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Original article

Effects of density dependence on diet composition of North American elk *Cervus elaphus* and mule deer *Odocoileus hemionus*: an experimental manipulation

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We examined interactions related to resource partitioning and competition with density-dependent processes among mule deer *Odocoileus hemionus* and North American elk *Cervus elaphus* at two different population densities of elk. We used an experimental approach to examine changes in diet diversity, selection of diets, dietary importance, niche breadth and overlap among sympatric species of large herbivores with changes in population density of one species. We hypothesized that diets of both species would change with changing population density and dietary niche would be expanded to include forages of lower quality in the areas with increased competition for resources. We used microhistological analysis corrected for differential digestibility of forages to estimate diets of mule deer and elk from faeces in two study areas with high and low population densities of elk. For both mule deer and elk, dietary niche was expanded in the high-density area compared with the low-density area, and included forages of lower quality and palatability. Our results indicate that negative feedbacks associated with density-dependent processes interact with competitive interactions among sympatric species of large herbivores.

Key words: Cervus elaphus, competition, density dependence, diet diversity, diet overlap, experimental manipulation, mule deer, niche breadth, North American elk, Odocoileus hemionus

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Resource partitioning among coexisting species is underpinned by the divergence in resource use between species, which once had greater overlap in their requirements (Connell 1980, Walter 1991, Stewart et al. 2010). Resource partitioning is believed to have developed through coevolutionary divergence among sympatric species resulting from interspecific competition (Connell 1983, Schoener 1983, Sinclair 1985, Jenkins & Wright 1988, Stewart et al. 2002, 2003, 2010). Niche partitioning among species traditionally has been evaluated along three niche axes: spatial separation, temporal avoidance and dietary differences (Ben-David et al. 1996, Keddy 2001, Kronfeld-Schor et al. 2001, Stewart et al. 2002, 2003). Exploring niche separation among large herbivores along all three niche axes is often a formidable task because those mammals occupy relatively large home ranges and exhibit broad dietary niches (Stewart et al. 2002).

Most aspects of the ecology of large mammals are influenced by density-dependent mechanisms (McCullough 1979, 1999, Kie et al. 2003) which is important for understanding competitive interactions among large herbivores (Stewart et al. 2002).

Density-dependent mechanisms operate through intraspecific competition, via per capita availability of food, and the subsequent influence of nutrition on reproduction and recruitment of young into the population (McCullough 1979, Kie et al. 1983, Sæther & Haagenrud 1983, Kie & White 1985, Robbins 1993, Schwartz & Hundertmark 1993, Keech et al. 2000, Barboza et al. 2009). Moreover, density-dependent processes often interact with other variables affecting populations including predation, harvest and genetics, as well as density-independent factors such as climate (McCullough 1979, 1990, White & Bartmann 1997, Bowyer et al. 1999, Aanes et al. 2000, Kie et al. 2003). Interspecific competition among sympatric species of large herbivores also may compound effects of density dependence, such that density-dependent feedbacks from one species may have a strong effect on population dynamics of sympatric species.

Stewart et al. (2002) suggested that at high population density, the ability of large herbivores to partition space would be reduced and dietary and habitat partitioning would be intensified. As availability of forage declines, herbivores expand their dietary niche to include lower-quality forages, resulting in greater breadth of dietary niche (Pianka 1988). Although, narrowing of dietary niche has been observed in some areas because species richness declined as intensive herbivory removed more palatable species of plants (Nicholson et al. 2006). Thus, niche partitioning among populations at high densities may become more difficult as resources become more limiting and spatial overlap increases, leading to more intense competition (Stewart et al. 2002).

Few areas in the western United States have only a single species of large herbivore, and mule deer *Odocoileus hemionus* and North American elk *Cervus elaphus* are sympatric throughout much of their range (Mower & Smith 1989, Stewart et al. 2002). Moreover, few studies have examined how niche partitioning among sympatric large herbivores interacts with density-dependent processes in affecting population ecology of large herbivores in an ecosystem, and even fewer have used an experimental approach. Our objectives were to examine plant-species composition, dietary niche breadth and diet selection of mule deer and elk at high and low population densities of elk. We hypothesized that density-dependent processes would result in increased intraspecific and interspecific competition, and that diets of both mule deer and elk would differ between population densities of elk. We predicted that at low population density of elk, competition between mule deer and elk would be low, and that both mule deer and elk would differ in diet selection for high-quality forages, which would be greater in availability than at a high-population density of elk. We further hypothesized that diets of elk would differ between high- and low-density populations of elk, and palatable species of high-quality forage would be more common in elk diets at low population density, because of low intraspecific competition for forage. We also hypothesized that density dependence in elk would affect diet composition of mule deer, which co-occur in our two study areas. We predicted that at low population density of elk, mule deer would select for primarily palatable species of forbs and browse of higher quality than in the area with the high population density of elk. We further postulate that diet divergence among high- and low-density populations of elk would be greater for mule deer, which tend to require higher-quality forages than do elk.

Material and methods

Study area

We conducted research in 2000 and 2001 on the Starkey Experimental Forest and Range of the U.S. Forest Service. Starkey (45°13'N, 118°31'W) is situated in the Blue Mountains of northeastern Oregon, USA. Elevations on Starkey range from 1,120 to 1,500 m a.s.l. Starkey encompasses 10,125 ha, and since 1987 has been surrounded by a 2.4-m fence that prevents immigration or emigration of large herbivores (Rowland et al. 1997, Stewart et al. 2002, Kie et al. 2005, Stewart et al. 2006, 2009). As a consequence, elk no longer migrate from our study area to traditional winter ranges. Animals were, therefore, maintained throughout winter in a holding area where they were fed a maintenance diet of alfalfa hay (Rowland et al. 1997, Stewart et al. 2006). Elk were concentrated and contained within a winter feeding ground from early December to late April each year (Stewart et al. 2006). Few elk remained on our study area during winter (November - March). Thus, herbivory by elk was constrained primarily to spring (April - June), summer (July - September) and autumn (October) as defined by Stewart et al. (2002). Elk were moved among study areas via a system of fenced alleyways across Starkey, and densities of elk were manipulated by selectively returning animals to study areas via those alleys. Consequently, we manipulated population density non-lethally for this study (Stewart et al. 2006).

