NICHE OVERLAP AND THE POTENTIAL FOR COMPETITION BETWEEN REINTRODUCED BISON AND OTHER UNGULATES IN SOUTHWESTERN YUKON

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Yukon
Environment

September 2013

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Yukon Department of Environment
Fish and Wildlife Branch
Technical Report TR-13-15

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Acknowledgements

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Suggested citation:

JUNG, T. S., AND S .M. CZETWERTYNSKI. 2013. Niche overlap and the potential for competition between reintroduced bison and other ungulates in southwestern Yukon. Yukon Fiah and Wildlife Branch report TR-13-15. Whitehorse, Yukon, Canada.

Summary

After their reintroduction in the 1980s, the bison population in southwestern Yukon grew rapidly, resulting in unexpected management challenges. Despite formerly being indigenous to the region, local people had substantial concern over potential competition between reintroduced bison and resident ungulates. Consequently, a key management action arising from a community-based management plan for bison in the region was to better understand the potential impact of bison reintroduction on moose, caribou, and sheep.

We looked at the question of competition from the perspective of niche overlap: **Do species need the same resources (e.g., food and habitat) and obtain them from the same places at the same time?**

Between 2009 and 2010, we initiated field studies to investigate the overlap in the diets of bison and other ungulates. We used available data to also look for potential competition for habitat. In addition, we conducted a late-winter aerial survey of range to determine the overlap in time and space of these species during this critical season.

Key Findings

- There is little potential for competition between bison and caribou, or bison and moose, and low-moderate potential for bison and sheep, based on a combined assessment of seasonal diet, habitat and spatial overlap.
- There was little overlap in the summer and winter diets of reintroduced bison and moose, and bison and caribou.
- There was high overlap in the summer and winter diets of bison and sheep, and bison and semi-feral horses. This means that there is a potential for competition for food resources. However, because forage availability was likely not limiting, the potential for competition may be substantially less than would be suggested by our analyses.
- Habitat overlap was low for all species pairs and seasons considered.
- Low habitat overlap between bison and caribou, sheep, and moose suggests a low potential for competition between these bison and these species during the seasons we investigated.
- Our aerial survey indicated that none of the species pairs were statistically associated with one another. That is, their distribution on the landscape was not influenced by interactions with each other.
- Our results are not surprising, given that bison were once a numerically dominant species in the region and likely co-evolved with caribou and sheep to partition resources and co-exist.
- Given the low potential for competition between reintroduced bison and resident ungulates, no management interventions are suggested at this time.

- We do not recommend any further work to investigate potential competition between bison and moose and bison and caribou. There may be value in monitoring sheep ranges, however, for impact by bison.

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Introduction

Background

From the end of the last ice age until the late 1800s, wood bison (*Bison bison athabascae,* hereafter bison) were a numerically dominant species in northwestern North America (Soper 1941). They lived alongside other large mammals in the boreal cordillera, such as caribou (*Rangifer tarandus*) and thinhorn sheep (*Ovis dalli*; Guthrie 1968). By the turn of the 19th century, however, wood bison in northwestern North America were on the brink of extinction, with population declines largely attributed to excessive hunting and habitat loss (Soper 1941, Sanderson et al. 2008). Extensive recovery efforts ensued in northwestern Canada, beginning in the late 1950s, and in 1980 a program was initiated to re-establish bison in southwestern Yukon, Canada (Government of Yukon 2012). They are currently listed as a threatened subspecies in Canada's *Species at Risk Act.*

The bison population in southwestern Yukon grew rapidly post-reintroduction (Government of Yukon 2012), resulting in unexpected management challenges. Despite formerly being indigenous to the region, local people had substantial concern over potential competition between reintroduced bison and resident ungulates, which they depended on culturally and economically.

Consequently, a key management action arising from a community-based management plan for bison in the region was to better understand the potential impact of the bison reintroduction project on resident ungulates, specifically moose (*Alces americanus*), caribou, and sheep (Government of Yukon 2012).

Here, we provide the results on the niche overlap and potential for competition between reintroduced bison and other ungulates in southwestern Yukon. The ungulate assemblage in this region is dynamic, and currently consists of 8 species, with varied histories. Woodland caribou, moose, thinhorn sheep, and mountain goats are native resident species that have been extant in the region for ≥200 years. Wood bison were extirpated from the region ≥350 years ago, but were reintroduced in 1988–1992 as part of a national recovery program (Government of Yukon 2012). Elk (*Cervus canadensis*) were introduced into the study area in the 1950s (population augmentations occurred in the 1990s) with the aim of providing another ungulate species to local area hunters (Yukon Elk Management Planning Team 2008). Mule deer (*Odocoileus hemionus*; hereafter deer) have been naturally colonizing the region over the last few decades; but, there were no records of deer prior to the 1940s in the region (Hoefs 2001).

Semi-feral horses (*Equus ferus caballus*) have been free-ranging in portions of the study area for probably ≥125 years, and local people have been concerned that bison may compete with them for food. Thus, 4 species were considered native residents (caribou, moose, sheep, and goats), 2 were introduced (elk and horses), 1 was naturally colonizing (deer) and another was reintroduced (bison). Populations of some of the "new" species (bison, elk, and deer) had been increasing in the past 20 years (Hoefs 2001, Florkiewicz et al. 2007, Jung and Egli 2012), while those of native resident species (caribou, moose, and sheep) were the focus of substantial population recovery efforts (Hayes et al. 2003).

Given the dynamic nature of the ungulate assemblage in the region it is not surprising that some local residents have been concerned that changes in diversity and abundance of ungulates may have consequences on the population status of valued species, such as moose, caribou, and sheep. The overall aim of our work was to investigate the potential for competition between reintroduced bison and resident ungulates. We used a multi-dimensional approach to investigate niche overlap between bison and resident ungulates, focusing on overlap and the potential for competition for food and habitat resources, as well as winter spatial distribution.

Objectives

Our specific objectives for this work were to:

1) Determine the seasonal dietary overlap and the potential for competition for food resources between reintroduced bison and resident caribou, moose, and sheep, as well as other ungulates.
2) Determine the seasonal habitat overlap and the potential for competition for habitat between reintroduced bison and resident caribou, sheep, and moose.
3) Determine spatial co-occurrence patterns of reintroduced bison and resident moose, caribou, and sheep.
4) Develop general, evidence-based conclusions on the potential for competition between reintroduced bison and resident moose, caribou and sheep.
5) If necessary, provide recommendations for further research or management interventions, regarding the potential for competition between reintroduced bison and resident moose, caribou, and sheep.
6) As an ancillary objective, determine winter diet overlap and the potential for competition for food resources between introduced elk and resident moose and other ungulates. (This is an objective of the Yukon management plan for elk [Yukon Elk Management Planning Team 2008] and accomplished within the framework of our bison impacts research.)

Report Organization

In the main body of this report (this section) we provide a general coverage of our methods and results, along with overall conclusions and recommendations. More detailed accounts of the various components of the study follow as appendices to the main report. Each appendix is intended as a standalone report of a specific aspect of the work. To reduce duplication, most tables and figures in the appendices are not reproduced in this section.

General Methods

Study Area

Our study was conducted in a 19,710 km² area that approximated the range of the reintroduced Aishihik population (herd) of wood bison and the Aishihik population of woodland caribou in southwestern Yukon, Canada (see: Hayes et al. 2003, Hegel et al. 2012). The study area was in the Boreal Cordillera Ecozone (Yukon Ecoregions Working Group 2004), east of the village of Haines Junction (60.8°N, 137.5°W; Figure 1). Elevation ranges from 502–2345 meters above sea level (ASL). Much of the area is above treeline (approximately ≥1000 m ASL), with several mountain peaks ≥1600 m ASL and extensive alpine plateaus. Alpine areas are bisected by several large lakes, including Aishihik Lake and Taye Lake, and deeply incised river valleys.

Vegetation at lower elevations and valley bottoms include open canopy black spruce (*Picea mariana*), white spruce (*P. glauca*) and trembling aspen (*Populus tremuloides*) forest, dwarf willow (*Salix* spp.), and dwarf birch (*Betula nana*) shrublands interspersed with mesic sedge (*Carex* spp.) meadows. Remnant boreal grasslands occur as small patches on south-facing slopes, also at low elevations. Alpine plant communities are dominated by willow and dwarf birch, graminoid species, and mosses (*Sphagnum* spp.; Hayes et al. 2003). Climate is cold and semi-arid, with snow cover extending from early-October to mid-May.

