

Spatial Distributions of Mule Deer and North American Elk: Resource Partitioning in a Sage-Steppe Environment

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ABSTRACT.—We examined spatial distributions and resource partitioning among female mule deer (*Odocoileus hemionus*) and female North American elk (*Cervus elaphus*) during summer and winter in southeastern Idaho, USA. Our objective was to understand differences in distributions and habitat selection by these two species of large herbivores in a sagebrush-steppe ecosystem. We used multi-response permutation procedures to examine seasonal distributions of mule deer and elk. We compared animal locations with random locations on a GIS-based habitat map to examine habitat selection and importance. Both species were more widely distributed during summer than winter, when distributions of both species were more restricted. During winter, habitat selection differed among mule deer and elk in use of aspect; east facing slopes were selected by elk and west-facing slopes by mule deer. Mule deer also were located closer to roads than random locations, which may have resulted from avoidance of elk. We observed no differences in habitat selection between mule deer and elk during summer, although these large herbivores showed resource separation by strongly partitioning use of habitats. Conversely, both species used the shrub-steppe ecosystem during winter, but partitioned habitat mostly via use of aspect and distance to roads. Our research provides insights into niche partitioning between these large mammals.

INTRODUCTION

Sympatric species of large mammals exploit their environment in different ways (Schwartz and Ellis, 1981). Resource partitioning among species traditionally has been evaluated along three niche axes: spatial separation (including differential use of habitats), temporal avoidance and dietary differences (Keddy, 1989; Ben-David *et al.*, 1996; Kronfeld-Schor *et al.*, 2001; Stewart *et al.*, 2002, 2003). Resource partitioning is believed to have arisen through coevolutionary divergence among sympatric species resulting from interspecific competition (Connell, 1983; Schoener, 1983; Sinclair, 1985; Jenkins and Wright, 1988). Typically, when there is a large overlap on ≥ 1 niche axes, avoidance or partitioning is expected on another axis (McCullough, 1980; Kie and Bowyer, 1999; Stewart *et al.*, 2002). Consequently, resource partitioning among co-existing species is the divergence in resource use between species, which once had greater overlap in their requirements, termed the ghost of competition past (Connell, 1980; Walter, 1991). Exploring niche separation among large herbivores often is a

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formidable task, because those mammals occupy relatively large home ranges and exhibit broad spatial and dietary niches (Kie *et al.*, 2003; Stewart *et al.*, 2003).

Populations of mule deer (*Odocoileus hemionus*) have been declining across much their historic range in the western United States (Fuller, 1998; Ballard *et al.*, 2001; Cook *et al.*, 2007; Bishop *et al.*, 2009). Although reasons for waning populations are numerous and sometimes unclear, competition with North American elk (*Cervus elaphus*), which are sympatric with mule deer through much of their distribution, may contribute to that decline (Ballard *et al.*, 2001). Stewart *et al.* (2002) inferred competition primarily via interference mechanisms among mule deer, elk and cattle in the Blue Mountains of eastern Oregon, USA. Stewart *et al.* (2002) reported that mule deer were more strongly affected by movements of elk than were elk by mule deer, and postulated that models for habitat selection by mule deer were driven by mule deer avoiding elk.

Resource partitioning among sympatric species and the potential for competition likely varies seasonally. Resources are most limiting during winter when animals are geographically confined by snow; thus, the potential for competition may be intense during that season (Jenkins and Wright, 1988). Moreover, distributions of mule deer and elk are more likely to overlap during winter, when animals are concentrated into limited habitats and tend to use smaller portions of their home range than during summer (Nelson, 1982). Indeed, Jenkins and Wright (1988) noted strong potential for interspecific competition among cervids using lowland *Picea* forests during severe winters in Flathead Basin, Montana, USA.

