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TEMPOROSPATIAL DISTRIBUTIONS OF ELK, MULE DEER, AND CATTLE: RESOURCE PARTITIONING AND COMPETITIVE DISPLACEMENT

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Rocky Mountain elk (*Cervus elaphus nelsoni*), Rocky Mountain mule deer (*Odocoileus hemionus hemionus*), and cattle frequently co-occur on landscapes in the northwestern United States. We hypothesized that niche overlap would be greatest between introduced cattle with either of the 2 native herbivores because coevolution between native elk and mule deer should have resulted in strong patterns of resource partitioning. We observed strong differences among species in use of space, especially elevation, steepness of slope, and use of logged forests. We used 2 temporal windows to examine both immediate (6 h) and long-term (7 days) effects of competition. We noted strong avoidance over a 6-h period among the 3 ungulates. That effect was weaker for the previous 7 days. Cattle were generalists with respect to habitat selection; the 2 native herbivores avoided areas used by cattle. Mule deer and elk avoided one another during the short temporal window (6 h), although spatial differences in habitat use often were not maintained over 7 days. Elk used lower elevations when cattle were absent and moved to higher elevations when cattle were present, indicating shifts in niche breadth and competitive displacement of elk by cattle. We demonstrated strong partitioning of resources among these 3 species, and presented evidence that competition likely has resulted in spatial displacement.

Key words: *Cervus elaphus*, competition, competitive exclusion, elk, free-ranging cattle, mule deer, niche partitioning, *Odocoileus hemionus*, Oregon

Understanding how habitat selection affects distributions of large mammals across the landscape is a necessary prerequisite for examining patterns of resource partitioning and competition (Cooke 1997). Competition is difficult to assess without experimentation, because niche partitioning among coexisting species may have resulted from past competitive interactions (e.g., the ghost of competition past; Connell 1980). Despite numerous studies, causes and consequences of competition among large herbivores remain uncertain. This paucity of information on competition among large mammals is unfortunate because their life-history strategies should make them among the most competitive of all organisms (McCullough 1979, 1999; Stearns 1992). Moreover, a growing body of literature suggests that browsing and grazing by large herbivores can have far-reaching effects on the structure and function of ecosystems (see Bowyer et al. 1997; McNaughton 1985; Turner et al. 1997 for reviews).

An experimental approach to the study of competition among large, herbivorous

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mammals has been problematic, because conducting addition or removal experiments concerning competition among ungulates have not been feasible. Indeed, reviews by Keddy (1989) and Schoener (1983) included few examples of competition among large mammals. Thus, most studies of large herbivores infer effects of competition from the amount of resource or niche partitioning (Jenkins and Wright 1988; McCullough 1980; Putnam 1996; Sinclair 1985). Interactions between native herbivores and domestic cattle are among the few studies where interference or exploitive mechanisms among large herbivores have been proposed (Hobbs et al. 1996; Jenks et al. 1996; Julander 1958; Kie et al. 1991; Mackie 1970). Indeed, Bowyer and Bleich (1984) and Loft et al. (1987) reported that cattle reduced vegetative cover essential for fawning habitat for mule deer (*Odocoileus hemionus*). Johnson et al. (2000) demonstrated that elk (*Cervus elaphus*) affected the distribution of mule deer during spring but not vice versa. Likewise, Coe et al. (2001) reported stronger competitive interactions between cattle and elk than for mule deer and cattle in summer. Nonetheless, important theoretical and applied questions regarding competition remain unresolved.

We tested hypotheses concerning resource partitioning, habitat selection, and competition among free-ranging cattle, Rocky Mountain elk (*C. e. nelsoni*), and Rocky Mountain mule deer (*O. h. hemionus*). We predicted that resource partitioning would be most pronounced and competition minimized between the 2 native cervids, because past competitive interactions should have resulted in strong patterns of habitat separation. We expected the reverse pattern for relationships of nonnative cattle with mule deer or elk. We also predicted that the 2 species with high dietary overlap that consumed mostly graminoids (elk and cattle—Stevens 1966) would exhibit greater competitive interactions than either cattle or elk with the species that concentrated on forbs (mule deer—Bowyer 1984). We examined the temporospatial relationships among the 3 large herbivores to better understand how niche partitioning of habitats was affected by differing use of space and whether such differences were maintained over time. Finally, because cattle were added to our study area in spring and removed in autumn, we tested for competitive displacement of native herbivores by cattle during those seasons. We further hypothesized that if competition occurred, niche relations between 2 species would differ when a 3rd was added or removed.

Materials and Methods

Study area.—We conducted research from 1993 through 1995 on the Starkey Experimental Forest and Range (hereafter, Starkey) of the United States Forest Service. Starkey (45°12′N, 118°3′W) is situated in the Blue Mountains of northeastern Oregon and southeastern Washington and is located 35 km southwest of La Grande, Oregon. The area encompasses 10,125 ha, and is surrounded by a 2.4-m-high fence that prevents immigration or emigration of large herbivores (Rowland et al. 1997). Elevations range from 1,120 to 1,500 m. This site supports a mosaic of forests and grasslands, with moderately sloping uplands dissected by drainages, which are typical of summer ranges for elk and mule deer in the Blue Mountains (Rowland et al. 1997). Seasons were delineated with a climograph and were defined by months that grouped within similar ranges of temperature and precipitation (Fig. 1), and reflected changes in plant phenology.

