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WINTER HABITAT USE BY MULE DEER IN IDAHO AND MONTANA

By

SONJA MARLENE SMITH

B.S., University of Arizona, Tucson, Arizona, 2008

Thesis

presented in partial fulfillment of the requirements for the degree of

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THESIS FORMAT

I wrote this thesis for submission to *The Journal of Wildlife Management*. Because of collaboration with other researchers, co-authors are listed and I use the collective "we" throughout the thesis.

Winter Habitat Use by Mule Deer in Idaho and Montana

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ABSTRACT

Winter survival for species such as Rocky Mountain mule deer (Odocoileus hemionus hemionus) depends on an energy conservation strategy where they use habitats at lower elevations and on south facing slopes with adequate thermal or canopy cover. However, not all mule deer habitats are equivalent in components or weather conditions, which contribute to differences in habitat use patterns and behavior among wintering populations. We examined winter habitat use by mule deer on the East Front of the Rocky Mountains, Montana and Warm Springs and Sink Creek, east-central Idaho to determine how weather and vegetation affect habitat use in different winter ranges. We used radiotelemetry to locate adult female mule deer and estimated microsite habitat conditions including wind speed, snow depth, percent cover of individual plant species, hiding cover, and canopy cover during winter 2010–2011. We compared data at deer locations to random locations across each study area using logistic regression, developing models based on pooled data for each study area, times of snow accumulation, and times of high wind speeds (for the East Front). We evaluated model fit using a Receiver Operating Characteristic (ROC). Our final models indicated that deer use different habitat components on different winter ranges. On the East Front, a combination of landscape

and weather variables predicted probability of deer use of areas. These included percent cover of trees, creeping juniper (*Juniperus horizontalis*), buffaloberry (*Shepherdia canadensis*), curly sedge (*Carex rupestris*), prairie sagewort (*Artemisia frigida*), whitemargin phlox (*Phlox albomarginata*), percent slope, snow depth, wind speed, and exposure to wind. These and additional covariates changed in magnitude depending upon weather conditions. Model covariates also changed depending on deer behavior. In Idaho, tall threetip sagebrush (*A. tripartita tripartita*) and phlox (*Phlox* spp.) were important predictors of mule deer habitat use, while tall threetip sagebrush and cumulative forbs predicted use of areas under snow conditions. Mule deer habitat use differed between Idaho study areas. In the Warm Springs study area, covariates related to foraging predicted habitat use. Differences among all 3 study areas indicate that deer use different habitat components under different winter conditions. Discrepancies among winter ranges are important considerations for habitat requirements of mule deer.

KEY WORDS habitat use, Idaho, Montana, mule deer, *Odocoileus hemionus*, winter range.

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In northern latitudes, most annual mortality for ungulates occurs during winter (White et al. 1996) when forage quality and availability declines (Short et al. 1966, Wallmo et al. 1977) and snow accumulation limits access to forage and increases energy demands (Gilbert et al. 1970, Parker et al. 1984). Cold temperatures, wind, and precipitation also increase energy expenditure for thermoregulation (Short 1966, Mysterud and Ostbye 1999). These factors force ungulates such as Rocky Mountain mule deer (*Odocoileus hemionus hemionus*) into negative energy balance for \geq 4 months, inducing physiological stress and catabolization of fat and protein reserves (Wallmo et al. 1977, Torbit et al. 1985, Moen and Delgiudice 1997). Winter survival

primarily depends on accumulating body reserves prior to winter and selecting landscapes that provide adequate forage and protection from weather and predators (Mautz 1978, Mackie et al. 1998).

Winter habitat use for most northern-temperate ungulates is based on a strategy of energy conservation (Moen 1976, Mautz 1978, Mackie et al. 1998). Important mule deer winter range includes areas that reduce the rate of energy loss by providing shallow snow, adequate food resources, security cover, and thermal environments (Garrott et al. 1987, Armleder and Waterhouse 1994, Mackie et al. 1998, Doerr et al. 2005, D'Eon and Serrouya 2005). Thus, winter ranges for mule deer usually have lower elevations, south-facing slopes, and moderate to high canopy cover (Carson and Peek 1987, Garrott et al. 1987, Armleder and Waterhouse 1994, D'Eon and Serrouya 2005, Doerr et al. 2005).

These habitat components are juxtapositioned in various ways. In Montana, winter range characteristics vary in vegetation community, topography, structure, and climate. Some mule deer populations in Montana occupy pine (*Pinus* spp.), juniper (*Juniperus* spp.), sagebrush (*Artemisia* spp.), or prairies during winter (Lovaas 1958, Martinka 1968, Mackie 1970, Dusek 1975). Elsewhere, mule deer occupy riparian bottoms or mountain shrub communities (Carson and Peek 1987). Some mule deer populations winter in steep, rugged terrain (Carson and Peek 1987, Nicholson et al. 1997, D'Eon and Serrouya 2005), while others concentrate on level to gently sloping sites (Mackie 1970, Schoen and Kirchoff 1990, Armleder and Waterhouse 1994). Other mule deer use irrigated and non-irrigated agricultural fields that overlap winter ranges (Mackie 1978, Vogel 1989, Garrott et al. 1987, Thomas and Irby 1991).

In east-central Idaho, winter ranges vary in topography and precipitation, forming a gradient of habitat quality based on vegetation types and available forages. For instance, one

winter range near Challis, Idaho (hereafter, Sink Creek) has steeper topography, less precipitation, and lower forage availability for mule deer, whereas another winter range < 70 miles away outside Tendoy, Idaho (hereafter, Warm Springs) receives more precipitation, has more vegetation heterogeneity, more potential forages, and gentler topography. Due to differences in habitat conditions, mule deer in these areas may exhibit different patterns of habitat use. For example, mule deer on the Warm Springs winter range may be able make gradual movements down in elevation as winter progresses and snow levels fluctuate, whereas steeper topography and less vegetation on the Sink Creek winter range force deer to concentrate at the lowest elevations for most of the winter. In addition, mule deer on the Sink Creek winter range may be forced into a more rigid energy conservation strategy where disturbance levels and thermal and hiding cover may be more important factors in habitat selection than on winter ranges with more available forage resources. If these habitat use and behavioral patterns occur, it is important to understand these differences as habitat prioritization will vary for each area.

In some mountain ranges, mule deer populations contend with energy deficits of longer or shorter duration than what mule deer in other areas experience (Mackie et al. 1998). The Eastern Front of the Rocky Mountains in north-central Montana (i.e., East Front) has a characteristically diverse climate, where high winds affect temperature and snow cover. Arctic fronts followed by high winds cause sub-zero temperatures and create snow drifts that make winter forage inaccessible to mule deer in some areas, while at other times warmer chinook winds melt snow and provide foraging opportunities that deer on other ranges may lack (Mackie et al. 1998). Mountain ranges outside the "chinook zone" on the East Front retain low-elevation snowpack from late-autumn through early spring (Mackie et al. 1998), but because these winds melt or redistribute snow (leaving some areas virtually snow-free), mule deer on the East Front can exploit greater foraging opportunities than previously reported in other studies. These extended foraging opportunities could allow mule deer to maintain their body condition and face a lower energy-deficit than other mule deer populations. Previous studies on the East Front in the 1980s and early 1990s examined mule deer distributions and movements (Kasworm 1981, Ihsle 1982, Pac et al. 1988, Baumeister 1994), but not mule deer habitat use patterns. Whereas there are numerous studies on deer-habitat relationships across Montana (Wilkins 1957, Lovaas 1958, Martinka 1968, Mackie 1970, Dusek 1975), habitat use with constantly changing snow depths has not been examined.

Whereas it is possible to make general assumptions about mule deer habitat use across landscapes, previous research contributes little to predicting more specialized winter habitat use and distributions of unstudied populations (Pauley et al. 1993). Many studies examining winter range also fail to address habitat use under diverse climatic conditions. Furthermore, little is published on important winter ranges. For example, the Idaho Department of Fish and Game (IDFG) recently updated its mule deer management plan, and in central and east-central Idaho, wildlife managers are particularly interested in winter range components that are important for long-term maintenance and viability of mule deer herds.

Mule deer habitats vary, but by definition they provide for viable populations and a means of comparing behavior and use among various habitat components such as cover and forage (Mackie et al. 1998). Our objective was to study female mule deer habitat use on 3 winter ranges with variable quality and availability of forage resources and different weather conditions. First, we tested the hypothesis that weather on the East Front affects mule deer habitat use differently than for mule deer on winter ranges in Idaho. If wind on the East Front affects mule deer habitat use, mule deer will use exposed sites over sheltered sites because of

lower snow depths, however during periods of high winds (i.e., ≥ 5 m/s) that decrease thermoregulation (Mautz 1978), mule deer will seek unexposed aspects. Feeding sites and bedding areas would vary due to wind and its effects on snow accumulation. Bedding areas would have greater hiding and canopy cover and be less exposed to wind when compared to feeding sites and random locations. Bedding areas may also have greater snow cover than feeding sites in areas where drifts accumulate among trees. Shrub composition will vary among feeding sites and bedding areas. For instance, feeding sites will have mule deer forage species such as creeping juniper (*Juniperus horizontalis*) and chokecherry (*Prunus virginianus*), whereas bedding areas will contain other trees and shrubs such as limber pine (*Pinus flixibilis*) or Canada buffaloberry (*Shepherdia canadensis*), which are not as important as forage species.

