Winter resource selection by female mule deer Odocoileus hemionus: functional response to spatio-temporal changes in habitat

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Original article

Winter resource selection by female mule deer *Odocoileus hemionus*: functional response to spatio-temporal changes in habitat

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Populations of mule deer *Odocoileus hemionus* have declined throughout most of their historic range in recent decades, and habitat alteration has been hypothesized as one potential cause of those declines. Consequently, understanding how patterns of behaviour change as landscapes are altered through time may provide important insights into mechanisms underlying observed demographic trends in populations of mule deer. We examined resource selection in relation to habitat change by mule deer on the Tex Creek winter range in southeastern Idaho, USA. We created a GIS-based map of habitats available to mule deer during two time periods, past (1985-1986) and current (2007-2009), to document changes in habitat over time. We then modeled past and current patterns of resource selection by mule deer based on locations obtained from visual observation, radio-telemetry and GPS collars. Abundance and distribution of juniper *Juniperus* spp., aspen *Populus tremuloides*, sagebrush steppe *Artemisia* spp. and riparian habitat did not change significantly between past and current time periods. In contrast, we documented an increase in grassland from 3.5 to 30.7% of our study area, and a corresponding decrease in agricultural land, which provides high-quality forage for mule deer, from 37.8 to 12.5% of our study area. Patterns of resource selection largely were similar between the two time periods. Nevertheless, mule deer significantly increased selection of agricultural fields and areas far from roads between the 1980s and 2007-2009. In addition, juniper stands were strongly selected in all years, and importance values (use × availability rescaled to 100%) for grassland and sagebrush steppe increased between past and current time periods. Our results indicated that mule deer responded behaviourally to declining availability of high-quality forage (i.e. agricultural land) by increasing selection of agricultural fields. Such functional responses in habitat selection may have important consequences for dynamics of mule deer populations, but additional research is necessary to link those responses to demography and population performance. Although juniper encroachment often is thought to have affected mule deer negatively on many summer ranges, strong selection for juniper in our study highlights the potential importance of that species on winter range, likely because it provides both thermal and hiding cover.

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Understanding relationships between wildlife and their habitat is critical for effective management of natural resources (Morrison 2001), because survival and reproduction are directly related to access to food and water, concealment cover to hide from or elude predators, space to avoid interspecific competition and arrangement of habitats (Connolly 1981). Accordingly, individual species often exhibit patterns of behaviour that allow them to meet those needs, such as using some resources in greater proportion than their availability on the landscape (i.e. 'selection'; Manly et al. 2002), while avoiding others. Correctly identifying those patterns of behaviour and how they change as landscapes are altered through time can provide crucial insights into the mechanisms underlying observed demographic trends in populations of large mammals.

Mule deer *Odocoileus hemionus* are both socially and economically important in the western USA (Heffelfinger & Messmer 2003). Nevertheless, populations of mule deer have been declining throughout most of their historic range in recent decades (Johnson et al. 2000, Stewart et al. 2002), which has led several agencies to reexamine their management strategies for this large herbivore (Heffelfinger & Messmer 2003). Previous research on mule deer has evaluated potential effects of predators (Whittaker & Lindzey 1999, Pierce et al. 2004, Bishop et al. 2005), weather (Bowyer et al. 1998, Unsworth et al. 1999), hunting (White et al. 2001), grazing by domestic livestock (Bowyer & Bleich 1984, Kie et al. 1991, Ragotzkie & Bailey 1991), interspecific interactions (Oedekoven & Lindzey 1987, Johnson et al. 2000, Ager et al. 2003, Poole & Mowat 2005, Stewart et al. 2006, 2010) and changes in habitat (Gamo & Anderson 2002, Sawyer et al. 2009) on mule deer demographics. The relative importance of those factors across the range of mule deer, however, is poorly understood, and continues to be debated.

Mule deer in the Intermountain West often migrate to meet their nutritional and energetic requirements for reproduction and survival. Moving from summer range at high elevation to winter range at lower elevation helps mule deer survive the climatic stress of winter (Nicholson et al. 1997, Sawyer et al. 2005, Monteith et al. 2011). Although mule deer typically cannot maintain body weight during winter, the rate that fat reserves are lost at can be slowed. Forage availability (typically browse) on winter range can reduce the loss of fat reserves accumulated during summer and autumn until new forage becomes available in spring (Mautz 1978, Pederson & Harper 1978). Winter range for ungulates at lower elevations, however, often is near human populations. Anthropogenic activities that can negatively affect mule deer on winter range include grazing by domestic livestock (Smith et al. 1979), development or degradation of natural resources (McCorquodale 1999, Sawyer et al. 2009), recreation (Rost & Bailey 1979), urban development and agriculture (Thomas & Irby 1991).

