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HABITATS OCCUPIED BY ELK (*CERVUS ELAPHUS*) IN DESERT GRASSLAND–SCRUBLANDS OF NORTHWESTERN NEW MEXICO

LOUIS C. BENDER,* ROGER A. BALDWIN, AND JESSICA R. PIASECKE

Extension Animal Sciences and Natural Resources, New Mexico State University, P.O. Box 30003 MSC 3AE, Las Cruces, NM 88003 (LCB)
Department of Animal and Range Sciences, New Mexico State University, Las Cruces, NM 88003 (RAB)
Department of Fisheries and Wildlife, New Mexico State University, Las Cruces, NM 88003 (JRP)
**Correspondent: lbender@nmsu.edu*

ABSTRACT—We studied habitat relationships of elk (*Cervus elaphus*) at scales of landscape, home range, and site on and adjacent to Chaco Culture National Historical Park, San Juan and McKinley counties, New Mexico. Across scales, use of habitats was driven by needs for cover. Pinyon–juniper and rocky habitats were used most often. Accrual of body fat was related most strongly to lactation and precipitation but also was influenced by several habitats, most strongly by semi-desert shrub-steppe. Habitats positively related to accrual of body fat were used less than available at scales of landscape and home range. Conversely, habitats preferentially included and used in home ranges were related negatively to accrual of body fat, further highlighting the importance of cover. At the level of site, feeding sites had greater cover by shrubs ($\geq$23% versus <12%) and grass–forbs (>25% versus <11%) than did bedding sites, whereas bedding sites had higher overstory cover ($\geq$46% versus $\leq$4%). Bedding sites most frequently were under pinyon or juniper trees or rocky overhangs and caves. Activity during midday was avoided when mean high temperatures exceeded thermal tolerance. Aspect and distance to roads, streams, or water did not affect distribution, but presence of elk was associated positively with higher elevations in some years.

RESUMEN—Estudiamos las relaciones del hábitat del alce (*Cervus elaphus*) a las escalas de paisaje, ámbito hogareño y sitio en el Chaco Culture National Historical Park y sus cercanías en los condados de San Juan y McKinley en Nuevo México. A través de las escalas, el uso de hábitats fue dirigido por necesidades de cobertura. Áreas de piñón–junípero y hábitat rocoso fueron los usados más frecuentemente. La acumulación de grasa corporal se relacionó más fuerte con la lactancia y precipitación, pero también fue influenciada por varios hábitats, más fuerte por la estepa arbustiva semi-desértica. Los hábitats que se relacionaron positivamente con la acumulación de grasa corporal fueron usados menos que su disponibilidad a la escala de paisaje y ámbito hogareño. A la inversa, los hábitats preferencialmente incluidos y usados en los ámbitos hogareños fueron relacionados negativamente a la acumulación de grasa corporal, destacando aún más la importancia de la cobertura. A nivel de sitio, los sitios de alimentación tuvieron mayor cobertura por arbustos ($\geq$23% versus <12%) y pastos-matorrales (>25% versus <11%) que los sitios para dormir, mientras que los sitios para dormir tuvieron mayor cobertura de dosel ($\geq$46% versus $\leq$4%). Los sitios para dormir se encontraban más frecuentemente bajo árboles de piñón o junípero o en salientes rocosas y cuevas. La actividad durante el mediodía fue evitada cuando el promedio de la temperatura máxima excedía la tolerancia termal. El aspecto y la distancia a caminos, arroyos, o agua no afectaron la distribución, pero la presencia del alce estuvo asociada positivamente con elevaciones más altas en algunos años.

Elk (*Cervus elaphus*) have flexible habitat requirements, although usually associated with rugged mountains or canyons containing forests and grasslands (Skovlin et al., 2002). Southwestern deserts and other arid habitats historically were considered marginal for elk (Skovlin et al., 2002). Presumed detriments of arid habitats included scarcity of water, low quantity and quality of forage, lack of vegetative cover, and thermal stress. These potentially result in nutritive deficiencies, dehydration, high thermoregulatory costs, and increased risk of predation and harvest (Young, 1988; Skovlin et al., 2002). Colonization and continued use of arid habitats by elk, i.e., in Washington (McCorquodale et al., 1986), Texas (Carpenter and Silvy, 1991), Idaho (Strohmeyer and Peek, 1991), and Wyoming (Sawyer et al., 2007), suggest that many arid environments have sufficient forage and water. Moreover, security cover also may be less critical in areas where disturbance by humans is low (McCorquodale et al., 1986; Merrill, 1991).

In about January 2000, the area on and around Chaco

Culture National Historical Park, San Juan and McKinley counties, New Mexico, was colonized by ca. 20 elk that immigrated into the area. The area is primarily desert grassland–scrublands, and this population subsequently increased at ca. 15%/year (Bender and Piasecke, 2010). While many studies have been conducted on movements and use of habitats (i.e., Skovlin et al., 2002), little is known of habitat relationships in southwestern desert grassland–scrublands or the suitability of such areas for elk because of the infrequency of occurrence in these and other arid habitats (Carpenter and Silvy, 1991). Further, of the studies conducted in arid ranges (McCorquodale et al., 1986, 1989; Carpenter and Silvy, 1991; Strohmeyer and Peek, 1996; Sawyer et al., 2007), each looked primarily at distributional patterns and none assessed how presence in, or use of, these habitats affected fitness. Thus, our goals were to document habitat relationships of elk and identify factors associated with fitness in these habitats. Our specific objectives were to determine selection of habitats at the levels of landscape and home range, to identify key features at the level of site, to identify other features of habitats that affect distribution, and to identify factors in habitats associated with condition and fitness.