Next, we addressed whether differences in topography and vegetation between 2 winter ranges in Idaho contributed to differences in habitat use between wintering mule deer. We hypothesized that due to limited forage resources available from less annual precipitation in Sink Creek mule deer wintering there may rely on energy conservation more than foraging as an influence of winter habitat use than deer on the Warm Springs winter range that receives more annual precipitation and has a greater diversity of plant species. In doing so, they would be more likely to use habitat characteristics that contributed to thermal or hiding cover and bedding behavior rather than available forages than deer would use in Warm Springs. Deer in Warm Springs may use a wider variety of habitat characteristics that allow for foraging and bedding.

STUDY AREAS

East Front, Montana

A portion of this study took place on the Theodore Roosevelt Memorial Ranch (TRMR) on the East Front and surrounding private lands within Hunting District 441 (Figure 1). The

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2,448 ha TRMR was located 14 km southwest of Dupuyer, in Township 27 North, Ranges 8 and 9. The East Front consisted of agricultural lands, open prairie, and foothills at lower elevations, and steep canyons and limestone reefs of the Continental Divide. Total relief exceeds 1,500 m (Baumeister 1994). The TRMR and neighboring ranches to the north and south were bordered by Lewis and Clark National Forest, the Bob Marshall Wilderness to the west, and private and state-owned lands to the east.

The East Front is characterized by long, cold (\leq -41°C) winters and short, warm summers (\leq 30°C; Aune and Kasworm 1989, Baumeister 1994). Average annual precipitation varied from 150—200 cm in the high alpine zones to 30—40 cm along the limestone reefs, foothills, and into the prairie, mostly occurring between April and July (Thompson 1981, Moeckel 1997). Snow can fall at any time of the year and accounted for 45—80% of annual precipitation (Baumeister 1994). Winds averaged 18.5 km/hr annually (Western Regional Climate Center 2008), but can exceed 194 km/hr during winter.

The East Front consisted of an ecotone between the northern Great Plains and the central Rocky Mountains. It was characterized by >20 vegetation communities (Offerdahl 1989, Barker and Whitman 1998, Baumeister 1999). Prairie grassland and limber pine savannas interspersed with aspen (*Populus tremuloides*) groves and riparian corridors dominated lower-elevation regions. Higher-elevation forests included Douglas-fir, lodgepole pine (*P. contorta*), or sub-alpine fir (*Abies lasiocarpa*) communities (Baumeister 1994).

The East Front provided important summer and winter range for game species including elk (*Cervus canadensis*), mule deer, white-tailed deer (*O. virginianus*), and sharp-tailed grouse (*Pedioecetes phasianellus*). It also included top predators including grizzly bear (*Ursus arctos*), black bear (*U. americanus*), mountain lion (*Felis concolor*), golden eagle (*Aquila chrysaetos*),

and gray wolf (*Canis lupus*). The TRMR was part of a management complex important for the long-term persistence of wildlife along the East Front that included Glacier National Park, the Blackleaf Wildlife Management Area, Pine Butte Swamp Preserve, and the Sun River Wildlife Management Area (Offerdahl 1989), complementing the Crown of the Continent Ecosystem, which remains 1 of the largest, intact natural ecosystems remaining in North America (Fagre 2003). Livestock grazing, farming, and recreation were the primary land uses.

Sink Creek, Idaho

The Sink Creek study area lies along the eastern edge of Game Management Unit (GMU) 36B around Centennial Flats and the nearby Bayhorse/Sink Creek areas, Custer Country, Idaho (Figure 2). Elevation ranged from 1,585—2,500 m, and the rolling foothills graded into steep slopes of Bald Mountain to the west and characterize much of the terrain (Hurley and Miyasaki 2005). Small cuts draining into the Salmon River, which comprises the study area's eastern border, add to complex relief.

Average temperatures ranged from 3—10°C and precipitation ranged from 25—120 cm (IDFG 2005). The majority of precipitation occurred during autumn, winter, and spring; most summer precipitation evaporated at lower elevations (IDFG 2005). The area was also influenced by prevailing winds from the west; average wind speeds at Challis were 6.75 km/hr with gusts up to 21.1 km/hr, but winds could occasionally exceed 100 km/hr (IDFG 2005, WWRC2008).

Vegetation was characteristic of xeric shrubland-steppe areas, and largely consisted of Wyoming big sagebrush (*A. tridentata wyomingensis*)—grass communities at lower elevations with mountain mahogany (*Cercocarpus* spp.) and mixed subalpine forest, lodgepole pine, and whitebark pine (*P. albicaulis*) at higher elevations (Hurley and Miyasaki 2005, Yeo 2005).

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Mule deer and elk occupied GMUs 36B and 36 to the west, and used the lower-elevation 36B in winter and migrate west to national forests within GMU 36 (Yeo 2005). The 36B winter range was mainly BLM-administered lands but contained some private agricultural lands on its eastern border along the Salmon River. Livestock grazing and recreation were the primary land uses of the Challis winter range study area.

Warm Springs, Idaho

The Warm Springs study area occurred in GMU 30 near Warm Springs and Reese Creek, Lemhi County, Idaho (Figure 3). While similar to the Sink Creek site with rolling hills and drainages below and steep mountain slopes above, the terrain is neither as complex nor steep; elevations ranged from 1,433—2,743m (Hurley and Miyasaki 2005).

Precipitation was greater at the Warm Springs area than in Sink Creek, which contributes to more heterogeneous vegetation and mule deer forages available at this site. The area received 25-127 cm annual precipitation, most of which fell as snow during autumn, winter, and spring (IDFG 2005). This area was characterized by cold winters, with average annual temperatures ranging from 2° to 8°C (IDFG 2005).

Vegetation in this region was also largely Wyoming big sagebrush—grass communities. Xeric shrubland and steppe vegetation types dominated lower elevations, which graded into dry conifer forests and subalpine forests at higher elevations (IDFG 2005). Common plants found on winter range included Wyoming big sagebrush, basin big sagebrush (*A t. tridentata*), mountain big sagebrush (*A. t. vaseyana*), tall threetip sagebrush (*A. tripartita tripartita*), fourwing saltbush (*Atriplex canescens*), greasewood (*Sarcobatus vermiculatus*), and a variety of forb and grass species.

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The majority of the Salmon mule deer winter range was BLM-administered public lands and private lands along the Salmon River. While livestock grazing was the dominant land use in the area, timber harvesting, mining, and outdoor recreation also occurred (IDFG 2005).

METHODS

Data Collection

In February and March 2010, we captured 13 adult female mule deer and fitted them with very high-frequency (VHF) collars (Telonics, Mesa, Arizona) on and surrounding the TRMR. Mule deer were captured with Clover traps baited with alfalfa hay and sweet feed. We captured an additional 18 female mule deer from December 2010—March 2011. Deer in the Warm Springs and Sink Creek study areas were captured using Clover traps, helicopter-netgunning, drive-netting, and drop-net techniques, and fitted with VHF and global positioning system (GPS) radiocollars. We selected 16 females from the Warm Springs study area and 12 females from the Sink Creek study area to monitor for habitat use. These mule deer were selected based on previous knowledge of capture locations and accessibility to locate them during winter. We used the same radiotelemetry techniques and vegetation sampling methods in all study areas.

We began locating deer by triangulation and homing (White and Garrott 1990) after the deer were radiocollared for ≥ 1 week (i.e., to eliminate potential capture-related changes in behavior). We visually located all collared deer and recorded behavior (e.g., feeding, moving, bedded) at their initial location. If the collared deer fled from the observer when first seen, we ceased tracking efforts and attempted to determine initial location via tracks. If we were unable to do so, data were not recorded for her that day.

Because weather can be variable throughout the day, we measured temperature and wind speed with a Kestrel 3500 pocket weather meter (Nielsen Kellerman, Boothwyn, Pennsylvania,

USA), and recorded time, wind direction, and precipitation at each deer location. We also noted the number, age and sex class of other deer ≤ 50 m to the radiocollared individual (or within the same group; Clutton-Brock et al. 1982). If > 1 radiocollared deer was observed in a group, we used data from only 1 of those deer to prevent pseudoreplication. We also recorded presence of cattle, white-tailed deer, elk, and predators.

After the radiocollared deer left the area, we collected microsite habitat data. At each location, we recorded UTM coordinates with a handheld GPS unit, slope $(0-5, 6-10, 11-15, 16-20, 21-30, \text{ or } \ge 31^\circ)$ with a clinometer, position on the slope (i.e., bottom, low, middle, upper, ridge), aspect $(0-360^\circ)$, with a compass, and elevation (m). We also listed the most prominent vegetation within a 0.04 ha microhabitat sampling plot (Hendricks 2000) and measured snow depth (cm) with a tape measure at 3 sites per Daubenmire frame (described below) and then averaged the measurements.

