MODELING SEASONAL DISTRIBUTION AND SPATIAL RANGE CAPACITY OF MOOSE IN SOUTHEASTERN WYOMING

Phillip E. Baigas[1], Richard A. Olson[1], Ryan M. Nielson[2], Scott N. Miller[1], and Frederick G. Lindzey[3]

[1]University of Wyoming, Department of Renewable Resources, 1000 E. University Ave., Laramie, WY 82071, USA; [2]Western Ecosystems Technology, Inc. 2003 Central Ave., Cheyenne, WY 82001, USA; [3]17 Millbrook Rd. Laramie, WY 82070, USA.

ABSTRACT: Predictive maps of Shiras moose (*Alces alces shirasi*) habitat associations have not been created for most Wyoming populations. For the state's most recently established population in the southeastern mountains, a literature-based winter habitat suitability index (HIS) model was developed and assessed with locations of 23 moose wearing global positioning system (GPS) radio-collars in 2005-2006. Overall, the winter HSI model was poorly predictive of habitat occupancy. The relationship between individual utilization distributions and landscape variables was modeled with resource selection functions (RSF) during winter and non-winter periods. In winter, moose generally responded in a similar fashion to distance variables to riparian shrub, to deciduous forest and forest edge, and slope and slope^2. Due to snow pack differences, 2 separate models were created for each winter; thermal aspect (warm vs. cool slopes) rather than slope and slope^2 was more predictive in the winter of deeper snow. The non-winter model demonstrated the nearly exclusive importance of riparian shrub habitat in close proximity to forest cover across a wide range of elevations. Non-winter moose locations were best explained by the total area of riparian shrub patches within a surrounding 1 km radius. Distance to forest edge had a considerably stronger influence on non-winter habitat use. The association with deciduous forest was still significant, although less than during winter; slope was also explanatory. The models were validated and a spatial algorithm was employed to estimate carrying capacity within the study area based on the predicted RSF habitat quality and size of winter home range.

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Shiras moose (*Alces alces shirasi*) habitat in the Rocky Mountains of North America has been described by many authors. While moose are most commonly found in riparian shrub habitat types, other important habitats include mixed mountain shrub, aspen (*Populus spp.),* and conifer forest (Benson et al. 1987, WGFD 1990). Willow (*Salix spp.*) is considered the crucial forage of most moose in winter (Harry 1957, Houston 1968, Dorn 1970, Peek 1974) as well as the growing season (Zimmermann 2001, Dungan and Wright 2005). However, the spatial distribution of Wyoming's Shiras moose relative to available habitat and forage resources is poorly documented for most populations, hence, seasonal range maps used by the Wyoming Game and Fish Department (WGFD) are undeveloped. The range of environmental situations exploited by moose during different seasons has only been defined recently for a single population in northwestern Wyoming (Becker 2008).

Moose became established in the Snowy Range of the Medicine Bow Mountains in southeastern Wyoming following introductions in North Park, Colorado (approximately 50 km to the south) in the late 1970s (Duvall and Schoonveld 1988). The population has

grown to a point that habitat condition is of concern and harvest has been liberalized. Of 38 moose hunting areas, the Snowy Range area is among those allowing highest opportunity with 45 permits (WGFD 2009). Harvest data and sightings suggest that the population continues to be very productive, whereas populations in western Wyoming are mostly in decline.

Relationships among environmental variables and the distribution of wildlife are commonly described by spatially explicit models of habitat capability using geographic information systems (GIS). Species-habitat relationships and related maps are commonly used to develop expert opinion-based habitat suitability index (HSI) models. Allen et al. (1987) published one of the first HSI models for moose range in the Lake Superior region; subsequent models have been developed for several other regions (Romito et al. 1999, Koitzsch 2002, Snaith et al. 2002, Dussault et al. 2006). Advances in geospatial databases and remote animal observation technologies have compelled the development of more statistically reliable habitat modeling techniques. For example, resource selection functions (RSF) allow creation of maps that allow probabilistic predictions of habitat selection across large areas (Manly et al. 2002).

Estimating Shiras moose populations in the Rocky Mountains is a management challenge. Although population surveys are generally reliable in areas where moose winter among extensive floodplains, their effectiveness may be limited by high cost or unfavorable weather conditions (Ward et al. 2000). However, population estimates are arguably necessary to develop management strategies and engage the public; likewise, carrying capacity estimates are desirable and useful to assess big game and domestic livestock range. Carrying capacity estimates require extensive information about vegetation dynamics and population demographics, and even with comprehensive data about forage biomass and nutritional quality, estimates differ by site, season, and even daily (Hanley and McKendrick 1983). Such variation makes an accurate carrying capacity estimate impossible in most cases, particularly where animals utilize multiple habitat types within variable habitats (McLeod 1997).

It has been suggested that statistically robust RSF models can be combined with knowledge of a species' behavioral ecology to estimate carrying capacity (Boyce and MacDonald 1999). A recent focus of many species-habitat studies is to relate habitat selection models (i.e., RSF maps) to various population metrics including home range (Boyce and Waller 2003, Apps et al. 2004, Mowat et al. 2004, Nielsen et al. 2005, Aldridge and Boyce 2007, Ciarniello et al. 2007; see Johnson and Seip 2008). Home range defines an accumulation of resources necessary for an animal's survival and reproduction (Mitchell and Powell 2004) as determined by energetic requirements (McNab 1963), is considered economical (Powell 2000), and some minimum level of total habitat quality should be within a home range (Roloff and Haufler 1997, Mitchell and Powell 2004, 2007). Ecological and physiological factors are thought to influence home range size above a threshold level of habitat quality (McLoughlin and Ferguson 2000); home ranges are expected to contain approximately equal levels of total habitat quality assuming minimal variation in individual resource requirements. If habitat characteristics used to predict species distribution reflect those factors limiting survival and reproduction, then spatial calculations based on home range size and quality can estimate carrying capacity (Roloff and Haufler 1997).

Moose density varies widely across their range (Maier et al. 2005) with individual variation in habitat use strategies (Osko et al. 2004, Dussault et al. 2005b). Resource requirements within a population are best compared during the critical winter period when forage is often limiting (Peterson and Allen 1974, WGFD

1990). We explored the total habitat quality of winter ranges as predicted by winter RSF models relative to winter range size. Our goal was to identify key habitat parameters of winter range for use in spatial calculations to predict carrying capacity of Shiras moose in southeastern Wyoming.

STUDY AREA

This study was conducted in the Snowy Range of the Medicine Bow Mountains of southeastern Wyoming. The study area is defined by the original boundary of Moose Hunt Unit 38, approximately 5,950 km^2 (Fig. 1). Most moose range lies within the Medicine Bow National Forest (MBNF) that occupies approximately 35% of the study area. Another 15% of the study area was public land managed by the Bureau of Land Management, the State of Wyoming, and WGFD. Private lands dominating the surrounding Laramie Basin and North Platte River Valley accounted for nearly half the study area (2,890 km^2).

The climate is generally characterized by long, cold winters and short, dry summers. Most precipitation comes as snowfall in November-April, with accumulation varying greatly with elevation and exposure. Snow pack provides most of the available moisture during the short growing season (Knight 1994). Total annual precipitation typically ranges from 50-125 cm (USDA-NRCS 2007a), increasing with elevation due to snowfall accumulation. Much of the study area frequently experiences high velocity westerly winds that widely redistribute snowfall.

Elevations range from 2,011 m above mean sea level along the North Platte River to 3,663 m atop Medicine Bow Peak. The greatest rise in elevation is in the central portion of the study area where the Snowy Range is formed by a steep face of uplifted granite. The remainder of the Medicine Bow Mountains is generally characterized by rolling, less dramatic topography. However, many creeks cut steep ravines or canyons through the foothills as they descend from montane elevations on all sides.