The objective of our study was to quantify habitat change over ~ 25 years, and evaluate how such change has affected resource selection by female mule deer. We hypothesized that temporal and spatial changes in the distribution and abundance of different habitat types on winter range would affect resource selection by mule deer, because those changes would have influenced the availability and distribution of forage and cover. Thomas & Irby (1991) documented selection of agricultural fields by mule deer during winter in the mid-1980s. The introduction of the Conservation Reserve Programme (CRP) during the mid-1980s, however, resulted in the conversion of habitat on winter range in southeast Idaho that once was actively farmed for winter wheat *Triticum* spp. to grassland. The CRP is a national cost-share programme that was passed by the U.S. Congress as part of the Farm Bill in 1985. Under this programme, agricultural producers receive payment from the federal government to plant private ground that is highly erodible or environmentally sensitive into permanent vegetative cover (U.S. Department of Agriculture Farm Service Agency 2011). Enrollment in the CRP since its inception has increased throughout the range of mule deer, and in Idaho it has increased from 15,777 ha in 1986 to 313,210 ha in 2008 (U.S. Department of Agriculture Farm Service Agency 2011). We therefore predicted that as availability of high-quality forage (i.e. agricultural land) declined between the 1980s and present, female mule deer would increase the magnitude of their selection for agricultural fields to help enhance intake of high-quality forage. Additionally, several studies have documented selection of sagebrush *Artemisia* spp. and bitterbrush *Purshia tridentata* as winter forage by mule deer (Clements & Young 1997, Pierce et al. 2004). Therefore, we also predicted that mule deer would increase selection of sagebrush-steppe habitat to offset the loss of critical fat reserves as availability of agricultural lands declined.

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Material and methods

Study area

Our study was conducted on the Tex Creek winter range (historically known as the Willow Creek winter range; Thomas 1987), approximately 29 km east of Idaho Falls, Idaho, USA (43°27'N, 111°41'W; Fig. 1). Our study area was focused around the Tex Creek Wildlife Management Area, which encompassed approximately 1,900 ha. Land ownership within our study area included several federal agencies (Bureau of Land Management, United States Forest Service and Bureau of Reclamation), state agencies (Idaho Department of Lands and Idaho Department of Fish and Game), as well as multiple private landowners. Approximately 13,000 ha of winter range at Tex Creek are managed by the Idaho Department of Fish and Game specifically for wintering ungulates. A network of roads allows the public to use this area for a variety of recreational activities throughout much of the year. Motorized access is restricted, however, from 1 December to 15 April, providing security for wintering ungulates from motorized traffic. Primary predators occurring on our study site included mountain lion *Puma concolor*, black bear *Ursus americanus* and coyote *Canis latrans*.

Elevations in our study area range from 1,551 m a.s.l. on the northern boundary to 2,248 m a.s.l. on the eastern boundary and the topography is characterized by a series of canyons and plateaus. Annual precipitation ranges from 30 to 40 cm and occurs mostly as snow and spring storms, and annual temperatures range from -17 to 37°C (Thomas 1987). Mean precipitation recorded during winters (January-April) of 2007, 2008 and 2009 by the nearest National Climatic Data Center site was 2.0, 4.3 and 4.1 cm, respectively (U.S. Department of Commerce National Climatic Data Center 2009). Mean temperatures recorded during winters (January-April) of 2007, 2008 and 2009 were -1.0, -4.1 and -1.2°C, respectively. Mean monthly precipitation and temperature for winter (January-April) of 1985 was 2.5 cm and -3.7°C and was 5.3 cm and 0.8°C, respectively, during 1986 (U.S. Department of Commerce National Climatic Data Center 2009).