Our objective was to understand broad-scale differences in the seasonal distributions and habitat selection by female mule deer and female North American elk in a sagebrush-steppe ecosystem with potentially severe winters. We tested hypotheses that habitat selection and resource partitioning between mule deer and elk in a sage-steppe ecosystem would occur during summer and winter, and that seasonal differences in the strength of resource partitioning between these cervids would likewise be evident. We predicted that distributions of mule deer and elk would be most similar during winter when mule deer and elk were using similar areas and that distributions of mule deer and elk would be more variable during summer when more habitats or space are available to both species. Furthermore, we postulated that mule deer and elk would partition habitat most strongly during winter when spatial overlap likely was highest. We also predicted that those cervids would be more similar in selection of habitats during summer when spatial distributions likely were less constrained. Answers to these questions are critical for understanding resource needs and managing habitats for mule deer and elk.

STUDY AREA

We studied distributions of female mule deer and female North American elk in southeastern Idaho, USA (Fig. 1). Vegetation communities were broadly defined as forests, shrublands characteristic of Great Basin Desert, meadows, riparian areas, barren lands without vegetation (*e.g.*, lava flows, mudflats or rock), areas with urban development or other human-influenced lands, areas of open water and agricultural crops. The terrain was rugged and streams were distributed throughout the study area; elevations ranged from 1327 to 3017 m. Roads were well distributed and were concentrated around urban areas. The area contains additional large herbivores, including moose (*Alces alces*), and predators including mountain lions (*Puma concolor*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*) and black bears (*Ursus americana*).

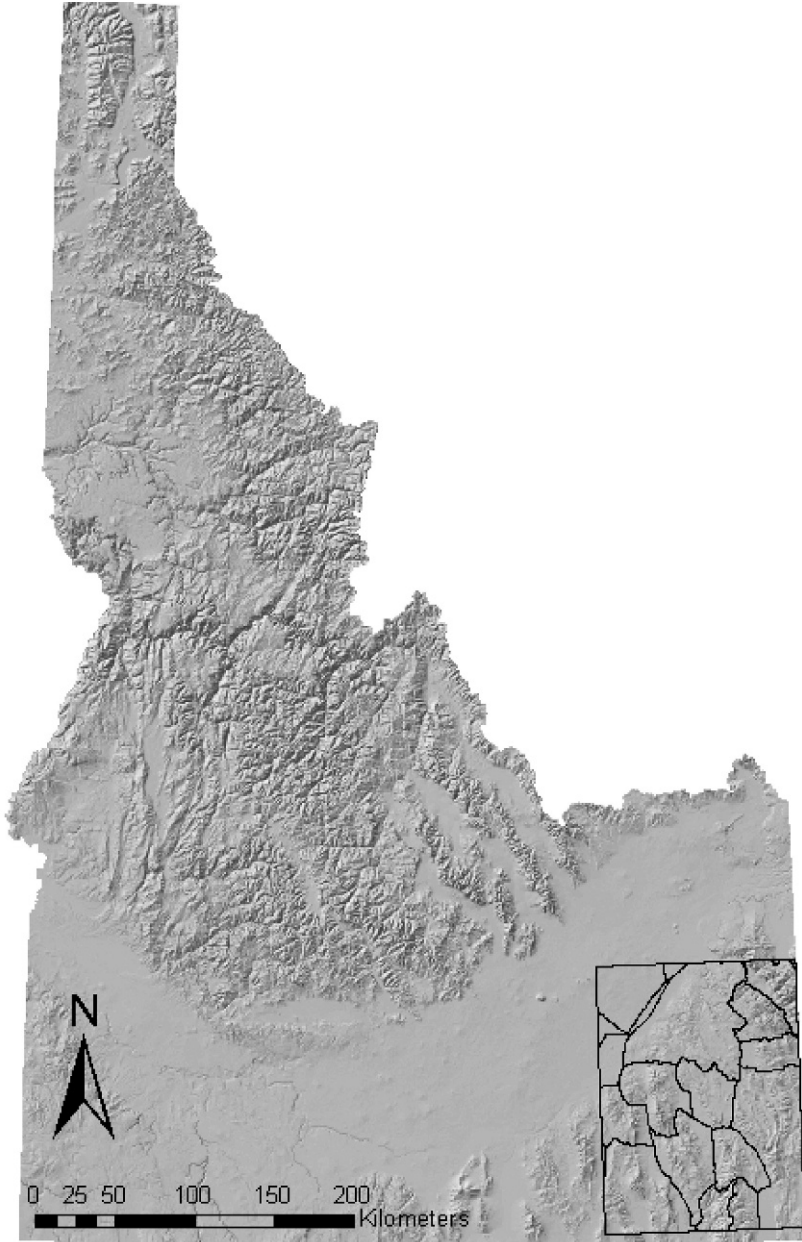


FIG. 1.—Location of study area in southeastern Idaho, USA, with associated game management units (Idaho Dept. Fish and Game), indicated by outlines