We restricted collection of data and our analyses to the northeast experimental area on Starkey, which was separated from the remainder of Starkey by a fence (Rowland et al. 1997). This northeast area contained 1,453 ha and consisted of 4 major habitats including: mesic forest dominated by grand fir (*Abies grandis*; 25% of the study area); xeric forest characterized by Ponderosa pine (*Pinus ponderosa*; 6% of the study area); xeric grassland dominated by a few grasses and forbs, such as onespike oatgrass (*Danthonia unispicata*), Idaho fescue (*Festuca idahoensis*), and low gumweed (*Grindelia nana*; 25% of the study area); and logged forest, harvested during 1991–1992 and then seeded with

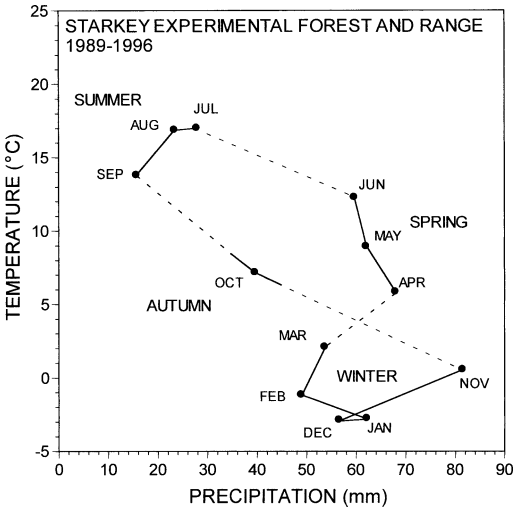

FIG. 1.—Climograph of mean monthly temperature and precipitation that define seasons on the Starkey Experimental Forest and Range, Oregon, 1989–1996. Solid lines indicate months within a particular season and dotted lines separate seasons.

rhizomatous grasses such as orchardgrass (*Dactylis glomerata*) and bluegrasses (*Poa*; 34% of the study area—Rowland et al. 1998). The logged forest was defined as a separate habitat because the composition of plant species, canopy cover, and responses of ungulates differed from the initial forest type. Grand fir in the northeast area suffered widespread mortality (>90%) from spruce budworm (*Choristoneura occidentalis*), and timber was harvested in 1991–1992, predominantly in areas where most trees had been killed (Rowland et al. 1997).

Our analyses included periods when all 3 species of ungulates were present on the study area, which typically was from mid-June through mid-October and included spring (only June), summer, and autumn (Fig. 1). Cattle were present on Starkey from mid-June until mid-October each year; most elk were fed a maintenance diet in a separate facility during winter (Rowland et al. 1997). Hence, only mule deer were present on the study area year-round. All 3 species occurred at moderate population densities relative to carrying capacity (Rowland et al. 1997). Population sizes in the northeast area were approximately 50 adult female cattle (with young), 75 mule deer, and 130 elk, as determined from stocking rate and helicopter census (Rowland et al. 1997). We collected data on locations of 118 individual females equipped with radiocollars, including 14 cattle, 18 mule deer, and 25 elk. Cattle were stocked at a moderate to high population density for the Blue Mountains of Oregon (Rowland et al. 1997). Annual recruitment of young elk on Starkey was 35–50 young:100 adult females and averaged 41 ($\pm$9.6 *SD*) from 1989 to 1995. Recruitment rate on our study area indicated that the population was increasing; however, this increase was well below the maximum finite rate of growth (λ = 1.46) reported for elk (Kimball and Wolfe 1974). Thus, some resources may have been in short supply, and competition among large herbivores was likely.

Definitions.—We defined exploitive and interference competition in accordance with Park (1962), Birch (1957), Case and Gilpin (1974), and Keddy (1989). Exploitive competition occurs when 1 species uses a limited resource at a rate that reduces its availability to coexisting species. Interference competition results when an individual of a dominant species causes direct harm to another individual via physical, chemical, or behavioral mechanisms; this may occur when 1 individual directly attacks another or in subtler forms, such as threat behavior or territoriality. Thus, interference competition precludes the use of a resource by a competing species, but does not necessarily remove that resource from the environment.

Both mathematical (Lotka 1932) and empirical (Brown et al. 1979) approaches to understanding competition recognize 2 important components to this process: number of competitors, and their ability to compete (i.e., their competition coefficients). We focus on this second component of competitive interactions among large herbivores, including niche overlap and aspects of past competition (Connell 1980) or avoidance along particular niche axes.

Geographic information system (GIS) analyses.—Locations of mule deer, elk, and cattle were collected with a rebroadcast civilian long-range navigation (LORAN-C) system from 1993 to 1995 (Findholt et al. 1996). This automated telemetry system located each radiocollared animal approximately every 1.5 h over 24 h from June to early November each year (Rowland et al. 1997). Data on animal locations and habitat variables were determined on a 30-m^2 pixel basis from a raster-based GIS maintained by the

Oregon Department of Fish and Wildlife and the United States Forest Service (Rowland et al. 1998). A spatial window of 25 pixels (5 pixels by 5 pixels; 2.25 ha) was centered on each animal location to account, in part, for error associated with telemetry locations of animals (Findholt et al. 1996; Johnson et al. 1998).

The telemetry system exhibited differences in location rates of animals that varied spatially across the study area (Johnson et al. 1998). Thus, statistical analyses were weighted by the inverse of the correction factor developed for Starkey in each year to mitigate effects of telemetry error on our analyses.

Habitat values for percentage of each plant community and means for elevation (m), slope (%), aspect (°), distance to permanent and intermittent water (m), distance to the ungulate-proof fence (m), and distances to roads (m) were calculated for each 25-pixel window. These derived variables characterized the spatial window.

Availability of water varied among seasons, and permanent sources of water consisted primarily of developed springs. Intermittent sources of water, which included a riparian area, typically retained water until mid summer (July or August), depending on rainfall in June and early July.

We controlled for effects of the ungulate-proof fence by including distance to the fence (m) in stepwise logistic analyses. Potential effects of roads on animals were evaluated on the basis of different levels of traffic. One road, open to the general public (hereafter, open road), was located outside the ungulate-proof fence on the southwestern border of the study area. Restricted roads were distributed throughout the study area and were used moderately by Forest Service and other research personnel. Closed roads had no traffic. We also calculated an index of diversity of terrain for each spatial window by multiplying standard deviation of the slope by mean angular deviation of aspect (Nicholson et al. 1997).

We created a database using 1 randomly chosen location per day for each elk, deer, and cow (June–October, 1993–1995) to help minimize the lack of independence of sample locations. For each animal, we determined the habitat values for its spatial window. We also recorded the total number of telemetered mule deer, elk, and cattle within each window 3 h before and after (6 h total) and during the previous 7 days from the time an animal was located. We chose 6-h and 7-day windows to examine immediate (6 h) and accumulated (7 days) effects of potential competitors over time. Six hours was required to obtain an adequate sample size without encompassing >1 activity period. Seven days was the longest period that allowed for a sufficient number of samples during spring (June) and autumn (October) once data were time-lagged for those seasons. We then sampled all telemetered animals without replacement for that day and excluded any animals located within a previously sampled window for that day to maintain independence of animal locations. We repeated that procedure until all animals of each species with radiocollars were located for that day.