Winter range was characterized as semi-arid sagebrush steppe (Thomas & Irby 1991). Sagebrush steppe included shrubs such as sagebrush, bitterbrush, rabbitbrush *Ericameria* spp., service berry *Amelanchier arborea* and chokecherry *Prunus virginiana*. Stands of juniper *Juniperus* spp. occur on south-facing slopes and stands of aspen *Populus tremuloides* occur on north-facing slopes. Willows *Salix* spp. dominate the riparian zones within
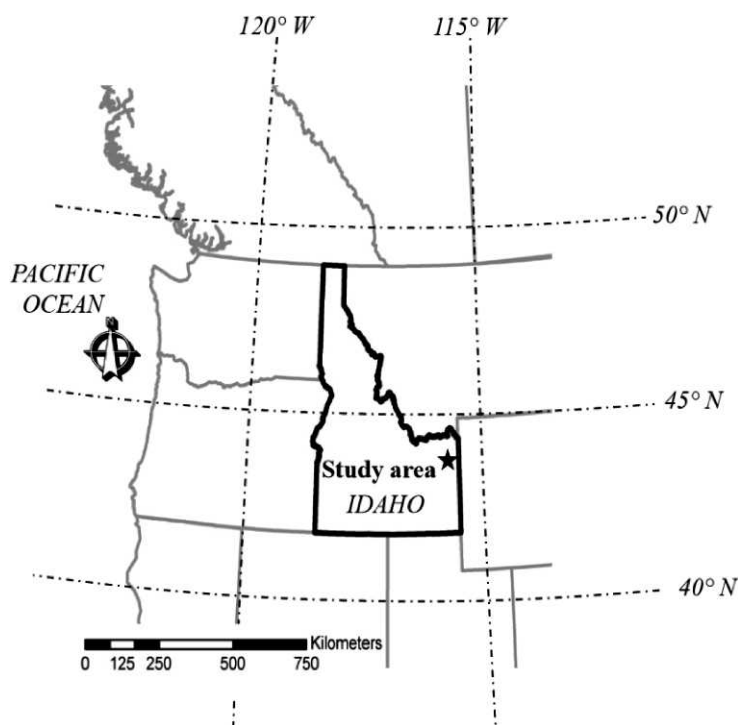

Figure 1. Location of our study area centered on the Tex Creek Wildlife Management Area located near Idaho Falls, Idaho, USA.

canyons. Common species of native forbs include lupine *Lupinus* spp., penstemon *Penstemon* spp. and milkvetch *Astragalus* spp. Alfalfa *Medicago sativa* and sainfoin *Onobrychis viciifolia* are common introduced forbs. Native grasses include bluebunch wheatgrass *Pseudoroegneria spicata* and Idaho fescue *Festuca idahoensis*, and introduced grasses, such as smooth brome *Bromus inermis* and crested wheat grass *Agropyron cristatum*, persist in the former agricultural fields.

Animal capture and telemetry

During 2007-2009, personnel from the Idaho Department of Fish and Game captured adult ($\geq$ 2.5 years of age) and yearling (1.5 years of age) female mule deer in January. Capture methods included net gunning from a helicopter, drive nets and drop nets (Barrett et al. 1982, Thomas & Novak 1991). Each mule deer was hobbled and blindfolded at the site of capture, and study animals were fit with GPS collars. We used two different collar manufacturers and three models in our study (models GPS 3300 & 4400, Lotek Wireless Inc., Newmarket, Ontario, Canada and model TGW-4500, Telonics, Inc., Mesa, Arizona, USA). We fitted mule deer with collars that included a release mechanism programmed to drop off prior to exhaustion of battery life to facilitate retrieval of locational data stored on each collar. The GPS collars also had very high frequency (VHF) transmitters attached to them, which allowed us to monitor animals for mortality and to locate the collar once it had dropped off. Based on the recommendation of Lewis et al. (2007) for simultaneously retaining the maximum amount of information and minimizing the effects of location error on analyses of space use, we retained all GPS locations with a 3-D fix in our analyses, and excluded locations with a 2-D fix that also had a dilution of precision > 5.

We selected capture sites from six subunits documented by Thomas & Irby (1991) within our study area. We distributed our collars among those capture sites to facilitate dispersion throughout our study area each year. Collars were programmed to obtain a location at 2-hour intervals during a 24-hour period through the duration of our study. We followed protocols approved by the Institutional Animal Care and Use Committee at Idaho State University (protocol # 6171008), and guidelines adopted by the American Society of Mammalogists Animal Care and Use Committee for handling of wild mammals (Gannon et al. 2007).

We used locations obtained between January and April in our analyses in 2008 (N = 19 deer) and 2009 (N = 15 deer). As a result of a mild winter in 2007, animals migrated off of the winter range by late March (N = 17 deer), and consequently, we did not include data from April 2007. We used 10,778 locations obtained in 2007, 14,345 locations obtained in 2008 and 9,975 locations obtained in 2009.