We restricted our experiment to the northeast area on Starkey, which encompassed 1,452 ha and was separated from the remainder of our study area by a high fence (Stewart et al. 2002, 2006, 2009). This northeast area was divided into two study sites with the same 2.4-m high fence, east (842 ha) and west (610 ha), to accommodate experimental comparisons of two populations densities of elk (Stewart et al. 2006, 2009). We divided the northeast area in a manner that resulted in plant communities being near equal in proportions in the east and west study areas (Stewart et al. 2005, 2006). Such study sites are sufficiently large to allow natural movements and other behaviours of large herbivores (Hirth 1977, McCullough 1979, Stewart et al. 2002). Stewart et al. (2002) examined locations of elk in the northeast study area and reported no significant effects of the high fence on habitat selection by elk.

The northeast area consisted of four major plant communities: 1) mesic forest, 2) xeric forest, 3) xeric grassland and 4) logged forest as defined by Stewart et al. (2002). Mesic forests occur on north-facing slopes with overstory composition dominated by grand fir *Abies grandis*. Xeric forests generally occur on south- and east-facing slopes and tree composition consisted primarily of Ponderosa pine *Pinus ponderosa*, with the understory dominated by elk sedge *Carex geyeri* (Stewart et al. 2002). Xeric grasslands occur primarily on south- and east-facing slopes and are dominated by a few grasses such as Idaho fescue *Festuca idahoensis* and bluebunch wheatgrass *Pseudoroegneria spicata*, and forbs such as low gumweed *Grindelia nana* (Stewart et al. 2002). Logged forests comprise areas where timber was harvested during 1991-1992. Grand fir on Starkey suffered widespread mortality (> 90%) from spruce budworm *Choristoneura occidentalis* during the late 1980s, and timber was harvested in areas where most trees were killed (Rowland et al. 1997, Stewart et al. 2002). Following removal of trees, those areas were seeded with several species of grasses including orchardgrass *Dactylis glomerata* and bluegrass *Poa* spp. (Stewart et al. 2002). Functional groups of plants included forbs, grasses, sedges, mat-forming shrubs, such as twinflower *Linnaea borealis*, and upright shrubs, such as serviceberry *Amelanchier alnifolia*. Plant nomenclature follows Hitchcock & Cronquist (1996) and Table 1.

Table 1. Acronyms, scientific and common names associated with forage composition of faeces of North American elk and mule deer as determined from microhistological analysis on the Starkey Experimental Forest and Range, northeastern Oregon, USA, 2000-2001. Palatability was indexed from Johnson (1998) and Miller et al. (1981).

Acronym	Plant species	Common name	Palatability
Forbs			
ERCH	*Erigeron chrysopsidis*	Dwarf yellow fleabane	Unpalatable
Grasses			
AGSP	*Agropyron spicatum*	Bluebunch wheatgrass	Palatable
AREL	*Arrhenatherum elatus*	Tall oatgrass	Moderate
BRCA	*Bromus carinatus*	Mountain brome	Moderate
DACA	*Danthonia californica*		Low
DAGL	*Dacylis glomerata*	Orchardgrass	Moderate
FEID	*Festuca idahoensis*	Idaho fescue	Low
STOC	*Stipa occidentalis*	Western needlegrass	Moderate
TRCA	*Trisetum canescans*	Tall trisetum	Moderate
Sedges			
CAGE	*Carex geyeri*	Elk sedge	Moderate
Carex spp.	*Carex* spp.	Other species of sedges, excluding elk sedge	Low
Shrubs			
AMAL	*Amelanchier alnifolia*	Serviceberry	Palatable
PHMA	*Physocarpus malvaceus*	Ninebark	Low
RICE	*Ribes cereum*	Straw current	Low
VAME	*Vaccinium membranaceum*	Big huckleberry	Palatable
VASC	*Vaccinium scoparium*	Grouse whortleberry	Unpalatable

Experimental design

During 1997, we began an experiment to examine effects of population density of elk on their physical condition and reproduction (Stewart et al. 2005) and on ecosystem processes (Stewart et al. 2006, 2009). We created two populations of elk at high and low density relative to carrying capacity (K), in the northeast east and west study areas on Starkey. The high-density population was maintained near K (20.1 elk/km^2) based on physical condition of elk on Starkey. At low densities of elk, near or below maximum sustained yield, we set the density of elk at 4.1 elk/km^2 (Stewart et al. 2006, 2009). The high-density population was randomly assigned to the northeast study area and the low-density population to the northwest study area. This manipulation of population density of elk began in 1998, which was a pretreatment year, and each study area was stocked with moderate densities of elk (Stewart et al. 2006). The experimental manipulation of high and low population density began in 1999, but a gate was left open between study areas. Thus, elk densities were moderately high (10.8 elk/km^2) and low (6.6 elk/km^2; Stewart et al. 2006, 2009). Finally in 2000 and 2001, we restricted access to our study areas and maintained our targeted high (20.1 elk/km^2) and low (4.1 elk/km^2) densities of elk (Stewart et al. 2006). We restricted our analyses on diet composition and available plants to two years (2000 and 2001) when elk densities were maintained at high and low density. Unlike elk, which move down to the winter feedground, mule deer remain on our study area the entire year. Thus, populations of mule deer were not manipulated and were similar in both study areas based on surveys of mule deer conducted by Oregon Department of Fish and Wildlife. All aspects of this research were approved by the Institutional Animal Care and Use committees at the University of Alaska Fairbanks (IACUC # 01-34) and the United States Forest Service Starkey Project, and were in keeping with protocols adopted by the American Society of Mammalogists for field research involving wild mammals (Gannon et al. 2007).