MATERIALS AND METHODS—Our study area covered ca. 308 km^2 on and adjacent to Chaco Culture National Historical Park in northwestern New Mexico, centered at ca. 36°00′N, 108°00′W. Elevations were 1,670–2,079 m, and topography was rolling plains and mesas interspersed with steep canyons. Average high temperature in July was 32°C, and average low temperature in December and January was −11°C. Average annual precipitation was 23 cm, with 52% falling in July–October, and average annual snowfall was 37 cm.

Dominant plants on mesas were four-wing saltbush (*Atriplex canescens*), rubber rabbitbrush (*Crysothamnus nauseosus*), mountain mahogany (*Cercocarpus intricatus*), winterfat (*Ceratoides lanata*), galleta grass (*Hilaria jamesii*), blue grama (*Bouteloua gracilis*), Indian ricegrass (*Oryzopsis hymenoides*), bigelow sage (*Artemisia bigelovii*), pinyon pine (*Pinus edulis*), one-seed juniper (*Juniperus monosperma*), and Utah juniper (*J. osteosperma*). Vegetation of canyons descending from mesas included mound saltbush (*Atriplex obovata*), galleta grass, blue grama, alkali sacaton (*Sporobolus airoides*), bigelow sage, winterfat, Mormon tea (*Ephedra*), and one-seed juniper. Vegetation in large washes included four-wing saltbush, galleta grass, giant dropseed (*S. giganteus*), sand dropseed (*S. cryptandrus*), saltcedar (*Tamarix pentandra*), willows (*Salix*), and cottonwoods (*Populus*). Only ca. 15% of the type of ecosystem represented by Chaco Culture National Historical Park remains intact in North America (Ricketts et al., 1999).

We captured adult females by darting them from a Bell 206B Jet Ranger helicopter (Bell Helicopter Textron, Inc., Hurst, Texas) using carfentanil citrate and xylazine hydrochloride in April and November 2003–2006. We blindfolded elk to minimize stress during handling and administered penicillin, vitamin B, vitamin E–selenium, and an 8-way *Clostridium* bacterin to alleviate stress of being captured. We radiocollared each with a VHF collar (Advanced Telemetry Solutions, Asanti, Minnesota) with unique numbered markers attached.

We located each radiocollared elk from the ground ≥1 time/week, both diurnally and nocturnally, during June 2004–June 2007. When located, we recorded location, size and composition of group, type and structure of habitat, and behavior (e.g., bedded, feeding, moving). We recorded locations with a handheld GPS unit and plotted these using the geographic information system software package ArcMap 9.1 (Environmental Systems Research Institute, Redlands, California).

We delineated habitats from the United States Geological Survey, Southwest land-cover-classification coverage (http://fws-nmcfwru.nmsu.edu/swregap). We reclassified the original 57 habitats into eight habitats that reflected the general composition of communities in the study area and comprised >0.001% of the study area. These eight habitats were used in our analyses.

We calculated 95% minimum convex polygons (Mohr, 1947) for each elk annually and for locations recorded during spring–autumn (April–November) and a composite 100% minimum convex polygon with a 2.5-km buffer from all locations pooled to define the overall area used. We used the combined 100% buffered area of home range using the minimum convex polygon to define the study area in terms of available habitats. We compared the proportion of habitats within annual home ranges with the proportion of habitats available in the study area (i.e., selection of landscape). We took the resultant difference by habitat for each elk and randomly selected with replacement $n = 10,000$ combinations of difference values (Bender et al., 2007). We then averaged each bootstrap replicate and used the $n = 10,000$ mean-difference values to create a frequency distribution of differences. We ranked the frequency distribution and excluded the extreme 500 values from each tail to develop 90% bootstrap confidence intervals for the mean difference for each habitat. If the confidence interval included 0, elk were distributed randomly with respect to that habitat. We also calculated selection ratios (percentage of habitat in home range:percentage of habitat available in the study area) for habitats overrepresented or underrepresented in home ranges. For selection ratios, a value >1 indicated selection, whereas a value <1 indicated avoidance.

We also compared proportions of locations with proportional availability of habitats within home ranges annually and in spring–autumn (i.e., selection of habitat). We also determined overuse and underuse as described.

At each location, we classed habitats by dominant species and structure of vegetation. We classed habitats around bedding and feeding sites (selection of site; Johnson, 1980) by visually estimating percentage of overhead cover (cover above a standing elk), percentage shrub cover, and percentage herbaceous (grass–forb) cover within a radius equal to approximate length of body of an elk from the center point of the bedding or feeding station. We assessed each component of cover from the exact bedded or standing position of the elk and used ocular estimates because structure of vegetation was simple enough that rapid ocular assessments produced similar data to transect-based methods ($r > 0.8$) and precluded the need to carry sampling equipment on surveys conducted on foot. We estimated visual obscurity or vertical cover for bedding sites by estimating the percentage of a bedded elk obscured by vegetation or other factors from an above-ground height of ca.

1.5 m averaged over the four cardinal directions. We estimated all variables of cover on a scale of 1–100%. We compared proportions of each class of cover within bedding and feeding sites using the Kruskal–Wallis analysis of variance (ANOVA; Zar, 1996). We also modeled size of groups at feeding and bedding sites as a function of proportions of cover for each type of cover using linear regression (Zar, 1996). We compared proportions of feeding observations by time of day between the time of highest ambient temperatures (from 3 h after sunrise to 3 h before sunset) and the remainder of the day to assess behavioral responses to high ambient temperatures in desert habitats. For this, we compared months (i.e., June–September) when mean daily high temperatures exceeded thermal tolerance of elk (26.5°C; Parker and Robbins, 1983) against all other months (October–May) using Fisher's exact test (Zar, 1996).