For comparison with current locations of mule deer, we obtained historical locations from 1985 and 1986 from Thomas (1987). This data set included locations obtained from aerial flights to locate 26 deer with VHF collars, and visual observations of deer wearing highly visible urethane collars. In addition, ground surveys recorded all visible deer within the six subunits of winter range at Tex Creek (Thomas 1987). Thomas (1987) recorded deer within groups; however, to avoid pseudoreplication resulting from assigning multiple locations to family groups, we used a single deer location for each group documented. We obtained a total of 456 deer locations distributed among the six subunits for our analysis. Mean number of locations per animal for VHF-collared deer was 8.2.

Environmental variables

We used panchromatic aerial photography from 1987 (0.5-m resolution) and 2004 (1-m resolution) obtained from the National Agricultural Imagery Programme (NAIP) to quantify habitat types in our study area. We classified habitats across our study area using IDRISI Taiga image-processing software (Clark Labs, Worcester, Massachusetts, USA), and used the SEGCLASS module to create habitat polygons based on spectral similarity in six bands of Landsat 5 imagery (bands 1, 2, 3, 4, 5 and 7). We used one historical (July 1987) and one modern (June 2004) image for our analysis. By adjusting the similarity threshold, we were able to assign pixels to segments based on changes in the variance among segments. We subjectively used a large threshold, which allowed us to derive habitat polygons that were heterogeneous, but also avoid classifying very small areas (i.e. a single pixel) as separate patches of habitat. We imported these habitat-segmentation polygons into ArcGIS 9.3, and overlaid them onto aerial photographs of our study area from 1987 and 2004. We then adjusted segmentation polygons visually to match habitat boundaries observed in the aerial photos, thereby producing a more accurate habitat map for both time periods. Using the spectral segmentation polygons and habitat layers obtained

from the Idaho Department of Fish and Game and the Farm Service Agency, we created a categorical habitat layer with six vegetation types: aspen (aspen-dominated forest), juniper (juniper-dominated forest), sagebrush steppe (sagebrush-dominated), riparian, grassland (former agricultural land converted primarily to grass) and agriculture (dryland winter-wheat crops, stubble fields and alfalfa-dominated fields cut for hay). We validated the habitat map by casting 200 random points throughout our study area. We then visited each random location on the ground and determined which of the six habitat classifications were present, and the resulting classification accuracy was 80%, and varied little by habitat type. Given the identical procedures used to produce both past (1980s) and current (2007-2009) habitat maps, we assumed similar accuracy for the 1980s map in the absence of validation data from that period.

Several continuous variables were derived from a digital elevation model and a roads layer for our study area with a 30-m^2 resolution: elevation (m), slope (%), aspect (degrees) and distance (m) to the nearest open road. In addition, we transformed aspect into two variables using sine and cosine functions to measure eastness and northness, respectively (Zar 1996). To aid in interpreting biological significance of our modeling results in addition to statistical significance, we transformed elevation, slope and distance to roads prior to analysis so that a 1-unit change in elevation represented 50 m, a 1-unit change in slope represented 10% and a 1-unit change in distance to roads represented 100 m. Consequently, odds ratios for those variables indicate the predicted change in probability of selection by mule deer for every 50-m change in elevation, 10% change in slope and 100-m change in distance to roads. Mean, minimum and maximum values of each continuous variable, prior to transformation, are presented by habitat type in Table 1.

We defined habitat available to the population of mule deer on Tex Creek winter range based on a 99% fixed-kernel utilization distribution (UD) calculated using the reference bandwidth (Silverman 1986, Worton 1989) in the Home Range Tools extension for ArcGIS 9.3 (Rodgers et al. 2007). We calculated a single population-level UD using all deer locations from both the 1980s and 2007-2009, and the outer boundary of that UD was then used to define the spatial extent of our analyses, and thus habitat availability. Use of a consistent outer boundary for defining availability was important given our primary goal of evaluating changes in habitat selection as the proportion of grassland and agriculture in our study area changed between the 1980s and 2007-2009.

Resource selection functions and model averaging
We used ArcGIS 9.3 to cast one random location for every deer location within the boundary of the population-level UD from 2007-2009, and 14 random locations for every deer location in the 1980s. The larger ratio of random to used locations in the 1980s was necessary for producing consistent estimates of habitat availability, because of the substantially smaller number of deer locations obtained during that time period. Resource availability was quantified at the scale of the winter range, and thus all of our models represent second order selection (Johnson 1980). We assigned all locations, both used and random, to 10 × 10 m pixels, and spatially joined each location with the corresponding values from the underlying habitat layers (slope, elevation, aspect, distance to roads and habitat type).