We located sampling sites with three replications in each of the four plant communities: mesic forest, logged forest, xeric forest and xeric grasslands per study area (Stewart et al. 2006). We determined species composition and cover of plants to estimate availability of forage using step-point transects at established locations for vegetation sampling (Bowyer & Bleich 1984, Bleich et al. 1997, Stewart et al. 2006). We recorded a cover 'hit' if the step-point (< 1 mm in diameter) fell within the canopy of a shrub or stem or leaf of a plant. Each transect contained approximately 200 step-points and was 300 m in length (Stewart et al. 2006). Adequate sample size was determined by plotting the number of species against cumulative number of points sampled until the line reached an asymptote (Kershaw 1964, Geysel & Lyon 1980, Stewart et al. 2006).

We obtained vegetation samples each month, which were collected by Stewart et al. (2006), at each of the 12 established sampling locations in each study area, for estimating seasonal productivity. We analyzed those vegetation samples by functional group for forage quality. Stewart et al. (2006) sampled vegetation by clipping in and outside of temporary and permanent exclosures monthly and seasonally to examine biomass in the presence and absence of herbivory. Stewart et al. (2006) clipped vegetation monthly in 0.25 m^2 plot frames and sorted them by category (forbs, grasses, sedges and current annual growth of shrubs). We obtained those samples clipped with herbivores present, and analyzed them by forage category for forage quality. Samples were composited by sampling location by forage categories with 12 replications per study area. We determined percent crude protein, percent *in vitro* dry matter digestibility (IVDMD; Tilley & Terry 1963) and performed a complete Van Soest fiber analysis (Van Soest 1994). For IVDMD, we used cervid rumen fluid from five caribou *Rangifer tarandus*, equipped with rumen canulas, that had been acclimated to forages from Starkey for about 10 days prior to collection of rumen fluid for IVDMD analysis (see Stewart et al. 2006 for complete description). Neutral detergent fiber (NDL), acid detergent fiber (ADF) and acid detergent lignin (ADL) consist primarily of cell wall contents with increasing levels of fiber (cellulose, hemicellulose and lignin), and represents the relatively indigestible components of plants compared with cell soluble (Van Soest 1994). Acid insoluble ash (AIA) consists of mineral content of those plants following all fiber analyses (Van Soest 1994). All analyses for forage quality were conducted by the Chemical Nutrition Laboratory of the Institute of Arctic Biology at the University of Alaska Fairbanks (see Stewart et al. 2006 for complete description).

We collected faeces weekly from May through October in 2000 and 2001, when elk were present on our study area. We collected fresh, insect-free pellet groups in each of our study areas. Pellets were placed in plastic bags and frozen until dietary analysis was conducted. Pellet groups were collected opportunistically and along 12 transects per study area located at least 1 km apart and one day per week across each study area to minimize the potential for overrepresentation by a single individual. We collected a total of 195 pellet groups (152 elk and 43 mule deer). We analyzed 1-2 faecal pellets from each group using microhistological analysis of plant fragments recovered from faeces. Those plant fragments were identified to species level (100 views) and corrected for differential digestibility of forages (Sparks & Malechek 1968, McInnis et al. 1983).We separated elk sedge from other species of sedges because of differences in morphology and palatability (see Table 1; Miller et al. 1981, Johnson 1998). All microhistological analyses were conducted under contract at Eastern Oregon Agricultural Research Center, Union, Oregon, USA.

Statistical analyses

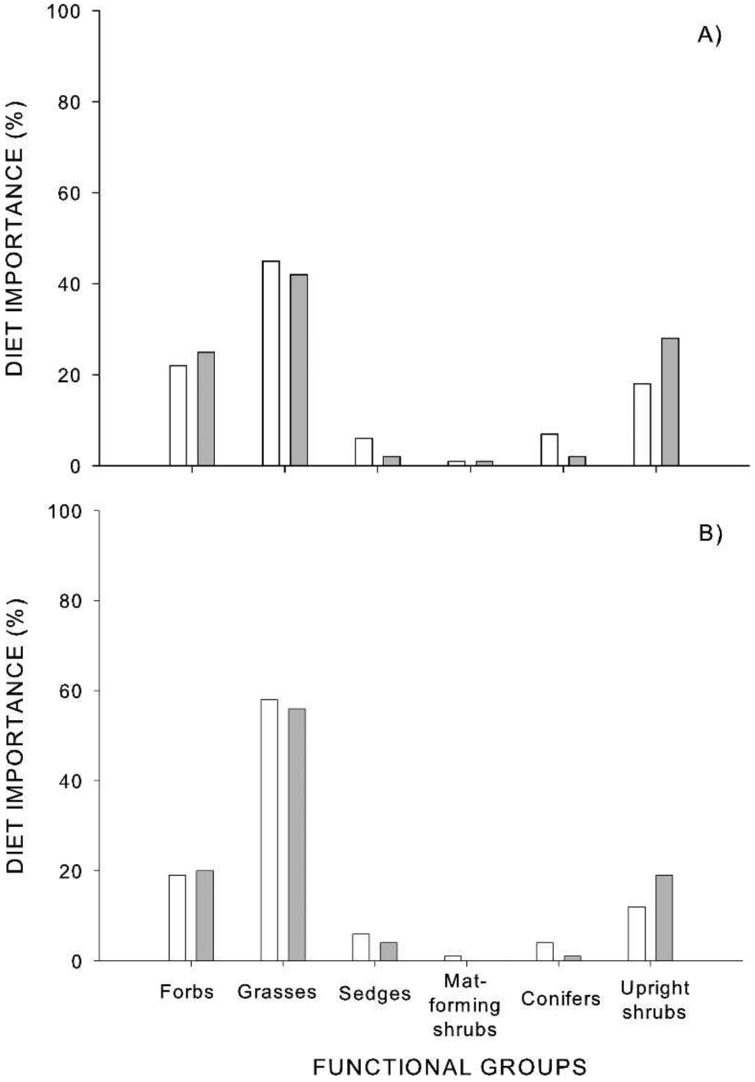
We calculated diet importance as use × availability, then rescaled to 100% (Bowyer & Bleich 1984, Bleich et al. 1997, Manly et al. 2002). We calculated diet diversity using Shannon-Weiner index as modified by Ricklefs & Miller (2000). We tested for differences in diet diversity by functional groups of plants for mule deer and elk between varying densities of elk using formulas from Zar (2004). Diet selection was calculated using proportion of plant species in faecal pellets to estimate forages used by herbivores, and availability of forages was estimated using frequency of cover of plant species obtained from the step-point transects. We used multivariate analysis of variance (MANOVA) to test for differences in diet composition of mule deer and elk with available forage by functional groups to estimate selection (i.e. use minus available; Ricklefs & Miller 2000) among the two population densities of elk, and we tested for effects of season and year. Significant differences between plants identified in the diets of either species of herbivore compared with their corresponding availability indicated that selection (use > available) or avoidance (use < available) occurred (Bowyer & Bleich 1984, Ricklefs & Miller 2000). In addition, we used MANOVA to test use of forage categories within species by treatment, and for mule deer and elk by plant species among high- and low-density populations of elk, followed by analysis of variance (ANOVA) for significant MANOVAs. Prior to release of elk onto our study area, availability of plant species among treatments were similar ($F_{1,\ 854} = 0.28$, $P = 0.5987$). We used MANOVA followed by ANOVA to test for differences in forage quality, from IVDMD, crude protein and Van Soest analyses, among forage categories and treatments. Percentage data were arcsin, square-root transformed to ensure additivity of treatment effects (Kie & Bowyer 1999, Stewart et al. 2003). We calculated diet overlap using Schoener's Index, which has been recommended as the best overall index of niche overlap (Schoener 1968, Abrams 1980, Mysterud 2000).