After we determined the number of animal locations sampled, we then cast an equal number of random points to calculate availability of habitats and physical characteristics for each spatial window centered on each random point (i.e., 1 random point for each animal location). Using this methodology, we recorded a total of 10,386 animal locations, based upon 57 telemetered animals and 10,386 random points. Locations for radiocollared animals had varying sample sizes depending on the number of years that an animal was present in the study area. To prevent a single animal from having a disproportionate effect on analyses, we divided our data into subsets with 1 location per animal per month per year, for a total of 465 animal locations and 465 random locations, randomly drawn from our data set of 57 individuals. To assure the aptness of this method, we selected, at random, 10 subsets of those data for all collared animals and tested means with multivariate analysis of variance (MANOVA) for all habitat variables among subsets of those data. Means of habitat variables were not significantly different ($P > 0.15$) between our data subsets, and we randomly selected 1 subset for further analyses.

Statistical design.—We used a hierarchical approach for understanding habitat selection and potential competition among cattle, elk, and mule deer (Table 1). First, multiresponse permutation procedures (MRPP—Slauson et al. 1991) were used to test for differences in spatial distributions among cattle, elk, and mule deer, as well as from random locations (the null model). MRPP offers a powerful method to assess the distributions of mammals (Nicholson et al. 1997; Pierce et al. 2000).

TABLE 1.—Hypotheses related to niche partitioning by cattle, elk (*Cervus elaphus*), and mule deer (*Odocoileus hemionus*), and statistical procedures used to test them; further descriptions and rationale for statistical tests and their citations are provided in ''Materials and Methods'' section in text.

Hypotheses	Statistical tests
Null model	
Animals are distributed randomly across the landscape	MRPP[a] (locations used versus random locations for each species)
Species use of space differs across the landscape	MRPP (locations used by each species)
Habitat selection	
Habitat variables are selected, avoided, or are important for each species	Stepwise logistic regression by species (used versus random locations)
Species select habitat components differently	MANOVA[b] with main effects location (used, random), species (mule deer, elk, cattle), and season (spring, summer, autumn)
Interspecific associations	
Relative influence of interference versus exploitive competition	Multiple regression 6-h and 7-day regression models for each species
Effects of cattle	
Mule deer and elk are displaced by cattle	MANOVA with main effects species (mule deer, elk), habitat (slope, elevation), and season (spring, autumn)

[a] Multiresponse permutation procedures.
[b] Multivariate analysis of variance.

We used logistic regression to identify habitat variables selected (or avoided) by each species (Bowyer et al. 1998, 1999). We employed MANOVA to test for differences in relative use and availability (selection or avoidance) of habitat variables among species (Bowyer et al. 1998, 1999; Nicholson et al. 1997). We then evaluated the relative importance of the 4 plant communities for each ungulate species (Bowyer and Bleich 1984; Weixelman et al. 1998).

We developed multiple-regression models to test for any remaining competition between those large herbivores with effects of resource partitioning held constant (Fox and Luo 1996; Luo et al. 1998). We incorporated a temporal window of 7 days into multiple-regression models and compared them with the near-instantaneous (6 h) multiple-regression models to evaluate relative effects of accumulated time on potential competitive interactions. A regression approach may be used to determine competition coefficients under field conditions for sympatric species (Crowell and Pimm 1976; Hallett and Pimm 1979; Schoener 1974). Moreover, the regression method controls for effects of past competitive interactions on existing partitioning of niches (Hallett and Pimm 1979). This method, however, was problematic because estimated coefficients were qualitatively inconsistent and contained statistical artifacts in the relation between competitive ability and census variance (Rosenzweig et al. 1985). Application of a standardization procedure eliminates effects of census variance on coefficients of competition (Fox and Luo 1996; Luo et al. 1998). Thus, the multiple-regression approach allows evaluation of competitive interactions while controlling for niche partitioning among species.

Statistical analyses.—Before addressing competition among species, we used MRPP to test the null model that species were distributed randomly across the landscape and that species distributions were random compared with one another. MRPP are distribution-free statistics that rely on permutations of data based on randomization theory and allow analyses of spatial differences not possible with logistic regression, such as partitioning of space within a habitat type (Slauson et al. 1991; Zimmerman et al. 1985). Significant differences from the distribution of random locations by a particular species indicate some type of habitat selection, and

significant differences among the distributions of species indicate that there is spatial separation.

We used stepwise logistic regression (α = 0.15 to enter and remain) to evaluate variables associated with animal locations (coded 1) and to determine habitat variables that differed significantly from random locations (coded 0) for each species (SAS Institute Inc. 1987). We controlled for multicollinearity (Bowyer et al. 1998, 1999) by eliminating 1 of any pair of variables with $r^2 > 0.45$. Distance to open road was negatively correlated with elevation ($r = -0.70$, $P < 0.001$). Because the open road was outside the study area, that variable was eliminated from our analyses, to avoid problems with multicollinearity. We evaluated the aptness of logistic models with a Homser–Lemeshow test for goodness-of-fit (Agresti 1990). Because animals may have been present at a random location other than when we sampled, our analysis provided a conservative measure of habitat selection (Bowyer et al. 1998). A logistic model was fit for all species (including species as a coded variable), and then separate models were analyzed for each species to reduce dimensionality of data. This approach has been used previously to examine habitat selection within and among species of mammals (Bowyer et al. 1998, 1999).

Habitat variables selected from logistic regression were used to develop a MANOVA model to evaluate differences in habitat selection among species. We performed an arcsine square-root transformation on percentage data and a square-root transformation on the number of animals within each spatial window, to satisfy distributional assumptions of MANOVA (Johnson and Wichern 1992). We transformed aspect (a circular variable) to Cartesian coordinates (sine and cosine) prior to analyses (Zar 1996).

