Original Research

Diet Content and Overlap of Sympatric Mule Deer (*Odocoileus hemionus*), Moose (*Alces alces*), and Elk (*Cervus elaphus*) During a Deep Snow Winter in North-central British Columbia, Canada

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Abstract

Diet content and overlap have been used extensively to index and compare resource use among sympatric herbivores. In this study, we looked at diet content and overlap among Mule Deer (*Odocoileus hemionus*), Elk (*Cervus elaphus*) and Moose (*Alces alces*) on Mule Deer winter range areas in north-central British Columbia, Canada. We used micro-histological analyses of fecal pellet samples to assess diet content. Using multivariate analysis of variance to compare differences in forage class composition among ungulate species and Pianka's formula to calculate diet overlap, we found that Mule Deer and Moose primarily foraged on different types of conifers while Elk mostly utilized deciduous shrubs in winter. Our findings suggest that there is low diet overlap among the three species (Mule Deer vs. Elk = 31.4%; Mule Deer vs. Moose = 24.1%; and Elk vs. Moose = 11.3%) possibly indicating that a diet niche separation is occurring on Mule Deer winter ranges in north central British Columbia. Although these findings seem to suggest low competition among these large herbivores, further research on spatial and temporal use of winter ranges by these ungulates is required before solid conclusions can be made.

Key Words: *Alces alces*, British Columbia, *Cervus elaphus*, diet overlap, Elk, fecal analysis, Moose, Mule Deer, *Odocoileus hemionus*, sympatric, ungulate, winter range.

INTRODUCTION

Environmental conditions at northern latitudes during winter (e.g., topography, dominant vegetation, snow depth, etc.) affect how ungulates utilize the landscape (Boyce 1991; Nicholson *et al.* 1997; Poole and Mowat 2005). Movement patterns during foraging affect an animal's energy expenditures, exposure to adverse weather conditions, predation risk and access to food items (Stephens and Krebs 1986;

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Moen *et al.* 1997; Yearsley *et al.* 2002; Bailey and Provenza 2008). The amount of time large herbivores spend in plant communities is proportional to the amount of suitable resources available (Senft 1989) which matches the effort of foraging with the amount of food that is available (Senft *et al.* 1987; Owens *et al.* 1991). Abiotic factors such as slope, thermal cover, temperature, and topographic barriers can also affect foraging behaviour (Bailey *et al.* 1996). In addition, snow depth can directly impact foraging success of large herbivores (Johnson *et al.* 2001). Temperature and snow conditions contribute to forage availability, energy expenditures, and ultimately the energy costs associated with feeding (Mackie *et al.* 2003).

Mule Deer (*Odocoileus hemionus*) and Elk (*Cervus elaphus*) have restricted winter ranges in regions of deep snowpack (Armleder *et al.* 1994; Poole and Mowat 2005) that limit their ability to maintain a positive energy balance. While Moose (*Alces alces*) are well adapted to moving through deep snow, snow depths of 15-30 cm may be sufficient to force smaller ungulates such as Mule Deer to seek sheltered winter ranges (Mackie *et al.* 2003; Parker *et al.* 1984). Accumulations of more than 40 - 50 cm of snow may preclude the use of an area by Mule Deer and Elk, respectively (Poole and Mowat 2005) while Moose tolerate snow depths up to 80 cm (Hundertmark *et al.* 1990). In areas of deep snowpack, ungulates may seek habitats with less snow as refugia, potentially causing sympatric species to compete for common food resources in these areas (Frisina *et al.* 2008).

In this study, we explored forage content and diet overlap between sympatric Mule Deer, Elk, and Moose on Mule Deer winter ranges in north-central British Columbia. Mule Deer winter ranges are formally classified as necessary for the survival of Mule Deer at the northern extent of their range in the interior of British Columbia (Sulyma and Vinnedge 2003). We hypothesized that there would be diet overlap between Mule Deer and Elk because of preferences for similar habitats during winter. We predicted that there would be little overlap between Mule Deer and Moose due to the smaller body size of Mule Deer and the adaptations of Moose to utilize greater portions of the landscape in deep snow conditions. In addition, we predicted that Elk and Moose would have the least amount of diet overlap due to different foraging behaviours (mixed feeders vs. browsers, respectively).