We determined shrub canopy cover with the line intercept method (Canfield 1941, Higgins et al. 2005) by forming 2 transects (i.e., 1 transect going upslope—downslope, 1 transect going left-slope—right-slope), counting only 1 transect through the center to eliminate doublesampling. We estimated canopy cover with a spherical densiometer (Lemmon 1956, Bunnel and Vales 1990) at the center and ends of each transect and averaged values for canopy coverage of the study plot. We estimated shrub cover and canopy cover as an index of potential browse, hiding (shrub cover only), thermal, and snow-interception cover. We also measured percent cover of forbs and grasses using a Daubenmire frame (Daubenmire 1959). In spring 2010, we placed the frame at the center of each location and at 5 and 10 m along each transect used to measure shrub canopy cover (n = 9 frames per location). We increased the number of Daubenmire frame measurements to the center of, and at 3, 6, and 9m along each transect (n = 13 frames per location) for the 2010/2011 winter field season to obtain a better estimate of available plant species. We measured hiding cover (i.e., visual cover, vegetative or non-vegetative barriers that conceal deer; Rahme 1991) with a cover pole (Griffith and Youtie 1988).

In the 2010-2011 field season, we established a paired random site for each deer location. In 2010 we determined the mean and standard deviation of distances between consecutive deer locations, estimating a range of 270-900 m. Therefore, the random locations ranged from 270-290 m from the radiocollared deer locations. We made the same microsite habitat measurements described above for deer locations at random sites.

Data Analysis

To determine deer habitat use from what was available across each study area, we developed models using multivariate logistic regression (Hosmer and Lemeshow 2000, Manly et al. 2002, Keating and Cherry 2004). We derived the relative probability of deer-use via the equation:

$$\widehat{\omega}(x) = \exp(\widehat{\beta_1}x_1 + \widehat{\beta_2}x_2 + \dots + \widehat{\beta_n}x_n) \quad (1)$$

Where $\hat{\omega}(x)$ is the relative likelihood of a location being a deer-use site as a function of covariates x_n and coefficents β_n (Hosmer and Lemeshow 2000, Manley et al. 2002). We assumed random locations represented habitat availability within the home range. Logistic regression makes no assumptions about normal distribution of the independent variables, but because many of the covariates were left-skewed, we used the transformation $\ln(x + 1)$ on all variables representing plant cover to normalize the distribution of cover given presence while still including the observations where species x = 0 (thus, maintaining a presence/absence component).

We used microsite habitat data collected at mule deer use and random locations as a basis for our models. In the process of, and in addition to data collected, we selected variables based on findings from previous literature, what was biologically relevant, and characteristics of the study area. Because mule deer winter resource use is scale-dependent (D'Eon and Serrouya 2005), we defined resource selection at the 3rd-order scale, or locations within the home-range (Johnson 1980). These variables included slope, wind speed, temperature, exposure, solar radiation, hiding cover, canopy cover, snow depth, and a combination of line-intercept and Daubenmire frame plant cover data.

Elevation and aspect are the most important predictors of home range selection in mule deer (D'Eon and Serrouya 2005), however they were not included as predictor variables because at the 3rd-order scale, deer are already at lower elevations, and aspect is often analyzed as a circular or categorical (e.g., north, north-east) variable, which by itself is of little relevance to mule deer. Instead of aspect, we used solar radiation and wind exposure. Aspect is generally used as a covariate in habitat use studies because of its influence on snow depth, vegetation, and temperature (Bilbao 2008). However, solar radiation (measured as insolation, W/m²) is a continuous surrogate for aspect and a more direct measure of sun exposure and ensuing thermal or snow conditions that still correlates with aspect (Figure 4; Rich et al. 1994, Fu and Rich 2002, D'Eon and Serrouya 2005). To account for the effects of high winds on the East Front, we generated a covariate based on Beers' transformation of aspect, where we compared the inverse of wind direction with aspect we measured at each use and random location to get a continuous variable representing exposure, where a value of 2 indicated that a deer was completely sheltered from wind while a value of 0 indicated complete exposure (Beers et al. 1966).

Other weather-related variables included temperature and wind speed collected directly from the deer use or random site. Random locations may not always represent weather conditions for the study area. (e.g., a random location behind a sheltered slope during high winds), we also gathered information from Snotel sites (http://www.wcc.nrcs.usda.gov/snow/) and weather stations to assess snow accumulation and average daily winds across the study area.

We used STATA 11 (StataCorp, College Station, TX) for all data analyses. Before developing our models, we assessed the potential contribution of each variable to the sample by evaluating the number of occurrences in each observation of the dataset, eliminating all variables that occurred in $\leq 5\%$ of the data. Therefore, plant species that were documented only on rare occasions were not included in data analysis. We tested all variables for correlations (using a cutoff threshold of r = 0.5), and applied univariate logistic regression to choose candidate variables (P < 0.25) to be included in the final model (Hosmer and Lemeshow 2000). We applied manual stepwise selection to assess variable and model significance.

For the East Front, we constructed 4 models constrained under different weather or behavior conditions. Our first model was a pooled model containing all use and random locations under all weather conditions and behaviors. Next, we constructed a model based on snow accumulation by data from Snotel sites for each study area and summing the total accumulation (i.e., positive, negative) for the 3-day period up to the date of each deer use and random location. If snow accumulation for that period > 0 cm, we included that observation in the snow accumulation model. If snow accumulated for that 3-day period \leq 0 cm, the observation was included in our 3rd model pertaining to deer habitat use during periods when no snow accumulated or snow melted. We also made a wind model, using data from weather stations at each study area (http://www.wunderground.com/weatherstation/index.asp?MR=1). Whereas we measured wind speed at each site, we did not solely rely on these measurements as a description of wind across the study area, due to the influences of site-specific topography and vegetation. Similar to the snow accumulation model, we ran a model for observations measured on windy days, when daily average wind speed ≥ 5 m/s. We chose a 5 m/s threshold because wind speeds \geq 5 m/s are enough to begin moving snow particles, and the volume of snow movement increases at wind speeds from 7-9 m/s (Winstral et al. 2002, Katlein 2009). With a sustained daily average wind speed of 5 m/s, individual wind measurements taken hourly or throughout the day sufficiently exceeded 5 m/s (enough to move snow particles) and the cutoff still provided a sufficient sample size. Finally, we ran a multinomial logistic regression using behavior categories (i.e., feeding/moving and bedding) and random locations as response variables to examine differences in coefficients and covariate significance based on deer behavior. In Idaho, we also ran 4 models: pooled locations from both of the study areas and all weather conditions, pooled locations and snow accumulation, Sink Creek locations, and Warm Springs locations. Daily average wind speed never exceeded 14 km/hr in either Idaho study area and thus, wind condition was not a variable for habitat use in Idaho.

We then applied Akaike's Information Criterion (AIC) adjusted for small sample size (AICc) to select the most parsimonious models if >1 candidate model was generated for each set of weather/study area circumstances. We used a Receiver Operating Characteristic (ROC) to evaluate models, which determined sensitivity, the probability that the model returns a positive prediction when the animal is present (y = 1) and specificity, where the model predicts a low probability when the animal is absent (y = 0; Cumming 2000). We used the area under the ROC curve, AUC, to assess model fit (Cumming 2000). An AUC of 0.8 indicates that the model has

roughly an 80% chance of correctly predicting use from a randomly-selected observation if use occurred (Fielding and Bell 1997).

RESULTS

We gathered microsite habitat data from 535 combined use and random locations across the East Front, Warm Springs, and Sink Creek study areas. On the East Front, we classified 142 observations as receiving snow accumulation and 243 observations as non-snow accumulation or snow-melt conditions in the analysis. Also on the East Front, we collected data on 114 observations during periods when daily average wind speeds \geq 18 km/hr. Due to smaller sample sizes from Warm Springs and Sink Creek (n = 47 and 50, respectively), both Idaho study areas were pooled and 34 observations were used in assessing habitat use under snowy conditions. Landscape and weather variables could be used to predict probability of deer use in the East Front and Idaho models.

East Front

The East Front presented a unique suite of characteristics for mule deer winter range. Snow depths at used or random locations ranged from 0—47.9 cm. On some days, average wind speeds reached 40 km/hr, with high winds exceeding 100 km/hr. These winds redistributed snow, creating large snow drifts in some areas and leaving swaths of bare ground and accessible forage in others.

Mule deer on the East Front used habitat variables contributing to thermal/hiding cover, environmental variables affecting thermoregulation and forage accessibility, and forage quality and availability. Cover variables included tree cover and percent cover buffaloberry, environmental variables included slope, wind speed, exposure, and snow depth, and forage variables included creeping juniper, whitemargin phlox (*Phlox albomarginata*), curly sedge (*Carex rupestris*), and prairie sagewort (*A. frigida*; $\chi_{10}^2 = 75.07$, *P* < 0.0001; Table 1). The area under the AUC curve totaled 0.81, indicating good model fit (Fielding and Bell 1997).