Bison and moose are common in both alpine and lowland habitats. Bison occur predominately in the eastern part of the study area; moose are ubiquitous. Caribou and sheep are also common, but patchily distributed throughout the study area, and found predominately in alpine habitats. Caribou occur largely in the western portion of the study area (Fischer and Gates 2005). Elk, deer, and horses are uncommon and largely restricted to the southern quarter of the study area. Bison, caribou, and sheep occur at low densities; however populations of bison and caribou were increasing during our study (Hegel et al. 2012). Current abundance trends for other ungulates are unknown, but presumed stable.

Dietary Overlap

To assess the potential for competition among ungulates we investigated the dietary overlap of 7 species during 2009–2010 by examining the contents of fecal samples collected in the field ($n = 438$). Briefly, composite fecal samples ($n = 66$) were sent to a commercial lab (Wildlife Habitat Nutrition Laboratory, Washington State University, Pullman, WA, USA) for microscopic analysis by an experienced analyst. Lab methods followed established procedures outlined in many similar studies (e.g. Hansen et al. 1973, Dearden et al. 1975, Li et al. 2008, Vila et al. 2009). Diet composition at the forage class level (e.g. grasses, lichens, shrubs, etc.) and composite diet indices (diversity, evenness, niche breadth) were compared among species found at 2 elevations (high and low) and during 2 broad seasons (summer and winter). Dietary overlap index values were generated from species-specific diet data for the various species pairs, during each season and at each elevation. Overlap index values ranged from 0 to 1, with 0 indicating no overlap and 1 indicating total overlap (reviewed in Krebs 1999). We considered species pairs with overlap indices of <0.40, 0.40–0.79, and ≥0.80, to have low, moderate, and high diet overlap, respectively.

Further details of our field, lab and analytical methods can be found in Appendix A.

Habitat Overlap

We used available data sets to develop habitat selection models and assess habitat niche breadth and overlap for bison, caribou, sheep, and moose. Briefly, spatial data for bison ($n = 2951$ geo-referenced locations) were obtained from global position system (GPS) collars affixed to adult bison during 2005–2009. Caribou spatial data ($n = 1961$ geo-referenced locations) was collected from adult caribou equipped with very high frequency (VHF) collars that were subsequently relocated periodically during aerial telemetry surveys conducted 1997–2007. For sheep, the best available information was spatially distinct polygons depicting known (mapped) seasonal ranges based on aerial surveys of sheep during the lambing, rut, and late-winter, and local knowledge interviews. Spatial data for moose came from observations of moose during winter aerial surveys aimed at inventorying populations. Unfortunately, inadequate spatial data was available from our study area for sheep during the summer, or for moose outside the winter months. While the sheep population in our study area was surveyed in summer 2011, not enough geo-referenced locations were obtained to permit detailed habitat modeling.

Our examination of habitat overlap between bison and caribou and bison and sheep was based on an ecological niche factor analysis (ENFA, Hirzel et al. 2002, Hirzel et al. 2006).

This analysis is based on the concept of ecological niche and implemented in Biomapper (ver. 4.0) software (Hirzel et al. 2002, Hirzel et al. 2006; Hirzel and Le Lay 2008). One of the main advantages of this approach is that it does not require any information on absences. ENFA is an approach that requires only presence data for model development (Hirzel et al. 2002). This was critical for comparing niches of species for which data sources are disparate. ENFA is based on the computation of marginality (M) and specialization (S) factors that explain the realized niche of a species within the available niche space (Hirzel et al. 2002, Hirzel et al. 2006). The marginality factor is the absolute difference between the global mean and species mean, and describes how far the species optimum is from the mean global distribution of environmental variables describing the study area (Hirzel et al. 2002). M close to 1 indicates that the species habitat differs from the mean conditions in the study area. The specialization factors, the ratio of the standard deviation of the global distribution to that of the focal species, describe how specialized the species is with regard to the available covariates in the study area (Hirzel et al. 2002, Hirzel et al. 2006). When S is greater than 1 it indicates that there is some degree of specialization.

For this analysis we used a geographic information system (GIS) to overlay animal locations with environmental data (e.g. habitat type [meadow, alpine, conifer forest, etc.], elevation, slope, etc.), and calculated habitat models and habitat suitability maps for each species. We then used these models to calculate the habitat niche breadth of each species and the niche overlap of bison and caribou and bison and sheep.

For a comparison of bison and moose habitat overlap we took a somewhat similar analytical approach, but we used resource selection probability function (RSPF; Lele and Keim 2006, Lele 2009) as our analytical tool. An RSPF is a function that describes the probability that a particular resource, as described by a series of environmental covariates, will be selected by an individual animal (Manly et al. 2002). Recent advances in computational algorithms make it possible to estimate probability of selection with logistic regression models (Hosmer and Lemeshow 2000). These models provide stronger inferences compared to other, commonly used models that often are not an accurate representation of natural processes and can result in biased probability maps. These models represent the "mean" habitat selection observed. In this case our end product was a calculation of the percent of the study area that was predicted to be highly suitable habitat for both bison and moose.
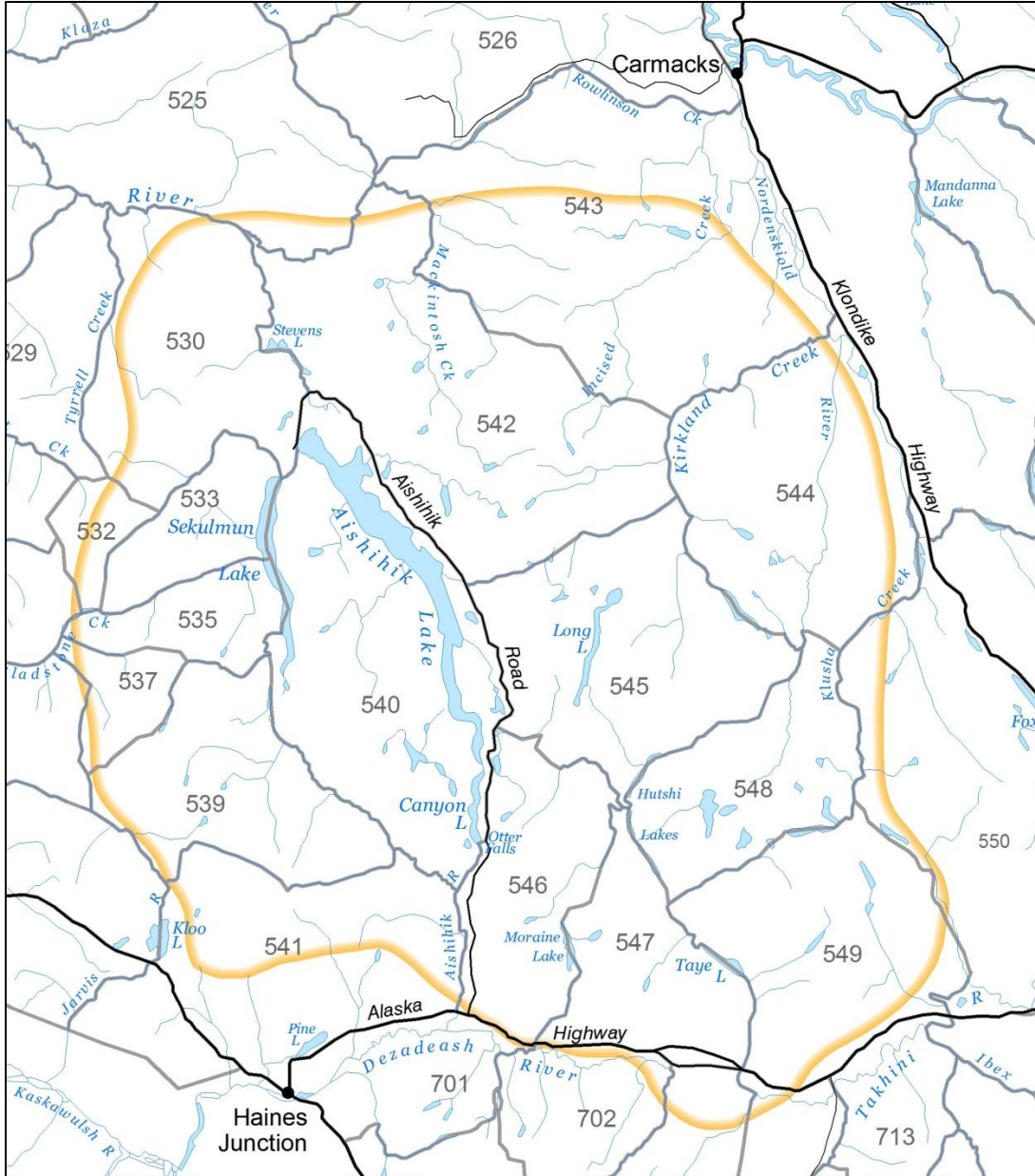
Figure 1. Location of the general study area in southwestern Yukon. The solid orange line delineates the core bison management zone, where most bison occur. Numbered polygons are the Game Management Subzones.

