RESPONSES OF ELK AND MULE DEER TO CATTLE IN SUMMER

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Abstract

Cattle graze seasonally on national forests in the Western United States, and mule deer (*Odocoileus hemionus*) and/or elk (*Cervus elaphus*) are sympatric with cattle in most of these areas. But the effects of interspecific interactions in terms of both the resources selected and animal distributions across landscapes are poorly understood. At the USDA Forest Service Starkey Experimental Forest and Range (Starkey), located in northeast Oregon, USA, elk and mule deer were free ranging within a 78 km^2 study area enclosed by a 2.4 m high fence while cattle were moved among pastures in summer on a deferred-rotation schedule. Elk, mule deer, and cattle were located with an automated telemetry system from 1993 - 1996 and locations were linked to a geographic information system (GIS) of Starkey. Our objective was to examine responses of elk and mule deer to cattle at several spatial and temporal levels. We compared elk and mule deer distributions, use of plant communities, and resource selection functions in one cattle pasture (24 km^2) during early summer (cattle present in odd-numbered years) and late summer (cattle present in even-numbered years). Elk and deer differed in their spatial and temporal responses to presence of cattle.   When cattle were present, the proportion of elk locations within the pasture decreased and use of the ponderosa pine/Douglas fir (*Pinus ponderosa/Pseudotsuga menziesii*) plant community within the pasture decreased in early summer and increased in late summer. The cattle resource selection function variable for early summer was not a predictor of elk distributions when cattle were present, but it was a predictor on years when cattle were absent. In late summer, the cattle resource selection function variable was a predictor of elk distributions regardless of presence of cattle. For mule deer distributions the cattle resource selection function variable was not a significant predictor in early summer (cattle present or absent), or in late summer when cattle were present, but it was a negative predictor of mule deer distributions when cattle were absent in late summer.   Mule deer use increased or decreased in opposite direction from elk use in 3 of 4 season/year combinations for both pasture and ponderosa pine/Douglas fir. Our results suggest that competition for forage could occur between elk and cattle in late summer and that species interactions may be stronger between elk and cattle than mule deer and cattle.

Introduction

Allocating forage and maintaining proper stocking levels of domestic and wild ungulates are fundamental concepts of range management (Stoddart and Smith 1955). Managing rangelands for cattle, elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) in montane habitats is complicated because interspecific interactions vary from potential competition (Skovlin et al. 1968, Lindzey et al. 1997, Mackie 1970, Dusek 1975, Knowles and Campbell 1982, Nelson 1982, Austin and Urness 1986, Loft et al. 1991, Wallace and Krausman 1987, Peek and Krausman 1996) to commensalism (Anderson and Scherzinger 1975, Frisina and Morin 1991, Peek and Krausman 1996). Further complicating our understanding of the interactions among these ungulates is that the response of elk or mule deer to cattle may vary seasonally depending on forage availability and quantity (Peek and Krausman 1996, Wisdom and Thomas 1996). Competition occurs when individuals or species use the same resources that are in short supply. Short supply of forage may decrease nutritional planes such that population performance of 1 or more species decreases (Birch 1957, Putnam 1996). In contrast, commensalism occurs when an action of 1 species benefits a second species. Clear understanding of distributions and resource selection of elk and mule deer with and without cattle present is necessary to identify possible interspecific relationships among cattle, elk, and mule deer to better manage the resources.

Elk and mule deer may respond to cattle grazing at several levels or scales. When cattle are present, elk and mule deer may leave a pasture, shift distributions within pastures but not change in how they select resources, stay within a pasture and select resources differently, or not respond in any measurable manner. Indeed, most studies of the interactions of either elk or mule deer with cattle describe changes in distribution when cattle are introduced into pastures (Skovlin et al. 1968, Knowles and Campbell 1982, Wallace and Krausman 1987, Kie et al. 1991, Loft et al. 1991, Clegg et al. 1994), but few studies have contrasted patterns of habitat selection of elk and mule deer with and without cattle present. Our objectives were to examine responses of elk and mule deer to cattle at several spatial and seasonal scales. We tested if elk and mule deer (1) left the pasture, (2) shifted distributions among habitats within a pasture, and (3) changed resource selection when cattle were present compared to when cattle were absent in early summer and late summer.

Materials and Methods

Study Area

Starkey Experimental Forest and Range (Starkey) is located on the Wallowa-Whitman National Forest, 35 km southwest of La Grande, Ore (45 deg 15' N, 118 deg 25' W). An ungulate-proof fence (2.4 m high) of New Zealand woven wire surrounds Starkey enclosing the 101 km^2 area (Bryant et al. 1993). Ungulate-proof fences also divide Starkey into 3 study areas, and we conducted our study within Main Area (78 km^2) (fig. 1). Main Area is divided by barbed-wire fences into several cattle pastures (hereafter "Main Area" refers to the area available to elk and mule deer, while the term "pasture" refers to one of the cattle pastures within Main Area). Cattle grazed Smith-Bally, Halfmoon, and Bear pastures annually. Plant communities characterizing the vegetation include bunchgrass (*Festuca idahoensis* Elmer, *Poa sandbergii* Vasey, *Agropyron spicatum* (Pursh) Scribn. & Smith), ponderosa pine (*Pinus ponderosa* Dougl.), Douglas fir (*Pseudotsuga mensiesii* (Mirbel) Franco), grand fir (*Abies grandis* (Dougl.) Forbes), and lodgepole pine (*Pinus contorta* Dougl.) (fig. 2). Elevations range between 1100 and 1500 m and from 1993 through 1996 annual precipitation averaged 636 mm. Skovlin (1991), Noyes et al. (1996), and Rowland et al. (1997) provide detailed descriptions of Starkey.

Elk and mule deer ranged freely throughout Main Area from spring through fall. In winter a portion of the animals were trapped and fed on a feedground where animals were sampled and radio-collars were attached and maintained. Elk and mule deer were also caught in portable traps in winter in Main Area and released after radios were attached. Annual point estimates of population size for elk ranged from 311 to 367 female elk (Noyes et al. 1996, Johnson et al. 2000) and 175 – 218 female mule deer prior to parturition from 1993 – 1996 (B. K. Johnson, unpublished data). Elk and mule deer were exposed to similar kinds and extents of human activities from spring through fall as found on adjacent national forests. Elk and mule deer populations were hunted in late summer or fall, and roads were open to the public from 1 May to mid-December each year. Between mid-December and the end of April each year the Experimental Forest was closed to the public.

From 15 June to 15 October each year, 500 cow-calf pairs were grazed in Main Area on a deferred rotation system. Cattle grazed Smith-Bally pasture from 15 June – 1 August on odd numbered years, and then moved on a set schedule to Halfmoon, and Bear pastures, and left Main Area about 15 September. On even-numbered years, cattle began grazing Bear pasture around 15 July and were then moved through Main Area

pastures in reverse order, grazing Smith-Bally pasture last from approximately 1 September – 15 October. Cattle grazed Bear pasture for approximately 6 weeks and Halfmoon pasture for 1 week in this rotation schedule, and the dates of cattle grazing in Bear pasture overlapped between even and odd years.