METHODS

We used locations of female mule deer and female elk obtained from the Idaho Department of Fish and Game (IDF&G). During Dec. and Jan. of each year mule deer ($n = 104$, ≥ 12 individuals per year, 2004–2007, 4 individuals 2008) and elk ($n = 22$, 2006–2007) were captured in southeastern Idaho, USA, with a drive net in the Soda Hills (Game management unit 72) and Indian Creek (Game management unit 76), which were wintering areas for mule deer and elk. Elk were restrained with Carfentanil prior to handling to protect animals and human handlers from injury. All animals were handled under permits held by IDF&G and were in compliance with guidelines for use of wild mammals in research approved by the American Society of Mammalogists (Gannon *et al.*, 2007).

All locations were determined by aerial VHF telemetry. Flights occurred about one time per month, weather permitting, and as many animals were located as possible during that flight. We obtained at least one location for each animal and we located each animal one to four times per year with ≥ 1 location per season. Multiple locations from an individual animal were obtained no more often than one time every 3 mo, to help minimize statistical difficulties related to pseudoreplication, and to prevent numerous locations for an individual biasing results of analyses (Stewart *et al.*, 2002; Boyce, 2006). Locations for mule deer encompassed 2004–2007, whereas locations for elk only included 2006–2007. We assumed that yearly differences in the distributions of deer were not substantial. We also combined years to help assess the broad-scale pattern of distribution of these large herbivores over time.

We obtained a digital elevation model (DEM) with a 30-m horizontal grid spacing with vertical units in meters (Idaho Geospatial Data Clearinghouse, 2004). From that DEM, we used the spatial analyst extension for ArcGIS (ESRI, 2006) to create layers for slope and aspect. We used 100 points randomly distributed across the study area to estimate availability of vegetation types, slopes, aspects and elevations. We transformed aspect, a circular variable, to Cartesian coordinates (sine and cosine) prior to analyses (Zar, 1999). We obtained GIS layers for streams, roads and game management units (GMUs) from Idaho Department of Fish and Game, with 30-m pixel size, and calculated distances from each random and animal location to roads and streams using ARCGIS 9.2 (ESRI, 2006). We acquired a vegetation map with 30-m pixel size from Idaho State University-GIS Training and Research Center (Weber, 2001), and determined habitat type for each animal and random location.

We used multiresponse permutation procedures (MRPP) to examine distribution patterns between female mule deer and female elk by season (Blossom software, Cade and Richards, 2005). Winter was defined as Nov. through Apr.; summer consisted of May through Oct. MRPP are distribution-free statistics that rely on permutations of data based on randomization theory and allow analyses of spatial differences not possible with other methods, especially partitioning of space within a habitat type (Cade and Richards, 2005; Zimmerman *et al.*, 1985; Stewart *et al.*, 2002). Thus, MRPP offers a powerful method to assess the distributions of large mammals, even when sample sizes are relatively small (Nicholson *et al.*, 1997; Pierce *et al.*, 2000; Stewart *et al.*, 2002). We first tested the null model that neither mule deer nor elk locations differed from random points by season, to determine if habitat selection occurred by either mule deer or elk. We then compared distributions of mule deer and elk with separate analyses by season and alternated mule deer and elk as the excess group. The excess group is used to determine if the distribution of a particular species could be obtained from a random draw of the joint distribution of both species (Cade and

Richards, 2005), and is a powerful method for examining small spatial differences in distributions of animals.