Fig. 1. Location of study area in Moose Hunt Area 38 in southeast Wyoming, USA.

Over 50% of the forest area is comprised of lodgepole pine (*Pinus contorta*) at various densities. These stands typically have a sparse understory of scattered buffaloberry (*Sheperdia canadensis*) and common juniper (*Juniperus communis*), with heartleaf arnica (*Arnica cordifolia*) as the primary herbaceous species. An Engelmann spruce (*Picea engelmanii*)–subalpine fir (*Abies lasiocarpa*) association typically occurs at higher elevations with an understory primarily of mosses and dwarf huckleberry (*Vaccinium scoparium*); Englemann spruce and subalpine fir also grow within sheltered ravines and along stream corridors at lower elevations. Interspersed within the coniferous forest and commonly in drainage bottoms are clones of quaking aspen (*P. tremuloides*) at elevations up to 2,900 m. Common aspen associates are serviceberry (*Amelanchier alnifolia*), snowberry (*Symphoricarpos* spp.), gooseberry/currant (*Ribes* spp.), redosier dogwood (*Cornus sericea*), Woods rose (*Rosa woodsii*), and Scouler willow (*Salix scouleriana*).

Willow communities occur in riparian areas, varying in species composition by elevation. In general order of greatest abundance, willow species included planeleaf (*Salix planifolia*), Booth (*S. boothii*), Wolf (*S. wolfii*), Drummond (*S. drummondiana*), Geyer (*S.*

geyeriana), whiplash (*S. lasiandra*), mountain (*S. monticola*), strapleaf (*S. eriocephala* var. *ligulifolia*), Bebb (*S. bebbiana*), and yellow (*S. eriocephala* var. *watsonii*). There are approximately 53 km^2 of willow communities within the study area, accounting for 1.3% of the MBNF. Bog birch (*Betula glandulosa*) is widely distributed in association with shorter willow species on moderately sloping stream gradients. At lower elevations, cottonwood species such as balsam poplar *(Populus balsamifera)* and narrowleaf cottonwood (*P. angustifolia*) create forest corridors along stream margins with taller willows (Drummond, Bebb, whiplash, and yellow) in the adjacent floodplain. Irrigated hay meadows are adjacent to most major streams below the forest.

Approximately 20% of the MBNF is not forested occurring as alpine meadows, natural openings or parks, regenerating clearcuts, riparian meadows, or dry slopes. Mountain big sagebrush (*Artemisia tridentata ssp. vaseyana*) and antelope bitterbrush (*Purshia tridentata*) dominate a mixed grass-shrub community at foothill elevations with southern exposure. Associated thickets of true mountain mahogany (*Cercocarpus montanus*), serviceberry, and snowbrush ceanothus (*Ceanothus velutinus*) are widely scattered.

Traditional land uses in the forested portion of the study area include timber extraction, mining, and livestock grazing, although these activities have declined. Consumptive and non-consumptive recreational use is increasingly important due to the proximity of human population centers in southeastern Wyoming and north-central Colorado. Cattle ranching operations dominate non-forested private lands.

METHODS

Moose Captures

Moose were tranquilized from a helicopter (n = 23) or the ground (n = 3) in December 2004 (5 M, 11 F) and 2005 (4 M, 6 F). A CO_2-injection powered rifle (Dan-inject North America, Fort Collins, CO) was used to fire 13 mm, 1.5 mL darts equipped with 32 mm barbed needles (Pneu-dart, Williamsport, PA) containing a dose of 10 mg thiafentanil (Kreeger et al. 2005). Immobilized moose were blindfolded and blood, hair, and swab samples of fecal and ear material were collected. The antibiotic oxytetracycline was administered to protect against dart wound infection, and Imovec was injected for endo- and ectoparasite control. Thiafentanil was antagonized with 300 mg naltrexone. Adult females were captured preferentially over males at a 3:1 ratio (Kreeger et al. 2005) to document female productivity, yet provide comparison of habitat use between sexes. Captures were performed in accordance with the University of Wyoming Institutional Animal Care and Use Committee protocols.

Each moose was fitted with a store-on-board Global Positioning System (GPS) collar (Model *TGW 3700*, Telonics, Mesa, AZ) programmed to collect locations every 1.5 h. A CR-2a release mechanism allowed for pre-programmed collar release. Sixteen collars were deployed December 2004; 8 were programmed to release in June 2005 and 8 in August 2006. The 8 collars collected in June 2005 and 2 collars from bulls harvested in October 2005 were redeployed in December 2005 and programmed to release in June 2006. Two bulls captured in December 2005 did not survive and 1 cow captured in December 2005 was an unintentional recapture. In total, 23 moose were studied; 16 were 1-winter animals (6 M, 10 F) and 7 were 2-winter animals (1 M, 6 F). GPS locations and other spatial datasets were projected in NAD 83, UTM Zone 13 and managed with ArcGIS 9.2 (Environmental Systems Research Inc., Redlands, CA 2007).

Vegetation and Spatial Data

A classified 30-m Landsat ETM+ image of the study area was obtained (Driese and

Nibbelink 2003) and used as the foundation for a preliminary HSI model. The Resource Information System (RIS; USFS 1995), a forest stand polygon database maintained by the MBNF, was used to develop observation-based RSF models. The RIS layer provided an effective basis for calculating a distance to forest edge variable. However, inconsistent results from queries of this database to identify forest attributes believed important to moose (e.g., species mix, percent cover, stand age, stand density) made it necessary to generalize forested polygons into 3 forest types: coniferous, deciduous, and mixed forest. Polygons attributed as containing >95% conifer forest were grouped together, regardless of species composition. RIS polygons with >75% aspen were identified as deciduous forest. Conifer stands with >5% aspen were classified as mixed forest; mixed forest polygons were often pure coniferous stands containing small patches of deciduous forest. Such cases were isolated by visual review of 1-m color infrared (CIR) orthophotography (2002) and the deciduous patches were heads-up digitized.

The RIS layer did not cover the entire study area, so additional editing was required to define the distribution of important cover types. Landsat image pixels beyond the extent of the RIS dataset were classified as deciduous forest and converted to polygons that were modified where necessary to better reflect aspen stand boundaries; polygons were deleted where misclassification occurred. Lastly, deciduous forest stands not identified by either vegetation layer were heads-up digitized using the CIR imagery. Likewise, because neither dataset accurately delineated riparian cover types, all riparian shrub communities discernable on the CIR photos were digitized across the study area. The National Wetland Inventory (NWI; USFWS 2007) dataset was used to identify riparian areas and polygons were modified to the boundaries of riparian shrub communities. New polygons were created around riparian shrub communities in locations not identified by the NWI. Euclidean distances to deciduous forest and riparian shrub polygons were calculated as variables. We calculated distances to snowmobile trails and maintained gravel roads. Distance to "high resolution" flowlines of the National Hydrography Dataset, derived from 1:24,000 topographic maps (USGS 2000), was calculated as a variable. For each distance variable, a centered 2nd order polynomial term was calculated for consideration in statistical model building (Kutner et al. 2003).

Additional predictor variables were compiled to explore topographic influences on habitat use. A 30-m digital elevation model (DEM; USGS 1999) was obtained and the Spatial Analyst extension (Environmental Systems Research Inc., Redlands, CA 2007) was used to calculate slope (degrees) and aspect. Grid cells with slope >4º were assigned to 1 of 8 categories (N, NE, E, SE, S, SW, W, or NW). Areas with slight slopes (≤4º) were considered flat and assigned to a reference category. A thermal aspect was created to differentiate between warm and cool slopes. Slopes ≥4º facing NW, N, NE, or E were assigned a "cool" value of 0, and south- or west-facing slopes were assigned a "warm" value of 1. To account for potential interaction between these variables, a site severity index (SSI; Nielsen and Haney 1998 in Boyce et al. 2003) was calculated from slope (%) and aspect (*A*, in degrees) as follows:

$$SSI = \sin(A + 225) * \left(\frac{slope}{45}\right) \quad (1)$$

Values ranged from -3.59 on steep northeast slopes to 4.23 on steep southwest slopes, with moderate slopes having values ±0.