We limited our analysis of resource selection and plant community uses to Smith-Bally pasture, because cattle were either present in the pasture or concentrated in the southeast portion of, or absent from, Main Area.

Habitat Variables

We developed a geographical information system (GIS) for Starkey (Rowland et al. 1998), and identified 26 variables from the literature (Reynolds 1962, Julander and Jeffery 1964, Cook 1966, Mackie 1970, Perry and Overly 1977, Lyon 1979, Thomas et al. 1979, Lyon 1983, Hershey and Leege 1982, Thomas and Toweill 1982, Irwin and Peek 1983, Senft et al. 1983, Skovlin et al. 1968, Edge et al. 1987, Pedersen et al. 1980, Collins and Urness 1983, Leckenby 1984, Bracken and Musser 1993, Wisdom 1998) that were correlated with elk, mule deer, and cattle distributions. We tested for collinearity (PROC CORR; SAS Institute 1987) among these variables. When 2 variables were correlated ($r > 0.37$), we deleted the variable we judged to be more difficult to measure accurately or interpret resulting in 15 variables to measure habitat in Smith-Bally pasture (Table 1). Rowland et al. (1998) and Johnson et al. (2000) provide detailed descriptions of derivations of these variables and their representation in the GIS habitat database. Figures 2 and 3 show habitat features from which most variables were derived.

Monitoring Animal Locations

Locations of a sample of female elk, mule deer, and cattle were monitored in Main Area with a LORAN-C automated telemetry system (Dana et al. 1989, Rowland et al. 1997) from April or early May through late fall each year. We attempted to locate a telemetry collar once every 20 seconds with the automated telemetry system. The automated telemetry system operated 24 hours day^{-1} except during periods of equipment testing, maintenance, or repair. We assigned each animal location to a 30- $\times$ 30-m grid cell. Mean positional error of the automated telemetry system was $\pm$ 53 m (SE = 5.9 m) (Findholt et al. 1996). We weighted each location by the inverse of the observation rate for each grid cell to correct for spatial bias (Johnson et al. 1998). We annually monitored from 25 to 55 elk, 12 to 36 mule deer, and 35 to 42 cattle in Main Area from 1993 – 1996, and we used subsets of 78,359 cattle locations, 117,773 elk locations, and 54,014 mule deer locations from the time periods in our analysis.

Statistical Analysis

Grouping animal locations—We grouped daily totals of elk and mule deer locations that occurred in Smith-Bally, Bear, and Meadow Creek/Horse pastures temporally into Interval, Period and Rotation (Fig. 4.). We identified 2 grazing intervals when cattle were moved among pastures at Starkey, adjusting the dates to be comparable to alternate years. We defined early summer (Interval A) as 20 June – 6 July and late summer (Interval B) as 5 September – 12 October. Early summer dates encompass a shorter interval than the actual cattle grazing dates to match the dates that cattle entered Main Area on alternate years. "Period" identified a day as to whether it was within the first 5 days (0), last 5 days (1), or another day (2) of the interval. "Rotation" denoted whether a year was even or odd.

To test for elk and mule deer responses to cattle presence within Smith-Bally pasture, we selected the same dates from alternate years when cattle were not in the pasture. We compared locations from 1993 and 1995 with locations from 1994 and 1996. We summarized elk and mule deer use of Bear and Meadow Creek/Horse pastures during these intervals to provide information on general distributions throughout Main Area.

Shifts in pasture use—To determine if elk and mule deer left the pasture when cattle were introduced, we calculated the number of elk and mule deer locations within the pasture and the total number of elk and mule deer locations in Main Area each day. We modeled daily elk numbers as a temporally correlated Poisson process using the GLIMMIX macro in SAS (Wolfinger and O'Connell 1993). Elk and mule deer counts were modeled using a Poisson distribution to account for the discrete nature of count data, and temporal auto-correlation was modeled using an autoregressive correlation model. The autoregressive parameter [Ar(1)] represents the correlation between consecutive days. We estimated separate autocorrelation coefficients for each year/ treatment combination. In general, Ar(1) ranges between -1.0 and 1.0 with large positive values reducing the effective degrees of freedom for estimation. Consequently, hypothesis tests were adjusted to account for autocorrelation among days. When autocorrelation was positive, effective degrees of freedom and consequently the power of statistical tests were reduced.

To test for cattle effects, we compared the first 5 day period with the last 5 day period (Period) when cattle were present and when cattle were absent (Rotation) within early summer and late summer (Interval). An interaction between Period and Rotation within an Interval was interpreted as an effect due to cattle. For example, if elk counts for the first five day period were similar to elk counts in the last 5 day period when cattle were absent, but elk numbers were disimilar between the first 5 day period and the last 5 day period when cattle were present, this effect was interpreted as an interaction between Period and Rotation (Period*Rotation). Count of locations in the pasture day $^{-1}$ was the response variable. To account for variations in daily counts of locations in Main Area each day, total count of locations from Main Area day $^{-1}$ was included as an offset term in the model. To investigate the effects of this reduction in degrees of freedom, we also conducted analyses under the assumption of independence of days (PROC GENMOD; SAS Institute 1987) and often effects which were significant under the assumption of independence were not detected when we accounted for autocorrelation. In some cases the GLIMMIX macro did not converge (a unique optimal set of parameters was not found). In those cases we assumed that the percentage of elk in each pasture was approximately normally distributed and analyzed the data as a repeated measures design with autoregressive error structure using PROC MIXED.

Shifts in plant community use—To determine if elk or mule deer changed their use of plant communities in response to cattle presence, we used locations within a plant community as the response variable and the total number of locations within the pasture as the offset.

Resource selection of cattle, elk, and mule deer—We used logistic regression (PROC GENMOD; SAS Institute 1997) in a stepwise backwards-approach to identify variables to include in the resource selection function for each species. Our sampling unit was one animal to avoid pseudoreplication (Pendleton et al. 1998, Otis and White 1999), but the variance from PROC GENMOD was underestimated, because it was based on locations. Consequently, we used a jackknife process (Efron 1982) to test the significance of the coefficients by repeating the analysis and sequentially dropping a different animal in each iteration of the data set to reduce the potential problem of autocorrelation among locations. The resulting coefficients were accumulated and the variance of each variable was examined for significance with Wald X^2 tests. We used $P < 0.05$ for determining if variables remained in the model for cattle and elk, but used $P < 0.10$ for mule deer. We relaxed the criterion for mule deer because we had a smaller sample of mule deer and wanted to avoid deleting a variable even though it could be significant (Type II error). Starting with all 15 variables, we deleted 1 or 2 variables from the model statement that had the highest P value and repeated the analysis until all variables were significant. Finally, we calculated the resource selection probability for each grid cell as RSF = $\exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 \ldots + \beta_n x_n)$ using non-standardized coefficients of the significant variables (Manly et al. 1993).