We used multivariate analysis of variance (MANOVA) to test for difference in relative use and availability (selection or avoidance) of habitat variables between mule deer and elk (Nicholson *et al.*, 1997; Bowyer *et al.*, 1998, 1999; Stewart *et al.*, 2002). Habitat variables included elevation (m), slope (%), distance to nearest road (m), distance to water (m), sine and cosine of aspect, and proportions of meadows, shrublands and forests. We then evaluated the relative importance (use \times availability, rescaled to sum to 100%) of the vegetation communities for each ungulate species seasonally (Bowyer and Bleich, 1984; Weixelman *et al.*, 1998; Stewart *et al.*, 2002) and calculated 95% confidence intervals for comparisons (Zar, 1999). We used a Z-test for proportions (Zar, 1999) with a Bonferroni correction for multiple comparisons (Rice, 1989) to compare importance between mule deer and elk by season. This statistical test is especially appropriate for our data because it allows sampling with replacement. The critical value for the Bonferroni correction was 0.0063. We adopted an $\alpha = 0.05$ for other statistical tests, all of which were two tailed.

RESULTS

Results from MRPP indicated that distributions of female mule deer differed from random during winter ($P < 0.001$, Fig. 2a) and summer ($P < 0.001$, Fig. 2b). Distributions of female elk also differed from random locations during both seasons ($P < 0.001$), indicating that habitat selection occurred for both species. When mule deer were used as the excess group in analyses with MRPP, those deer differed significantly from the joint distribution of mule deer and elk during winter ($P = 0.003$), and summer ($P < 0.001$). Conversely, when elk were included as the excess group in MRPP, that cervid did not differ significantly from the joint distribution of mule deer and elk during summer ($P = 0.999$) or winter ($P = 0.311$). Thus, distributions of mule deer were clustered within those of elk and not vice versa.

We compared habitat characteristics at locations used by elk with random locations to understand habitat selection between these species during winter (Table 1) and summer (Table 2). Habitat selection differed between seasons for these two large herbivores (*Wilks' lambda* $F_{13,427} = 3.24$, $P < 0.001$). During winter, MANOVA revealed a species (mule deer, elk) by location (used, random) interaction (*Wilks' lambda* $F_{13,427} = 3.01$, $P = 0.003$), indicating differences in selection of some habitat variables between species. Univariate analyses following MANOVA identified distance to roads and sine of aspect as the only variables in which selection differed between species (Fig. 3). Elk used areas farther from roads, whereas mule deer were located closer to roads than random locations (Fig. 3). Elk selected east-facing slopes, whereas mule deer selected more west-facing aspects (Fig. 3). The interaction between species (mule deer, elk) and location (used, random), however, was not significant during summer (*Wilks' lambda* $F_{14,284} = 0.89$, $P = 0.572$), indicating no differences in selection of habitat variables between species.

We observed no significant ($P > 0.006$) differences in importance of coarse-scale vegetation communities between mule deer and elk during winter. Nonetheless, shrub-steppe clearly is critical habitat for both species during winter (Fig. 4). Conversely, during summer, mule deer and elk differed in importance of forests and agricultural lands (Fig. 4). Forests were more important vegetation communities for elk; and agricultural lands, likely alfalfa, were more important to mule deer during summer than for elk.

