low fetal rates, and individuals did not reach maximum reproductive output until after 4 years of age. Adult survival was high and relatively stable over the study period; however, declines in survival were evident at old age, and in years with very low levels of precipitation (Fig. 3). Those findings support our hypothesized relationships between resource limitation and population regulation, where intraspecific competition for resources results in delays in age at first reproduction, reproductive pauses, and decreased litter size.

These same relationships have been observed in other studies of density-dependence in ungulates including mule deer and elk (McCullough 1999, Kie et al. 2003, Bowyer et al. 2005, Stewart et al. 2005). Adult survival generally is predicted to remain constant and is affected only at very high levels of resource limitation (Gaillard et al. 1998), which is consistent with our results. Additionally, we identified effects of habitat composition or precipitation on body condition, fetal rate, recruitment and survival, lending further support for population regulation occurring as a function of available resources. Moreover, senescent declines in body condition and survival with increasing age tend to only be observed during periods of high intraspecific competition for resources, where the population may be experiencing greater reproductive costs in both young and old females (Festa-Bianchet et al. 1998). In deer populations not limited by resource availability, yearlings are generally pregnant and often produce twins, and adults consistently produce 2 offspring, with documented cases of triplets in some populations (Monteith et al. 2014). If this population was not limited by resource availability and was able to reach its full biotic potential, we would expect to consistently see individuals carrying 2 fetuses, which we did not.

In semi-arid ecosystems precipitation can shape resource availability by influencing plant productivity and nutritional quality of forage (Tollefson et al. 2010). Years with above-average rainfall can mitigate the effect of density-dependent processes by increasing resource availability, thereby reducing animal density per unit resource, with very little change in population size (McCullough 1999). Nevertheless, this release from resource limitation can translate into increases in population (Marshal et al. 2005b). Conversely, years with low precipitation can exacerbate effects of density dependence. Many studies of ungulate populations in the western United States attribute population declines to patterns of precipitation, particularly instances of prolonged drought (McKinney 2006, Lawrence et al. 2004, Bender et al. 2013), with concomitant reductions in adult body condition, adult survival, and survival of young during dry years contributing to those declines (Bender et al. 2007a). As a result, mule deer populations may be held at low absolute numbers during drought and then increase during years with high precipitation, highlighting the need to incorporate climatic variables when evaluating population status with respect to ecological carrying capacity, and the associated regulatory mechanisms (Bowyer et al. 2014, Owen-Smith 2014, Bergman et al. 2015), and confounds the management of mule deer occupying arid and unpredictable environments (Mackie et al. 1990). The ability of this population to increase productivity in years when forage resources were more abundant is suggestive of a population regulated by bottom up, rather than top down forcing.

We observed a much clearer relationship between precipitation and reproductive output (fetal rates and recruitment) than we did between precipitation and body condition or survival. Our findings of relatively high and stable adult survival with greater variation in fetal rates relative to changes in resource availability (precipitation), are consistent with a conservative or slow-paced life history strategy, where individuals attempt to balance energetic requirements for both cell maintenance and reproduction to maximize survival (Ricklefs and Wikelski 2002, Stearns 1992, Hamel et al. 2010). Individuals in this population may have altered their behavior to maintain adequate body condition over a range of environmental conditions by adjusting reproductive output as evident by the variation in fetal rates and recruitment. This reduction in reproductive output during years with greater scarcity in resources has been documented by others in their studies of ungulate reproductive ecology (Bardsen et al. 2008, Morano et al. 2013, Monteith et al. 2013). The fact that we were able to identify an effect of precipitation and habitat composition on survival and body condition is not trivial, especially since survival of adults is generally the last trait to be impacted by resource limitation in long-lived organisms such as ungulates. This effect is most commonly observed in populations nearing nutritional carrying capacity in which high intraspecific competition for resources results in a greater proportion of adults and neonates in poor condition (Gaillard et al. 1998, Hamel et al. 2010). Reduced survival during dry years indicates that during droughts a greater number of adult females were unable to meet their metabolic demands. Low fetal rates and recruitment, in addition to lower body condition during dry years lends further support to our hypothesis that resource limitation is regulating this population. We identified multiple lines of evidence to suggest that weather and its effect on resource availability likely had a larger regulatory effect on this population than any potential regulation associated with predation. Our findings of high average survival (0.95), a 20% decrease in survival between wet and dry years, and substantial declines in recruitment during dry years support our hypothesis of population regulation associated with availability of resources in the White Mountains. In a study on mule deer where predation was thought to be the regulating factor, predator removal had little influence on population rate of change and enhanced nutrition resulted in an increase in population growth rate (Bishop et al. 2009). This is not to say that predation could not have some effect on population growth during those productive years, which has been demonstrated in other studies of mule deer (Pierce et al. 2012).

The duration of our study was modest, and given the correlative nature of weather metrics and the importance in timing of seasonal precipitation in semi-arid environments, we view precipitation as an inclusive measure of annual variation in climatic conditions. Annual precipitation experienced during the years of our study was representative of below average, average, and above average conditions when compared with the 10-year mean (Fig. 2) and, thus, our study incorporated the range of values we would expect to observe in this ecosystem. Ultimately, we found strong support for precipitation effects across almost all measured demographic characteristics, suggesting that the correlations we observed with precipitation reflect true population-level phenomena and were not simply a sampling artifact.

Demographic buffering through habitat and precipitation

In semi-arid ecosystems heterogeneous distribution of resources associated with differences in soil composition, groundwater, and elevation, can allow individuals inhabiting higher quality or more optimal habitats to be buffered against climatic fluctuations and be able to survive and reproduce more consistently than others.

Individuals inhabiting lesser quality habitat, however, may be more sensitive to periods of high and low precipitation (Owen-Smith 2014). As a result we identified variable effects of habitat composition among our suite of individual demographic traits (fetal rates, body condition and survival). We also identified a modifying effect of precipitation on relationships between habitat composition and individual demographic rates, whereby the influence of habitat composition was evident only when we accounted for dry versus wet years. For instance, the influence of habitat composition on body condition was evident only during periods of high precipitation, where periods of low precipitation seemed to override many of the potential influences of high quality habitat (Fig. 4). Conversely, habitat effects on survival were evident only during periods of low precipitation otherwise individuals were able to maintain relatively high survival regardless of habitat composition within their home range (Fig. 6).

Characteristics of high-quality habitat seemed to vary between wet and dry years. During periods of high precipitation, high-quality habitat, as defined by having a positive relationship to individual demographic rates (fetal rate, body condition, and survival), included areas with productive shrub communities and high-elevation vegetation associations, such as, alpine meadows, sub-alpine and alpine shrub communities, bristlecone, mountain mahogany, and high AET sites. Conversely, these relationships were either not apparent or were negative during dry years, suggesting that productive high-elevation habitats may only be beneficial during periods with adequate precipitation, and that use of those areas may actually be maladaptive during periods of drought, possibly related to timing of green-up and senescence of vegetation. For example, Gugger et al. (2015) suggested that high elevation plant species are more likely to respond to drought conditions by increasing the onset of green-up and shortening the duration of the growing season. Moreover, the positive correlation between home range size and use of alpine-shrub associations suggests that this vegetation type may be lower quality and require that individuals make greater movements to obtain adequate resources (Bender et al. 2013). We identified a similar relationship with home range size for low elevation desert scrub communities, indicating that those areas may also be sub-optimal habitat during summer.

Our finding of a negative relationship between demographic rates and areas with greater amounts of woody vegetation, such as, pinyon-juniper woodland, and mid-elevation shrub communities, particularly during years with high levels of precipitation, suggests that those plant communities do not contain adequate foraging opportunities even in years when precipitation and herbaceous vegetation likely is more abundant. Mule deer diets are generally comprised of forb and shrub vegetation (Krausman et al. 1997) but, given their high nutritional demands during lactation, mule deer require diets high in digestible energy during this period (Barboza et al. 2001, Tollefson et al. 2010), and individuals likely concentrate in more productive forb-shrub communities, such as sub-alpine shrub, or wet meadows. Conversely in dry years herbaceous growth is suppressed, areas with greater abundances of woody shrubs, such as sagebrush and bitterbrush, may become a more important component of diet, as reported during winter months when herbaceous vegetation is unavailable (Kucera 1997, Pierce et al. 2012).

Our results support previous research highlighting the importance of riparian areas with water resources in arid or semi-arid regions (Bleich et al. 2010, McKee et al. 2015). We found that individuals whose home ranges contained areas that were on average farther from riparian zones had much larger home range size than those individuals that were using areas that were on average closer to riparian vegetation, and that home range size decreased with increasing amounts of riparian vegetation within the home range. Moreover riparian vegetation was associated with increased fetal rates during dry years. Nevertheless, in the absence of diverse forb and herbaceous cover, riparian areas may not be as beneficial, aside from providing access to associated water resources. The value of riparian vegetation can be diminished in areas with concentrated use by livestock or horses (Beever 2003, Roever et al. 2015), or if predation risk is greater in such areas. This could explain why we did not see a positive effect of riparian vegetation on fetal rates during wet years when presumably herbaceous resources are more widely distributed.

Model results suggested a negative influence of PJ woodland across multiple demographic metrics. In areas with increased PJ densities, understory biomass declines causing a reduction in forb and shrub species (Tausch et al. 1981, Tausch and Tueller 1990). In the big sagebrush vegetation association of southeastern Oregon, sagebrush cover declined by roughly 80% with a 50% increase in juniper cover, and there were concurrent declines in herbaceous cover and species diversity (Miller et al. 2000). Pinyon-juniper vegetation is also efficient on capitalizing on water resources, given their long lateral roots, further reducing soil water content available to other plants with shallow root systems such as forbs, which can be exacerbated during periods of drought (Breshears et al. 1997, Pierson et al. 2010). Moreover, mule deer whose home range contained greater amounts of PJ woodland did not experience the same increase in IFBFat during wet years, indicating that greater amounts of PJ woodland may suppress the ability of an individual to capitalize on periods of high plant productivity consistent with the notion that PJ may outcompete other plant species for water resources. Indeed, our results are consistent with results from northern New Mexico where the proportion of PJ woodland within an individual's home range was negatively correlated with body condition of mule deer (Bender et al. 2013). In addition, our observed decline in survival for individuals with increased amounts of PJ woodland within their home range during years with low precipitation lend further support to the notion that PJ woodland represents low-quality habitat for mule deer. Individuals may be able to persist in these sub-optimal habitats during years of otherwise good conditions, dependence on habitat dominated by PJ woodland may exacerbate the negative effects of drought on the population. Pinyon -juniper and other woody vegetation may, nonetheless, create beneficial microclimatic conditions during hot, dry periods, which can reduce thermoregulatory costs for animals (Giotto et al. 2013) as a result PJ may be beneficial at low densities (see Chapter 1). Our results suggest that habitat heterogeneity at increased elevations that support more productive shrub and herbaceous vegetation associations are beneficial to mule deer.

The mule deer population in the White Mountains appears to be regulated largely by bottom-up processes. Annual variation in precipitation, presumably through its effect on plant growth, affected demographic rates directly but, in some instances, individuals were able to buffer themselves against poor climate years by selecting high-quality habitat. In arid ecosystems, it is important to consider weather when attempting to understand population regulation and nutritional carrying capacity, as both are interconnected where annual variation in precipitation can cause major shifts in nutritional carrying capacity over short time periods. Results from this study support the results of other research demonstrating that the ability to detect density-dependence can be affected by temporal variation in climate related to shifts in nutritional carrying capacity and by spatial heterogeneity of resources (Mysterud et al. 2001, Wang et al. 2006, 2009). Managing landscapes to promote heterogeneous plant communities and to reduce the amount of large contiguous stands of PJ—while preserving areas of higher productivity and shrub and herbaceous vegetation—could mitigate some of the negative effects of drought on mule deer populations and increase nutritional carrying capacity for the population. These relationships between habitat, climate, and demographics are particularly important to consider in the context of changing climatic patterns and landscape composition. This research demonstrates the utility of using demographic rates and environmental factors to assess population regulation and nutritional carrying capacity, and are consistent with guidelines for habitat management in the intermountain west (Cox et al. 2009), and with recommendations for managing mule deer ranges in this region (Taylor 1997, Cox et al. 2009).

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Table 1. Life-history characteristics of ungulates used to determine population status in relation to carrying capacity (*K*), relationships reflect the relative differences in populations being regulated by top-down forcing (predation), versus bottom-up processes (*K*). (modified from Bowyer et al. 2005)

Life-history characteristic	**Top-down regulated**	**Bottom-up regulated**	**Data used to asses predicted relationships**
Physical condition of adult females	Better	Poorer	Body Condition Scores and Fat Depth from Ultrasound
Pregnancy rate of adult females	Higher	Lower	Ultrasound Pregnancy Data
Pause in annual production by adult females	Less likely	More likely	NA
Yearlings pregnant [a]	Usually	Seldom	Ultrasound Pregnancy Data and Age Data from Tooth Extraction
Corpora lutea counts of adult females	Higher	Lower	Ultrasound Pregnancy Data
Litter size [a]	Higher	Lower	Ultrasound Pregnancy Data
Age at first reproduction for females	Younger	Older	NA
Weight of neonates	Heavier	Lighter	NA
Survivorship of young [b]	Higher (additive)	lower (compensatory)	Fawn: Adult Ratios from helicopter surveys
Age at extensive tooth wear	Older	Younger	NA
Diet Quality	Higher	Lower	NA

[a] Some species of ungulates may show limited variability in particular characteristics.
[b] In the absence of efficient predators.

Table 2. Results from generalized linear mixed models identifying the effects of age, precipitation and summer home range composition on body condition (ingesta-free body fat), fetal rates (probability of having twins) and recruitment (young:adult ratios) for mule deer in the White Mountains, California and Nevada, USA from 2006-2009. Recruitment only contained variables related to annual variation in precipitation because it was a population level metric and individual-level information about habitat composition and age was not available. The structure of the base model is identified in italics and was used as noted in all subsequent models. Models containing Age^2 or an interaction between two variables also contained the singular terms for those variables (see full model results in AppendixA,B).