Using methods of Cook (2000), we used a SonoVet 2000 ultrasound (Samsung Medison, Seoul, South Korea) with a 5-mHz probe to measure thickness of subcutaneous fat along a straight line midway between the spine, at its closest point to the coxal tuber and ischial tuber (thickness of subcutaneous fat) of each elk at capture. Also following Cook (2000), we determined a rump–body-condition score by palpation of the soft tissue of the rump near the base of the tail and scored rump–body condition from standards that ranged from 1 (emaciated) to 5 (obese) in intervals of 0.25. As outlined by Cook et al. (2001), we combined rump–body-condition score and thickness of subcutaneous fat into an index, where the index equaled the rump–body-condition score when thickness of subcutaneous fat was <0.3 cm and equaled (thickness of subcutaneous fat minus 0.3) plus the rump–body-condition score when thickness of subcutaneous fat was ≥ 0.3 cm, and estimated percentage of body fat from the index using body fat equals -7.1527185 plus 7.323081 times the index minus 0.98980456 times the index^2 plus 0.057445567 times the index^3.

We used analysis of covariance (ANCOVA; Zar, 1996) to explore relations between levels of body fat and characteristics of the annual home range while accounting for status of lactation. We used ANOVA (Zar, 1996) to explore relations between size and characteristics of home ranges annually and in spring–autumn, including proportions of habitats. We included annual (based on calendar January–December and biological June–May years) and seasonal (seasons corresponding with important periods of life history) precipitation in models of body fat and size of home range. Periods of life history included: conception through parturition, January–June; primary lactation, June–August; and post-primary lactation through senescence of forage, September–November.

We modeled presence of elk using Maximum Entropy 3.1 (Phillips et al., 2006) to identify attributes of habitats associated with presence. This approach uses known locations to determine important attributes of habitats, thereby eliminating the need for data on absence and provides a less-biased alternative to other approaches that require generation of non-use areas (Baldwin and Bender, 2008). We modeled variables shown to affect distribution (Skovlin et al., 2002), including elevation, distance to roads, distance to sources of water, distance to streams, slope, and aspect.

We compared models using receiver–operating-characteristic plots to assess relative performance and to establish thresholds for identifying the likelihood of a site being used by elk (Phillips et al., 2006). The receiver–operating-characteristic plot is a plot of sensitivity and specificity (specifically, 1 minus specificity), with sensitivity representing how well the data correctly predict presence, while specificity provides a measure of correctly predicted absences (Fielding and Bell, 1997). We then used the area-under-the-curve to assist in selecting the most-appropriate model (Fielding and Bell, 1997; Phillips et al., 2006). Area-under-the-curve provides an index of accuracy of models; values range from 0.5 to 1.0 with values of 0.5 indicating no fit greater than that expected by chance alone, and models with area-under-the-curve >0.7 indicate good fit (Swets, 1988). We used 30% of locations as testing data to approximate standard errors around area-under-the-curve scores. We used the critical-ratio test outlined in Pearce and Ferrier (2000) to compare the general model (containing all variables) to simpler models to determine if the increase in explanatory value was significant at $\alpha = 0.05$. Because models were constructed using the same data, Spearman's rank correlation coefficients were calculated between competing models and were incorporated into the critical-ratio test (Pearce and Ferrier, 2000). We identified thresholds and direction of effect of significant variables of habitats on distribution (Baldwin and Bender, 2008). Because maximum entropy is an exponential model, the probability assigned to a pixel is proportional to the exponential of the selected combination of variables; thus, allowing construction of response thresholds and curves to illustrate the effect of selected variables on probability of use (Phillips et al., 2006).

RESULTS—We monitored 16–24 radiocollared adult females annually during 2003–2006. Extensive aerial surveys indicated that size of annual samples included virtually all adult females in the population (Bender and Piasecke, 2010). We obtained a total of 657, 814, and 984 locations in 2004, 2005, and 2006, respectively, with a range of 3–89 locations/elk annually. Lower values were for elk caught in November that had few opportunities to be detected before the end of December and, thus, were not included in analyses of home range or distribution for that year.

Mean annual size of home range calculated using the 95% minimum convex polygon varied ($F_{2,49} = 4.2$; $P = 0.021$), with home ranges in 2005 (112.4 km^2; $SE = 12.2$; $n = 21$) and 2006 (101.8 km^2; $SE = 5.7$; $n = 24$) being larger than those in 2004 (60.3 km^2; $SE = 12.4$; $n = 7$; $P \leq 0.023$). The sample for size of annual home ranges was small in 2004 because only seven of 17 elk had locations for January–March. Size of home range in spring–autumn varied ($F_{2,59} = 13.7$; $P < 0.001$) among years: 2005 (118.4 km^2; $SE = 12.6$; $n = 21$) $>$ 2006 (85.9 km^2; $SE = 7.5$; $n = 24$) $>$ 2004 (47.0 km^2; $SE = 4.6$; $n = 17$; $P \leq 0.012$).

Semi-desert grassland (34% of landscape), semi-desert shrub–steppe (31%), and pinyon–juniper woodland (15%) were the three most common habitats (Table 1). Inclusive of years, home ranges had more pinyon–juniper (selection ratio = 1.8–2.4) than was present on the landscape and less sagebrush shrubland (selection ratio = 0.4–0.9), semi-desert grassland (selection ratio = 0.5–0.7), and semi-desert shrub-steppe (selection ratio = 0.8–0.95; Table 1). Barren rocky habitats (selection ratio = 1.9–2.6) also were included consistently in home ranges signifi-

TABLE 1—Differences and 90% confidence intervals (CI) between proportional composition of the landscape and annual home ranges of elk (*Cervus elaphus*) around Chaco Culture National Historical Park, San Juan and McKinley counties, New Mexico, 2004–2006; asterisks indicate significant differences ($P < 0.10$).

