Spatial and Temporal Interactions of Elk, Mule Deer and Cattle

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Introduction

Elk (*Cervus elaphus)*, mule deer (*Odocoileus hemionus*) and cattle share millions of acres of public and private forests and rangelands across the western United States and Canada. These three species have important social, ecological and economic values. Understanding their interspecific interactions may clarify two recurring issues in their management: competition for food and competition for space, both may result in decreased animal fitness. Animal unit equivalents (AUEs) among these three species have been based on equivalent body mass (Society for Range Management 1989), whereby one cow is equivalent to two and one-half elk or to six mule deer. Hobbs and Carpenter (1986) argue that AUEs should be based on dietary overlap, and the argument can be extended to include spatial overlap. Consequently, the ecological impact of one species on the landscape may not be equivalent to another species. Furthermore, allocating forage becomes challenging if managers do not clearly understand the spatial and dietary overlap among these three species. Accurate

predictions of ungulate distributions over time and space may help managers regulate densities and understand effects of specific ungulates on ecosystem processes.

Many factors may influence the seasonal distribution of domestic and native ungulates, including vegetation composition, topography and distance to water (Mueggler 1965, Leckenby 1984, Peek and Krausman 1996, Wisdom and Thomas 1996). Ungulates also distribute themselves in response to disturbances, such as traffic (Rowland et al. 2000), hunting (Johnson et al. 2004) and logging (Pederson et al. 1980). In addition, there may be inter- and intraspecific influences on animal distribution. These interactions may produce different patterns of distribution at different scales of investigation (Bowyer et al. 1997). This paper summarizes studies of ungulate interactions at Starkey Experimental Forest and Range (Starkey) in terms of how interactions among ungulate species may affect animal distributions over space and time.

Past studies of interspecific interactions among elk, mule deer and cattle have indicated potential competition (Skovlin et al. 1968, Mackie 1970, Dusek 1975, Knowles and Campbell 1982, Nelson 1982, Austin and Urness 1986, Wallace and Krausman 1987, Loft et al. 1991, Peek and Krausman 1996, Wisdom and Thomas 1996, Lindzey et al. 1997), while others have inferred commensalism (Anderson and Scherzinger 1975, Frisina and Morin 1991, Peek and Krausman 1996). Competition occurs when individuals or species use similar resources that are in short supply. Inadequate forage quality or quantity may decrease nutritional planes such that population performance of one or more species decreases (Birch 1957, Putnam 1996). In contrast, commensalism occurs when one species benefits from association with another species, while the other species is unaffected (Martin 1990).

Simple descriptive approaches to interactions among large herbivores result in inherent difficulties (Painter 1980). Overlapping distributions could be evidence for competition or dependence. Nonoverlap could be an expression of active avoidance or ecological separation, which occurs when two species evolved together. Although sexual segregation, or spatial separation of sexes outside the mating season, is nearly ubiquitous among polygamous ungulates (Bowyer 1984, McCullough et al. 1989, Scarbrough and Krausman 1998, Kie and Bowyer 1999), our paper concentrates on distribution of females. Comparisons of distribution with and without one ungulate species present during the same season and on the same ground should help to illuminate whether competition is

occurring. Diet studies of ungulates during different seasons, both with and without prior grazing also should help to establish competitive interactions.

Studies of ungulate interactions began at Starkey in 1954 (Skovlin et al. 1968). Deer were summer-long residents while elk were spring (May to June) and fall migrants through the area. The investigators monitored use by deer and elk in two replicates of pasture systems supporting light (40 acres per animal unit [16 ha/animal unit]), moderate (30 acres per animal unit [12 ha/animal unit)]) and heavy (20 acres per animal unit [8 ha/animal unit]) cattle grazing. Over a period of 11 years (1954–1964), elk and mule deer use was measured from pellet groups and plant utilization surveys. They found that both elk and mule deer used pastures not grazed by cattle more than any of the cattle-grazed pastures, with use declining as cattle stocking rate increased. They found less of an effect by cattle on mule deer than on elk, indicating possible competition between elk and cattle only.