Due to the high complexity and variability of the diets of mule deer and elk, we used principal components analysis (PCA), based on the variance-covariance matrix, to reduce dimensionality of those data (SAS Institute 1988, McGarigal et al. 2000). We used MANOVA to compare treatments on diet composition of mule deer and elk separately, using principal components (PCs) 1 and 2 as dependent variables; the main effect was treatment (high and low density of elk). We used MANOVA to compare treatments on diet composition of elk by season (spring and summer) using PC 1 and PC 2 as dependent variables and main effects of treatment and season. We did not analyze data by season for mule deer, because a limited number of samples were obtained during spring ($N = 4$) in the low-density area.

Results

Diet importance for mule deer and elk was similar among high- and low-density populations (Fig. 1). Diets of elk also were similar in importance to those of mule deer, with grasses being the most important to both species in both our study areas (see Fig. 1). Upright shrubs were more important to mule deer in the low-density population compared with the high-density area (see Fig. 1). Diets of mule deer had greater plant diversity ($P < 0.05$) in the high-density area ($H' = 1.41$, $N = 24$) compared with the low-density area ($H' = 1.31$, $N = 19$). Diets of elk also were greater in diversity ($P < 0.001$) in the high-density area ($H' = 1.94$, $N = 85$) compared with the low-density area ($H' = 1.83$, $N = 67$). In the high-density study area, diets of elk had greater diversity ($P < 0.001$) than those of mule deer, and elk diets in the low-density area also had greater diversity ($P < 0.001$) than those of mule deer. Diet overlap between mule deer and elk was greater in the high-density (Schoener's Index = 0.862) than the low-density area (Schoener's Index = 0.664).

Figure 1. Dietary importance (use x available, then rescaled to 100%) of forage categories for mule deer (A) and North American elk (B) in high- (white bars) and low-density (grey bars) populations of elk on the Starkey Experimental Forest and Range, Oregon, USA, 2000-2001.



Mule deer and elk exhibited similar patterns of dietary selection. Both large herbivores selected for forbs, grasses and upright shrubs (Fig. 2). We observed an interaction between species and available forage (mule deer, elk and available forage) and treatment (high and low density of elk) for selection of forage categories (Wilks' λ: $F_{10, 462} = 2.41$, $P = 0.0085$), therefore we analyzed treatments separately (see Fig. 1). In the high-density area, sedges were used in proportion to availability by both cervids (see Fig. 2). Mule deer use of sedges did not differ from availability in either treatment, although in the low-density area elk exhibited slight selection for sedges (see Fig. 2). Mule deer exhibited stronger selection for upright shrubs than did elk, and elk exhibited stronger selection for grasses in both study areas than did mule deer (see Fig. 2). When we compared forage composition of mule deer and elk among treatments, mule deer selected more strongly for forbs and upright shrubs in the low-density area, and did not differ from elk in use of forbs in the high-density area (see Fig. 2). Elk selected more strongly for grasses in both study areas and used mat-forming shrubs in the low-density area to a much lesser extent than did mule deer, for which use did not differ significantly from available forage (see Fig. 2).