Table 1. Descriptive statistics for three topographical variables and distance to roads, for pixels in each of six habitat types, in Tex Creek Wildlife Management Area, Idaho Falls, Idaho, USA. Distribution of grassland and agriculture changed substantially over our study period, and thus both past (1985-1986) and current (2007-2009) values are presented for those habitat types.

| Habitat type | Elevation (m) | | | Slope (%) | | | Aspect (degrees) | | | Distance to roads (m) | | |
	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
Juniper	1688	1554	1841	36	0	235	194	0	360	1124	0	3476
Aspen	1888	1562	2223	28	0	224	171	0	360	1219	0	3692
Riparian	1690	1553	1982	17	0	198	185	0	360	1023	0	3519
Sagebrush steppe	1795	1553	2223	27	0	312	197	0	360	1169	0	3849
Grassland (past)	1805	1653	1987	13	0	94	182	0	360	979	0	2755
Grassland (current)	1767	1560	2067	10	0	231	197	0	360	767	0	3812
Agriculture (past)	1765	1612	2067	7	0	173	204	0	360	903	0	3849
Agriculture (current)	1752	1635	1981	6	0	125	206	0	360	1250	0	3849

We used conditional logistic regression (PROC LOGISTIC; SAS Institute, Cary, North Carolina, USA) to model resource selection by mule deer on winter range (Hosmer & Lemeshow 2000, Manly et al. 2002, Boyce 2006). Prior to modeling, we used a correlation matrix to evaluate collinearity among predictor variables (PROC CORR; SAS Institute, Cary, North Carolina, USA). No variables were removed (all |r| values were < 0.60). As a preliminary means of evaluating potential differences in patterns of resource selection between past (1985-1986) and current (2007-2009) time periods, we fitted a global model that included all main effects along with the five possible main effect*time period interaction terms. Statistical significance of an interaction term indicated a difference in selection for that variable between time periods. Results of that analysis must be interpreted with caution, however, because the stratifying variable differed between the two time periods. For current years, models were conditioned upon the individual animal (Boyce 2006). For past years, however, fewer data were available, and we could not use animal ID as a stratifying variable. As a result, we chose to stratify data from 1985-1986 by subpopulations of mule deer that occupied the various subunits within the Tex Creek winter range (N = 6). In contrast to topographical predictor variables and distance to roads, which were continuous, habitat type was included as a categorical predictor variable. Consequently, a reference category was required. In our analysis, we used sagebrush steppe as the reference category because of its abundance and history of consistent importance to mule deer (Stewart et al. 2010).

Following evaluation of the global model, we produced a separate model set for each time period (past and current) that included all possible combinations of the environmental predictor variables. For each individual model, we calculated Akaike's Information Criterion adjusted for small sample size (AIC$_c$), ΔAIC$_c$ and the Akaike weight (w_i; Burnham & Anderson 2002). We then selected a 95% confidence set of models from each full set based on w_i values, and used the confidence set to calculate weighted, model-averaged parameter estimates and unconditional standard errors (SE) for each predictor variable (Burnham & Anderson 2002). Model-averaged parameter estimates were then converted to odds ratios by exponentiation for ease of interpretation. If the confidence interval around an odds ratio contained 1, then that variable was not significant. Moreover, we considered odds ratios for each

predictor variable to differ significantly between time periods if the 95% confidence intervals did not overlap.

In addition to our resource selection functions, we also assessed the relative importance of the different habitat types each year by calculating 'importance' values (use × availability rescaled to 100%, where use = the proportion of deer locations in each habitat type and availability = the proportion of the total available area occupied by each habitat type; Bowyer & Bleich 1984, Manly et al. 2002). This analysis helps to identify habitats that are critical to animals but may not be selected (i.e. use > availability) because of their abundance in the landscape.

Results

Habitat classification
The percent of our study area occupied by aspen ($\sim$ 10%), juniper ($\sim$ 5%), sagebrush steppe ($\sim$ 40%) and riparian areas ($\sim$ 3%) did not change substantially between the 1980s and 2007-2009 (Table 2). In contrast, availability of grassland increased from 3.5 to 30.7% between the 1980s and 2007-2009, whereas availability of agricultural land decreased from 37.8 to 12.5% between the 1980s and 2007-2009 (see Table 2).