Variables were computed to describe cover type arrangement and the amount of forest edge surrounding a given point on the landscape within 2 distances, since habitat selection occurs at different scales (Johnson 1980). Eight variables were derived using the moving window algorithm (Focal Sum) of

the Spatial Analyst extension (Environmental Systems Research Inc., Redlands, CA 2007). The approximate mean distance between consecutive locations (80 m) and the mean cumulative 24-h distances among locations (1 km) defined the radius of 2 circular windows that were centered on each raster cell. Within each buffer distance the area of intersecting coniferous forest, deciduous forest, and riparian shrub was summed; the total distance of forest edge within these 2 buffers was also calculated.

Winter HSI Model Creation

A knowledge-based HSI model was developed with 5 variables identified as important to Shiras moose in western North America: elevation (SI_1), slope (SI_2), distance to willow (SI_3), food availability (SI_4), and willow patch size (SI_5) (Table 1). Locations at elevation of 2,439-2,896 m were assigned an optimum suitability index value ($SI_1 = 1$), lower elevations were assigned $SI_1 = 0.5$, and higher elevations were set at 0. Optimal slopes were those ≤10º and suitability decreased linearly with increasing slope to $SI_2 = 0$ at slope ≥60º. Similarly, locations within 120 m of a riparian shrub polygon had $SI_3 = 1$ and decreased linearly with increasing distance to $SI_3 = 0$ at distances ≥360 m. Foraging habitat capability was determined based on the assumed vegetation quality and production within the Landsat cover class. Riparian forest, mesic shrubland, and mixed mountain shrubland were assigned optimal suitability; deciduous forest, mixed forest, and mixed mountain shrub were assigned $SI_4 = 0.5$. Cover classes deemed least suitable for foraging ($SI_4 = 0$) included grassland and conifer forest, among others (Table 1). Because larger willow patches may accumulate more snow and provide less protective cover for moose, the extent of contiguous riparian shrub pixels was calculated using the moving window algorithm (150 x 150 m) of the Spatial Analyst extension. Optimal riparian shrub patches ($SI_5 = 1$) were defined

Table 1. Description of 5 variables considered important to Shiras moose in western North America that were used to develop a preliminary habitat suitability index (HSI) model in southeastern Wyoming.

Variable		Criteria	HIS	Reference
		> 2,896 m	0	
SI_1	Elevation	< 2,439 m	0.5	Personal Observations; and
		≤ 2896 & ≥ 2439 m	1	WGFD Annual Reports
		≥ 60º	0	Langley 1993;
SI_2	Slope	> 10º & < 60º	0 – 1	Rudd and Irwin 1985; and
		≤ 10º	1	Van Dyke 1995
		> 360 m	0	
SI_3	Distance to willow	≥ 120 & ≤ 360 m	0 – 1	Kufeld and Bowden 1996; and
		< 120 m	1	Halko et al. 2001
		Grassland, sagebrush shrubland, rock, etc.	0	Peek 1974;
SI_4	Food availability	Deciduous forest, mixed forests, mixed mountain shrubland	0.5	Harry 1957;
		Riparian forest, mesic shrubland, riparian shrubland	1	Houston 1968
		> 2 ha	0	
SI_5	Willow patch size	≤ 2 ha & ≥ 1.75 ha	0.5	Personal Observations
		< 1.75 ha	1	

as those >0 ha and <1.75 ha, medium-size patches of ≥1.75 ha and ≤2 ha had $SI_5 = 0.5$, and larger patches >2 ha were assigned $SI_5 = 0$. Variables were stored in GRID format and a linear combination was spatially projected across the study area as:

$$HSI = \left(SI_1 * SI_2 * SI_3 * SI_4 * SI_5\right)^{1/5} \quad (2)$$

This HSI model was evaluated with the winter locations of moose.

RSF Model Estimation

The definition of winter was determined by reviewing the contraction and expansion of moose range, as energy and forage availability are constrained by snow depth. A 95% kernel density estimate polygon was created from locations of each moose in 2-week time steps using Hawth's Tools (Beyer 2006). The bi-weekly interval in which moose movement became dramatically limited was defined as the start of winter, lasting until range expansion was observed in spring. The rest of the year was considered a single non-winter period.

Resource selection functions (Manly et al. 2002) were calculated following methods described by Marzluff et al. (2004), Millspaugh et al. (2006), and Sawyer et al. (2006, 2007). Individual animals defined the sample unit, rather than GPS point locations, which allows for the identification of individual differences in habitat selection (Osko et al. 2004) and avoids concerns about spatial autocorrelation and pseudoreplication (Sawyer et al. 2007). The domain of analysis was defined by a 100% minimum convex polygon around all moose locations, as recommended by McClean et al. (1998). Sampling points (n = 68,387) were created within this area from the centroids of a 125-m raster grid. The number of locations within each grid cell was tallied for each moose separately as a surrogate utilization distribution (UD; Marzluff et al. 2004), and transferred as an attribute of each sampling point using Hawth's Tools (Beyer 2006). Each sampling point was also intersected with the underlying grid value of each potential variable layer. Predictor variables were screened for collinearity and if correlations were large (r >0.6), they were not included in the same model.

RSF models were developed for both winter and non-winter using locations from both years. Separate winter 2005 and winter 2006 RSF models were also created because cover type selection and diet composition differed between years (Baigas 2008). A general linear model (GLM; Eq. 3) was fit for each individual moose, assuming a zero-inflated negative binomial (NB) distribution in order to allow for overdispersion (i.e., clustering):

$$\ln\left[E(r_i)\right] = \ln(total) + \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_p x_p \quad (3)$$

where r_i is the expected number of point locations for that moose within grid cell i, *total* is an offset term equal to the total number of GPS points collected from that individual, and predictor variables $x_1 \ldots x_p$ have coefficients $\beta_1 \ldots \beta_p$ (Millspaugh et al. 2006). Using a forward stepwise modeling approach, variable entry was determined by considering the collective direction and strength of individual moose responses (Sawyer et al. 2006). After running the NB GLM model for each moose, coefficients of each variable were assumed to be a random sample taken from a standard normal distribution. Using the mean and standard error, a t-statistic was calculated to test the likelihood of the coefficient's deviation from normality. Variable entry was permitted at P ≤0.15 (Sawyer et al. 2006). For significant variables, coefficients were averaged among all moose to create population-level RSF models.

After GLM coefficients were estimated for each RSF model, a log-linear model was used to calculate and spatially project the probability of use (w) for each 30 x 30 m raster cell. Coefficients (β_1) were multiplied by each cell (x_i) in the respective raster of predictor

variables $x_1 \ldots x_p$ as:

$$w(x) = \exp(\beta_0 + \beta_1 x_1 + \ldots + \beta_p x_p) \quad (4)$$

For easier visualization and comparison, the resulting raster values were scaled from 0-1 with a linear stretch with the following equation:

$$\hat{w} = \left(\frac{w(x) - w_{\min}}{w_{\max} - w_{\min}} \right) \quad (5)$$

where $w_{\min}$ and $w_{\max}$ represent the smallest and largest RSF values, respectively (Johnson et al. 2004). Relative probability of use values ($\hat{w}$) were classified using the common approach of identifying quartile breakpoints. The 25th, 50th, 75th, and 100th percentiles were assigned to low, medium-low, medium-high, or high habitat value classes, respectively. Alternatively, a map of continuous $\hat{w}$ values was maintained to present finer distinctions among RSF values.