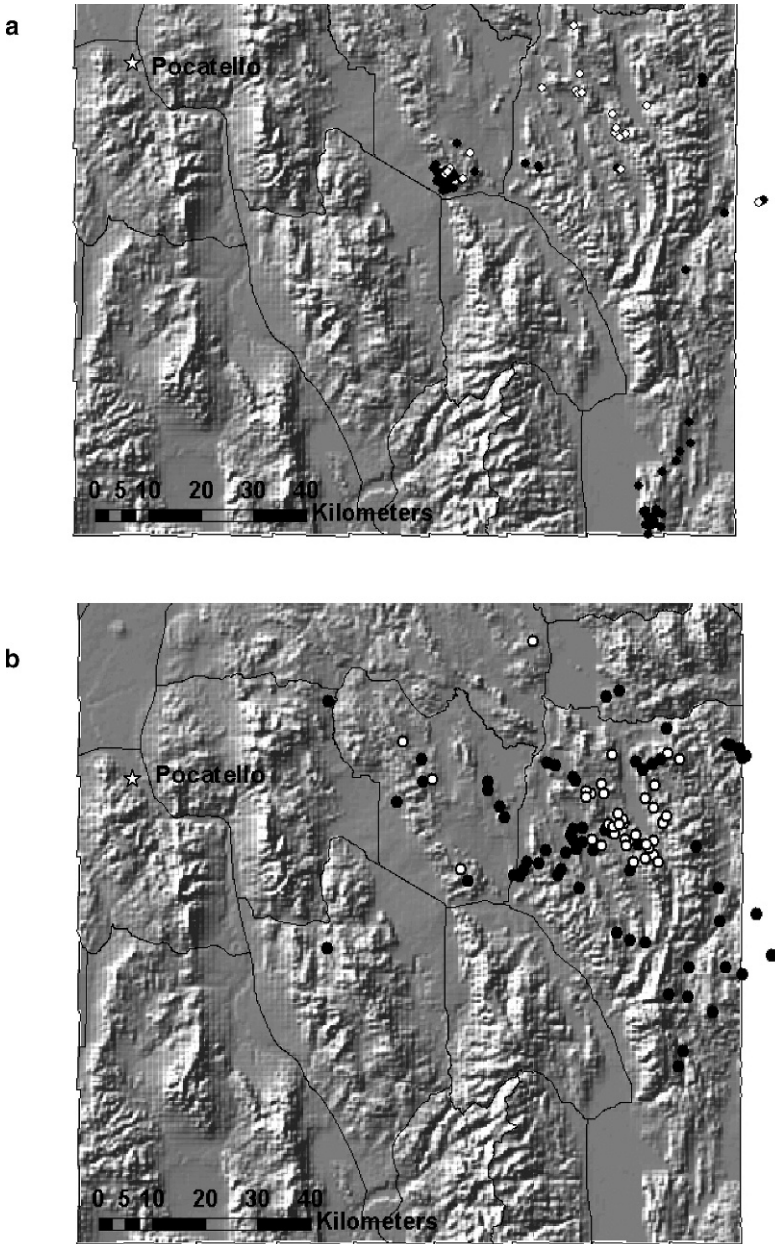


FIG. 2.—(a) Winter locations for female mule deer (black) and female North American elk (white) in southeastern Idaho, USA, on hillshade of digital elevation model. Clustered distributions of mule deer and elk occurred at Soda Springs and East Bear Lake wintering areas in 2004–2008. (b) Summer locations for female mule deer (black) and female North American elk (white) in southeastern Idaho, USA, on hillshade of digital elevation model. Black outlines on the map are game management units

TABLE 1.—Habitat features used and available (random) to female mule deer (69 individuals, 2004–2008) and female North American elk (19 individuals, 2006–2007) during winter (Oct.–Apr.) in southeastern Idaho, USA. Sample sizes indicated in table are number of locations used in analyses

Habitat variables	Mule deer				Elk			
	Used (n = 139)		Random (n = 100)		Used (n = 19)		Random (n = 100)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Winter								
Elevation (m)	2015	186.9	1779	277.1	2039	307.3	1872	262.8
Slope (%)	9.5	4.17	7.1	7.12	11.3	6.71	8.0	7.96
Distance to Roads (m)	2159	818.5	2771	2673.7	3653	1142.8	2913	2567.1
Distance to Streams (m)	2790	1803.4	1644	2816.2	1965	2050.0	1806	3053.5
Aspect	205.6	59.19	261.6	52.80	227.7	105.33	92.42	53.08
Sine	-0.370	0.6847	0.082	0.6861	0.147	0.7231	-0.050	0.7389
Cosine	0.118	0.6217	0.091	0.7249	-0.106	0.7057	-0.084	0.6742