We estimated 2 resource selection functions for cattle (early summer and late summer) and 4 resource selection functions for both elk and mule deer (early summer and late summer, with and without cattle). To examine differences between models within an interval for elk and mule deer, we tested the interaction of Rotation with each variable that was significant in either of the initial models for each species. We used cattle locations obtained within 4 hours after sunrise or 4 hours before sunset when foraging is highest for cattle and all locations obtained for elk and mule deer. We used the peak foraging period for cattle to describe where cattle foraged and where potential interactions between elk and mule deer may be highest. We used all locations for elk and mule deer because if we used only locations from peak foraging periods (i.e., within 2 hours of sunrise or sunset), we would not have a sufficient number of locations from enough animals to estimate resource selection. We used locations from 16 mule deer, 35 elk, and 52 cattle in odd years and 21 mule deer, 45 elk, and 48 cattle in even years, and we had a minimum of 32 locations from each animal in an interval. Leban (1999) recommended using a minimum of 20 animals and 50 locations per animal when estimating resource selection in Starkey.

To evaluate if elk or mule deer were selecting resources similar to cattle, we incorporated the cattle resource selection function score (cattle RSF) from the appropriate Interval as a variable in the logistic regression for the elk or mule deer. We tested for collinearity of the cattle variables with the 15 variables used in the logistic regression and deleted variables that were correlated ($r > 0.37$) with the cattle or elk resource selection function prior to the analysis.

Results

Shifts among pastures

The proportion of elk locations declined in both early summer (43%) and late summer (21%) when cattle were present, compared to when cattle were absent (6% early, 33% increase late) (Table 2, Fig. 5a., b.). The proportion of elk locations increased in Bear and Meadow/Horse pastures during the same intervals that they were decreasing in Smith-Bally pasture (Table 3).

The proportion of mule deer locations within the pasture increased 35% in early summer, but decreased 23% in late summer when cattle were present, compared to when cattle were absent (2% increase early, 8% increase late)(Table 2, Fig. 6a., b.). The proportion of mule deer locations in Bear and Meadow/Horse pastures concurrently stayed level or changed in opposite directions to mule deer proportions in Smith-Bally pasture (Table 3).

Shifts among plant communities

Only in the ponderosa pine/Douglas fir plant community were consistent changes evident in amount of use during intervals for elk and mule deer. However, mule deer response was generally opposite from that of elk (Table 2). In early summer, the mean daily proportion of elk locations in the ponderosa pine/Douglas fir community decreased 81% when cattle were present but increased 21% when cattle were absent (Table 2, Fig. 5c.). In late summer the proportion of elk locations in the ponderosa pine/Douglas fir community increased 36% when cattle were present and decreased 44% when cattle were absent (Table 2, Fig. 5d.). In early summer the proportion of mule deer locations increased 33% when cattle were present and increased 54% when cattle were absent. In late summer the proportion of mule deer locations decreased 33% when cattle were present and increased 133% when cattle were absent (Table 2, Fig 6c.,d.). In all other plant communities, significant shifts in use were not evident. Proportion of cattle use in the 4 plant communities declined in the bunchgrass community and increased in lodgepole pine and grand fir communities from early summer to late summer (Table 4).

Resource selection models

Contrasting patterns emerged for variables included in resource selection functions for cattle between early summer and late summer (Table 5). When we included the interaction term for early or late summer, the standardized coefficients (β) for cosine of aspect (β = 0.302, SE = 0.135, P = 0.02, n = 68 cows), distance from water (β = -0.384, SE = 0.135, P = 0.004), herbage production (β = 0.181, SE = 0.047, P < 0.001), and canopy cover (β = 0.408, SE = 0.129, P = 0.002) were significantly different between Intervals. That is, compared to early summer, cattle in late summer selected resources with northerly aspects, closer proximity to water, higher herbage production, and greater canopy cover.

For elk, 11 variables were identified in resource selection functions during early summer (Table 6) and 9 variables during late summer (Table 7). During early summer, variables that differed whether cattle were present in the pasture included slope (β = -0.346, SE = 0.174, P = 0.047, n = 56 elk), convexity (β = -0.163, SE = 0.083, P = 0.049), distance to edge of stand (β = -0.117, SE = 0.055, P = 0.034), distance to roads with low rates of traffic (β = 0.609, SE = 0.193, P = 0.002), and canopy cover (β = 0.129, SE = 0.065, P = 0.046). That is, when cattle were absent in early summer, elk selected sites with more gentle slopes, less convex topography, closer to edge of forest stand, further from roads with low traffic rates, and lower canopy cover. During late summer, only canopy cover differed (β = 0.236, SE = 0.084, P = 0.008, n = 52 elk) whether cattle were present or absent from the pasture. Elk selected for denser canopy when cattle were present in the pasture.

For mule deer during early summer, 6 variables were identified in resource selection models when cattle were either present or absent (Table 8). Only distance to edge of the stand (β = 0.211, SE = 0.118, P = 0.07, n = 19 mule deer) was significantly different whether cattle were present or absent in the pasture; mule deer selected for areas further from the edge of a forest stand when cattle were absent. During late summer 7 variables were significant in resource selection functions when cattle were either present or absent in the pasture (Table 9) and soil depth (β = 0.30, SE = 0.001, P = 0.01, n = 24 mule deer) and herbage production (β = -0.163, SE = 0.004, P < 0.001) differed whether cattle were present or absent. When cattle were present, mule deer selected sites with deeper soils and lower herbage production, which at Starkey are associated with coniferous forests.

We included cattle resource selection function as a variable in the models for elk and mule deer. That is, we calculated the probability of use for each pixel from the cattle resource selection function, and then included that variable (cattle RSF) as a habitat variable and repeated the model selection process for both elk and mule deer. In early summer the cattle RSF variable was not significant in the elk model when cattle were present (P = 0.41, n = 32 elk) but was significant when cattle were absent (β = 0.313, P <0.001, n = 31 elk). During late summer, the cattle RSF variable was significant in the elk model regardless of cattle presence (β = 0.2252, P < 0.001, n = 38 elk) or absence (β = 0.1793, P <0.001, n = 25 elk). In early summer the cattle RSF variable was not significant in the mule deer model whether cattle were present (P = 0.70, n = 12 mule deer) or absent (P = 0.17, n = 13 mule deer). In late summer, the cattle RSF variable was not significant in the mule deer model when cattle were present (P = 0.70, n = 20 mule deer) but was significant when cattle were absent, but the estimate is negative (β = -0.3954, P = 0.016, n = 12 mule deer). That is, when cattle were absent, mule deer were selecting

resources that cattle do not select.