Further details of our modeling and analytical methods can be found in Appendix B (bison, caribou, and sheep) and Appendix C (bison and moose).

Spatial Overlap

We took a null model approach to examine spatial co-occurrence patterns (Gotelli 2000) in the ungulate community in southwestern Yukon. We focused our effort during late-winter, a time when food resources are most limiting and niche overlap for northern ungulates may be greatest (Jenkins and Wright 1987). We divided the study area into a grid comprising 779 hexagonal cells that were each 12 km^2 (Figure 2). Occurrence of bison, moose, caribou and sheep was determined through the observation of animals or their tracks in the snow (e.g. Jenkins and Wright 1988, Jung et al. 2009, Bowman et al. 2010) during 11 aerial surveys conducted 10–31 March 2010. Each cell was surveyed 1–5 times to increase our confidence in determining species presence (Bowman et al. 2010). With each subsequent survey we strived to enter and exit cells from a different angle, increasing our spatial coverage of each cell. Altogether we flew 7,670 km during 73.5 hours of aerial survey. We used a GIS to calculate the number of observed cells occupied by a species, as well as the number and percentage of cells where bison and each of the other species co-occurred. Co-occurrence was assessed through a null model analysis (Gotelli 2000).

Further details of our aerial survey or analytical procedures can be found in Appendix D.

General Results

Dietary Overlap

Composite diet indices and use of major forage classes differed substantially among species during summer and winter and at both high and low elevations. Dietary overlap for most species pairs was low to moderate (0.10–0.70). However, for reintroduced bison and native sheep, and bison and horses, it was high (≥0.80) during both summer and winter (Table 1), indicating a potential of competition for food. Elk and caribou had moderate dietary overlap with several species, but did not highly overlap with any other species.

We found that dietary overlap increased during winter among species at low elevations, but not for species found at high elevations. Dietary overlap between species appeared to be correlated primarily to their feeding mode (i.e., browser-intermediate-grazer), rather than body size. Bison, horses, and sheep are all grazers.

We concluded that the potential for competition for food resources between bison and sheep and bison and horses is high, but that for all other species pairs in our study area is low to moderate, based on dietary overlap.
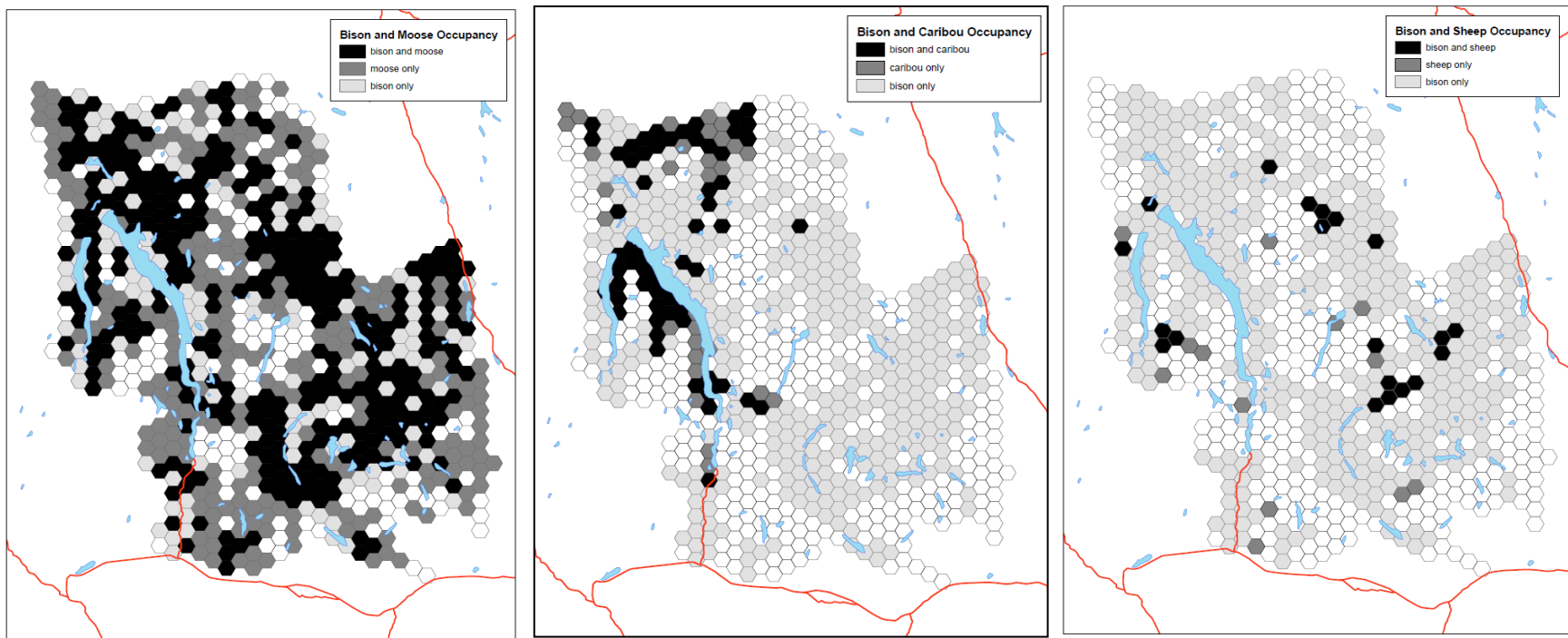
Figure 2. Late-winter occurrence of a) bison and moose, b) bison and caribou, and c) bison and sheep in 12 km2 hexagon cells (n = 779) in southwestern Yukon, Canada. Occurrence was determined by observations of animals or their tracks in snow as seen during 11 aerial surveys in March 2010.

Table 1. Dietary overlap index values for ungulate species pairs at high (≥1000 m ASL) and low (≤1000 m ASL) elevations during summer and winter in southwestern Yukon, Canada. Particularly high overlap values (≥0.80) are in bold. Index values range from 0–1, with 0 indicating no overlap and 1 representing complete overlap.

Elevation	Season	Species Pair	Pianka's Overlap Index	Morisita's Overlap Index	Horn's Overlap Index
High	Summer	Bison & Moose	0.12	0.12	0.32
		Bison & Caribou	0.55	0.51	0.65
		Bison & Sheep	**0.98**	**0.96**	**0.94**
		Moose & Caribou	0.54	0.44	0.62
		Moose & Sheep	0.21	0.19	0.43
		Caribou & Sheep	0.68	0.67	0.74
High	Winter	Bison & Moose	0.15	0.13	0.23
		Bison & Caribou	0.23	0.23	0.51
		Bison & Sheep	**0.82**	**0.80**	**0.90**
		Moose & Caribou	0.14	0.12	0.21
		Moose & Sheep	0.62	0.60	0.53
		Caribou & Sheep	0.28	0.28	0.60
Low	Summer	Bison & Moose	0.24	0.23	0.49
		Bison & Horse	**0.84**	**0.83**	**0.92**
		Moose & Horse	0.19	0.18	0.41
Low	Winter	Bison & Moose	0.42	0.42	0.59
		Bison & Horse	**0.98**	**0.97**	**0.97**
		Bison & Deer	0.08	0.07	0.31
		Bison & Elk	0.48	0.44	0.66
		Moose & Horse	0.38	0.38	0.52
		Moose & Deer	0.19	0.19	0.41
		Moose & Elk	0.63	0.59	0.72
		Horse & Deer	0.10	0.10	0.35
		Horse & Elk	0.59	0.57	0.71
		Deer & Elk	0.48	0.46	0.73

The availability of forage resources was unknown but likely not limiting to any species, given that they occur at the low densities in our study area. Thus, while diet overlap may be substantial between bison and horses and bison and sheep, the actual potential for competition is probably markedly lower as a result of seemingly abundant forage.