MANOVA revealed a season (spring and summer) by treatment (high and low density of elk) interaction for diet composition of elk (Wilks' λ: $F_{14, 135} = 2.31$, $P = 0.0070$). Thus, we analyzed the seasons separately. During spring, diet composition of elk differed by sedges (*Carex* spp.), excluding elk

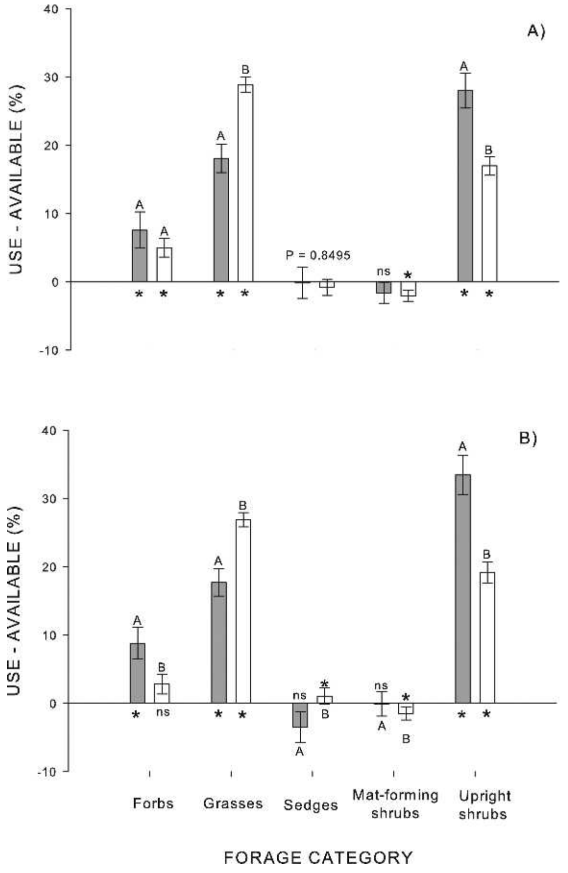


Figure 2. Least squared means (± SE) of dietary composition compared with availability of forage classes for mule deer (grey bars) and North American elk (white bars) in high- (A) and low-density (B) populations on the Starkey Experimental Forest and Range, Oregon, USA, 2000-2001. Comparisons are from ANOVA following significant MANOVA for differences among treatments (Wilks' λ: $F_{2, 231} = 5.54$, $P < 0.0001$). Letters over bars indicate comparisons between species, different letters indicate significant differences ($P < 0.05$), * indicates that the indicated bar differs significantly from availability, 'ns' denotes that the indicated bar is not significantly different from available forage. Note that analyses were conducted on arcsin-squareroot transformed data and data were back transformed and presented as percentages for ease of interpretation.

sedge and one species of grass, western needlegrass *Stipa occidentalis*. No other plant species differed among treatments during spring (Fig. 3). During summer, elk diets differed by several species of grasses, sedges and upright shrubs (see Fig. 3). In general, species with higher palatability (see Table 1) occurred to a greater extent in the diets of elk in the low-density treatment (see Fig. 3). We observed a treatment by plant species interaction for mule deer (Wilks' λ: $F_{12, 25} = 4.36$, $P = 0.009$). Plant species of higher palatability (see Table 1) occurred to a greater extent in the diets of mule deer in the low-density area compared with the high-density population (Fig. 4). Mule deer foraged on several palatable species of shrubs, but only serviceberry and big huckleberry *Vaccinium membranaceum* were selected to a greater extent in the area with low density of elk than in the high-density population of elk (see Table 1 and Fig. 4).

We combined treatments for analysis of quality, because MANOVA revealed a significant effect of functional groups of plants (Wilks' λ: $F_{6, 222} = 113.84$, $P < 0.001$), although differences in quality among treatments were not significant (Wilks' λ: $F_{7, 218} = 0.96$, $P = 0.458$). We observed significant differences in quality among years (Wilks' λ: $F_{7, 218} = 7.24$, $P < 0.001$), although there were no significant interactions between year and treatment (Wilks' λ: $F_{7, 218} = 0.96$, $P = 0.460$) nor between year and forage class (Wilks' λ: $F_{14, 436} = 1.13$, $P = 0.327$). Therefore, we combined treatments and years for our final analysis (Fig. 5). The shrub category included both upright and mat-forming shrubs, although mat-forming shrubs were of very low importance in the diets of both mule deer and elk. IVDMD was greatest for forbs and graminoids and was lowest for shrubs (see Fig. 5). Our estimates of crude protein for the three forage categories indicated that values were greater for forbs than the other two categories (graminoids and shrubs) which did not differ in crude protein content (see Fig. 5). Results from Van Soest fiber analysis represents the relatively indigestible components of forage. In decreasing order of digestibility, each of the three forage categories (forbs, graminoids and shrubs) differed from one another in NDF, which was greatest for graminoids and lowest for forbs, with shrubs having intermediate NDF (see Fig. 5). ADF was lower for forbs than graminoids and shrubs, which did not differ significantly ($P > 0.05$) from one another (see Fig. 5). Finally, ADL, the most indigestible component of forage, was greatest for shrubs and lowest for graminoids with forbs having intermediate ADL levels (see Fig. 5). AIA was greatest for graminoids and lowest for shrubs with forbs having intermediate AIA levels (see Fig. 5).

We used PCA and MANOVA to test for differences in diet composition among treatments. Due to the low importance of mat-forming shrubs and conifers to both mule deer and elk, we used forbs, grasses, sedges and upright shrubs as variables in our PCAs. Two PCs explained 94% of the variation: PC $1 = 80\%$ and PC $2 = 14\%$. PC 1 ranged from shrubs and forbs (negative loadings) to grasses and sedges