STUDY AREA AND MATERIALS

Study Area

Our study area was in and adjacent to the John Prince Research Forest (JPRF; 54°40'14" N; 124°25'13" W) located near Fort St. James, British Columbia, Canada. The JPRF is characterized by rolling terrain with low mountains (700 - 1500m a.s.l.) and is within the Sub-Boreal Interior ecoprovince with representation of the Babine Uplands, Manson Plateau and Nechako Lowlands ecosections. It represents the northern extent of contiguous Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) forests in the interior of British Columbia and is dominated by the Sub-Boreal Spruce biogeoclimatic (BGC) zone. The BGC zone within the study area is dominated by the Dry

Warm (dw3), the Dry Cool (dk), and the Moist Cool (mk1) subzones (Delong *et al.* 1993). In these subzones, Douglas fir is most common on sub-mesic and drier sites that are of medium richness and richer. The area has experienced a wide variety of logging activities over the past 50 years and contains a mosaic of old and young coniferous forests with interspersed deciduous stands. The stands have a relatively rich understory of deciduous shrubs and regenerating conifers.

The stands defining Mule Deer winter ranges are predominantly (>50%) Douglas fir. Lodgepole pine (*Pinus contorta* var. *latifolia*) and hybrid White spruce (*Picea glauca* x *engelmannii*) are also common in these ranges with Sub-alpine fir (*Abies lasiocarpa*) dominating the understory. There are approximately 14,000 ha of south-facing stands where Douglas-fir represents a majority of the mature canopy (Sulyma and Vinnedge 2003). White-tailed Deer (*Odocoileus virginianus*) also occur in these areas occasionally. However, anecdotal results from aerial surveys have not identified White-tailed Deer using these winter range areas.

The average total snowfall for the 15 years prior to our study was 102 cm. The winter of 2007-2008 was the highest recorded total snowfall (197 cm) in the previous 15 years. The average snow accumulation across winter range areas during the winter was 75 cm. The mean temperature from December 1, 2007 to April 15, 2008 for the study area was -7°C. Snow conditions remained deep and relatively intact until the last week of April.

Pellet Sample Collections

In late winter 2007-2008, we conducted track surveys on snowshoe along 20 km of line transects (spaced 500 m apart) that dissected winter range areas. Surveys were conducted on 7 days between March 17 and April 20, 2008. We collected Mule Deer (*n* = 30), Elk (*n* = 30) and Moose (*n* = 28) pellet group samples found along transects. Samples were collected from pellet groups sighted (typically <30 m from transect) on the snow as they were encountered along each transect. Each transect was visited once during the winter. Concentrated accumulations of pellet groups along transects were not common; however, in areas where pellet concentrations did occur, we collected every third pellet group encountered to reduce the potential of sampling pellets from the same individual. Samples collected in this manner typically maintained a minimum distance between pellet groups of approximately 20 m.

Fecal Analysis

Fecal pellet samples were air dried and sent to the Wildlife Habitat Laboratory at Washington State University (B. Davitt, Pullman, Washington, USA) where plant matter content was quantified using microhistological analysis. Microhistological analysis of herbivore fecal samples is a technique that involves microscopic identification and quantification of discernible food fragments in animal fecal material used for determining food habits (Sparks and Malechek 1968; Holechek *et al.* 1982; La Morgia and Bassano 2009). Fifty microscope views per sample were used to discern density values for plant fragments in fecal samples to determine forage content. Fifty

views are comprised of 25 randomly located microscope views on each of two slides. This technique is widely used (e.g., Kirchoff and Larsen 1998; Stewart *et al.* 2003; Tortenson *et al.* 2006) because it is a reliable method of evaluating diet content of large herbivores (Mohammad *et al.* 1995). There are biases in content due to differential digestibility of forage plants (Holechek *et al.* 1982); however, correction factors are not necessary when the technique is used to estimate diet overlap among cervids with similar digestive processes (Hansen *et al.* 1973; La Morgia and Bassano 2009). Nevertheless, researchers must acknowledge that this technique does underestimate the proportion of highly digestible diet items such as forbs and lichens.

Data Analysis

We used Pianka's formula to calculate % overlap of diets between species (Pianka 1974; La Morgia and Bassano 2009):

$$O_{jk} = \frac{\sum P_{ij} P_{ik}}{\sqrt{\sum P^2_{ij} \sum P^2_{ik}}}$$

where Pij and Pik are the proportions of i resources used by the j species and the k species. Index values range from 1 (complete overlap) to 0 (no overlap). A Kolmogorov-Smirnov test was used to test assumptions of normality and a Fligner-Killeen test was used to test homogeneity of variances. To determine differences in forage class composition among species of animal, we used multivariate analysis of variance (MANOVA) and subsequent ANOVAs for pair-wise comparisons (Zar 2010). We then used principal components analysis (PCA) to reduce the dimensionality (Maindonald and Braun 2007).