Model	*K*	AICc	Delta AICc
Ingesta-Free Body Fat Models			
Base + WPrecip*Pinyon-Juniper	8	249.46	0.00
Base + Wprecip*Aspen	8	251.57	2.11
Base + WPrecip*Sagebrush	8	252.19	2.73
Base + PJ	7	252.82	3.36
Base + Alpine Meadow	7	253.09	3.63
Base + WPrecip* Riparian	8	253.70	4.24
Base + Wprecip*Alpine Meadow	8	253.74	4.28
Base + WPrecip *Bristlecone	8	253.84	4.38
Base + WPrecip *Sub-Alpine Shrub	8	253.85	4.39
Base *(WPrecip + Age^2)*	6	254.37	4.91
.	.	.	.
Age^2	5	254.39	4.94
Null *(Intercept + Random effect Year)*	3	264.00	14.09
Fetal Rate Models			
Base + WPrecip*Alpine Shrub	7	86.29	0.00
Base + WPrecip*Riparian	7	87.82	1.54
Base + WPrecip*NDVI	7	90.75	4.46
Base + IFBFat	6	91.75	5.46
Base *(WPrecip + Age^2)*	5	91.76	5.47
Base + WPrecip*PJ	7	92.00	5.71
.	.	.	.
Age^2	4	94.93	8.64
Null (*Intercept + Random effect Year)*	2	97.39	11.10
Recruitment Models			
Annual Precip. Jan-Jan	3	230.98	0.00
Winter-Summer Precip. Nov-Nov (t-1)[1]	3	234.47	3.49
Base (*Year- Categorical + Random effect Year*)	6	235.33	4.35

Snow Water Content March (t-1)	3	236.47	5.49
Null *(Intercept + Random effect Year)*	2	249.40	18.42
Winter Precip (t)	3	249.87	18.89

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[1] (t-1) relates to precipitation that fell in the year prior to when data was collected and signifies a lag effect.

Table 3. Results from survival models (known-fate, program MARK) identifying the effects of age, precipitation and summer home range on annual survival for mule deer in the White Mountain, California and Nevada, USA from 2006-2009. The structure of the base model is identified and was used as noted in all subsequent models. Models containing an interaction between two variables also contained the singular terms for those variables (see full model results in AppendixC).

Survival Model	***K***	**AICc**	**Delta AICc**
Base + APrecip*Tree + $Tree^2$	6	215.89	0.00
Base + APrecip*AET	5	216.31	0.43
Base + APrecip*Shrub-NDVI	5	217.26	1.37
Base + APrecip*MM	5	217.35	1.46
Base + $Tree^2$	5	217.41	1.53
Base + APrecip*Tree	5	217.76	1.88
Base + Mountain Mahogany	4	217.82	1.94
Base + Shrub-NDVI	4	218.03	2.14
Base *(Annual Precip + Age)*	**3**	**218.09**	**2.20**
.	.	.	.
Age	2	221.39	5.50
Null *(Intercept)*	**1**	**227.86**	**11.97**

Table 4. Results from generalized linear models identifying the effects of habitat composition on size of summer home range for mule deer in the White Mountain, California and Nevada, USA from 2006-2009 (see full model results in Appendix D). All covariates were z-standardized prior to analysis so β values indicate magnitude and direction on the covariate effect on home range size, with the standard error and lower and upper 85% confidence interval indicated.

HR Size Model	*K*	AICc	Delta AICc	Habitat variable *(β)*	SE	LCI	UCI
Dist. to Riparian	2	71.68	0.00	0.45	0.07	0.31	0.59
Riparian	2	87.02	15.34	-0.34	0.08	-0.51	-0.18
Aspen	2	91.82	20.13	-0.29	0.09	-0.46	-0.12
Desert Scrub	2	95.70	24.02	0.23	0.09	0.05	0.41
Alpine Shrub	2	97.99	26.31	0.19	0.09	0.00	0.37
Fetal Rate	2	98.23	26.55	-0.31	0.16	-0.62	0.01
IFBFat	2	98.66	26.98	-0.29	0.16	-0.61	0.02
Snow Water Content	2	98.88	27.20	-0.16	0.09	-0.35	0.02
Null *(Intercept)*	**1**	**99.68**	**28.00**	**-**	**-**	**-**	**-**
Winter Precipitation	2	100.26	28.57	-0.12	0.10	-0.31	0.06
Bristlecone	2	100.36	28.68	0.12	0.10	-0.07	0.31
Shrub-NDVI	2	100.45	28.77	-0.12	0.10	-0.30	0.07
Mountain Mahogany	2	100.96	29.28	0.09	0.10	-0.09	0.28
Tree	2	101.62	29.94	-0.06	0.10	-0.25	0.13

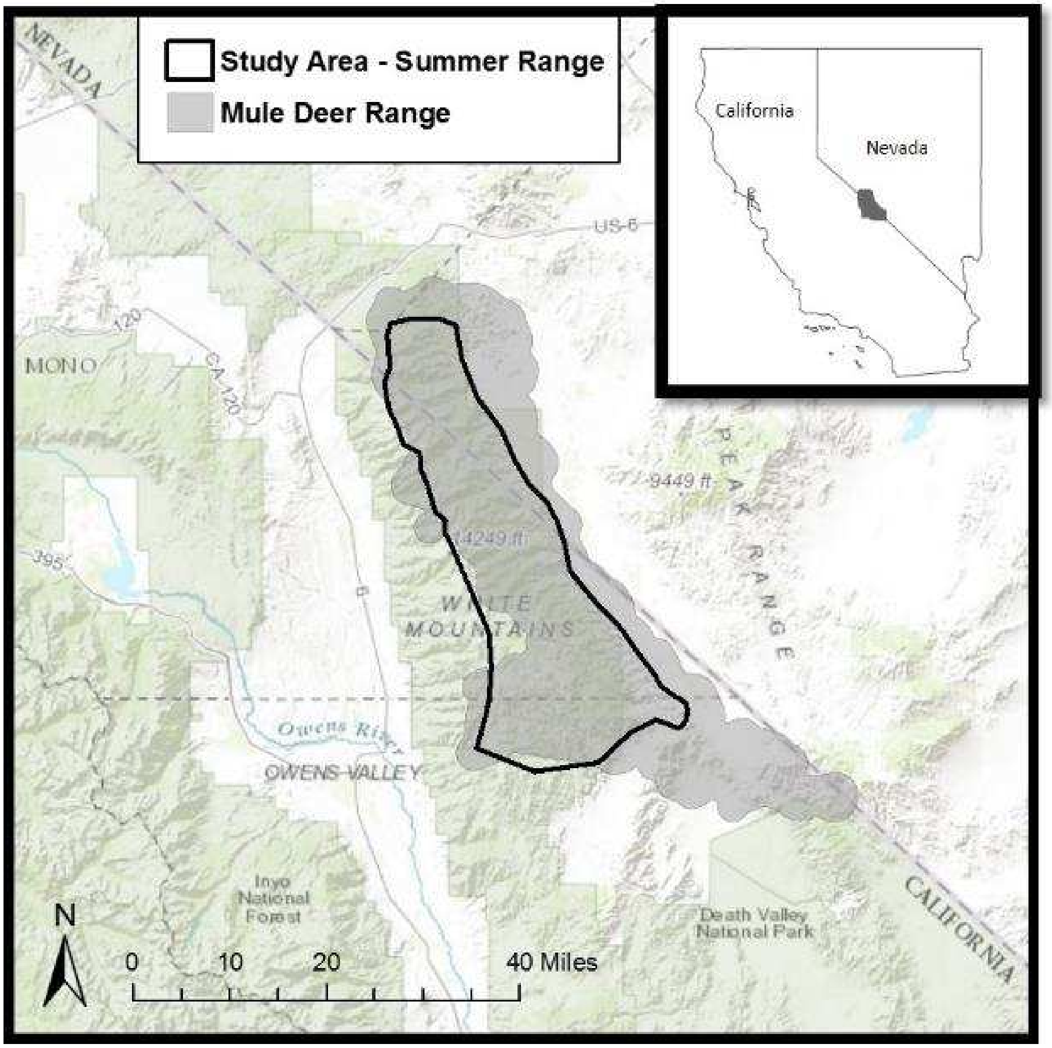

Fig. 1. Study area in the White Mountains of eastern California and western Nevada, USA. Mule deer range occurred primarily on the eastern side of the mountains with summer range extending from 2,900 m to 4,000 m and deer using lower elevations during the winter months.

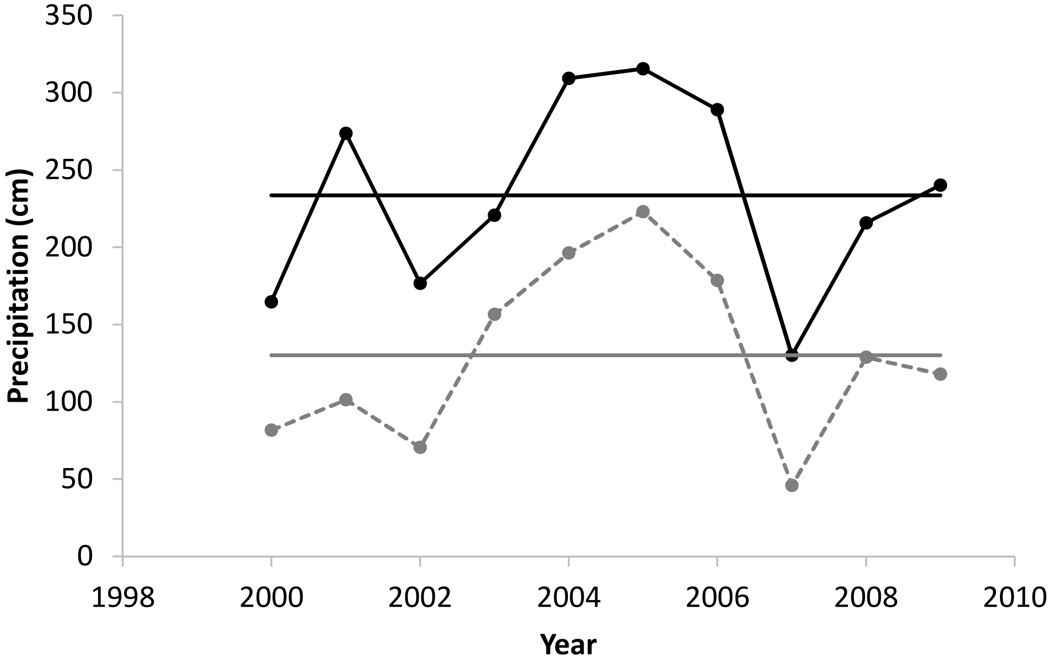

Fig. 2. Mean annual (top solid line) and winter (dashed bottom line) precipitation obtained for summer range in the White Mountains, California and Nevada, USA, 2000-2009 (PRISM Group, 2010). Straight lines represent the mean value over that time period, highlighting years with above and below average precipitation during our study period.

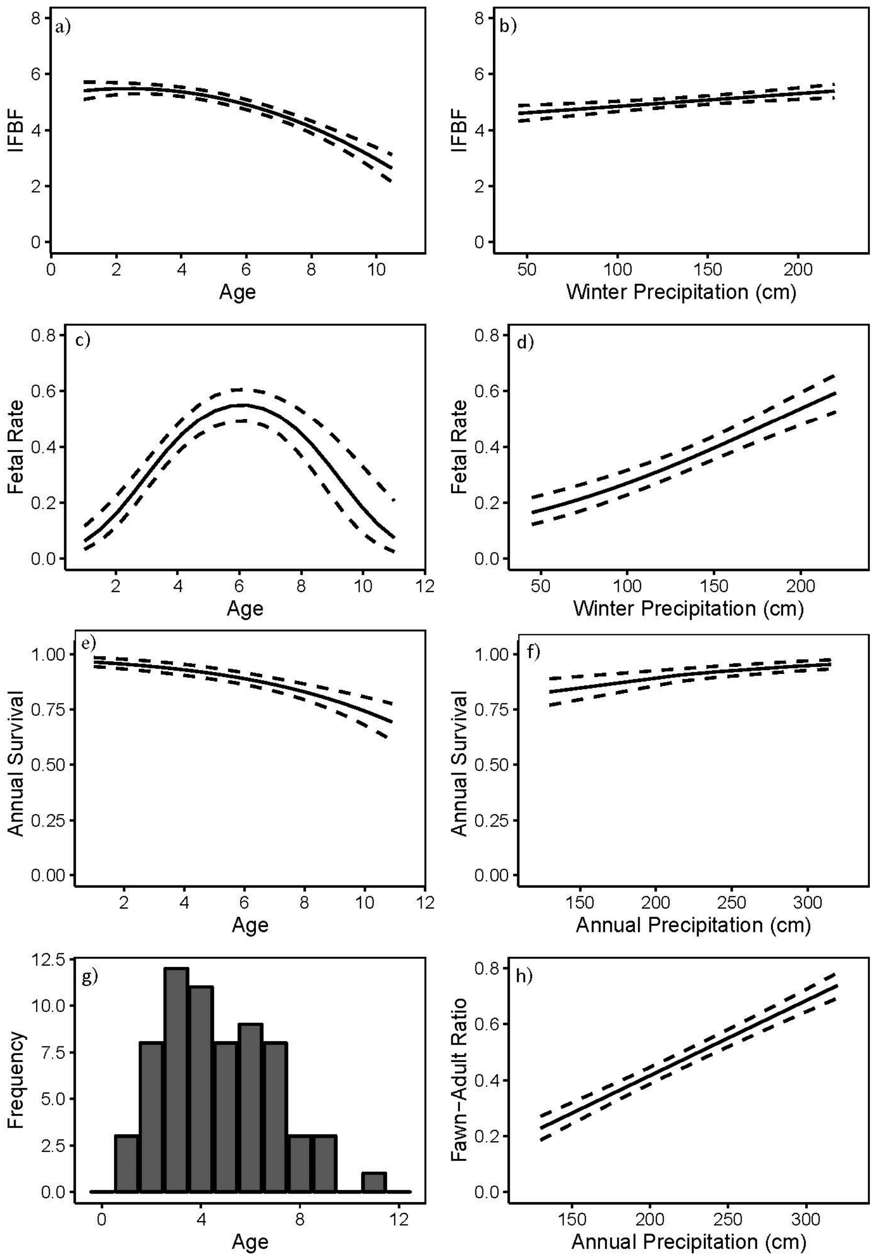

Fig. 3. Effects of age or precipitation (± SE) on body condition (IFBF; a, b), fetal rate (probability of having twins; c, d), annual survival (e,f), and young-adult ratios (h) for a mule deer population in the White Mountains California and Nevada, USA from 2005 to 2009. Predicted values were estimated from generalized linear mixed models which contained the intercept, the predictor variable of interest, and a random intercept term for year (a-d, h). Survival models were generated from known fate models (MARK) which contained the intercept term and predictor variable of interest. Frequency of individuals in each age class over the study period is also shown (g).