Further details of our results and their interpretation may be found in Appendix A.

Habitat Overlap

For bison, caribou, and sheep, our ENFA models suggested that sheep generally were the most selective of specific habitat types, followed by caribou and bison. Consequently, sheep had the narrowest niche breadth and are described as habitat "specialists". Niche breadth values for bison and caribou suggest that they are more "generalists" in their habitat requirements. Furthermore, their niche breadth varied seasonally, being wider in the early-winter and late-winter than in other seasons (spring, summer and fall). Consequently, habitat niche overlap between bison and caribou was greater during both early-winter and late-winter, compared to the other seasons. For bison and sheep, habitat niche overlap was very low in all seasons.

Our main finding was that habitat niche overlap was low for bison and caribou and bison and sheep (Figures 3 and 4), suggesting limited potential for competition for habitat.

Although we did not detect niche overlap between bison and sheep during any season, our results should be interpreted with caution given the specialized niche exhibited by sheep and the wide breadth of habitats used by bison in summer. Specifically, winter range (with graminoid cover) is critical in the welfare of sheep (Oldemeyer et al. 1971) and heavy use of these areas by bison may result in changes in graminoid cover from grazing, trampling, and wallowing (Knapp et al. 1999). Although our results do not provide evidence for resource competition, the wide summer niche breadth of bison could have a time-lag effect on the quality of sheep range, which may be either detrimental or beneficial to sheep.

Our RSPF models for bison and moose were restricted to winter, given available data. In both early-winter and late-winter, bison and moose selected for very different habitat types. In late-winter, for example, bison generally avoided deciduous forest areas whereas this habitat type was the strongest predictor of moose habitat selection. Given the difference in habitat use between moose and bison, they overlapped on only 0.5% and 6.6% of the study area during early-winter and late-winter, respectively, based on the most selected third of the area by each species (Figure 5).
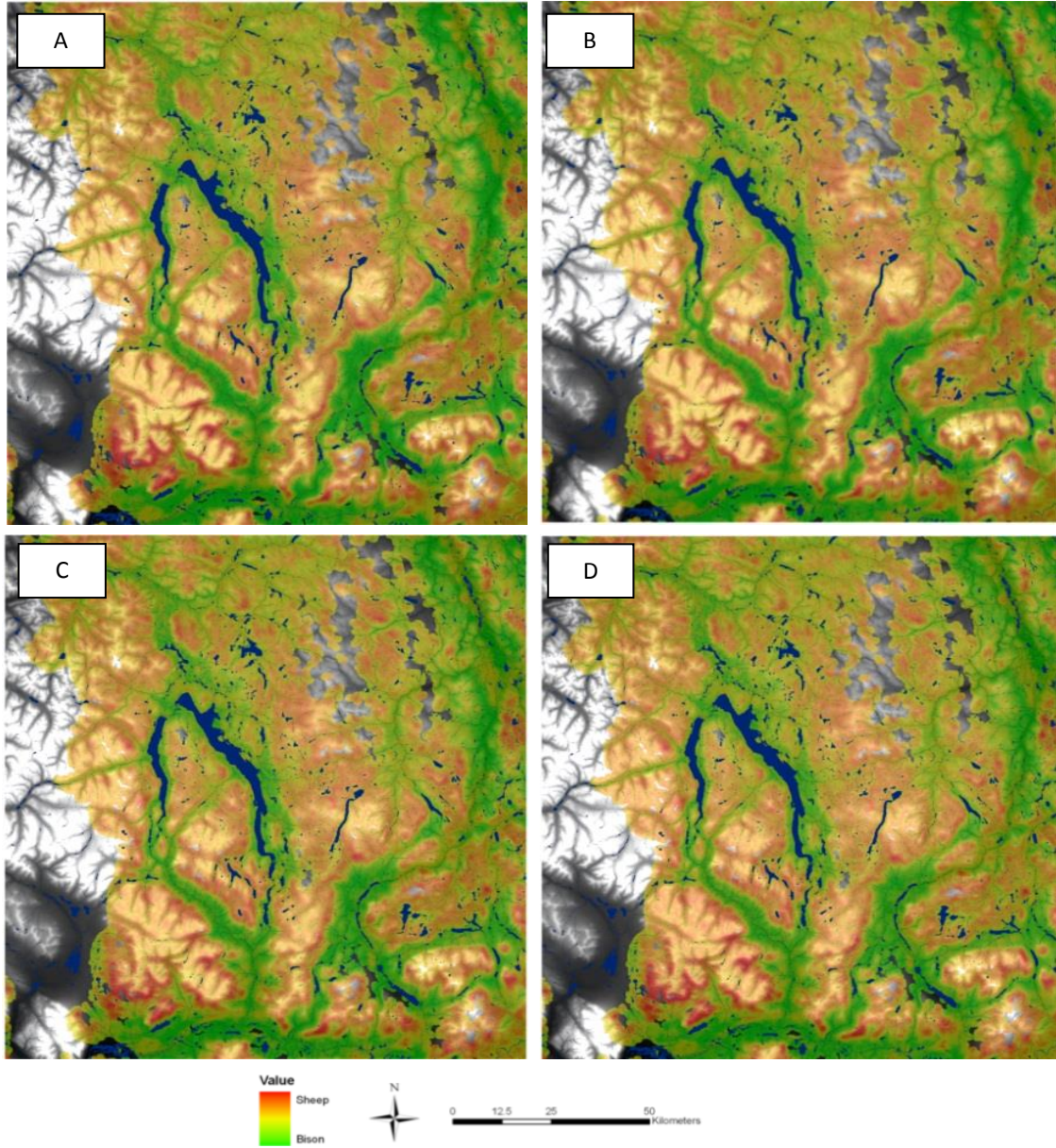
Figure 3. Niche differentiation map between bison and sheep for A) spring, B) fall, C) early-winter, and D) late-winter. Green areas represent conditions favouring bison whereas red areas represent environmental conditions favouring sheep. No sheep data was available for summer
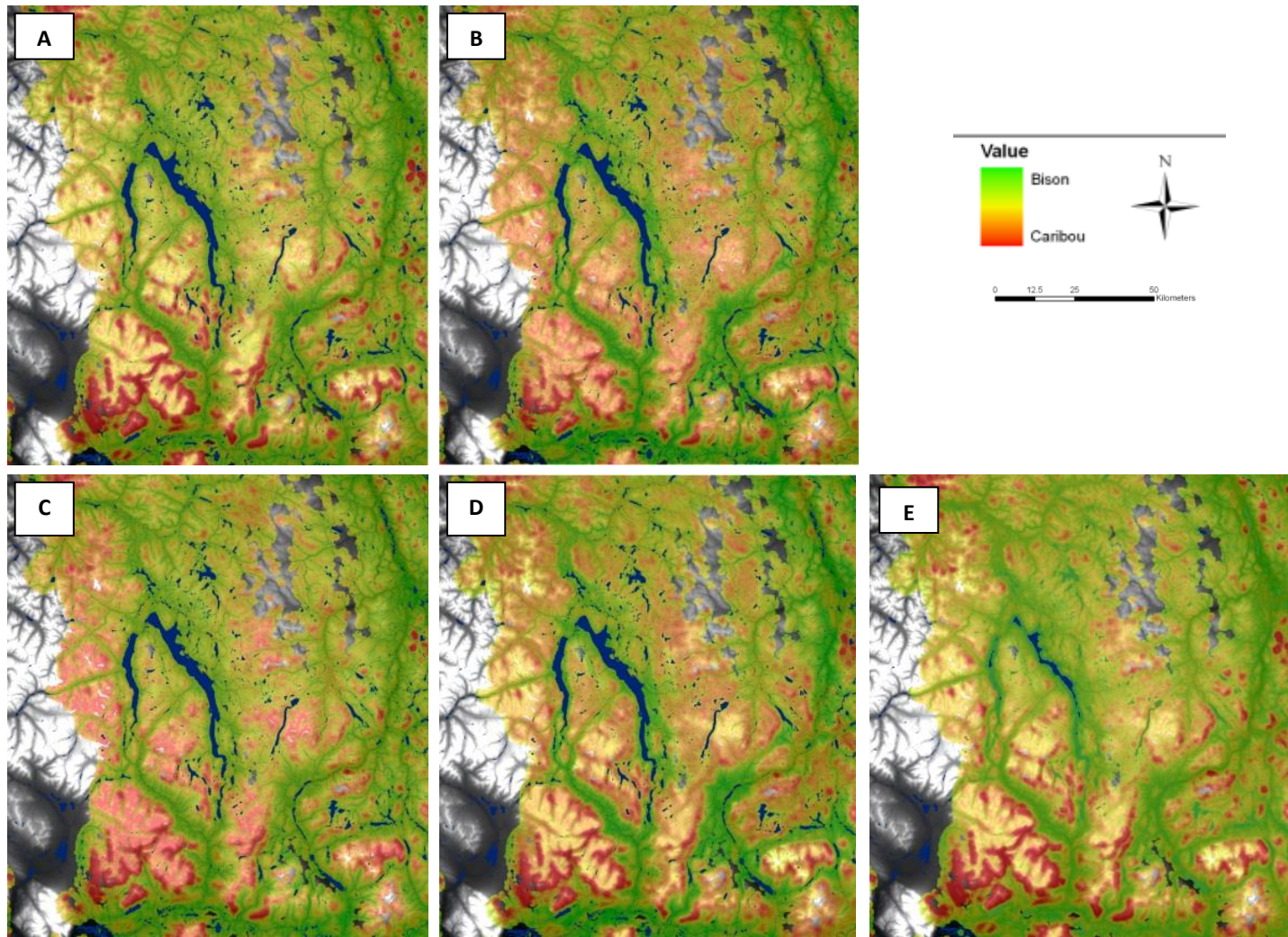
Figure 4. Niche differentiation map between bison and caribou for A) spring, B) summer, C) fall, D) early-winter, and E) late-winter. Green areas represent conditions favouring bison whereas red areas represent environmental conditions favouring caribou.
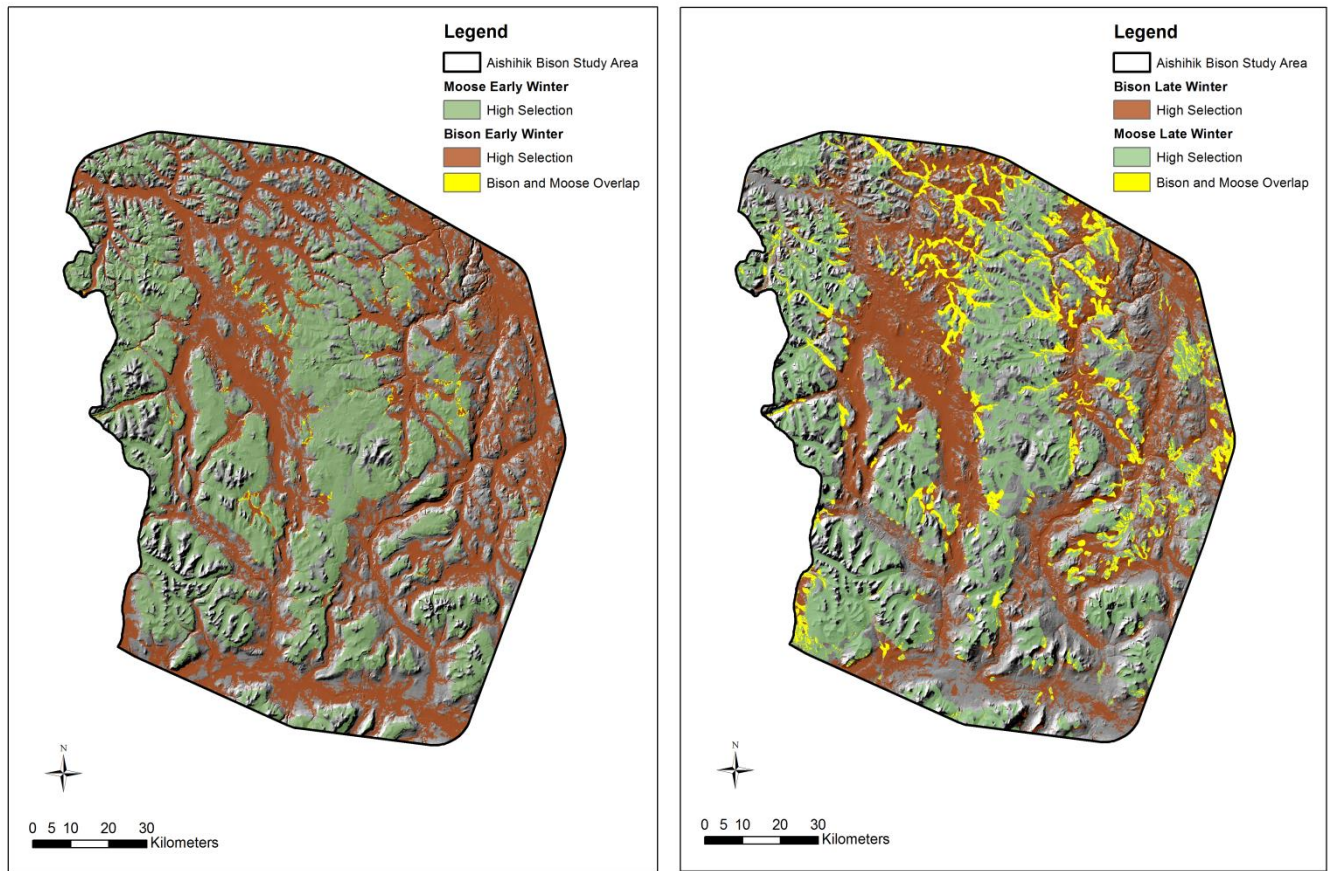
Figure 5. Areas of predicted high habitat selection for bison (brown shading) and moose (green shading) and their overlap (yellow shading) during early-winter (left panel) and late-winter (right panel) in southwestern Yukon, Canada. Grey areas were not predicted to be highly suitable habitat for either species. Areas of predicted high habitat selection were based on 3 equal sized bins from the RSPF model, see text for details.