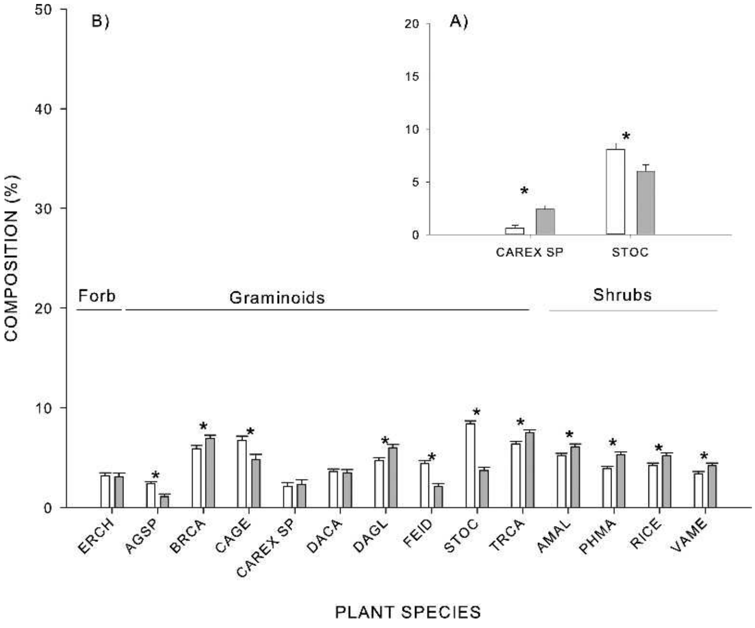


Figure 3. Least squared means (± SE) of dietary composition of North American elk in spring (A) and summer (B) at high (white bars) and low (grey bars) population densities of elk. Comparisons are from ANOVA following significant MANOVA for differences among treatments (Wilks' λ: $F_{14, 134} = 8.80$, $P < 0.001$), * indicates plant species that differed significantly ($P < 0.05$) in the diets of elk at high and low population density on the Starkey Experimental Forest and Range, Oregon, USA, 2000-2001. Acronyms along the x-axis are explained in Table 1. Note that for spring the same plant species were analyzed, but only two differed significantly.

(positive loadings) and likely represented a continuum from graminoids to broadleaved plants (Fig. 6). PC 2 ranged from shrubs (positive loadings) to grasses (negative loadings) and probably represented a grazing to browsing continuum (see Fig. 6). Following PCA, we used MANOVA to test for differences in high- and low-density treatments among seasons for elk following significant season by treatment interaction (Wilks' λ: $F_{2, 147} = 6.44$, $P = 0.0021$). Neither, PC 1 ($F_{1, 54} = 3.36$, $P = 0.072$), nor PC 2 ($F_{1, 54} = 0.64$, $P = 0.426$) differed significantly for elk at high or low densities during spring (see Fig 5). During summer, PC 1 did not differ between treatments ($F_{1, 96} = 2.46$, $P = 0.120$), but PC 2 differed significantly ($F_{1, 94} = 11.0$, $P = 0.0013$) between high and low population density during summer (see Fig. 6). For mule deer, PC 1 differed significantly ($F_{1, 41} = 12.73$, $P = 0.0009$) between high and low densities of elk, although there were not significant differences in PC 2 ($F_{1, 41} = 0.23$, $P = 0.634$) among treatments (see Fig. 6).

Discussion

We hypothesized that diets of mule deer and North American elk would contain more palatable species

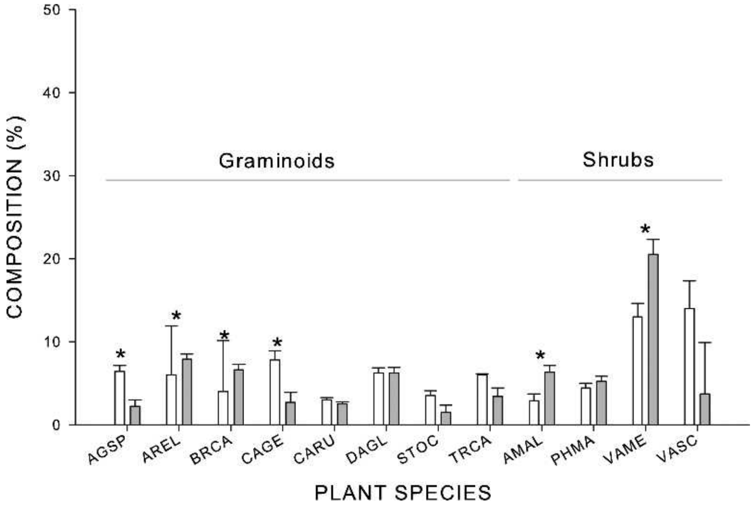


Figure 4. Least squared means (± SE) of dietary composition of mule deer in summer at high (white bars) and low (grey bars) population densities of elk. Comparisons are from ANOVA following significant MANOVA (Wilks' λ: $F_{12, 25} = 4.36$, $P = 0.009$), * indicates plant species that differed significantly ($P < 0.05$) in the diets of mule deer at high and low population density of North American elk on the Starkey Experimental Forest and Range, Oregon, USA, 2000-2001. Acronyms along the x-axis are explained in Table 1.

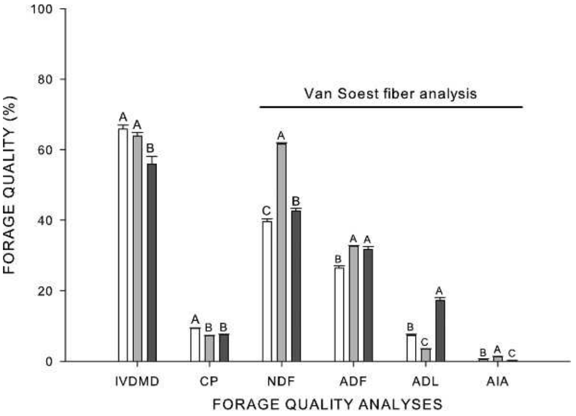


Figure 5. Forage quality (%) of forbs (white bars), graminoids (light grey bars) and shrubs (dark grey bars). Increasing values of *in vitro* dry matter digestibility (IVDMD; $F_{2, 119} = 13.24$, $N = 120$, $P < 0.001$) and crude protein (CP; $F_{2, 119} = 27.03$, $N = 120$, $P < 0.001$) represent increasing quality of forage. The Van Soest analysis included percent neutral detergent fiber (NDF; $F_{2, 120} = 418.09$, $N = 121$, $P < 0.001$), percent acid detergent fiber (ADF; $F_{2, 120} = 44.08$, $N = 121$, $P < 0.001$), percent acid detergent lignin (ADL; $F_{2, 120} = 297.66$, $N = 121$, $P < 0.001$), and percent acid insoluble ash (AIA; $F_{2, 120} = 99.25$, $N = 121$, $P < 0.001$), which all indicate proportion of indigestible components of forage classes. Thus, increasing values from Van Soest analysis indicates declining quality of forage, from high- and low-density populations of North American elk on the Starkey Experimental Forest and Range, Oregon, USA, 2000-2001. Means are from ANOVA following significant MANOVA for forage classes (Wilks' λ: $F_{6, 222} = 113.84$, $P < 0.001$). Note that for quality analyzes, all shrubs (mat-forming and upright) were combined. Letters over the bars indicate results of comparison of means within quality variables where different letters indicate significant differences ($P < 0.05$).