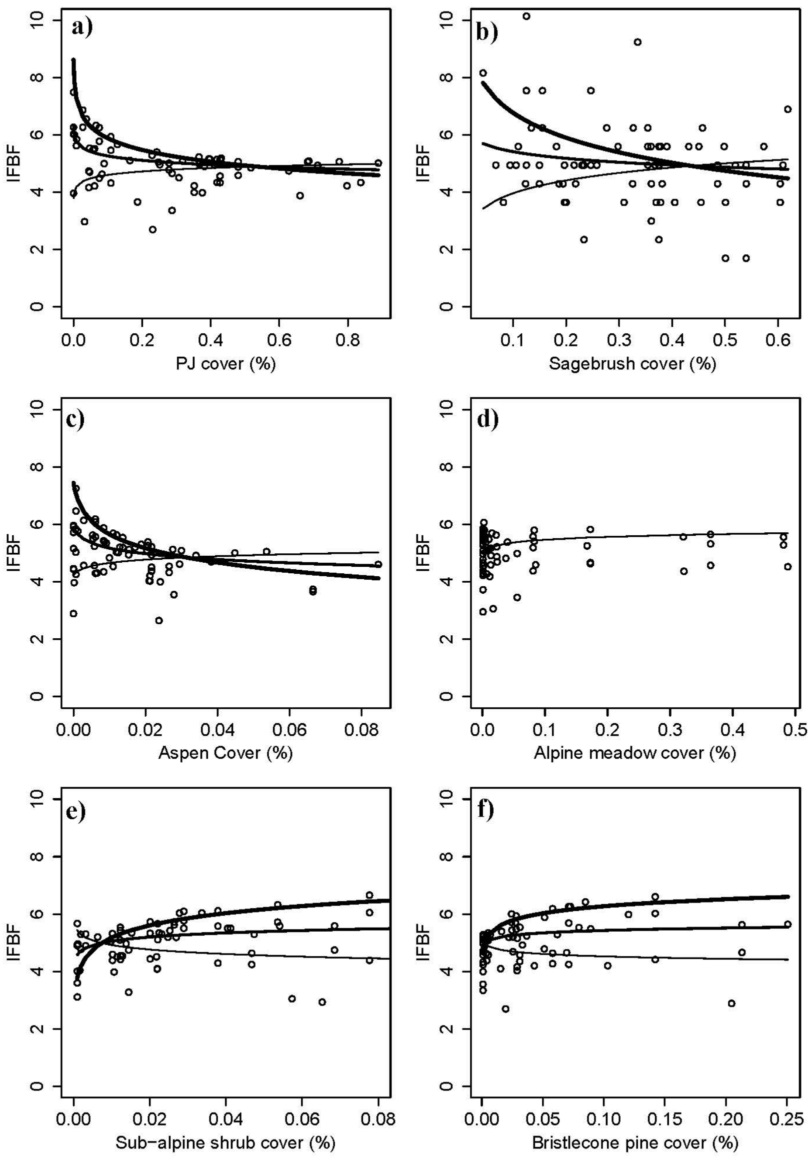

Fig 4. Interactive effects between summer habitat composition; (a)pinyon-juniper, (b)sagebrush, (c) aspen, (d) alpine meadow, (e) sub-alpine shrub, or (f) bristlecone pine cover, and winter precipitation on body condition (IFBFat) of female mule deer in the White Mountains, California and Nevada, USA, 2005-2009, from generalized linear mixed effects models. Predicted values were estimated from models which contained a parameter for the habitat variable, and interaction with winter precipitation, in addition to the base model (Age+Age^2+Winter Precipitation+Random intercept for year). Thicker lines indicate years with greater amounts of winter precipitation, the three lines are representative of the range in dry, average and wet conditions experienced over the study period.

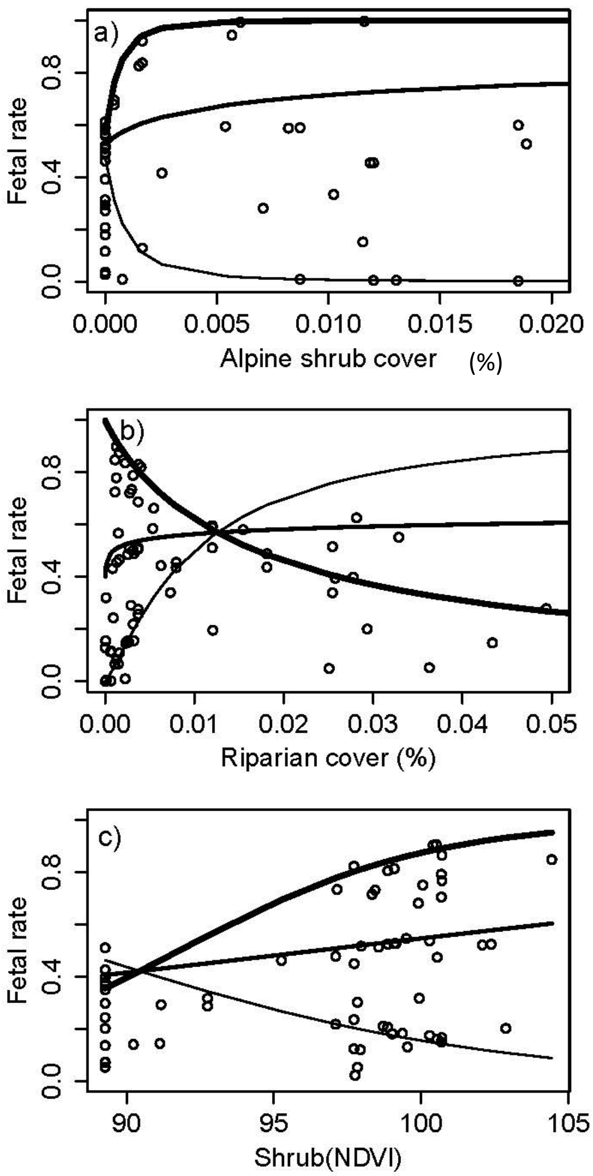

Fig. 5. Interactive effects between summer habitat composition; (a) alpine shrub cover, (b) riparian cover, or (c) shrub NDVI, and winter precipitation on fetal rate (probability of having twins) of female mule deer in the White Mountains, California and Nevada, USA, 2005-2009, from generalized linear mixed effects models. Predicted values were estimated from models which contained a parameter for the habitat variable of interest, and interaction with winter precipitation, in addition to the base model (Age+Age^2+Winter Precipitation+ Random intercept for year). Thicker lines indicate years with greater amounts of winter precipitation, the three lines are representative of the range in dry, average and wet conditions experienced over the study period.

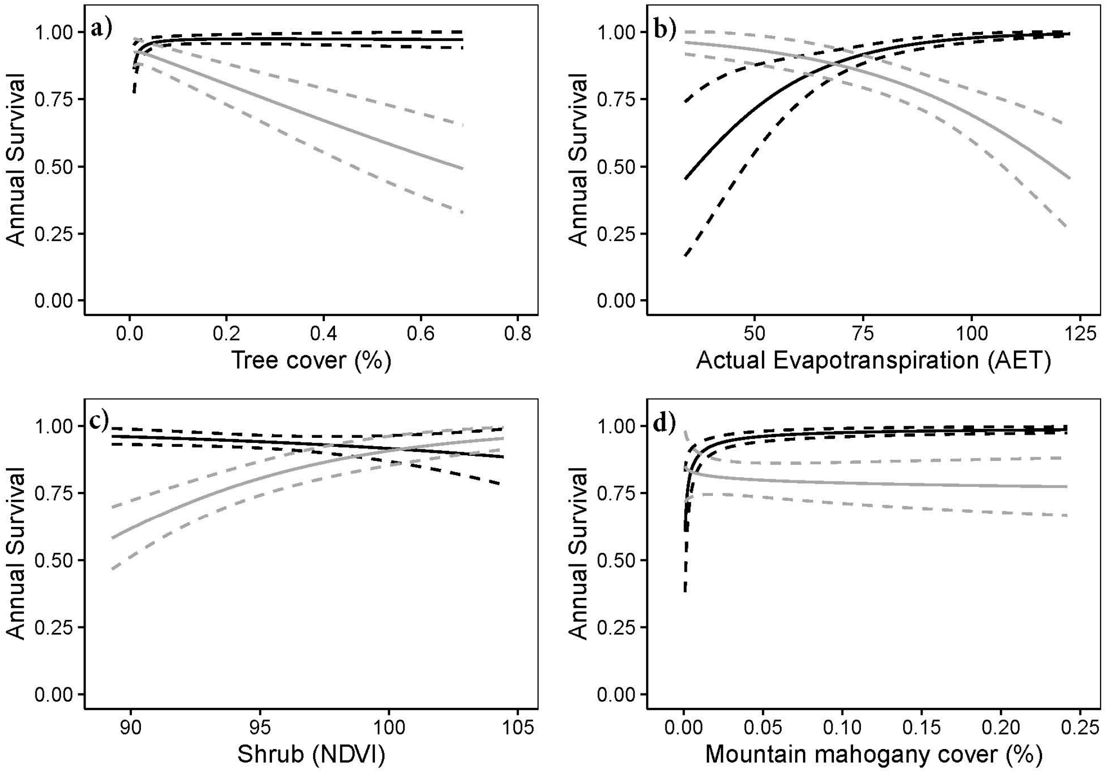

Figure 6. Interactive effects of summer habitat composition and precipitation on **a**nnual survival rates (± 85% CI) of female mule deer in the White Mountains, California and Nevada, USA, 2005-2009, from known-fate analysis (program MARK). Predicted values were estimated from models which contained a parameter for the habitat variable of interest, and interaction with annual precipitation, in addition to the base model (Age+Annual Precipitation). The dark line indicates years with greater amounts of winter precipitation and the grey line represents years with below average the three lines are representative of the range in dry and wet conditions experienced over the study period.

SUPPLEMENTAL MATERIAL

Appendix A. Results from generalized linear mixed models identifying the effects of age, precipitation and summer home range composition on body condition (ingesta-free body fat) for mule deer in the White Mountain, California and Nevada, USA from 2005-2009. The structure of the base model is identified in italics and was used as noted in all subsequent models. Models containing Age^2 or an interaction between two variables also contained the singular terms for those variables. K refers to the number of parameters in each model.

IFBFat Model	**K**	**AICc**	**Delta AICc**
Stage 3) Habitat Variables			
Base + PJ*WPrecip	8	249.46	0.00
Base + Aspen*WPrecip	8	251.57	2.11
Base + Sagebrush*WPrecip	8	252.19	2.73
Base + PJ	7	253.36	3.90
Base + Alpine Meadow	7	253.63	4.17
Base + Riparian*WPrecip	8	253.70	4.24
Base + Alpine Meadow*WPrecip	8	253.74	4.28
Base + Bristlecone*WPrecip	8	253.84	4.38
Base + Sub-Alpine Shrub*WPrecip	8	253.85	4.39
Base ***(Age^2+PrecipJ)***	**6**	**254.37**	**4.91**
Base + Recruitment Index*WPrecip	8	254.69	5.22
Base + Sagebrush	7	255.03	5.57
Base + Aspen	7	255.15	5.69
Base + AET	7	255.25	5.79
Base + Limber Pine*WPrecip	8	255.36	5.90
Base + Sub-Alpine Shrub	7	255.54	6.08
Base + Bristlecone	7	255.74	6.28
Base + Tree	7	255.86	6.40
Base + Riparian	7	255.96	6.50
Base + AET*WPrecip	8	256.12	6.66
Base + NDVI	7	256.42	6.96
Base + Tree*WPrecip	8	256.44	6.98
Base + Limber Pine	7	256.47	7.01
Base + Recruitment Index	7	256.51	7.05
Base + NDVI*WPrecip	8	256.56	7.10
Base + Alpine Shrub	7	256.95	7.49
Base + Dist to Riparian	7	257.01	7.55
Base + Mountain Mohagany	7	257.01	7.55
Base + Desert Scrub	7	257.23	7.77
Base + Bitterbrush	7	257.25	7.79
Base + Tree	7	257.31	7.85

Base + Bare Ground	7	257.33	7.87
Base + Willow	7	257.38	7.91
Base + Density	7	257.38	7.92
Base + Bitterbrush*WPrecip	8	257.87	8.41
Base + Desert Scrub*WPrecip	8	258.76	9.30
Base + Bare Ground*WPrecip	8	258.83	9.37
Base + Alpine Shrub*WPrecip	8	258.85	9.39
Base + Dist to Riparian*WPrecip	8	259.00	9.54
Base + Mountain Mohagany*WPrecip	8	259.01	9.55
Base + Tree*WPrecip	8	259.28	9.82
Base + Willow*WPrecip	8	259.35	9.89
Base + Density*WPrecip	8	259.38	9.92
Stage 2) Environmental Variables			
Age^2 + Winter Precip (t)	6	254.37	0.00
Age^2	5	254.39	0.02
Age^2 + Recruitment Index	6	255.16	0.78
Age^2 + Annual Precip J-J	6	256.49	2.12
Age^2 + WPrecip (t) + Winter- Summer Precip (t-1)	7	256.63	2.25
Age^2 + Density	6	256.70	2.32
Age^2 + Snow Water Content (t-1)	6	256.74	2.36
Age^2 + Winter- Summer Precip (t-1)	6	256.76	2.38
Stage 1) Age Variables			
Age^2	5	254.39	0.00
Age	4	254.67	0.28
Null (Intercept)	3	263.55	9.16

Appendix B. Results from generalized linear mixed models identifying the effects of age, precipitation and summer home range composition on fetal rates (probability of having twins) for mule deer in the White Mountain, California and Nevada, USA from 2005-2009. The structure of the Base model is identified in italics and was used as noted in all subsequent models. Models containing Age^2 or an interaction between two variables also contained the singular terms for those variables. K refers to the number of parameters in each model.

