

University of Nevada, Reno

**Resource Partitioning and Dietary Overlap of Mule Deer and Elk in Eastern
Nevada**

A thesis submitted in partial fulfillment of the requirements for the degree of Master of
Science in Natural Resources and Environmental Science

By

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Abstract

In semi-arid environments, such as the Great Basin, low productivity and frequent drought conditions increase the complexity of understanding the potential for competition, habitat selection, and dietary separation between native ungulates and cattle. I studied resource partitioning and spatial patterns of habitat use by female mule deer (*Odocoileus hemionus*) and female elk (*Cervus elaphus*) in eastern Nevada during winter, spring, and summer. I also examined dietary composition and overlap of mule deer, elk, and cattle. To assess resource partitioning and spatial distributions I used ecological niche factor analysis (ENFA) to analyze the areas used by radio-collared mule deer and elk and create habitat suitability maps for both species. I found that both species were using habitats close to dirt roads and that areas with high pinyon-juniper cover were avoided during all seasons. Nonetheless, there was selection for low-density pinyon-juniper areas and areas in proximity to pinyon-juniper. Mule deer selected for specific elevational ranges (2300m to 2500m) and areas close to springs during the summer. Elk selected for higher elevations during spring and summer. Slope and proximity to springs were also important during summer. I found that habitat use was more restricted during summer than for the other seasons for both species, but especially mule deer. My results suggest that in these semi-arid watersheds, mule deer and elk may be more restricted by availability of water and high quality forage during summer.

To assess dietary composition and overlap between mule deer, elk, and cattle, diet utilization was quantified from microhistological analysis of rumen and fecal samples. I observed that that there was not substantial dietary overlap among elk and mule deer from October to December, but that dietary overlap was greatest in summer. Elk and

mule deer showed greater dietary overlap than elk and cattle. I observed a slight dietary separation among male and female elk, with female elk diets having a greater graminoid component than male elk. Elk and cattle exhibited greater dietary separation in my study area that included a crested wheatgrass seeding, suggesting either that elk avoided areas of high cattle concentration (i.e. crested wheatgrass seedings), or that cattle preferred the seeded grasses and utilized less of other forage species favored by elk.

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Table of Contents

Abstract.....	i
Acknowledgments.....	iii
Table of Contents.....	iv
List of Tables.....	vi
List of Figures.....	ix
Chapter 1.....	1
Introduction.....	1
Literature Cited.....	5
Chapter 2.....	8
Resource Partitioning and Habitat Overlap of Mule Deer and Elk in Eastern Nevada.....	8
Abstract.....	9
Introduction.....	9
Methods.....	11
<i>Study Area</i>	11
<i>Species' Presence Data</i>	12
<i>Environmental Variables</i>	12
<i>Data Analysis</i>	13
<i>Validation</i>	15
Results.....	16
<i>Spatial Distributions</i>	16
<i>Mule Deer</i>	16
<i>Elk</i>	17
<i>Habitat Overlap</i>	17
Discussion.....	18
Management Implications.....	23
Literature Cited.....	25
Tables.....	33
Figure Legend.....	39
Chapter 3.....	47
Diet Composition and Overlap among Elk, Mule Deer, and Cattle in Eastern Nevada.....	47
Abstract.....	48
Introduction.....	49

Methods.....	52
<i>Study Area</i>	52
<i>Field Methods</i>	54
<i>Statistical Analysis</i>	55
Results.....	56
Discussion.....	61
Management Implications.....	65
Literature Cited.....	67
Chapter 4.....	85
Summary.....	85

List of Tables

Chapter 2

Table 1. Environmental predictor variables used to determine habitat use and overlap between mule deer and elk, and the transformation used for each variable.	33
Table 2. Overall marginality for each environmental variable examined for mule deer and elk during winter, spring, and summer. Marginality values indicate whether the species habitat differs from the average habitat conditions in the study area. Bolded variables indicate variables that contribute the most to each factor or component of overall suitability. The elk winter model is not included due to poor model performance.	34
Table 3. Overall specialization for each environmental variable examined for mule deer and elk during winter, spring, and summer. Specialization factors indicate the breadth of the habitat conditions the species is willing to tolerate. Bolded variables indicate variables that contribute the most to each factor or component of overall suitability. The elk winter model is not included due to poor model performance.	35
Table 4. Overall Marginality and specialization values for mule deer and elk for winter, spring, and summer. Larger marginality values indicate that the species range is different than average conditions in the study area, and large specialization factors indicate that species niche is narrow. Elk winter values are not included due to poor model performance.	35
Table 5. Boyce index for mule deer and winter for winter, spring, and summer for habitat suitability models. A Boyce index of 0 indicates that the model did not differ from the random model. The elk winter model was dropped due to poor model performance.	36

Table 6. Amount of habitat (km ²) for each habitat suitability classification for mule deer and elk in winter, spring, and summer. Habitat suitability is divided into 4 categories, low, moderate, good, and prime habitat. The elk habitat suitability model for winter is not included due to poor model performance.	37
---	----

Chapter 3

Table 1. Descriptive statistics for diet composition (%) for elk, mule deer, and cattle collected during winter (October to December) and summer (June to September) in Duck Creek (Duck Creek) and Horse and Cattle Camp (Horse and Cattle Camp), near Ely, Nevada 2005-2006. Rumen samples were not available for cattle.	73
--	----

Table 2. Plant species that make up $\geq 10\%$ of average diet of male and female elk and mule deer in Duck Creek (Duck Creek) and Horse and Cattle Camp (Horse and Cattle Camp) during winter (October to December) 2005-2006 as determined by microhistological analysis of rumen samples. Rumen samples were not available for cattle.	75
---	----

Table 3. Plant species that make up $\geq 10\%$ of average diet of elk, mule deer, and cattle in Duck Creek (Duck Creek) and Horse and Cattle Camp (Horse and Cattle Camp) during summer (June to September) 2005-2006 as determined by microhistological analysis of fecal samples.	76
---	----

Table 4. Results from Shannon-Wiener calculations for winter (October to December) and summer (June to September) for elk, mule deer and cattle. Samples were collected from Duck Creek (Duck Creek) and Horse and Cattle Camp (Horse and Cattle Camp) near Ely, Nevada 2005-2006.	77
---	----

Table 5. Results from Morisita's similarity index calculations for winter (October to December) and summer (June to September) for elk, mule deer and cattle. Samples were collected from Duck Creek (Duck Creek) and Horse and Cattle Camp (Horse and Cattle Camp) near Ely, Nevada 2005-2006.....	78
---	----

List of Figures

Chapter 2

- Figure 1. Climograph of mean monthly temperature and precipitation used to define seasons for Ely, Nevada 2003-2004. Solid lines indicate months and dotted lines separate seasons. 39
- Figure 2. Habitat suitability maps for mule deer. Green indicates low quality habitat, orange indicates medium quality habitat, and red indicates high quality habitat. 39
- Figure 3. Box plots presenting the distributions among sites at which mule deer were present and the entire study site during the winter months for the predictor variables contributing to mule deer habitat suitability. Predictor variables are a.) slope, b.) elevation, c.) pinyon-juniper cover, d.) distance from road, and e.) distance from spring. 39
- Figure 4. Box plots presenting the distributions among sites at which mule deer and elk were present and the entire study site during the spring months for the predictor variables contributing to mule deer habitat suitability. Predictor variables are a.) slope, b.) elevation, c.) pinyon-juniper cover, d.) distance from road, and e.) distance from spring. 39
- Figure 5. Box plots presenting the distributions among sites at which mule deer and elk were present and the entire study site during the summer months for the predictor variables contributing to mule deer habitat suitability. Predictor variables are a.) aspect, b.) distance from stream, c.) elevation, d.) pinyon-juniper cover, e.) distance from road, f.) slope, and g.) distance from spring. 39
- Figure 6. Habitat suitability map depicting the difference in mule deer and elk habitat selection during the spring and summer. During the spring mule deer used slopes varying

from 4 to 17% and elevations from 2400 to 19950m. Elk used slopes varying from 2 to 12% and elevations from 2400 to 2050m. During the summer mule deer used slopes varying from 9 to 16% and elevations from 2300 to 2500m and elk used slopes varying from 5 to 18% and elevations from 2100 to 2700m. Green indicates low habitat overlap, orange indicates moderate habitat overlap, and red indicates high overlap. 39

Chapter 3

Figure 1. Climograph of mean monthly temperature and precipitation used to define seasons for Ely, Nevada 2003-2004. Solid lines indicate months and dotted lines separate seasons. 79

Figure 2. Dietary overlap among species in winter, shown using principal component analysis (PCA) on forage classes determined from microhistological analysis of rumen samples collected in Duck Creek (DC) and Horse and Cattle Camp (HCC) for elk (Duck Creek=36; Horse and Cattle Camp=33) and mule deer (Duck Creek=31;Horse and Cattle Camp=8). Rumen samples were collected from hunters that harvested a mule deer or elk near Ely, Nevada for October to December 2005. Ellipses are 95% confidence intervals of PCA axis scores. 79

Figure 3. Dietary overlap among species in summer, shown using principal component analysis (PCA) on forage classes determined from microhistological analysis of feces collected in Duck Creek (DC) and Horse and Cattle Camp (HCC) from cattle (Duck Creek=4; Horse and Cattle Camp=4), elk (Duck Creek=4; Horse and Cattle Camp=8), and mule deer (Duck Creek=5; Horse and Cattle Camp=5) near Ely, Nevada from June to

September, 2005. Ellipses represent 95% confidence intervals of PCA axis scores. Note:
scale is different from rumen sample graphs. 79

Figure 4. Dietary overlap among sexes of elk in winter, shown using principal
component analysis (PCA) on forage classes determined from microhistological analysis
of rumen samples collected in Duck Creek (DC) and Horse and Cattle Camp (HCC) from
female elk (Duck Creek=16; Horse and Cattle Camp=10) and male elk (Duck Creek=20;
Horse and Cattle Camp=23). Rumen samples were collected from hunters that harvested
elk near Ely, Nevada from October to December 2005. Ellipses are 95% confidence
intervals of PCA axis score. 79

Chapter 1
Introduction

Sympatric species with similar life-history strategies typically exhibit resource partitioning on three niche axes: spatial separation, temporal avoidance, and dietary differences (Stewart et al. 2002). Mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) are known to co-exist throughout the western states and both of these species are thought to have coevolved; therefore a high degree of resource partitioning is expected (Connell 1980). Habitat selection coupled with dietary requirements add a complex dimension to competition in the Intermountain West where native large herbivores, such as elk and mule deer, utilize the same rangelands as domestic livestock (Stewart et al. 2002).

Many studies have shown resource partitioning and dietary differences between mule deer, elk, and cattle (Vavra et al. 1989; Kingery et al. 1996; Stewart et al. 2002; Stewart et al. 2003, Beck and Peek 2005; Torstensen et al. 2006; Stewart et al. 2010). However, few studies (Beck and Peek 2005; Beck et al. 2006) have been conducted in regions with a semi-arid climate, which can dramatically impact resource selection and competition. In semi-arid environments, low levels of precipitation and frequent drought conditions add to the complexity of understanding ungulate use of their environment and have the potential to increase competition, resource partitioning, and dietary separation.

Low levels of precipitation and drought conditions affect body condition, survival, distribution, and habitat use (Marcum and Scott 1985; McKinney 2003; Bender et al. 2007). Levels of precipitation, especially in semi-arid environments, have impacts on plant productivity and nutritional quality, which affect the overall body condition of mule deer and elk (Smith and LeCount 1979; McKinley et al. 2003; Marshal et al. 2006; Bender et al. 2007) and are likely to affect habitat selection. Competition among large

herbivores is most evident where forage productivity is low, and population densities of native herbivores or stocking rates of domestic species are high (Hobbs et al. 1996a). Semi-arid rangelands, such as those in Nevada, are likely to have intensified competitive interactions among large herbivores because of low primary productivity (Manier and Hobbs 2007). As availability of forage declines, herbivores expand their dietary niche to include sub-optimal, but often less contested forages resulting in greater niche breadth (Pianka 1988; Nicholson et al. 2006). The resulting increase in dietary overlap among sympatric large herbivores may increase the likelihood and intensity of competition (Hobbs et al. 1996b).

Elk were reintroduced in 1932 northeastern Nevada, and the increasing elk population has prompted concerns about the interactions between elk, mule deer, and cattle. Moreover, declining mule deer populations are of great concern and competition with cattle and elk may exacerbate the decline (Fuller 1998; Ballard et al. 2001; Wasley 2004; Cook et al. 2007; Bishop et al. 2009). Thus, niche partitioning and competitive interactions are important components of management decisions regarding these three species of large herbivores and the ecosystems that they inhabit.

I conducted a study of habitat selection and overlap of mule deer, elk, and cattle in eastern Nevada. This thesis is divided into two parts. First, I examined resource partitioning and habitat overlap among mule deer and elk, using statistical modeling approaches based on environmental variables constructed within a GIS. I hypothesized that habitat overlap would be greatest during the winter, when resources were most limiting, and that habitat overlap would be least during the summer. Secondly, I examined dietary overlap between mule deer, elk, and cattle. My objectives were to

determine levels of dietary overlap between elk, cattle, and mule deer in eastern Nevada. I hypothesized that greater dietary overlap will occur during winter when resources are more restricted. In addition, I expected dietary overlap to be the greatest between native intermediate feeder, elk, and the non-native grazer, cattle, because of digestive morphology, physiology, and lack of coevolution, than either species with mule deer. I also predicted that female elk would consume fewer graminoids than their male counterparts, because females are more selective for higher quality forage due to greater metabolic demands and smaller body size than males. Lastly, I hypothesized that there would be greater dietary overlap in my more arid study site due to differences in precipitation, elevation, and plant communities.

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Chapter 2

Resource Partitioning and Habitat Overlap of Mule Deer and Elk in Eastern Nevada

Abstract

I studied habitat selection and overlap and patterns of spatial distribution for female mule deer (*Odocoileus hemionus*) and female elk (*Cervus elaphus*) in eastern Nevada during winter, spring, and summer. My objective was to examine the degree of resource partitioning and habitat overlap between mule deer and elk in a semi-arid environment. I used ecological niche factor analysis (ENFA) implemented in Biomapper software to analyze known locations of radio-collared mule deer and elk and to create habitat suitability maps. I found that both species were commonly found close to roads and that areas with high pinyon-juniper cover were avoided during all seasons. During the summer, mule deer selected for specific elevational ranges and areas close to springs. Elk selected for higher elevations during spring and summer. Steeper slopes and areas closer to springs were also important during summer. I found that habitat use was more restricted during summer than other seasons for both species, indicating that mule deer and elk are more restricted during the summer by availability of water and high quality forage.

Introduction

Mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) are known to co-exist throughout the western states, and concerns about declining mule deer populations have prompted concerns about competition between mule deer and elk (Fuller 1998; Ballard et al. 2001; Stewart et al. 2002; Wasley 2004; Cook et al. 2007; Bishop et al. 2009; Stewart et al. 2010). Many studies have shown resource partitioning between mule deer and elk (Vavra et al. 1989; Stewart et al. 2002; Torstensen et al. 2006; Stewart et al. 2010).