		2004			2005			2006		
Habitat	Landscape	Annual home range	Difference	90% CI	Annual home range	Difference	90% CI	Annual home range	Difference	90% CI
Barren rocky	0.064	0.167	+0.103*	0.090 to 0.118	0.130	+0.066*	0.050 to 0.084	0.123	+0.059*	0.049 to 0.070
Pinyon–juniper woodland	0.147	0.346	+0.200*	0.157 to 0.241	0.275	+0.129*	0.092 to 0.164	0.266	+0.120*	0.102 to 0.144
Sagebrush shrubland	0.079	0.029	−0.050*	−0.054 to −0.045	0.054	−0.025*	−0.033 to −0.016	0.069	−0.010*	−0.017 to −0.002
Mixed salt-desert scrub	0.021	0.024	+0.003	−0.001 to 0.006	0.022	+0.002	−0.0004 to 0.0036	0.025	+0.005*	0.003 to 0.007
Semi-desert shrub-steppe	0.313	0.241	−0.072*	−0.088 to −0.052	0.254	−0.060*	−0.075 to −0.046	0.298	−0.015*	−0.028 to −0.002
Semi-desert grassland	0.343	0.167	−0.176*	−0.213 to −0.135	0.215	−0.127*	−0.161 to −0.091	0.231	−0.111*	−0.139 to −0.096
Riparian woodland	0.003	0.003	0	<−0.001 to <0.001	0.003	<0.001*	<0.001 to <0.001	0.003	<+0.001*	<0.001 to 0.001
Greasewood	0.032	0.024	−0.007	−0.016 to 0.002	0.047	0.015*	0.006 to 0.024	0.036	+0.004	−0.005 to 0.011

cantly more than their occurrence in the landscape (Table 1). These habitats were associated primarily with bedding sites. Other habitats were included in home ranges in excess or less than their availability, but these were generally minor components of home ranges (Table 1).

Numbers of locations of elk in each habitat were similar among years (Fisher's exact $P = 0.441$). Because of limited numbers of locations per habitat each year, we pooled locations over years and used mean composition of annual and seasonal home ranges to identify patterns of preference. We further combined habitats into six classes that reflected all observed locations: pinyon–juniper; grass–forb (desert grasslands and grass–forb areas <0.5 ha in other habitats); desert shrub (shrub-steppe and desert scrub); sagebrush shrublands; riparian; and barren rocky. Elk were located in pinyon–juniper (selection ratios = 1.4–1.5), grass–forb (selection ratios = 1.2–1.4), and riparian (selection ratios = 47–54) habitats more frequently ($P < 0.100$) than expected annually and during spring–autumn based on availability of these habitats within home ranges (Table 2). Conversely, elk were located less frequently ($P < 0.100$) than expected in desert shrub (selection ratios = 0.30), sagebrush shrublands (selection ratios = 0.40), and barren rocky (selection ratios = 0.4) habitats.

Percentage ground cover varied among feeding and bedding sites in 2005 ($H_5 = 151.2$; $P < 0.001$) and 2006 ($H_5 = 333.5$; $P < 0.001$); data for use of sites were not collected in 2004 (Table 3). In 2005, bedding sites had higher ($P < 0.001$) overstory cover than did feeding sites, whereas feeding sites had greater shrub ($P < 0.001$) and grass–forb ($P < 0.001$) cover than did bedding sites. In 2006, bedding sites similarly had greater overstory cover ($P < 0.001$) but less shrub ($P < 0.001$) and grass–forb cover ($P < 0.001$) than did feeding sites. Vertical cover was similar ($U = -0.9$; $P = 0.388$) in 2005 and 2006 at bedding sites (Table 3).

We identified 203 bedding sites. The most common overstory cover at bedding sites included caves–rock ledges (34.9%), pinyon or juniper trees (27.1%), saltcedars (14.3%), dirt banks–overhangs (6.4%), cottonwood trees (3.4%), other trees (1.0%), and boulders (1.0%). No overstory cover was present at 11.8% of bedding sites. However, 35% of these sites had a shrub (sage, greasewood, four-wing saltbush) vertical-cover component, and one (4.3%) was on an island in Chaco Wash.

Overstory cover ($r = -0.621$; $F_{1,186} = 116.9$; $P < 0.001$) and visual obscurity (vertical cover; $r = -0.444$; $F_{1,122} = 22.9$; $P < 0.001$) were related inversely to size of group at bedding sites. Herbaceous cover was related positively to size of group ($r = 0.408$; $F_{1,185} = 36.9$; $P < 0.001$) at bedding sites, while shrub cover was unrelated to size of groups at bedding sites ($r = 0.078$; $F_{1,186} = 1.1$; $P = 0.291$). Similarly, at feeding sites, size of group was related

Table 2—Differences and 90% confidence intervals (CI) between proportional composition of home ranges and proportions of locations of elk (*Cervus elaphus*) annually and during spring–autumn around Chaco Culture National Historical Park, San Juan and McKinley counties, New Mexico, 2004–2006; asterisks indicate significant differences ($P < 0.10$).