Methods

In 1989 an ungulate-proof fence was built around Starkey for long-term studies of elk, mule deer and cattle (Rowland et al. 1997). Three studies of spatial interactions among elk, mule deer and cattle took place in the enclosed areas. The largest-scale study was conducted in main study area (19,026 acres [7,700 ha]) during spring, when only elk and mule deer were present (Johnson et al. 2000). In a smaller (5,930-acre [2,400-ha]) subpasture of Main Study Area, Smith-Bally, responses of elk and mule deer to cattle were investigated during early and late summer, and elk and mule deer distributions were analyzed with and without cattle present (Coe et al. 2001). Finally, in the 3,459-acre (1,400-ha) Northeast Study Area, spatial and temporal competitive interactions among all three species were documented (Stewart et al. 2002). Scale of analysis was defined by spatial extent (the size of the study area), spatial grain (the smallest spatial unit used in analysis), temporal extent (the time span of the study) and temporal grain (the smallest unit of time used in analysis; Table 1).

In the Main Study Area, we investigated interactions of elk (n = 88) and mule deer (n = 45) during spring, when cattle were not present (Johnson et al. 2000). Resource selection functions were estimated for both species. A resource selection function is a value for a resource unit that is proportional to the probability of the unit being used by an animal (Manly et al. 1993). Resource units

Table 1. Scales of species interaction analyses at Starkey Experimental Forest and Range, northeast Oregon

Measure of scale	Elk and mule deer[a]	Elk, mule deer and cattle[b]	Elk, mule deer and cattle[c]
Spatial extent acre (ha)	19,012 (7,700)	19,012 (7,700[d]), 5,926 (2,400)[e], 5,926 (2,400)[f],	3,457 (1,400)
Spatial grain acre (ha)	0.22 (0.09)	5,926 (2,400)[d], 19 (7.7)[e], 0.22 (0.09)[f]	5.55 (2.25)
Temporal extent (yrs)	4	2	3
Temporal grain (mean number of days	56.5	27	7[g], 0.25[h]

[a] Spring (Johnson et al. 2000)
[b] Summer (Coe et al. 2001)
[c] Spring, summer and fall (Stewart et al. 2002)
[d] Pasture level analysis
[e] Plant community level analysis
[f] Pixel level analysis (resource selection functions)
[g] Seven-day model
[h] Six-hour model

were represented as 98.4 by 98.4 feet (30 x 30 m) cells. A resource selection function may be mapped as a probability of use by the species across a landscape. To investigate interspecific interactions between mule deer and elk, the probability of use for one species was used as a variable to estimate a resource selection function for the other species.

In Smith-Bally pasture we investigated responses of elk and mule deer to cattle at several spatial grains (Coe et al. 2001; Table 1). We analyzed counts of animal locations (n = 25–55 elk, 12–36 mule deer and 35–42 cattle) at the pasture and habitat level within the pasture. We estimated resource selection functions at the pixel level. To examine species use at the pasture level, we used relative counts of elk and mule deer locations within the pasture versus the rest of main study area during years when cattle were present and the same days during years when cattle were absent. A temporally correlated Poisson regression accounted for autocorrelation among days and nonnormally distributed count data. The same process was used to investigate whether elk and mule deer changed their use of four major habitat types within the Smith-Bally pasture when cattle were present, compared to when they were absent. Finally, resource selection functions were estimated for both elk and mule deer at the pixel level when cattle were present and when they were absent in Smith-Bally pasture. Cattle resource selection functions were also estimated for the same time periods and at the same spatial grain.