Fetal Rate Model	***K***	**AICc**	**Delta AICc**
Stage 3) Habitat Variables			
Base + Alpine Shrub*WPrecip	7	86.29	0.00
Base + Riparian*WPrecip	7	87.83	1.54
Base + NDVI*WPrecip	7	90.75	4.46
Base + IFBFat	6	91.75	5.46
Base(Age+Age^2+PrecipJ)	5	91.76	5.47
Base + Aspen	6	91.86	5.57
Base + NDVI	6	91.92	5.62
Base + PJ*WPrecip	7	92.01	5.71
Base + Limber Pine*WPrecip	7	92.06	5.77
Base + Aspen*WPrecip	7	92.41	6.12
Base + Dist to Riparian	6	92.62	6.33
Base + Tree*WPrecip	7	92.90	6.61
Base + Bristlecone*WPrecip	7	93.01	6.72
Base + Alpine Meadow	6	93.08	6.79
Base + Sub-Alpine Shrub	6	93.15	6.86
Base + Annual Precip	6	93.22	6.93
Base + Tree	6	93.33	7.04
Base + Willow	6	93.49	7.20
Base + Limber Pine	6	93.50	7.21
Base + Snow Water Content (t-1)	6	93.68	7.39
Base + IFBFat*WPrecip	6	93.68	7.39
Base + Sagebrush	6	93.72	7.43
Base + Snow Water Content (t-1)*WPrecip	7	93.74	7.45
Base + Bristlecone	6	93.76	7.46
Base + PJ	6	93.77	7.48
Base + Mountain Mohagany	6	93.80	7.51
Base + Density	6	93.89	7.59
Base + Recruitment Index	6	93.89	7.60
Base + AET	6	93.93	7.64
Base + Recruitment Index*WPrecip	7	93.98	7.69
Base + Sagebrush*WPrecip	7	93.98	7.69

Base + Desert Scrub	6	94.01	7.72
Base + Delete Age *WPrecip	7	94.03	7.74
Base + Alpine Shrub	6	94.08	7.79
Base + Bare Ground	6	94.09	7.80
Base + Riparian	6	94.09	7.80
Base + Bitterbrush	6	94.14	7.85
Base + Tree	6	94.15	7.86
Base + Sub-Alpine Shrub*WPrecip	7	94.23	7.94
Base + Dist to Riparian*WPrecip	7	94.47	8.18
Base + Tree^2	7	94.70	8.40
Base + Density*WPrecip	7	95.12	8.82
Base + Desert Scrub*WPrecip	7	95.37	9.08
Base + Alpine Meadow*WPrecip	7	95.45	9.16
Base + Willow*WPrecip	7	95.75	9.46
Base + Tree^2	7	96.00	9.71
Base + Bare Ground*WPrecip	7	96.08	9.78
Base + PJ^2	7	96.09	9.80
Base + Mountain Mohagany*WPrecip	7	96.17	9.88
Base + AET*WPrecip	7	96.40	10.11
Base + Bitterbrush*WPrecip	7	96.60	10.31
Base + Tree*WPrecip	7	96.62	10.33
Stage 2) Environmental Variable			
Age^2 + WPrecip (t)	5	91.76	0.00
Age^2 + WPrecip (t) + Winter- Summer Precip (t-1)	6	93.40	1.64
Age^2	4	94.93	3.17
Age^2 + Snow Water Content (t-1)	5	96.53	4.77
Age^2 + Winter- Summer Precip (t-1)	5	96.65	4.89
Age^2 + Density	5	96.89	5.13
Age^2 + Recruitment Index	5	97.02	5.26
Age^2 + Annual Precip J-J	5	97.25	5.49
Stage 1) Age Variables			
Age^2	4	94.93	0.00
Null	2	97.39	2.46
Age	3	98.50	3.57

Appendix C. Results from survival models (known-fate, program MARK) identifying the effects of age, precipitation and summer home range on annual survival for mule deer in the White Mountain, California and Nevada, USA from 2006-2009. The structure of the Base model is identified and was used as noted in all subsequent models. Models containing an interaction between two variables also contained the singular terms for those variables. K refers to the number of parameters in each model.

Survival Model	**AICc**	**K**	**Delta AICc**
Stage 3) Habitat Variables			
Base + APrecip*Tree +Tree2	215.89	6	0.00
Base + APrecip*AET	216.31	5	0.43
Base + APrecip*NDVI	217.26	5	1.37
Base + APrecip*Mountain Mohagany	217.35	5	1.46
Base + Tree2	217.41	5	1.53
Base + APrecip*Tree	217.76	5	1.88
Base + Mountain Mohagany	217.82	4	1.94
Base + NDVI	218.03	4	2.14
Base *(Annual Precip + Age)*	**218.09**	**3**	**2.20**
Base + Density	218.46	4	2.57
Base + Aspen	218.93	4	3.04
Base + Willow	219.13	4	3.24
Base + Dist to Riparian	219.23	4	3.34
Base + Tree	219.97	4	4.09
Base + AET	220.09	4	4.21
Base + Riparian	220.09	4	4.21
Base + Sagebrush	220.10	4	4.21
Base + PJ	220.10	4	4.21
Base + APrecip*Riparian	220.35	5	4.46
Base + APrecip*Density	220.44	5	4.56
Base + APrecip*Aspen	220.94	5	5.05
Base + APrecip*Dist to Riparian	221.11	5	5.22
Base + APrecip*PJ	221.76	5	5.88
Stage 2) Age Variables			
APrecip + Age	218.09	3	0.00
APrecip+ Age2	220.01	4	1.92
Age	221.39	2	3.30
Stage 1) Environmental Variables and Time			
Annual Precip (Jan-Jan)	223.81	2	0.00
Winter Precip (t)	224.36	2	0.56
Snow Water Content (t-1)	227.23	2	3.43

Null *(Intercept)*	**227.86**	**1**	**4.05**
Year	228.36	5	4.55
Winter/Summer	229.81	2	6.01
Month	241.32	11	17.52

Appendix D. Results from generalized linear models identifying the effects of habitat composition on size of summer home range for mule deer in the White Mountain, California and Nevada, USA from 2006-2009. The Null model contains only the intercept term, and K refers to the number of parameters in each model.

Home Range Size Model	**K**	**AICc**	**Delta AICc**
Dist to Riparian	2	71.68	0.00
Riparian	2	87.02	15.34
Aspen	2	91.82	20.13
Desert Scrub	2	95.70	24.02
Alpine Shrub	2	97.99	26.31
Fetal Rate	2	98.23	26.55
IFBFat	2	98.66	26.98
Snow Water Content (t)	2	98.88	27.20
Null (*Intercept*)	**1**	**99.68**	**28.00**
Winter Precipitation	2	100.26	28.57
Bristlecone	2	100.36	28.68
NDVI	2	100.45	28.77
Mountain Mohagany	2	100.96	29.28
Bitterbrush	2	101.35	29.67
Willow	2	101.54	29.86
Limber Pine	2	101.56	29.88
Snow Water Content (t-1)	2	101.58	29.89
Tree	2	101.62	29.94
Sagebrush	2	101.65	29.97
Sub-Alpine Shrub	2	101.68	30.00
Age	2	101.71	30.03
Alpine Meadow	2	101.74	30.06
Bare Ground	2	101.75	30.06
PJ	2	101.78	30.09
Tree	2	101.84	30.16
Annual Precip	2	101.92	30.24
AET	2	101.95	30.26
Recruitment Index	2	101.95	30.27
Density	2	101.96	30.28

Chapter 3 - Resource selection of female mule deer during parturition: influence of forage and cover

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Abstract

Neonatal survival and juvenile recruitment often drive populations of ungulates. Maternal condition and availability of high-quality habitat has a direct influence on neonate survival. Females often select habitat to maximize predator avoidance while also meeting nutritional demands of lactation. In mule deer (*Odocoileus hemionus*) newborns adopt a hiding strategy and rely on adequate concealment cover and optimal placement of bed-sites for survival. Our main objective was to characterize habitat selection of adult females during parturition in the White Mountains of California, Nevada. We placed GPS collars on 51 female mule deer from 2005 to2008 and analyzed movement data from June and July to determine timing of parturition and associated habitat use. We assessed selection at two spatial scales, the landscape scale which considered summer range for the entire population, and the local scale which considered within home range selection. GIS-derived variables related to vegetation associations, tree cover, site productivity, topography, and terrain ruggedness were assessed at the landscape scale, in addition to those variables ground-sampled variables related to concealment cover, plant composition and tree density were assessed at the local scale. Female mule deer selected areas with greater amounts of shrub cover, NDVI, structural cover and landscape ruggedness, and avoided areas with a higher percent of bare ground at the local scale. At

the landscape scale females selected areas with intermediate levels of tree cover and site productivity, lower elevations, less steep slopes, greater NDVI and greater amounts of sagebrush cover. Our results suggest that female mule deer selected habitat that maximized hiding cover for newborns (greater shrub densities and structural cover), while still providing foraging opportunities (greater NDVI and shrub cover). It is possible that females underutilized areas that contained optimal forage such as riparian corridors, high AET sites, higher elevation shrub communities, and areas with less tree cover, to avoid conspecifics or decrease predation risk for neonates during parturition. Nevertheless, in this semi-arid ecosystem it is likely areas that contained robust understory cover also contained suitable foraging opportunity minimizing the tradeoffs which occurred between predator avoidance and forage availability.

1. Introduction

Large herbivores have evolved life history strategies where relatively high and constant adult survival is often maintained through greater variability in reproductive effort (Gaillard et al. 1998). As a result population dynamics of these species are often driven by changes in survival and recruitment of young (Gaillard et al. 2000). Survival of neonates is influenced by maternal condition and availability of high-quality habitat (Monteith et al. 2014, Shallow et al. 2015). Although predation tends to be a proximate cause of mortality for newborns, nutritional condition and forage availability often drive the demographics of ungulate populations, particularly in semi-arid ecosystems (Bishop et al 2009, Parker et al 2009, Monteith et al. 2014). Nevertheless, in populations where nutritional carrying capacity has not been achieved (i.e. $N < K$) predation can limit population growth (Pierce et al. 2012).

Given their limited mobility, neonates are especially vulnerable to predation following parturition (White et al. 1972, Salwasser 1974, Bleich et al. 2006). Many ungulates adopt a hiding strategy for predator avoidance, so robust structural cover is critically important for survival of young (White et al. 1972, Shallow et al 2015). Additionally, nutritional requirements for adult females are high late in gestation and during lactation, making access to abundant forage with high protein content and high digestible energy especially during this period (Sadlier 1980, Barboza and Bowyer 2001, Tollefson et al. 2011). Consequently, during parturition, females often select areas with adequate forage, to meet increased nutritional demands for lactation, and hiding cover to minimize the risk of predation on young (Bowyer et. al 1998). Moreover, habitat quality, through direct influences on physical condition of adult females and indirect effects on survival of young, has a pronounced effect on productivity of a population (Verme and Ullrey 1984, Lomas and Bender 2007, Monteith et al. 2014, Shallow et al. 2015).

Mule deer (*Odocoileus hemionus*) neonates are most vulnerable to predation during the first month of life and mortality rates as high as 70% have been documented in some populations (Salwasser et al. 1978, Bleich et al 2006, Shallow et al. 2015), with daily survival probabilities increasing over time as newborns become more mobile (Monteith et al. 2014). To minimize risk of predation on newborns, adult females often adopt one or more antipredator behaviors associated with parturition including termination of contact with conspecifics (Ozoga et. al 1982, Schwede et al. 1993), isolation from conspecifics, and reduction of home range size or overlap (Fox and Krausman 1994, Schwede et al. 1993). Parturient females often will select habitat characteristics associated with low predator activity and increased concealment cover for young to enhance offspring survival and subsequently their own reproductive fitness (Main and Coblentz 1996, Shallow et al. 2015, Jacques et al. 2015). Studies have shown that bed sites with higher shrub densities and steeper slopes can increase survival of young by reducing exposure to coursing predators, such a coyotes (Cook et al. 1971, Smith and Lecount 1979, Shallow et al. 2015), which are a common predator of mule deer neonates (Hurley et al. 2011). Females may select habitat containing lower quality forage in exchange for increased accessibility to cover or escape terrain (Bleich et al. 1997, Rachlow and Boyer1998, Bangs et al. 2005), suggesting that selection of habitat during parturition may be driven by structural components in the landscape related to predator avoidance rather than forage (Bowyer et al. 1998).

Determining habitat selection during parturition is important for understanding how mule deer use the landscape during this life-history stage, and has implications for demographics of the population (Gaillard et al. 2000). Declines in mule deer (*Odocoileus hemionus*) populations have been documented since the late 1950s throughout the western portions of their range (Carpenter 1998; Gill 2001, Heffelfinger and Messmer 2003). Many hypotheses have been raised regarding causes of declines, including competition with wild or domestic herbivores, predation, over harvest, habitat loss, fire exclusion, and extreme weather (Clements and Young 1997; Gill 2001). Additionally the intermountain west, has experienced a large-scale shift in landscape composition where areas that were once shrub dominated have transitioned into woodlands. Over the past 120 years there has been an increase in distribution and density of pinyon-juniper woodland throughout the western United States (Miller and Wigand 1994, Romme et al. 2009).