		Annual		Spring–autumn	
Habitat	Home range	Difference	90% CI	Difference	90% CI
Barren rocky	0.133	−0.086*	−0.094 to −0.076	−0.083*	−0.092 to −0.073
Pinyon–juniper woodland	0.282	+0.112*	0.073 to 0.154	+0.135*	0.094 to 0.176
Sagebrush shrubland	0.055	−0.036*	−0.042 to −0.030	−0.033*	−0.039 to −0.026
Desert shrub	0.337	−0.237*	−0.252 to −0.221	−0.243*	−0.262 to −0.227
Grass–forb	0.217	+0.081*	0.060 to 0.103	+0.038*	0.016 to 0.059
Riparian woodland	0.003	+0.138*	0.111 to 0.163	+0.159*	0.129 to 0.186

inversely to overstory ($r = -0.115$; $F_{1,260} = 3.5$; $P = 0.064$) and shrub ($r = -0.200$; $F_{1,260} = 10.9$; $P = 0.001$) cover and positively related to herbaceous ($r = 0.311$; $F_{1,260} = 27.9$; $P < 0.001$) cover. Visual obscurity was not recorded at feeding sites.

Elk spent significantly less time feeding during midday during months when mean daily high temperatures were >26.5°C (Fisher's exact $P < 0.001$). Of feeding observations, 18% occurred during midday in June–September (mean daily high temperatures = 30.6, 32.2, 30.6, and 27.2°C, respectively) versus 56% in October–May (mean daily high temperatures = 6.1–24.4°C).

Because accrual of body fat is driven by nutrition in spring–autumn (Cook, 2002), we used only characteristics of home ranges in spring–autumn to model body fat. Status of lactation ($F_{1,52} = 8.3$; $P = 0.006$) had the strongest effect on accrual of body fat. Accounting for status of lactation, levels of body fat that elk were able to accrue were related positively to proportions of sagebrush shrublands ($F_{1,52} = 2.9$; $P = 0.095$) and semi-desert shrub-steppe ($F_{1,52} = 3.4$; $P = 0.071$). Levels of body fat that elk were able to accrue were related negatively ($F_{1,52} = 3.0$; $P = 0.089$) to proportion of barren rocky habitats in home ranges in spring–autumn. The strongest effect was associated with semi-desert shrub-steppe, which accounted for 56% of the variance in body fat.

Annual size of home ranges was not influenced by status of lactation ($F_{1,50} = 2.5$; $P = 0.117$) but was related positively to proportion of sagebrush shrubland and semi-desert shrub-steppe in annual home ranges (Table 4). Annual size of home ranges was related negatively to proportions of barren rocky and pinyon–juniper habitats. The strongest effect was associated with sagebrush shrubland; presence of this habitat explained 30% of variation in size of home ranges.

Status of lactation ($F_{1,60} = 1.9$; $P = 0.173$) was not related to size of home ranges in spring–autumn. Size of home ranges in spring–autumn was related negatively to proportions of barren rocky and pinyon–juniper habitats and positively related to proportions of sagebrush shrubland, semi-desert shrub-steppe, and semi-desert grassland (Table 4). The strongest effect was associated with barren rocky habitats, which explained 63% of variation in size of home ranges.

Accounting for status of lactation, body fat of individuals was related positively to total annual precipitation during the June–May biological year ($F_{1,52} = 4.4$; $P = 0.040$; $\beta = 0.38$; $SE = 0.16$) and to cumulative precipitation during September–November ($F_{1,52} = 25.5$; $P < 0.001$; $\beta = 5.8$; $SE = 1.2$), the period immediately following the peak of lactation. Body fat of individuals was related negatively to cumulative precipitation during January–June ($F_{1,52} = 3.1$; $P = 0.082$; $\beta = -0.46$; $SE = 0.26$). Precipitation during January–June was related positively to survival of offspring (Bender and Piasecke, 2010); hence, the negative association with body fat likely was due to increased survival of offspring, which lowered fat reserves of the adult female.

Annual size of home range was not related to seasonal or annual precipitation ($F_{1,50} \leq 2.6$; $P \geq 0.113$). Size of home range in spring–autumn was related negatively to total annual precipitation during the June–May biological year ($F_{1,60} = 2.8$; $P = 0.099$) and cumulative precipitation during September–November ($F_{1,60} = 14.9$; $P < 0.001$).

Neither aspect (area-under-the-curve ≤0.585, $SE = 0.019$), slope (area-under-the-curve ≤0.551, $SE = 0.016$), distance to stream (area-under-the-curve ≤0.630, $SE =$

Table 3—Mean and *SE* of percentage of overhead, vertical, shrub, and herbaceous cover at bedding and feeding sites of elk (*Cervus elaphus*) in the area of Chaco Culture National Historic Park, San Juan and McKinley counties, New Mexico, 2005 and 2006; means in the same column that do not share a letter differ ($P < 0.10$).

		2005		2006	
Site	Cover	Mean	*SE*	Mean	*SE*
Bedding	Overhead	46.0a	3.2	55.6a	2.7
	Vertical	54.5	2.1	62.6	2.2
	Shrub	11.5c	1.7	13.7d	1.4
	Herbaceous	10.6c	1.7	6.9e	1.1
Feeding	Overhead	4.0d	1.2	2.0f	0.5
	Shrub	23.0b	1.7	24.8c	1.7
	Herbaceous	25.2b	2.4	32.1b	2.0

0.019), distance to road (area-under-the-curve $\leq$0.649, *SE* = 0.022), nor distance to source of water (area-under-the-curve $\leq$0.669, *SE* = 0.020) significantly influenced distribution. Elevation (area-under-the-curve = 0.700, *SE* = 0.020 and 0.739) in 2004 and 2006 was related positively with distribution but not in 2005 (area-under-the-curve = 0.632, *SE* = 0.017).