Thus, we conclude that there is little evidence for the potential for competition for habitat between bison and moose in the study area during winter.

Further details on our results and their interpretation may be found in Appendix B (bison and caribou; bison and sheep) and Appendix C (bison and moose).

Spatial Overlap

No evidence of ungulate occurrence was observed in 119 (15.3%) of the 12 km^2 cells. Only 1 species of ungulate was observed in 313 (40.2%) of the cells, whereas 309 (39.7%) and 38 (4.9%) cells had evidence of 2 and 3 species of ungulates, respectively. Moose were observed in the largest percentage of cells surveyed (66%), followed by bison (54%), caribou (12%), and sheep (4%; Figure 2).

Moose were found in a much higher percentage of cells (28%) without bison than caribou (4%) or sheep (2%). However, the percentage of cells that were occupied by moose, caribou, and sheep, but not bison, was similar among species (37–43%).

Caribou and sheep, and bison and sheep, had the greatest co-occurrence of our species pairs, indicating a somewhat positive association. Conversely, bison and moose, and bison and caribou had the lowest co-occurrence, indicating an association that tended to be negative.

Nevertheless, none of the interactions were statistically significant, suggesting that overall the interactions among our species pairs were neutral; that is, they did not influence each other's distribution on the landscape.

The main finding of this part of our study is that we did not find evidence that the late-winter spatial distribution of reintroduced bison impacted that of resident caribou, moose, or sheep. The ungulate community in our study area was randomly distributed (i.e., neutral interactions; Darmon et al. 2012) with respect to interactions between its member species.

We have no data on the distribution of ungulates prior to bison reintroduction; however this part of the study can provide an analysis of whether reintroduced bison appear to have displaced any of the resident ungulates during late-winter.

While none of our species pairs were statistically associated with one another, bison and sheep were substantially more positively associated than were bison and caribou or bison and moose. This suggests that there may be some potential for interspecific competition between bison and sheep, given that they are similarly distributed across the landscape, even though that association is weak. Conversely, our data suggest that the potential for competition between bison and caribou and between bison and moose during late-winter is low, given that they do not co-occur on the landscape. Further details on our results and their interpretation may be found in Appendix D.