In the Great Basin single leaf pinyon pine (*Pinus monophylla*) and Utah juniper (*Juniperus osteosperma*) have shifted from historical mid-elevations, to higher and lower elevations (Tausch and West 1988) with increased tree densities throughout their range (Tausch et al. 1981). As expansion and infilling by pinyon-juniper woodland occurs, tree densities increase and understory biomass declines (Tausch et al. 1981, Everett and Ward 1984, Pieper 1990). This trend is most prevalent on south facing slopes, where canopy cover can range from 20-30%, with understory cover containing 5% shrubs, grasses and forbs, and nearly 70% bare ground (Miller and Wigand 1994). Loss of productive sagebrush-steppe habitat resulting from expansion and infilling of pinyon-juniper woodland alters understory composition and forage resources, resulting in reduction of habitat quality for mule deer. This reduction in habitat quality for adult females (Bender et al. 2007b, 2013) and reduction in understory cover for young (Riley and Dood 1984) and has the potential to negatively impact mule deer populations.

Our goal was to assess habitat selection by female mule deer during parturition and to evaluate which habitat characteristics were most important when neonates are most vulnerable to predation. We were also interested in assessing whether adult females made trade-offs between forage availability and hiding cover, selecting areas based on predator avoidance for young rather than for meeting their own nutritional requirements.

We used location data from female mule deer in the White Mountains of eastern California and western Nevada to evaluate patterns of resource selection during the time period surrounding parturition. Given that deer exhibit substantial reductions in movements surrounding parturition (Bertrand et al. 1996, Carstensen et al. 2003) we were able to estimate timing of birth using movement data from GPS-collared females and identified location clusters corresponding to habitat used during that time period (Long et al. 2009, Bush et al. 2015). Females will often alter their behavior and habitat use as offspring become more mobile and nutritional constraints change (Long et al. 2009); therefore, we focused on habitat use during parturition, which did not require us to make assumptions about continued survival of young.

We hypothesized that parturient females would select habitat that provided greater protection for neonates, such as increased understory cover, steeper slopes, and proximity to escape terrain, rather than solely focusing on prime foraging locations, during this period when neonates are most vulnerable to predation. We also hypothesized that pinyon- juniper woodlands would not contain characteristics, such as understory cover, necessary to conceal newborns and therefore would be avoided by parturient females. We evaluated these hypothesis at both a local and landscape scale to examine the influence of fine scale structural characteristics in addition to larger landscape scale processes related to topography and vegetation associations on resource selection of female mule deer during parturition.

2. Materials and methods

2.1 Study area

The White Mountains are a semi-arid mountain range located northeast of Bishop, California (37.4° N, 118.5° W) at the western edge of the Great Basin, within Inyo and Mono counties in California and Esmeralda County in Nevada. The mountain range extends approximately 20 km from their base at 1,400 m to their crest, which ranges from 3,000 m to 4,000 m (Hall 1991). They fall within the rain shadow of the Sierra Nevada, resulting in low rainfall for a mountain range of this size and elevation. Average precipitation for this region was between 12.7 cm at lower elevations and 50.8 cm at highest elevations with the majority of precipitation falling during the winter months (Hall 1991). Mule deer populations tended to occur on the eastern side of the range, which had a more gradual elevation profile and typifies the basin and range topography and plant communities of the Great Basin. Our study area extended 80 km along the east side of the mountain range from the foothills to the mountain crest, and transitioned through the associated plant communities along the elevational gradient.

Sagebrush (*Artemisia* spp.), ephedra (*Ephedra* spp.) and rabbitbrush (*Ericameria nauseosus*) were dominant at low elevations (<2,000 m). Intermediate elevations (2,000 m to 2,900 m) contained large expanses of single-leaf pinyon pine and Utah juniper overstory (PJ woodland), with the understory dominated by sagebrush, bitterbrush (*Purshia spp*.), ephedra, and rabbitbrush. Those intermediate elevations tended to contain large stands of closed canopy PJ woodland interspersed with patches of more open shrub-woodland dominated vegetation. The Subalpine Zone (2,900 m to 3,500 m) consisted of a patchy mosaic of shrub, forb and wet meadow vegetation interspersed with open forests consisting of lodgepole pine (*P. contorta*) and limber pine (*P. flexilis*), with bristlecone pine (*P. longaeva*) at higher elevations in more acidic soil; quaking aspen (*Populus tremuloides*) occurred in moist areas, and dense stands of curl-leaf mountain mahogany (*Cercocarpus ledifolius*) occurred along dry slopes at lower elevations. Elevations above 3,500 m, comprise the Alpine Zone, which is characterized by dolomite or granite fields with sparse, dwarfed vegetation such as phlox (*Phlox* spp.), buckwheat (*Eriogonum* spp.), and dwarf sagebrush (*A. arbuscula*; Hall 1991). Perennial water sources are generally scare and occur only in a few major drainages, with riparian areas at lower elevations dominated by cottonwood (*Populus* spp.) and higher elevations by willow (*Salix* spp.) and quaking aspen. Seeps, wet meadows, and intermittent streams also occur throughout the landscape from spring to late summer, however the region relies heavily on snowmelt for water recharge and plant growth (Comstock and Ehleringer 1992, Fan et al. 2014).

The majority of mule deer in the White Mountains exploit resources by shifting up and down in elevation to capitalize on seasonal availablility of forage. They used low elevation (1,800 m) shrub habitat during the winter and spring, then transitioned to intermediate elevation and alpine habit during the summer months (2,900 m - 4,000 m; Hall 1991. Sagebrush and bitterbrush are major components of mule deer diets, especially during winter (Kucera 1997, Pierce et al. 2004, Pierce et al. 2012), but deer have a greater dependence on forbs and new plant growth during summer months when nutritional requirements are high. Carnivore species generally occurred at low population densities and included coyotes (*Canis latrans*), mountain lions (*Puma concolor*), bobcats (*Lynx rufus*), black bears (*Ursus americana*), and golden eagles (*Aquila chrysaetos*), each of which are predators of young mule deer (Shallow et al. 2015, Monteith et al. 2013).

2.2 Animal capture and location data

Adult female mule deer (>1yr old) were captured during winter and spring of 2005-2008 using a net gun fired from a helicopter (Krausman et al. 1985). Once captured, animals were transported to a central processing area where biological samples were collected. Pregnancy and fetal rates were determined by abdominal ultrasound for individuals captured during the spring. We deployed a standard global positioning system (GPS) telemetry collar (Advanced Telemetry Systems, Isanti, Minnesota, USA) on each individual, which were programmed to gather location data every 3 or 7 hours during summer. Individuals were monitored bi-weekly to determine mortality, otherwise, collars were recovered after approximately one year, at which time the location data were retrieved for analysis and for ground sampling. We attempted to distribute capture efforts evenly across the study area to maintain independence among our sampled individuals. All capture and handling of mule deer was compliant with procedures outlined by the California Department of Fish and Wildlife, were in keeping with guidelines established by the American Society of Mammalogists for research involving mammals (Sikes et al. 2011), and were approved by the Institutional Animal Care and Use Committee at the University of Nevada Reno (IACUC: 00109).

2.3 Timing of parturition

To determine timing and corresponding habitat used at parturition, we estimated daily movement rates from GPS location data for individual adult females during the period of peak parturition (June through July). Previous studies have recognized that females markedly reduce movements just prior to parturition (Bertrand et al. 1996, Carstensen et al. 2003, Long et al. 2009). Behavioral studies have also identified a reduction in movement several days following parturition, when the neonate has limited mobility (Ozoga et al.1982; Huegel et al. 1985). Based on this behavior we considered parturition to occur when the hourly movement rates dropped markedly (generally to ≤ 30m) over a 24-hour period and remained so for multiple days (>1; Bush et al. 2015). We then visually identified the cluster of points that corresponded to these reduced movements and considered that the fawning cluster. Similar cluster analyses have been used to identify kill sites for mountain lions and grizzly bears (Anderson and Lindzey 2003, Cristescu et al. 2014). This method allowed us to evaluate habitat selection related to the birth-site, without the use of more invasive techniques, and in a mountain range with very limited access. Once the cluster of points was identified we randomly selected 2 points from within that cluster as representative of the birth-site. We then paired those used sites with a random site located between 200 m and 500 m from the centroid of the fawning cluster, to determine selection at the local scale. To assess habitat selection at the landscape scale we compared locations associated with the fawning cluster to random points generated throughout the summer range for the population.

2.4 Predictor variables

Ground Sampling- We measured environmental variables related to forage availability, hiding cover, and topography from both ground-sampled data and GIS datasets, which allowed us to combine fine-scale measures of habitat composition with GIS-derived variables over a larger spatial extent. For each location (birth-site or random), we estimated ground data related to structural hiding cover and plant composition along two 30 meter transects radiating in opposite directions (generated at random) from the GPS location; transect data were averaged over the 60 m for each point. We used a vegetation profile board (Nudds 1977) to determine amount of structural hiding cover available at the site, to approximate the view shed of an approaching predator. We estimated the percent obstruction (cover) of the profile board, at three height intervals (ground to 0.5 m, 0.5 m-1.0 m, 1.0 m-1.5 m) along each 30m transect at 5m increments from the plot center, for each location. We then averaged the cover values over the length of the transect for the 0 m -1.5-m height class and the 0-0.5-m height class, to focus both on concealment cover in general, and that which is relevant for a hiding neonate, respectively. To determine the dominant plant community and species composition, we identified the linear cover for each plant species along the 30-m transect (Kershaw 1964). Given that pinyon and juniper trees often have a shrub-like form in this region, we included tree species in our linear cover estimates. Using these vegetation data, we identified 4 broad cover types: bare ground, forb, grass, shrub, and tree. We also estimated percent cover of the most dominant shrub and tree species individually, which included bitterbrush, sagebrush, rabbitbrush, mountain mahogany, and pinyon pine. In addition, we generated a secondary estimate of tree density using point quarter sampling at 2 random locations along each transect (Avery and Burkhart 2002). Tree density was estimated as the mean distance to the closest tree averaged over the entire transect, in general tree densities within this region are low, making the linear cover method a more useful measure of tree composition.

GIS-derived variables – In addition to ground sampling, we also incorporated GIS-derived variables to assess resource selection at the landscape scale. This technique allowed us to estimate landscape characteristics for a larger number of used and available points, and to calculate additional landscape metrics related to topography, vegetation composition and water resources. We identified variables that are thought to influence selection of birth sites, such as slope, elevation, aspect, and ruggedness using a 10-m Digital Elevation Model (DEM; United States Geological Survey 2010). To describe landscape ruggedness we calculated a vector ruggedness measure (VMR; Sappington et al. 2007) that combined the variation in slope and aspect of a region to create an index of ruggedness, which ranged between 0 (no terrain variation) and 1 (high terrain variation), with most landscapes containing values from 0 to 0.4. We also calculated an index of topographic position (TPI; ArcGIS 10.0 ESRI, Redlands, California, USA) where negative values indicate lower hillslope position and positive values indicate higher hillslope position than the surrounding area, with zero indicating either a flat or mid-slope position. We calculated a site-based measure of actual evapotranspiration (AET) to estimate potential plant growth for a given pixel based on abiotic factors. To do this we used elevation, solar radiation, temperature, soil, water, slope, and aspect, and calculated AET from a Thornthwaite water balance model (Stephenson 1998, Dilts et al. 2015) with 30-year average PRISM climate data (PRISM Group 2010). We calculated an annual AET value (Jan-Jan) and a spring AET value (May-June), which characterized sites along a gradient from hot, dry and generally less productive, to cooler, wetter and more productive (Stephenson 1998, Dilts et al. 2015).

We delineated land cover types based on the U.S. Forest Service 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 Forest Service 1981). We reclassified the map into 8 broad vegetation associations based on dominant plant species: (1) wet meadow, (grasses and forbs); (2) bare ground; (3) bristlecone pine; (4) sagebrush; (5) bitterbrush; (6) mountain mahogany; (7) pinyon- juniper woodland; (8) upper montane pine (lodge pole and limber pine). Vegetation associations related to high alpine shrub or desert shrub communities were not included in the analysis because they were rare in the dataset. To derive finer resolution data on vegetation composition and structure we employed maximum likelihood classification in ArcGIS 10.0 (ESRI, Redlands, California, USA) using 1m resolution orthophoto imagery from the National Agriculture Imagery Program (NAIP, USDA Farm Service Agency August 2008) to categorize sites as bare ground, tree, shrub, and riparian cover (willows, aspen, cottonwood, and see Chapter 1 for more detail). Using those broad classifications, we generated estimates for percent tree cover, riparian cover, and distance to riparian zones. Tree cover included all non-riparian trees with pinyon-juniper being the dominant vegetation type (70%), followed by mountain mahogany (20%), bristlecone pine (5%), and limber-lodge pole pine (5%), based on CALVEG classifications. Using the same orthophoto imagery we also calculated shrub-NDVI, an index of greenness using NDVI for all non-tree, non-riparian pixels to differentiate between shrub areas with robust plant cover versus areas with greater amounts of bare ground (see Chapter 1). NDVI has been shown to correlate with plant productivity and increased forage availability (Pettorelli et al. 2005).

2.5 Statistical analysis

We used generalized linear mixed models (package lme4 in R2.15.3; R Development Core Team 2013) to estimate resource selection at 2 spatial scales (1) local scale (within home range) and (2) landscape scale (within summer range). We included animal ID as a random effect to account for unequal numbers of locations among individuals. The local-scale models contained variables estimated from ground sampled data, in addition to GIS-derived variables related to topography and broad vegetation associations. Variables included in the landscape-scale models were all GIS-derived. A separate analysis was performed to determine resource selection at each spatial scale, and the same modeling process and evaluation was employed for each analysis. We also estimated Pearson product-moment correlation coefficients for the ground sampled and GIS-derived variables to assess covariance among habitat variables in addition to understanding relationships between habitat components (Zuur et al. 2009).