Resource selection functions and habitat importance
A global resource selection model for mule deer containing all main effects and interaction terms between each main effect and time period (past or current) indicated potentially important differences in patterns of selection for habitat (P = 0.03 for the habitat type*time period interaction) and distance to roads (P < 0.0001 for the roads*time period inter-

Table 2. Percentage of each habitat type within the boundary of available habitat defined by a 99% fixed-kernel utilization distribution (availability), and importance values (use × availability rescaled to 100%; importance) for each habitat type used by mule deer during winter (January-April) in southeastern Idaho, USA. Past values are for 1985-1986 and current values are for 2007-2009.

Habitat type	Availability		Importance	
	Past	Current	Past	Current
Juniper	5.1	5.0	3.8	3.5
Aspen	9.9	9.9	1.6	1.6
Grassland	3.5	30.7	0.2	8.9
Agriculture	37.8	12.5	13.6	2.6
Riparian	2.8	2.7	0.4	0.3
Sagebrush steppe	40.7	38.8	80.3	83.0

action) between the 1980s and 2007-2009. Consequently, we produced separate resource selection functions for each time period. The 95% confidence set of models for each time period is presented in Table 3. Models of resource selection by female mule deer on winter range indicated that patterns of selection for topography and roads largely were similar between the 1980s and 2007-2009. Not unexpectedly, a substantially smaller sample size from the 1980s resulted in wider confidence intervals around odds ratios for that time period (Fig. 2). Nevertheless, some differences were evident between the two periods. The odds ratio for distance to roads was significantly higher (indicated by non-overlapping 95% confidence intervals) for current than for past years (see Fig. 2), and this indicated that probability of selection by mule deer increased by an average of 5.7% for every 100-m increase in distance to the nearest open road during 2007-2009. In contrast, selection by mule deer did not appear to be influenced by roads during the 1980s (see Fig. 2). The only significant topographical variable in the 1980s model was elevation, which also was significant in the model for current years (see Fig. 2). In both instances, odds ratios indicated that probability of selection by mule deer declined by roughly 25% for every 50-m increase in elevation. Aspect was not significant in either model, and odds ratios for slope indicated that mule deer likely selected steep slopes during both time periods, although the odds ratio for slope in the 1980s model was not statistically significant (see Fig. 2).
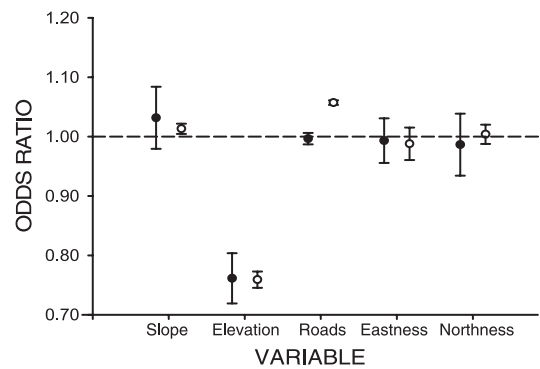

Figure 2. Odds ratios for five continuous variables related to topography and roads obtained from model-averaged resource selection functions for past (1985-1986; •) and current (2007-2009; ○) years for female mule deer on the Tex Creek winter range, southeastern Idaho, USA. Past models were conditioned on spatially explicit subunits (N = 6) and current models were conditioned on individual deer (N = 51). Odds ratios indicate the percent change (1 = no change) in probability of use by mule deer for every 10% increase in slope, 50-m increase in elevation, 100-m increase in distance to roads and 45° change in aspect (eastness and northness). Error bars represent 95% confidence intervals.

Table 3. Ninety-five percent confidence set of models of resource selection for mule deer during winter (January-April) in southeastern Idaho, USA. Past models are for 1985-1986 and current models are for 2007-2009. Variables modeled included habitat type (hab), elevation (elev), percent slope (slope), eastness of aspect (east), northness of aspect (north) and distance to the nearest open road (roads). Number of variables in the model (K), AIC value adjusted for small sample size (AIC_c), change in AIC_c (ΔAIC_c) and the Akaike weight (w_i) are presented for each model.