DISCUSSION—Commonalities in associations across scales indicated that selection of habitats by elk was driven primarily by cover. Location of home range showed strong positive selection for pinyon–juniper and rocky cover habitats (Table 1). Similarly, use of habitats within home ranges showed strong positive selection for pinyon–juniper and riparian habitats. Moreover, factors most influential in size of home range, a measure of quality of habitats (Wickstrom et al., 1984; Bender et al., 2007), showed that size of home range was smaller, and hence, quality of habitat higher, when they included more pinyon–juniper and barren rocky habitats, which occurred mainly at higher elevations on mesas and in canyons. Collectively, these preferences demonstrate the importance of cover. At the scale of site, bedding sites included high overstory (>46%) and vertical (>55%) cover that provided elk with thermal and security benefits, and these sites were associated primarily with barren rocky (35%), pinyon–juniper (27%), and riparian (24%) habitats. These results highlight interrelationships in selection of habitats across scales and the importance of evaluating selection of habitats at multiple scales to understand selection at any single scale. Moreover, no habitat consistently preferred in relationships between landscape and home range was related positively to accrual of body fat, further demonstrating preference for cover.

The importance of cover in selection of habitats likely was influenced by small size of the population and vegetative characteristics. These relatively open desert grassland–scrublands were inherently limited in cover (>85% in grass, shrub, or other open habitats). Cover decreases vulnerability to human and nonhuman predators, reduces disturbance and losses of energy, and is used for comfort or thermoregulation during summer because of high ambient temperatures (Young, 1988; Carpenter and Silvy, 1991; Strohmeyer and Peek, 1996; Cook et al., 1998; Skovlin et al., 2002; Sawyer et al., 2007). Ungulates also preferentially use hiding cover when size of groups are small because they face greater hazards foraging in the open when alone than when in large groups of conspecifics (Geist, 2002). In Chaco Culture National Historical Park, size of groups were related negatively to overstory cover; elk preferred to be in large groups when in open areas. Because the population in Chaco Culture National Historical Park was only ca. 53 elk (Bender and Piasecke, 2010) and mean size of groups was 2.5, elk may have avoided open areas because safety in numbers often was not possible.

Disturbance by humans and other predators was relatively low in Chaco Culture National Historical Park; only one elk was harvested during our study and none was predated (Bender and Piasecke, 2010). There also was limited foot and vehicular traffic. Such conditions previously have been associated with less use of security cover (McCorquodale et al., 1986; Merrill, 1991). Despite this, elk showed a noticeable preference for habitats and sites that provided security cover. Elk also preferred bedding under substantial cover, i.e., average canopy cover of bedding sites was >46%.

The need for thermal cover has been discounted in winter (Cook et al., 1998), but requirements in summer are less certain. Ruminants suffer from thermal stress (Young, 1988) and alter behavior to avoid activity during hot diurnal hours (Carpenter and Silvy, 1991; Strohmeyer and Peek, 1996). Thermal stress may be particularly problematic for elk in southwestern deserts that have much higher ambient temperatures than arid habitats occupied in the inland northwestern region or northern Rocky Mountains (Strohmeyer and Peek, 1996; Sawyer et al., 2007). In Chaco Culture National Historical Park, elk were less active during midday during months when average daily high temperatures exceeded thermal tolerance. Behavior therefore suggested that preference for cover was associated with avoidance of heat. In Guadalupe Mountains National Park, Carpenter and Silvy (1991) similarly noted that elk preferentially used woody ravines, ostensibly for shade. They reported that 90% of resting areas were in full or partial shade when ambient temperatures were >12°C.

Despite preference for cover, elk also need adequate nutrition to accrue sufficient body fat for survival and production of young (Cook, 2002; Bender et al., 2008; Bender and Piasecke, 2010). Accrual of body fat was associated with open habitats (sagebrush, shrub-steppe, and grasslands) in Chaco Culture National Historical Park; habitats that generally were avoided at scales of landscape and home range and positively associated with annual and seasonal size of home range, an indication of poor habitat for elk. Condition (body fat) is related to quantity and quality of forage, which in desert systems is related closely to precipitation (McKinney, 2003; Marshall et al., 2005). Condition of individual females also was related to precipitation following primary lactation and prior to senescence of forage (September–November), which is when females potentially can recover reserves used in raising a neonate to weaning. Condition also was related positively to total annual precipitation during the biological year (June–May). Thus, both timing and amount of precipitation affected condition of females, likely through effects on quantity and quality of forage during critical periods in the biological year. However, even given favorable patterns of precipitation, habitats

TABLE 4—Relationships between size and composition of annual and spring–autumn home ranges of adult female elk (*Cervus elaphus*) in the area of Chaco Culture National Historical Park, San Juan and McKinley counties, New Mexico, 2004–2006. In addition to *F*-values, *P*-values, and size of sample (*n*), the coefficient (β) and standard error (*SE*) of the variable in the regression model are provided.

	Annual					Spring–autumn				
Cover	*F*	*P*	β	*SE*	*n*	*F*	*P*	β	*SE*	*n*
Barren rocky	3.9	0.055	−290	148	52	77.4	<0.001	−903	103	62
Pinyon–juniper woodland	3.8	0.057	−63	53	52	64.3	<0.001	−302	38	62
Sagebrush shrubland	13.4	0.001	690	188	52	54.5	<0.001	1,217	165	62
Mixed salt-desert scrub	<0.1	0.995	—	—	52	1.0	0.326	—	—	62
Semi-desert shrub-steppe	8.6	0.005	434	148	52	25.5	<0.001	701	139	62
Semi-desert grassland	0.4	0.523	—	—	52	69.3	<0.001	383	46	62
Riparian woodland	0.5	0.464	—	—	52	1.2	0.283	—	—	62
Greasewood	2.1	0.117	—	—	52	1.6	0.206	—	—	62

need to have forage present to respond to precipitation. Preferred forages were more common in open habitats on Chaco Culture National Historical Park (L. C. Bender, in litt.), and consequently, body fat was related positively to open habitats.