We used MANOVA to determine interspecific differences in habitat selection within seasons, and to test for significant species (cattle, elk, or mule deer) by location (animal or random) interactions (i.e., differences in selection among species). Habitat characteristics were dependent variables and main effects were animal location (use versus random), species (cattle, elk, mule deer), and season (spring, summer, autumn). Significant location-by-species interactions indicated differences in selection (use > availability) or avoidance (use < availability) among species (Bowyer et al. 1998, 1999; Nicholson et al. 1997; Rachlow and Bowyer 1998; Weixelman et al. 1998). We then used analysis of variance with planned contrasts to separate significant differences ($P \leq 0.05$) in means of habitat variables between species.

For descriptive purposes only, mean values for each habitat variable for random locations (available) were subtracted from mean values of animal locations (used) and divided by the sum of those values to allow for comparisons without extreme differences in units measured; a positive result typically indicated selection and a negative one indicated avoidance (Powell et al. 1997). Bivariate plots of 95% confidence interval for variables that differed among species were plotted to further elucidate resource partitioning among species. We also determined the relative importance of each habitat type seasonally. Importance was defined as use multiplied by availability rescaled to 100% (Bowyer and Bleich 1984; Weixelman et al. 1998). This approach allows evaluation of habitat components that are crucial to a species but are not limited in supply. Logistic regression will not identify such habitats (Bowyer et al. 1999).

We determined interspecific associations using multiple-regression analyses for each species with habitat variables that differed in selection among species included as covariates (Fox and Luo 1996; Luo et al. 1998). We used Mallow's *Cp* to aid in model selection; this statistic provides information similar to that from Akaike's information criterion (Atilgan 1996). Variables representing number of animals within each spatial window (for either 6 h or 7 days) were standardized prior to analyses to prevent biases associated with the correlation between regression coefficients and variances of independent variables (Fox and Luo 1996; Luo et al. 1998; Marquandt 1980). We used separate regression models to evaluate temporal effects (e.g., 6 h and 7 days) for each species. Model fit was evaluated with adjusted coefficient of multiple determination (R_a^2), to account for the number of independent variables in the multiple-regression model (Zar 1996). The dependent variable for both regression models (6 h and 7 days) consisted of 1 of the 3 species within 6 h of a particular animal location. For example, number of elk within 6 h of an animal location was the dependent variable in regression models to evaluate effects of cattle and mule deer on elk. Independent variables for 6-h models included the number of the 2 sympatric species within 6 h ($\pm$3 h) of the time of

location, and habitat variables from MANOVA that differed in selection among species. For 7-day models, independent variables included the accumulated number of all species within the previous 7 days and habitat variables from MANOVA that differed in selection among species. Those habitat variables that were included in the regression model behaved as covariates in multiple-regression analyses (Zar 1996). Standardized regression coefficients of independent variables for sympatric species, located within each spatial window (6 h or 7 days), were estimated coefficients of association (α_{ij}) and indicated the effect of the 2 sympatric species on the third species (e.g., dependent variable). Fox and Luo (1996) provide a more complete description of this method. Because our data for animal counts within the spatial windows were standardized prior to analyses, the estimated coefficients of association ranged between 1 and -1. A coefficient of 1 indicates complete spatial overlap, a coefficient of -1 indicates spatial avoidance, and a value of 0 or nonsignificance for that variable indicates no effect.

Our interpretations of results from multiple-regression analyses differ slightly from traditional competition coefficients, because those coefficients likely represented differential use of space among species rather than intensity of competition. This different interpretation is required because our dependent variables in multiple-regression analyses are strongly representative of where those species already occur across the landscape and are less dependent on locations of competitors. Strongly negative regression coefficients in our models indicate low spatial overlap among species, rather than 1 species being a more efficient competitor (Fox 1999).

After reviewing results from multiple regressions, we observed that avoidance among species was not maintained over a long time period. Moreover, because we suspected that the 2 native herbivores avoided cattle, we performed an a posteriori test of competition between native herbivores and cattle. We returned to the original data and selected 2 periods, 2 weeks before and 2 weeks after cattle were introduced to the study area during spring and removed from the study area in autumn of each year. We again divided data in subsets to prevent any single animal from having a disproportionate effect on analyses; thus, this data set contained 492 locations for elk and 244 locations for mule deer. We used the presence of cattle as a treatment effect and compared relative responses of mule deer and elk to the introduction of cattle using MANOVA. The 2 variables in which cattle and the 2 native herbivores partitioned resources were slope and elevation. Thus, MANOVA model used those variables to compare responses of elk and mule deer to introduction and removal of cattle.

RESULTS

Nearest-neighbor distances of elk (1,971 m), mule deer (1,487 m), cattle (2,011 m), and random locations (2,038 m) indicated some differences in use of space across seasons. Both elk ($P < 0.01$) and mule deer ($P < 0.01$) differed from random locations (e.g., the null model), signifying that selection of habitat occurred (i.e., locations of animals were clumped spatially compared with random samples). Cattle did not differ ($P = 0.10$) spatially from random points. When distributions of species were compared, all 3 species differed ($P < 0.01$) spatially from one another with seasons combined ($P < 0.001$), and also when seasons were tested separately ($P \leq 0.001$). During spring, however, locations of elk and mule deer did not differ ($P = 0.18$) spatially from each other.

We modeled habitat selection for each species of large herbivore with logistic regression, including plant community, physical characteristics of the landscape, distances to roads, distances to sources of water, and distance to the fence (Table 2). None of our models deviated from a logistic fit ($P > 0.26$, Homser–Lemeshow tests for goodness-of-fit). Year did not enter any logistic model ($P > 0.15$), indicating no yearly differences in habitat selection among species. Likewise, no fence effect on habitat selection by cattle, elk, or mule deer occurred ($P > 0.15$). Distances to water sources and either elevation or slope entered all logistic models, and strongly influenced the distribution of the 3 species (Table 3). The logistic model for cattle was 66% concordant and indicated strong ef-

TABLE 2.—Summary statistics of habitat characteristics for locations of 3 species of large herbivores (used) and random locations (available) on the Starkey Experimental Forest and Range, northeast Oregon, 1993–1995. Habitat types are expressed as the mean percentage of each habitat in a spatial window (150 by 150 m) surrounding each animal and random locations.