Model	K	AIC_c	ΔAIC_c	w_i
Past				
hab+elev+slope	3	2913.97	0.00	0.29
hab+elev+slope+roads	4	2914.09	0.12	0.27
hab+elev	2	2915.69	1.72	0.12
hab+elev+roads	3	2915.95	1.98	0.11
hab+elev+slope+east+north	5	2916.65	2.69	0.08
hab+elev+slope+east+north+roads	6	2916.72	2.75	0.07
hab+elev+east+north	4	2918.21	4.24	0.03
Current				
hab+elev+slope+east+north+roads	6	78411.56	0.00	0.51
hab+elev+slope+roads	4	78411.76	0.20	0.46

Patterns of selection for habitat type also were relatively similar between the two time periods. In both past and current years, juniper was the only habitat type with a higher probability of selection than sagebrush steppe (the reference type in our analyses). All other habitat types had a probability of selection lower than or equivalent to sagebrush steppe (Fig. 3). Resource selection functions predicted a 120-276% higher probability of selection for juniper than sagebrush steppe in past years, and a 224-285% higher probability of selection for juniper in current years (ranges based on 95% confidence intervals). The only statistically significant change in habitat selection by mule deer between past and current years was for agriculture, which increased in predicted probability of selection relative to sagebrush steppe by 50% between the 1980s and 2007-2009 (model-averaged odds ratios for agricultural habitat were 0.33 and 0.50 for past and present models, respectively; see Fig. 3).

In general, importance (use × availability rescaled to 100%) values for riparian areas, aspen stands and juniper stands were relatively consistent through time (see Table 2). In contrast, the importance value for agricultural lands declined by 81% between the 1980s and 2007-2009 (see Table 2), whereas the importance value for grasslands increased by 97% (see Table 2). In addition, the importance value for sagebrush steppe increased slightly between the 1980s and 2007-2009 (see Table 2).
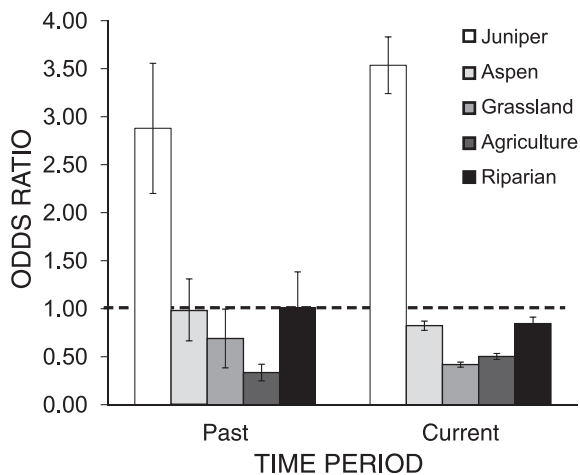
Figure 3. Odds ratios for juniper, aspen, grassland, agriculture and riparian habitat obtained from model-averaged resource selection functions for past (1985-1986) and current (2007-2009) years for female mule deer on the Tex Creek winter range, southeastern Idaho, USA. Past models were conditioned on spatially-explicit subunits (N=6) and current models were conditioned on individual deer (N = 51). Odds ratios indicate the percent change (1 = no change) in probability of use by mule deer for each habitat type relative to sagebrush steppe. Error bars represent 95% confidence intervals.

Discussion

We evaluated resource selection by female mule deer on winter range as availability of agricultural and grassland habitats changed from the 1980s to 2007-2009. Our hypothesis that changes in habitat availability would influence patterns of resource selection by deer was supported.

One of our primary goals was to use resource selection functions to rank habitat types according to degree of selection by mule deer on winter range, and determine how the relative importance of each habitat changed as availability of agriculture and grasslands was altered. Using this approach, we documented patterns of resource selection that largely were similar between the two time periods of our study. One limitation of such analyses, however, is that they can fail to highlight the importance of habitats that comprise a large proportion of the study area, because mule deer would have to spend an inordinate amount of time in those habitats for selection to be detected statistically. Consequently, we combined our resource selection analyses with an analysis of habitat importance (use × availability; Bowyer & Bleich 1984, Manly et al. 2002). This combined approach demonstrated the importance of both juniper (selection) and sage-brush-steppe (importance) habitats to mule deer on the Tex Creek winter range, as well as increased selection for agricultural fields that provide high-quality forage, as availability of those fields declined.