However, few studies have been conducted in semi-arid conditions (Beck and Peek 2005; Beck et al. 2006), which can dramatically impact resource selection and competition.

Mule deer and elk habitat preferences are diverse, species- and season-specific, and often particular to a given study area, making it difficult to determine the interaction between animals and their habitats. In semi-arid environments, low levels of precipitation and frequent drought conditions add to the complexity of understanding ungulate use of their environment and have the potential to increase interspecific competition and resource partitioning. Naturally occurring low levels of precipitation and drought conditions affect body condition, survival, habitat use and distribution for mule deer and elk (Marcum and Scott 1985; McKinney 2003; Bender et al. 2007). In semi-arid environments, plant productivity and nutritional quality are strongly influenced by water availability during the growing season, and in turn influence the overall body condition of mule deer and elk (Smith and LeCount 1979; McKinney et al. 2003; Marshal et al. 2005; Bender et al., 2007).

Resource partitioning, or the division of resources among multiple co-occurring species, is generally divided into three categories: temporal, spatial, and dietary (Schwartz and Ellis 1981; Stewart et al. 2002; Mobaek et al., 2009; Stewart et al. 2010). Seasonality likely influences the degree of resource partitioning and the degree of competition between mule deer and elk due to fluctuation of availability high quality habitat. Mule deer and elk separate on multiple niche axes both spatially and temporally along environmental and resource gradients (Stewart et al. 2002; 2010). During autumn and winter months, resources become scarce due to low plant productivity (Cook et al. 2001) and limited access due to snow (Peek et al. 1982; Parker et al. 1984). This

decrease in productivity and availability may result in increased spatial overlap (Stewart et al. 2002), especially as elk and mule deer populations migrate to lower elevations to avoid snow at higher elevations. During spring and summer months resources are more plentiful and spatial overlap is generally less but may be higher if resources are not limiting. However, the degree of spatial overlap may be less pronounced in semi-arid environments. The combination of these factors may cause overlap on one niche axis but separation on another niche axis (Pinaka 1988) and in some cases force one species to utilize less desirable habitats (Kie et al. 2003).

My objective was to examine the degree of resource partitioning and habitat overlap between mule deer and elk in eastern Nevada. I hypothesized that resource partitioning would occur during all seasons but would be most pronounced during the winter due to limited availability of resources. I predicted that distributions of both species would be similar during the winter, when available habitats are restricted, and that distribution during summer would show greater variability. I also predicted that during the summer elk and mule deer would select for more similar habitat variables than during winter or spring, times of year when essential resources are expected to be more limiting.

Methods

Study Area

My field site was located near Ely, Nevada (39.17°N, 114.51°W) in the Schell Creek Mountain Range. The 5292-km² study area ranged in elevation from 1286 to 3980m. Seasonal temperatures range from -9° to 31°C, with an average precipitation of 23cm (Western Regional Climate Center 2008). The study area is managed by the

Bureau of Land Management and the United States Forest Service, with some private holdings. The area is open to cattle grazing from late May to October; in addition, the area receives hunting pressure for elk and mule deer from late summer into early winter. General habitat types include pinyon-juniper (PJ) stands dominated by singleleaf pinyon (*Pinus monophylla* Torr. & Frém.) and Utah juniper (*Juniperus osteosperma* Torr. (Little)), quaking aspen (*Populus tremuloides* Michaux), planted and natural meadows, big sagebrush (*Artemisia tridentata* [Rybd.] Beetle) steppe, and crested wheatgrass (*Agropyron cristatum* [L.] Garertn) seedings.

Species' Presence Data

A total of 10 female elk and 10 female mule deer were captured July 2005 and fitted with a GPS store-on-board radio collar (Sirtrack Ltd.). Collars were programmed to record a GPS location every 4 hours until retrieval of the collars. One adult female deer was harvested in August (2005), and 1 mule deer collar and 1 elk collar were not recovered. Data downloaded from the collars were randomly subset; one point was randomly sampled for each collar for each day (Stewart et al. 2002). Those data were then sampled to reflect the times of greatest activity for the study species, by selecting only those points that were recorded two hours before or after sunrise and sunset (Stewart et al. 2002).

Environmental Variables

A total of 8 environmental variables (Table 1.1) were chosen to be used for determining habitat suitability because they have been shown to affect habitat selection of mule deer and elk in other studies (Stewart et al. 2002, Marshal et al. 2006, and Stewart et al. 2010.). All of the variables were calculated using ArcGIS (ESRI 2006) and then

converted to IDRISI (Eastman 1999). Snow depth was calculated using ArcGIS (ESRI 2006) based on slope, aspect, local exposures, and the average wind speed, dominant wind direction, and amount of snowfall for the previous 10 years (Western Regional Climate Center, 2008). Aspect was converted into a measure of “northeastness” ($\cos[\text{aspect}-45^\circ]$). Pinyon and juniper tree crowns were classified from 1-m resolution digital orthophotography quadrangles (DOQ images) from 1996, using eCognition Professional 4.0 software (Definiens Imaging), following the object-oriented classification approach of Greenwood and Weisberg (2009). Tree canopy cover was then aggregated to a 30-m pixel resolution using a neighborhood summation function in ArcGIS (version 9.3).

SWReGAP (USGS National Gap Analysis Program 2004) data were used for broad scale vegetation classification, and only areas comprising 1 km² or greater were considered for further analysis. Vegetation types considered in the analysis included Intermountain mountain basins big sagebrush shrubland, Intermountain basins montane sagebrush steppe, Great Basin xeric mixed sagebrush shrubland, crested wheatgrass seeding, Intermountain basins mixed salt desert scrub, pinyon and juniper woodlands, Intermountain basin mountain mahogany woodland and shrubland, aspen and mixed conifer woodland, subalpine limber pine and bristlecone pine, and aspen woodlands.

Data Analysis

I used ecological niche factor analysis (ENFA) implemented in Biomapper software v. 4.0 (Hirzel et al., 2008) to analyze the presence data for each species. This software was chosen for its ability to calculate habitat suitability based on presence-only data (Hirzel et al., 2002). Biomapper uses ENFA to compute habitat suitability (HS)

maps based on habitat variables that are important for the study species (Hirzel et al. 2002). Habitat suitability maps provide a visual depiction of habitat suitability, as well as a GIS tool for further model exploration. ENFA compares the distribution of the predictor variables between the set of locations where the species is known to have occurred and the global distribution of the study area by summarizing the predictor variables into a few uncorrelated factors (Hirzel et al., 2008). Biomapper computes two parameters to create HS maps: 1.) marginality, which is the difference between the species distribution and the global distribution with respect to a given predictor variable, and 2.) specialization, which is the ratio between the variances of the global distribution and the species distribution (Hirzel et al. 2002). The ENFA provides marginality factors, specialization factors, and habitat suitability maps. The marginality factors indicate whether species habitat requirements differ from the average habitat conditions while the specialization factors indicate the breadth of habitat conditions the species is willing to tolerate. A large marginality factor indicates that the species range is different from the average conditions of the study area, while a large specialization factor indicates that the niche range is narrow.

Biomapper was run with all environmental variables listed in Table 1, using the geometric mean algorithm to calculate the habitat suitability (Hirzel and Arlettaz 2003). MacArthur's broken stick advice was used to determine the number of factors used in developing the habitat model (MacArthur 1957). Habitat models were developed for each species by season. Seasons were defined using a climograph by grouping months that had similar ranges of temperature, and reflected changes in plant phenology (Stewart et al. 2002; Fig. 1.1). Because autumn was a transitional period and consisted of only a

single month, I combined autumn and winter samples. This does not account for the importance of autumn as a critical time period for both mule deer and elk for both dietary needs and migration; however, the objectives of the study did not allow for a single month to provide adequate data to examine habitat suitability. Thus, the October through December period was classified as winter, March through May was classified as spring, and June through September was classified as summer (Fig 1.1)

Validation

The predictive power of the HS maps generated by the habitat model was evaluated using 10-fold cross validation (Fielding and Bell 1997). The k-cross fold validation uses all of the available locations. Animal locations are randomly partitioned into k identically sized groups (10 groups in our study) and $k-1$ set are used to create the suitability map. This process is repeated k times and each subset is left out one time. The relationships between the observed and expected number of validation points at different habitat suitability values are evaluated to determine the predictive power (Boyce et al. 2002). I used the continuous Boyce index, with a window size of 25 for all model validations within Biomapper to determine the HS maps performance. Biomapper uses a moving window with computation starting with a first class covering the suitability range chosen (i.e. a window size of 25) which contains a proportion of the maps total area and a proportion of validation points (observations left out during the cross-validation), this provides the predicted to expected frequency. Then the moving window is shifted a small amount upwards and the predicted to expected ratio is again calculated. The Boyce index is finally computed by the Spearman's rank between the PE and the class rank,

varying from -1 to 1 , with 0 indicating a random model (Boyce et al. 2002; Hirzel et al. 2006).

Results

Spatial Distributions

Mule Deer

During winter, mule deer selected for areas of gradual slope but across a broad range of elevations, and avoided areas with high pinyon and juniper tree cover (Table 1.2). During the winter mule deer also selected for areas close to roads. Selection for areas of steeper slopes and avoidance of areas with higher pinyon and juniper tree cover continued during the spring. During the summer, I found that mule deer selected for areas of higher elevation and closer to springs. The specialization factors indicate that mule deer were sensitive to slope, elevation, and distance to springs during all seasons (Table 1.3). During summer, however, mule deer habitat use appeared confined to a narrow range of environmental conditions for pinyon and juniper tree cover, distance to roads, distance to springs, and aspect (Figures 1.3, 1.4, and 1.5).

Mule deer had a more restricted range of habitat conditions during the summer than in the spring or winter (Table 1.4 and Figures 1.3, 1.4, and 1.5). Habitat suitability maps provide a visual representation of the seasonal expansion and contraction of mule deer habitat within the study area (Figure 1.2).

Model validation for mule deer during the winter indicates that this model performed better than the random model. The spring model performed only slightly better than the random model, while the summer model performed much better than the random model (Table 1.5)

Elk

Elk habitat selection during the spring was driven by selection for areas at higher elevation and areas closer to roads. During the summer elk selected for areas at higher elevation with steeper slopes (Table 1.2). The specialization factors indicate that elk were sensitive to the distance to streams during all seasons. Slope, elevation, and distance to springs were important during the spring and summer. Distance to roads was important only during the summer (Table 1.3). Both elk and deer were more selective in their habitat requirements in summer than in spring, although mule deer exhibited the higher degree of specialization (Table 1.4).

Model validation for elk during the winter indicates that this model did not perform better than the random model, and was dropped from further analysis. Lack of model performance is likely caused elk by being generalist during the winter in regards to suite environmental variables examined and therefore selection was not occurring at a level that was able to be detected. The spring model performed only slightly better than the random model, while the summer model performed much better than the random model (Table 1.5)

Habitat Overlap

Areas that were predicted to be of greatest habitat suitability (i.e. top 25%) for elk and mule deer were examined for spatial overlap using GIS overlays of predictive habitat suitability maps. During the spring, deer had approximately 243 km² of high-quality habitat, elk had approximately 280 km² high-quality habitat. Of the total area of high-quality habitat, only 55 km² were shared by mule deer and elk. Mule deer used steeper slopes than elk, while elk used higher elevations (Figures 1.2 and 1.4). During the

summer, mule deer had 11 km² of high-quality habitat, while elk had 109 km². There was a total of 3 km² of prime habitat that was used by both species (Table 1.6).

However, during the summer elk used steeper slopes than mule deer. Elk continued to use higher elevations than mule deer, and mule deer were confined to a narrower range of elevations (approximately 2300m to 2500m) (Figure 1.5).

Vegetation types were then identified within areas of prime habitat for mule deer and elk (Table 1.7). During the winter, deer used a total of 16 vegetation types, while elk only used 7 vegetation types. Both utilized big sagebrush shrublands, montane sagebrush steppe, xeric mixed sagebrush shrublands, and pinyon and juniper woodlands. During spring, the number of vegetation types used decreased to 5 for mule deer, while the number used by elk remained the same as for winter. During the spring, both species continued to utilize the same vegetation types as during the winter with the addition of mountain mahogany woodlands and shrublands. Elk also utilized two additional vegetation types, crested wheatgrass seeding and a mixed salt desert scrub. During the summer, mule deer used 6 vegetation types, while elk used 4 vegetation types. The only shared vegetation type was montane sagebrush steppe. Mule deer prime habitat consisted primarily of montane sagebrush steppe and pinyon and juniper woodlands. Prime elk habitat consisted of montane sagebrush steppe, pinyon and juniper woodlands, and mountain mahogany woodlands and shrublands.

Discussion

It is important to identify the factors that influence habitat selection in areas with environmental extremes. Processes of segregation may be most distinct, and hence amenable to study, in environments with severe resource limitation. Semi-arid

environments add to the complexity of understanding resource selection and habitat overlap. In the present study, I examine habitat variables that are known to effect mule deer and elk resource selection and habitat overlap. In particular I examined only those time periods in which mule deer and elk are most likely to be actively foraging. By focusing on only active foraging times, habitats used for other purposes are likely to underrepresented.

My findings for mule deer selection during winter for elevation and slope are similar to other studies (Poole and Mowat 2005; Stewart et al. 2010). Elevation and slope are often correlated to snow depth (Poole and Mowat 2005; Keating et al. 2007) and selection for less steep areas at lower elevations is interpreted as mule deer avoiding areas of high snow depth. However, my proxy variable for snow depth did not contribute significantly to the mule deer winter habitat model, indicating either that snow depth was not a driving factor in mule deer habitat selection in my study area, or that snow depth was inadequately estimated by my topographically defined algorithm. Areas of high pinyon and juniper cover were avoided, but areas with low pinyon-juniper cover or areas that were adjacent to denser pinyon-juniper stands were used, which is consistent with other studies (Anderson et al. 2005).

Mule deer and elk selected particular habitats during the spring. I found that mule deer and elk differed in their use of slopes, elevations, and distance to roads. Mule deer used areas of steeper slopes than elk. Other studies have documented that mule deer and elk have exhibited segregation by selecting areas of differing slopes (Stewart et al. 2002). Elk used a more restricted range of elevation than mule deer, which is consistent with the findings of Stewart et al. (2010). The restricted elevation use may have been a result of

selectivity for certain forage types from spring green up. Both species were found closer to roads than expected and unlike other studies, elk were found closer to roads than mule deer (Johnson et al. 2000; Stewart et al. 2010)

During the summer, mule deer used an extremely narrow elevational range and were found close to springs. Selection for elevation and distance from springs may be related, as many of the springs are located at higher elevations. Nevertheless, this does not completely explain the small range of elevation used by mule deer. I hypothesize that habitat preferences for a small range of elevation and proximity to springs is driven by the lack of available water sources and the propensity of high quality forage near water sources. In addition, areas near water sources often have taller grasses and shrubs which can provide hiding cover. The requirement for high quality vegetation during lactation may strongly influence habitat selection of female mule deer during the summer.