DISCUSSION

Patterns of movement and distribution of North American elk (Bowler, 1981; Preisler *et al.*, 2004; Kie *et al.*, 2005; Anderson *et al.*, 2005, 2008) and mule deer (Bowler, 1984; Eberhardt *et al.*, 1984; Thomas and Irby, 1990; D'Eon and Serrouya, 2005; Long *et al.*, 2009) continue to be studied intensively, in part because such data can reveal insights into the ecology of these cervids, including their potential competitive interactions (Stewart *et al.*, 2002, 2003; Ager *et al.*, 2003; Poole and Mowat, 2005). Moreover, understanding factors affecting movements between summer and winter ranges (*i.e.*, migrations) can be critical for managers to sustain viable populations of these large vagile mammals (Thomas and Irby, 1990; Berger, 2004; McClure *et al.*, 2005; Sawyer *et al.*, 2005). Our purpose was to understand

TABLE 2.—Habitat features used and available (random) to female mule deer (59 individuals, 2004–2008) and female North American elk (21 individuals, 2006–2007) during summer (May–Sept.) in southeastern Idaho, USA. Sample sizes indicated in table are number of locations used in analyses

Habitat variables	Mule deer				Elk			
	Used (n = 73)		Random (n = 100)		Used (n = 38)		Random (n = 100)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Summer								
Elevation (m)	1913	547.8	1779	277.1	2195	157.9	1872	262.8
Slope (%)	8.6	6.41	7.1	7.12	11.9	5.34	8.0	7.96
Distance to Roads (m)	2571	2250.5	2771	2673.7	3124	1745.8	2913	2567.1
Distance to Streams (m)	1590	1716.3	1644	2816.2	950	992.9	1806	3053.5
Aspect	167.6	111.8	261.6	52.80	166.8	112.3	92.42	53.08
Sine	-0.072	0.718	0.082	0.6861	-0.184	0.6548	-0.050	0.7389
Cosine	-0.053	0.701	0.091	0.7249	-0.0553	0.7485	-0.084	0.6742

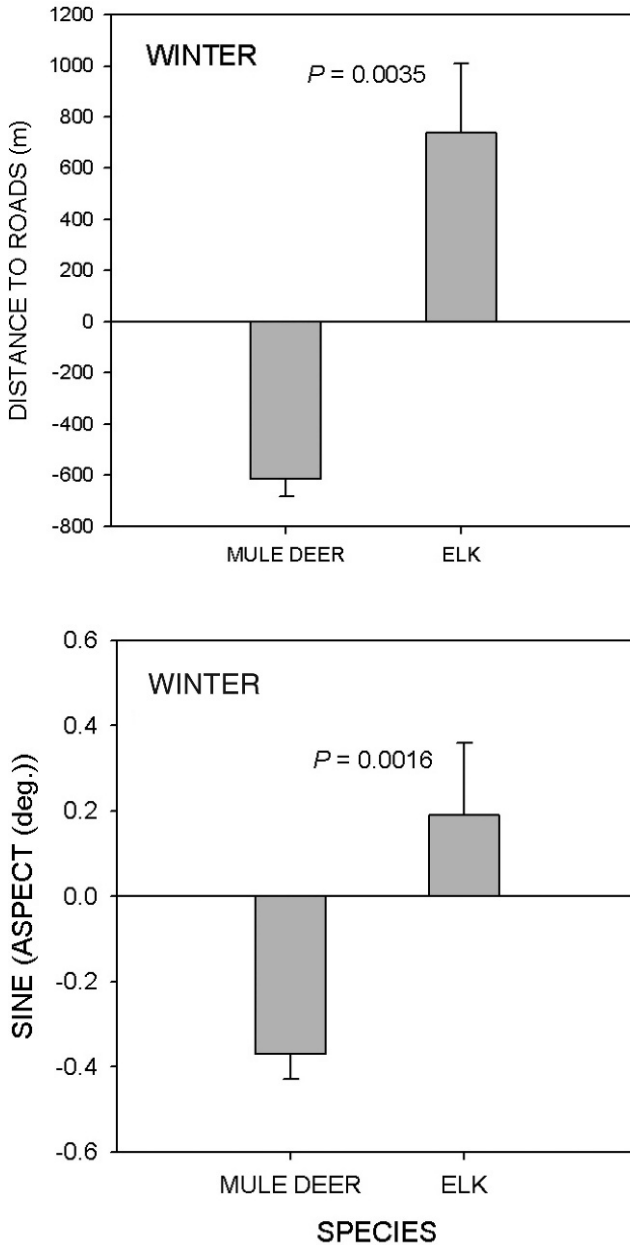


FIG. 3.—Selection of habitat variables (used minus available) for female mule deer and female North American elk during winter in southeastern Idaho, USA, 2004–2008. Negative values for selection (i.e., animals are closer than predicted at random). P-values are from analysis of variance followed by significant differences in selection or avoidance of habitat characteristics determined from MANOVA (Wilks' lambda, P = 0.003)