We documented little or no change in the abundance or distribution of sagebrush steppe, juniper, aspen and riparian habitat types during our study, but we documented a substantial change in agricultural practices that resulted in decreased abundance of agricultural fields (see Table 2). We predicted that as availability of agricultural habitat declined, female mule deer would increase selection of winter wheat plantings on winter range to enhance intake of high-quality forage. Our results supported this prediction. Indeed, the only statistically significant difference in habitat selection by mule deer between the 1980s and 2007-2009 was the increased selection of agricultural fields. Such functional responses in habitat selection (i.e. changing degree of selection as availability changes; Mauritzen et al. 2003, Godvik et al. 2009) may represent an important behavioural adaptation for coping with habitat change through time. Nevertheless, the degree to which such responses can compensate for declines in quality or abundance of forage is unclear, and future research should focus on linking patterns of selection to population performance and demographics. Increased selection of agricultural lands during 2007-2009 may also explain the change in the influence of roads between past and current years. During the 1980s, agriculture was the habitat type most closely associated with roads (see Table 1). In contrast, during 2007-2009, agricultural lands were, on average, located further from roads than all other habitat types (see Table 1). As a result, increased selection of agricultural lands during current years likely was coincident with increased use of areas located farther from roads.

Our results also highlighted both the past and current importance of sagebrush-steppe habitat to mule deer on southeastern Idaho winter range. The importance value for sagebrush steppe was an order of magnitude higher than for any other habitat type besides agriculture in the 1980s, and for all other habitat types in current years. Several other authors have reported similar results. For example, Oedeko-ven & Lindzey (1987) documented the extensive use of a sagebrush-steppe ecosystem on winter range in southwestern Wyoming, USA. Similarly, Stewart et al. (2010) observed high relative value of sagebrush steppe on a winter range in southeastern Idaho. Clements & Young (1997) suggested the importance of bitterbrush as forage in sagebrush-steppe com-

munities during winter to help reduce loss of fat reserves. In addition, Pierce et al. (2004) noted that bitterbrush was important forage for mule deer. At the scale of our study, we were not able to separate areas of bitterbrush within the sagebrush steppe. Nonetheless, our results, combined with others, highlight the importance of conserving native sagebrush-steppe communities throughout the range of mule deer.

Aspen communities have long been described as critical summer habitat for mule deer, because they often contain a rich diversity of forbs, grasses and shrubs that provide cover and forage (Leckenby et al. 1982). Beck & Peek (2005) documented that aspen habitat can provide high-quality forage for mule deer during summer; however, during winter these aspen communities may not provide the same nutritional value. On the Tex Creek winter range, aspen typically occur on the north-facing slopes where snow accumulation can be substantial. Although we did not detect a difference in selection between aspen and sagebrush-steppe habitats during the 1980s, we did document significantly higher selection of sagebrush than aspen in current years. We hypothesize that mule deer selected sagebrush steppe over aspen because of the energetic costs associated with accessing aspen habitat, and the low availability of forage in that habitat during winter. We therefore conclude that aspen management, which is an important part of many mule deer management plans, should be focused on key summer range when high-quality forage is more accessible to deer.

The consistently high degree of selection for juniper stands by mule deer on winter range at Tex Creek was unexpected. Miller et al. (2008) noted that juniper habitat occupied only 5-10% of its current distribution prior to the 1860s, and expansion of juniper was rapid between 1880 and 1920. This expansion has been related to seed sources (Miller et al. 2008), fire frequency, grazing by domestic livestock (Miller et al. 1995), and higher precipitation and milder winters compared with long-term averages (LaMarche 1974, Graumlich 1987). After the 1950s, the rate of juniper expansion declined (Miller et al. 2008), and during our study we did not document juniper expansion over about 25 years (see Table 2). We hypothesize that selection for juniper may be related to the need for thermal cover on winter range (Parker & Gillingham 1990, Bowyer & Kie 2009). Nevertheless, we propose that an analysis of juniper stands at a finer scale may provide additional clarification of this result. More specifically, we propose examining the density of juniper stands in relation to the understory, which may be providing forage and protection from the elements.

We suggest that mule deer in southeast Idaho have used sagebrush-steppe habitats more as agricultural lands have diminished. Prior to European settlement, mule deer likely used sagebrush steppe more intensively. As settlers cleared sagebrush to plant crops, however, mule deer likely shifted their patterns of resource selection toward agricultural crops and away from sagebrush steppe. Consequently, as productive agricultural fields have been replaced with a permanent grass-dominated cover, mule deer may again be relying more heavily on sagebrush steppe for winter forage. Our results indicate a high dependence on sagebrush steppe by mule deer on winter range. This outcome warrants further investigation as to how this may affect life-history traits and population trends of mule deer in the Intermountain West. We encourage management practices for mule deer on winter range that include the maintenance and sustainability of a healthy sagebrush-steppe ecosystem. We also caution against aggressive juniper removal on winter range, because that habitat may provide important thermal or concealment cover for mule deer on winter range.

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