	Cattle (n = 124)		Elk (n = 183)		Mule deer (n = 158)		Random (n = 465)	
Habitat variables	$\bar{X}$	*SE*	$\bar{X}$	*SE*	$\bar{X}$	*SE*	$\bar{X}$	*SE*
Mesic forest (%)	0.37	0.03	0.41	0.02	0.41	0.03	0.40	0.01
Xeric forest (%)	0.09	0.02	0.04	0.01	0.11	0.02	0.07	0.01
Logged forest (%)	0.26	0.03	0.33	0.02	0.24	0.03	0.26	0.01
Xeric grasslands (%)	0.27	0.03	0.22	0.02	0.25	0.02	0.29	0.01
Slope (%)	13.3	0.46	15.3	0.39	15.5	0.49	15.3	0.25
Aspect (°)	119.3	8.88	136.6	6.97	140.2	7.26	131.7	4.07
Elevation (m)	1,252	5.5	1,287	3.9	1,299	3.4	1,267	2.6
Terrain	118.84	12.52	115.56	8.46	113.77	8.76	131.18	5.90
Distance to permanent water (m)	357.60	19.53	387.86	14.00	326.84	12.88	401.10	9.35
Distance to intermittent water (m)	726.37	51.18	803.59	38.22	739.14	39.54	859.55	26.18
Distance to fence (m)	581.79	30.88	596.05	23.80	598.29	27.63	625.88	17.66
Distance to open roads (m)	1,170.43	56.05	918.40	37.96	750.99	30.85	1,113.35	25.52
Distance to restricted roads (m)	86.53	6.05	92.92	4.62	96.94	5.52	85.02	2.67
Distance to closed roads (m)	546.73	32.72	677.60	25.82	593.75	23.12	602.27	16.31

fects of slope and distance to sources of permanent water (Table 3). Logistic models for elk (67% concordant) and mule deer (73% concordant) indicated selection for several vegetation communities; elk selected both mesic forests and logged forests, and mule deer avoided xeric grasslands (Table 3). Elevation and distance to sources of intermittent water also entered logistic models for both elk and mule deer (Table 3).

Habitat selection differed among seasons for these 3 large herbivores (Wilks' lambda, $P = 0.015$). MANOVA revealed a species (cattle, elk, mule deer) by location (used, random) interaction (Wilks' lambda, $P < 0.001$), indicating differences in selection of some habitat variables among species. Univariate analyses following MANOVA identified logged forest, slope, and elevation as the only variables in which selection differed among species ($P < 0.01$; Fig. 2). Although there were some differences in selection of xeric grasslands, those differences were marginally not significant ($P = 0.075$; Fig. 2). Both native herbivores (elk and mule deer) selected higher elevations and steeper slopes than did cattle, especially during spring and summer (Fig. 2). Bivariate plots of 95% confidence interval indicated that cattle differed from the native herbivores by avoiding steeper slopes and high elevations, particularly during spring and summer (Fig. 3). Hence, during all seasons elk and mule deer partitioned physical characteristics of the landscape from cattle by occupying higher elevations and steeper slopes (Figs. 2 and 3). Mule deer and elk strongly overlapped in use of slope and elevation, and partitioned use of vegetation communities (Figs. 2 and 3). Elk selected logged forest and differed ($P < 0.01$) from mule deer and cattle; this differential use of logged forests and possibly of xeric grasslands was particularly evident during autumn (Figs. 2 and 3).

Mesic forest habitat was of greatest importance to all 3 species (Fig. 4), although there was no difference in selection of that habitat among species (Fig. 3). Logged forests and xeric grasslands were of intermediate importance, and xeric forests were the least important plant communities to these large herbivores (Fig. 4).

Differences in habitat use by cattle, elk, and mule deer were stronger over the 6-h

TABLE 3.—Results of weighted logistic-regression from models of habitat selection for cattle, elk (*Cervus elaphus*), and mule deer (*Odocoileus hemionus*) on the Starkey Experimental Forest and Range, northeastern Oregon, 1993–1995. Animal locations were coded 1 and random locations were coded 0. Hosmer–Lemshow tests for goodness-of-fit indicated models did not deviate ($P > 0.10$) from logistic fit.

Variable	Parameter estimate	*SE*	*P*
All species			
Intercept	−7.74	2.020	<0.001
Logged forest	0.44	0.198	0.027
Elevation	0.01	0.002	<0.001
Slope	−0.04	0.016	0.001
Distance to restricted roads	<0.01	0.001	0.016
Distance to permanent water	<−0.01	<0.001	0.016
Distance to intermittent water	<−0.01	<0.001	<0.001
Cattle			
Intercept	2.35	0.696	<0.001
Slope	−0.12	0.035	<0.001
Distance to permanent water	<−0.01	<0.001	0.037
Elk			
Intercept	−9.53	3.255	0.003
Mesic forest	0.64	0.361	0.075
Logged forest	1.16	0.367	0.002
Elevation	0.01	0.002	0.007
Distance to restricted roads	<0.01	0.002	0.070
Distance to intermittent water	<−0.01	<0.001	0.015
Mule deer			
Intercept	−21.86	4.781	<0.001
Xeric grasslands	−0.78	0.426	0.068
Aspect	−0.34	0.228	0.140
Elevation	0.02	0.004	<0.001
Distance to permanent water	<−0.01	<0.001	0.022
Distance to intermittent water	<−0.01	<0.001	0.027

period than for the previous 7 days (Table 4). Coefficients of association for the 6-h models were strongly negative, indicating strong avoidance among all species during all seasons (Table 5). The relative effect of resource partitioning on habitat selection was controlled in both 6-h and 7-day models, because habitat variables from MANOVA that differed in selection among species were included as covariates in those models. We also included xeric grasslands because they were marginally nonsignificant ($P = 0.075$).