Model covariates changed and the predictive capabilities of the covariates varied depending upon weather conditions. During or following periods of snow accumulation (i.e., any positive accumulation in the last 3 days), only a subset of these variables (wind speed, percent cover creeping juniper and buffaloberry), in addition to the covariates, canopy cover and percent cover rough fescue (*Festuca campestris*) had predictive power ($\chi_8^2 = 75.07, P < 0.0001$, AUC = 0.88; Table 2). In lieu of canopy cover, mean hiding cover, percent tree cover, and percent cover of limber pine were also contributors along with the other covariates, but were all correlated with canopy cover (r > 0.5) and none gave the model any better predictive capabilities than canopy cover alone. Canopy cover was not related to decreased snow depths ($t_{427} = -0.35$, P = 0.725), but it exhibited a negative relationship with wind speed ($t_{426} = 2,47, P = 0.014$). Snow depth was an important univariate predictor (Z = -2.64, P = 0.008) during periods of snow accumulation but lost significance when combined with the other covariates in the model, and it was also negatively correlated with rough fescue (r = -0.37) when observations were constrained to the given weather conditions. Also, mean snow depth after snow accumulation was $14.0 \pm$ 14.2 cm. Snow depth at use sites averaged 10.7 ± 9.84 cm, snow depth at random locations averaged 17.3 ± 17.3 cm.

During periods without snow accumulation or if snow melted, variables associated with thermoregulation and potential forages predicted deer habitat use. These variables included a cover variable (limber pine), environmental variables (wind speed, exposure), and vegetation/forage variables (creeping juniper, slender wheatgrass [*Elymus trachycaulus subsecundus*], and fringed sagewort ($\chi_6^2 = 63.46$, *P* < 0.0001, AUC = 0.79; Table 3).

Under high wind conditions, tree cover, exposure to wind, percent cover of forage species (the 5 main browse species reported as used by deer on the TRMR), junegrass (*Koeleria macrantha*) and curly sedge were the top model predictors ($\chi_5^2 = 55.40$, P < 0.0001, AUC = 0.84; Table 4). There was also a negative relationship between tree cover and wind speed ($t_{141} = -4.64$, P < 0.001) and exposure and wind speed ($t_{141} = -4.18$, P < 0.001) under windy conditions. Snow depth did not contribute to predicting deer use in the model (Z = -1.80, P = 0.071), nor as a univariate predictor (Z = -1.05, P = 0.296). Also, under windy conditions, mean snow depth was 0.611 ± 1.08cm.

Some model covariates varied depending upon deer behavior (Table 5). For instance, snow depth (Z = -2.41, P = 0.016) predicted deer feeding and moving locations but not bedding locations, while buffaloberry (Z = 3.20, P = 0.001) and tree cover (Z = 5.09, P < 0.001) predicted of deer bedding locations but not feeding or moving locations.

Idaho

When data from both study areas were pooled, tall threetip sagebrush and phlox were the best predictors of mule deer use locations versus available ($\chi_3^2 = 16.89$, P = 0.0007, AUC = 0.73; Table 6). Increasing each covariate increased probability of deer use in Idaho, however, the only term with coefficient standard errors not overlapping 0 was phlox (Z = 2.11, P = 0.035).

During or after snow accumulation, increasing percent cover of tall threetip sagebrush and cumulative forbs predicted mule deer use over random locations ($\chi_2^2 = 9.86$, P = 0.0072, AUC = 0.78; Table 7) with both terms contributing to the model.

For the Warm Springs study area, increasing percent cover of tall threetip sagebrush, all forbs, and possibly wind speed increased probability of deer use ($\chi_3^2 = 19.14$, P = 0.0002, AUC = 0.81; Table 8). Wind speed approached significance in the model (Z = 1.79 P = 0.073) and in

univariate regression (Z = 1.94, P = 0.053). While wind speed did not end up in the final Sink Creek model, exposure was included as a variable due to its influence on the AUC curve (AUC without exposure = 0.71). Longleaf phlox (*Phlox longifolia*) and mean hiding cover also positively contributed to the Sink Creek model ($\chi_3^2 = 11.37$, P = 0.0099, AUC = 0.77; Table 9), albeit mean hiding cover only approached significance (Z = -1.81, P = 0.071).

DISCUSSION

Habitat characteristics such as forage quality and quantity and appropriate cover determine the strategies that mule deer employ to effectively maintain themselves and reproduce. Survival and reproduction of a mule deer is improved when it uses appropriate habitats characteristics for maintenance periods like winter. As expected, winter habitat use on the East Front coincided with an energy conservation strategy, in which the data exhibited a positive relationship for probability of deer use favoring lower snow depths and thermal/security cover and a combination of potential forages.

Whitemargin phlox in our East Front models is as a potentially important forb for female mule deer. Phlox species, particularly Hood's phlox (*Phlox hoodii*), have been noted as present in mule deer rumen samples or forage sites (Lovaas 1958, Constan 1972, Mackie 1970). Bryoides phlox (*Phlox bryoides*) was an important forage for mule deer in Colorado after other browse species such as Saskatoon serviceberry (*Amelanchier alnifolia*), mountain snowberry (*Symphoricarpos oreophilus*), and yellow rabbitbrush (*Chrysothamnus viscidiflorus*) were depleted (Carpenter et al. 1979). While Hood's phlox was not an important covariate in our study, it was present in both use and random sites, therefore its availability across the study area may not have limited mule deer habitat use. Alternatively to phlox, there was a negative relationship between probability of deer use and percent cover of curly sedge. There were no

known published accounts of mule deer selection or avoidance of curly sedge, however due to its tendency to grow in dry areas with a low moisture gradient, it has been noted as avoided by another ungulate, muskox (*Ovibos moschatus*), in winter (Schaefer and Messier 1994, 1995). In Utah, it is a dominant plant on dry, rocky south faces above timberline (Lewis 1958). Curly sedge was positively correlated with elevation (r = 0.49) in our study.

Canopy cover, slope exposure, and percent cover of shrubs like buffaloberry, may aid in reducing wind speeds and providing thermal cover for mule deer during or following snowstorms. Unlike other studies, which report that mule deer use habitats with moderate to high canopy cover due to lower snow depths from tree interception (Armleder and Waterhouse 1994, D'Eon and Serrouya 2005), we report no negative relationship between canopy cover and snow depth. Armleder and Waterhouse (1994) reported that mule deer used old-age tree stands with high canopy cover and used these areas more when overall snow depths were high. In our study, canopy cover was important under all conditions but had its greatest effect after snow accumulation. Observations during data collection support our findings, in fact, several areas of high canopy cover contained deep snow, especially on leeward aspects where vegetation in these areas trapped snow particles during windy conditions.

It is possible that deer use of other habitat characteristics such as thermal/hiding cover superseded selection for lower snow depths when snow was accumulated across the study area. Our snow accumulation model was rather conservative, because any locations that had received > 0 cm snow in a 3-day period were included in the model. Therefore, days in which a 2—3 centimeters of snow had accumulated were treated similarly to days that received > 20 cm. Due to sample size we did not restrict locations to higher snow accumulations, but because distinctions in habitat use occurred even at this level, it is possible that relationships would be

more apparent if the model was restricted to higher snow depth conditions. High variability in mean snow depth at both use and random locations in addition to overlapping standard deviations make it difficult to determine relationships between snow depth and probability of deer use.

Top model covariates on windy days also varied from covariates in the full model; the negative relationship between tree cover and wind speed, and exposure and windspeed, indicates that tree cover and exposure may decrease wind speeds experienced by deer in some areas. Tree cover was a more effective predictor of probability of deer use than canopy cover under these circumstances because it was likely a better indicator of thermal protection than overhead canopy cover by itself. Snow depths were not indicative of deer use vs. availability on windy days, but because mean snow depths at this time were < 1 cm, snow depths during these conditions would not have restricted deer foraging or moving opportunities. Gilbert et al. (1970) suggests that at snow depths > 46 cm are sufficient to impeded deer travel and foraging.

Our data suggest that wind conditions on the East Front may remove enough snow cover to open up greater foraging opportunities for mule deer than what deer on other winter ranges experience. The importance of creeping juniper on the East Front was reflected by its presence in nearly every model, regardless of weather conditions. However, the data provided some evidence that wind speeds may decrease snow depths and allow deer more foraging opportunities, as creeping juniper by itself was not the most important forage variable in the wind model. Rather, the 5 main browse species (i.e., creeping juniper, chokecherry, silverberry, serviceberry, and snowberry; Hemmer 2005) were collectively more effective at describing probability of deer use than creeping juniper alone.

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While there are many studies on mule deer diet, results are site-specific and forage selection is based on the available vegetation in a given range. However, the most commonly-used browse species across various habitats in Montana are junipers (Lovaas 1958, Martinka 1968, Mackie 1970, Dusek 1975). For instance, Hemmer (2005) reported that creeping juniper was among the top 5 commonly-used browse species by mule deer on the TRMR. While traditionally considered a low-palatability, emergency browse for deer (Hill 1946, Smith and Hubbard 1954, Julander 1962), other studies note it is used in varying degrees and situations (Hill and Harris 1943, Anderson et al. 1965). Junipers contain oils and terpenoids that at high levels, can harm rumen microflora (Schwartz et al. 1980*a*), however when multiple plant species are available, deer can consume various amounts of juniper without inhibiting rumen function (Schwartz et al. 1980*b*). When juniper is the only palatable species for mule deer on winter range, winter condition and survival may be affected (Schwartz et al. 1980*b*).