Semi-desert shrub-steppe was the habitat most positively related to accrual of body fat; similarly, proximity to shrublands (Sawyer et al., 2007) and mountain shrublands (Carpenter and Silvy, 1991) were associated positively with presence of elk in other arid habitats, likely reflecting availability of foods, particularly foods (browse) that were more drought tolerant than herbaceous species (Marshall et al., 2005). In Chaco Culture National Historical Park, most foods (forbs, cool-season grasses, and mountain mahogany; L. C. Bender, in litt.) were associated with little overstory canopy (<4%; Table 3). Feeding sites also showed greater coverage of grasses–forbs (>25%) and shrubs (>23%; Table 3) than did bedding sites. Despite the importance of these open habitats for condition and productivity of populations (Bender and Piasecke, 2010), they generally were avoided in relationships between landscape and home range. Faced with a need to feed to survive and produce viable young (Piasecke, 2006; Bender et al., 2008; Bender and Piasecke, 2010), elk apparently decreased real or perceived vulnerability by increasing size of groups while foraging (Geist, 2002). This behavioral adaptation allowed elk to access needed nutrition, which was most abundant in open habitats (L. C. Bender, in litt.). Because condition is dependent upon nutrition (Cook, 2002) and condition strongly affected production and survival of young in Chaco Culture National Historical Park (Bender and Piasecke, 2010), presence and use of open habitats is critical to persistence of elk. This was further illustrated by the strong effect of status of lactation on body fat. As quality and quantity of forage declined, differences in body fat between lactating and non-lactating females increased (Piasecke and Bender, 2009). The negative effect of status of lactation on levels of body fat indicated that high-quality foraging areas were limited, particularly during years with limited precipitation.

Size of annual home range in Chaco Culture National Historical Park (60, 102, and 112 km^2) was much smaller than determined by McCorquodale et al. (1989) in arid eastern Washington (162 km^2) and Strohmeyer and Peek (1996) in arid southeastern Idaho (544–555 km^2). Conversely, size of home ranges generally was larger than for most populations in forested habitats (3–112 km^2; Strohmeyer and Peek, 1996). Size of home range varies extensively with habitat and large home ranges are associated with inferior habitats (Wickstrom et al., 1984; Bender et al., 2007). Strohmeyer and Peek (1996) attributed the extremely large home ranges in sagebrush habitats in southeastern Idaho to aridity (resulting in dispersed food and water), juxtaposition of components of habitats (elk foraged in agricultural fields, which were distant from bedding sites in sagebrush habitats), and disturbance by humans. Size of home ranges in Chaco Culture National Historical Park was related negatively to precipitation in June–May and September–November, similarly indicating that quality of habitat increased as precipitation increased; presumably, because of positive effects on availability of food and possibly water. Elk apparently had to search less for food during the period most related to accrual of body fat (September–November) during wet years, resulting in smaller size of home ranges in spring–autumn. In contrast to elk in the Chihuahuan Desert of Guadalupe Mountains National Park, where distribution was associated most strongly with availability of water (Carpenter and Silvy, 1991), we detected no association between distribution and presence of water. Thus, excluding precipitation, few of these other factors apply to Chaco Culture National Historical Park, and none of these studies (McCorquodale et al., 1989; Carpenter and Silvy, 1991; Strohmeyer and Peek, 1996) actually modeled size of home range as a function of components of habitats, limiting the strength of their inferences.

Size of home ranges both annually and in spring–

autumn were related positively to open habitats (shrublands and grasslands) and negatively related to habitats preferred for bedding (barren rocky and pinyon–juniper), indicating that the need for cover primarily determined size of home ranges in Chaco Culture National Historical Park despite the relative lack of disturbance, which would deemphasize the need for security cover (McCorquodale et al., 1986; Merrill, 1991). However, large ungulates experience thermal stress (Young, 1988) and, because of thermal stress, may show diurnal bedding and nocturnal feeding (particularly if disturbance by humans is high; Strohmeyer and Peek, 1996), strong preference for shaded bedding sites (Carpenter and Silvy, 1991), and use of cooler aspects in hotter months if topography allows (Sawyer et al., 2007). Elk in Chaco Culture National Historical Park were not solely nocturnal in foraging (L. C. Bender, in litt.); perhaps because disturbance by humans was low. However, elk chose high overhead cover at bedding sites (Table 3) and limited activity during midday in months when mean daily high temperatures exceeded their thermal tolerance. These results support a thermal-stress effect on behavior and likely contributed to the importance of habitats that provide desired attributes for bedding (overhead cover) affecting placement and size of home ranges. Cover, especially overstory cover, is limited in southwestern deserts (i.e., primarily to riparian washes and higher-elevation mesas), and modeling of home ranges clearly indicated a need to increase size of home range to include cover in cover-limited habitats of Chaco Culture National Historical Park. This may be particularly important given the high ambient temperatures in southwestern deserts compared to northern arid habitats (McCorquodale et al., 1989; Strohmeyer and Peek, 1996).

Elk were able to meet annual life requisites in southwestern desert grassland-scrublands, particularly given favorable patterns of precipitation. Coupled with high rates of increase in size of population (15%/year; Bender and Piasecke, 2010), this indicates that southwestern desert grassland-scrublands are worth consideration in long-term management plans. However, elk required cover for security and thermal benefits, but habitats that provide these needs are limited in these landscapes (<15% of the landscape) and, thus, require careful management to maintain their presence. In the area around Chaco Culture National Historical Park, pinyon–juniper habitats that are not owned by the National Park Service are being cleared to promote perennial grasses for cattle. This manipulation may decrease overall quality of habitats if sufficient areas of higher canopy coverage (i.e., >45%) are not retained to meet requirements for cover. Likewise, high-quality foraging areas also are important for success of populations, but forage, nutrition, and condition are influenced strongly by precipitation in Chaco Culture National Historical Park and other arid environments. While elk apparently are able to obtain sufficient water as evidenced by the lack of a relationship between distribution and location of water in Chaco Culture National Historical Park, condition and, consequently, fitness likely will be limited during drought years in these landscapes (Bender and Piasecke, 2010).