We used $a = 0.05$ and a confidence level of 95% in all analyses which we conducted using Stata (StataCorp. 2009. Stata Statistical Software: Release 11. College Station, TX: StataCorp LP).

RESULTS

Ungulates in our study area exhibited restricted diets during winter compared to reports from other areas of their range with Mule Deer diets comprising 24 plant species; Elk 25 plant species; and Moose 17 plant species. Mule Deer consumed mostly conifers, but also consumed shrubs and lichens. Elk consumed mostly shrubs with lichens and conifers, while Moose foraged largely on conifers and fewer shrubs (Table 1).

Mule Deer pellets contained *Pseudotsuga* sp. (48%) and *Abies* sp. (12%) as the bulk of their diet with the remainder comprising a variety of deciduous shrubs (Table 1). The diets of Elk were the most variable and consisted primarily of shrubs (70.8%), *Pseudotsuga* sp. (13.9%), and lichens (9.4%) (Table 1). Moose had a more restricted diet and selected *Abies* sp. (45.3%), shrubs (35%), and *Pseudotsuga* sp. (16.8%).

There were significant differences in diet selection among ungulate species (Wilk's Lambda F$_{12, 160}$= 23.13; P<0.01). Pairwise comparisons between ungulate species indicated that there were

differences between Mule Deer and Elk in all forage classes (P<0.01), except in the lichen (P<0.08), other conifers (P<0.67), and other (P<0.91) categories. Elk and Moose winter diets differed (P<0.01) except in the *Pseudotsuga* sp. (P<0.37) and other conifer (P<0.75) categories. Moose and Mule Deer diets differed (P<0.01) except in
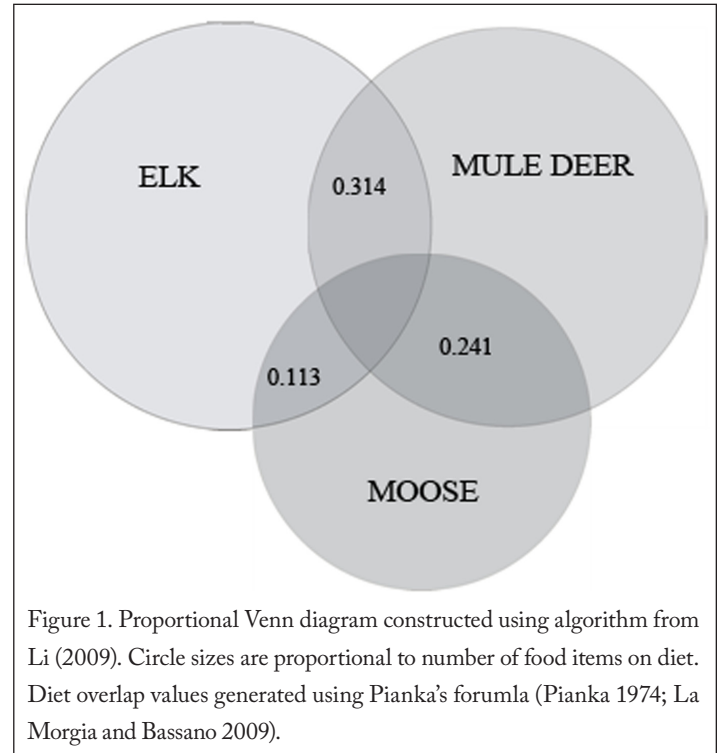

Figure 1. Proportional Venn diagram constructed using algorithm from Li (2009). Circle sizes are proportional to number of food items on diet. Diet overlap values generated using Pianka's forumla (Pianka 1974; La Morgia and Bassano 2009).

the other conifer (P<0.50) and shrub (P<0.17) forage classes. The diet overlap values calculated using Pianka's formula were greatest between Elk and Mule Deer (0.31), less so between Mule Deer and Moose (0.24), and least between Moose and Elk (0.11; Figure 1).