RSF Model Validation

The winter and non-winter RSF models developed from locations of both years combined were evaluated using a 5-fold cross validation method (Boyce et al. 2002, Hirzel et al. 2006). The 23 moose were randomly partitioned into 5 groups (3 groups of 5 and 2 groups of 4). A RSF model was developed (Eq. 3) from moose within 4 groups (training set) and intersected with locations of moose in the withheld group (test set). This calibration and test procedure was performed 5 times, once for each training and test set combination. Estimated RSF models were projected to 30-m rasters (Eq. 4) that were classified into 20 equal area classes (vingtiles) occupying approximately 297 km^2. For each individual moose in the test group, a Spearman rank correlation coefficient (r_s) was calculated between the 20 model classes (i.e., 1, 2, 3, . . . 20) and the number of intersecting locations. The use of 20 bins, twice what Hirzel et al. (2006) recommended, was necessary to adequately separate locations among higher predictive classes and increased the sensitivity of the rank correlation. A good predictive model is defined as having high correlation (r_s >0.90; Boyce et al. 2002) since an increasing number of animal locations fall within higher model classes. An overall measure of model fit was assessed by averaging the 5 r_s values.

One-winter RSF models were evaluated with the independent sample of moose from the other winter, excluding 7 moose collared both winters. Similar to 2-winter models, 1-winter RSF maps were classified by vingtiles and the number of locations within each class was tallied. Spearman rank correlations were calculated between the numeric RSF model classes and the counts of locations. The lower classes containing no locations were assumed to be unsuitable habitat.

Because the exponential model can be an incorrect combination of estimated regression parameters and RSF models may not necessarily measure the absolute probability of use (Keating and Cherry 2004), further evaluation of 1-winter RSF maps was performed to determine if map predictions were indeed proportional to the likelihood of use. Within the portion of the study area identified as suitable moose habitat (occupied 2-winter RSF map vingtiles), the relative probability of use values ($\hat{w}$) of 1-winter RSF maps were reclassified into 10 equal-interval classes having values 0-1 at intervals of 0.1. The expected utilization value, $U(x_i)$, was then calculated as:

$$U(x_i) = \frac{A(x_i) * w(x_i)}{\sum_i w(x_i) * A(x_i)} \quad (6)$$

where $A(x_i)$ is the area and $w(x_i)$ is the RSF midpoint value of the ith class (i.e., 0.05, 0.15, 0.25, . . . 0.95; Boyce and McDonald 1999). The resulting $U(x_i)$ values describe the relative proportion of locations expected to occur within each of the 10 equal-interval classes, adjusted by area. The observed proportion of locations (N_i) from the other winter was calculated by dividing the frequency of

points within the *i*th class by the total number of points. A simple linear regression model of N_i vs. U_i was fit to assess the relationship between observed and expected observation frequencies. A RSF model that is relatively proportional to the probability of use has a high R^2 and slope not significantly different from 1 (Johnson et al. 2006).

Statistical analyses were performed in the open-source programming application R, version 2.4.0 (R Foundation for Statistical Computing 2006). RSF modeling was performed using the "glm.nb" routine in the "MASS" library.

Range Capacity Approximation

Spatial calculations based on predicted winter RSF values and observed home range sizes (Roloff and Haufler 1997, 2002) were performed to provide a rough approximation of potential moose range capacity. Winter home ranges were delineated using the 95% adaptive local convex hull (a-LoCoH) method with the Getz and Wilmers (2004) ArcGIS toolbox. This algorithm connects each GPS point with a convex polygon to all neighboring points "within a radius, *a,* such that the distances of all points within the radius to the reference point sum to a value ≤ to *a*" (Getz et al. 2007). The union boundary of these polygons is taken to represent the home range boundary. A winter a-LoCoH home range was delineated for each moose with multiple *a*, and the appropriate value was determined when the estimated range size increased towards asymptote. The performance of each home range polygon was also visually reviewed with respect to the spatial distribution of locations.

The 1-winter RSF model validated as best predictive of habitat use was used to explore how winter range size related to predicted home range quality. That model was applied to a 10 x 10 m raster with Eqs. 4 and 5. An overall home range "quality" was calculated by adding the relative probability of use values ($\hat{w}$) of raster cell within each moose a-LoCoH winter range. This number is equivalent to an arbitrary habitat units (HU) measurement, where 1 HU equals 1 ha at maximum resource potential ($\hat{w}$ = 1) (Plume and Roloff 2005). Accordingly, 1 HU can be achieved with 100 cells having $\hat{w}$ = 1, 200 cells having $\hat{w}$ = 0.5, or 400 cells having $\hat{w}$ = 0.25, and so forth.

Home range size was plotted against its HU value to evaluate whether an RSF-based spatial calculation was appropriate for making capacity approximations. A lack of correlation between the 2 values would tend to provide support to the approach. The HomeGrower application developed by Plume and Roloff (2005) was used to estimate the number of moose home ranges that the study area could conceivably support. Its algorithm places a large number of random seed points (e.g., > 20,000) on the habitat quality map (i.e., RSF) and "grows" a home range outward until the target HU with a defined minimum threshold is accumulated. A successful home range occurs when the total RSF value meets or exceeds the HU target value before a defined maximum home range size is reached. Iterations of the procedure are run and successes are tallied until the grid is filled to capacity with hypothetical home ranges. A range of potential capacity approximations was computed by adjusting the target habitat quality parameter based on the mean, 25% quartile, and 75% quartile of HU values. These same summary statistics of winter home range size, including the maximum, were used to define the maximum allowable home range size.

RESULTS

Habitat Models

Winter HSI model -- A winter HSI model based on classified Landsat satellite imagery indicated that the best moose habitat occurred alongside streams at low elevations below the forest boundary (Fig. 2). These extensive floodplain willow complexes were among the most accurately predicted areas of highly suitable winter habitat. In addition,

moose that wintered within riparian shrub or aspen communities were mostly found within higher HSI prediction regions. However, the HSI model was poorly predictive of all winter locations. Pooled observations did not occur at increasing frequency within cells having higher HSI value (r_s = 0.15), and approximately 50% of locations were in areas with HSI ≤0.5 (Fig. 2). Several moose occupied conifer forest or upland shrub cover types for a substantial part of winter, habitats classified as unsuitable winter range based on the input land cover parameters. Also, the HSI map produced questionable predictions of high suitability next to streams surrounded by rangelands at lower elevations. In fact, moose are rarely documented to occupy the 2 largest concentrations of predicted high quality winter habitat.

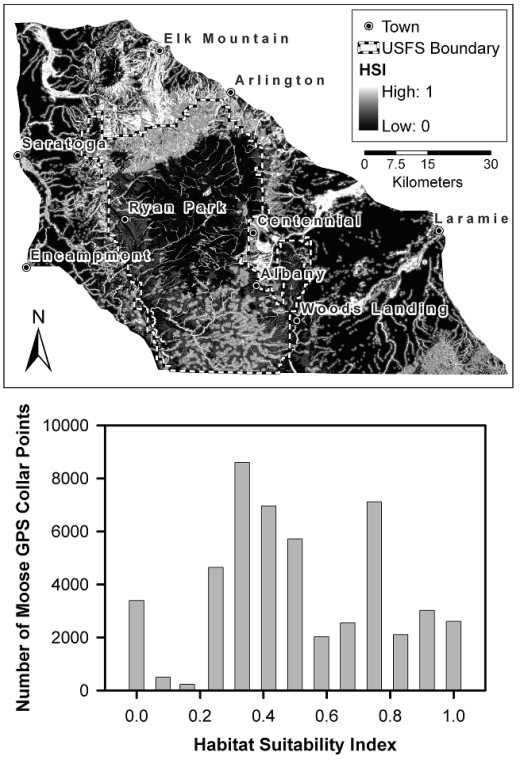

Fig. 2. Map of a preliminary winter habitat suitability index (HSI) model based on the influence of elevation, slope, distance to willow, food availability, and willow patch size in southeastern Wyoming. This HSI model was validated with GPS collar points collected on a sample of moose during winter 2005 (n = 7) and winter 2006 (n = 9).