Model selection was performed in an iterative process, whereby we first investigated single term models containing the variable of interest, then determined if that variable was supported over the Null model (intercept only), and next increased model complexity where appropriate. Sample size for the local-scale models was low, so we were cautious when including multiple correlated variables in those models. Additionally, given the nature of transect based sampling, many of our ground-sampled variables were highly correlated. By first assessing them as single term models, we were able to identify which variables were best supported and compare the magnitude of the effects. Models were ranked using Akaike's information criterion corrected for small sample size (AICc), which identifies the most parsimonious model by balancing model complexity with the amount of variance explained, and where the best model had the lowest AICc value (Burnham and Anderson 2002). Covariate effects were considered to be supported if inclusion of the parameter improved model fit, over the Null model and the 85% confidence intervals of the beta estimates did not overlap zero (Arnold et al. 2010). All habitat variables were converted to standard normal values ($\mu = 0$, SD >1) to allow for direct comparison of covariate effects (Zar 2010, McKee et al. 2015). For consistency we used the same process to evaluate resource selection for our landscape scale analysis, although at that scale we did not have the same degree of covariance among our suite of variables (Pearson correlations < 0.6). Once we identified the variables with the greatest support within our suite of single term models (supported over the Null model), we then explored more complex model structures. First we used the supported variables from the suite of single term models to create a global model. To simplify this global model we then iteratively removed each variable individually and assessed the change in AICc value. Variables were retained in the global model only if removing them caused a decrease or increase in AICc of greater than 2 (Arnold et al 2010). We then identified all possible combinations of those variables in our final analysis. Given that shrub cover and bare ground were highly correlated (Pearsons correlation >0.7) we did not allow those variables to occur in the same model. We then identified the suite of top models from each analysis (AICc weight >0.05) and model averaged among those top models to derive parameter estimates. Model averaging was employed for our analysis at the local scale. The landscape level analysis identified only one top model and model averaging was not necessary.

3. Results

3.1 Timing of parturition

We identified decreased movement rates over multiple days, consistent with behaviors observed during parturition for 51 female mule deer during the summers of 2005 through 2008. The majority of individuals (*n*=47) showed decreased movement rates indicative of parturition between the 5th and 28th of June (Fig. 2), with four individuals giving birth during the first 2 weeks of July. We estimated the mean parturition date as June17 (SD± 5 days), with a peak in activity on June 18th (Fig. 2). We included all of these individuals in our analysis of resource selection at the landscape scale, but could only conduct ground sampling of fawning clusters for 35 individuals for the analysis of resource selection at the local scale due to constraints on the timing of sampling.

3.2 Vegetation summaries

Data collected from the ground transects identified sagebrush, pinyon pine, bitterbrush, mountain mahogany, rabbitbrush and willow as the most common plant species. Additionally bare ground comprised on average 53% (SD±15%) of the transect length with mean shrub cover of 24% (SD±18%) and mean tree cover of 11% (SD±13%). We identified a strong negative correlation between shrub cover and bare ground, where transects that contained greater shrub abundance had less bare ground, and greater forb and grass abundance (Table 1). Shrub cover along the transect was highly correlated with greater structural cover from 0-0.5m in height as measured by a cover board. There was also a negative correlation (-0.60, $p<0.05$) between tree cover and shrub cover for all measures of tree abundance; tree cover along transects, tree density from point-quarter sampling, and our remotely sensed estimate of tree cover from geospatial data. We also identified a negative correlation between our measures of tree cover and both grass and forb abundance, while tree density was positively correlated with bare ground (Table 1). Interestingly tree cover was positively correlated with structural cover, at 1m and 1.5 m heights and less so at 0.5 m. This relationship suggests that as tree cover increased it provided concealment cover at the higher height classes, but less understory structural cover.

3.3 Local scale resource selection

Results from our models of resource selection suggest that during parturition, female mule deer selected habitat for structural cover and forage availability at the local scale. Females avoided areas with greater amounts of bare ground and selected areas with greater concealment cover, shrub cover, mountain mahogany cover, and higher productivity (NDVI) in addition to a greater degree of landscape ruggedness at the local scale (Tables 2 and 3, Fig. 3). These variables were retained in our global model for local scale resource selection. Our single term model results also identified avoidance of bare ground, to be the strongest predictor of relative habitat use, followed by selection for greater shrub NDVI, concealment cover (0-0.5m in height) and overall shrub cover (Appendix A). Models that contained variables related to forb cover, grass cover, or individual species of plants were largely unsupported and were ranked below the null model (Appendix A). Female mule deer selected areas with greater landscape ruggedness (VMR; Fig. 3c), but other terrain variables such as slope, topographic position and elevation were not significant at the local scale. A positive effect of mountain mahogany cover was supported by model selection, however the 85% CI surrounding the beta estimates overlapped zero and indicated high variability in the relationship. Structural cover was also supported in model selection with 85% confidence intervals overlapping zero and again indicated high variability in the effect (Table 3 and Fig. 3e). We also failed to find support for any influence of tree cover, either sampled along the line transect or from our remote sensed vegetation layer, with models containing those variables performing worse than the null model (Appendix A).

3.4 Landscape scale resource selection

During parturition female mule deer selected lower elevation areas, with gradual slopes, greater shrub NDVI and intermediate site productivity (AET) than available summer habitat at the landscape scale, with these variables contained in our global model and top ranked model (Table 4). Females also selected areas containing sagebrush, pinyon-juniper or meadow vegetation associations, which tend to occur at mid-elevations. Additionally females were less likely to use vegetation associations that occurred at high or low elevations, such as lodgepole pine, mountain mahogany, and bitterbrush vegetation associations, or areas of predominantly bare ground (Fig. 4e).

Females selected areas with potentially greater foraging opportunities, such as areas of high NDVI (Fig. 4d). Conversely, riparian vegetation did not significantly influence location of birth sites, and was not included in the global model. Moreover, single term models identified slight avoidance of riparian areas (Appendix B) indicating some selection for areas with greatest foraging opportunities as indexed by shrub NDVI, and avoidance of other productive habitat such as riparian areas. Additionally, females selected areas with low to intermediate tree cover, suggesting that trees provide some benefit as structural cover during parturition, but areas with high levels of tree cover were generally avoided (Fig. 4a). Interestingly the influence of hillslope position and terrain ruggedness (VMR) were not supported at this larger scale.

4. Discussion

Selection of habitat components may vary based on life-history stages, such as during parturition. Mule deer likely select habitats differently during different stages of their life history to obtain resources necessary for growth, reproduction, and survival, as well as the needs of their offspring. By analyzing GPS movement data from adult female mule deer, we were able to identify periods of decreased and clustered movements that matched parturient behaviors observed in other studies (Carstensen et al. 2003, Long et al. 2009, Bush et al. 2015). Incidentally, we captured one female that was not pregnant and consequently did not demonstrate a decrease in movement rates consistent with our parturient females. Identifying parturition through the use of movement data allowed us to assess habitat selection associated with parturition even though we were unable to visually observe birth-sites. Since survival of newborns is highly variable during the first week of life (Monteith et al. 2014), selection of birth-sites and habitat during this period when young are the least mobile directly influences survival (Riley and Dood 1984 Main and Coblentz 1996, Jacques et al. 2015, Shallow et al. 2015). We identified substantial variation in estimated date of parturition for this population (Fig. 2), which can be influenced by nutritional condition of females, where females that conceive later and extends the duration of which births occur (Asher et al. 2005, Clements et al. 2011).

Our findings suggest that during parturition, female mule deer select sites that optimize security of newborns, which contain greater amounts of concealment cover, productive shrub vegetation (NDVI), terrain ruggedness (VMR), and less bare ground.

Nevertheless by selecting these area which had a greater abundance of productive forb and shrub vegetation, adult females may also increase their access to forage resources which is critical given the high energetic demands of late term gestation and lactation (Sadlier 1980, Barboza and Bowyer 2001, Tollefson et al. 2011). Poor maternal condition can influence offspring survival by predisposing neonates to early mortality through low birth weights or malnutrition, especially during the first 2 weeks of life (Monteith et al. 2014), though characteristics of habitat that relate to concealment cover and escape from predators may have equally important effects on survival of young (Lomas and Bender 2007, Shallow et al. 2015).

Within the eastern Sierras and parts of the great basin, newborn mule deer are likely most vulnerable to predation by coyotes, felids (bobcats and mountain lions), and black bears (Monteith et al. 2014). In more mesic forested regions black bear predation may be the dominant cause of mortality, conversely in more arid regions, such as the White Mountains, canids and felids are the predominant predators (Monteith et al. 2014, Shallow et al. 2015). Concealment cover has been shown to increase survival probability of neonates (White et al. 1972, Shallow et al. 2015), and our data indicate that females selected areas that had less bare ground, greater shrub abundance and greater concealment cover than random locations, at the local scale (Fig. 3). Steeper slopes and higher hill-slope positions may aid in avoidance of coursing predators such as coyotes (Cook et al. 1971, Main and Coblentz 1996), but we found that females were more likely to use lower elevation and flatter areas during parturition (Table 2 and Fig.4). Females also selected areas with a greater degree of landscape ruggedness (Fig. 3). These findings are consistent with other studies, where mule deer fawns selected areas with dense concealment cover and typically used areas associated with mid-slopes or lower hill-slope positions (Riley and Dood 1984, Shallow et al. 2015). This mid-to lower-portion of the hillslope in semi-arid regions may have the greatest available moisture and support more robust vegetation while still providing opportunities to escape from predators. Females also selected vegetation associations which occurred at mid-elevations, (sagebrush and pinyon-juniper) to a greater extent than those found at higher elevations (bristlecone pine, lodge pole pine, and mountain mahogany). Selection for mid-elevation sites may correspond with earlier green-up in summer and higher night-time temperatures. Temperatures in high elevation sites may still drop to below 5°C during early June (PRISM). Mule deer migration often corresponds to snow-melt and green-up of vegetation to allow individuals to exploit seasonally available forage resources (Monteith et al. 2011). Additionally, Wallace and Krausman (1990), observed that bed-site selection of elk young varied in elevation related to seasonal snow-melt and green-up.

Parturition sites we identified were characterized by greater plant productivity (NDVI), shrub abundance and sagebrush vegetation associations, which highlights the importance of adequate foraging opportunities. In many ungulate species timing of birth often coincides with onset of green-up and peak NDVI (Bowyer et al. 1991, Whiting et al. 2012). NDVI in our study area was correlated with greater forb and grass abundance, and negatively correlated with bare ground (Table 1), and has been shown to correlate with plant productivity and increased forage availability (Pettorelli et al. 2005).

Generally, sagebrush and bitterbrush are thought to be fundamental components in the diets of mule deer, especially during winter (Kucera 1997, Pierce et al. 2004, Pierce et al. 2012) however, given their high nutritional requirements during summer, mule deer often concentrate feeding on forbs and new plant growth (Barboza and Bowyer 2001, Tollefson et al. 2011). Forbs are generally scarce in this semi-arid ecosystem, and shrubs likely provide an important food resource for mule deer during summer months (Krausman et al. 1997, Bartmann 1983). Our ground sampling occurred the season preceding the location data and as a result, there could be some annual variability in forb or grass abundance that obscured our results at the local scale. Shrub abundance is unlikely to change dramatically from one year to the next.

Riparian areas are often considered an important component of habitat for mule deer in semi-arid regions and they provide important forage and water resources (Hazam and Krausman 1988, Mckee et al. 2015). Conversely, our results indicated avoidance of riparian habitat during parturition (Tables 2 and 4, and Appendix B). Although, there was some evidence that mule deer selected sites closer to riparian areas at the larger spatial scale, the effect was weak (Appendix B). Riparian areas tend to attract domesticated ungulates such as sheep, cows, and horses that likely diminish the value of riparian vegetation as a forage resource or for structural cover (Loft et al. 1987, Beever 2003, Roever et al. 2015) and can act as travel corridors for predators making riparian areas riskier for newborn mule deer. Females attempt to minimize interactions with other conspecifics and predators during parturition; thus use of riparian areas during parturition may be limited however, the forage and water resources are likely still critical for adult females especially during lactation (Hazam and Krausman 1988, Parker et al. 2009) and use of riparian areas has been shown to increase later in the season as young become more mobile (Long et al. 2009).

We identified variable use of pinyon-juniper woodland and tree cover during parturition for this population. Females selected intermediate amounts of pinyon-juniper woodland and avoided areas of high cover at the larger spatial scale; although tree cover did not directly influence decisions about fine scale habitat selection (Fig. 4a). At low-to-intermediate cover tree cover may provide beneficial structural characteristics such as concealment and escape from predators (Altendorf et al. 2001), or optimal microclimate conditions (Giotto et al. 2013, Tull et al. 2001). Many studies of bed-site selection of newborns have identified selection for areas with robust hiding cover generally comprised of shrubs or dense vegetation, with juniper trees also being utilized to a lesser extent (Butler et al. 2009, Grovenburg et al. 2010). In semi-arid ecosystems, understory biomass tends to decline as PJ cover increases (Tausch et al. 1981, Pieper 1990, Tausch and Tueller 1990), particularly on drier sites where trees are able to outcompete forbs and shrubs for resources and especially for water (Breshears et al. 1997, Pierson et al. 2010). In addition, viewshed may decline with increasing PJ density, making it difficult to detect predators and increasing perceived risk (Altendorf et al. 2001). Within our study area tree density was positively correlated with structural cover (0-1.5 meters) indicating that it may provide concealment cover for adult deer, however there was no significant correlation with understory cover (0-0.5m), which is most critical for newborn mule deer (Table 1;Shallow et al. 2015). Moreover areas with greater tree densities tended to have greater amounts of bare ground, and lower shrub cover, which is significantly correlated with structural cover for neonates (0-0.5m; Table 1). Tree cover was also negatively correlated with the abundance of important forage resources (sagebrush, bitterbrush, forbs, and grasses), and suggest a decline in foraging opportunities as tree cover increases (Table 1).

Our results are consistent with research conducted in southeast Oregon, where a 50% increase in juniper cover resulted in an 80% decline in sagebrush cover followed by a reduction in herbaceous vegetation and species diversity (Miller et al. 2000). Moreover, areas of high PJ cover where understory biomass has declined lose beneficial structural components, resulting in less concealment cover for newborns and forage for adults. Previous research conducted in this mountain range identified a negative relationship between annual survival and tree cover, during years with low precipitation (chapter 2). Further, Bender et al. (2007) identified a negative relationship between body condition and amount of pinyon-juniper within an individual's home range for mule deer in north-central New Mexico. These findings support our hypothesis areas dominated by pinyon-juniper cover have lower habitat value for mule deer.