Discussion

We examined interspecific relationships and resource selection of cattle, elk, and mule deer by analyzing locations of these 3 ungulates obtained from an automated telemetry system and linked to a GIS of habitat variables. Elk and mule deer differed in their responses to presence of cattle within the pasture. Mule deer responses were consistently opposite to changes in elk distribution. Elk use of a pasture declined after cattle entered the pasture in both early and late summer, use of the ponderosa pine/Douglas fir plant community declined in early summer but increased in late summer, and elk resource selection functions changed when cattle were present in early summer.

The responses of elk and mule deer to cattle may be due to differences in plant phenology and forage quality between early and late summer. In early summer, grasses and forbs within the bunchgrass community were actively growing but by late summer most were cured, with the only growing (green) herbaceous vegetation was along riparian areas and under forest canopy (Edgerton and Smith 1971). Digestible energy and crude protein of grasses and forbs are high in upland range types in early summer but decline by late summer (Skovlin 1967, Svejcar and Vavra 1985, Sheehy 1987). Declines in percent protein in shrubs are less pronounced as summer progresses (Cook and Harris 1950, Holechek et al. 1981, Svejcar and Vavra 1985) and in vegetation under shade (McEwen and Dietz 1965). Shrubs are common but heavily utilized in many of the forested plant communities in Starkey.

When the variable for cattle RSF was offered for inclusion into the elk resource selection function model, the pattern of inclusion was not consistent between early and late summer, and the pattern can be explained by changes in plant phenology. Because high quality forage was still abundant and wide spread in early summer, elk could shift distributions and select other resources and still obtain adequate nutrition to meet the demands of lactation, as evidenced by the differences in variables in the early summer models and that the variable for cattle RSF was not significant when cattle were present. In late summer, the cattle variable that related to the elk resource selection function was significant, regardless of cattle presence, and there were few differences between the elk models with and without cattle present. In late summer, elk and cattle selected resources with some of the same characteristics, presumably because forage quality was low in much of the pasture, thus the animals converged on sites that had higher quality forage in late summer (Holechek et al. 1981).

Anatomical and body size differences among the 3 ungulates may also explain some of the differences we saw in elk and mule deer response to cattle. In winter, adult female mule deer weigh approximately 60 kg, adult female elk weigh about 200 kg at Starkey (B. Johnson, unpublished data), and cattle in summer weigh about 550 kg at Starkey (B. Johnson unpublished data). Wickstrom et al. (1984) concluded that mule deer were well adapted to exploit low-biomass, shrubby habitats, while elk were adapted to forage in high-biomass, herbaceous or mixed communities. Because of their larger body size, cattle are even better adapted to forage in high-biomass herbaceous communities. Consequently, the niche separation between mule deer and cattle is much more pronounced than between elk and mule deer or elk and cattle. Shrubs and grasses dominate diets of elk (Korfhage et al. 1980) and cattle (Holechek et al. 1982) in late summer in northeast Oregon. Similarly, Jarman (1974) concluded that African antelope separate feeding styles based on body size.

Annual variation in early summer precipitation may have played a part in how resources were selected. 1993 and 1995 were characterized by higher precipitation and lower temperatures while in both 1994 and 1996 precipitation was lower and temperatures higher in the summer (Fig. 7.). However, the shifts in distribution and in habitat use were counter to what we would expect if precipitation was driving selection. For example, we would expect to see a decrease in elk use of the ponderosa pine/Douglas fir plant community in late summer on a drought year, but we observed the opposite response. Total herbage production in an adjacent pasture was 22% lower in the ponderosa pine/Douglas fir community in 1994 and 1996, compared to 1993 and 1995 (P. Coe, unpublished data). Additionally, we would not have expected elk resource selection functions in late summer 1993 and 1995 to be similar to 1994 and 1996 if weather variability were driving distributions of elk and mule deer.

Proportions of elk locations within Smith-Bally and Bear pastures were dynamic and fluctuated in response to cattle grazing. When elk use decreased in Smith-Bally, it was increased in Bear pasture and vice versa (Tables 2 and 3). In contrast, elk use of Meadow Creek/Horse pastures gradually increased from early summer through fall, but use by mule deer gradually declined (P.Coe, unpublished data). Increasing use of Meadow Creek/Horse pastures may reflect effects of both intra- and interspecific competition for forage. By fall, 500 cow-calf pairs had grazed pastures 1-3 of Main Area (6681 ha) for 3 months. Based on ocular estimates, forage was more abundant in Meadow Creek in fall than in either Smith-Bally or Bear pastures.

Demonstrating competition between 2 species in natural situations is difficult, seldom proven and, hence,

is usually inferred. In addition to the analysis of habitat variables and animal locations it requires manipulations of populations and measures of animal performance (i.e. body weight, measures of productivity) (Schoener 1983). The common traits between resource selection functions for cattle and elk provide evidence of potential competition between the 2 species for forage. Elk responses to cattle provide evidence to support both interference and exploitative competition. The potential for interference competition is evident in early summer because elk resource selection shifted from areas also selected by cattle when cattle were absent to areas not selected by cattle when cattle were present. In late summer elk resource selection changed little whether cattle were present or absent and the cattle RSF was a significant variable in the elk interspecific resource selection function model, indicating cattle and elk were selecting for some of the same resources, thus the potential for exploitative competition exists. Elk use of Meadow Creek/Horse pastures increased through early summer, late summer, and fall, indicating the potential that forage was limiting in the other pastures. Mule deer use fluctuated inversely to elk use in many of the comparisons we made with cattle. This suggests that mule deer may be avoiding elk, a requirement of interference competition. Holechek et al. (1981) found that cattle lost weight in late summer at Starkey, compared to early summer because of the decline in forage quality. Our analysis does not incorporate stocking densities, forage removal, estimates of dietary similarity, or animal performance (i.e. weight dynamics, productivity) that need to be quantified before competition can be documented. Research is being conducted at Starkey to quantify dietary overlap among elk, cattle, and mule deer on shared ranges in the Blue Mountains.

Management Recommendations

Understanding the ecological and nutritional consequences of the stocking densities of wild and domestic ungulates on landscapes is vital for proper management and our results show a high degree of interaction between elk and cattle at Starkey. Elk distributions changed in response to cattle grazing but clear patterns of response of mule deer to cattle were not evident. Instead, we observed mule deer changes in distribution to be correlated with changes in elk distribution. Cattle, therefore, cause changes in distributions of both elk and mule deer. We recommend that managers look closely at stocking levels in late summer because elk and cattle select some of the same resources during that period, and effects on both animal and plant productivity could be detrimental depending on stocking levels. Particular attention should be paid to the ponderosa pine/Douglas fir plant communities where we found significant cattle and elk interactions. Resource selection functions can be used to predict distributions of sympatric populations of cattle, elk, and mule deer (Johnson et al. 2000) and these predicted distributions can be incorporated into a forage allocation model for resource managers (Johnson et al. 1996). While developing coordinated management plans for forage allocation is complicated by social values, understanding the interactions of cattle, elk, and mule deer will help managers make decisions involving these three species.