Two-winter RSF model -- Movement of all moose became substantially limited the first week of January until mid-April; winter was thus defined as 1 January-15 April. A population-level winter RSF was first created from 48,992 locations obtained from 23 individuals during both winters; there were 1,656-1,665 locations/moose each winter.

Moose responded similarly to 4 predictor variables (Table 2). Distance to forest edge explained the most variance of habitat use, followed by distance to deciduous forest and distance to riparian shrub; slope and slope^2 were also significant variables. The model was applied to predict the probability of moose occurrence with Eq. 4 as:

$$w(x) = \exp\left(\begin{array}{l}-10.329 - 0.0024(DistToRipShrub) - 0.0035(DistToDecidForest) - \\ 0.0039(DistToForestEdge) + 0.0782(Slope) - 0.0042(Slope^2)\end{array}\right)$$

Cross validation of this model indicated that it performed well ranking the value of winter habitat. Locations of moose in 5 cross-validation sets occurred with increasing frequency among bins of higher RSF values, producing Spearman rank correlations of 0.972, 0.919, 0.962, 0.866, and 0.925 (r_s = 0.93). There were no moose observations in the lower 8 of 20 classes for any cross-validated model; therefore, approximately 40% of the study area could essentially be considered unsuitable winter habitat. If those unoccupied lower bins were ignored, 3 of 5 cross validation sets had r_s = 1.

One-winter RSF models -- Snow depth in 2005 averaged 87% of normal, ranging 82-90% at 4 SNOTEL sites distributed across the mountain range. In 2006, mean depth at these sites was 126% of normal, ranging 115-134% (USDA-NRCS 2007b). To account for this annual difference, separate RSF models were estimated for each winter using 26,607 locations obtained from 16 moose in 2005, and 22,385 points from 14 moose in 2006.

Table 2. Mean negative binomial regression coefficients (b), standard errors (SE), and significance level (P) from 4 seasonal population-level resource selection function (RSF) models created to predict moose distribution in the Snowy Range of the Medicine Bow Mountains in southeast Wyoming, December 2004 – August 2006. Models were applied to predict the probability of occurrence with the equation, $w(x) = \exp(b_0 + b_1x_1 + \ldots + b_px_p)$. Non-significant variables are identified as "ns".

	All Winter			Winter 2005			Winter 2006			Nonwinter		
	b	SE	P	b	SE	P	b	SE	P	b	SE	P
Intercept	-10.329	0.2664	<0.0001	-10.2939	0.4056	<0.0001	-10.5371	0.2977	<0.0001	-10.0327	0.2652	<0.0001
Dist. to Rip. Shrub	-0.0024	0.0009	0.0164	-0.0022	0.0013	0.0139	-0.0021	0.0007	0.0089	ns	ns	ns
Dist. to Decid. Forest	-0.0035	0.0009	0.0027	-0.0027	0.0009	0.0083	-0.0039	0.0012	0.0066	-0.0017	0.0004	0.0004
Dist. To Forest Edge	-0.0039	0.0012	0.0006	-0.0038	0.0013	0.0127	-0.0028	0.0015	0.0767	-0.007	0.0011	<0.0001
Focal Willow 1km.	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.0004	0.0001	0.0001
Slope	0.0782	0.0484	0.12	ns	ns	ns	0.1162	0.0401	0.0125	-0.0964	0.0293	0.0033
Slope^2	-0.0042	0.0016	0.0169	ns	ns	ns	-0.0045	0.0012	0.003	ns	ns	ns
Thermal Aspect	ns	ns	ns	0.3162	0.1458	0.0665	ns	ns	ns	ns	ns	ns

Moose generally responded in a similar fashion both winters to the same 3 distance variables identified as important in the 2-winter model (i.e., riparian shrub, deciduous forest, and forest edge) (Table 2). However, the thermal aspect variable better explained habitat use during winter 2005, whereas slope and slope^2 were significant predictors in winter 2006. A winter 2005 RSF map (Fig. 3) was produced with Eq. 4 as:

$$w(x) = \exp\left(\begin{array}{l} -10.2939 - 0.0022(DistToRipShrub) - 0.0027(DistToDecidForest) - \\ 0.0038(DistToForestEdge) + 0.3162(ThermalAspect) \end{array}\right)$$

A winter 2006 RSF map (Fig. 3) was produced with Eq. 4 as:

$$w(x) = \exp\left(\begin{array}{l} -10.5371 - 0.0021(DistToRipShrub) - 0.0039(DistToDecidForest) - \\ 0.0038(DistToForestEdge) + 0.1162(Slope) - 0.0045(Slope^2) \end{array}\right)$$

The resulting winter RSF maps for 2005 and 2006 were evaluated with the 7 and 9 independent moose of the opposing winter, respectively. In both cases, moose occupied areas classified as higher quality with greater frequency (Fig. 4). The locations of these independent moose occurred within the highest vingtile of the 2005 RSF map at 26-82% and at 24-69% for the 2006 model. The locations of 6 of 7 independent moose from 2006 increased as expected within 2005 RSF classes ($r_s = 1$), indicating that the winter 2005 model distinguished high probability use areas from less likely ones. Only 1 moose in winter 2006 did not increasingly occupy higher vingtile classes of the 2005 RSF map ($r_s = 0.369$). Similar predictive power was found for the winter 2006 model. Four of 9 moose from winter 2005 increasingly occupied higher RSF classes to produce $r_s = 1$; locations of 4 other moose produced $r_s > 0.8$. Again, locations of 1 moose occurred mostly within the lower prediction classes ($r_s = 0.53$).

The Johnson et al. (2006) test for a 1:1 relationship between observed and expected occurrence was applied to 60% of the study area that was determined suitable as moose habitat in the 2-winter RSF model. Within 10 new equal-interval map classes of the 1-winter RSF models, the proportion of observed moose locations (N_i) regressed against the expected proportion of locations (U_i) produced models with slopes different from 0 ($P < 0.0001$) with moderately strong fits (2005: $R^2 = 0.87$; 2006: $R^2 = 0.86$) (Fig. 5). This suggests the RSF models from each winter made sensible predictions of probability of occurrence. The slope of the regression line fitted to the winter

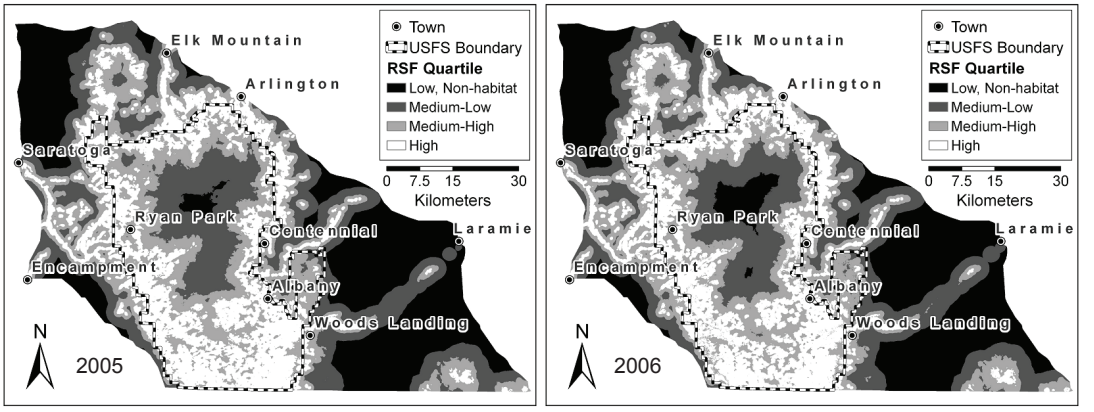

Fig. 3. Predicted quantile categories of probability of occurrence of moose in the Snowy Range of the Medicine Bow Mountains in southeast Wyoming during 2 winters of different snow depth: 2005 (left) was below average and 2006 (right) was above average snow depth. Maps represent the results of population-level resource selection function (RSF) models.