We observed an interaction of season by species by treatment (Wilks' lambda, $P = 0.046$), as well as a species by treatment interaction (Wilks' lambda, $P = 0.002$) for use of slope and elevation by elk and mule deer following introduction and removal of cattle during spring and autumn. We then analyzed species (elk and mule deer) and seasons (spring and autumn) separately. Presence or absence of cattle did not affect use of slopes by elk (Fig. 5). Mule deer moved to lower elevations following introduction of cattle during spring. Addition of cattle did not affect use of slope by mule deer during spring, although mule deer moved to more-level slopes following removal of cattle during autumn (Fig. 5). Elk used higher elevations following addition of cattle during spring and moved to lower el-

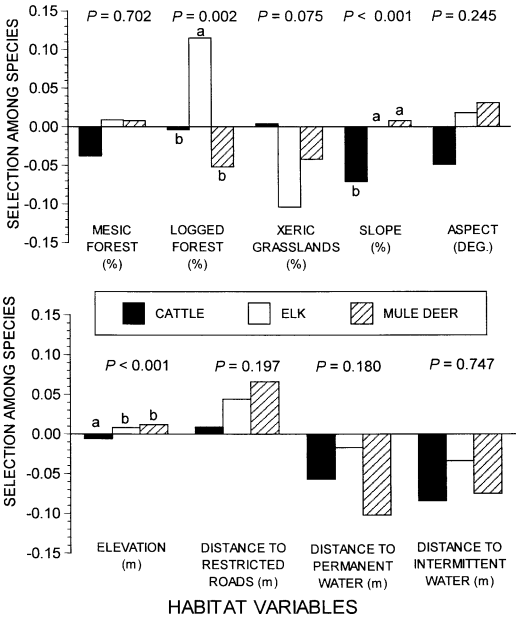

FIG. 2.—Selection of habitat variables (used minus available, divided by used plus available) among cattle, elk (*Cervus elaphus*), and mule deer (*Odocoileus hemionus*) on the Starkey Experimental Forest and Range, Oregon, 1993–1995. Values for selection vary from +1 to −1, and negative values for distance measurements indicate selection (i.e., animals are closer than predicted from random). *P*-values are from analysis of variance with planned contrasts, following significant differences in selection or avoidance of habitat determined from MANOVA (Wilks' lambda, $P < 0.001$). Differences in lowercase letters indicate significant differences ($P < 0.05$).

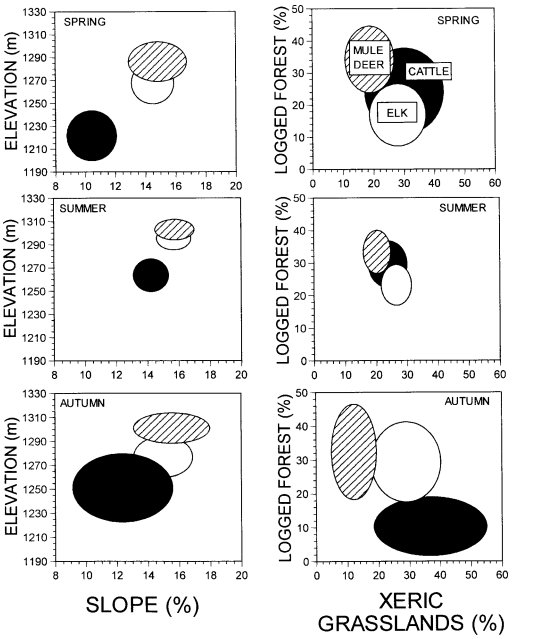

FIG. 3.—Bivariate plots of niche partitioning based on elevation and slope (left) and on logged forest and xeric grasslands (right). Ellipses are 95% *CI* for cattle, elk (*Cervus elaphus*), and mule deer (*Odocoileus hemionus*), across seasons on the Starkey Experimental Forest and Range, Oregon, 1993–1995.

evations following the removal of cattle during autumn (Fig. 5).

DISCUSSION

We predicted that resource partitioning would be more pronounced between the 2 native herbivores than for either cervid with introduced cattle. Coexistence between deer and elk was expected to result in evolution of strong patterns of habitat or dietary separation. Indeed, we observed strong evidence of resource partitioning of habitats and space among all 3 species of large herbivores (Figs. 2 and 3). Cattle differed from mule deer and elk in avoidance of steep slopes and high elevations. Although native herbivores selected similar slopes and elevations, mule deer and elk strongly partitioned use of vegetation communities (Figs. 2 and 3). These observations also are supported by significant differences among species in use of space, as indicated by MRPP. Mule deer (Bowyer 1984), elk (Bowyer 1981), and cattle (Kie and Boroski 1996) are constrained in their distribution by availability of free water; all 3 species selected areas near water rather than at random (Table 3). These herbivores did not differ, however, in selection of water resources (Fig. 2).

Some characteristics of our study site held the potential to affect our results. Distance to the ungulate-proof fence failed to enter any of the logistic models for evaluating habitat selection. This outcome indi-

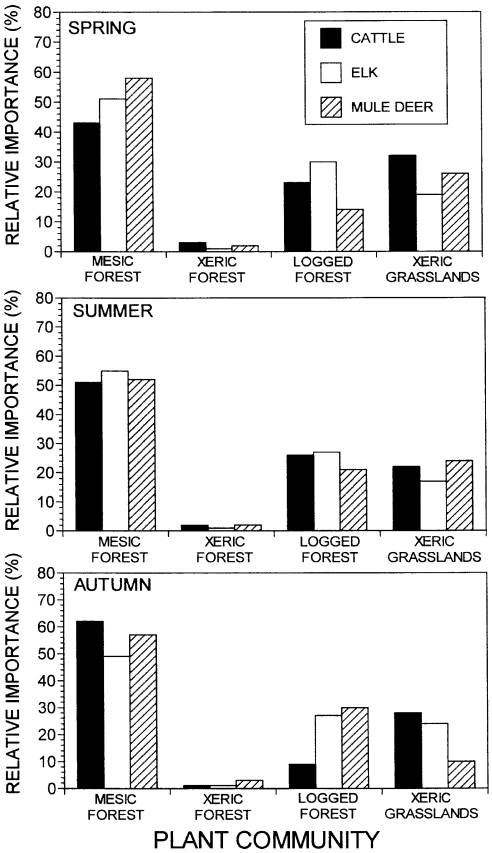

FIG. 4.—Seasonal importance of vegetation communities for cattle, elk (*Cervus elaphus*), and mule deer (*Odocoileus hemionus*) on the Starkey Experimental Forest and Range, Oregon, 1993–1995. Importance is defined as use multiplied by availability, scaled to 100%.

cated the fence was not a significant factor in affecting habitat selection or distributions of animals on Starkey. Although restricted roads entered logistic models for elk, no differences existed in selection or avoidance of roads among species, indicating that use of restricted roads did not affect our analyses. Likewise there were no differences among years in selection of habitats by the 3 herbivores.