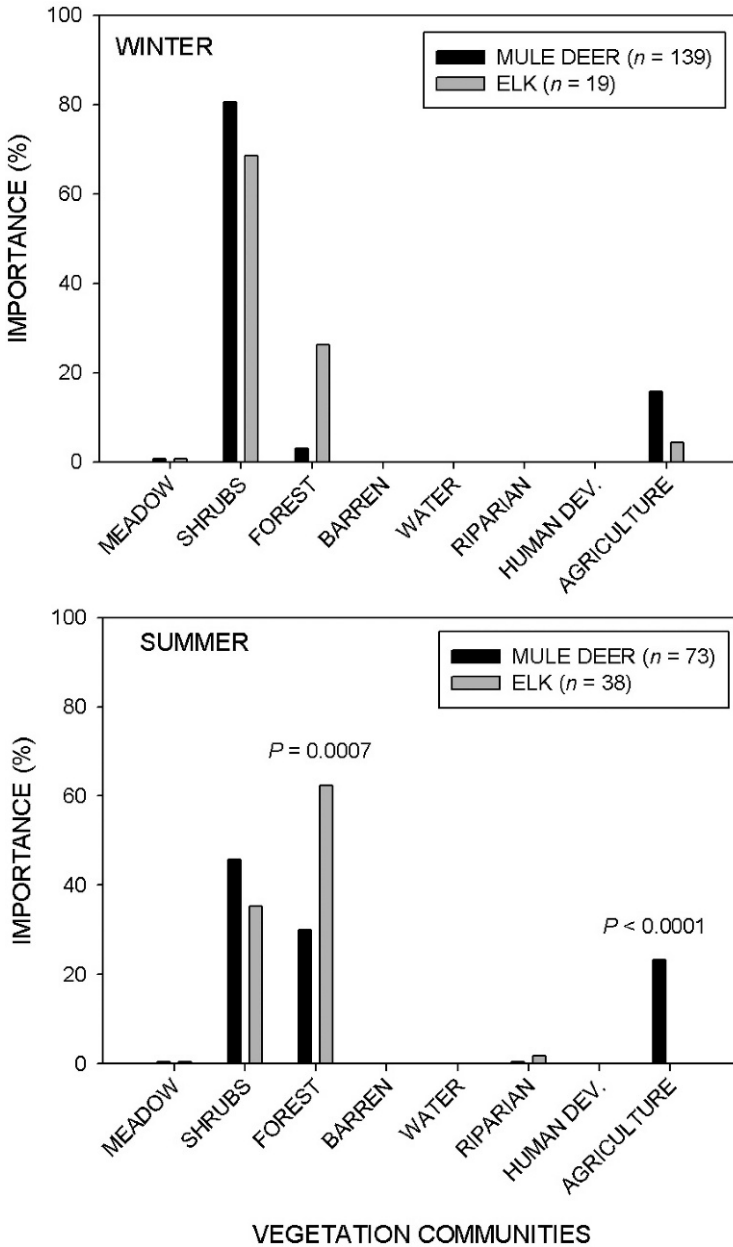


FIG. 4.—Seasonal importance of vegetation communities for mule deer and North American elk in southeastern Idaho 2004–2008. Sample sizes indicated are total number of locations used in analysis for each season. Importance is defined as use multiplied by availability, scaled to 100%. P-values are following Z-test for proportions with Bonferroni correction for multiple comparisons with a significance level of 0.006

broad-scale differences in the distribution and habitat selection by elk and mule deer in a sagebrush-steppe ecosystem with potentially severe winters.