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Table 1. Variables used in logistic regression to estimate resource selection of cattle, elk, and mule deer in early and late summer in Smith-Bally pasture at Starkey Exp. Forest and Range, northeast Ore. 1993 - 1996.

Variable[a]	Mean	Minimum	Maximum
Herbage (kg ha^{-1})	332	0	2200
Canopy closure of trees > 12 cm dbh (%)	28	0	80
Distance to nearest grid cell with >40% cover (m)	100	0	976
Distance to edge of forest stand (m)	45	0	297
Soil depth of the A and B horizons (cm)	28	9	60
Slope (%)	20	0	84
Sine of aspect (east and west)	-0.024	-1.0	1.0
Cosine of aspect (north and south)	-0.034	-1.0	1.0
Convexity (of terrain)	500	466	525
Distance to nearest permanent water (m)	217	0	933
Circularity index (shape of polygon)	0.128	0.006	0.917
Zero traffic—distance to nearest road with 0 traffic (m)[b]	204 - 322	0	1406
Low traffic—distance to nearest road with >0 but $\leq$ 1 vehicle 12 hours^{-1} (m)[b]	325 - 1291	0	4011
Medium traffic—distance to nearest road with >1 but $\leq$ 4 vehicles 12 hours^{-1} (m)[b]	815 - 1582	0	6391
High traffic—distance to nearest road with >4 vehicles 12 hours^{-1} (m)[b]	880 - 1355	0	3776

[a] Variables considered for inclusion, but omitted because of collinearity with other variables, were area of stand, perimeter of stand, elevation, percent shrub cover, percent herbaceous cover, distance to forage, distance to nearest stand with seedling and sapling trees, distance to nearest open road, distance to nearest closed road, distance to nearest administrative road, distance to nearest game-proof fence.
[b] Traffic rates varied among the 4 years and seasons, so distances varied among intervals.

Table 2. Elk and mule deer use of Smith-Bally pasture and ponderosa pine/Douglas fir (PP/DF), lodgepole pine (LP), grand fir (GF), and grassland, shrubland, and meadow (BG/MD) plant communities in response to cattle grazing rotation. Mean proportions (Mean) and standard errors (SE) are of daily elk or mule deer observations in pasture or plant community during the first 5 days (0) and last 5 days (1) of the interval. Pasture proportions are for Main Area and plant community proportions are for within Smith-Bally pasture. Cattle grazed Smith-Bally pasture in early summer in 1993 and 1995 (Odd) and in late summer in 1994 and 1996 (Even). Significance levels were determined from PROC MIXED and adjusted for autocorrelation among days within a 5 day period within an interval within a year.

		Early Summer (20 Jun-6 Jul)					Late Summer (5 Sep-12 Oct)				
		Mean		SE		P	Mean		SE		P
First 5(0)/Last 5(1)		0	1	0	1		0	1	0	1	
Elk: Pasture	Even	.35	.33	.03	.02	0.0166	.33	.26	.03	.02	0.0489
	Odd	.30	.17	.03	.02		.21	.28	.02	.02	
PP/DF	Even	.14	.17	.02	.03	0.0099	.11	.15	.01	.04	0.1113
	Odd	.16	.03	.03	.01		.09	.05	.02	.01	
LP	Even	.03	.04	.01	.01	0.4320	.05	.08	.01	.02	0.2813
	Odd	.02	.08	.01	.03		.04	.03	.01	.01	
GF	Even	.65	.60	.03	.01	0.2924	.66	.61	.02	.04	0.7693
	Odd	.57	.72	.02	.02		.67	.62	.03	.03	
BG/MD	Even	.18	.18	.02	.02	0.3783	.15	.16	.01	.02	0.2171
	Odd	.24	.16	.03	.03		.20	.29	.03	.03	
Deer: Pasture	Even	.46	.47	.04	.04	0.1197	.40	.31	.02	.02	0.0212
	Odd	.23	.31	.02	.01		.37	.40	.02	.02	
PP/DF	Even	.11	.17	.02	.05	0.0118	.15	.10	.02	.01	0.0210
	Odd	.12	.16	.02	.03		.09	.21	.02	.03	
LP	Even	.08	.05	.02	.02	0.2641	.12	.16	.04	.05	0.2202
	Odd	.11	.14	.03	.03		.11	.04	.04	.01	
GF	Even	.47	.47	.06	.04	0.0441	.50	.55	.05	.05	0.3232
	Odd	.48	.46	.03	.05		.47	.44	.04	.03	
BG/MD	Even	.34	.29	.04	.04	0.3051	.23	.18	.02	.02	0.8229
	Odd	.27	.24	.04	.04		.32	.31	.04	.02	

Table 3. Elk and mule deer use of Bear and Meadow Creek pastures in response to cattle grazing rotation in Smith-Bally pasture. Mean proportions (Mean) and standard errors (SE) are of daily elk or mule deer observations in pasture during the first 5 days (0) and last 5 days (1) of the interval. Cattle grazed Smith-Bally pasture in early summer in 1993 and 1995 (Odd) and in late summer in 1994 and 1996 (Even). Significance levels were determined from PROC MIXED and adjusted for autocorrelation among days within a 5 day period within an interval within a year.

		Early Summer (20 Jun-6 Jul)					Late Summer (5 Sep-12 Oct)				
		Mean		SE		P	Mean		SE		P
First 5(0)/Last 5(1)		0	1	0	1		0	1	0	1	
Elk: Bear	Even	.50	.49	.04	.03	0.0057	.44	.46	.02	.02	0.7621
	Odd	.51	.58	.04	.01		.44	.44	.06	.04	
Deer: Bear	Even	.23	.17	.05	.04	0.2422	.30	.34	.04	.03	0.5580
	Odd	.39	.39	.03	.01		.39	.41	.02	.02	
Elk: Meadw	Even	.10	.14	.01	.02	0.9272	.20	.21	.02	.03	0.4789
	Odd	.12	.20	.01	.01		.26	.19	.04	.04	
Deer: Meadw	Even	.27	.24	.04	.04	0.3019	.24	.23	.03	.02	0.6977
	Odd	.28	.22	.02	.02		.17	.14	.01	.03	

Table 4. Cattle locations (%) within 4 plant communities in Smith-Bally pasture in early and late summer, 1993-1996, Starkey Exp. Forest and Range, northeast Ore. Locations were obtained within 4 hours after sunrise or 4 hours before sunset. Cattle grazed this pasture in early summer in 1993 and 1995 and late summer in 1994 and 1996.