Concealment cover for young and adequate foraging opportunities for mothers are critically important for neonatal survival (Monteith et al. 2014, Shallow et al 2015) and appear to be key determinants of habitat use during parturition. Mule deer in this region did not appear to select habitat based solely on forage resources and knowing that maternal condition has direct effects on offspring survival, it is not surprising that we identified strong selection for robust forb and shrub vegetation. Nevertheless, females avoided or underutilized areas that many consider to provide optimal foraging opportunities such as riparian corridors, higher elevation shrub communities, greater AET sites, or areas with less tree cover. Avoidance of these areas might minimize interactions with conspecifics or increase security from predators during parturition (Cook et al. 1971, Ozoga et. al 1982, Schwede et al. 1993, Main and Coblentz 1996). Given the arid nature of this landscape, it is likely that areas that provide adequate hiding cover for young in the form of robust understory vegetation likely have adequate soil moisture and growing conditions to support forage resources for adult females until young are more mobile. Further, this study demonstrated the utility of GPS derived movement data to identify habitat selection when visual observations of birth-site or timing of birth is unknown. This method can be particularly useful in populations where timing of parturition is highly variable and individuals are dispersed. Given that survival, and ultimately, the recruitment of young generally have the greatest influence on population growth and persistence for many species of large mammals, it is important to identify critical habitat during the time periods when young are most vulnerable. In semi-arid ecosystems managing for optimal habitat during parturition such as productive shrub vegetation, and ample concealment cover has the potential to positively influence the dynamics of mule deer populations in this region. Maintaining areas with low-to-intermediate tree cover, where there is still abundant shrub understory and sufficient concealment cover, may also be beneficial for mule deer.

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Table 1. Pearson Correlation coefficients for ground sampled data (T) and GIS derived variables (G) used in local scale analysis of fawning-habitat selection of female mule deer in the White Mountains, California and Nevada, USA from 2005 to 2008. Stars indicate significance levels (p-values) based on a two-sided pairwise comparison.

		Transect Data				Geospatial Data	
	Sample Type	Bare Ground	Shrub	Tree	Tree Dens (log)	Shrub NDVI	Tree cover (30m)
Artemisia tridentata	T	-0.50 ***	0.70 ***	-0.53 ***	-0.60 ***	0.12	-0.52 ***
Ericameria spp.	T	-0.23 **	0.38 ***	-0.27 **	-0.31 ***	-0.05	-0.24 **
Purshia tridentata	T	-0.47 ***	0.56 ***	-0.22 **	-0.37 ***	0.16 .	-0.27 **
Salix spp	T	-0.22 **	0.27 **	-0.05	-0.10	-0.03	-0.05
Cercocarpus ledifolius	T	-0.08	0.21 *	-0.11	0.13	-0.05	0.28 ***
Pinus monophylla	T	0.00	-0.56 ***	0.98 ***	0.61 ***	0.06	0.55 ***
Structural cover (0-0.5m height)	T	-0.53 ***	0.40 ***	0.13	-0.01	0.04	0.05
Structural cover (0-1.5m height)	T	-0.15 .	-0.14	0.53 ***	0.41 ***	-0.02	0.41 ***
Bare ground	T	1.00	-0.70 ***	0.02	0.31 ***	-0.28 ***	0.08
Forb	T	-0.29 ***	0.39 ***	-0.47 ***	-0.41 ***	0.21 *	-0.44 ***
Grass	T	-0.20 *	0.20 *	-0.41 ***	-0.41 ***	0.23 **	-0.32 ***
Shrub	T	-0.70 ***	1.00	-0.60 ***	-0.64 ***	0.05	-0.45 ***
Tree cover	T	0.02	-0.60 ***	1.00	0.64 ***	0.09	0.58 ***
Riparian vegetation	G	-0.14	0.12	0.04	0.08	0.14 .	-0.10
Distance to riparian vegetation	G	0.04	0.06	-0.21 *	-0.12	-0.38 ***	-0.21 *
Elevation	G	-0.25 **	0.33 ***	-0.36 ***	-0.38 ***	0.34 ***	-0.13
AET12	G	-0.08	-0.01	0.10	0.05	0.33 ***	0.20 *

Significance codes: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.' 0.1, ' ' 1

Table 2. Ranking of local scale models for habitat selection during parturition of female mule deer in the White Mountains California and Nevada, USA from 2005 to 2008. These are the top models (model weight >0.05) from the GLMM analysis which were used for model averaging of beta estimates shown in table 2. All models contained a random intercept term for animal ID in addition to habitat variables and the intercept. K indicates the number of parameters in a given model. The global model contained % cover of bare ground or % cover of shrub, and mountain mahogany, shrub NDVI, ruggedness (VMR) and structural cover (0-0.5m).

Model	**K**	**AICc**	**Δ AICc**	**Weight**
Bare ground+NDVI+ruggedness	5	187.79	0.00	0.12
Bare ground+Mohogany+NDVI+ruggedness	6	187.93	0.15	0.11
NDVI+shrub+ruggedness	5	188.30	0.51	0.09
Cover+NDVI+ruggedness	5	188.77	0.98	0.07
Cover+NDVI+shrub+ruggedness	6	188.82	1.03	0.07
Mohogany+cover+NDVI+ruggedness	6	188.93	1.15	0.07
Mohogany+NDVI+shrub+ruggedness	6	189.00	1.22	0.07
Bare ground+cover+NDVI+ruggedness	6	189.09	1.30	0.06
Bare ground+Mohogany+cover+NDVI+ruggedness	7	189.45	1.66	0.05

Table 3. Model averaged parameter estimates from local-scale resource selection models (GLMM) of female mule deer during parturition, in the White Mountains, California and Nevada, USA from 2005 to 2008. Parameter coefficients (β), standard error and lower and upper 85% confidence intervals are shown.

			85% Confidence Interval	
Model Parameters	**β**	**SE**	**Lower**	**Upper**
Intercept	0.07	0.18	-0.19	0.33
Bare Ground (%)	-0.39	0.21	-0.69	-0.08
Shrub NDVI	0.51	0.20	0.22	0.80
Ruggedness (VMR)	0.50	0.20	0.21	0.79
Shrub cover (%)	0.33	0.20	0.04	0.61
Structural Cover (0-0.5m)	0.28	0.22	-0.03	0.60
Cercocarpus ledifolius	0.27	0.21	-0.04	0.57

Table 4. Ranking of landscape scale models for habitat selection during parturition of female mule deer in the White Mountains, California and Nevada, USA from 2005 to 2008. These are the top models from the GLMM, all models contained a random intercept term for animal ID in addition to habitat variables and the intercept. K indicates the number of parameters in a given model. The global model contained vegetation association, actual evapotranspiration, elevation, shrub NDVI, slope, and tree cover 30m from remote sensed data.

Models	**K**	**AICc**	**ΔAICc**	**Weight**
Veg Assoc.+AET+AET^2+elev+NDVI+slope+Tree30m+Tree30m^2	16	2268.0	0.00	0.96
Veg Assoc.+AET+elev+NDVI+slope+Tree30m+Tree30m^2	15	2274.6	6.53	0.04
Veg Assoc.+AET+elev+slope+Tree30m+Tree30m^2	15	2287.9	19.89	0.00
Veg Assoc.+elev+NDVI+slope+Tree30m+Tree30m^2	14	2289.0	20.98	0.00
Veg Assoc.+AET+slope+Tree30m+Tree30m^2	15	2289.1	21.11	0.00
Veg Assoc.+AET+NDVI+slope+Tree30m+Tree30m^2	14	2292.4	24.40	0.00
Veg Assoc.+elev+slope+Tree30m+Tree30m^2	15	2308.0	39.92	0.00
Veg Assoc.+AET+elev+NDVI+Tree30m+Tree30m^2	14	2351.1	83.09	0.00
Veg Assoc.+AET+elev+NDVI+slope	15	2351.4	83.36	0.00

Table 5. Parameter coefficients (β), standard error and lower and upper 85% confidence intervals from the top landscape-scale model of resource selection (GLMM) for female mule deer during parturition, in the White Mountains, California and Nevada, USA from 2005 to 2008. The model also contained a random intercept for animal ID.

			85% Confidence Interval	
Model Parameters	**β**	**SE**	**Lower**	**Upper**
Intercept	-0.64	0.13	-0.83	-0.46
Vegetation Association				
Bare ground	-0.06	0.30	-0.49	0.36
Bristlecone	-0.58	0.36	-1.10	-0.05
Meadow	-0.16	0.41	-0.75	0.44
Bitterbrush	-1.58	0.39	-2.14	-1.01
Mahogany	-2.25	0.53	-3.01	-1.50
Pinyon-juniper	-0.25	0.15	-0.47	-0.03
Lodge pole	-1.76	0.74	-2.83	-0.69
Elevation	-0.51	0.10	-0.65	-0.37
Tree cover (30m)	0.63	0.12	0.46	0.79
Tree cover^2 (30m)	-0.65	0.09	-0.77	-0.52
Annual site productivity (AET)	-0.39	0.07	-0.49	-0.28
Annual site productivity^2 (AET)	-0.31	0.06	-0.39	-0.23
Slope	-0.39	0.06	-0.47	-0.30
Shrub NDVI	0.23	0.08	0.12	0.34

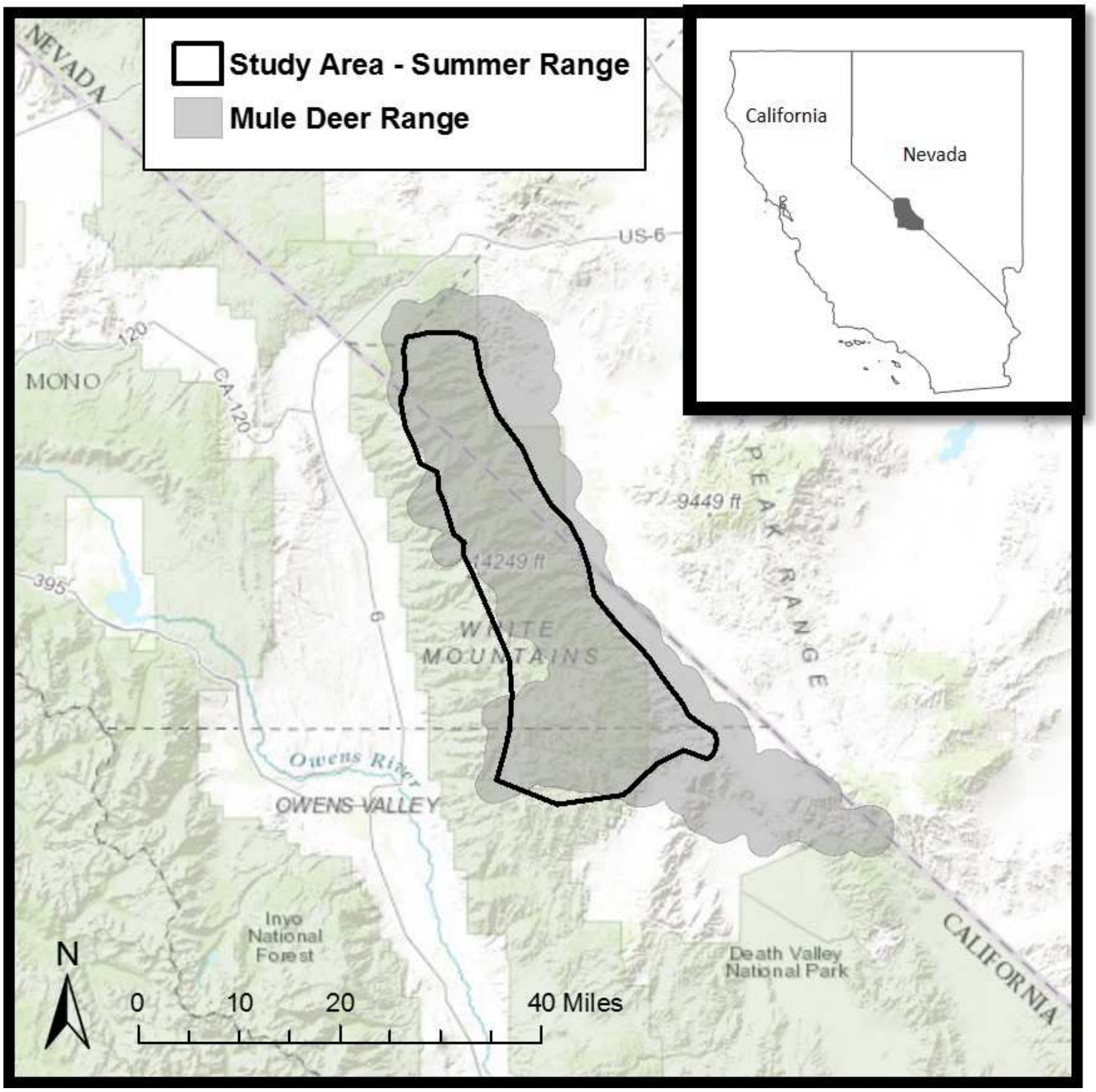

Fig. 1. Study area in the White Mountains of eastern California and western Nevada, USA, from 2005 to 2008. Mule deer range occurred primarily on the eastern side of the mountains with summer range extending from 2,900 m to 4,000 m and deer using lower elevations during the winter months.