Conclusions

Utility of Niche Overlap

Our study was conducted with the intent of examining the potential for interspecific competition between reintroduced bison and resident ungulates, specifically moose, caribou, and sheep.

Documenting competition between 2 species, however, is difficult with free-ranging animals in a natural environment (Mishra et al. 2004, Ritchie et al. 2009). We examined the question of competition from the perspective of niche overlap; that is, do species require the same resources (e.g., food and habitat) and obtain them from the same places at the same time?

It is generally believed that for competition to occur, species must use the same resources (food, habitat) and overlap in time and space (de Boer and Prins 1990).

According to the competitive exclusion principle, 2 species that overlap niches in the same place cannot do so over the long term – eventually one will outcompete the other (Hardin 1960). Many similar studies interested in the potential for competition between ungulates have also examined niche overlap as a proxy for competition (e.g. Jenkins and Wright 1988, Baldi et al. 2004, Prins et al. 2006, Liu and Jiang 2009, Vila et al. 2009, Darmon et al. 2012). However, this assumption is debated.

It should be noted that overlap of any or all of these niche dimensions (food, habitat, time, and space) by 2 species would not necessarily demonstrate that competition is occurring between those species (Holt 1987, de Boer and Prins 1990). Niche overlap does not imply competition; it demonstrates an association and the possibility of competition. Moreover, to infer competition between species a multi-dimensional approach along several niche axes, as well as an assessment of resource availability, is necessary (Holt 1987, de Boer and Prins 1990). Truly, only an experimental approach can determine a cause and effect relationship between species.

Nonetheless, work such as ours provides an important assessment of the potential for competition between reintroduced bison and resident ungulates.

Documenting the extent of niche overlap may be used as an aid in determining if management interventions are warranted, or if further resources should be concentrated to determine if competition is occurring between species, and where and when to focus those efforts.

Potential for Competition

An overall assessment by species pair is provided below:

Bison and Moose. — Our analyses of the diet, habitat, and spatial overlap between reintroduced bison and moose failed to find significant niche overlap between these species. However, we lacked data on habitat or spatial overlap between these species during summer. Regardless, moose had a specialized diet and very narrow niche breadth. Bison, on the other hand, were less specialized and they tended to use different forage resources than moose. Likely due to the large difference in their diets (Appendix A), moose and bison exhibited substantial niche differentiation. Given the lack of niche overlap between reintroduced bison and moose, the potential for exploitative competition between these species is likely quite low.

Bison and Sheep. — The results for bison and sheep were mixed. As both species are grazers, they had a very high overlap of seasonal diets, suggesting a potential for competition for food. However, seasonal habitat overlap between bison and sheep was very low.

We found a weak positive association in the spatial overlap between bison and sheep in late-winter. Taken together, the results suggest that reintroduced bison have a low-moderate potential for competition with sheep, since they don't necessarily occupy the same habitats, even though their diets are similar. However, bison could have a time-lagged negative impact on sheep winter range in specific areas of high-use in their range.

Bison and Caribou. — Similar to the earlier work by Fischer and Gates (2005), we did not find much evidence of interspecific competition between reintroduced bison and caribou. Caribou are intermediate in terms of their diet, and have fairly diverse seasonal diets. Hegel et al. (2012) noted that despite the concern over the potential for competition between bison and caribou, populations of both species were currently increasing. Indeed, changes in abundance between 2 potentially competing species are perhaps a litmus test for whether competition is occurring or not (Forsyth and Hickling 1998), as competing species should not both be increasing (Hardin 1960).

Overall, we found little evidence for the potential for exploitative competition between reintroduced bison and resident moose, caribou, or sheep. Niche overlap between bison and these species was low, with the exception of diet overlap with sheep.

Our results are consistent within the context of the nutritional requirements and diet choices of these species. As grazing animals, bison have the least in common from a diet perspective with moose and the most with sheep (*sensu* Hofmann 1989). It stands to reason that differences in the seasonal diets of these species will lead to differences in where and when they will be found on the landscape and in relation (association) to one another.

Moreover, while the potential for competition may be a cause for concern because of the insertion of a large ungulate (bison) into an existing species assemblage by humans (Voeten and Prins 1999, Mishra et al. 2004), our finding that the potential for competition among these species is low is consistent with the theory of the "ghost of competition past" (Connell 1980). While bison have been absent from our ungulate community for ≥350 years, they were once a numerically dominant species in northwestern North America that coexisted with caribou, moose, and sheep (Guthrie 1968).

For these species to have coexisted on a shared range for thousands of years during the late Pleistocene and early Holocene they would have likely mutually evolved mechanisms to partition resources along various niche axes (Connell 1980, Hopf et al. 1993).

Ecological niches filled by caribou, moose, and sheep in our study area had perhaps already co-evolved such that spatial or temporal segregation, or sharing of resources (food and habitat), was not incompatible with respect to bison. In this sense, it is plausible that bison reintroduced to this species assemblage may in fact be filling an ecological niche that has been largely vacated since they were locally extirpated.

Recommendations

Given our general conclusion that bison present a low potential for competition with resident ungulates (moose, caribou, and sheep) we have few recommendations for potential management interventions or future research and monitoring. Our recommendations are below.

- There does not appear to be a need to further examine potential exploitative competition between bison and moose. We recognize that our lack of data for moose habitat use in seasons other than winter is a constraint.

However, bison and moose are quite far apart in their diet needs, and our data for winter suggests very low habitat and spatial overlap. Therefore, the evidence indicates that it is unlikely that bison and moose compete for resources in any season. No management interventions related to reintroduced bison are recommended on behalf of moose populations in the Aishihik area.

- Similarly, we do not recommend any management interventions or further research on the potential for competition for resources between reintroduced bison and caribou. Seasonal data on diet and habitat use by caribou and bison suggest that there is little overlap and, hence, a low potential for competition. Indeed, both species are currently increasing in abundance (Hegel et al. 2012).

- We lacked data on habitat use by sheep during summer, the time of year that bison tend to be found most commonly at high elevations. While we conclude that our analyses suggest limited (likely low) potential for competition between bison and sheep, further investigation may be warranted. Specifically, it may be informative to gather data on the habitat use of these species during summer and provide an assessment of overlap. This is of particular interest given the summer diet overlap between these species.

Also, we suggest that monitoring of the condition of sheep range that is used by bison would likely be of management interest and there may be a benefit for further investigation. No management interventions related to reintroduced bison are recommended on behalf of sheep populations in the Aishihik area are suggested at this time.

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Appendix A:

Dietary Overlap and Potential Competition in a Dynamic Ungulate Community in Northwestern Canada

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ABSTRACT: The potential for interspecific competition for scarce food resources is a key consideration when newly introduced ungulates occupy a shared range with resident native species. To assess potential competition among ungulates we examined dietary overlap of 7 species during 2009–2010 in southwestern Yukon, Canada. Diet composition at the forage class scale and composite diet indices (diversity, evenness, and niche breadth) were compared among species found at 2 elevation classes (high and low) during 2 broad seasons (summer and winter), using diet data derived from microhistological analyses. Composite diet indices and use of major forage classes differed among species during summer and winter and at both high and low elevations. Dietary overlap for most species pairs was low to moderate (0.10–0.70). However, for reintroduced bison (*Bison bison*) and thinhorn sheep (*Ovis dalli*), and bison and semi-feral horses (*Equus ferus caballus*), it was high (≥0.80) during both summer and winter, indicating a potential of competition for food. Dietary overlap between species appeared to be based primarily on morphophysiological classification (i.e., browser-intermediate-grazer), rather than body size. Bison, horses, and sheep were all grazers. Intermediate species such as introduced elk (*Cervus canadensis*) had moderate dietary overlap with several species, but did not highly overlap with any other species. We conclude that the potential for competition for food resources between bison and sheep and bison and horses is high, but that for all other species pairs in our study area is low to moderate.

Keywords: bison, competition, deer, diet, elk, exotic species, moose, niche breadth, niche overlap, ungulate, reintroduction, sheep, Yukon

INTRODUCTION

In his seminal paper, Hutchinson (1959) asked why there were so many animals. In the decades since then, understanding the degree of, and mechanisms for, niche separation has been a fundamental pursuit of ecologists. In communities composed of potential competitors, a key prediction is that species need to exhibit niche separation to reduce interspecific competition (Hairston et al. 1960, Sale 1974, Tilman 1987).