2006 RSF model bins was not different from 1 ($P = 0.009$); the 2005 regression model slope differed from 1 ($P = 0.226$). This indicates that some bins from the winter 2005 RSF were occupied by moose at a frequency different than expected from a model that is proportional to the probability of use. Therefore, the 2006 RSF model was considered to be a slightly better predictor of winter habitat use of the study moose.

Non-winter RSF model. -- The UD of 59,111 locations combined from both years during non-winter (16 April-31 December) was best explained by the total area of willow within a surrounding 1 km radius (Table 2). Distance to forest edge was the second most important predictor, with considerably stronger influence than during winter. Moose also occupied locations close to stands of deciduous forest, but the association was not as strong as in winter. Slope was also significant, with greater influence than in winter. This model was used to produce a non-winter RSF map with Eq. 4 as:

$$w(x) = \exp\left(\begin{array}{l} -10.0327 - 0.0021(FocalRipShrub1Km) - 0.0017(DistToDecidForest) - \\ 0.0070(DistToForestEdge) + 0.0964(Slope) \end{array}\right)$$

Areas predicted as high quality extended to higher elevation than during winter, but also included many areas of low elevation willow

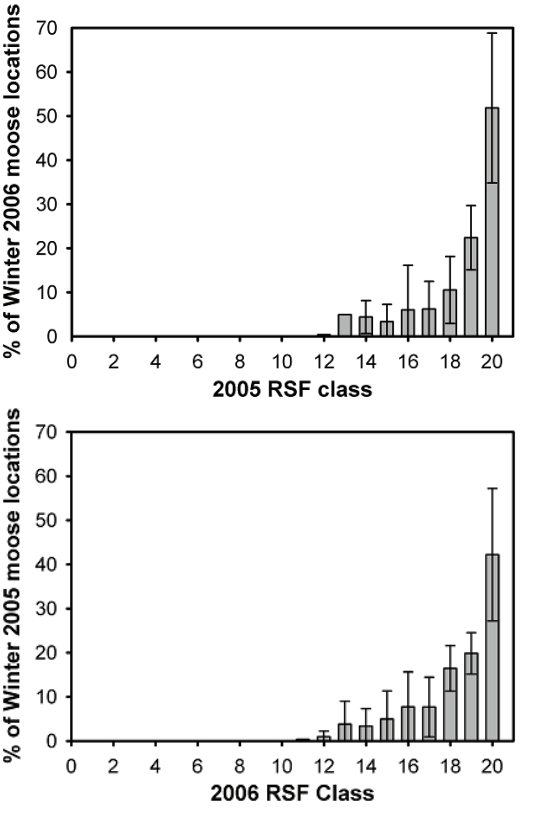

Fig. 4. Validation of winter 2005 and winter 2006 resource selection function (RSF) models of moose habitat capability in southeast Wyoming using locations of independent moose in the other winter (2005: $n = 7$, 2006: $n = 9$). Bars represent the mean percent and standard deviation of locations within 20 mapped equal area RSF classes during winter (1 January-15 April).

concentrations, overlapping with most floodplain winter ranges (Fig. 3).

The non-winter RSF map predicted non-winter locations well. Cross validation showed that locations of withheld test groups were strongly rank-correlated with RSF vingtile classes, having r_s values of 0.87, 0.98, 0.92, 0.91, and 0.97 ($\bar{r}_s = 0.93$). Similar to the winter models, approximately 40% (8 of 20 bins) of the study area calculated as having lower probability of use was not occupied by any moose in the 5 test groups.

Spatial Capacity Approximations

Predicted home range quality -- Winter a-LoCoH home range of 28 of 30 moose varied from 83-370 ha ($X = 213.8$, $SD = 81.9$). One bull each winter had an extensive home range (628 and 669 ha) that was composed of nearly twice the HUs of other sampled moose (189 and 186 ha). These 2 bulls were considered outliers for the purpose of defining winter habitat requirements of typical moose. Difference in range size between years was not observed among the entire sample ($t_{28} = -0.305$, $P = 0.763$), nor between paired 2-winter moose ($t_6 = 0.958$, $P = 0.188$). The 1-winter RSF model that included slope and slope^2, rather than the thermal aspect variable, was adopted for HomeGrower abundance approximation routines since it was similar to the winter 2006 model that was validated as slightly more robust. Based on those map predictions, HU totals among home ranges were 25-105 ($X = 55.4$, $SD = 21.3$). Home range size was not strongly correlated with predicted HU value ($r = 0.46$), generally supporting the hypothesis that cumulative habitat quality of home ranges does not depend on size. That is, larger home ranges necessarily included more poor quality habitat. Although variation among predicted home range quality was larger than expected, HU values were tightly clustered about the mean with over 50% of home ranges having 40-65 HUs.

HomeGrower estimates -- After confirming evidence of a habitat quality threshold defining moose winter home range, the HomeGrower application seemed a reasonable approach to generate an estimate of the study area carrying capacity. Among the HU totals of 28 home ranges, the 25% quartile, mean, and 75% quartile of 40, 55, and 65 HU, respectively, were used as target "habitat quality" levels. The maximum permissible size of simulated home ranges was tested at the 25% quartile (169 ha), mean (213 ha), 75% quartile (285

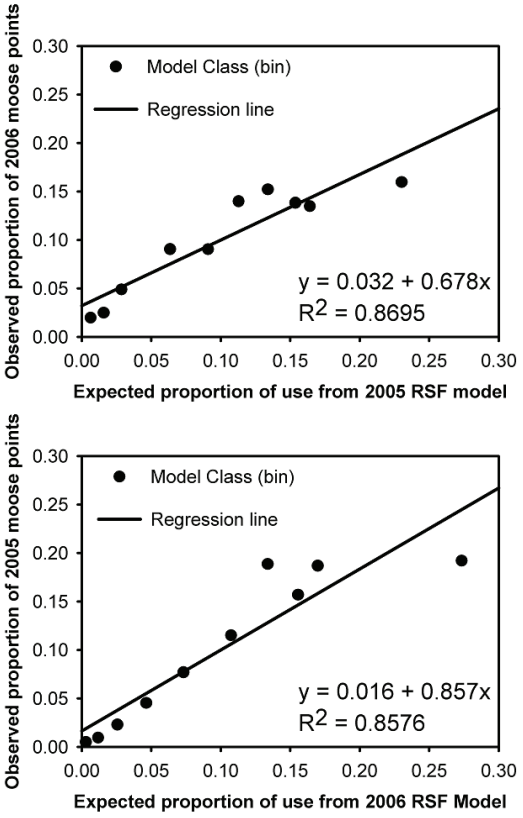

Fig. 5. Expected vs. observed proportion of moose locations within 10 equal interval resource selection function (RSF) classes (bins) for: (top) an independent sample of 7 moose from winter 2006 compared to predictions of a winter 2005 model, and (bottom) an independent sample of 9 moose from winter 2005 compared to predictions of a winter 2006 model. RSF model predictions are proportional to the probability of use if the fitted regression line has an overall goodness of fit (R^2) and is not significantly different from 1 (Johnson et al. 2006).

ha), and maximum (370 ha) levels.