In addition to snow storms on the East Front affecting deer habitat use, snowstorms in Idaho may have also affected deer habitat use on these winter ranges. Tall threetip sagebrush provided both a cover and forage resource, and combined with the cumulative forage variable indicates that deer may be forced to broaden their range of forage selectivity when snow cover prohibits foraging on low-growing species such as phlox. Tall threetip sagebrush grows up to 1.8 m high, has introgressed with Wyoming big sagebrush in the Salmon, Idaho area, and is palatable for mule deer and other wildlife (McArthur et al. 1979, Wambolt 2001, Rosentreter 2004). At higher snow depths in Colorado, Carpenter and Wallmo (1979) reported that mule deer consumed taller plant species like shrubby vegetation, but lower-profile plant species (forb and grass) consumption increased with lower snow depths, and the authors concluded that snow depths limited dietary complexity.

Top model covariates between Sink Creek and Warm Springs differed, providing some evidence that deer in Sink Creek versus deer in Warm Springs rely more heavily on cover and conserving energy while exhibiting limited foraging opportunities. In Warm Springs, a combination of cover, forage, and environmental variables had predicted deer use. The positive relationship between probability of deer use and percent cover of tall threetip sagebrush and cumulative forbs may be an indication that mule deer in the Warm Springs area have a combination of foraging and bedding opportunities that influence habitat use. The final model for Sink Creek provides some evidence that environmental conditions and thermal or hiding cover may be important to mule deer in this area. The presence of phlox in the Sink Creek model further supports our findings on the East Front that phlox species may be an important forage resource for mule deer. Adequate hiding cover and thermal cover aid in energy conservation (Mysterud and Ostbye 1999), while a forb such as phlox which remains green during winter (Carpenter et al. 1979) could provide some important forage.

We did not have a sufficient sample size to determine whether deer altered their behaviors and increased foraging or bedding time given certain weather conditions, but we were able to ascertain behavior-specific habitat attributes, or differences in the magnitude of these attributes influenced probability of deer use. These relationships indicate that certain habitat characteristics, while important for deer use in general, suit different purposes in meeting or sustaining deer energy requirements. Environmental factors or catastrophic events cause resource limitations and induce periods of stress for mule deer. However, mule deer have evolved unique strategies to cope with these situations. In addition to using appropriate habitat, deer must also alter their behavior to mitigate for winter's higher energy requirements and suboptimal forage conditions. Travel and foraging time increases with decreasing forage

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availability (Collins et al. 1978, Wickstrom et al. 1984), and energetic costs of locomotion are greatly influenced by snow cover (Parker et al. 1984). Foraging represents a significant cost to an ungulate's daily energy requirements, and there is a threshold at which energy expenditure required for foraging (i.e., locomotion, thermoregulation, eating, digestion) exceeds the energetic gains from forage (Short 1975). This relationship is reinforced with increasing snow depths and cold winds (Mautz 1978). Numerous studies indicate that ungulates modify their foraging behavior and conserve energy through reduced food intake during winter (Thompson et al. 1973, Mautz 1978) concomitant with decreases in metabolic rate and activity levels (Ozoga and Verme 1970, Moen 1976, Mautz 1978, Taillon et al. 2006).

Comparing habitat-use characteristics across multiple winter ranges in association with weather conditions provides further insight into winter adaptations and how mule deer mitigate for winter conditions. Across study areas, winter ranges varied in topography, vegetation, and weather, resulting in different patterns of habitat use by mule deer. We hypothesized that wind conditions on the East Front would affect mule deer habitat use, and we provide evidence to support this hypothesis. For instance, whereas other studies report mule deer use of south-facing slopes or areas with higher solar radiation due to lower snow depths, solar radiation was not a final variable in our models (D'Eon and Serrouya 2005). Rather, in our study, exposure was an appropriate surrogate for aspect; mule deer used sheltered sites under nearly all weather conditions, indicating that high wind speeds on the East Front may take a significant toll on thermoregulation and energy conservation. We further support this with the relationship between deer use and lower wind speeds in all 5 of our East Front models. However, cumulative forage species (rather than solely creeping juniper) were important covariates during or following periods of high winds (Z = 4.07, P = <0.001), suggesting that winds on the East Front

may provide extended foraging opportunities for mule deer. Also, feeding and bedding locations differed via magnitude and significance of coefficient. Bedding areas were less exposed to wind and contained more variables indicative of hiding and thermal cover than feeding sites. In Idaho, deer in Sink Creek used habitat characteristics more in line with thermal and hiding cover than a broader suite of forage species, supporting our hypothesis that differences in topography and vegetation among study areas contribute to different habitat use patterns in mule deer.

MANAGEMENT IMPLICATIONS

On the East Front and east-central Idaho, understanding mule deer habitat use and discrepancies in winter habitat use among winter ranges will define optimal mule deer use of these areas. In our study, we analyzed data from 1 winter, which we did not consider a major winter event and therefore did not identify limiting factors for these deer populations. However, we were still able to identify habitat relationships in each area.

For instance, mule deer reliance on variable topography and vegetation indicates that maintaining heterogeneity, rather than prioritizing singular habitat components such as elevation, canopy cover, south-facing aspects on the East Front landscape is important to ensure mule deer use of this winter range during varying weather conditions. Because different habitat use patterns arose among study areas, it is important to understand these differences as habitat prioritization will vary for each winter range.

Mule deer wintering and transitional ranges are located on or adjacent to private lands which have more potential for habitat loss (e.g., subdivisions) or degradation (e.g., livestock grazing, farming; Carpenter and Wallmo 1981, Mackie et al. 1982, Thomas and Irby 1991, Sawyer et al. 2005). Winter ranges that lie within federal lands are also more prone to greater threat of exploitation (e.g., oil and gas development, livestock grazing; Sawyer et al. 2006) than the less-accessible summer ranges.

There are important considerations regarding where and how to implement habitat conservation or improvement projects, for instance, key factors in identifying important habitat in areas with suboptimal forage resources (e.g., Sink Creek) may be the abundance of quality thermal or hiding cover and low levels of disturbance along with presence of key forb species such as phlox. Because these deer are already limited in their winter range, focus on transitional and summer ranges may better enable them to accumulate fat reserves prior to, or regain body condition more rapidly following, winter. Depending on population size and objectives, deer in higher-quality winter ranges may not require specific habitat management, better enabling agencies to focus on more sensitive areas.

Conversely, understanding which winter ranges provide suitable or less than suitable habitat for mule deer will aid in prioritizing land use. For instance, energy development is becoming an increasing threat to mule deer winter ranges in the west. Through direct habitat loss and increased disturbance, oil and gas development negatively impacts mule deer (Sawyer et al. 2006), yet increasing demands for energy put greater pressure on federal lands for these developments. Landscape conservation strategies increasingly focus on areas where populations are more likely to persist in the long term (Margules and Pressey 2000). If an oil well, or any other land use that will negatively impact mule deer is to be placed on a given winter range, managers will be able to triage winter ranges, potentially conserving the higher-quality winter range where deer are more likely to persist than on winter ranges where deer are sensitive to disturbance.

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LITERATURE CITED

- Anderson, A. E., W. A. Snyder, and G. W. Brown. 1965. Stomach content analysis related to condition in mule deer, Guadalupe Mountains, New Mexico. Journal of Wildlife Management 29:352—365.
- Armleder, H. M., and M. J. Waterhouse. 1994. Winter habitat use by mule deer in the central interior of British Columbia. Canadian Journal of Zoology 72:1721—1725.
- Aune, K. and W. Kasworm. 1989. Final report: East Front grizzly bear study. Montana Fish, Wildlife, and Parks, Helena, Montana, USA.
- Barker, W. T. and W. C. Whitman. 1988. Vegetation of the Northern Great Plains. Rangelands 10:266–272.
- Baumeister, T. R. 1994. Evaluation of mule deer hunting on Theodore Roosevelt Memorial
 Ranch and observations on white-tailed deer. Paper 94-9, Boone and Crockett Wildlife
 Conservation Program, University of Montana, Missoula, USA.
- Baumeister, T. R. 1999. Field-testing the accuracy and generality of selected wildlife-habitat models. Dissertation, University of Montana, Missoula, USA.
- Beers, T. W., P. E. Dress, and L. C. Wensel. 1966. Aspect transformation in site productivity research. Journal of Forestry 64:691—692.
- Bilbao, J. V. 2008. Predicting feeding site selection of mule deer on foothill and mountain rangelands. Thesis, Montana State University, Bozeman, USA.
- Bunnel, F. L. and D. J. Vales. 1990. Comparison of methods for estimating forest overstory cover: differences among techniques. Canadian Journal of Forestry Research 20:101— 107.

- Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. Journal of Forestry 39:388—394.
- Carpenter, L. H., O. C. Wallmo, and R. B. Gill. 1979. Forage diversity and dietary selection by wintering mule deer. Journal of Range Management 32:226–229.
- Carson, R. G. and J. M. Peek. 1987. Mule deer habitat selection patterns in northcentral Washington. Journal of Wildlife Management 51:46—51.
- Collins, W. B., P. J. Urness, and D. D. Austin. 1978. Elk diets and activities on different lodgepole pine habitat segments. Journal of Wildlife Management 42:799–810.
- Constan, K. J. 1972. Winter foods and range use of three species of ungulates. Journal of Wildlife Management 36:1068—1076.
- Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. Red deer: behavior and ecology of two sexes. University of Chicago Press, Chicago, Illinois, USA.
- Cumming, G. S. 2000. Using between-model comparisons to fine-tune linear models of species ranges. Journal of Biogeography 27:441—455.
- Daubenmire, R. 1959. A canopy coverage method for vegetation analysis. Northwest Science 33:43—64.
- Doerr, J. G., E. J. Degayner, and G. Ith. 2005. Winter habitat selection by Sitka black-tailed deer. Journal of Wildlife Management 69:322—331.
- D'Eon, R. G. and R. Serrouya. 2005. Mule deer seasonal movements and multiscale resource selection using global positioning system radiotelemetry. Journal of Mammalogy 86:736—744.
- Dusek, G. L. 1975. Range relations of mule deer and cattle in prairie habitat. Journal of Wildlife Management 39:605—616.

- Fagre, D. B. 2003. Glacier National Park Biosphere Reserve: its suitability for the Mountain Research Initiative. Pages 99—108 *in* Global change research in Mountain Biosphere Reserves, Proceedings of the International Launching Workshop. The United Nations Educational, Scientific, and Cultural Organization. 10—13 November 2003, Entlebuch Biosphere Reserve, Switzerland.
- Fielding, A. H. and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38— 49.
- Fu, P. and P. M. Rich. 2002. A geometric solar radiation model with applications in agriculture and forestry. Computers and Electronics in Agriculture 37:25—35.
- Garrott, R. A., G. C. White, R. M. Bartmann, L. H. Carpenter, and A. W. Alldredge. 1987.Movements of female mule deer in northwest Colorado. Journal of WildlifeManagement 51:634—643.
- Gilbert, P. F., O. C. Wallmo, and R. B. Gill. 1970. Effect of snow depth on mule deer in Middle Park, Colorado. Journal of Wildlife Management 34:15–23.
- Griffith, B. and B. A. Youtie. 1988. Two devices for estimating foliage density and deer hiding cover. Wildlife Society Bulletin 16:206—210.
- Hemmer, S. A. 2005. Winter feeding ecology and browse effects of mule deer, elk, white-tailed deer, and cattle on the Theodore Roosevelt Memorial Ranch. Thesis, University of Montana, Missoula, USA.
- Hendricks, C. W. 2000. Mule deer habitat use of the Buckskin Mountain winter range. Thesis, Utah State University, Logan, USA.

- Higgins, K. F., K. J. Jenkins, G. K. Clambey, D. W. Uresek, D. E. Naugle, J. E. Norland, and W. T. Barker. 2005. Vegetation sampling and measurements. Pages 524—553 *in* C. E. Braun, editor. Techniques for wildlife investigations and management. Sixth edition. The Wildlife Society, Bethesda, Maryland, USA.
- Hill, R. R. 1946. Palatability ratings of Black Hills plants for white-tailed deer. Journal of Wildlife Management 10:47—54.
- Hill, R. R. and D. Harris. 1943. Food preferences of Black Hills deer. Journal of Wildlife Management 7:233—235.
- Hosmer, D. W. and S. Lemeshow. 2000. Applied logistic regression. Second edition. John Wiley & Sons, New York, New York, USA.
- Hurley, M. and H. Miyasaki. 2005. Mule deer ecology. Idaho Department of Fish and Game, Federal Aid in Wildlife Resoration, Job Progress Report, Project W-160-R-31. Boise, Idaho, USA.
- Idaho Department of Fish and Game [IDFG]. 2005. Idaho Comprehensive Wildlife Conservation Strategy. Idaho Conservation Data Senter, Idaho Department of Fish and Game, Boise, ID. http://fishandgame.idaho.gov/cms/tech/CDC/cwcs.cfm. Accessed 17 September 2011.
- Ihsle, H. B. 1982. Population ecology of mule deer with emphasis on potential impacts of oil and gas development along the east slope of the Rocky Mountains, northcentral Montana. Thesis, Montana State University, Bozeman, USA.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecological Monographs 54:187–211.

- Julander, O. 1962. Range management in relation to mule deer habitat and herd productivity in Utah. Journal of Range Management 15: 278–281.
- Kasworm, W. F. 1981. Distribution and population characteristics of mule deer along the Eats Front, north-central Montana. Thesis, Montana State University, Bozeman, USA.
- Katlein, C. 2009. Physics of snow drift. Infrastructure in a Changing Climate. University
 Centre in Svalbard, Svalbard, Norway. http://www.katlein.de/media/dokumente/physik/
 Physics of Snow drift Personal Report Christian Katlein AT301.pdf>. Accessed 19
 September 2011.
- Keating, K. A. and S. Cherry. 2004. Use and interpretation of logistic regression in habitatselection studies. Journal of Wildlife Management 68:774—789.
- Lemmon, P. E. 1956. A spherical densiometer for estimating forest overstory density. Forest Science 2:314—320.
- Lewis, M. E. 1958. Carex its distribution and importance in Utah. Brigham Young University Science Bulletin: Biological Series 1. Brigham Young University, Provo, Utah, USA.
- Lovaas, A. L. 1958. Mule deer food habits and range use, Little Belt Mountains, Montana. Journal of Wildlife Management 22:275–283.
- Mackie, R. J. 1970. Range ecology and relations of mule deer, elk, and cattle in the Missouri River Breaks, Montana. Wildlife Monographs 20:1—79.
- Mackie, R. J. 1978. Impact of livestock grazing on wild ungulates. Transactions of the North American Wildlife and Natural Resources Conference 43:462—476.
- Mackie, R. J., K. L. Hamlin, and D. F. Pac. 1982. Mule deer. Pages 862—877 *in*: J. A.
 Chapman and G. A. Feldhamer, editors. Wild mammals of North America—biology, management, economics. John Hopkins University Press, Baltimore, Maryland, USA.

- Mackie, R. J., D. F. Pac, K. L. Hamlin, and G. L. Dusek. 1998. Ecology and management of mule deer and white-tailed deer in Montana. Montana Fish, Wildlife, and Parks, Federal Aid in Wildlife Restoration Project W-120-R, Helena, USA.
- Manley, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002.Resource selection by animals: statistical analysis and design for field studies. Second Edition. Kluwer, Boston, Massachusetts, USA.
- Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. Nature 405:243–253.
- Martinka, C. J. 1968. Habitat relationships of white-tailed deer and mule deer in northern Montana. Journal of Wildlife Management 32:558—565.
- Mautz, W. W. 1978. Sledding on a bushy hillside: the fat cycle in deer. Wildlife Society Bulletin 6:88—90.
- McArthur, E.D., A.C. Blauer, A.P. Plummer, and R. Stevens 1979. Characteristics and hybridization of important intermountain shrubs. III. Sunflower family. USDA Forest Service Research Paper INT-220, Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.
- Moen, A. N. 1976. Energy conservation by white-tailed deer in the winter. Ecology 57:192–198.
- Moen, R. and G. D. Delguidice. 1997. Simulating nitrogen metabolism and urinary urea nitrogen: creatinine ratios in ruminants. Journal of Wildlife Management 61:881—894.
- Mysterud, A. and E. Ostbye. 1999. Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. Wildlife Society Bulletin 27:385—394.

- Nicholson, M. C., R. T. Bowyer, and J. G. Kie. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. Journal of Mammalogy 78:483—504.
- Offerdahl, R. J. 1989. A description of the major plant communities on the Theodore Roosevelt Memorial Ranch. Thesis, University of Montana, Missoula, USA.
- Ozoga, J. J. and L. J. Verme. 1970. Winter feeding patterns of penned white-tailed deer. Journal of Wildlife Management 34:431—439.
- Pac, H. I., W. F. Kasworm, L. R. Irby, and R. J. Mackie. 1988. Ecology of the mule deer, *Odocoileus hemionus*, along the east front of the Rocky Mountains, Montana. Canadian Field Naturalist 102:227—236.
- Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. Journal of Wildlfie Management 48:474—488.
- Pauley, G. R., J. M. Peek, and P. Zager. 1993. Predicting white-tailed deer habitat use in northern Idaho. Journal of Wildlife Management 57:904—913.
- Rahme, A. H. 1991. Visual cover and site selection by mule deer. Thesis, Simon Fraser University, Burhaby, British Columbia, Canada.
- Rich, P. M., W. A. Hentrick, S. C. Saving, and R. O. Dubayah. 1994. Using viewshed models to calculate intercepted solar radiation: applications in ecology. American Society for Photogrammetry and Remote Sensing Technical Papers: 524—529.
- Rosentreter, R. 2004. Sagebrush identification, ecology, and palatability relative to sage-grouse. USDA Forest Service Proceedings RMRS-P-000.
- Sawyer, H. R., F. Lindzey, and D. McWhirter. 2005. Mule deer and pronghorn migration in western Wyoming. Wildlife Society Bulletin 33:1266—1273.