Niche dimensions of key interest with respect to interspecific competition being food, habitat, space, and time. In their reviews of studies on a wide range of plant and animal communities, Connell (1983) and Schoener (1983) found evidence of interspecific competition in about half of the studies they examined.

In recent years, several studies have focused on niche separation within ungulate communities (e.g., Sinclair 1985, Singer and Norland 1994, Ihl and Klein 2001, Prins et al. 2006). From a conservation perspective, the introduction of a new species (exotic or reintroduced, intentional or otherwise) to a community raises the spectre of interspecific competition, with concomitant impacts on resident native species. Globally, native ungulates are frequently among the most culturally and socio-economically important wildlife species to local people, and threats to their persistence are often of critical concern. As a result, several studies were prompted by the introduction of livestock (e.g. Hansen and Reid 1975, Olsen and Hansen 1977, Awan et al. 2006, Hong-Jun et al. 2008, Liu and Jiang 2009) or introduced species (e.g. Kirchoff and Larsen 1998, Faas and Weckerly 2010) onto native ungulate ranges. Yet, other studies have investigated the potential impact of interspecific competition on threatened species (e.g. Li et al. 2008, Vila et al. 2009, Namgail et al. 2010). Most of these studies have reported some degree of overlap in diet or habitat among some species pairs within these communities. In some cases, the degree of overlap has been substantial, indicating a potential for interspecific competition and leading to suggested management interventions.

Ungulate communities are not static. Over longer time scales, the abundance and distribution of species change, and the species within a community change. Recently, however, anthropogenic changes to climate and landscapes, as well as management actions, have the potential to dramatically affect ungulate community composition in relatively short timeframes. For example, Laliberte and Ripple (2004) documented significant range contractions ($\geq$20%) in 8 of 12 species of North American ungulates since settlement by Europeans, with the greatest losses coming from areas with the most human influence. Rapid changes in ungulate community composition may have negative impacts on native species, which may be undesirable by local people.

Currently, the ungulate community in southwestern Yukon, Canada, is particularly dynamic. The community is composed of 7 members, of varied histories. Woodland caribou (*Rangifer tarandus caribou*; hereafter, caribou), moose (*Alces americanus gigas*) and thinhorn sheep (*Ovis dalli dalli*; hereafter, sheep) were long-standing members ($\geq$200 years) of the species assemblage. Wood bison (*Bison bison athabascae*; hereafter, bison) were extirpated from the region $\geq$350 years ago, but were reintroduced in 1988–1992 as part of a national recovery program (Government of Yukon 2012). Elk (*Cervus canadensis manitobensis*) were introduced into the study area in the 1950s (population augmentations occurred in the 1990s) with the aim of providing another ungulate species to local area hunters (Strong et al. 2013). Mule deer (*Odocoileus hemionus hemionus*; hereafter deer) have been naturally colonizing the region over the last few decades; but, there were no records of deer prior to the 1940s in the region (Hoefs 2001). Semi-feral horses (*Equus ferus caballus*) have been free-ranging in portions of the study area for probably $\geq$125 years. Thus, 3 species were considered native residents (caribou, moose, and sheep), 2 were introduced (elk and horses), 1 was naturally colonizing (deer) and another was reintroduced (bison).

Populations of some of the "new" species (bison, elk, deer) had been increasing in the past 20 years, while those of resident species (caribou, moose, and sheep) were the focus of substantial population recovery efforts (Hayes et al. 2003). Local populations of bison and caribou were listed as species at risk in Canada's *Species at Risk Act*.

Given this dynamism in the regional ungulate community, local people had become concerned about the potential for interspecific competition among species. Particularly, there was concern that the growing bison and elk populations competed for food with caribou, moose, and sheep. As a result, community-based management plans for elk (Yukon Elk Management Planning Team 2008) and bison (Government of Yukon 2012) in southwestern Yukon, both called for local studies on the diet overlap between these species and resident native ungulates.

Much is already known of the diets of the component species in this ungulate community; however, few studies have examined overlap among the various species pairs in this community. Indeed, community-level analyses of dietary overlap in ungulate assemblages appear to be rare. Notable exceptions include work by Sinclair (1985), Singer and Norland (1994), Mysterud (2000), and Hong-Jun et al. (2008), who took a community-level approach to ungulate dietary overlap in the Serengeti, Yellowstone, Fennoscandia, and the Qinghai-Tibet Plateau, respectively. Most studies contrast diet overlap in a subset of the community (e.g. Li et al. 2008; Namgail et al. 2010). Specific to our study area, Fischer and Gates (2005) previously examined diet overlap between bison and caribou, during winter. They found that winter diet overlap was about 10% and concluded that there was low potential for food competition. Their study, however, did not consider diet overlap during other seasons. Diet overlap between bison and caribou in other seasons, or any other species pairs, in our study area were unknown.

Our aim was to investigate seasonal diets, niche breadth, and dietary overlap within this dynamic ungulate community in order to provide information on the potential for interspecific competition. We used microhistological analyses of fecal material (Sparks and Malechek 1968) to assess broad seasonal diets between species pairs, during 2 seasons (summer and winter) and at 2 elevations (alpine and lowland). These data should be useful in assessing the potential for competition in species pairs and developing appropriate management responses.

Some authors have noted that body mass is a key factor shaping dietary overlap and competition within ungulates (e.g. Gordon and Illius 1989, Mysterud 2000). In our ungulate community, species range in body mass from about 50 to 900 kg, with bison being the largest species, followed by horse, moose, elk, caribou, deer, and sheep. As such, we predicted that, in general, species with similar body masses would have the highest diet overlap values and those with the widest divergence the least. However, we acknowledge that different feeding strategies (grazing, browsing, etc.) would likely be an important mediating factor in determining the amount of diet overlap, as suggested by Hofmann (1989). We also predicted that diet overlap would be greater during winter, when forage availability was likely to be reduced (Jenkins and Wright 1987, Gordon and Illius 1989, Mysterud 2000, Li et al. 2008).

METHODS

Study Area

Our study was conducted in an 8,000 km^2 area that approximated the range of reintroduced wood bison in southwestern Yukon, Canada. The study area was in the Boreal Cordillera Ecozone (Yukon Ecoregions Working Group 2004) east of the village of Haines Junction (60.8°N, 137.5°W). Much of the area is above treeline (approximately ≥1000 m ASL), with several mountain peaks ≥1600 m ASL and extensive alpine plateaus. Alpine areas are bisected by several large lakes, including Aishihik Lake and Taye Lake, and deeply incised river valleys. Lowland areas are largely open canopied forest, dominated by either white spruce (*Picea glauca*) or trembling aspen (*Populus tremuloides*). Small areas of wet sedge meadows and wet shrub meadows occur at low elevations. Remnant boreal grasslands occur as small patches on south-facing slopes, also at low elevations. Climate is cold and semi-arid, with snow cover extending from October to May.

Bison and moose are common and occur throughout the study area, in both alpine and lowland habitats. Caribou and sheep are also common, but patchily distributed throughout the study area, and found predominately in alpine habitats. Horses, deer and elk are restricted to the southern third of the study area and occur in low numbers in lowland habitats only. Mountain goats (*Oreamnos americanus*) also occur in the region, but are rare and none were observed in our study area. White-tailed deer (*Odocoileus virginianus*) are not known from the region, but occur within 400 km (Hoefs 2001) and a few individuals may have ranged into the study area. We did not consider mountain goats or white-tailed deer to be extant in our study area.

Diet Samples

We assumed that forage availability would vary relative to snow cover. To account for seasonal differences in diet we collected fecal samples from ungulates in our study area during 2 broad seasons: summer (15 May – 14 October) and winter (15 October – 14 May), which corresponded to the snow-free and snow-covered season, respectively. Given the mountainous nature of the study area, we also assumed that forage availability would differ by elevation, and that different ungulate communities would occur in the alpine versus lowland areas. To account for elevational differences we collected fecal samples from 2 different elevations: high (≥1000 m ASL) and low (≤1000 m ASL). Thus, our sampling design permitted both seasonal and elevational contrasts.