The resulting 12 runs of the HomeGrower algorithm produced a wide range of home range tallies (114-791) (Fig. 6). If a moose winter home range can be defined as requiring only HU <40, as observed for 25% of collared moose, carrying capacity of the study area was >500 moose. However, when the HU threshold was adjusted higher to the mean predicted winter home range quality (55 HU), capacity approximations were substantially less (250-550 moose) depending on the maximum permissible home range size. Since every moose is not energetically capable of occupying the maximum observed winter home range size or competing for the highest quality habitats, a realistic maximum home range size may be represented by the mean or 75% quartile and an average habitat quality threshold. Given those parameters, the carrying capacity estimate was 400-500 moose (Fig. 6).

DISCUSSION

The reliability of a species-habitat relationship model depends explicitly on the accuracy of the land cover base map (Roloff and Kernohan 1999). Presumably, the poor predictive ability of the preliminary winter HSI model was largely due to classification error of land cover. Substantial misclassification occurred with the Landsat image from which 3 of 5 variables were derived. For example, there was systematic error within a large forested region where pixels within conifer stands were frequently classified as mixed forest, producing inflated HSI values. Also, irrigated agricultural land uses were often confused as riparian shrub communities and calculations of willow patch size falsely assigned high suitability to small groups of misclassified riparian shrub pixels. Because patches of vegetation were repeatedly occupied, locations typically occurred as clusters in localized areas and often near forest edges. Thus, hundreds of locations potentially intersected pixels that were either misclassified or confused with adjacent cover types. We conclude that using satellite-based vegetation

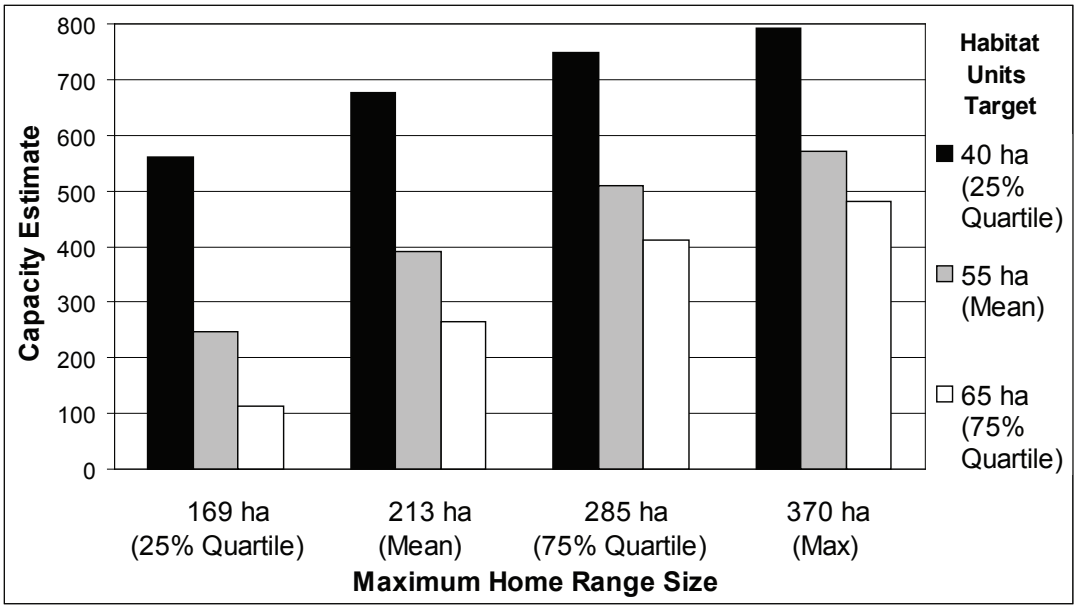

Fig. 6. Estimated range capacity approximations for moose in the Snowy Range of the Medicine Bow Mountains, Wyoming, 2005-2006. Estimates are derived from the HomeGrower algorithm (Plume and Roloff 2005) given different values of 2 key input parameters, a habitat units target, and the maximum home range size. A habitat unit is equal to 1 ha of maximum resource potential (RSF = 1).

maps with highly resolved GPS locations can be troublesome without improved classification of vegetative cover.

The incorporation of distance functions into RSF models greatly improved preliminary RSF models estimated with categorical land cover variables, because a fine scale gradient of habitat quality is perceived by animals (Arlt 2007). Distance variables were quite accurate since willow and aspen patches were easy to distinguish on the CIR orthophotographs, although error still exists with digitized features (Corsi et al. 2000, Dussault et al. 2001); for example, small patches of willow and aspen were obscured by conifer forest and not digitized. The 2006 winter locations of a cow and calf were not within an area defined as high quality winter habitat by the winter 2005 RSF model. The relatively open, north-facing lodgepole pine was too distant from riparian shrub, deciduous forest, and forest edge to be calculated as high RSF. If small aspen clones and Scouler willow nearby were identified, their winter habitat selection would have corresponded to prediction.

The predictive ability of species-habitat models requires inclusion of variables that are related directly to the mechanisms involved in habitat selection (Corsi et al. 2000). Models created from locations in both winters were similar in their estimated coefficients for distance to riparian shrub, deciduous forest, and forest edge (Table 2). These seem to be valid predictors since concentrations of important browse species in proximity to thermal cover determine quality of foraging and resting habitat (Allen et al. 1987, Courtois and Beaumont 2002, Dussault et al. 2005b). The combination of these variables with either slope or thermal aspect accounted for the distribution of willow, subalpine fir, mountain mahogany, and antelope bitterbrush in proximity to forest cover. The non-winter RSF model explained the nearly exclusive importance of riparian shrub habitat and nearby thermal cover across a wider range of elevations than in winter.

Accurate delineation of willow communities was critical to developing robust predictive maps because willow is the key winter forage constituting approximately 60% of the diet (Baigas 2008), and is probably >90% of the summer diet (McMillan 1953, Zimmermann 2001, Dungan and Wright 2005). During winter 50% of moose occupied a willow community >25% of the time, and >50% of winter locations of 19 of 23 moose (83%) were within 200 m of a riparian shrub patch. However, the other 4 moose rarely utilized willow (<5% locations) during winter; distance to forest edge, distance to deciduous forest, and thermal aspect were more influential. Two cows did not winter in riparian willow habitat; instead, they appeared to use/forage mostly on bitterbrush or serviceberry. In non-winter every moose spent >36% time in riparian shrub habitat ($\bar{X}$ = 52%), apparently exploiting the highest concentrations of willow.

Subalpine fir was the second most important winter forage (Baigas 2008), as also found in Yellowstone National Park (Tyers 2003) and to a lesser degree in Montana (Knowlton 1960, Dorn 1970, Stevens 1970). Subalpine fir grows mainly in association with aspen at elevations (~2,400-2,800 m) below the spruce-fir forest type in the Snowy Range that corresponded remarkably well with winter locations. Distance to deciduous forest at this elevation did not exceed 1 km, the threshold distance at which univariate RSF = 0. Most (80%) winter locations were <200 m from deciduous forest where univariate RSF was >0.5. No moose moved higher during winter to forage on fir within spruce-fir stands (WGFD 1990). Although elevation is an important predictor of moose habitat in the Rocky Mountains (Stevens 1970, Pierce and Peek 1984, Van Dyke 1995) due to snow depth and thermal influence (Poole and Stuart-Smith 2006), it did not influence the seasonal distribution of moose in the RSF models. Rather, distance to deciduous forest explained much of the same variation in habitat use, being collinear

enough with elevation (r = 0.68) to prevent model convergence.