Plant community	% of area	Locations in early summer (15 Jul - 28 Jul)	Locations in late summer (4 Sep - 15 Oct)
Lodgepole pine	11.5	8.6	13.0
Ponderosa pine/ Douglas fir	12.7	11.2	10.6
Grand fir	48.1	48.9	50.8
Bunchgrass, meadows, and shrublands	27.2	31.3	25.6

Table 5. Variables in resource selection functions of cattle in early summer and late summer in Smith-Bally pasture, using locations obtained within 4 hours after sunrise or 4 hours before sunset with a LORAN-C automated telemetry system, Starkey Exp. Forest and Range, northeast Ore. 1993 – 1996.

Variable	Cattle resource selection in early summer				Cattle resource selection in late summer			
	β	Standardized β	SE[a]	P	β	Standardized β	SE	P
Intercept	-1.4328	-1.5282	0.07890	<0.001	1.6725	-1.8773	0.0727	<0.001
Slope	-0.03159	-0.4078	0.05351	<0.001	-0.01164	-0.1525	0.5604	0.006
Convexity				Ns[b]	-0.007063	-0.04269	0.02163	0.045
Sine of aspect	-0.1784	-0.1285	0.03679	<0.001	-0.09065	-0.06463	0.03230	<0.001
Cosine of aspect	0.1245	0.08536	0.02944	0.003	0.2206	0.1534	0.3801	0.0484
Distance to water	0.000584	0.09856	0.02995	0.002	-0.000589	-0.09542	0.03689	0.010
Herbage				Ns	0.000487	0.1176	0.01953	<0.001
Soil depth	0.000756	0.09643	0.01793	<0.001	0.0107	0.1369	0.04026	<0.001
Distance to edge	-0.001952	-0.08518	0.02074	<0.001	-0.001635	-0.07182	0.01874	<0.001
Canopy	-0.01121	-0.2516	0.02412	<0.001	0.002345	0.0525	0.02464	0.033
Distance to cover	-0.001143	-0.1475	0.02404	<0.001	-0.001141	-0.1454	0.03929	<0.001

[a] Standard error (SE) is of standardized β
[b] Not significant

Table 6. Variables in resource selection functions of elk in early summer with (1993 and 1995, n = 38 elk) and without (1994 and 1996, n = 43 elk) cattle present within Smith-Bally pasture, using locations obtained 24 hours day^{-1} with a LORAN-C automated telemetry system, Starkey Exp. Forest and Range, northeast Ore.

Variable	Elk resource selection with cattle present				Elk resource selection without cattle present			
	β	Standardized β	SE[a]	P	β	Standardized β	SE	P
Intercept	-32.9801	-2.5270	0.1905	<0.001	-26.854	-2.97614	0.08587	<0.001
Slope				Ns[b]	-0.2232	-0.2912	0.0710	<0.001
Convexity	0.0616	0.3718	0.05793	<0.001	0.04778	0.2857	0.0479	<0.001
Sine of aspect	-0.2199	-0.1560	0.04701	<0.001	-0.27014	-0.190	0.03919	<0.001
Distance to water				Ns	0.00154	0.2510	0.05689	<0.001
Soil depth				Ns	0.0169	0.1601	0.04673	<0.001
Distance to edge	0.00343	0.1529	0.0407	<0.001				Ns
Canopy	0.00599	0.1338	0.0407	0.001				Ns
Dist. roads low traffic	-0.00112	-0.7159	0.1684	<0.001	-0.000457	-0.2906	0.07942	<0.001
Dist. to cattle fence	0.000781	0.3012	0.0638	<0.001	0.00744	0.28918	0.0736	<0.001
Circularity				Ns	-0.7677	-0.1289	0.0483	0.007
Distance to cover	-0.00201	-0.2580	0.0618	<0.001	-0.00213	-0.2750	0.06612	<0.001

[a] Standard error (SE) is of standardized β
[b] Not significant

Table 7. Variables in resource selection functions of elk in late summer with (1994 and 1996, n = 38 elk) and without (1993 and 1995, n = 25 elk) cattle present within Smith-Bally pasture, using locations obtained 24 hours day $^{-1}$ with a LORAN-C automated telemetry system, Starkey Exp. Forest and Range, northeast Ore.

Variable	Elk resource selection with cattle present				Elk resource selection without cattle present			
	β	Standardized β	SE[a]	P	β	Standardized β	SE	P
Intercept	-19.924	-2.0965	0.07611	0.001	-9.4488	-2.2977	0.1795	<0.001
Convexity	0.033754	0.2009	0.02398	<0.001	0.01520	0.0908	0.0426	0.033
Cosine of aspect	0.3540	0.2476	0.07611	0.001	0.3326	0.2324	0.1082	0.032
Distance to water	0.001486	0.2446	0.04438	<0.001	0.001621	0.2639	0.08214	0.001
Forage	-0.000407	-0.08735	0.03781	0.021	-0.001269	-0.2739	0.09554	0.004
Soil depth	0.01705	0.2204	0.03568	<0.001				Ns[b]
Distance to edge	0.00138	0.06239	0.02124	0.003				Ns
Canopy	0.01301	0.2949	0.03403	<0.001				Ns
Circularity				Ns	-0.6781	-0.1137	0.03531	0.001
Distance to cover	-0.001951	-0.24939	0.07450	<0.001	-0.003058	-0.3904	0.08593	<0.001

[a] Standard error (SE) is of standardized β
[b] Not significant

Table 8. Variables in resource selection functions of mule deer in early summer in Smith-Bally pasture when cattle are present (1993 and 1995, n = 12 deer) and absent (1994 and 1996, n = 13 deer) using locations obtained 24 hours day^{-1} with a LORAN-C automated telemetry system, Starkey Exp. Forest and Range, northeast Ore.

Variable	Mule deer resource selection with cattle				Mule deer resource selection without cattle			
	β	Standardized β	SE[a]	P	β	Standardized β	SE	P
Intercept	-2.2703	-3.1861	0.2197	<0.001	-25.4169	-3.7745	0.2960	<0.001
Convexity				Ns[b]	0.0457	0.2695	0.1381	0.075
Distance to water					0.0024	0.3352	0.1264	0.006
Distance to edge	-0.00393	-0.1725	0.0683	0.011				ns
Canopy				Ns	-0.01496	-0.3331	0.1003	<0.001
Distance to cover				Ns	-0.00280			0.019
Distance to roads with high traffic rates	-0.000555	-0.4432	0.2147	0.039	-0.00790			0.107

[a] Standard error (SE) is of standardized β
[b] Not significant

Table 9. Variables in models of resource selection functions of mule deer in late summer when cattle were present (1994 and 1996, n = 21 deer) or absent (1993 and 1995, n = 16 deer) in Smith-Bally pasture, using locations obtained with a LORAN-C automated telemetry system, Starkey Exp. Forest and Range, northeast Ore.