In the Northeast Study Area, Stewart et al. (2002) investigated the relative influence of interference versus exploitive competition among elk, mule deer and cattle, after accounting for niche partitioning. Stewart et al. (2002) used multivariate analysis of variance (MANOVA) to examine seasonal niche partitioning among these three species of large herbivores by examining the interactions of animal locations with random locations ($n = 465$) for independent variables associated with habitat selection (e. g. habitat type, distance to water, distance to roads, slope and aspect). Habitat variables included in MANOVA models had been selected previously from species-specific logistic regression to determine which variables were important to that species (Stewart et al. 2002). Multiple regression was used to examine competition among the three species while accounting for niche partitioning, by including habitat variables that had been selected from logistic regression being held in the model, and the number of sympatric species and conspecifics within a 5.55-acre (2.25-ha) area surrounding a focal animal location. Stewart et al. (2002) used two temporal windows to examine the relative effects of interference and exploitive competition in those multiple-regression models. One window was a 6-h temporal window to investigate interference competition, based on the number of sympatric animals that were present within the 5.55-acre (2.25-ha) window plus or minus 3 hours of a focal animal location. And, the other window was a 7-day temporal window to examine effects of exploitive competition, based on the number of animals that were present 7 days prior to the focal animal location. Finally, Stewart et al. (2002) compared movements of mule deer and elk 2 weeks before and after cattle were introduced to the study area (early summer) and removed (autumn) to examine potential competitive displacement of mule deer and elk by cattle.

Results

Elk and Mule Deer—Spring

In Main Study Area during spring, elk were found on flatter and more westerly aspects than mule deer, and they were found further from roads with high (more than four vehicles per day) and medium (one to four vehicles per day) traffic (Figure 1). Several of the habitat attributes that mule deer selected were opposite from those elk selected; for example, mule deer selected steeper and northeast-facing aspects, and they selected sites closer to high and medium

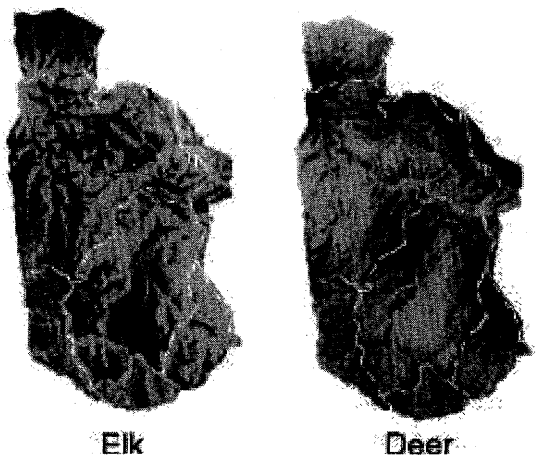

Figure 1. Resource selection function values for elk and mule deer during spring at Starkey Experimental Forest and Range. Light to dark shading indicates increasing proportion of use by each species (from Johnson et al. 2000).

traffic (Johnson et al. 2000). When the mule deer resource selection function was incorporated into the elk resource selection function, and vice versa, the resulting coefficients for the incorporated resource selection functions were negative and significant, indicating that each species selected resources that the other did not. The magnitude of the elk resource selection function in the mule deer model was greater, however, indicating that mule deer were more strongly affected by elk than elk were by mule deer. Further investigation revealed that mule deer use of five habitat types ranked according to elk resource selection function (RSF) was inverse of elk selection. Elk habitat selection within the ranked mule deer resource selection function, however, displayed no pattern. This is further indication that mule deer may have been avoiding elk more than elk were avoiding mule deer.