We used PCA to reduce the dimensionality of the data with the first two principal components explaining 93% of the variation in diet composition. We considered principal component 1 (59%) a forage content axis that represented conifers (negative loadings) to shrubs (positive loadings) with diets containing lichen and other categories demonstrating slightly positive loadings. Principal component 2 represented a browsing axis from Abies (negative) to *Pseudotsuga* (positive) with all other classes loading neutral or slightly positive. The distribution of the scores for principal components 1 and 2 clearly show a separation of diet items consumed by Mule Deer, Elk and Moose (Figure 2).

DISCUSSION

We predicted that diet overlap would be greatest between Mule Deer and Elk. While this was true (31%) it was lower than what we had expected and suggests that in our study area there is diet niche separation between Elk and Mule Deer occurring during winter. This overlap is lower than other reported values for Mule Deer and Elk

Table 1. Descriptive statistics for diet items (%) found in fecal pellets of Mule Deer (*n* = 30), Elk (*n* = 30), and Moose (*n* = 28) in the John Prince Research Forest, north-central British Columbia, Canada. Forage species that were >5% of the diet of at least one ungulate species were included.

Species and Forage class	Mean	SD	Minimum	Maximum
Mule Deer				
Abies lasiocarpa	12.2	13.9	0	58.7
Pseudotsuga menziesii	48.5	24.3	1.6	83.4
Other Conifer	2.0	2.52	0	9.5
Total Conifer	**62.7**	**27.7**	**1.6**	**97.9**
Amelanchier alnifolia	1.5	2.5	0	12.3
Betula spp.	2.5	3.1	0	11.2
Populus spp.	3.8	4.2	0	16.6
Salix spp.	6.9	9.6	0	36.0
Viburnum edule	3.4	3.8	0	15.5
Other Shrub	10.4	1.2	0	4.5
Total Shrub	**28.7**	**23.0**	**0.7**	**88.8**
Lichen	**5.4**	**11.7**	**0**	**62.2**
Other	**3.4**	**5.2**	**0**	**20.8**
Elk				
Abies lasiocarpa	0.2	0.6	0.1	2.9
Pseudotsuga menziesii	13.9	13.0	0	45.0
Other Conifer	1.8	1.9	0	5.4
Total Conifer	**15.9**	**13.6**	**0**	**45.0**
Amelanchier alnifolia	8.9	5.7	0	20.0
Betula spp.	5.4	4.6	0	15.9
Populus spp.	6.4	4.5	0	17.0
Salix spp.	26.5	7.5	13.4	39.3
Viburnum edule	7.8	6.0	0	20.2
Other Shrub	15.6	0.5	0.8	3.5
Total Shrub	**70.4**	**15.5**	**29.9**	**95.0**
Lichen	**9.9**	**6.7**	**0**	**33.6**
Other	**3.6**	**5.4**	**0**	**20.8**
Moose				
Abies lasiocarpa	45.3	17.4	11.1	71.3
Pseudotsuga menziesii	16.9	11.5	0	36.9
Other Conifer	1.6	2.2	0	7.7
Total Conifer	**63.8**	**13.7**	**33.3**	**88.4**
Amelanchier alnifolia	4.0	3.7	0	13.4
Betula spp.	3.8	4.1	0	12.9
Populus spp.	3.3	4.2	0	15.1
Salix spp.	13.1	7.1	2.2	35
Viburnum edule	4.4	5.1	0	20.7
Other Shrub	6.9	0.5	0.1	2.3
Total Shrub	**35.5**	**13.6**	**10.9**	**66.7**
Lichen	**0.7**	**1.2**	**0**	**5.3**
Other	**0**	**0**	**0**	**0**

across their range: 64% in Alaska (Kirchoff and Larsen 1998), 37% in Colorado (Hobbs *et al.* 1983), 74% in Washington (Leslie *et al.* 1984), and 61% in Wyoming (Tortenson *et al.* 2006). Although data on densities of ungulates in our study area are unavailable, ecological conditions at the edge of Mule Deer range may result in lower densities and limited dietary overlap among these sympatric ungulates.

The lack of diet overlap between Elk and Mule Deer in our study may be explained by relatively low densities of both species at the northern extent of their ranges in the interior of British Columbia. In effect, this could mean that animals are eating whatever is available in currently selected suitable winter range areas and avoiding the energetic costs associated with long forays in deep snow and cold temperatures to search for higher quality food items, thereby potentially inducing spatial separation (Parker *et al.* 1984; Poole and Mowat 2005).