Variable	Mule deer resource selection with cattle				Mule deer resource selection without cattle			
	β	Standardized β	SE[a]	P	β	Standardized β	SE	P
Intercept	-0.9355	-2.5591	0.2166	<0.000	-1.6359	-2.5428	0.2798	0.002
Slope				Ns[b]	0.0207	0.2709	0.1668	0.10
Distance to water				Ns	0.001467	0.2364	0.09816	0.016
Herbage	-0.000858	-0.186	0.08976	0.038				Ns
Soil depth				Ns	-0.01949	-0.2459	0.1050	0.019
Distance roads with high traffic	-0.0011	-0.7811	0.3423	0.022	-0.000851	-0.5991	0.3375	0.075
Canopy				Ns	-0.007823	-0.1738	0.08748	0.047
Distance to cover	-0.00193	-0.2477	0.0527	<0.001				Ns

[a] Standard error (SE) is of standardized β
[b] Not significant

Figure Captions:

Fig. 1. Main Area at Starkey Exp. Forest and Range, northeast Oregon is summer range for about 300 elk and 200 mule deer. Solid lines depict livestock fences. Pastures are grazed by 500 cow-calf pairs of cattle on a deferred rotation schedule. Cattle grazed sequentially through Smith-Bally (1), Half moon (2), and Bear (3) on odd-numbered years from 15 June to 15 September and through pastures 3, 2, and 1 on even-numbered years from 15 July to 15 October. Meadow Creek pasture was not grazed except for the 3 pastures on the extreme east edge for 20 days each. Livestock did not graze Horse pasture.

Fig. 2. Distribution of 4 plant communities in Smith-Bally pasture, Starkey Exp. Forest and Range, northeast Ore. Plant communities were classified based on Hall (1973).

Fig. 3. Habitat variables used in the resource selection models were derived from digitized pasture, elevation, road, traffic, stream, water development, soil, and vegetation maps developed in a GIS for Starkey Exp. Forest and Range, northeast Ore. (Rowland et al. 1998).

Fig. 4. Daily elk and mule deer locations were grouped and analyzed temporally by Interval (grazing season), Period (first 5 days, last 5 days), and Rotation (odd or even year) for Smith-Bally pasture and plant community comparisons within Smith-Bally pasture. Resource selection models for elk, mule deer, and cattle were calculated by Interval and Rotation within Smith-Bally pasture, Starkey Exp. Forest and Range, northeast Ore.

Fig. 5. Proportion of elk locations in Smith-Bally pasture and in the ponderosa pine/Douglas fir plant community during early summer and late summer, when cattle were present (open circles, n = 20 days) compared to when cattle were absent (closed circles, n = 20 days), Starkey Exp. Forest and Range, northeast Ore., 1993 - 1996.

Fig. 6. Proportion of mule deer locations in Smith-Bally pasture and in the ponderosa pine/Douglas fir plant community during early summer and late summer, when cattle were present (open circles, n = 20 days) compared to when cattle were absent (closed circles, n = 20 days), Starkey Exp. Forest and Range, northeast Ore., 1993 - 1996.

Fig. 7. Average monthly maximum temperatures and total monthly precipitation (April – October) for the Starkey Exp. Forest and Range, northeast Ore., 1993 though 1996 (C. Borum, USDA For. Serv., La Grande, Ore., unpublished data).

Smith-Bally
1

Meadow Creek

Main

Area

Halfmoon
2

Bear
3

Horse

N

1   0   1   2 Kilometers

Plant Community
- Lodgepole
- Ponderosa Pine/ Douglas Fir
- Grand Fir
- Bunchgrass/ Meadow

0.5 0   0.5   1   Kilometers

N

Legend
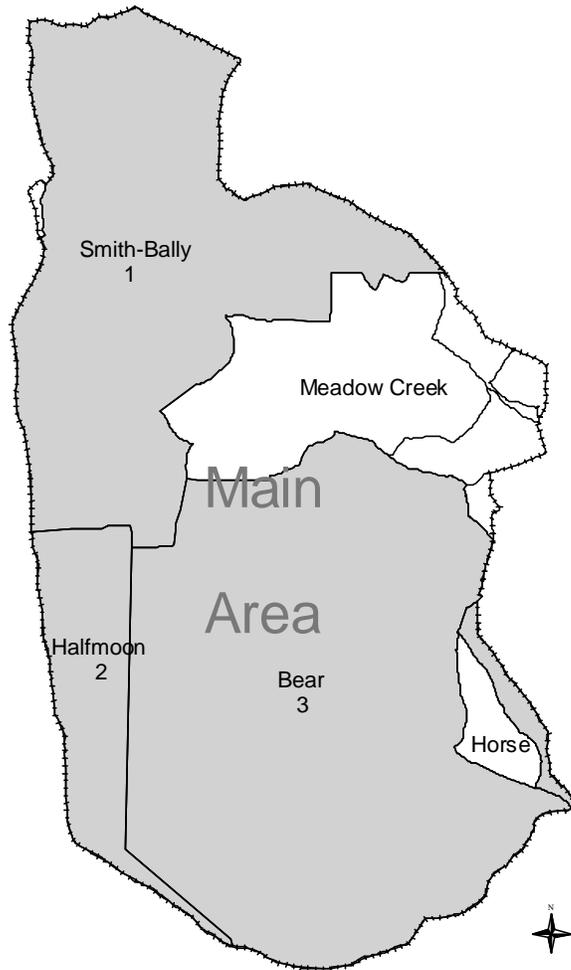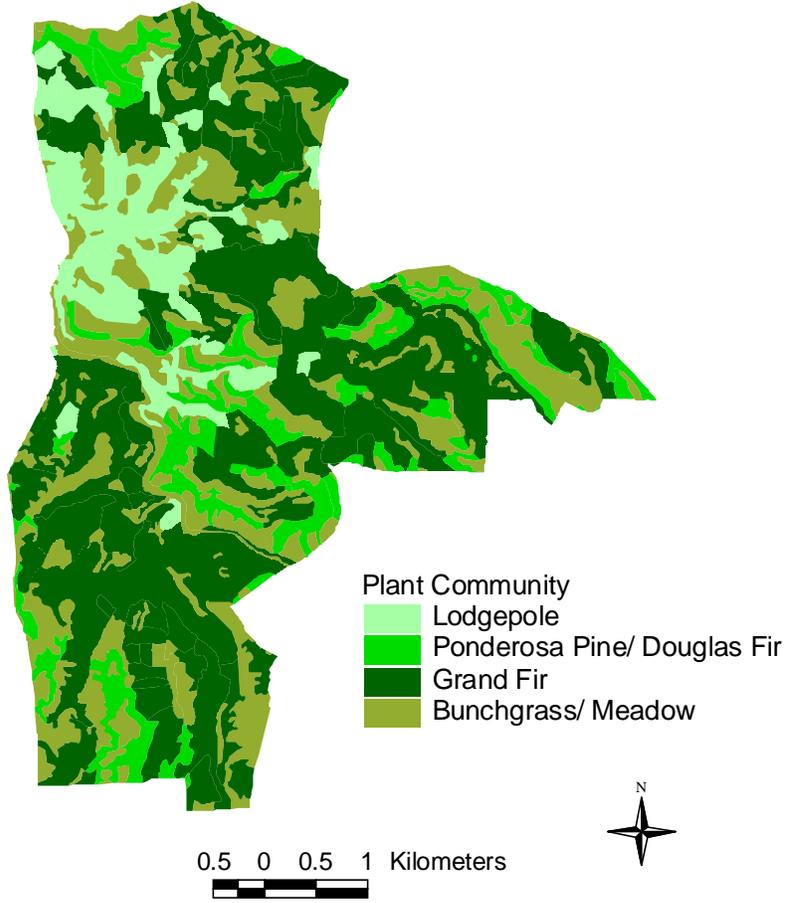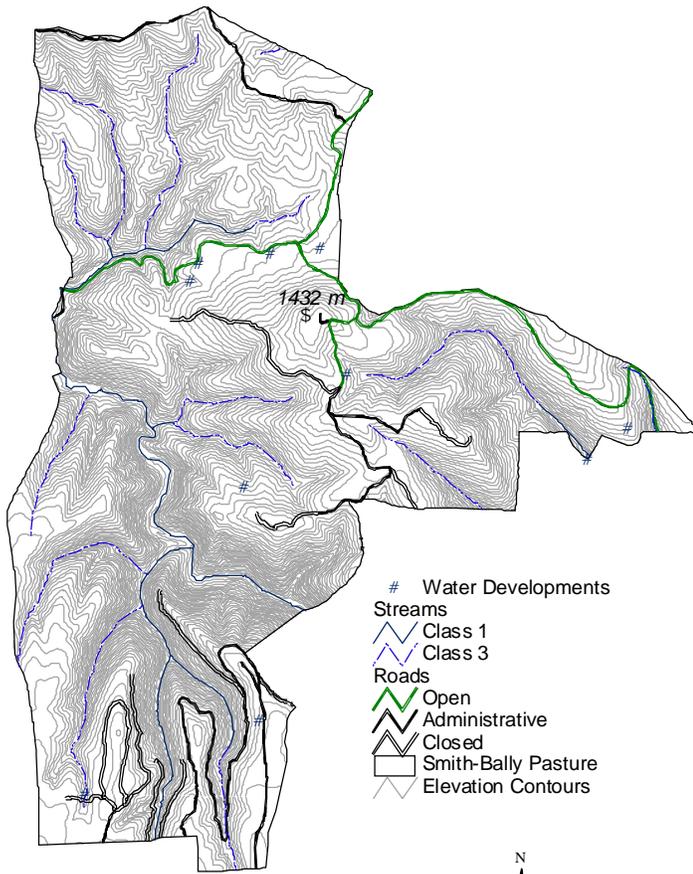
Water Developments
Streams
Class 1
Class 3
Roads
Open
Administrative
Closed
Smith-Bally Pasture
Elevation Contours