Coe et al. (2001) noted avoidance of cattle by elk on Starkey. Their results were based on differences between species in convexity, a variable associated with terrain that measured use of ridge tops and drainage bottoms. This outcome is similar to our findings of resource partitioning based on elevation and slope.

Cattle were habitat generalists when locations were pooled across seasons. Indeed, MRPP did not detect differences between cattle locations and random sites, and no vegetation types entered the logistic-regression models for cattle (Table 3). Cattle used more-level slopes and lower elevations than did elk or mule deer (Figs. 2 and 3).

Strong, negative coefficients of association in the 6-h regression models indicate spatial avoidance by either 1 or both species (Table 4). Indeed, MRPP indicated that all 3 species differed significantly from one another in use of space. Mule deer and elk may have avoided cattle, as indicated by strong negative coefficients in the 6-h models for cattle, and for the cattle variable in the mule deer and elk models. That analysis could not determine if negative coefficients between mule deer and elk in both 6-h models resulted from mutual avoidance or from 1 species consistently avoiding the other.

Effects of resource partitioning may be examined when the 6-h and 7-day models are considered together. Strongly negative coefficients for the 6-h period indicate spatial avoidance and any remaining effects that may be attributed to competition are indicated in the 7-day model. Negative coefficients indicate avoidance over the short term (e.g., 6-h models), and possibly interference or exploitive competition with maintained avoidance over the previous 7 days. Those patterns of avoidance may be maintained by interference effects or by the removal of resources by a competitor (e.g., exploitive competition). Conversely, positive coefficients in the 7-day models indicated that the avoidance observed in the 6-h models was not maintained and there was high spatial overlap for the longer period. Hence, those large herbivores used the same habitat, which may be indicative of exploitive competition, particularly during autumn. Large, positive values for coeffi-

TABLE 4.—Multiple-regression models for short-term (6 h) and long-term (7 days) effects. Models were weighted by correction factor for radio telemetry, to evaluate competitive interactions among cattle, elk (*Cervus elaphus*), and mule deer (*Odocoileus hemionus*) on the Starkey Experimental Forest and Range in northeastern Oregon, 1993–1995. All models were significant ($P < 0.001$).

Model and season	6-h model			7-day model		
	d.f.	*F*	R_a^2	*d.f.*	*F*	R_a^2
Cattle						
Spring	6, 92	36.07	0.682	7, 91	9.43	0.376
Summer	6, 277	113.55	0.705	7, 276	6.84	0.126
Autumn	6, 75	24.04	0.631	7, 74	12.26	0.493
Overall	6, 458	241.10	0.674	7, 457	20.25	0.225
Elk						
Spring	6, 92	41.33	0.712	7, 91	4.07	0.180
Summer	6, 277	141.74	0.749	7, 276	10.85	0.196
Autumn	6, 75	32.87	0.703	7, 74	12.44	0.497
Overall	6, 458	199.62	0.720	7, 457	16.93	0.194
Mule deer						
Spring	6, 92	43.47	0.722	7, 91	5.05	0.224
Summer	6, 277	131.02	0.733	7, 276	7.88	0.145
Autumn	6, 75	27.16	0.660	7, 74	4.83	0.249
Overall	6, 458	188.55	0.708	7, 457	11.34	0.135

cients among conspecifics in the 7-day models for mule deer support this observation. Intraspecific competition by female herbivores may be intense (McCullough 1979). When the 7-day models for elk and mule deer are considered together, coefficients of association for mule deer in the 7-day models for elk were consistently not significant; however, effects of elk on mule deer were significant for all seasons, except spring. Thus, mule deer are more strongly affected by the movements of elk than are elk by mule deer. Moreover, the strong habitat partitioning observed for summer indicated by significant negative coefficients in the mule deer model may be driven by mule deer avoiding elk. During autumn, coefficients of association for elk on mule deer were positive and significant, indicating spatial overlap; changes in forage quality as summer progresses to autumn likely forced mule deer to move into areas used by elk, thereby increasing spatial overlap and likely resulting in exploitive competition. Johnson et al. (2000) noted that mule deer ostensibly avoided elk in spring on Starkey. Although our data did not support their observations during spring, we observed similar patterns of movements by mule deer during summer.

Resource partitioning of dietary niche may result in high overlap in habitat use without increasing competitive interactions (Hanley 1984; Krebs et al. 1974; MacArthur and Pianka 1966). Although we did not measure dietary differences, habitat selection is highly correlated with forage availability in large herbivores (Hanley 1984); thus, high overlap on the habitat axis may be accompanied by low overlap on a dietary niche axis (Kie and Bowyer 1999; Krebs et al. 1974; MacArthur and Pianka 1966). Although overlap in habitat use has been reported to be high for deer and elk, diet overlap is probably relatively low when forage is abundant, because elk are more likely to feed upon graminoids than do mule deer, whereas mule deer feed primarily on forbs and browse (Bowyer 1984; Hanley 1984; McCullough 1980). Seasonal changes in forage availability, however, often lead to increased dietary overlap as forage resources become less available

TABLE 5.—Standardized competition coefficients (α) for 3 sympatric ungulates during spring, summer, and autumn as determined from weighted multiple regressions, Starkey Experimental Forest and Range, northeastern Oregon, 1993–1995. Number of conspecifics plus the focal animal in the 6-h models is the dependent variable for both 3-h and 7-day models.