Female mule deer and elk selected particular habitats during both summer and winter, although we observed different patterns in distributions of those cervids seasonally. During winter, mule deer had a restricted distribution and differed significantly from the distribution of elk, which were somewhat more widely distributed across winter range than were mule deer (Fig. 2a). Conversely, during summer, mule deer were more widely distributed across the study area than elk, although these cervids did show some selection of habitat components (Fig. 2b). We had a relatively small sample size for elk during winter ($n = 19$ total locations), but MRPP is robust for analysis with small sample sizes and can detect differences in distributions when making comparisons with unequal sample sizes (Cade and Richards, 2005).

We observed no differences in habitat selection between mule deer and elk during summer for the specific habitat variables that we measured. Because both mule deer and elk distributions differed significantly from random, those large herbivores were selecting habitat in a manner that did not differ from each other. During winter, however, elk and mule deer differed in use of aspect and distance to roads. Our results indicated that mule deer were located closer to roads than expected and elk were farther away. This outcome is consistent with other investigations of mule deer and elk, which reported that mule deer use areas closer to roads to avoid elk (Johnson *et al.*, 2000). Moreover, elk avoided areas near forest roads with high traffic levels, which also has been observed in previous studies of elk in other ecosystems (Perry and Overly, 1976; Witmer and deCalesta, 1985; Rowland *et al.*, 2000; Wisdom *et al.*, 2005; Gagnon *et al.*, 2007). Elk and mule deer also differed in use of aspect. Elk used more east-facing slopes, indicated by the positive value for sine of aspect, whereas mule deer used west-facing slopes, indicated by the negative value for sine of aspect. This outcome likely resulted from differences in habitat selection among those species, but may also have been a manifestation of mule deer avoiding elk.

When we examined importance of vegetation communities for mule deer and elk, we observed no differences during winter. The shrub-steppe community was most important wintering habitat for both species. During summer, however, we observed more variability in importance of vegetation communities, although shrub-steppe was essential for both cervids. Forests were more important communities to elk during summer and agricultural lands were more important to mule deer than elk. Agricultural lands are most likely to be helpful to mule deer if they consist of forb or newly emergent grain crops. In general, elk are more likely to feed upon graminoid forages than mule deer, which feed primarily on forbs and browse (McCullough, 1980; Bowyer, 1984; Hanley, 1984; Stewart *et al.*, 2002; Kie *et al.*, 2003).

During summer, mule deer and elk likely were partitioning use of vegetation communities and were widely distributed across the study area. An increasing elk population, however, might lead to competition in the future. Conversely, during winter, both species used the shrub-steppe habitats extensively. We were not able to directly address competition, because of the broad scale of our data, and manipulation of population density for either cervid was not possible (*sensu* Stewart *et al.*, 2006). More detailed data on spatial partitioning of resources and potential dietary differences between mule deer and elk would be necessary to rule out exploitive competitive interactions (Stewart *et al.*, 2003). Nonetheless, by partitioning other habitat characteristics such as use of different aspects and distance to roads, we hypothesize that if competition occurs in this ecosystem, it is most likely interference rather than exploitive competition. Such conclusions have been reached

previously for research concerning the spatial distributions and habitat selection by mule deer and elk (Stewart *et al.*, 2002).

We do not dismiss the potential for elk and mule deer to exhibit competitive interactions. For instance, Stewart *et al.* (2002) documented a strong avoidance of elk by mule deer during spring and summer. Our temporal windows for understanding seasonal distributions of elk and mule deer were necessarily broad to encompass longer-term movements of these migratory populations. A finer-scale assessment might yield additional insights, especially during the birthing season. Indeed, many ecological processes are extremely scale sensitive (Bowler and Kie, 2006; Boyce, 2006), and more resolute data might provide further information on the ecological interactions of these sympatric cervids. Finally, we believe that data on the distribution of male elk and mule deer, in concert with that for females, also would be of interest because the sexes of dimorphic ruminants sexually segregate for much of the year (Bowler, 2004). How spatial segregation of the sexes within a species affects competitive interactions between species has yet to be studied.

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