Summer forage intake rates have a great effect on black-tailed deer (*Odocoileus hemionus columbianus*) condition and elk (Parker 1988; Peek et al. 2002; Stewart et al. 2005) and the same is likely true for mule deer. In addition, mule deer that have fawns may be selecting for areas that are not favored by coyotes which can include factors such as hiding cover, elevation, and steepness slopes during the time period when their fawns are most susceptible to predation (Riley and Dood 1984; Fox and Krausman 1994; Bleich 1997; Brunjes et al. 2007).

Cattle and sheep grazing occur in portions of the study area during all seasons. The presence of cattle can influence resource selection and may cause avoidance of otherwise favorable habitats by mule deer and elk (Stewart et al. 2003; Beck and Peek 2005; Torstensen et al. 2006; Cooper et al. 2008). Although I was unable to investigate

the influence of cattle and sheep on habitat selection behavior of mule deer and elk, I suspect that their presence likely had an effect.

Both species selected for areas that were generally nearer to roads and in some cases they were found to be using the road itself in all seasons. This is counter to what most studies have found (Perry and Overly 1976; Morgantini and Hudson 1979; Thomas et al. 1979; Irwin and Peek 1983; Wisdom 1998; Wisdom et al. 2004; Sawyer et al. 2007, Stewart et al. 2010). However, if the type of road and the level of traffic that the road receives are taken into account my findings are similar to the other studies. I found that mule deer were farther from roads than elk during the spring, but during the summer mule deer were closer to roads than elk. Johnson et al. (2000) reported that mule deer use areas closer to roads than elk, as a means to avoid elk. Mule deer may also use areas near roadside due to greater cover associated with roadsides. I believe that in my study area the relationships among mule deer, elk, and distance roads are more complex and are related to the level of traffic levels. I included paved roads (323 miles), maintained dirt roads (2,171 miles), closed and abandoned roads, and seldom-used two-tracks (8,345 miles). The degree to which mule deer or elk avoid roads is likely influenced by the amount of motorized traffic the road receives (Naylor et al. 2009). Throughout the year, motorized traffic within the study area is primarily limited to paved highways. Some of the maintained dirt roads and two-tracks are only seasonally accessible due to snowy and muddy conditions. These roads are only used sparingly by the local human population and are less likely to be avoided by wildlife (Stubblefield et al. 2006; Gagnon et al 2007). In addition local land management agencies have closed some of the two-track roads, and as these roads no longer are accessible for motorized vehicles there is little reason for

mule deer or elk to avoid these areas. Roads that receive little traffic provide travel corridors for elk and mule deer. The energy expenditure is less for traveling along a road than it is when an animal traveling through brush, in a manner inversely related to body size (Parker et al. 1984).

Areas of high pinyon and juniper cover were avoided, but areas with low pinyon-juniper cover and areas that were adjacent to denser pinyon-juniper stands were used during all seasons. Nutritional condition is negatively related to the amount of pinyon-juniper (Bender et al. 2007; Hallbritter and Bender 2011). Pinyon-juniper communities that have high canopy cover produce little vegetation due to competition for water, lack of sunlight for understory vegetation, litter accumulation, phytotoxic exudates from roots, and binding of nutrients (Miller et al. 1979; Schott and Pieper 1985; Dahms and Geils, 1997). However, areas adjacent to denser pinyon-juniper woodlands or that have low cover of pinyon-juniper can provide security cover (Bender et al. 2007). These areas may also be important for thermal cover for mule deer during the summer (Bowyer and Kie 2009), but Cook et al. (1998) found that thermal cover did not provide energetic benefits for elk during winter. However, these areas have also been shown to be preferred by elk (Anderson et al. 2005) and by white-tailed deer (*Odocoileus virginianus*) during drought (Grovenberg et al. 2011). During the winter months open canopy pinyon-juniper woodlands may provide increased access for foraging and lower energetic cost for movement as the canopy can prevent heavy snow accumulation on the ground. In addition, open canopy pinyon-juniper woodlands can be associated with increased available ground water, which translates to increased forage in some areas. Our results

suggest that, in this semi-arid ecosystem, some degree of tree cover is an important component of habitat mosaics preferentially selected by both elk and mule deer.

In addition I expected to find that mule deer would have more restricted habitat use than elk, and that both species would select for a narrow range of habitat conditions within their critical winter range. However, I found that habitat use was more restricted during the summer for both species, suggesting that the dry summer season may be more limiting in semi-arid environment. Mule deer in particular may be more limited during the summer by availability of water and high quality forage. Mule deer exhibited greater specialization during the summer than elk. This finding is counter to the findings of Stewart et al. (2010) for mule deer and elk in southeastern Idaho, who found that mule deer were more widely distributed than elk; however this was not a water limited ecosystem.

Management Implications

I found evidence that mule deer and elk avoid areas of high pinyon-juniper cover during all seasons, but do utilize areas that have low levels of pinyon-juniper cover. Mule deer and elk also appeared to be more limited during the summer months possibly by water and high quality forage than during the winter. Focusing habitat restoration efforts in areas with moderate pinyon-juniper to decrease pinyon-juniper cover and maintaining mosaics of trees and shrub steppe may increase the available habitat for both species. This may also increase available summer habitat for both species.

The propensity of mule deer and elk to use seldom traveled roads, i.e. two-tracks, may provide additional travel corridors. As travel management plans are implemented for federal lands that close off some two-tracks new travel corridors may be created. If

habitat restoration projects were preferentially located along these travel corridors a larger useable area of high quality habitat could perhaps be created for both species.

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Tables

Table 1. Environmental predictor variables used to determine habitat use and overlap between mule deer and elk, and the transformation used for each variable.

Environmental Variable	Transformation
Slope	Square Root
Elevation	Box Cox
Tree Cover	Square Root
Distance to Roads	Box Cox
Distance to Springs	Square Root
Snow Depth	Square Root
Distance to Streams	Square Root
Aspect	-----

Table 2. Overall marginality for each environmental variable examined for mule deer and elk during winter, spring, and summer. Marginality values indicate whether the species habitat differs from the average habitat conditions in the study area. Bolded variables indicate variables that contribute the most to each factor or component of overall suitability. The elk winter model is not included due to poor model performance.

Species and Season	Environmental Variables							
	Slope	Elevation	Tree Cover	Distance to Roads	Distance to Springs	Snow Depth	Distance to Streams	Aspect
DEER								
Winter	0.69	0.45	0.40	0.29	0.19	0.17	0.16	0.04
Spring	0.73	0.29	0.55	0.05	0.10	0.02	0.25	0.07
Summer	0.33	0.60	0.21	0.35	0.52	<0.01	0.29	0.10
ELK								
Spring	0.05	0.53	0.31	0.64	0.29	0.17	0.31	0.04
Summer	0.40	0.83	<0.01	0.08	0.24	0.20	0.21	0.04

Table 3. Overall specialization for each environmental variable examined for mule deer and elk during winter, spring, and summer. Specialization factors indicate the breadth of the habitat conditions the species is willing to tolerate. Bolded variables indicate variables that contribute the most to each factor or component of overall suitability. The elk winter model is not included due to poor model performance.

Species and Season	Environmental Variables							
	Slope	Elevation	Tree Cover	Distance to Roads	Distance to Springs	Snow Depth	Distance to Streams	Aspect
DEER								
Winter	4.42	5.03	3.94	2.97	4.48	2.84	3.65	1.73
Spring	4.02	5.51	2.76	2.45	4.32	2.35	3.12	1.91
Summer	11.7	22.3	9.87	13.9	19.6	3.01	12.0	4.43
ELK								
Spring	3.18	4.51	2.69	3.16	4.27	2.77	4.92	2.18
Summer	5.33	5.06	3.69	4.61	4.10	2.00	5.52	1.50

Table 4. Overall Marginality and specialization values for mule deer and elk for winter, spring, and summer. Larger marginality values indicate that the species range is different than average conditions in the study area, and large specialization factors indicate that species niche is narrow. Elk winter values are not included due to poor model performance.

Species and Season	Marginality	Specialization
DEER		
Winter	0.40	1.28
Spring	0.25	1.25
Summer	0.74	2.30
ELK		
Spring	0.35	1.27
Summer	0.79	1.35

Table 5. Boyce index for mule deer and winter for winter, spring, and summer for habitat suitability models. A Boyce index of 0 indicates that the model did not differ from the random model. The elk winter model was dropped due to poor model performance.

Species and Season	Boyce index	Standard deviation
DEER		
Winter	0.73	0.33
Spring	0.63	0.32
Summer	0.97	0.04
ELK		
Winter	0.52	0.60
Spring	0.69	0.46
Summer	0.93	0.12

Table 6. Amount of habitat (km²) for each habitat suitability classification for mule deer and elk in winter, spring, and summer. Habitat suitability is divided into 4 categories, low, moderate, good, and prime habitat. The elk habitat suitability model for winter is not included due to poor model performance.

WINTER					
	Low Deer Habitat (0-25)	Moderate Deer Habitat (26-50)	Good Deer Habitat (51-75)	Prime Deer Habitat (76-100)	Total
	2230	771	446	156	3603

SPRING					
	Low Deer Habitat (0-25)	Moderate Deer Habitat (26-50)	Good Deer Habitat (51-75)	Prime Deer Habitat (76-100)	TOTAL
Low Elk Habitat (0-25)	1356	387	224	66	2033
Moderate Elk Habitat (26-50)	368	178	151	54	751
Good Elk Habitat (51-75)	190	125	156	68	539
Prime Elk Habitat (76-100)	89	53	83	55	280
TOTAL	2003	743	614	243	3603

SUMMER					
	Low Deer Habitat (0-25)	Moderate Deer Habitat (26-50)	Good Deer Habitat (51-75)	Prime Deer Habitat (76-100)	TOTAL
Low Elk Habitat (0-25)	2704	91	91	1	2887
Moderate Elk Habitat (26-50)	336	30	32	3	401
Good Elk Habitat (51-75)	116	65	21	4	206
Prime Elk Habitat (76-100)	45	45	16	3	109
TOTAL	3201	201	161	11	3603

Figure Legend

Figure 1. Climograph of mean monthly temperature and precipitation used to define seasons for Ely, Nevada 2003-2004. Solid lines indicate months and dotted lines separate seasons.

Figure 2. Habitat suitability maps for mule deer. Green indicates low quality habitat, orange indicates medium quality habitat, and red indicates high quality habitat.

Figure 3. Box plots presenting the distributions among sites at which mule deer were present and the entire study site during the winter months for the predictor variables contributing to mule deer habitat suitability. Predictor variables are a.) slope, b.) elevation, c.) pinyon-juniper cover, d.) distance from road, and e.) distance from spring.

Figure 4. Box plots presenting the distributions among sites at which mule deer and elk were present and the entire study site during the spring months for the predictor variables contributing to mule deer habitat suitability. Predictor variables are a.) slope, b.) elevation, c.) pinyon-juniper cover, d.) distance from road, and e.) distance from spring.

Figure 5. Box plots presenting the distributions among sites at which mule deer and elk were present and the entire study site during the summer months for the predictor variables contributing to mule deer habitat suitability. Predictor variables are a.) aspect, b.) distance from stream, c.) elevation, d.) pinyon-juniper cover, e.) distance from road, f.) slope, and g.) distance from spring.

Figure 6. Habitat suitability map depicting the difference in mule deer and elk habitat selection during the spring and summer. During the spring mule deer used slopes varying from 4 to 17% and elevations from 2400 to 19950m. Elk used slopes varying from 2 to

12% and elevations from 2400 to 2050m. During the summer mule deer used slopes varying from 9 to 16% and elevations from 2300 to 2500m and elk used slopes varying from 5 to 18% and elevations from 2100 to 2700m. Green indicates low habitat overlap, orange indicates moderate habitat overlap, and red indicates high overlap.

Figure 1.

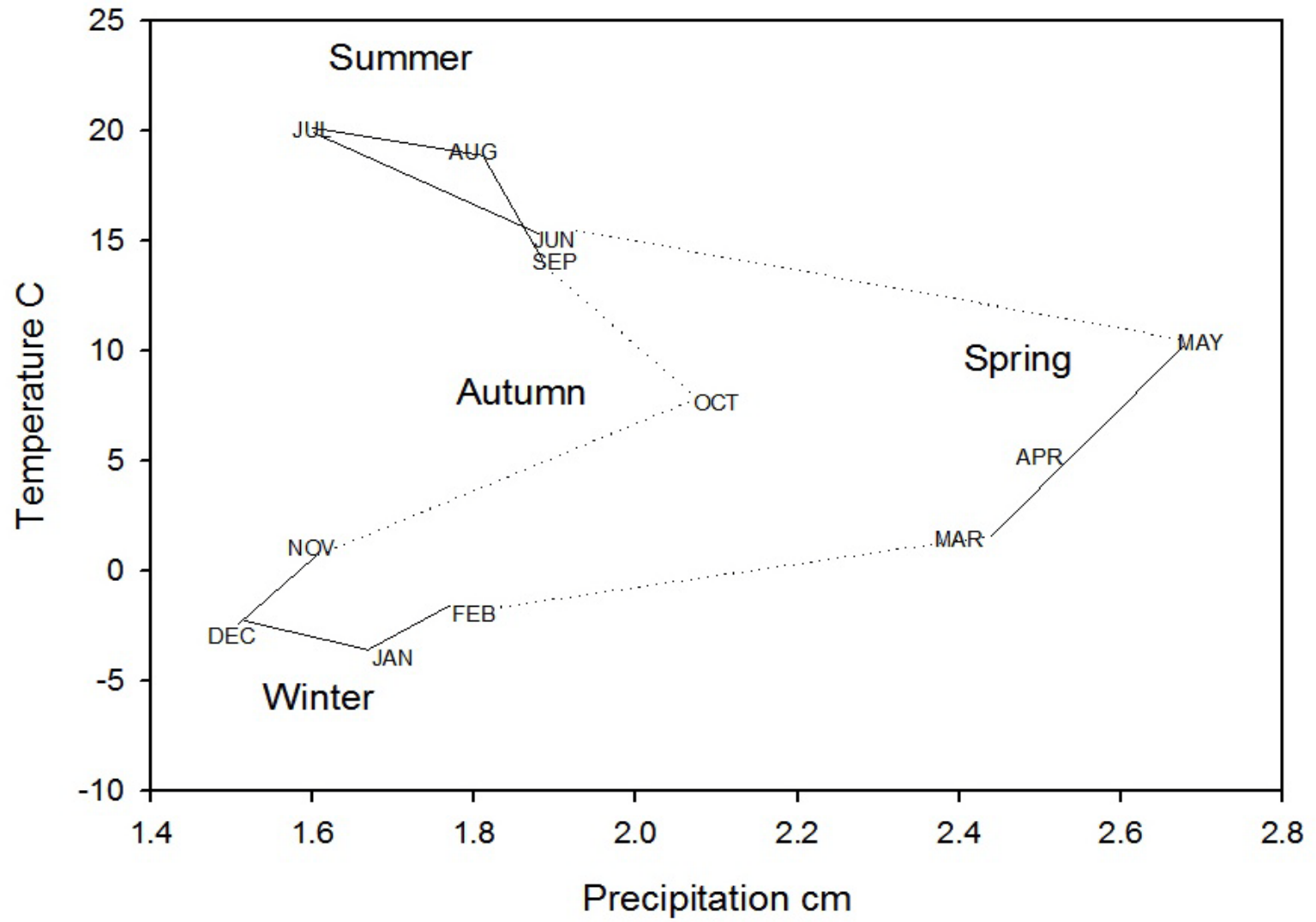
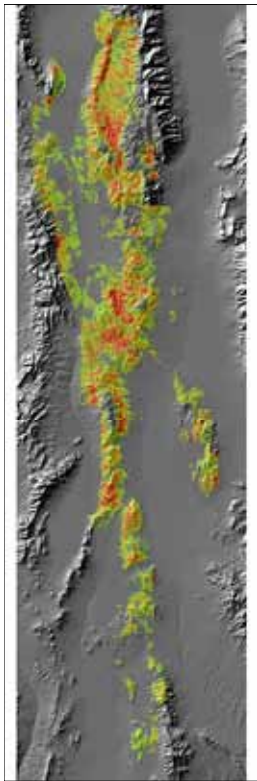
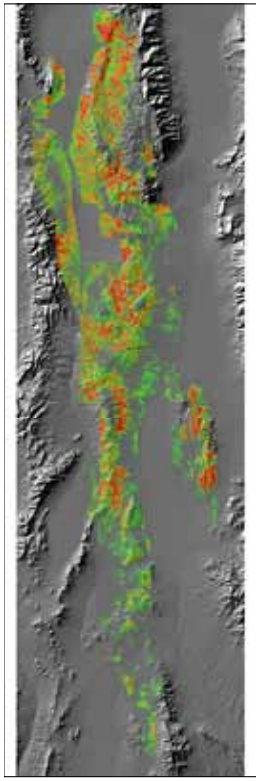