- Sawyer, H., R. M. Nielson, F. Lindzey, and L. L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management 70:396—403.
- Schaefer, J. A. and F. Messier. 1994. Composition and spatial structure of plant communities on southeastern Victoria Island, Arctic Canada. Canadian Journal of Botany 79:1264— 1269.
- Schaefer, J. A. and F. Messier. 1995. Habitat selection as a hierarchy: the spatial scales of winter foraging by muskoxen. Ecography 18:333—344.
- Schwartz, C. C., J. C. Nagy, and W. L. Regelin. 1980a. Juniper oil yield, terpenoid concentration, and antimicrobial effects on deer. Journal of Wildlife Management 44:107—113.
- Schwarz, C. C., W. L. Regelin, and J. G. Nagy. 1980b. Deer preference for juniper forage and volatile oil treated foods. Journal of Wildlife Management 44:114—120.
- Schoen, J. W. and M. D. Kirchhoff. 1990. Seasonal habitat use by Sitka black-tailed deer on Admiralty Island, Alaska. Journal of Wildlife Management 54:371—378.
- Short, H. L. 1966. Effects of cellulose levels on the apparent digestibility of feeds eaten by mule deer. Journal of Wildlife Management 30:163—167.
- Short, H. L. 1975. Nutrition of southern deer in different seasons. Journal of Wildlife Management 39:321—329.
- Short, H. L., D. R. Deitz, and E. E. Remmenga. 1966. Selected nutrients of mule deer browse plants. Ecology 47:222–229.

- Smith, A. D. and R. L. Hubbard. 1954. Preference ratings for winter deer forages from northern Utah ranges based on browsing time and forage consumed. Journal of Range Management 7:262—265.
- Taillon, J., D. G. Sauvé, and S. D. Côté. 2006. The effects of decreasing winter diet quality on foraging behavior and life-history traits of white-tailed deer fawns. Journal of Wildlife Management 70:1445—1454.
- Thomas, J. R. and K. R. Irby. 1991. Winter habitat use by mule deer with access to wheat fields and planted forb-grassland. Wildlife Society Bulletin 19:155—162.
- Thompson, M. J. 1981. Mountain goat distribution, population characteristics and habitat use in the Sawtooth Range, Montana. Thesis, Montana State University, Bozeman, USA.
- Thompson, C. B., J. B. Holter, H. H. Hayes, H. Silver, and W. E. Urban, Jr. 1973. Nutrition of white-tailed deer. I. Energy requirements of fawns. Journal of Wildlife Management 37:301—311.
- Torbit, S. C., L. H. Carpenter, D. M. Swift, and A. W. Alldredge. 1985. Differential loss of fat and protein by mule deer during winter. Journal of Wildlife Management 49:80—85.
- Vogel, W. O. 1989. Response of deer to density and distribution of housing in Montana. Wildlife Society Bulletin 17:406–413.
- Wallmo, O. C., L. H. Carpenter, W. L. Regelin, R. B. Gill, and D. L. Baker. 1977. Evaluation of deer habitat on a nutritional basis. Journal of Range Management 30:122—127.
- White, G. C. and R. A. Garrot. 1990. Analysis of wildlife radio-tracking data. Academic Press, New York, New York, USA.
- White, G. C., A. F. Reeve, F. G. Lindzey, and K. P. Burnham. 1996. Estimation of mule deer winter mortality from age ratios. Journal of Wildlife Management 60:37–44.

- Wickstrom, M. L., C. T. Robbins, T. A. Hanley, D. E. Spalinger, and S. M. Parish. 1984. Food intake and foraging energetics of elk and mule deer. Journal of Wildlife Management 48:1285—1301.
- Wambolt, C. K. 2001. Mule deer foraging preference among five sagebrush (*Artemisia* L.) taxa. Western North American Naturalist 61:490–494.
- Western Regional Climate Center. 2008. Climatological Summary Challis Airport, Idaho September 1998 to December 2008. http://www.wrcc.dri.edu/summary/llj.id.html. Accessed 17 September 2011.
- Winstral, A., K. Elder, and R. E. Davis. 2002. Spatial snow modeling of wind-redistributed snow using terrain-based parameters. Journal of Hydrometeorology 3:524—538.
- Yeo, J. J. 2005. Effects of grazing exclusion on rangeland vegetation and soils, east central Idaho. Western North American Naturalist 65:91—102.
- Wilkins, B. T. 1957. Range use, food habits, and agricultural relationships of the mule deer,Bridger Moutains, Montana. Journal of Wildlife Management 21:159—169.

Variable	Coefficient	S.E.	Р	95% CI for coefficient		
				Lower	Upper	
Tree (% tree cover)	0.478	0.131	< 0.001	0.222	0.734	
Buffaloberry	0.665	0.284	0.019	0.108	1.22	
Exposure to wind	0.706	0.174	< 0.001	0.365	1.04	
Wind speed (km/hr)	-0.065	0.019	0.001	-0.102	-0.028	
Slope (%)	0.091	0.031	0.004	0.029	0.152	
Snow depth (cm)	-0.023	0.011	0.034	-0.045	-0.002	
Creeping juniper	0.451	0.105	< 0.001	0.244	0.657	
Curly sedge	-0.648	0.173	< 0.001	-0.988	-0.309	
Prairie sagewort	-0.553	0.195	0.005	-0.935	-0.170	
Whitemargin phlox	1.00	0.397	0.012	0.224	1.78	
Constant	-1.22	0.421	0.004	-2.05	-0.397	

Table 1. Parameter estimates for a logistic regression model describing the probability of femalemule deer use of areas on the East Front, Montana, winter 2010—2011.

Table 2. Parameter estimates for a logistic regression model describing the probability of female mule deer use of areas within 3 days of snow accumulation on the East Front, Montana, winter 2010—2011.

Variable	Coefficient	S.E.	Р	95% CI for coefficient		
				Lower	Upper	
Canopy cover (100% = open)	-0.179	0.084	0.032	-0.343	-0.015	
Buffaloberry	2.33	0.679	0.001	0.995	3.66	
Wind speed (km/hr)	-0.362	0.095	< 0.001	-0.548	-0.177	
Creeping juniper	1.33	0.039	0.001	0.570	2.09	
Rough fesscue	0.976	0.210	< 0.001	0.563	1.39	
Constant	18.0	8.35	0.031	1.66	34.4	

Table 3. Parameter estimates for a logistic regression model describing the probability of female mule deer use of areas during periods without snow accumulation on the East Front, Montana, winter 2010—2011.

Variable	Coefficient	S.E.	Р	<u>95% CI for</u>	coefficient	
				Lower	Upper	
Limber pine	0.628	0.163	< 0.001	0.307	0.948	
Exposure to wind	0.662	0.223	0.003	0.225	1.10	
Wind speed (km/hr)	-0.050	0.021	0.017	-0.091	-0.009	
Creeping juniper	0.393	0.118	0.001	0.161	0.625	
Prairie sagewort	-0.551	0.230	0.017	-1.00	-0.100	
Constant	-0.693	0.417	0.097	-1.51	0.124	

Table 4. Parameter estimates for a logistic regression model describing the probability of female mule deer use of areas during periods of high winds (e.g., daily average ≥ 5 m/s) on the East Front, Montana, winter 2010—2011.

Variable	Coefficient	S.E.	Р	95% CI for Lower	<u>coefficient</u> Upper
Tree (% tree cover)	0.856	0.268	0.001	0.330	1.38
Snow depth (cm)	-0.058	0.030	0.052	-0.116	0.000
Exposure to wind	0.928	0.371	0.012	0.201	1.66
Wind speed (km/hr)	-0.064	0.030	0.033	-0.123	-0.005
Forage (% cover main browse spp.)	0.993	0.233	< 0.001	0.537	1.45
Prairie junegrass	-0.655	0.290	0.024	-1.22	-0.087
Constant	-0.738	0.742	0.320	-2.19	0.717

Table 5. Parameter estimates for a multinomial logistic regression model describing the probability of female mule deer use of areas and behavior (active, bedded) on the East Front, Montana, winter 2010—2011.