of forage at low density of elk because of reduced interspecific and intraspecific competition for forages. Indeed, for both mule deer and elk, the more palatable upright shrubs such as serviceberry and big huckleberry (see Table 1) occurred in the diets to a significantly greater extent in the low-density population. Conversely, species of somewhat lower quality, such as elk sedge and Idaho fescue were used to a greater extent in the high-density area by both mule deer and elk (see Figs. 2 and 3). During spring, elk used sedges (*Carex* spp. other than elk sedge) to a greater extent in the low-density area, likely because early growth was more available and of high quality (see Fig. 2). However, one graminoid, western needlegrass was present in faeces of elk to a greater extent in the high-density area during both spring and summer (see Fig. 3).

Diet importance was similar for both species of large herbivores with grasses, forbs and upright shrubs being the most important forages. Although, grasses were less important and shrubs more important to mule deer than for elk. Both plant communities and forages used by mule deer and elk were highly diverse, although about 60% of diets of elk consisted of grasses, with some slight differences among population-density treatments. Diets of both mule deer and elk had greater diversity in the high-density area, likely because dietary niche was expanded to include lower-quality forage in the presence of greater interspecific competition between mule deer and elk and increased intraspecific competition for elk at the high population density.

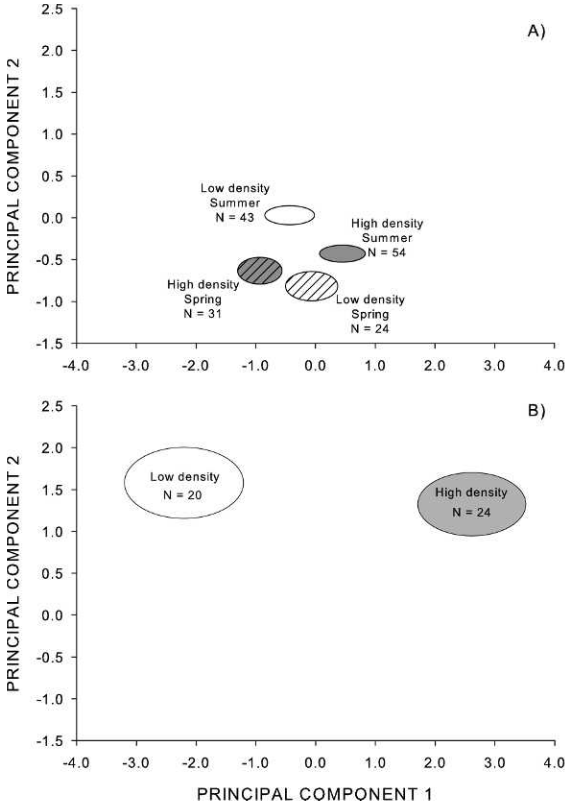


Figure 6. Results of principal components analysis on forage classes, determined from microhistological analysis of faeces of North American elk for principal components 1 and 2 (93% of variation explained). Ellipses are least squared means ± SE for elk (A) and mule deer (B) from MANOVA on the Starkey Experimental Forest and Range, Oregon, USA, 2000-2001. Dark circles indicate high population density and white circles indicate low population density. Elk data were analyzed by season, i.e. spring (hatched ellipses) and summer (open ellipses). Note that sample sizes for mule deer were too small during spring to allow for sampling by season.

We hypothesized that the potential for competition would be greater in the high-density area, which was supported by our observation that diet overlap was greater between mule deer and elk in the high-density area. We observed less divergence in diet where there was more competition for forage and likely less forage available; elk removed most net aboveground productivity of plants at high density (Stewart et al. 2006). Gordon & Illius (1989) cautioned that high degree of overlap may indicate an absence of competition thereby permitting sharing of common resources, particularly during seasons when forage is most abundant. Nevertheless, we were able to compare overlap among high- and low-density populations of elk and observed greater overlap where density, and hence competition, was likely greatest. That observation is consistent with niche theory wherein dietary niche is broadened where higher-quality resources become less available (Pianka 1988). Moreover, resources were most available in the low-density area (Stewart et al. 2006), where overlap in diet was lowest and palatable species of plants occurred to a greater extent in the diets of both cervid species. We did not have the option of examining resource partitioning during winter when resources are least abundant, because elk were not present on our study areas during that season (Stewart et al. 2005, 2006).

For both mule deer and elk, diet diversity was greater and dietary niche was expanded for both species in the high-density population of elk. Dietary niche likely was expanded in the high-density study area to include forage species of lower quality because species of higher-forage quality became less available. Conversely, Nicholson et al. (2006) observed a narrowing of dietary niche of mule deer during winter in a high-density population and hypothesized that per capita availability of forbs was reduced in the high-density population over winter causing a narrowing of dietary niche in the high-density area, although that relationship was not maintained during summer. Although palatable species of forage were less available in the high-density area at Starkey, there were ostensibly enough plant species of low palatability, particularly during summer, that dietary niche of both mule deer and elk could be broadened to include those species of lower palatability and quality. In general, grasses and sedges were used to a greater extent in the high-density area than the low-density area, and quality of those forages is lower than that of forbs (see Fig. 5).