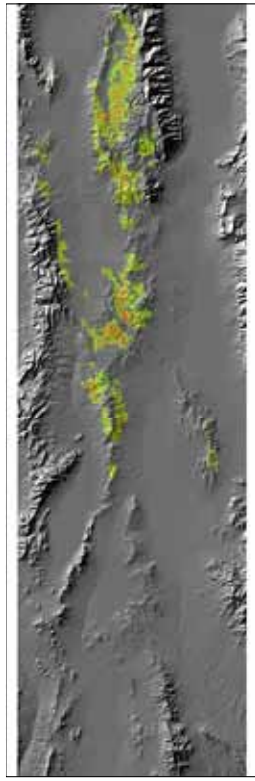
Figure 2.



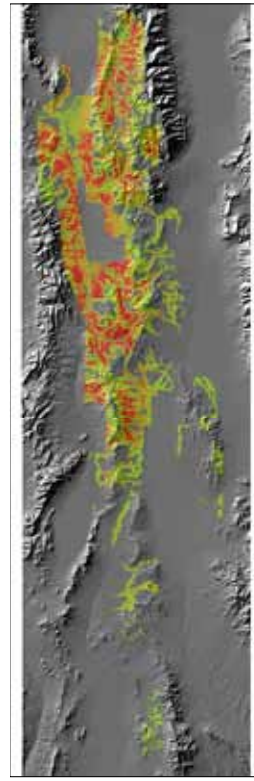
Deer Winter



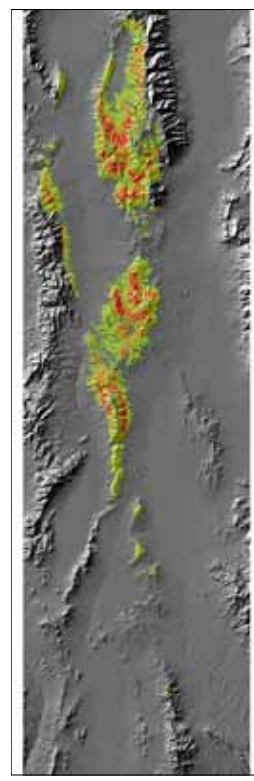
Deer Spring



Deer Summer



Elk Spring



Elk Summer

Figure 3.

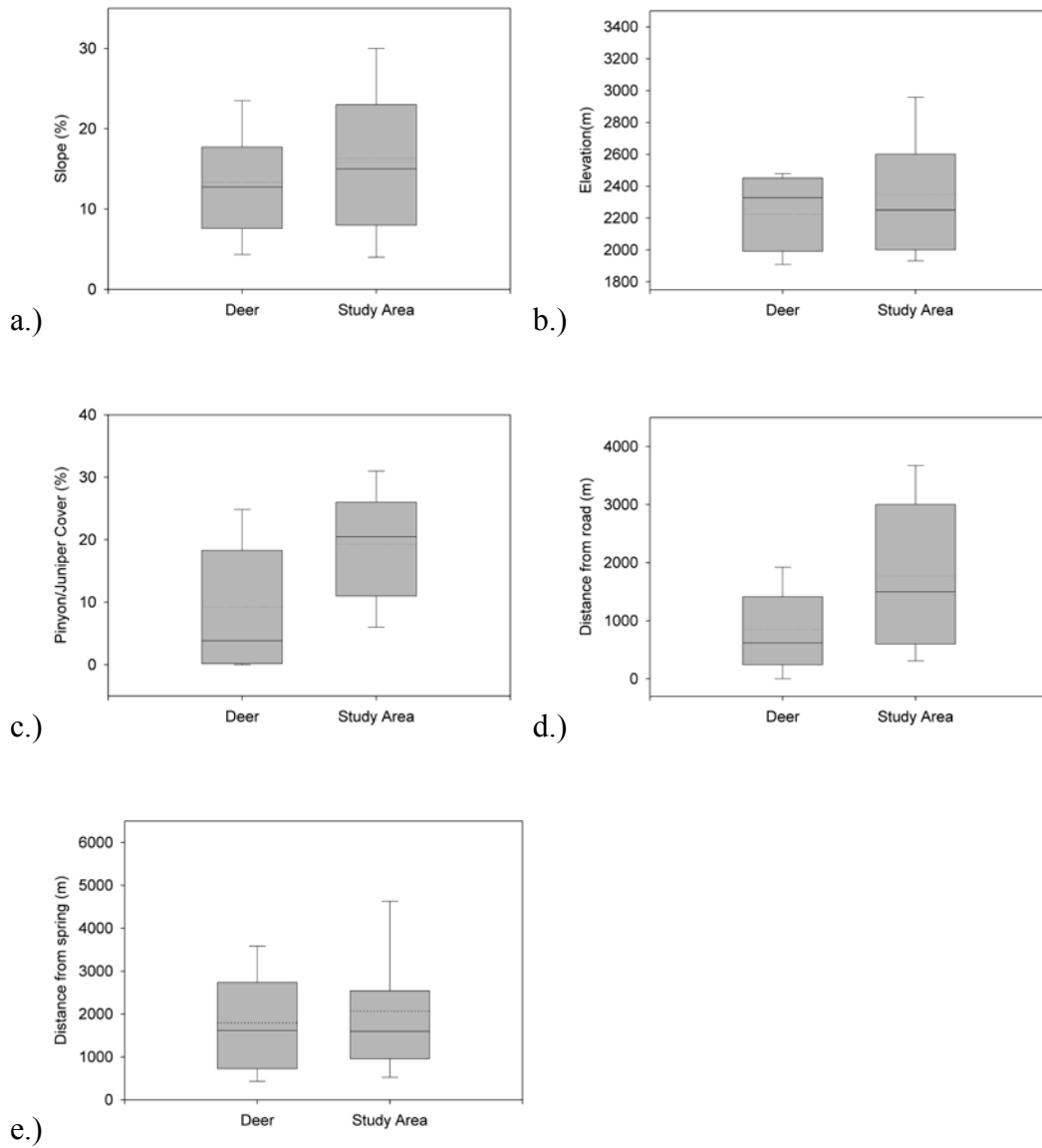


Figure 4.

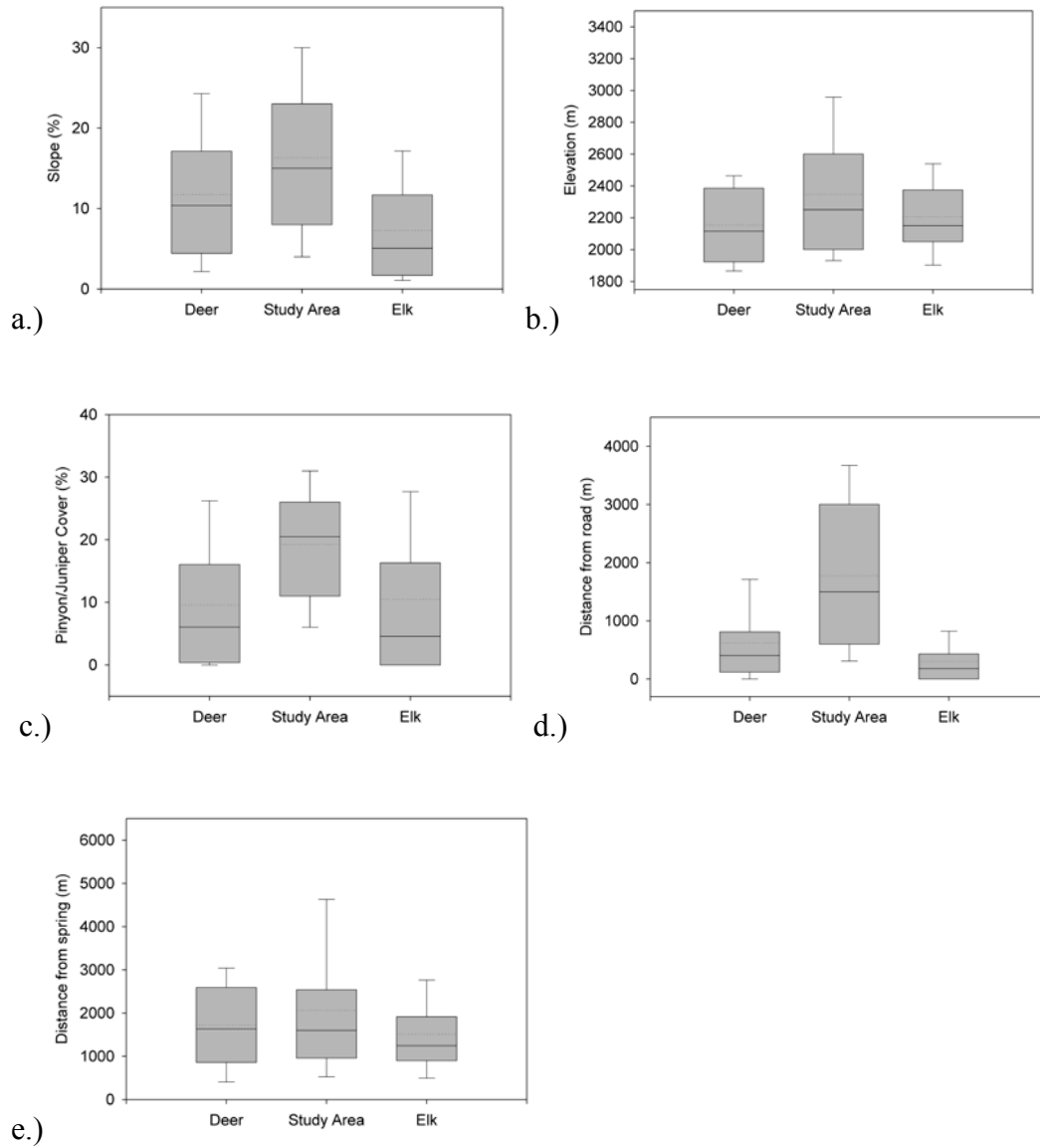


Figure 5.