Alternatively, the lack of diet overlap between Elk and Mule Deer may be explained by diet partitioning or behavioural separation leading Mule Deer to avoid Elk as reported from other parts of their range (Miller 2002; Stewart *et al.* 2002). Another potential explanation is that Elk, as a result of larger body size, may be able to foray into areas with deeper snow accumulation to access food items such as shrubs. Given the deep snow pack during this project, however, Elk movements would also likely be limited by snow conditions (Poole and Mowat 2005).

We also predicted that diets would be different between Mule Deer and Moose due to differences in body size and behavioural adaptations to winter (i.e., larger bodied Moose can tolerate much deeper snow). In agreement with Ludewig and Bowyer's (1985) work with Moose and White-tailed Deer in Maine, we found that Mule Deer and Moose
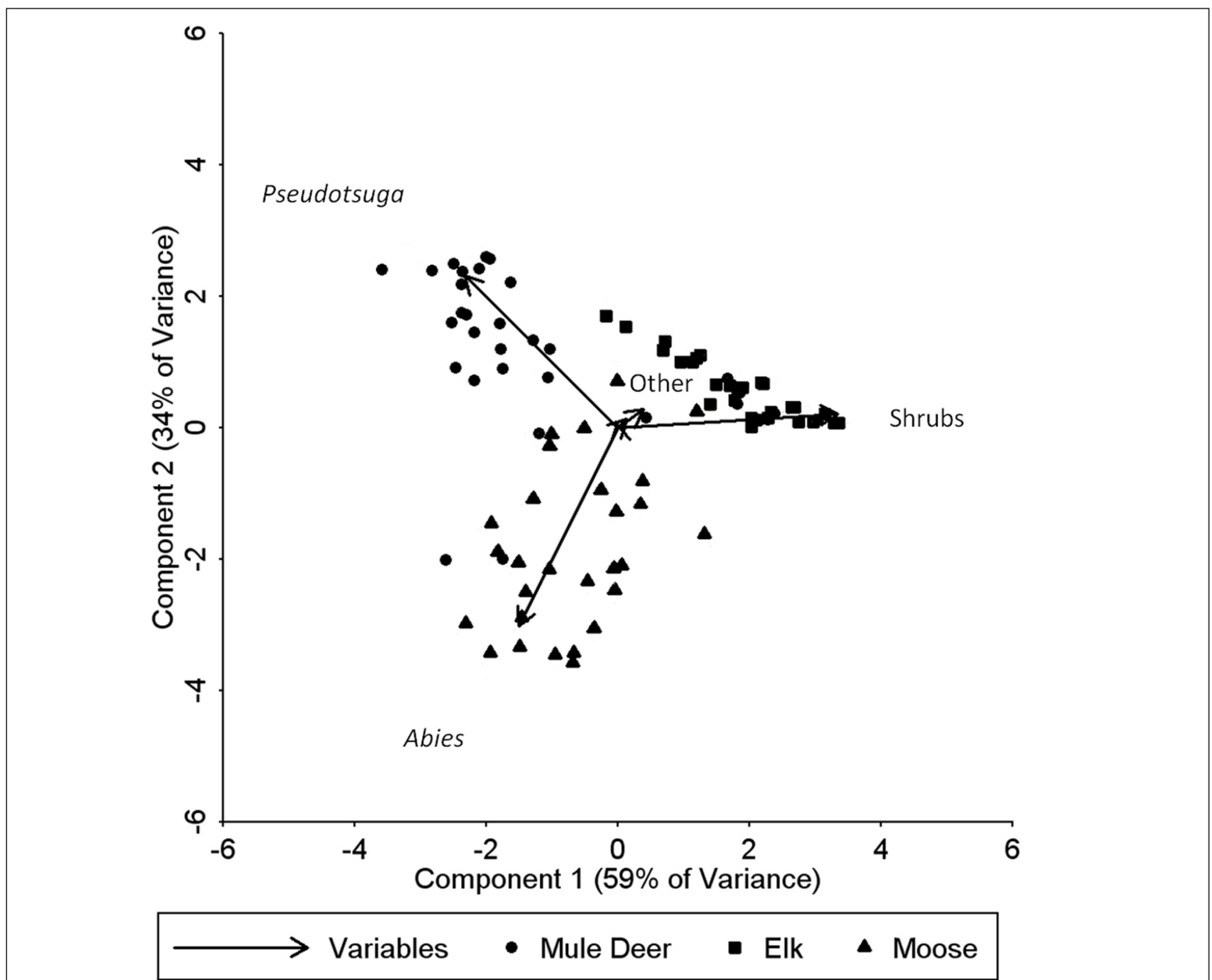