Stewart et al. (2005) observed negative feedbacks associated with density dependence in elk in the high-density area. Body condition and pregnancy rates in elk were significantly lower in the high-density population of elk compared with the low-density population. If elk exhibit reduced physical condition and reproduction in areas where they are sympatric with mule deer, we hypothesize that mule deer also were affected by density-dependent processes through reduced physical condition and reproduction, because of interspecific competition for shared resources. Measures of body condition and reproduction, however, were not available for mule deer. Indeed, Parker et al. (2009) noted that reduced forage quality and quantity had a direct effect on nutritional status of ungulates, which resulted in declines in both physical condition, indexed by body fat or protein stores, and reproduction.

Both mule deer and elk selected strongly (see Fig. 2) for forbs, which also were highest forage category in quality, both digestibility and crude protein (see Fig. 5). In addition, forbs were lowest in ADF, an indication of indigestible components of forage. Our measures of diet quality for shrubs probably were not reflective of the palatable species of shrubs that increased in use in the low-density compared with the high-density area, such as serviceberry and big huckleberry. Samples of shrub species were composited to forage class for nutrient analysis. Mat-forming shrubs, which likely were of very low palatability (Miller et al. 1981, Johnson 1998), were combined with other more palatable species for nutrient analyses and we sampled current annual growth consisting of both stems and leaves. Mat-forming shrubs appeared to be of low dietary importance to both mule deer and elk (see Fig. 2). If mule deer and elk were more selective for plant parts than current annual growth of stems and leaves those values also would be lower than leaves alone. Therefore, our values for quality of shrubs are reflective of combining species or plant parts of high and low palatability and are probably much lower than those specific species that were selected by mule deer and elk. Indeed, Alldredge et al. (2002) reported an average of 14.5% crude protein of serviceberry, which was greater than our composited samples of shrubs (7.5%; see Fig. 4). Mule deer and elk selected strongly for upright shrubs, while either avoiding or using mat-forming shrubs in proportion to their availability. Thus, mule deer and elk selected for forages of higher quality particularly in the low-density area and forages selected by mule deer and elk likely were of higher quality than our analyses of diet quality indicated. Elk selected strongly for graminoids, which were similar in digestibility to forbs, although much higher in NDF than forbs. Consequently, elk were selective for some forages with greater indigestible components than were mule deer. Indeed mule deer, with smaller body size than elk, used forages of lower quality to a significantly lesser extent than did elk.

We examined digestibility of forages directly using IVDMD, thus we did not examine plants for presence of secondary compounds. None of the plant species we observed contain toxins, although some of the species likely contain some level of tannins (Johnson 1998). Secondary compounds observed in some shrubs and forbs generally act to reduce digestibility of forages (McLeod 1974, Schwartz et al. 1980, Robbins 1993, Barboza et al. 2009). Our estimate of the differences in digestibility among forages accounted for the presence of secondary compounds because we used rumen fluid of cervids that had been acclimated to forages from our study areas. Thus, we measured digestibility directly using IVDMD, and did not specifically test for the presence of secondary metabolites in those forages.

Competition for resources by large herbivores is a function of both numbers of competitors and their ability to compete effectively, and as our data indicate, interacts with density-dependent processes (Putnam 1996, Stewart et al. 2002, 2005). Stewart et al. (2002) postulated that at high population densities, niche partitioning becomes more difficult as resources become more limiting, leading to increased likelihood of competition. Stewart et al. (2002) also observed a greater effect of interference than exploitive competition in the population prior to our manipulation of population density, although cattle were present in that system. Both interference and exploitive competition hold the potential to influence niche dynamics (Case & Gilpin 1974). Interference competition has been demonstrated among sympatric ungulates including mule deer and elk (Stewart et al. 2002), as well as axis deer *Axis axis* and white-tailed deer *Odocoileus virginianus* (Faas & Weckerly 2010). Roe deer *Capreolus capreolus* and fallow deer *Dama dama* have been reported to exhibit both interference (Ferretti et al. 2008, Ferretti 2011) and exploitive (Focardi et al. 2006) forms of competition. We hypothesize that at high-population density of elk both interference and exploitive mechanisms would be present because of both high numbers of elk, as well as extensive use of available resources. We were unable to address interference effects, but our data strongly indicate that exploitive competition occurred (especially at high density of elk), which resulted in changes in dietary niche for both species. We observed greater overlap of diets and use of forages of lower quality by both mule deer and elk in a high-density population of elk. In the low-density area, dietary overlap and diversity were lower and these ungulates appeared to be partitioning dietary niche to a greater extent than in the high-density area. Although mule deer occurred at much lower densities than elk, effects of density-dependent feedbacks on elk had cascading effects on mule deer. Those effects of density dependence in the elk population were evidenced by changes in diet selection, quality and diversity of diets of mule deer in the same study areas, and would have been difficult to detect without our experimental manipulation.

Our observed outcomes are consistent with niche theory (Pianka 1988). Dietary niches of both species broadened at higher population density and increased competition. Indeed, in the low-density area, dietary niche was narrowed and both species focused on forage types of higher nutritional quality. Those observations were supported by Stewart et al. (2005), where physical condition and reproduction of elk was greatest in the low-density population of elk. Although we infer that similar changes in physical condition and reproduction affected mule deer, an experiment that documents changes in those factors for both species at multiple population densities would increase our understanding of the interaction between density-dependent processes and interspecific competition. Mobæk et al. (2009) suggested that knowledge of the interactions between population density and temporal variation in foraging behaviour is important to understanding variation in vital rates and population dynamics. Our data indicate that those same interactions also are important to understanding competitive interactions among sympatric species that exhibit strong density dependence.

Our approach was unique in that we were able to examine effects of population density on niche breadth while controlling for effects of year. Removal experiments to study competition are inevitably confounded by temporal effects. Such manipulations of herbivore density are rare, but perhaps necessary to gain a full appreciation of competitive interactions among large herbivores exhibiting strong density dependence.

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