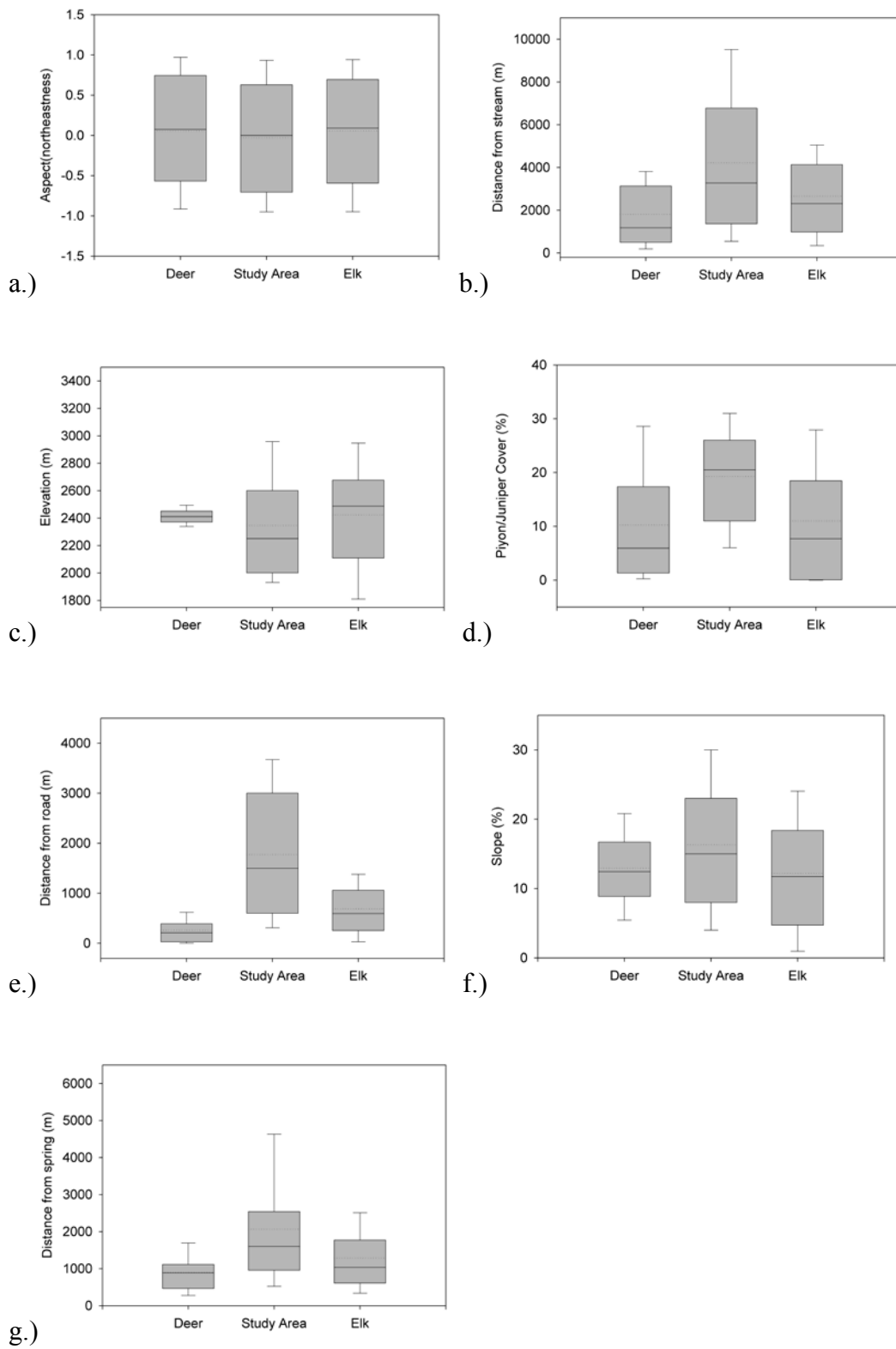
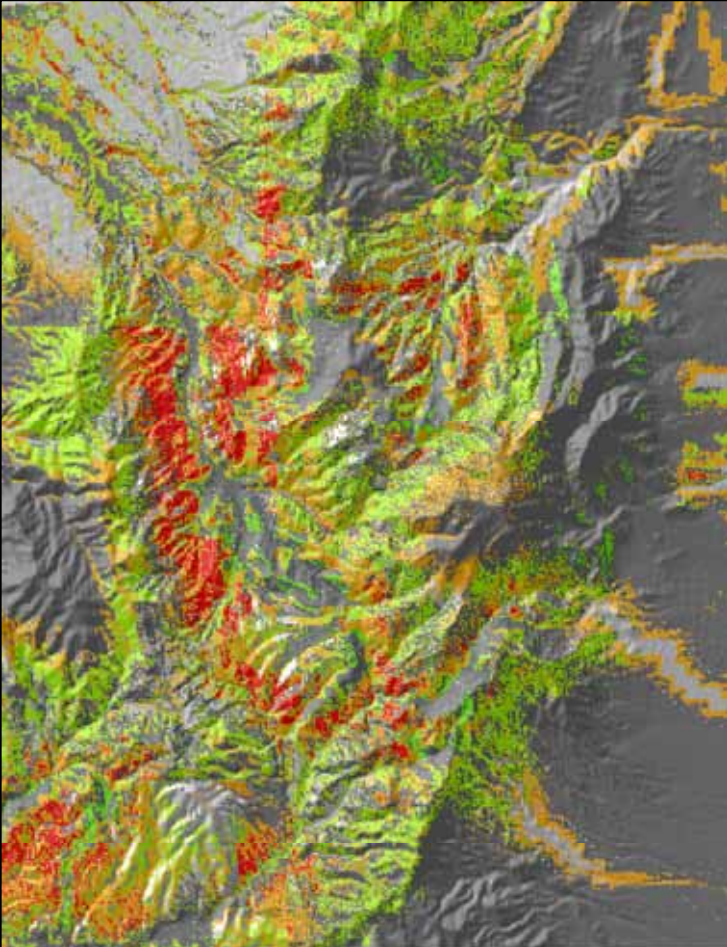
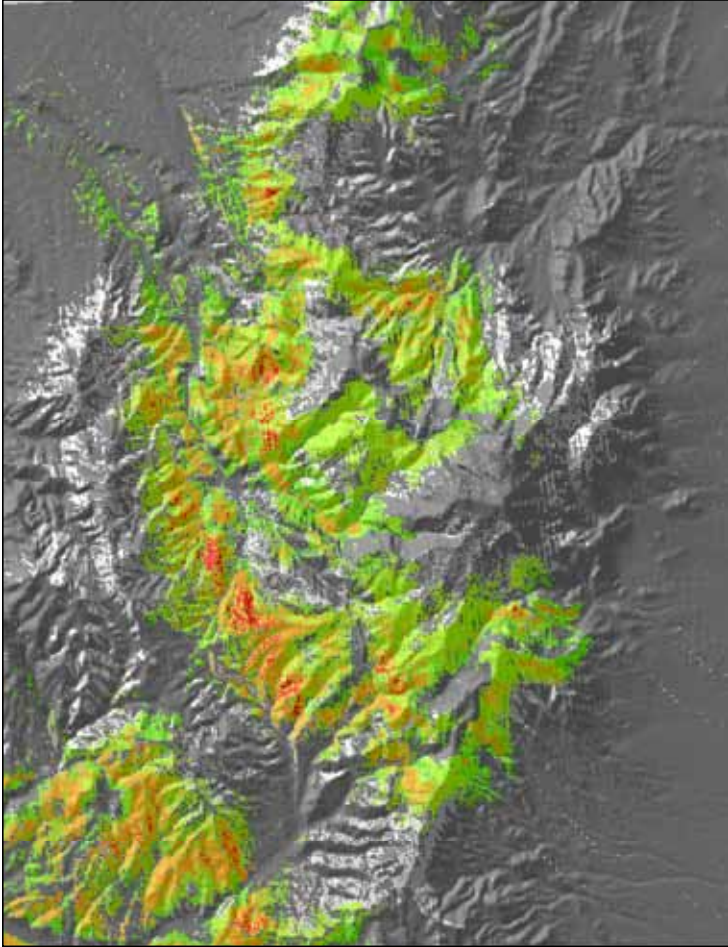


Figure 6.



Spring



Summer

Chapter 3

Diet Composition and Overlap among Elk, Mule Deer, and Cattle in

Eastern Nevada

Abstract

I examined the dietary composition and overlap of elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and cattle in eastern Nevada. Two study areas of 2679 km² and 2613 km², respectively, differed in aridity, livestock use, and extent of crested wheatgrass (*Agropyron spicatum* (L.) Gaertn.) seedings. Diet utilization was quantified from microhistological analysis of rumen and fecal samples. I hypothesized that dietary overlap among the three species is greatest during winter due to limited forage availability, and that dietary overlap is greatest between the native intermediate feeder, elk, and the non-native grazer, cattle, because of digestive morphology, physiology, and lack of coevolution. Additionally I hypothesized that female elk consume a lower proportion of graminoids than their male counterparts because of differences in digestion and dietary needs. I observed that there was not substantial dietary overlap among elk and mule deer from October to December, as hypothesized, but that dietary overlap was greatest in summer. Mule deer diets differed substantially between study areas. Elk and mule deer showed greater dietary overlap than elk and cattle. I observed a slight dietary separation among male and female elk, with female elk diets having a greater graminoid component than male elk. Elk and cattle exhibited greater dietary separation in our study area with the crested wheatgrass seeding, suggesting that elk avoided areas of high cattle concentration, or that cattle preferred the seeded grasses and utilized less of other forage species favored by elk. The increased dietary separation between elk and cattle may have caused an increase in dietary overlap between elk and mule deer on the site with the seeding. Observed dietary separation among species may be due either to spatial

segregation, to differential selection at the level of plant species within functional types, or selection for different plant parts due to differences in bite size.

Introduction

Sympatric species with similar life-history strategies typically exhibit resource partitioning on three niche axes, spatial separation, temporal avoidance, and dietary differences (Pianka 1988; Stewart et al. 2002). Competition for limited resources results in a reduction in resources available per individual or total exclusion of less competitive animals from the best resources (Nicholson et al. 2006). Habitat selection coupled with dietary requirements add a complex dimension to competition in the Intermountain West where native large herbivores, such as elk and mule deer, utilize the same rangelands as domestic livestock (Stewart et al. 2002).

Competition among large herbivores is most evident where forage productivity is low, and population densities of native herbivores or stocking rates of domestic species are high (Hobbs et al. 1996a). As availability of forage declines, herbivores expand their dietary niche to include sub-optimal, but often less contested forages resulting in greater niche breadth (Pianka 1988; Nicholson et al. 2006). The resulting increase in dietary overlap among sympatric large herbivores may increase the likelihood and intensity of competition (Hobbs et al. 1996b). During winter months when forage availability is low, the potential for competitive interactions among native herbivores may be intensified because both mule deer and elk occupy similar habitats, and both habitat and dietary overlap are increased (Torstenson et al. 2006).

Competitive interactions among large herbivores may be intensified in semi-arid rangelands, such as those in Nevada, because of low productivity of the plant community

(Manier and Hobbs 2007). In addition, elk have been reintroduced to northeastern Nevada in 1932, and the increasing population of elk has prompted concerns about the interactions between elk, mule deer, and cattle. Moreover, declining mule deer populations are of great concern and competition with cattle and elk may exacerbate the decline (Fuller 1998; Ballard et al. 2001; Wasley 2004; Cook et al. 2007; Bishop et al. 2009). Thus niche partitioning and competitive interactions are important components of management decisions regarding these three species of large herbivores and the ecosystems that they inhabit, particularly in semi-arid rangelands in the western United States.

Among ruminants, physiological and nutritional requirements differ in relation to body size (Jarman 1974; Demment and Van Soest 1985; Hoffman 1985; Robbins 1993; Barboza and Bowyer 2000; 2001; Stewart et al. 2003). Interactions among nutritional requirements, availability of forages, and occurrence of competitors determine diet selection among species of large herbivores (Anthony and Smith 1977; Singer 1979; Jenkins and Wright 1988; Mower and Smith 1989; Stewart et al. 2003). Large-bodied ruminants, such as elk and cattle, are able to subsist on lower quality forage than mule deer because of larger rumen size and greater retention time for digestion (Kleiber 1961; Hoffman 1985; Putnam 1988). Small-bodied ruminants, such as mule deer, require forages that are less fibrous and have a higher nutrient content (Kie et al. 2003; Stewart et al. 2003). Mule deer have traditionally in the Great Basin been considered browsers, especially during winter months; although the concept of deer as browsers by choice is perhaps one of the oldest and most persistent myths in ungulate ecology (Gill 1976; Kie et al. 2003; Stewart et al. 2003). Nutritional requirements of mule deer may exclude

them from using low quality forage, such as cured grasses, and cause them to consume larger amounts of woody browse during winter months (Kie et al. 2003). This result, however, is not evidence that mule deer are browsers by choice (Gill 1976) since when highly nutritious and digestible forage is available deer will readily consume it (Kie and Czech 2000).

In general, elk are believed to have more diverse diets than cattle and mule deer (Kingery et al. 1996; Beck and Peek 2005). Diet overlap between mule deer and elk is usually low when forage is abundant, because elk are more likely to feed upon graminoids than mule deer, which consume mostly forbs and browse (Bowyer 1984; Hanley 1984; Stewart et al. 2002; Stewart et al. 2003). Conversely, in semi-arid rangelands of the west, such as in Nevada, forage is often limiting and diet overlap among these species is likely to be great. Stewart et al. (2003) reported that mule deer had more variable diets than either elk or cattle in the Blue Mountains of Oregon, most likely because mule deer expanded their dietary niche in response to competition and reduced availability of forages. Cattle typically have the narrowest dietary niche, which is dominated by graminoids (Stewart et al. 2003; Beck and Peek 2005).

Sexual segregation outside the mating season is nearly ubiquitous among polygynous ungulates (Bowyer 2004) and resource partitioning between sexes occurs among habitat, dietary and spatial niche axes (Myserud 2000). Females often are more selective while foraging than males because of their smaller body size (Barboza and Bowyer 2000; 2001). Male ruminants have a larger ruminal capacity supporting longer forage retention, allowing them to utilize more fibrous forage than females (Barboza and Bowyer 2000). Smaller-bodied females often are better suited to post-ruminal digestion,

especially during reproduction and lactation when their energy requirements increase (Barboza and Bowyer 2000). Differences in metabolic demands among sexes for energy and nutrients may cause sexual segregation and niche partitioning among the sexes (Barboza and Bowyer 2000; 2001).

My objectives were to determine levels of dietary overlap between elk, cattle, and mule deer in eastern Nevada. I hypothesized that greater dietary overlap will occur during winter, when forage selection is diminished, and less overlap will occur during summer due to greater availability of forage. In addition, I expected dietary overlap to be the greatest between native intermediate feeder, elk, and the non-native grazer, cattle, because of digestive morphology, physiology, and lack of coevolution, than either species with mule deer. I also predicted that female elk would consume fewer graminoids than their male counterparts, because females are more selective due to greater metabolic demands and smaller body size than males. Lastly, I hypothesized that there would be greater dietary overlap in our more arid study site, Horse and Cattle Camp, than at Duck Creek Basin due to differences in precipitation, elevation, and plant communities.

Methods

Study Area

I selected two field sites, Duck Creek Basin (Duck Creek) and Horse and Cattle Camp, which are located near Ely, Nevada (39.17°N, 114.51°W) in the Schell Creek Range. The Duck Creek study area occupies 2679 km² and is located 28 miles north of Ely. Elevation ranges from 1553 to 3980 m. Seasonal temperatures range from -9° C to 31° C, and average annual precipitation is 23.31 cm (Western Regional Climate Center 2008). There are several springs and small creeks within the study area. The study area

is in mixed ownership, with 63% managed by the Forest Service, 26% by the Bureau of Land Management (BLM), and 11% in private holdings. Several homes are located within the basin, and one ranch has cattle present year round. Most grazing on the public lands is seasonal; cattle are introduced in late May and removed in October. The area is also popular for recreation and hunting from early spring into the winter. Population numbers for elk are estimated at 350-450 and mule deer 1200-1500 during the summer (C. Baughman personal communication, July 2007).

Habitat types include dense pinyon-juniper (PJ) stands, aspen (*Populus tremuloides* Michaux), planted and natural meadows, and big sagebrush (*Artemisia tridentata* [Rybd.] Beetle) steppe. Important plant species include singleleaf pinyon pine (*Pinus monophylla* Torr. & Frem), juniper (*Juniperus* spp.), big sagebrush, needle grass (*Stipa* spp.), serviceberry (*Amelanchier* spp.), snowberry (*Symphoricarpos* spp.), elderberry (*Sambucus* spp.), mountain mahogany (*Cercocarpus* spp.), arrowleaf balsamroot (*Balsamorhiza sagittata* (Prush) Nutt.), bluebunch wheat grass (*Agropyron* spp.), willow (*Salix* spp.) rose (*Rosa woodsii* Lindl), aspen, antelope bitterbrush (*Purshia tridentata* (Prush) DC), lupine (*Lupinus* spp.), and limber pine (*Pinus flexilis* James). There are also several seedings, primarily crested wheatgrass, located throughout Duck Creek which make up approximately 100km² of the study area.

The Horse and Cattle Camp study area (2613 km²) is located 15 miles southeast of Ely, with elevations ranging from 1286 to 1375 m. Average annual precipitation is 22.89cm, with average temperatures ranging from -9°C to 32°C (Western Regional Climate Center). The majority of the area is managed by the BLM, although there are several small parcels that are privately owned. The Horse and Cattle Camp has seasonal

(late June to October) cattle grazing managed by the BLM. The area is open to hunting for elk and mule deer from late August until December. Habitat types include dense pinyon-juniper and mountain mahogany stands, natural meadows, crested wheat seeding, and sagebrush steppe. Important plant species include pinyon-juniper, mountain mahogany, rabbitbrush (*Chrysothamnus* spp.), sagebrush, lupine, Indian paintbrush (*Castilleja* spp.), bluegrass (*Poa* spp.), bitterbrush, snowberry, and serviceberry. There is approximately 217 km² of crested wheatgrass (*Agropyron spicatum*) seeding located in the study area. Population numbers for the summer months are estimated at 250-300 elk and 150-200 mule deer.