Figure 2. A biplot of principal component scores with forage classes indicated by arrows for Elk (*n* = 30), Mule Deer (*n* = 30), and Moose (*n* = 28) diets on Mule Deer winter range areas in north-central British Columbia, Canada. Principal component 1 is a forage class axis ranging from conifers to shrubs, while principal component 2 is a browsing axis ranging from *Abies* sp. to *Pseudotsuga* sp.

demonstrate considerable diet separation on deer winter ranges. Our results suggest that, when Moose and Mule Deer occur in the same areas during the winter, they maintain about a 75% diet niche separation. This may be due to Mule Deer seeking sheltered winter ranges (Armleder *et al.* 1994) and Moose seeking winter habitats in proportion to habitat and browse availability (Telfer 1978), except in severe winter conditions (Mech *et al.* 1987; Hundertmark *et al.* 1990).

We expected that Elk and Moose would have the least amount of diet overlap of all species we tested due to different foraging behaviors (mixed feeders vs. browsers: Hofmann 1989). Indeed, this was the case with an overlap index between Moose and Elk of 11% in our study area. However, Miller (2002) and Bowyer *et al.* (2003) suggest that interspecific competition between Moose and Elk is possible.

We predicted that the smaller Mule Deer would be more selective in diet choice than the larger Elk and/or Moose. Our results showed that Mule Deer and Elk had more varied diets than Moose. While *Pseudotsuga* sp. dominated the diet (48%) of Mule Deer (similar to findings of Waterhouse *et al.* (1994) from the Cariboo region of British Columbia), other conifers typically found in winter ranges were also consumed with several shrubs, lichens and forbs. This finding suggests that Mule Deer may be restricted in diet choices because of deep snow conditions that limit their movements (Telfer 1978; Parker *et al.* 1984; Armleder *et al.* 1994) unlike Moose, which are capable of movement through deep snow conditions allowing for greater access to forage and selectivity in both mature and younger forest types.

In an examination of indicators of time and space, Stewart *et al.* (2002) showed that Mule Deer, Elk and Cattle (*Bos taurus*) exhibited overlap in habitat use. However, in a companion study, it was later reported that strong partitioning of diet niches did occur despite overlap in habitat use (Stewart *et al.* 2003). While diet overlap can be a useful index of interspecific competition among large herbivores, there are other temporal and spatial factors as well as behavioural avoidance mechanisms (Telfer 1978) that need to be investigated before strong conclusions regarding competition (or lack thereof) between Mule Deer, Elk and Moose on winter ranges can be made.

This work supports the theory that native sympatric herbivores exhibit resource partitioning and low diet overlap. This is in agreement with numerous other works (Hartnett *et al.* 1997; Stewart *et al.* 2003; Tortenson *et al.* 2006) and suggests, at current population levels, there is low diet overlap (and low competition for food resources) among Mule Deer, Elk, and Moose on Mule Deer winter ranges in north-central British Columbia.

Competition can cause avoidance and/or displacement of some herbivores and may be reflected in reduced diet overlap (van Wieren and van Langevelde 2008). Ranges used by Mule Deer in winter in north-central British Columbia are clearly used by other ungulates which consume forage used by Mule Deer for overwintering survival. Further research such as using marked individuals or population manipulations from hunting to investigate the spatial and temporal overlap of these ungulates could lead to more robust interpretations of how resources are partitioned within Mule Deer winter ranges. Collections of pellets in multiple seasons over multiple years would increase our ability to detect diet overlap under varying conditions (e.g., heavy vs. light snow winters).

MANAGEMENT CONSIDERATIONS

Currently, Mule Deer winter ranges in the Fort St. James Forest District of north-central British Columbia make up less than one percent of the total forest planning landscape. Wildlife managers have designated these areas as critical for the survival of Mule Deer (Sulyma and Vinnedge 2003); however, they are also used by Moose and Elk. Although there currently appears to be low diet overlap between Mule Deer, Elk, and Moose in these areas, an increase in Moose or Elk numbers could alter this relationship (Miller 2002; Frisina *et al.* 2008). To this end, managers must remain alert, not only to those habitat components required and used by Mule Deer, but also used by competitors such as Moose and Elk that can reduce critical resources required by Mule Deer occupying these habitats during critical deep snow winters.