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Literature Cited

Baldwin, R. A., and L. C. Bender. 2008. Den-site characteristics of black bears in Rocky Mountain National Park, Colorado. Journal of Wildlife Management 72:1717–1724.

Bender, L. C., and J. R. Piasecke. 2010. Population demographics and dynamics of colonizing elk in a desert grassland–scrubland in northwestern New Mexico. Journal of Fish and Wildlife Management 1:152–160.

Bender, L. C., L. A. Lomas, and T. Kamienski. 2007. Habitat effects on condition of doe mule deer in northcentral New Mexico. Rangeland Ecology and Management 60:277–284.

Bender, L. C., J. G. Cook, R. C. Cook, and P. B. Hall. 2008. Relations between nutritional condition and survival of elk in the Pacific Northwest. Wildlife Biology 14:70–80.

Carpenter, J., and N. Silvy. 1991. Movements and habitat relations of a small elk population in West Texas. Pages 64–68 in Proceedings of the elk vulnerability symposium (A. G. Christensen, L. J. Lyon, and T. N. Lonner, compilers). Montana State University, Bozeman.

Cook, J. G. 2002. Nutrition and food. Pages 259–349 in North American elk: ecology and management (D. E. Toweill and J. W. Thomas, editors). Smithsonian Institution Press, Washington, D.C.

Cook, J. G., L. L. Irwin, L. D. Bryant, R. A. Riggs, and J. W. Thomas. 1998. Relations of forest cover and condition of elk: a test of the thermal cover hypothesis in summer and winter. Wildlife Monographs 141:1–61.

Cook, R. C. 2000. Studies of body condition and reproductive physiology in Rocky Mountain elk. M.S. thesis, University of Idaho, Moscow.

Cook, R. C., J. G. Cook, D. L. Murray, P. Zager, B. K. Johnson, and M. W. Gratson. 2001. Development of predictive models of nutritional condition for Rocky Mountain elk. Journal of Wildlife Management 65:973–987.

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.

Geist, V. 2002. Adaptive behavioral strategies. Pages 389–433 in North American elk: ecology and management (D. E. Toweill and J. W. Thomas, editors). Smithsonian Institution Press, Washington, D.C.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluation resource preference. Ecology 61:65–71.

Marshall, J. P., P. R. Krausman, and V. C. Bleich. 2005. Rainfall, temperature, and forage dynamics affect nutritional quality of desert mule deer forage. Rangeland Ecology and Management 58:360–365.

McCorquodale, S. M., K. J. Raedeke, and R. D. Taber. 1986. Elk habitat use patterns in the shrub-steppe of Washington. Journal of Wildlife Management 50:664–669.

McCorquodale, S. M., K. J. Raedeke, and R. D. Taber. 1989. Home ranges of elk in an arid environment. Northwest Science 63:29–34.

McKinney, T. 2003. Precipitation, weather, and mule deer. Pages 219–237 in Mule deer conservation: issues and management strategies (J. C. deVos, Jr., M. R. Conover, and N. E. Headrick, editors). Jack H. Berryman Press, Logan, Utah.

Merrill, E. H. 1991. Thermal constraints on use of cover types and activity time of elk. Applied Animal Behaviour Science 29:251–267.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37:223–249.

Parker, K. L., and C. T. Robbins. 1984. Thermoregulation in mule deer and elk. Canadian Journal of Zoology 62:1409–1422.

Pearce, J., and S. Ferrier. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modelling 133:225–245.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190:231–259.

Piasecke, J. R. 2006. Relationships among condition, health, and reproduction in free-ranging elk (*Cervus elaphus*) populations throughout the United States. M.S. thesis, New Mexico State University, Las Cruces.

Piasecke, J. R., and L. C. Bender. 2009. Relationships between nutritional condition of elk and nutritional carrying capacity. Rangeland Ecology and Management 62:145–152.

Ricketts, T. H., E. Dinerstein, D. M. Olson, C. J. Loucks, W. Eichbaum, D. DellaSala, K. Kavanagh, P. Hedao, P. T. Hurley, K. M. Carney, R. Abell, and S. Walters. 1999. Terrestrial ecoregions of North America: a conservation assessment. Island Press, Washington, D.C.

Sawyer, H., R. M. Nielson, F. G. Lindzey, L. Keith, J. H. Powell, and A. A. Abraham. 2007. Habitat selection of Rocky Mountain elk in a nonforested environment. Journal of Wildlife Management 71:868–874.

Skovlin, J. M., P. Zager, and B. K. Johnson. 2002. Elk habitat selection and evaluation. Pages 531–555 in North American elk: ecology and management (D. E. Toweill and J. W. Thomas, editors). Smithsonian Institution Press, Washington, D.C.

Strohmeyer, D. C., and J. M. Peek. 1996. Wapiti home range and movement patterns in a sagebrush desert. Northwest Science 70:79–87.

Swets, J. A. 1988. Measuring the accuracy of diagnostic systems. Science 240:1285–1293.

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.

Young, B. A. 1988. Effect of environmental stress on nutrient needs. Pages 456–467 in The ruminant animal: digestive physiology and nutrition (D. C. Church, editor). Prentice Hall, Inc., Englewood Cliffs, New Jersey.

Zar, J. H. 1996. Biostatistical analysis. Prentice Hall, Inc., Upper Saddle River, New Jersey.

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