Elk, Mule Deer and Cattle—Summer

At the pasture level, elk occurred less frequently in Smith-Bally pasture when cattle were introduced, both in early summer and late summer (Figure 2, top). The elk that stayed in the pasture when cattle were present shifted their use of the ponderosa pine/Douglas fir type as a result of cattle (Figure 2, bottom). In early summer, elk were displaced from the ponderosa pine/Douglas fir habitat by cattle. In late summer, elk were displaced into the ponderosa pine/Douglas fir habitat by cattle (Coe et al. 2001). Forage in this habitat was most palatable and nutritious in early summer; consequently, elk likely were negatively affected by this displacement. At the pixel level, early summer resource selection functions for elk when cattle were present were significantly different from elk resource

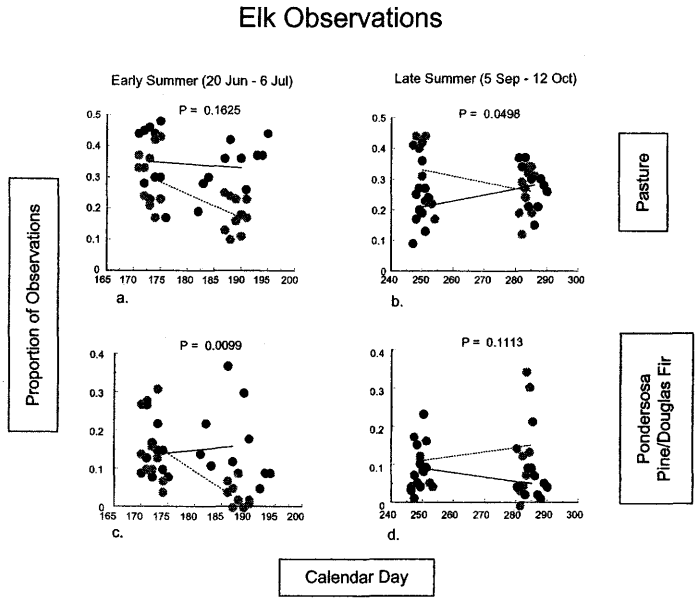

Figure 2. Comparison of the proportion of elk locations in Smith-Bally pasture and in the ponderosa pine/Douglas fir plant community within that pasture, when cattle were present (grey circles, n = 20 days) versus when cattle were absent (black circles, n = 20 days), Starkey Experimental Forest and Range, northeastern Oregon, 1993–1996 (from Coe et al. 2001).

selection functions when cattle were absent. Conversely, late summer resource selection functions for elk when cattle were present were similar to elk resource selection functions when cattle were absent (Coe et al. 2001). In early summer, elk selection for five habitat variables differed if cattle were absent; they selected for sites with gentler slopes, less convex topography, lower canopy, closer to edge of forest stand and further from roads with low traffic rates. In late summer, elk selected denser canopy when cattle were absent; otherwise, elk resource selection functions did not differ based on presence of cattle (Coe et al. 2001). When we included the cattle resource selection function in the elk models, we found that cattle could be used as a predictor of elk distribution in some conditions. With cattle absent, elk selected some of the same resources that cattle select in early spring. When cattle were present, however, elk selected different resources and were spatially separate from cattle. Conversely, in late summer elk resource selection functions were similar to those of cattle, regardless of cattle presence.

Mule deer reduced use of the Smith-Bally pasture in late summer when cattle were introduced but did not change use in early summer with regard to cattle presence. Mule deer use of the ponderosa pine/Douglas fir habitat type was opposite that of elk; mule deer were probably responding to elk movements rather than cattle movements. We observed mule deer changes in habitat use to be

opposite those of elk in three out of four season/year combinations. Mule deer resource selection functions were not affected by the presence of cattle.

Elk, Mule Deer and Cattle—Spring, Summer and Fall

In Northeast Study Area, habitat selection differed among seasons for elk, mule deer and cattle. Wilks' lambda (P = 0.015) revealed a species-by-location (used, random) interaction that indicated differences in selection of some habitat variables among species (Stewart et al. 2002). Bivariate plots of 95-percent confidence intervals indicated that cattle differed from mule deer and elk by avoiding steeper slopes and high elevations, particularly during spring and summer; by contrast, mule deer and elk overlapped in use of slope and elevation, but they partitioned use of vegetative communities (Stewart et al. 2002, Figure 3).