Behavior	Variable	Coefficient	S.E.	Р	<u>95% CI fo</u> Lower	or coefficient Upper
Active	Tree (% tree cover)	0.271	0.146	0.063	-0.015	0.558
	Buffaloberry	0.285	0.344	0.407	-0.388	0.958
	Exposure to wind	0.639	0.187	0.001	0.272	1.01
	Wind speed (km/hr)	-0.056	0.020	0.005	-0.095	-0.017
	Slope (%)	0.086	0.034	0.010	0.020	0.152
	Snow depth (cm)	-0.032	0.013	0.016	-0.058	-0.006
	Creeping juniper	0.470	0.109	< 0.001	0.258	0.683
	Curly sedge	-0.756	0.222	0.001	-1.19	-0.322
	Prairie sagewort	-0.462	0.202	0.022	-0.858	-0.066
	Whitemargin phlox	0.848	0.412	0.021	0.140	1.76
	Constant	-1.40	0.455	0.002	-2.29	-0.508

Behavior	Variable	Coefficient	S.E.	Р	<u>95% CI for</u> Lower	<u>coefficient</u> Upper
Bedded	Tree (% tree cover)	0.775	0.152	< 0.001	0.476	1.07
	Buffaloberry	1.02	0.320	0.001	0.396	1.65
	Exposure to wind	0.876	0.249	< 0.001	0.388	1.36
	Wind speed (km/hr)	-0.109	0.035	0.002	-0.177	-0.040
	Slope (%)	0.106	0.041	0.010	0.025	0.187
	Snow depth (cm)	-0.007	0.015	0.634	-0.036	0.022
	Creeping juniper	0.357	0.150	0.017	0.063	0.650
	Curly sedge	-0.458	0.231	0.048	-0.911	0.005
	Prairie sagewort	-0.870	0.308	0.005	-1.47	-0.266
	Whitemargin phlox	1.20	0.531	0.024	0.155	2.24
	Constant	-2.76	0.635	< 0.001	-4.01	-1.52

Table 5. (continued)

Variable	Coefficient	S.E.	Р	<u>95% CI for</u> Lower	<u>coefficient</u> Upper
Tall threetip sagebrush	0.595	0.345	0.084	-0.080	1.27
All phlox (% cover all <i>Phlox</i> spp.)	0.610	0.289	0.035	0.043	1.18
Bitterroot	0.919	0.613	0.134	-0.282	2.12
Constant	-0.619	0.303	0.041	-1.21	-0.026

Table 6. Parameter estimates for a logistic regression model describing the probability of femalemule deer use of areas for pooled Sink Creek and Warm Springs, Idaho, winter 2010—2011.

Table 7. Parameter estimates for a logistic regression model describing the probability of deer use of areas during or within 3 days of snow accumulation for pooled Sink Creek and Warm Springs, Idaho, winter 2010—2011.

Variable	Coefficient	S.E.	Р	95% CI for Lower	<u>coefficient</u> Upper
Tall threetip sagebrush	0.879	0.481	0.068	-0.064	1.82
All forbs (% cover all forb spp.)	0.989	0.405	0.015	0.196	1.78
Constant	-1.67	0.789	0.035	-3.21	-0.121

Table 8. Parameter estimates for a logistic regression model describing the probability of deer
use of areas from Warm Springs, Idaho, winter 2010-2011.

Variable	Coefficient	S.E.	Р	95% CI for Lower	<u>coefficient</u> Upper
Wind speed (km/hr)	0.140	0.079	0.073	-0.013	0.295
Tall threetip sagebrush	1.09	0.482	0.024	0.147	2.03
All forbs (% cover all forb spp.)	1.04	0.417	0.013	0.223	1.86
Constant	-2.80	0.977	0.004	-4.71	-0.890

Table 9. Pa	arameter estimates	s for a logistic reg	ression model	describing the probability of deer	
use of area	s from Sink Creek	, Idaho during, 20	10—2011.		

Variable	Coefficient	S.E.	Р	95% CI for Lower	<u>coefficient</u> Upper
Exposure	-0.790	0.490	0.107	-1.75	0.171
Mean hiding cover $(5 = no cover)$	-1.51	0.483	0.071	-3.14	0.127
Longleaf phlox	1.61	0.597	0.007	0.442	2.78
Constant	6.52	3.42	0.057	-0.194	13.2

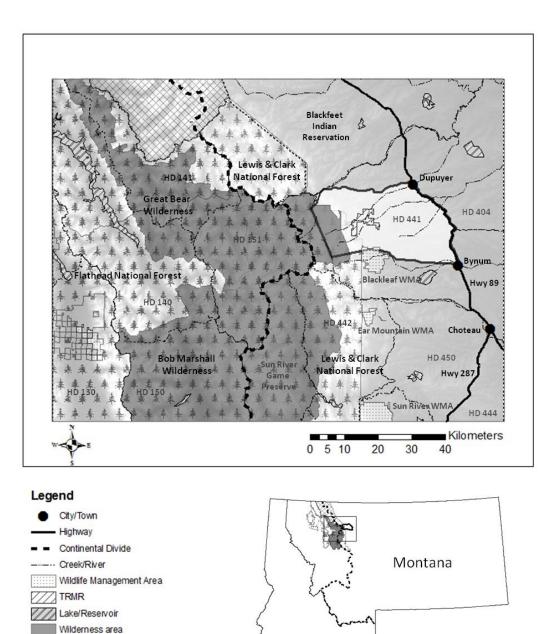


Figure 1. East Front study area, Montana, 2011.

StudyArea

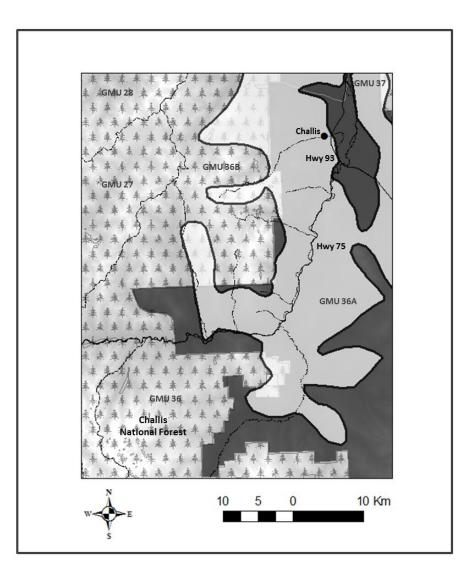
 National Forest

 Glacier National Park

 Hunting District Boundary

Idaho

Figure 2. Sink Creek study area, central Idaho, 2011.



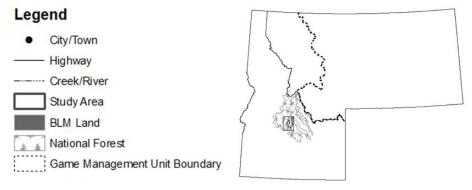
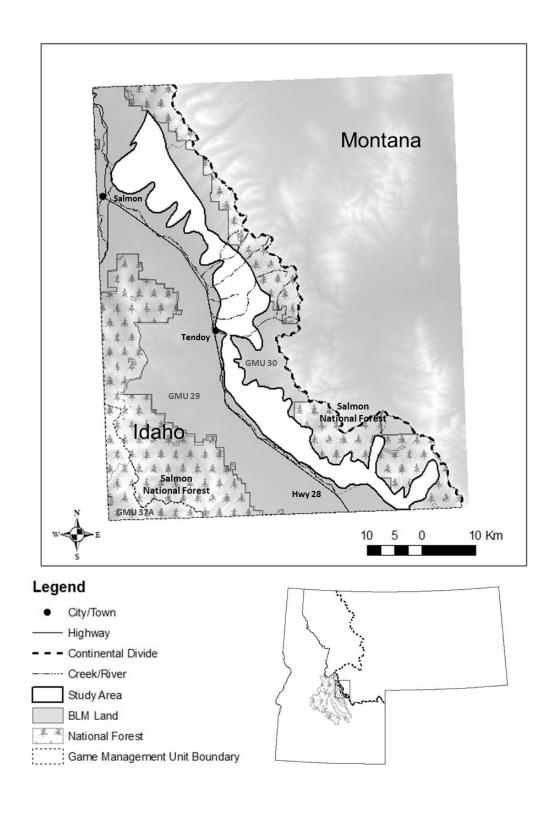


Figure 3. Warm Springs study area, east-central Idaho, 2011.



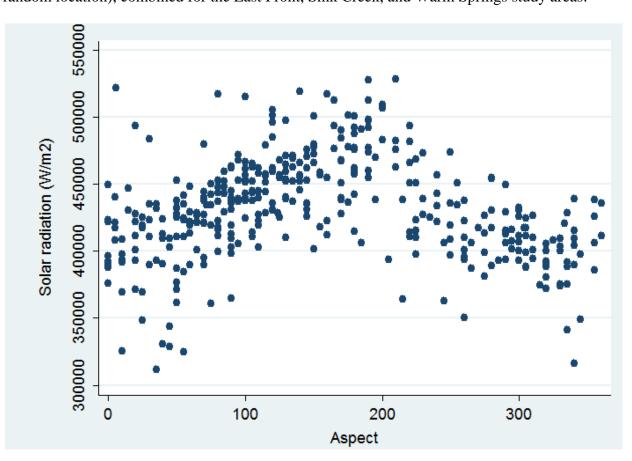


Figure 4. Relationship between aspect and solar radiation (at each female mule deer use and random location), combined for the East Front, Sink Creek, and Warm Springs study areas.