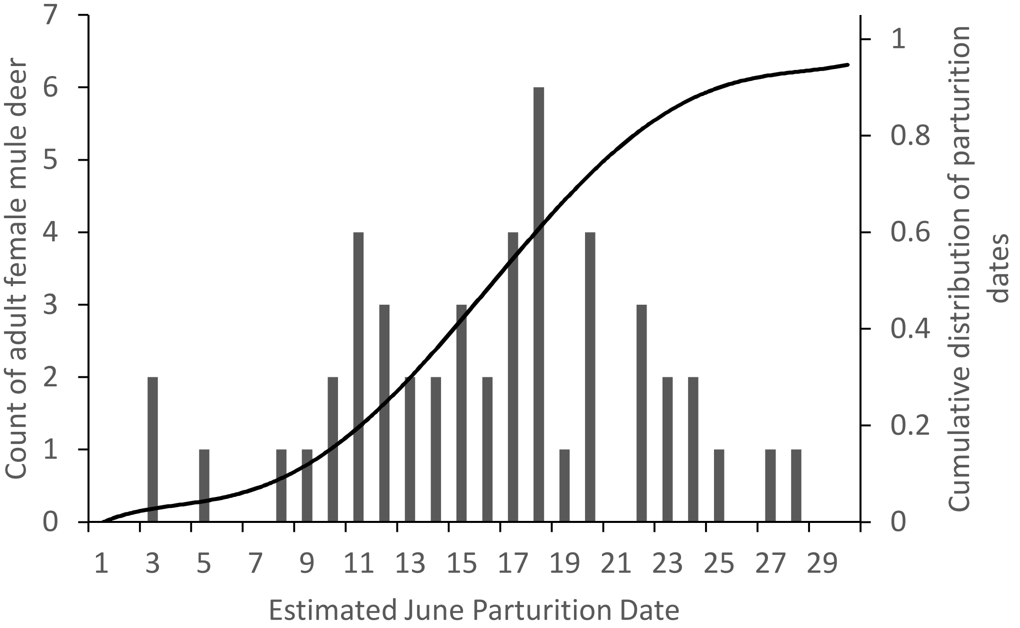

Fig. 2. Distribution of estimated June parturition dates, based on movement analyses of 51 adult female mule deer in the White Mountains, California and Nevada, USA from 2005 to 2008. Line indicates cumulative distribution, with 50% of births occurring on or before June 17.

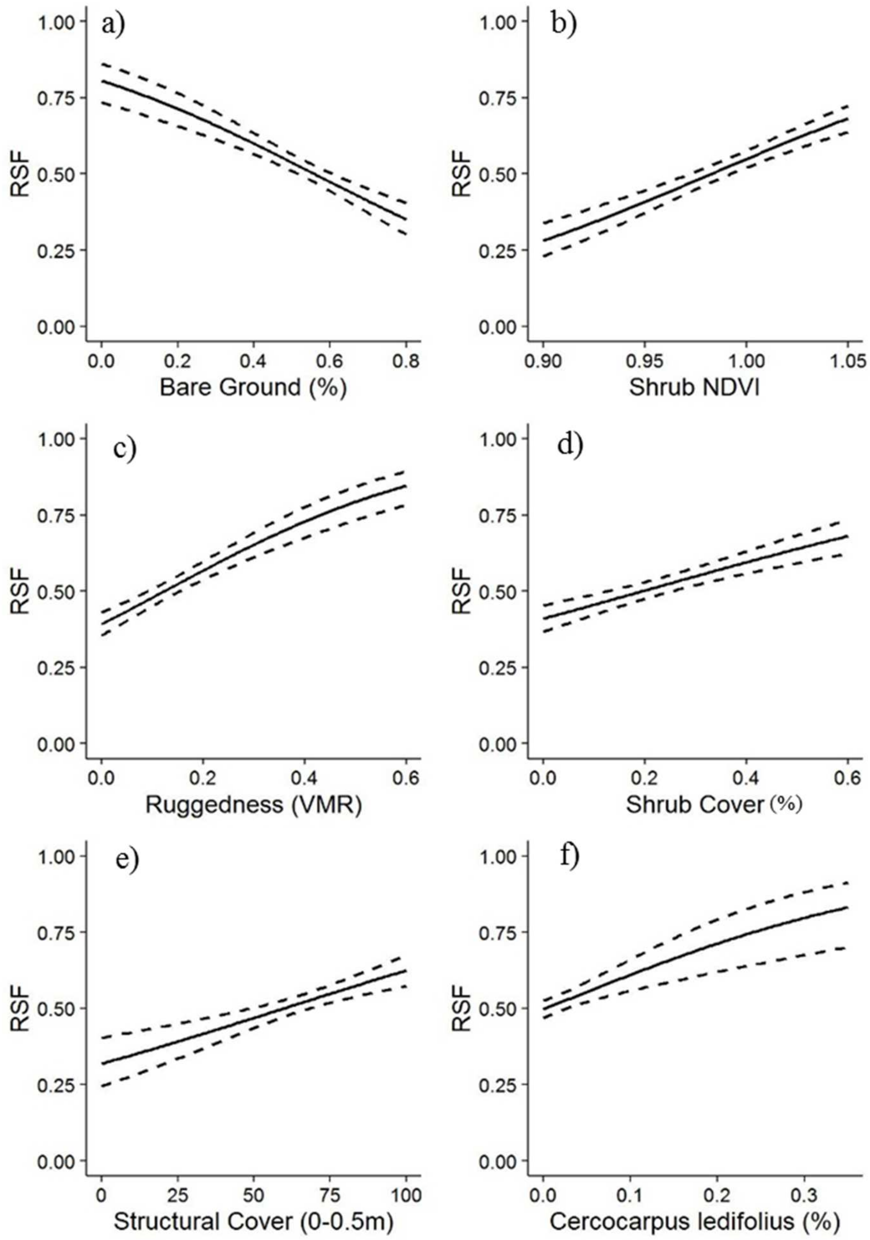

Fig. 3. Relative probability of selection (± SE) at the local scale for a given habitat variable for adult female mule deer during parturition in the White Mountains, California and Nevada, USA from 2005 to 2008. Predictions are based on results of model averaged betas from GLMM and correspond to habitat variables of interest: bare ground (a), shrub NDVI (b), terrain ruggedness (c), shrub cover (d), structural cover measured at 0 to 0.5m high (e), and curl-leaf mountain mahogany (*Cercocarpus ledifolius*, f).

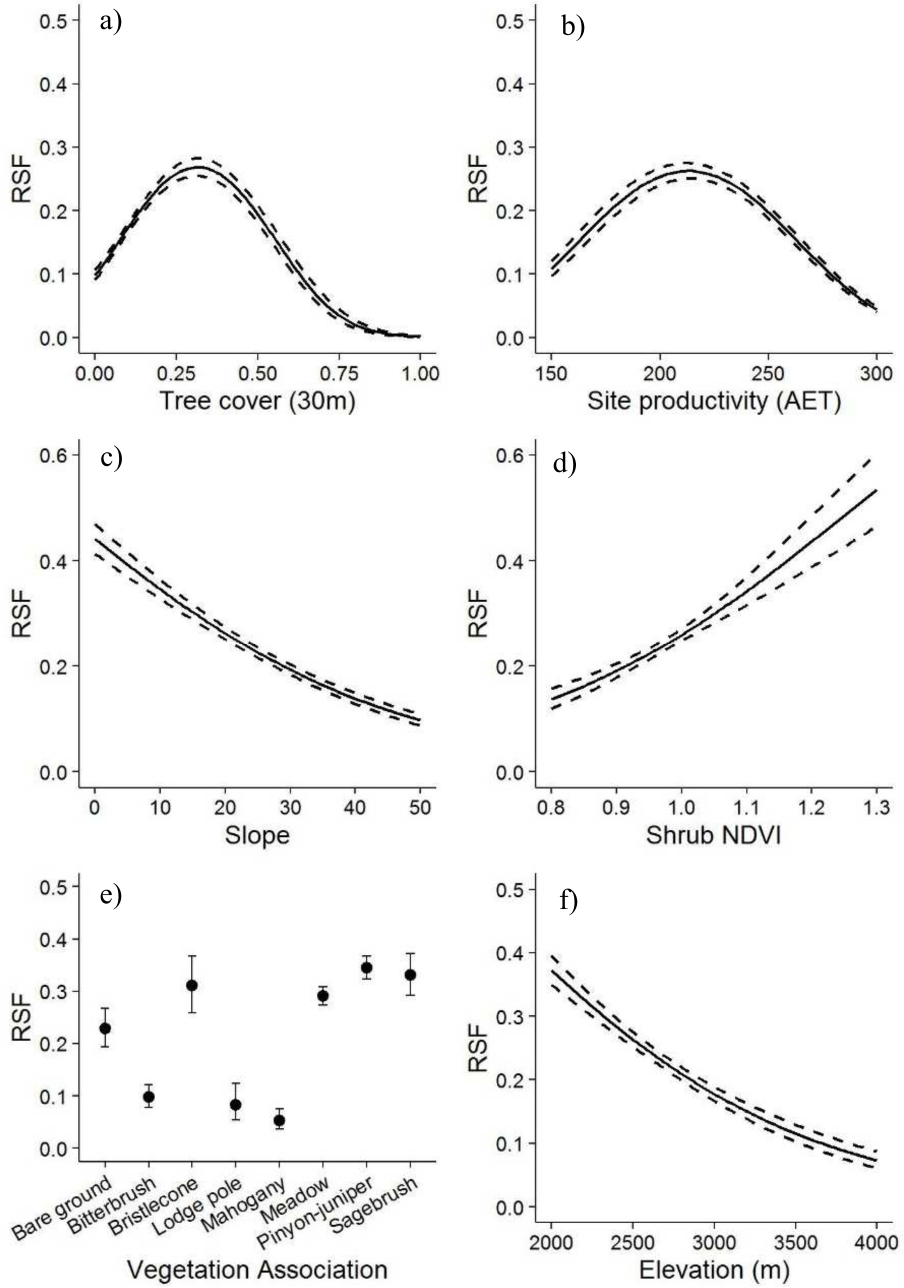

Fig. 4. Relative probability of selection (± SE) at the landscape scale, for a given habitat variable, by mule deer during parturition in the White Mountains, California and Nevada, USA from 2005 to 2008. Predictions are based on the top ranked model from the suite of GLMM that contained a random intercept (animal ID), amount of tree cover in a 30m buffer as calculated by our remotely sensed data (a), annual site productivity (b), slope (c), shrub NDVI (d), vegetation association (e), elevation (f).

Supplemental Material

Appendix A. Ranking of models estimating habitat selection during parturition, at the local scale, for female mule deer in the White Mountains, California and Nevada, USA from 2005 to 2008. Unless otherwise noted all models are single variable models, containing the habitat variable of interest (shown in table), an intercept term and random effect term (animal ID). Parameter coefficients (β) and SE and lower and upper 95% confidence intervals (LCI, UCI) are shown for the habitat variable of interest, along with number of parameters in model (*K*).

Habitat variable contained in model	**Habitat β**	**SE**	**LCI**	**UCI**	***K***	**AICc**
Bare ground	-0.47	0.18	-0.83	-0.12	3	195.5
Shrub NDVI	0.45	0.18	0.10	0.80	3	196.2
Structural cover (0-0.5m height)	0.43	0.18	0.08	0.78	3	196.8
Shrub	0.39	0.18	0.04	0.74	3	197.8
Ruggedness (VMR)	0.39	0.19	0.02	0.77	3	198.2
Cercocarpus ledifolius	0.30	0.21	-0.11	0.72	3	200.4
Null (intercept + random effect)	**-**	**-**	**-**	**-**	**2**	**200.8**
Riparian vegetation	0.45	0.57	-0.66	1.57	3	200.9
Forb	0.24	0.18	-0.11	0.59	3	201.0
Purshia tridentata	0.23	0.18	-0.13	0.59	3	201.2
Structural cover (0-1.5m)	0.22	0.17	-0.12	0.55	3	201.3
Tree cover (30m)	0.19	0.17	-0.14	0.52	3	201.7
Tree density (log) Pt-quarter	0.17	0.17	-0.16	0.50	3	201.9
Pinus monophylla	-0.15	0.17	-0.48	0.18	3	202.1
Tree cover	-0.13	0.17	-0.46	0.20	3	202.3
Elevation	0.12	0.17	-0.21	0.45	3	202.4
Annual site productivity (AET)	0.09	0.17	-0.24	0.42	3	202.7
Grass	-0.07	0.17	-0.40	0.26	3	202.7
Hillslope position	-0.05	0.17	-0.38	0.29	3	202.8
Slope	-0.04	0.17	-0.37	0.29	3	202.8
Artemisia tridentata	0.04	0.17	-0.29	0.37	3	202.9
Spring site productivity (AET)	-0.02	0.17	-0.35	0.31	3	202.9
Ericameria spp.	-0.01	0.17	-0.34	0.32	3	202.9
Distance to riparian veg	0.00	0.17	-0.33	0.33	3	202.9
Tree cover (30m)^2 *	0.26 (-0.14)	0.19 (0.17)	-	-	4	203.1
Annual site productivity (AET)^2 *	0.07 (-0.06)	0.17 (0.15)	-	-	4	204.6

* Models containing quadratic term also include the linear term, numbers in parentheses refer to quadratic term

Appendix B. Ranking of models estimating habitat selection during parturition, at the landscape scale, for female mule deer in the White Mountains, California and Nevada, USA from 2005 to 2008. Unless otherwise noted all models are single variable models, containing the habitat variable of interest (shown in table), in addition to an intercept term and random effect term (animal ID). Parameter coefficients (β), SE and lower and upper 95% confidence intervals (LCI, UCI) are shown for the habitat variable of interest, along with number of parameters in model (*K*).

Habitat variable contained in model	**Habitat β**	**SE**	**LCI**	**UCI**	***K***	**AICc**
Vegetation Association Type	**	**-**	-	-		2425.0
Tree cover $(30m)^2$ *	0.57 (-0.63)	0.08 (0.08)	-	-	4	2478.6
Elevation	-0.44	0.05	-0.54	-0.33	3	2514.0
Annual site productivity $(AET)^2$ *	-0.29 (-0.26)	0.06 (0.05)	-	-	4	2544.7
Annual site productivity (AET)	-0.18	0.05	-0.28	-0.09	3	2571.5
Slope	-0.18	0.05	-0.28	-0.09	3	2571.6
Shrub NDVI	0.16	0.05	0.06	0.26	3	2574.9
Riparian vegetation	-0.15	0.08	-0.30	0.00	3	2579.8
Distance to riparian veg	-0.10	0.05	-0.21	0.00	3	2581.1
Hillslope position	-0.09	0.05	-0.19	0.01	3	2581.8
Ruggedness (VMR)	0.07	0.05	-0.02	0.16	3	2582.8
Null (intercept + random effect)	-	-	-	-	**2**	**2583.0**
Spring site productivity (AET)	0.06	0.05	-0.04	0.16	3	2583.5
Tree cover (30m)	0.05	0.05	-0.04	0.15	3	2583.9

* Models containing quadratic term also include the linear term, numbers in parentheses refer to quadratic term

** Models containing categorical variables are displayed in figure 4.