Field Methods

Rumen and fecal samples were collected to determine dietary composition for elk, mule deer, and cattle. Of the two methods, rumen samples provide a more accurate description of dietary composition but represent only one feeding bout (Uden et al. 1982). Fecal samples may overestimate fibrous forages (such as mature graminoids) and underestimate highly-digestible forages (such as forbs or new grass growth), but represent multiple feeding bouts (Anthony and Smith 1974). Rumen samples were collected for elk and mule deer only. Fecal samples were collected for all three species.

Rumen samples were collected from hunters that harvested a mule deer or elk in hunt units comprising the study areas. Hunters also completed an information sheet for the rumen sample including date, species, sex, and basic habitat information for the animal that they harvested. Habitat information was classified by hunters as meadow, sagebrush, mountain mahogany, pinyon-juniper, or aspen. Rumen samples were frozen upon receipt and sent to Washington State University, Wildlife Habitat and Nutrition

Laboratory for microhistological analysis (Davitt 1979; Korhage 1974). Samples were analyzed for forage class (forb, shrub, conifer, grasses, and sedge/rush) and major forage plants (>5% of diet, usually 6-12 species).

I collected fecal samples for all three species by walking 8-km transects in each study area once each month from June through December. Transects were located perpendicular to 2-track dirt roads. GPS locations were recorded at transect endpoints (+/-5m) and the transect track was recorded in the GPS to allow repeated sampling. Fecal samples were also collected opportunistically in other areas. Fecal samples were only collected if the sample was determined to be fresh (i.e. still moist on the inside, with odor, and insect free). For each sample I recorded date collected, species, habitat type, and GPS location. Samples were frozen and sent to the Washington State University, Wildlife Habitat and Nutrition Laboratory, where they were analyzed for dietary composition using microhistological analysis of forage class and major plant species in the sample. Samples were not collected during spring, due to inaccessibility of areas where the animals were located.

Statistical Analysis

I performed analysis of variance (ANOVA) following significant ($\alpha \leq 0.05$) multivariate analysis of variance (MANOVA) tests for differences in mean diet composition among sexes (elk only), study site, and species. I applied an arcsine-square root transformation to percentage data to ensure additivity of treatment effects (Kie and Bowyer 1999; Stewart et al. 2002). I used a Shannon-Wiener Diversity Index to estimate niche breadth as forage component diversity for all three species (Krebs 1999; Nicholson et al. 2006). I used Morisita's Index of Similarity to measure niche overlap as similarity

in forage components utilized between ungulate species in a pairwise manner (Krebs 1999).

I performed principal components analysis (PCA) to reduce the number of variables for major forage classes and for ordination (McGarigal et al. 2000). I used MANOVA to test for differences in diet composition, expressed using principal components, among elk, deer, and cattle. This analysis was performed separately for each sample type (rumen or fecal), because of a weakly significant (*Wilk's Lambda* $F_{2, 141} = 2.85, P = 0.06$) interaction between ruminant species and sample type (Neter 1996). I observed a season by ungulate species interaction (*Wilk's Lambda* $F_{8, 232} = 2.26, P = 0.02$); therefore, I conducted separate analyses for each season and sample type. Seasons were defined using a climograph by grouping months that had similar ranges of temperature, and reflected changes in plant phenology (Stewart et al. 2002; Fig. 1). Because autumn was a transitional time period and consisted of only a single month, I combined autumn and winter samples. Thus, the June through September period was classified as summer and the October through December period was classified as winter.

Results

Microhistological analysis of rumen samples during winter indicated that there was a greater variety of species consumed by elk than mule deer. Elk consumed 40 plant species in Duck Creek and 42 plant species in Horse and Cattle Camp; mule deer consumed 35 plant species in Duck Creek and 15 species in Horse and Cattle Camp. In both study sites elk and mule deer diets consisted mainly of forbs, grasses, and some shrubs (Table 1). Grasses were the most important forage class for elk in both Duck Creek and Horse and Cattle Camp, while forbs and shrubs were more important for mule

deer in both Duck Creek and Horse and Cattle Camp (Table 2). Similarly, microhistological analysis of fecal samples indicated that elk had the most diverse diet during summer. Elk consumed 30 plant species in Duck Creek and 29 plant species in Horse and Cattle Camp; mule consumed 13 species in Duck Creek and 18 species in Horse and Cattle Camp; cattle consumed 15 species in Duck Creek and in Horse and Cattle Camp. I also note that although elk and mule deer consumed similar amounts of forbs, they consumed different plant species. The only forb species that were consumed by both species during winter months in noteworthy amounts were arrowleaf balsamroot and lupine, although these species made up less than 10% of the total diet. In both study areas elk and mule deer diets consisted mainly of shrubs and forbs, whereas cattle diets consisted mainly of grasses (Table 1 and Table 3).

Mean diet composition among ungulates differed between Duck Creek and Horse and Cattle Camp (*Wilk's Lambda* $F_{6, 101} = 2.768, P = 0.02$) for winter, but not for summer (*Wilk's Lambda* $F_{6, 23} = 1.038, P = 0.43$). Elk and mule deer demonstrated a significant difference in overall forage utilization in both Duck Creek and Horse and Cattle Camp (*Wilk's Lambda* $F_{6, 69} = 14.96, P < 0.01$; *Wilk's Lambda* $F_{6, 34} = 16.55, P < 0.01$). In Duck Creek, utilization of forbs ($F_{1, 65} = 3.32, P = 0.08$) and conifer ($F_{1, 65} = 3.64, P = 0.06$) forage classes differed weakly among species. In Horse and Cattle Camp, however, the only forage classes with significantly different utilization levels were shrubs ($F_{1, 39} = 89.1, P < 0.01$) and grasses ($F_{1, 39} = 40.8, P < 0.01$). All three species' diets in Duck Creek differed during summer (*Wilk's Lambda* $F_{12, 10} = 9.10, P > 0.05$), with forbs and conifers being the only forage classes that did not differ significantly. There was not a significant difference of consumption of overall forage classes among the three species in

Horse and Cattle Camp during summer (*Wilk's Lambda* $F_{12, 18} = 1.86, P = 0.11$). There were, however, significant differences in consumption of shrubs ($F_{2, 14} = 8.51, P < 0.01$), forbs ($F_{2, 14} = 3.78, P = 0.05$), and grasses ($F_{2, 14} = 12.7, P < 0.01$).

Male and female elk showed little variability in overall dietary composition in either season. Overall dietary composition between the sexes did not differ between Duck Creek and Horse and Cattle Camp (*Wilk's Lambda* $F_{6, 29} = 1.038, P = 0.42$; *Wilk's Lambda* $F_{6, 26} = 1.187, P = 0.34$). In Horse and Cattle Camp there was a significant difference in the grass consumption between the sexes ($F_{1, 31} = 6.88, P = 0.01$), males consumed more sedges and females had a greater proportion of crested wheatgrass in their diet (Table 2).

Diet diversity, indicated by the Shannon-Wiener index of diet diversity, varied by season, species, and study site (Table 4). During winter, elk had a slightly greater niche breadth in Duck Creek ($P = 0.76$), and mule deer had a slightly greater niche breadth in Horse and Cattle Camp ($P = 0.50$). However, neither of the differences was significant. Mule deer in Duck Creek during the winter had significantly different diet diversity from male elk (DC $P < 0.001$; HCC $P < 0.001$), both elk sexes combined (DC $P < 0.001$; HCC $P < 0.001$) for both study areas. During summer, elk and cattle had a greater niche breadth in Duck Creek while mule deer had greater niche breadth in Horse and Cattle Camp than in Duck Creek ($P = 0.50$). However, neither of these was significant. Mule deer and cattle had different diet diversity in Horse and Cattle Camp during the summer ($P = 0.06$). Finally, Morisita's measure of similarity showed a similar degree of overlap between elk and mule deer in both study areas, though the degree of overlap was slightly greater in Horse and Cattle Camp (Table 5).

I used PCA to reduce dimensionality of the rumen sample data for winter from six major forage classes to two components which explained 96.3% of the total variance, and 91.1% of the total variance for summer. I interpreted principal component 1 (PC1) as a grazing to browsing continuum for both winter and summer. PC1 explained 77.3% of the variation in winter diets and showed diets high in graminoids loading positively (0 to 0.7) and shrubs loading negatively (0 to -0.7). PC1 explained 73.3% of the variation in summer diet with diets high in graminoids loading negatively (0 to -0.7) and shrubs loading positively (0 to 0.6). Diets high in forbs loaded near zero for both seasons. Principal component 2 (PC2), explained 19.0 % of the variation for winter showed diets high in forbs loading positively (0 to 0.8), shrubs (0 to -0.5), and grasses (0 to -0.4) loading negatively in winter; PC2 explained 17.8% of the variation in summer and showed diets high in forbs loading positively (0 to 0.8) and shrubs (0 to -0.6) and grasses (0 to -0.3) loading negatively. PC2 was interpreted as a study site difference between Duck Creek and Horse and Cattle Camp due to difference in elevation and availability of water and a larger forb component in Duck Creek than Horse and Cattle Camp.

The PCA results showed that elk diets determined from rumen samples, during winter, were similar in both study areas (Figure 2). Mule deer, however, consumed more forbs in Duck Creek and more shrubs in Horse and Cattle Camp (Table 1, Figure 2). Elk loaded positively for PC1 and PC2 in both Duck Creek and Horse and Cattle Camp. This result indicates that elk diets were primarily composed of graminoids, although forbs were also an important portion of the diet for Duck Creek. Mule deer in Duck Creek loaded negatively for PC1 and positively for PC2, while they loaded negatively for both PC1 and PC2 in Horse and Cattle Camp. The loadings in Duck Creek indicate that diets

were high in shrubs, but forbs were also an important component. The negative loadings in for mule deer in Horse and Cattle Camp signify that shrubs were the primary component of the diet. An overall difference was present between elk and mule deer for Duck Creek (*Wilk's Lambda* $F_{2, 64}=33.92, P<0.01$) and Horse and Cattle Camp (*Wilk's Lambda* $F_{2, 38}= 49.65, P<0.01$).

PCA loadings for elk and mule deer were more variable during summer, than winter loadings (Fig. 3). Elk in Duck Creek loaded negatively for PC1 and slightly positively for PC2, indicating that diets were composed primarily of graminoids with some forbs. Mule deer loaded positively for PC1 and negatively for PC2 indicating that shrubs were the primary component. Cattle in Duck Creek loaded negatively for PC1 and slightly positively for PC2 showing that graminoids were the primary dietary component. Elk diets were more variable in Horse and Cattle Camp, loading near zero for PC1 and PC2. Shrubs were the primary component of mule deer diets, as they loaded positively for PC1 and slightly positively for PC2. Cattle loaded negatively for PC1 and PC2 indicating that grasses were an important component in the diet. An overall difference between species was detected for both study sites Duck Creek (*Wilk's Lambda* $F_{4, 18}= 22.55, P < 0.01$) and Horse and Cattle Camp (*Wilk's Lambda* $F_{4, 26}= 4.88, P<0.01$); however, an overall difference was not detected between study sites. Diet similarity determined from Morisita's measure during summer was greatest among elk and mule deer in both study areas. Elk and cattle had comparable dietary similarities in both study areas. Diets of mule deer and cattle were more similar in Horse and Cattle Camp than in Duck Creek (Table 5).

Slight differences in dietary composition were also noted between male and female elk during October to December (Figure 4). Female elk in Duck Creek loaded slightly more positively for PC1 (more graminoids, fewer forbs) and PC2 (more forbs, fewer shrubs) than male elk. In Horse and Cattle Camp female elk loaded positively for PC1 and negatively for PC2, while male elk loaded slightly less positive for PC1 and slightly more positive for PC2. There was not a significant difference between male and female elk for either study site or season for PC1 or PC2. However, dietary similarity was greater between the sexes in Duck Creek than in Horse and Cattle Camp (Table 5).

Discussion

I hypothesized that greater dietary overlap would occur during winter, because of diminished opportunity for selective foraging due to scarcity of forage resources. However, I observed evidence of dietary separation during winter, with elk consuming more grasses while mule deer consumed more shrubs on both sites. Mule deer diets were less diverse during winter months but were more diverse in Duck Creek, including 35 plant species in Duck Creek and only 15 species in Horse and Cattle Camp. Elk diets were more diverse during winter months which may indicate a decrease in nutritional quality and a concomitant decrease in selectivity or broadening of their dietary selection. In addition, elk can utilize cured grasses and forbs during the winter more effectively than mule deer, which contributes to dietary separation (Kie et al. 2003). The ability of elk to utilize the cured grasses and forbs is related to larger rumen size and longer retention time (Kie et al. 2003). Although elk and mule deer consumed similar amounts of forbs, they consumed different species, which may reflect a difference in dietary quality of the species consumed. The only forb species that were consumed by both

species during winter months in noteworthy amounts were arrowleaf balsamroot and lupine. Both forb species are common in Duck Creek. Consumption of different forb species indicates that although winter diets of elk and mule deer appear to be similar, there is utilization of different plant species. Analysis of plant functional groups only would not have detected an apparent separation in diet. This separation may be spatial with avoidance of areas occupied by a different ungulate species, or dietary with the ungulate species using the same areas but consuming different species of plants.

Differences in diets among these three species of large herbivores were more apparent during the summer months. I observed greater dietary separation between cattle and elk in Horse and Cattle Camp than in Duck Creek. Cattle concentrating in the seeded area of crested wheatgrass at the west side of Horse and Cattle Camp may decrease the chance of interactions between elk and cattle. I did not observe planted grass species in the diets of cattle at Horse and Cattle Camp, although cattle were observed to concentrate in these areas. This observation is most likely a result of low sample size for fecal samples from cattle in the area.

I hypothesized that cattle and elk would have the greatest dietary overlap but observed the greatest dietary overlap between elk and mule deer, which is comparable to other studies (Stewart et al 2003). In addition, I found that dietary overlap between mule deer and cattle was comparable to the dietary overlap of elk and cattle in Horse and Cattle Camp. I observed that cattle and elk had greater dietary separation in Horse and Cattle Camp than in Duck Creek. The differences in overlap between the study sites were most likely caused by greater acreages seeded to forage grasses in Horse and Cattle Camp than in Duck Creek.

I further hypothesized that female elk would prove more selective in their diet than males, as evidenced by lower utilization of graminoid species. However, I observed no overall difference between male and female elk diets, as determined by rumen samples, between the sexes for either study area. In Horse and Cattle Camp, however, female elk consumed a greater amount of grasses than male elk, while male elk consumed more sedges. Sedges have less nutritive value than crested wheatgrass (National Research Council, 1982). This may be due to gender-specific differences in digestion processes. Males are thought to consume more fibrous forages than females because they have larger rumen and body size and are better able to digest it (Barboza and Bowyer 2000; 2001). Males may actually do less well with high quality forages due to possibility of bloat (Kie et al. 2003). These forages may be more likely to be overestimated in the diets of females because they are less efficient at digesting them than are males. This hypothesis needs more research. In addition, this observation may indicate that there is some spatial segregation between male and female elk during feeding. However, the reason for feeding segregation cannot be determined by dietary analysis alone.