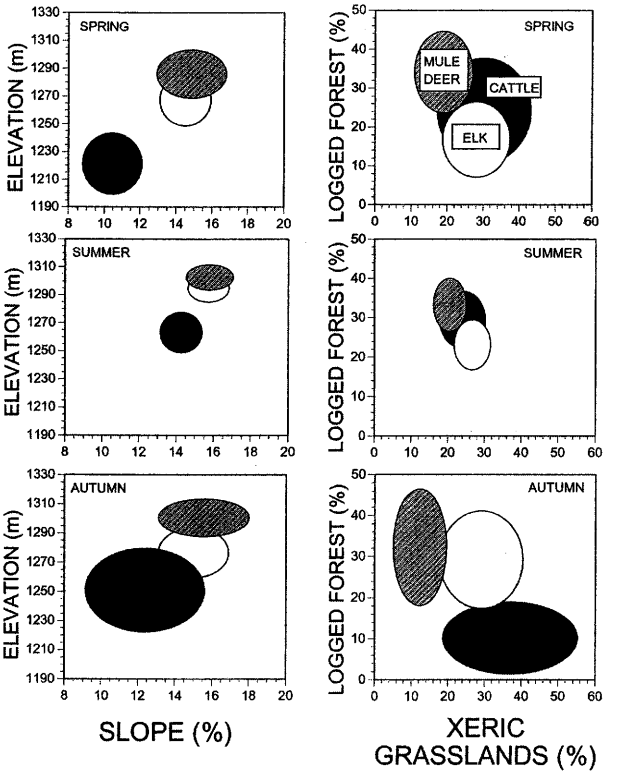

Figure 3. Bivariate plots of niche partitioning based on elevation and slope (left) and on logged forest and xeric grasslands (right). Ellipses are 95 percent confidence interval for cattle, elk and mule deer across seasons on the Starkey Experimental Forest and Range, northeastern Oregon, 1993–1995 (from Stewart et al. 2002).

Spatial avoidance among mule deer, elk and cattle was stronger for the 6-hour models than for the previous 7 days; coefficients of association from

multiple regressions were strongly negative for the 6-hour models, indicating strong avoidance among the three species during all seasons (Stewart et al. 2002). Stewart et al. (2002) observed an interaction of season by species by treatment (Wilks' lambda, $P = 0.046$) and an interaction of species by treatment (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. Because those interactions were significant, the authors analyzed species (elk and mule deer) and seasons separately. Elk moved to higher elevations following introduction of cattle during spring, and they returned to lower elevations following removal of cattle in autumn (Stewart et al. 2002). Conversely, mule deer moved to lower elevations following introduction of cattle during spring, possibly in response to displacement of elk following introduction of cattle (Stewart et al. 2002). The addition of cattle to the northeast did not affect the slope of habitats used by mule deer during spring; although, deer moved to more level ground following removal of cattle in autumn (Stewart et al. 2002).

Resource partitioning for the 6-hour models was interpreted as interference competition, and 7-day partitioning was interpreted as possible interference or exploitive competition. In autumn (September 15 to October 15), coefficients were strongly positive, compared to spring and summer, in all of the 7-day models, indicating spatial overlap among all species (Figure 4). The exception, during autumn, was the elk model, where elk continued to avoid cattle. Mule deer more strongly avoided elk than elk avoided mule deer as evidenced by nonsignificant mule deer variables in the elk models, but highly significant elk variables in the mule deer models. This occurred for all seasons except during the earliest period (June 15 to June 30).