ACKNOWLEDGEMENTS

LITERATURE CITED

Armleder, H. M., M. J. Waterhouse, D. G. Kiesker, and R. J. Dawson. 1994. Winter habitat use by mule deer in the central interior of British Columbia. Canadian Journal of Zoology 72: 1721-1724.

Bailey, D. W., J. E. Gross, and E. A. Laca. 1996. Mechanisms that result in large herbivore grazing distribution patterns. Journal of Range Management 49: 386-400.

Bailey, D. W., and F. D. Provenza. 2008. Mechanisms determining large herbivore distribution. Pages 7-28 *in* H. H. T. Prins and F. van Langevelde, editors. Resource ecology: Spatial and temporal dynamics of foraging. Springer Science, Amsterdam, Netherlands.

Boyce, M. S. 1991. Migratory behaviour and management of elk (*Cervus elaphus*). Applied Animal Behaviour Science 29: 239-250.

Bowyer, R. T., V. van Ballenberghe, and J. G. Kie. 2003. Moose (*Alces alces*). Pages 931-964 in G. Feldhammer , B. Thompson, and J.A. Chapman, editors. Wild mammals of North America: Biology, management, and conservation, Second Edition. John Hopkins University Press, Baltimore, Maryland, USA.

DeLong, C., D. Tanner, and M. J. Jull. 1993. A field guide for site identification and interpretation for the southwest portion of

the Prince George Forest Region. British Columbia Ministry of Forests, Victoria, B.C. Land Management Handbook No. 24.

Frisina, M. R., C. L. Wambolt, W. W. Fraas, and G. Guenther. 2008. Mule deer and elk winter diet as an indicator of habitat competition. Pages 123-126 *in* S. G. Kitchen, R. L. Pendleton, T. A. Monaco, and J. Vernon, comps. Proceedings - Shrublands under fire: Disturbance and recovery in a changing world. USDA, Forest Service, Rocky Mountain Research Station, Proc. RMRS-P-52.

Hansen, R. M., D.G. Peden, and R. W. Rice. 1973. Discerned fragments in feces indicates diet overlap. Journal of Range Management 26: 103-105.

Hartnett, D. C., A. A. Steuter, and K. R. Hickman. 1997. Comparative ecology of native and introduced ungulates. Pages 72-101 in F. L. Knopf and F. B. Samson, editors. Ecology and conservation of Great Plains vertebrates. Springer, Berlin Heidelberg, New York, New York, USA.

Hobbs, N. T., D. L. Baker, and R. B. Gill. 1983. Comparative nutritional ecology of montane ungulates during winter. Journal of Wildlife Management 47: 1-16.

Hofmann, R. R. 1989. Evolutionary steps of ecophysiology adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78: 443-457.

Holechek, J. L., M. Vavra, and R. D. Pieper. 1982. Botanical composition determination of range herbivore diets: a review. Journal of Range Management 35: 309–315.

Hundertmark, K. J., W. L. Eberhardt, and R. E. Ball. 1990. Winter habitat use by moose in southeastern Alaska: implications for forest management. Alces 26: 108-114.

Johnson, C. J., K. L. Parker, and D. C. Heard. 2001. Foraging across a variable landscape: behavioral decisions made by woodland caribou at multiple spatial scales. Oecologia 127: 590-602.

Kirchhoff, M. D., and D. N. Larsen. 1998. Dietary overlap between native sitka black-tailed deer and introduced Elk in southeast Alaska. Journal of Wildlife Management 62: 236-242.

La Morgia, V., and B. Bassano. 2009. Feeding habits, forage selection, and diet overlap in alpine chamois (*Rupicapra rupicapra L.*) and domestic sheep. Ecological Research 24: 1043-1050.

Leslie, D. M., E. E. S. Tarkey, and M. Vavra. 1984. Elk and mule deer diets in old-growth forests in western Washington. Journal of Wildlife Management 48: 762-775.

Li, S. 2009. Using SAS to create proportional Venn diagrams. Paper 217, SAS Global Forum 2009.

Ludewig, H. A., and R. T. Bowyer. 1985. Overlap in winter diets of sympatric moose and white-tailed deer in Maine. Journal of Mammalogy 66: 390-392.