Competitive effect	α_{ij}			
	Spring	Summer	Autumn	Overall
Cattle model				
6-h model				
Elk	−0.790***	−0.866***	−0.831***	−0.828***
Mule deer	−0.773***	−0.823***	−0.714***	−0.785***
7-day model				
Cattle	0.309***	0.178**	0.475***	0.275***
Elk	0.028^{ns}	−0.161**	−0.167*	−0.106**
Mule deer	−0.225**	−0.051^{ns}	−0.343***	−0.148***
Elk model				
6-h model				
Cattle	−0.714***	−0.736***	−0.669***	−0.716***
Mule deer	−0.818***	−0.803***	−0.738***	−0.790***
7-day model				
Cattle	−0.071^{ns}	−0.137**	−0.680***	−0.251***
Elk	0.386***	0.403***	0.046^{ns}	0.327***
Mule deer	0.079^{ns}	−0.071^{ns}	−0.011^{ns}	−0.049^{ns}
Mule deer model				
6-h model				
Cattle	−0.676***	−0.741***	−0.658***	−0.707***
Elk	−0.789***	−0.852***	−0.844***	−0.823***
7-day model				
Cattle	−0.182^{ns}	0.071^{ns}	0.413***	0.034^{ns}
Elk	−0.176^{ns}	−0.309***	0.252*	−0.212***
Mule deer	−0.135^{ns}	−0.161**	0.216*	0.168***

* = $P \leq 0.05$, ** = $P \leq 0.01$, *** = P 0.001, ns = $P > 0.05$.

(Schwartz and Ellis 1981). Indeed, increased dietary overlap has been reported between cattle and elk (Stevens 1966), mule deer and elk (Mower and Smith 1989), and mule deer and cattle (Bowyer and Bleich 1984) in other areas during periods when forage abundance and availability were reduced. We observed high spatial overlap of herbivores during autumn. Moreover, with the exception of elk, the strongly positive coefficients during autumn when resources are most limiting support this observation; intraspecific effects would be stronger than interspecific ones because of dietary overlap among conspecifics. Thus, we hypothesize that those large herbivores were competing for resources (Table 5). Moreover, positive coefficients of association, particularly during autumn, likely indicated exploitive competition.

We hypothesized, a posteriori, that the introduction of cattle to the study area might result in changes in niche breadth among the native herbivores, especially in use of slope and elevation. Indeed, cattle differed from native herbivores by using lower elevation sites with shallower slopes. Comparisons of elevation and slope prior to and following addition of cattle during spring and prior to and following removal of cattle in autumn indicated that competitive displacement likely occurred between cattle and elk, although we could not control for effects of season in that analysis. Indeed, during spring and autumn, elk used lower elevations when cattle were not in the study

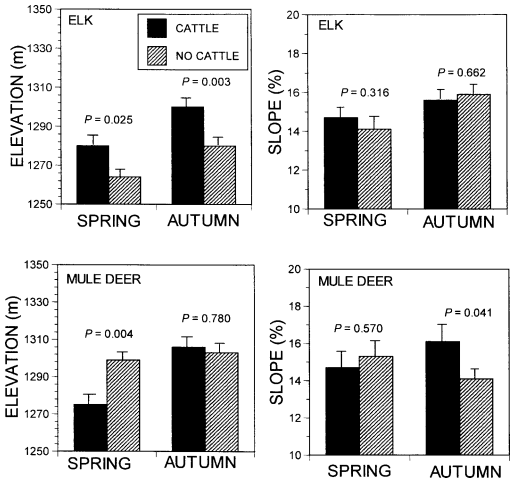

FIG. 5.—Mean (+*SE*) seasonal use of elevation and slope by elk (*Cervus elaphus*—above) and mule deer (*Odocoileus hemionus*—below) in response to presence and absence of cattle on the Starkey Experimental Forest and Range, Oregon, 1993–1995. *P*-values are from analysis of variance following significant treatment effects from MANOVAs (Wilks' lambda, $P < 0.05$).

area and used higher elevations when cattle were present. We suggest that the corresponding shift in niche breadth of elk indicates competitive displacement by cattle (Hardin 1960; Levin 1970). Mule deer shifted to more-level slopes following removal of cattle during autumn. During spring, however, shifts in use from higher to lower elevations following the introduction of cattle indicated a more complicated response. During spring, mule deer may have responded to elk movements to higher elevations following the addition of cattle to the study area.

Cattle seldom used areas with steep slopes and were widely distributed across vegetational communities at low elevations. These introduced herbivores selected nearness to sources of water, which included riparian zones. Consequently, we hypothesize that sensitive riparian areas at low elevations would require more protection from overgrazing by cattle than those on steep slopes or at high elevations with rugged terrain.

Most studies concerning niche partitioning among large herbivores have not considered cascading effects of competition between 2 species on a 3rd. Thus, studying only 2 of these large herbivores would not have revealed how the niche dynamics of cattle, elk, and mule deer were interconnected. Moreover, in the absence of data on cattle, measuring either habitat use or selection might lead to misinterpreting the habitat requirements of elk and mule deer and to subsequent errors in managing habitat for those ungulates.

We observed substantial resource partitioning in use of slope, elevation, and vegetative communities by cattle, elk, and mule deer. We also demonstrated changes in niche breadth of elk following the addition and removal of cattle from the study site, which likely indicated competitive displacement. Nonetheless, most aspects of the ecology of large mammals are influenced by density-dependent mechanisms (McCullough 1979, 1999), and that observation holds for understanding competitive interactions among large herbivores. Competition is a function of both number of competitors and their ability to compete effectively. When there is a large overlap on 1 or more niche axes, avoidance or partitioning would be expected on another axis (Kie and Bowyer 1999; McCullough 1980). Although we strongly inferred that competition occurred, the ungulates we studied were also strongly partitioning habitats and space. At much higher density, however, the ability to partition space would be reduced, and dietary and habitat partitioning might be intensified. Niche partitioning among populations at high densities becomes more difficult as resources become more limiting, leading to more competition. Such tradeoffs among use of space, diet, and habitats have been documented with increasing population density for the sexes of white-tailed deer (*Odocoileus virginianus*—Kie and Bowyer 1999). A manipulative experiment

examining the effects of density-dependent processes on partitioning of space, habitat, and diet holds the most promise for understanding both resource partitioning and competition among large herbivores.

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