I expected males to consume more fibrous forages due to differences in digestion between the sexes (Barboza and Bowyer 2000). Females are also generally considered to be more selective feeders (Clutton Brock et al. 1987), and therefore consume higher amounts of forages with better nutrient quality (Barboza and Bowyer 2000, 2001). There is some evidence that female elk took greater advantage of cattle feeding grounds than their male counterparts, as there is slightly more crested wheatgrass in the female diets. During the early winter months females may have been taking advantage of the new

growth that often occurs. In addition females were also seen utilizing the crested wheatgrass seedings with their calves in early summer.

I also hypothesized that there would be greater dietary overlap among species in Horse and Cattle Camp than in Duck Creek, due to differences in water availability, elevation, and plant community composition. Apparent study site differences in dietary overlap were not statistically significant. Mule deer would be the species most likely to be affected by study site differences, as they require forages with greater nutrient content (Kie et al. 2003; Stewart et al. 2003). Differences in forage consumption by mule deer between the two study sites may indicate that the mule deer selected the forages in each study area that had the highest nutrient content and digestibility. In addition, greater dietary separation was observed between male and female elk in Horse and Cattle Camp. Competition for forage may have been a limiting factor for female elk as they had a less diverse diet than males, and consumed a greater proportion of crested wheatgrass. During summer there were also differences in the amount of dietary separation between elk and cattle in Horse and Cattle Camp and elk and mule deer in Duck Creek. Mostly likely these changes in dietary separation were caused by differences in available vegetation and the corresponding nutritional quality. Differences in forage consumption may also be caused by Duck Creek having higher elk and mule deer populations than Horse and Cattle Camp, therefore having an increased potential for competition. Cattle use patterns may also be a contributing factor.

In comparing the differences of diet between seasons it is important to note that spring diets were determined using fecal samples while winter diets were determined using rumen samples. Detection rates for highly digestible species, such as new growth

or forbs, are less with fecal samples than with rumen samples due to differences in digestibility of plants and passage rates (Gill 1983). Furthermore, differences in rumen size and passage times between species may also influence the detection rates for plant species.

I observed resource partitioning in diets by examining dietary components of elk, mule deer, and cattle. Elk and mule deer exhibited dietary separation from October through December. This result suggests that forage was not likely limiting, and each species was able to select different forages. During summer there was greater dietary overlap, possibly indicating that forage abundance and quality were great enough to allow for increased spatial separation. In Horse and Cattle Camp both nutrient quality and forage quantity were likely diminished as grasses and forbs became cured, which may have caused elk to expand their diet and mule deer to be excluded from higher quality forbs. In addition, competition may have been increased between elk and mule deer on the arid site by the presence of crested wheatgrass seedings. Elk and cattle exhibited greater dietary separation on the site with the seeding, which may be indicative of elk avoiding areas of large cattle concentrations. By avoiding cattle, elk could have increased their interactions with mule deer, potentially excluding them from desirable forage. However, this observation requires further research and is not supported by an observed lack of crested wheatgrass in cattle diets, even though the presence of cattle was noted frequently on the crested wheatgrass seedings.

Management Implications

Our study indicates that cattle and elk exhibited less dietary overlap when areas of high grass production were available for cattle to graze. Elk and mule deer exhibited less

dietary overlap where diverse forage types were available. It may be possible to reduce potential competition among cattle and elk by increasing areas of high forage production, through improvement of low quality rangelands with a variety of plantings of native and non-native plant species which are able to withstand moderate grazing pressure. In addition, these areas provide favorable habitat and abundant forage resources for elk during spring and early summer. Habitat improvements that allow for an increase in high quality forage may reduce competition between sympatric species of large herbivores, by providing more abundant resources..

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Table 1. Descriptive statistics for diet composition (%) for elk, mule deer, and cattle collected during winter (October to December) and summer (June to September) in Duck Creek (Duck Creek) and Horse and Cattle Camp (Horse and Cattle Camp), near Ely, Nevada 2005-2006. Rumen samples were not available for cattle.

	<u>Winter (Rumen)</u>				<u>Summer(Fecal)</u>			
	<u>Elk Duck Creek n= 36</u>		<u>Elk Horse and Cattle Camp n=33</u>		<u>Elk Duck Creek n=4</u>		<u>Elk Horse and Cattle Camp n=8</u>	
	<u>Mean</u>	<u>SD</u>	<u>Mean</u>	<u>SD</u>	<u>Mean</u>	<u>SD</u>	<u>Mean</u>	<u>SD</u>
Forbs	12.11	18.79	9.21	14.80	17.28	6.71	25.40	21.08
Shrubs	10.25	16.66	9.81	13.46	14.53	9.41	32.60	15.53
Conifer	1.28	2.59	1.18	4.11	0	0	1.23	2.27
Grasses	73.88	26.46	72.52	22.63	62.45	5.03	37.54	31.92
Sedge/Rush	2.025	6.041	5.561	12.63	5.75	10.33	3.24	7.44
Other	0.456	1.436	1.724	4.586	0	0	0	0
	<u>Mule Deer Duck Creek n=31</u>		<u>Mule Deer Horse and Cattle Camp n=8</u>		<u>Mule Deer Duck Creek n=5</u>		<u>Mule Deer Horse and Cattle Camp n=5</u>	
	<u>Mean</u>	<u>SD</u>	<u>Mean</u>	<u>SD</u>	<u>Mean</u>	<u>SD</u>	<u>Mean</u>	<u>SD</u>
Forbs	20.62	24.42	7.51	8.69	13.56	13.15	38.72	31.94
Shrubs	57.55	35.87	75.09	21.87	83.80	15.01	54.52	26.58
Conifer	0.36	1.42	0.26	0.74	0.40	0.89	0	0
Grasses	21.46	28.22	16.88	18.67	0.64	0.92	4.44	9.93
Sedge/Rush	0	0	0	0	0.82	1.83	1.38	3.09
Other	0	0	0.263	0.742	0.78	1.74	0.94	1.37

Table 1. Continued.

					Cattle Duck Creek n=4 Mean	SD	Cattle Horse and Cattle Camp n=4 Mean	SD
Forbs	—	—	—	—	6.43	4.90	2.95	4.83
Shrubs	—	—	—	—	2.75	3.01	5.92	5.90
Conifer	—	—	—	—	0	0	0	0
Grasses	—	—	—	—	57.73	22.36	87.32	10.24
Sedge/Rush	—	—	—	—	33.10	27.05	3.80	2.59
Other	—	—	—	—	0	0	0	0

Table 2. Plant species that make up $\geq 10\%$ of average diet of male and female elk and mule deer in Duck Creek (Duck Creek) and Horse and Cattle Camp (Horse and Cattle Camp) during winter (October to December) 2005-2006 as determined by microhistological analysis of rumen samples. Rumen samples were not available for cattle.

Plant Species	Elk (male) Duck Creek	Elk (female) Duck Creek	Elk (male) Horse and Cattle Camp	Elk (female) Horse and Cattle Camp	Mule Deer (Duck Creek)	Mule Deer (Horse and Cattle Camp)
Lupine	—	—	—	—	7.2%	—
Milkvetch	—	—	—	—	51.3%	—
Alfalfa	—	5.4%	—	—	—	—
Bitterbrush (leaf)	6.5%	—	—	—	30.7%	48.7%
Bitterbrush(Stem)	—	—	—	—	—	9.0%
Needle and thread grass	—	13.4%	12.7%	15.9%	6.5%	—
Blue grass	15.7%	16.6%	17.6%	18.7%	5.4%	—
Wheat grass	19.4%	26.9%	21.4%	35.6%	—	—
Barley	7.9%	7.9%	—	—	—	—
Rush	9.9%	—	—	—	—	—
Sedge	—	7.2%	9.7%	—	—	—

Table 3. Plant species that make up $\geq 10\%$ of average diet of elk, mule deer, and cattle in Duck Creek (Duck Creek) and Horse and Cattle Camp (Horse and Cattle Camp) during summer (June to September) 2005-2006 as determined by microhistological analysis of fecal samples.

Plant Species	Elk Duck Creek	Elk Horse and Cattle Camp	Mule Deer Duck Creek	Mule Deer Horse and Cattle Camp	Cattle Duck Creek	Cattle Horse and Cattle Camp
Arrowleaf	—	—	—	7.2%	—	—
balsamroot						
Opuntia	—	16%	7.7%	29.0%	—	—
Bitterbrush (leaf)	5.9%	10.2%	56.5%	34.8%	—	—
Sagebrush	5.2%	—	—	10.0%	—	—
Squirrel tail	32.0%	9.7%	—	—	20.2%	26.5%
Brome	15.6%	11.3%	—	—	11.7%	35.5%
Tufted hairgrass	—	—	—	—	6.2%	—
Rush	—	—	—	—	25.3%	—
Flower	—	—	—	—	7.8%	—

Table 4. Results from Shannon-Wiener calculations for winter (October to December) and summer (June to September) for elk, mule deer and cattle. Samples were collected from Duck Creek (Duck Creek) and Horse and Cattle Camp (Horse and Cattle Camp) near Ely, Nevada 2005-2006.

Species	Winter				Summer			
	Duck Creek	n	Horse and Cattle Camp	n	Duck Creek	n	Horse and Cattle Camp	n
Elk(both sexes)	4.83	36	4.78	33	4.33	4	4.12	8
Female Elk	4.13	16	3.48	10	—		—	—
Male Elk	4.96	20	4.78	23	—		—	—
Mule Deer	3.27	31	3.44	8	4.13	5	4.84	5
Cattle	—		—		3.75	4	3.11	4

Table 5. Results from Morisita's similarity index calculations for winter (October to December) and summer (June to September) for elk, mule deer and cattle. Samples were collected from Duck Creek (Duck Creek) and Horse and Cattle Camp (Horse and Cattle Camp) near Ely, Nevada 2005-2006.

Species Comparison	Winter		Summer	
	Duck Creek	Horse and Cattle Camp	Duck Creek	Horse and Cattle Camp
Elk (both sexes) - Mule Deer	0.999	1.09		1.03
Elk (both sexes) - Cattle	—	—	0.994	0.783
Female Elk - Male Elk	1.07	0.996	—	—
Mule Deer - Cattle	—	—	0.390	0.813

List of Figures

Figure 1. Climograph of mean monthly temperature and precipitation used to define seasons for Ely, Nevada 2003-2004. Solid lines indicate months and dotted lines separate seasons.

Figure 2. Dietary overlap among species in winter, shown using principal component analysis (PCA) on forage classes determined from microhistological analysis of rumen samples collected in Duck Creek (DC) and Horse and Cattle Camp (HCC) for elk (Duck Creek=36; Horse and Cattle Camp=33) and mule deer (Duck Creek=31; Horse and Cattle Camp=8). Rumen samples were collected from hunters that harvested a mule deer or elk near Ely, Nevada for October to December 2005. Ellipses are 95% confidence intervals of PCA axis scores.

Figure 3. Dietary overlap among species in summer, shown using principal component analysis (PCA) on forage classes determined from microhistological analysis of feces collected in Duck Creek (DC) and Horse and Cattle Camp (HCC) from cattle (Duck Creek=4; Horse and Cattle Camp=4), elk (Duck Creek=4; Horse and Cattle Camp=8), and mule deer (Duck Creek=5; Horse and Cattle Camp=5) near Ely, Nevada from June to September, 2005. Ellipses represent 95% confidence intervals of PCA axis scores. Note: scale is different from rumen sample graphs.

Figure 4. Dietary overlap among sexes of elk in winter, shown using principal component analysis (PCA) on forage classes determined from microhistological analysis of rumen samples collected in Duck Creek (DC) and Horse and Cattle Camp (HCC) from female elk (Duck Creek=16; Horse and Cattle Camp=10) and male elk (Duck Creek=20; Horse and Cattle Camp=23). Rumen samples were collected from hunters that harvested

elk near Ely, Nevada from October to December 2005. Ellipses are 95% confidence intervals of PCA axis score.

Figure 1.

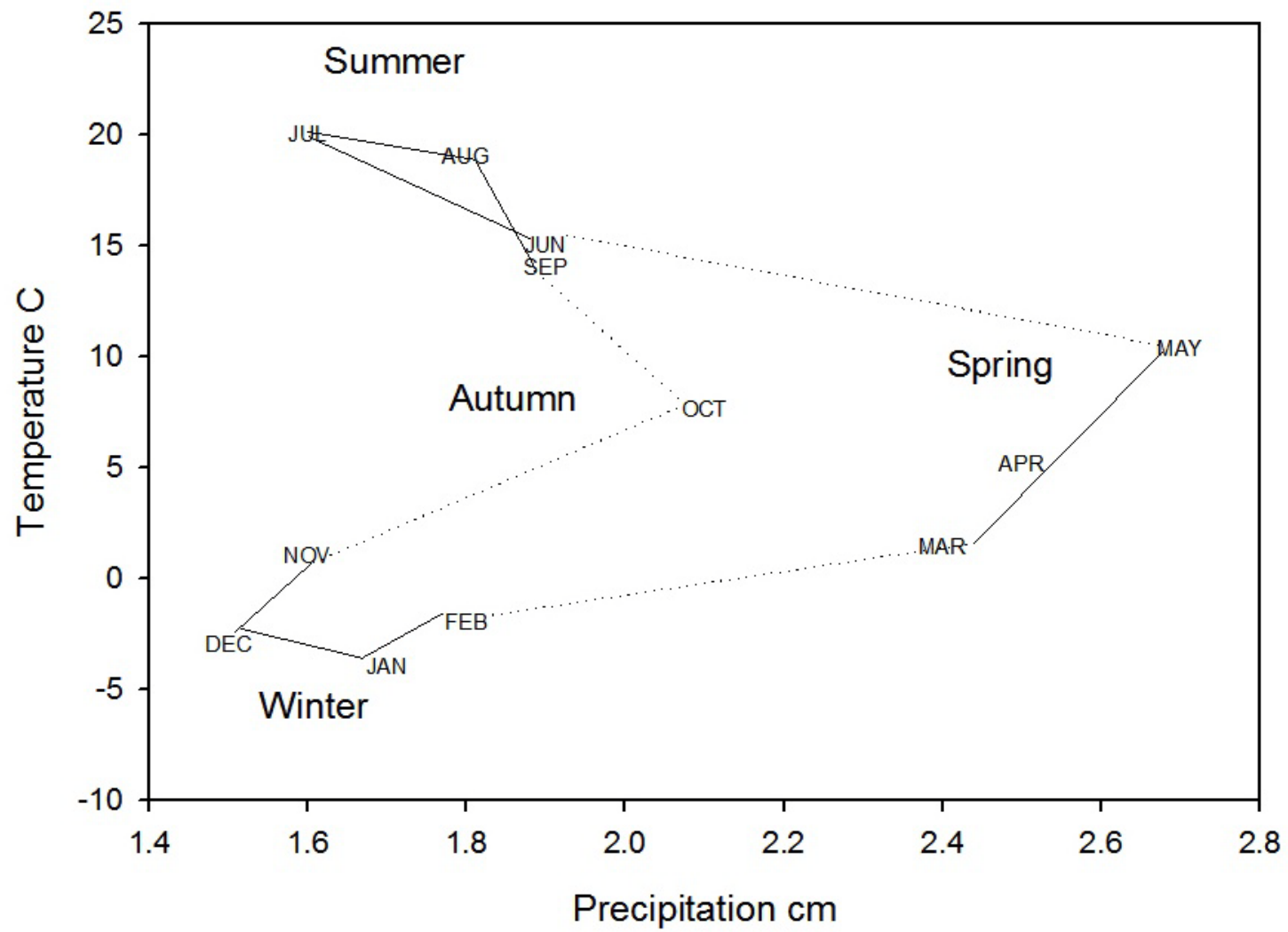


Figure 2.