1432 m
$

0.5 0 0.5 1 Kilometers

N

	Early Summer			Late Summer	
	20 June	15 July	5 Sept		15 Oct
Interval	**A**			**B**	
Period	⊢–┤ first	⊢–┤ last		⊢–┤ first	⊢–┤ last
Rotation: 1993 & 1995				**cattle present**	
1994 & 1996	**cattle present**				

Elk observations

Early Summer (20 Jun - 6 Jul)   Late Summer (5 Sep - 12 Oct)

a.

b.

c.

d.
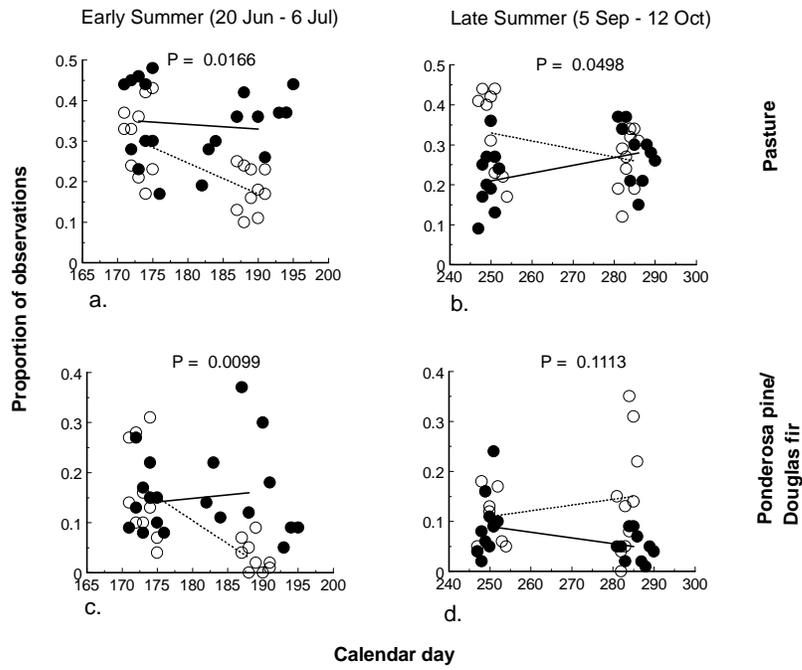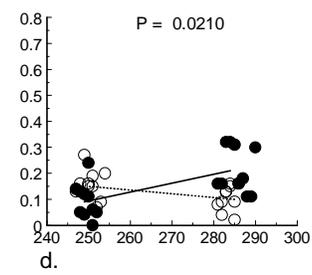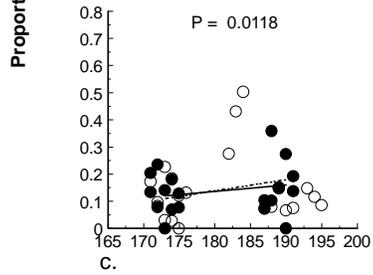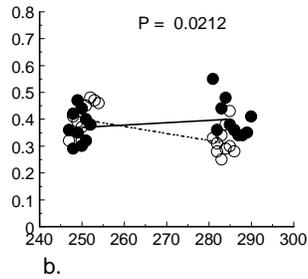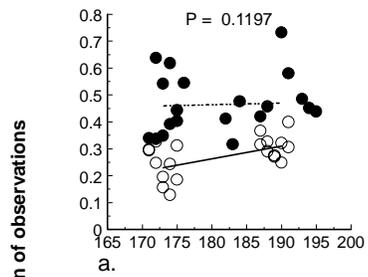
Calendar day

Pasture

**Ponderosa pine/
Douglas fir**

Proportion of observations

P = 0.0166

P = 0.0498

P = 0.0099

P = 0.1113

Mule deer observations

Early Summer (20 Jun - 6 Jul)

Late summer (5 Sep - 12 Oct)

Proportion of observations

Pasture

**Ponderosa pine/
Douglas fir**

P = 0.1197

P = 0.0212

P = 0.0118

P = 0.0210

a.

b.

c.

d.

Calendar day

Total Monthly Precipitation

Average Monthly Maximum Temperature