Mackie, R., J. Kie, D. Pac, and K. Hamlin. 2003. Mule deer (*Odocoileus hemionus*). Pages 889-905 *in* G. Feldhammer , B. Thompson, and J. A. Chapman, editors. Wild mammals of North America: Biology, management, and conservation, Second

Edition. John Hopkins University Press, Baltimore, Maryland, USA.

Maindonald, J. H., and J. Braun. 2007. Data analysis and graphics using R: an example based approach, Second Edition. Cambridge University Press, Cambridge, UK.

Mech, L. D., R. E. McRoberts, R. O. Peterson, and R. E. Page. 1987. Relationships of deer and moose populations to previous winters' snow. Journal of Animal Ecology 56: 615-627.

Miller, W. 2002. Elk interactions with other ungulates. Pages 435-447 *in* D. E. Toweill and J. W. Thomas, editors. North American elk ecology and management. Smithsonian Institution Press, New York, USA.

Moen, R., J. Pastor, and Y. Cohen. 1997. A spatially explicit model of moose foraging and energetics. Ecology 78: 505-521.

Mohammad, A. G., R. D. Pieper, J. K. Wallace, J. L. Holechek, and L. W. Murray. 1995. Comparison of fecal analyses and rumen evacuation techniques for sampling diet botanical composition of grazing cattle. Journal of Range Management 48: 202–205.

Nicholson, M. C., R. T. Boyer, and J. G. Kie. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. Journal of Mammalogy 78: 483-504.

Owens, M. K., K. L. Launchbaugh, and J. W. Holloway. 1991. Pasture characteristics affectingspatial distribution of utilization by cattle in mixed brush communities. Journal of Range Management 44: 118-123.

Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. Journal of Wildlife Management 48: 474-488.

Pianka, E. R. 1974. Niche overlap and diffuse competition. Proceedings of the National Academy of Sciences 71: 2141-2145.

Poole, K. G., and G. Mowat. 2005. Winter habitat relationships of deer and elk in the temperate interior mountains of British Columbia. Wildlife Society Bulletin 33: 1288-1302.

Senft, R. L. 1989. Hierarchical foraging models: effects of stocking and landscape composition on simulated resource use by cattle. Ecological Modeling 46: 283-303.

Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. Bioscience 37: 789-799.

Sparks, D. R., and J. C. Malechek. 1968. Estimating percentage dry weight in diets using a microscopic technique. Journal of Range Management 21: 264–265.

Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton, New Jersey, USA.

Stewart, K. M., R. T. Bowyer, J. G. Kie, N. J. Cimon, and B. K. Johnson. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. Journal of Mammalogy 83: 229-244.

Stewart, K. M., R. T. Bowyer, J. G. Kie, B. L. Dick, and M. Ben-

David. 2003. Niche partitioning among mule deer, elk and cattle: do stable isotopes reflect dietary niche? Écoscience 10: 297-302.

Sulyma, S., and J. Vinnedge. 2003. Mule deer ungulate winter range proposal: Fort St. James Forest District, Omineca Region. Ministry of Water, Land and Air Protection. Fort St. James, British Columbia, Canada.

Telfer, E. S. 1978. Cervid distribution, browse and snow cover in Alberta. Journal of Wildlife Management 42: 352-361.

Torstenson, W. L., J. C. Mosley, T. K. Brewer, M. W. Tess, and J. E. Knight. 2006. Elk, mule deer, and cattle foraging relationships on foothill and mountain rangeland. Rangeland Ecology and Management 59: 80-87.

van Wieren, S. E., and F. van Langevelde. 2008. Structuring herbivore communities: The role of habitat and diet. Pages 237-262 *in* H. H.T. Prins and F. van Langevelde, editors. Resource ecology: Spatial and temporal dynamics of foraging. Springer Science, Amsterdam, Netherlands.

Waterhouse, M. J., H. M. Armleder, and R. J. Dawson. 1994. Winter food habits of mule deer in the central interior of British Columbia. British Columbia Ministry of Forests Research Note No. 113.

Yearsley, J., I. M. Hastings, and I. J. Gordon. 2002. A lifetime perspective on foraging and mortality. Journal of Theoretical Biology 215: 983-986.

Zar, J. 2010. Biostatistical Analysis. Fourth Edition. Prentice Hall, Englewood Cliffs, New Jersey, USA.

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