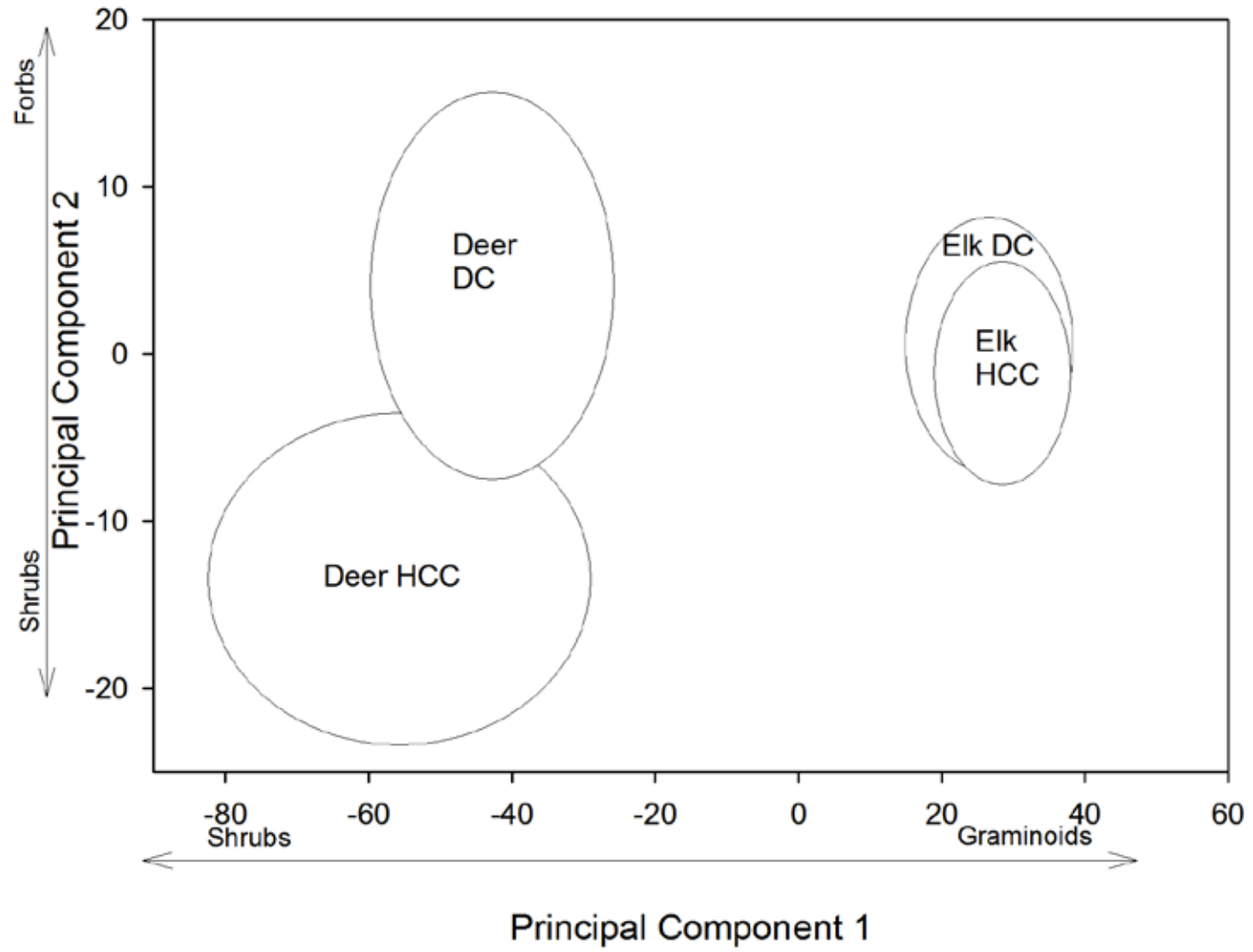


Figure 3.

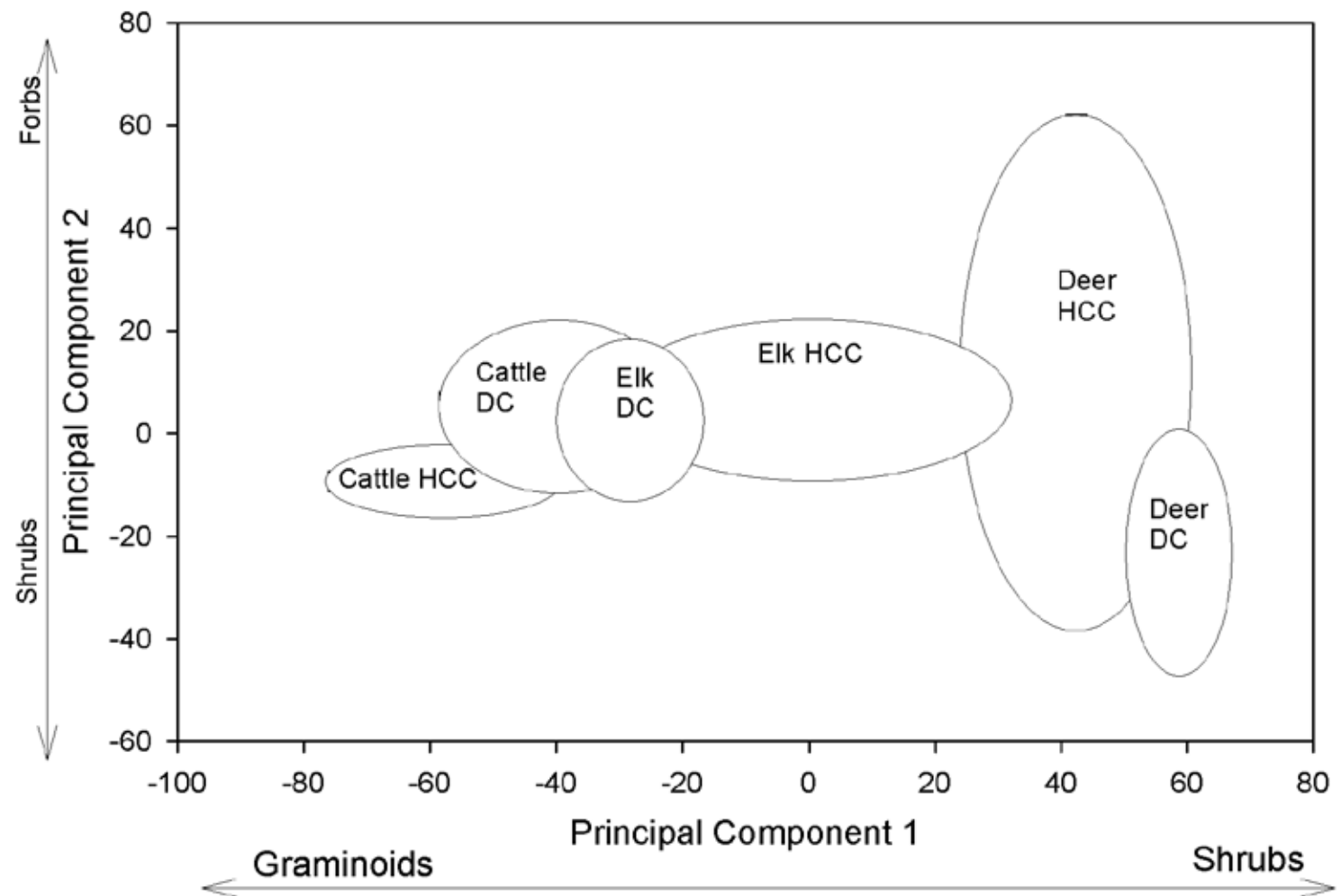
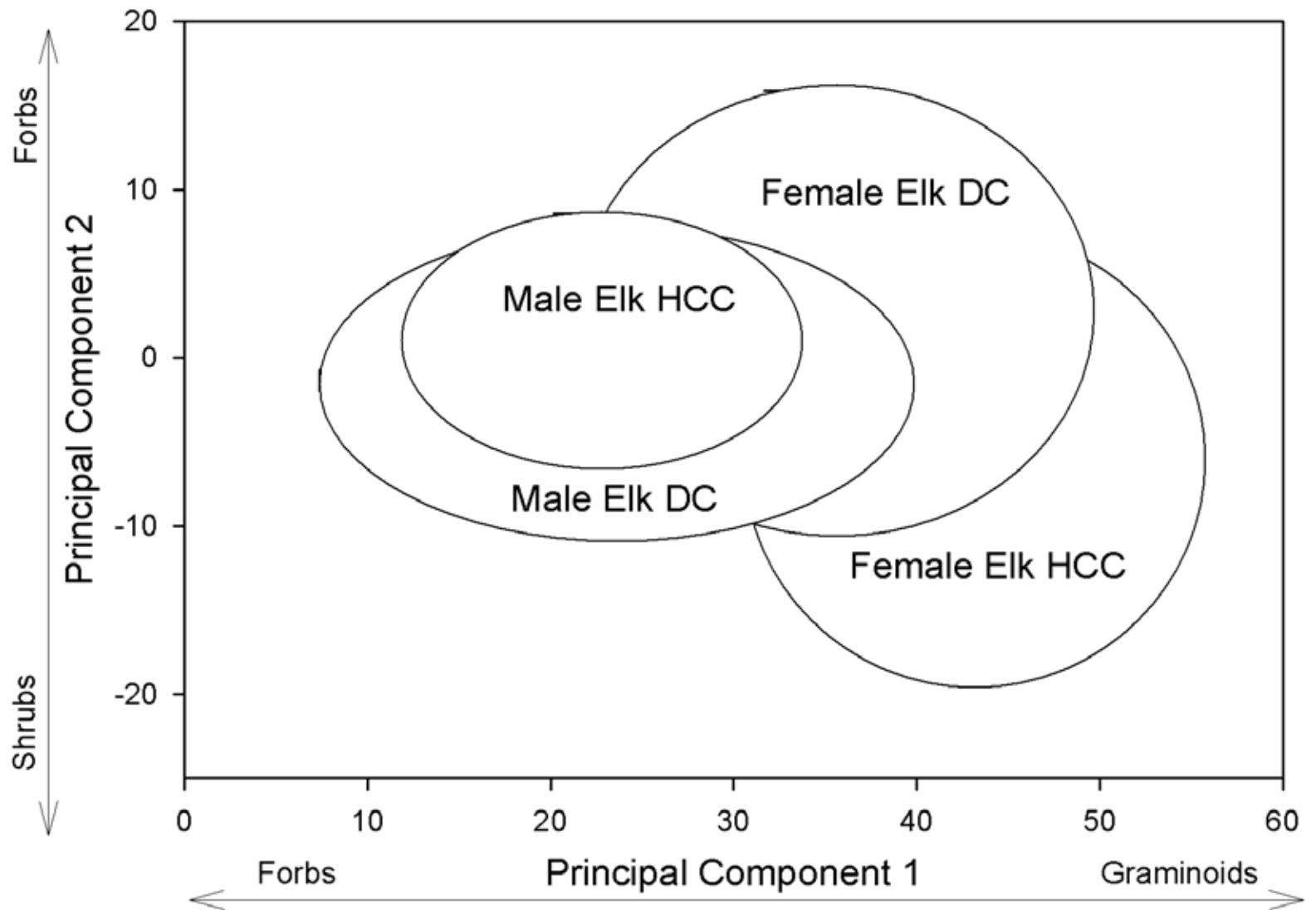


Figure 4.



Chapter 4**Summary**

Habitat selection and dietary overlap are commonly studied in large ungulates such as, mule deer, elk, and cattle. These species commonly co-occupy rangelands throughout the Great Basin which increases their likelihood of competition. There are several factors, such as low precipitation, low plant production, and pinyon-juniper encroachment, within the Great Basin that increases the complexity of understanding resource selection and habitat overlap.

Overall, our results are comparable with other studies (Stewart et al., 2005 and 2002 and Poole and Mowat 2005). During the winter, I found that there was dietary separation in the diets of mule deer and elk, indicating that forage was not a limiting factor. The lack of dietary separation may also indicate that mule deer and elk were able to separate spatially. However, due to poor model performance I was unable to examine the spatial aspect of the habitat selection during the winter.

During the summer, I found greater dietary overlap and greater spatial separation of mule deer and elk. I also found that during the summer, elk and cattle exhibited greater dietary separation in the part of the study area that had a large crested wheatgrass seeding. The greater separation exhibited by elk and cattle may be indicative of elk avoiding large areas of cattle concentrations and increasing their interactions with mule deer.

In addition, I found that mule deer and elk both exhibited a narrower distribution and were more selective for particular habitats during the summer than during the other seasons. The lack of spatial distribution across the landscape was counter to what I predicted because mule deer and elk in other regions have been reported to exhibit a narrower range of spatial distribution across their critical winter range. The narrow

distribution during the summer may be an indication that mule deer and elk in the Great Basin are more limited by water and availability of high quality forage during the summer than by deep snow in the winter.

In all seasons, I found that both mule deer and elk avoided areas of high pinyon-juniper cover, but areas with low pinyon-juniper cover or areas that were adjacent to denser pinyon-juniper stands were used. Dense stands of pinyon-juniper produce little understory vegetation; however, open canopy pinyon-juniper woodlands can be associated with increased available ground water and forage. Our results suggest that in our study area some degree of tree cover is an important component of habitat mosaics used by mule deer and elk. However, little work has been done on the habitat preferences of mule deer and elk with regard to pinyon-juniper cover.

I also found that mule deer and elk were closer to roads than expected. It has been suggested that mule deer may use areas closer to roads as a means to avoid elk. However, I believe that the relationship of mule deer, elk, and distance to road is more complex than simple avoidance. The degree to which the road is avoided is influenced by the amount of traffic that the road receives. In addition, some roads have been closed by local land management agencies making it unlikely that mule deer and elk would avoid these roads. Roads that have been closed or that receive little motorized vehicle traffic may provide travel corridors. These types of travel corridors require less energy expenditure than traveling through brush.

Influences of changes on the landscape may dramatically influence habitat selection by mule deer and elk, especially in semi-arid landscapes. Changes in availability of forage availability, cover, and travel corridors may influence the dietary

and habitat selection of mule deer and elk. However, many of these influences have not been studied in the context of semi-arid environments.