Elevations occupied in non-winter and winter were similar for most moose, making distance to deciduous forest a significant year-round predictor of habitat use; however, the effect of this variable was less during non-winter (Table 2). Ten moose (43%) in winter had >50% locations within 50 m of a deciduous forest stand, compared to 2 moose (9%) in non-winter. Therefore, an important distinction between seasonal models was that higher non-winter RSF values occurred at slightly higher elevations where deciduous forest is absent. Many studies in the region report that moose move to higher elevations during summer (Knowlton 1960, Halko et al. 2001, Poole and Stuart-Smith 2006), most likely to alleviate heat stress. Non-winter ranges of 2 moose were as high as 3,000 m and the largest seasonal elevational transitions were by moose that moved to higher elevations during summer. However, the mean winter elevation used by 7 of 23 moose (30%) was actually higher than their mean non-winter elevation. In 2005 one cow summered among tall floodplain willow complexes at ~2,400 m outside the forest, yet wintered at >2,800 m within the forest foraging on 1.5-2 m willow, underscoring the importance of high biomass, tall willow complexes during the growing season. Interestingly, in winter 2006 with deeper snow she occupied predominately forest habitat between her 2005 seasonal ranges.

Moose were close to forest edges at all times, more so than deciduous forest or riparian shrub communities. This association with forest edge could lead to the conclusion that fragmentation in the MBNF has benefited moose since a preference for edge habitat is widely reported across most of the boreal forest (Mastenbrook and Cumming 1989, Thompson and Stewart 1998), northwest Montana (Costain 1989, Matchett 1985), southeastern British Columbia (Poole and Stuart-Smith 2006), and Washington (Base et al. 2006). However, clearcuts with little or no browse regeneration are not utilized (Matchett 1985) and it is uncommon for site conditions in the southern Rocky Mountains to favor abundant browse production following harvest. Habitat use during winter was rarely near edges of timber harvests, as only 1 bull and 2 cows occupied clearcuts and only 1-2.5% of time; data from Colorado are similar (Kufeld and Bowden 1996). The preferred winter ecotone provided by edge was that between mature forest cover and upland or riparian shrub communities. However, it does appear that some moose were attracted to clearcuts >15 years old in August-October, particularly those adjacent to riparian areas with the requisite timber buffer (>100 m; USFS-MBNF 2004).

The influence of solar radiation on use of south- and west-facing slopes has been previously reported (Langley 1993, Halko et al. 2001). The effect was greater during the year with less snow pack and presumably reflects higher availability of low-growing mountain shrub communities. However, while the significance of the thermal aspect differed between years (2005: P = 0.067, 2006: P = 0.163), the difference in pattern of use between aspects was less apparent. All moose used warm (south- or west-facing) aspects >50% of time in winter 2006, but 3 moose occupied cool (north- or east-facing) aspects more in winter 2005. The significance of thermal aspect in winter 2005 was probably due to 5 moose occupying warm aspects >75% of time, whereas only 1 moose made such exclusive use of warm slopes in winter 2006. Although the 2005 winter RSF model that included thermal aspect was less predictive than models with slope and slope^2, the influence of solar insolation on snow depth and vegetation certainly influences moose distribution in the Snowy Range.

Moose generally used slopes up to 20º during winter; use declined with increasing frequency on steeper slopes. The influence of slope was less consistent during winter

2005 and was not included in the RSF model. That winter 7 of 16 moose (44%) used slopes between 0-5º most, and others occupied 5-10º slopes. In 2006, 11 of 14 moose (79%) were found most often on 5-10º slopes. The mean slope occupied by moose was 7.1º in 2005 and 9.3º in 2006; fewer observations were in flat areas (i.e., drainage bottoms) in 2006. The quadratic term of slope in the 2005 RSF had the effect of increasing suitability values to a maximum about 13º; suitability declined to 0 at approximately 40º. Underneath this curve all locations with slope <24º had univariate RSF >0.5. Lower slopes were occupied most frequently in non-winter because stream corridors were the preferred habitat, producing a model with highest suitability values in riparian areas.

A difficulty with species distribution modeling is that models based on a single population or landscape may not necessarily translate well to other situations (Boyce and Waller 2003, Apps et al. 2004), particularly if habitat preferences are not fixed in moose (Osko et al. 2004). The application of this model across Shiras moose range would be complicated by local resource availability (Mysterud and Ims 1998), land management activities that produce habitat variation, as well as competition, weather, predation, and harvest (Peek 1998). These processes may influence distribution at different scales (Dussault et al 2005b, Dussault et al. 2006) leading to locally poor performance of a large-scale model. Accounting for such parameters should improve model accuracy and enhance the applicability of a model.

The habitat quality values predicted by RSF models were assumed to correspond to the energetic efficiency of different habitat situations since they result from occupancy patterns of many individual moose. However, Saether and Andersen (1990) demonstrated that when moose are not able to select patches of highest quality, they modify their behavior to adapt to local conditions. The intensity of use (i.e., UD) may only describe the relative habitat value of different sites (North and Reynolds 1996), which could explain the wide variation observed in predicted home range quality. Other factors contributing to the observed 4-fold variation in home range size probably include maternal influences, sex, age, body size, health status, and a variety of unmeasured environmental influences. Nonetheless, the total predicted RSF values within winter ranges did not tend to increase with home range size; larger ranges incorporated more area of "low quality" resources. Dussault et al. (2005a) also found a negative relationship between food availability and a wide range of moose home range sizes during winter, and this relationship has also been reported for several mammalian species (Litvaitis et al. 1986, Ims 1987, Jones 1990, Tufto et al. 1996, McLoughlin and Ferguson 2000, Mitchell and Powell 2007).

The spatial approach to carrying capacity produced variable estimates, but were as accurate as those of a forage-based model that calculated willow production in North Park, Colorado (Kufeld and Steinert 1990) that had ~15% more riparian shrub habitat than our study area. Carrying capacity was estimated at ~1,800 animals (>29 moose per km^2), an obvious overestimation indicating that moose are not limited by availability of willow browse, and the difficulty of estimating carrying capacity from browse availability and consumption data. Because of variation in plant and animal nutrition (Hanley and McKendrick 1983), estimates of ungulate carrying capacity based on forage production and a nutritionally optimal diet are often tenuous (Hanley and Rogers 1989).

MANAGEMENT IMPLICATIONS

Moose are difficult to manage in Wyoming due to their solitary nature, low density, and preference for forest habitat. Our habitat models are useful to identify core areas critical for survival of moose in the southern Rocky

Mountains. Such locations include montane riparian willow galleries surrounded by forest, the bottoms of foothill drainages as they exit forested cover, the steep south- and west-facing hillsides above those drainages, aspen stands encroached by subalpine fir, and floodplain willow communities. This information should be useful to improve the efficiency of population sampling and to identify critical habitats for monitoring.

Although the empirical RSF models may be statistically objective in their explanation of habitat associations, a certain degree of subjectivity is necessary to apply them in other areas. Habitat models by nature cannot include every relevant parameter, and population density and habitat use are not always related to one defined set of predictor variables. Therefore, the RSF models described here may be difficult to apply directly to other areas, especially where such resolved vegetation data layers are not available. However, the relationships among cover, riparian shrub, and deciduous forest are probably similar for many other Rocky Mountain moose populations.

There exist at least as many "carrying capacities" as there are management objectives (Heady 1975). A population biologist seeks to reach a balance where the public and landowners are satisfied with animal numbers, while important habitats are sustained for biodiversity. The moose population in the Snowy Range has experienced an irruptive growth phase in the past 20 years, and arguably, will be regulated increasingly by nutritional constraints from competition and decline in forage resources. Although body condition and reproductive health of animals handled in this study do not indicate such conditions exist currently, high use of preferred browse exists in the study area. Poor range condition has often been implicated as the cause of population declines, and a fine-scale, habitat-based approach has long been recommended to manage moose populations (Timmermann and Buss 1998). A conservative management strategy would be to assume that moose have reached capacity in the Snowy Range, and the population should be maintained at a sustainable level relative to key habitats identified in this study.

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