Discussion

Three separate investigations yielded similar information about spatial relationships of elk, mule deer and cattle within Starkey at three different scales. Spatial separation was noted for elk and mule deer and for elk and cattle at all scales analyzed during spring and early summer. At the largest scale, the Main Study Area, remarkable spatial separation was seen for elk and mule deer (no cattle present) in spring, so much so that maps of resource selection functions for each species were nearly mirror images. In Smith-Bally pasture spatial

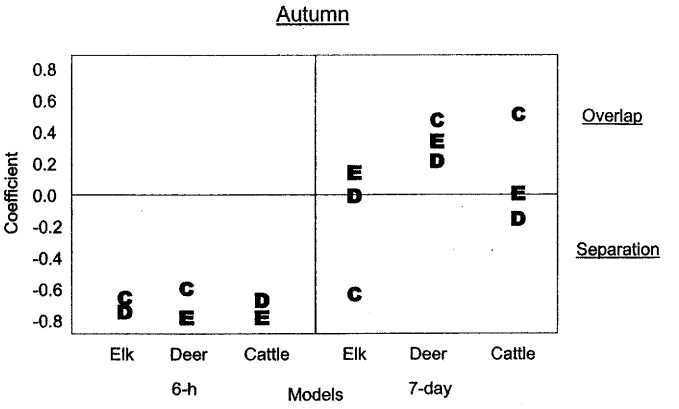

Figure 4. Standardized competition coefficients, determined from weighted multiple regressions for elk, mule deer and cattle during autumn (September 15 to October 15) in Starkey Experimental Forest and Range. Number of conspecifics (C = cattle, D = mule deer and E = elk) plus the focal animal,was the dependent variable for 6-hour and 7-day models (Stewart et al. 2002).

separation of elk and mule deer was evidenced in that mule deer response was opposite to that of elk in their use of plant communities. In Northeast Study Area, spatial separation between elk and mule deer was maintained in the 5.55-acre (2.25-ha) neighborhood surrounding each focal animal in early summer for both temporal scales analyzed.

Elk and cattle spatial separation occurred in the two studies where cattle were present. Both studies concluded that elk avoid cattle during summer. Both studies also noted more overlap among all ungulates during late summer; spatial overlap of all species during late summer and fall occurred in the two studies that encompassed these seasons. This overlap is indicative of possible exploitive competition between the three species of ungulates as forage resources become depleted later in the grazing season, especially in light of other findings at Starkey. Other Starkey studies have found nutritional deficits of both elk and cattle in late summer (Cook et al. 2004, Holechek et al. 1982). Spatial overlap, indications of nutritional deficits and diet overlap in grand fir (*Abies grandis*) habitats during August (Findholt et al. 2004) implicate competition for resources as a potential limiting factor in ungulate productivity during late summer and fall.

All of the analyses are consistent with the hypothesis of a cascading effect of larger ungulates displacing smaller ones. In both the Smith-Bally and in the Northeast Study Area analyses, cattle displaced elk, and all three studies cited evidence of elk displacing mule deer. If this hypothesis is true (i. e., if larger ungulates choose habitat first), elk could suffer nutritional deficits sooner than cattle, and deer could suffer sooner than elk in a limited-forage situation.

Policy Implications

Following is a list of the implications of this research:

- Cascading effects of larger herbivores choosing resources before smaller herbivores do imply that decisions that change distribution of cattle will likely change distributions of elk and mule deer.
- Cattle are the most easily manipulated and are the largest herbivore in northeastern Oregon; thus, they can be a tool in managing spatial distributions of elk and mule deer.
- Management of ungulate density in late summer and fall (e. g., stocking reductions in areas of high ungulate overlap) could ensure high productivity of both wild and domestic ungulates as forage resources become limited.
- Resource selection functions, which account for interspecific interactions of elk, mule deer and cattle, can predict animal distributions over a landscape and can act as part of a larger model to predict forage removal and animal productivity.
- Estimating animal unit equivalents is dependent on two basic factors—distributional overlap and dietary overlap. Animal unit equivalents cannot be based strictly on body weight; results from these studies indicate spatial separation occurs, effectively discounting the animal unit equivalencies for these three species.

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