Ungulate fecal samples were collected during 9 aerial- and 3 ground-based sampling sessions that occurred between January 2009 and September 2010. We distributed our sampling spatially across the study area, and temporally to include 2 summers and 2 winters. For aerial surveys, we located animals from a helicopter and then landed to search for and collect fecal material at the site. For ground-based surveys, we followed rough transects along game trails to search for feces, which were primarily found at low elevations. Ground-based surveys occurred only during the summer and were intended to supplement summer aerial surveys, which were generally less successful in locating some species (e.g., moose) than those in the winter.

At each fecal collection site we subsampled from available deposits to collect a pooled sample of ≥250 g from the site. Ungulates in our study area most often occurred in groups, so our sample was for the group, not a specific individual.

Because most ungulate species in our study area are sexually segregated for much of the year, and this may result in significantly different diets between the sexes (e.g. Post et al. 2001), we focused on maternal female groups rather than mature males, where possible. Only fresh feces (approximately ≤1 month old) were collected. In winter, we collected only feces that were on top of fresh snow. During summer, we determined the freshness of feces based on color, surficial cracking (Hibert et al. 2010), and relative moisture. Our study area was semi-arid and ungulate feces faded, cracked, and desiccated quickly (P. M. Kukka and T. S. Jung, Environment Yukon, unpublished report), making it easy to determine if feces were fresh or old.

Fecal samples ($n = 438$) were stored frozen at -20°C for 1–23 months before processing. We pooled fecal samples from each species collected during each sampling session ($n = 12$) to obtain a composite 30 g fecal sample ($n = 66$). Composite fecal samples were then dried in a forced-air oven at 60ºC for 48 hrs. Microhistological analysis of plant fragments (e.g., Todd and Hansen 1973, Dearden et al. 1975) in the feces was done by experienced analysts at a commercial lab (Wildlife Habitat Nutrition Laboratory, Washington State University, Pullman, WA, USA). Briefly, 4 microscopic slides were made from each composite fecal sample and 25 randomly placed microscopic views were examined, for a total of 100 views per sample. Diets were compiled as percent cover of plant fragments by species or genera at each of the 100 randomly placed microscopic views, using 100x magnification. A list of potential forage species from the study area was used to aid in identification of plant fragments in fecal samples. Composition of each sample was determined at the species or genera level for vascular plants, where possible. No attempt was made to identify lichens and mosses to the species levels. Botanical composition of diets was subsequently combined into 7 major forage classes, including: shrubs, conifer, forbs, sedges and rushes, grasses, lichens, and mosses. Percent diet composition was calculated for each forage class. No correction was made for the differential digestibility of forage species; thus, our compositional analyses are relative to the groups we contrasted.

Data Analyses

To obtain composite diet indices, we calculated Simpson's Diversity Index (1-*D*), Camargo's Evenness Index (E′), and Levin's Niche Breadth Index (*B*) values for each composite fecal sample ($n = 66$). Diet indices were computed using Ecological Methodology (ver. 7.2), which is based on the equations in Krebs (1999).

Our study design allowed us to make statistical comparisons of diet composition based on the following contrasts: a) between species at each elevation (high and low) and season (summer and winter) treatments; b) across seasons for each species at each elevation; and c) between elevations for bison and moose (no other species were found at both elevations). Prior to statistical analyses, data normality was tested with Shapiro-Wilk's test. Most data was not normal, and could not be adequately improved via transformations, so we used non-parametric statistics for all our tests. We compared use of the 7 forage classes and diet indices between species at each elevation and season using Kruskal-Wallis tests, followed by Conover-Inman post hoc pairwise comparisons. Seasonal and elevational effects on the diets of species were determined by Mann-Whitney *U*-tests. Statistical tests were conducted using Systat (ver. 13). We used $P \leq 0.05$ to denote statistical significance.

To determine dietary overlap, we calculated Pianka's, Morisita's, and Horn's overlap indices for each ungulate species pair, using the equations provided in Krebs (1999). We used 3 different overlap indices to better account for differences that may have been related to biases associated with the index chosen (e.g., Wallace and Ramsey 1981, Smith and Zaret 1982, Krebs 1999). For all overlap indices used the computed values range from 0–1, with 0 representing no overlap and 1 indicating complete overlap. Overlap indices were computed using Ecological Methodology (ver. 7.2).

RESULTS

Diet Indices and Key Forage Classes

At high elevations during summer (Table 1) and winter (Table 2), all composite diet indices and use of forage classes differed significantly between bison, moose, caribou, and sheep (Table 1). Caribou had the highest summer diet diversity, evenness, and niche breadth values, followed by sheep, bison, and moose. Shrubs were a key forage resource ($\geq$10% of the diet) for moose and caribou (Table 1). Sedges and rushes were a key summer forage resource for bison, sheep, and caribou. Bison and sheep both used grasses as a key forage resource. Lichens and mosses were a key forage resource only for caribou. No species used conifer or forbs as a key forage resource during summer at high elevations (Table 1). During winter at high elevations, post-hoc pairwise comparisons revealed similar patterns to those observed in summer. Exceptions being that caribou niche breadth and diet diversity and evenness decreased in winter compared to summer, whereas for sheep those values increased (Table 2).

At low elevations during summer, composite diet indices and use of forage classes differed significantly between bison, moose and horses (Table 3). The exception being the use of conifer and mosses, which were not key forage resources for any of these species. Shrubs and forbs were a key forage resource for only moose and horses, respectively. Bison and horses both made extensive use of grasses. Sedges and rushes were a key forage resource for all 3 species at low elevations during summer, particularly bison (Table 3).

During winter at low elevations, almost all composite diet indices and relative use of forage classes differed for bison, moose, horse, deer, and elk (Table 4). Use of mosses and lichens was not statistically different among these 5 species but neither were they a key forage resource for any of the species at low elevations during winter. Sedges and rushes were a key winter forage resource for all low-elevation species except deer. Grasses were a key forage resource for bison, horse, and elk. Conifer was important for deer and elk. Moose, elk, and deer depended on shrubs as a key winter forage resource at low elevations (Table 4).

Seasonal Diets

Key forage resources for bison at both elevations, during both summer and winter, were sedges and rushes (primarily *Carex* spp.) and grasses (primarily *Calamagrotis purpurea*, *Alopecurus alpinus*, and *Poa* spp.; Tables 1 and 2). Bison diet diversity, evenness and niche breadth, however, differed significantly between summer and winter, at both high and low elevations (Table 5). At high elevations, bison diets had significantly fewer sedges and rushes, and correspondingly more shrubs, mosses, and lichens in winter than in summer.

Conversely, at low elevations, bison diets contained significantly more sedges and rushes and less grasses during winter than in the summer (Table 5).

Moose diet did not differ seasonally at low elevations, but did so at high elevations (Table 5). At high elevations, moose fed almost exclusively on shrubs (primarily *Salix* spp., *Populus* spp., and *Betula glandulosa*) in winter but they broadened their summer diet to also include other forage classes. Although their use of other forage classes in summer was significantly different than in winter (Table 5), none of these were considered key forage resources (Table 1).

Key forage resources for caribou included ground-dwelling lichens (*Cladonia* spp., *Cladina* spp., and *Cetraria* spp.), mosses, and sedges and rushes (*Carex* spp.) in both seasons, and shrubs in the summer only (Tables 1 and 2). Caribou diet diversity and niche breadth differed significantly between seasons (Table 5). In winter, caribou relied significantly less on lichens and diversified their diet to include a larger percentage of other forage classes, particularly shrubs and sedges and rushes (Tables 1 and 2).

Sheep diets were relatively diverse in both seasons. Key forage classes used by sheep included sedges and rushes (primarily *Carex* spp.) and grasses (primarily *Poa* spp., *Calamagrostis purpurea*, and *Festuca* spp.) in both seasons, and shrubs (primarily *Artemisia frigida*) in winter. Their diet did not vary significantly between seasons (Table 5). Sheep diets, however, included substantially more shrubs and less sedges and rushes in winter than summer (Tables 1 and 2).

Key forage resources of horses included grasses and sedges and rushes in both seasons, and forbs (primarily *Equisetum* spp.) in the summer (Tables 3 and 4). However, only the difference in the percent of grasses in the diet of horses was significantly different between seasons (Table 5). Horse diets contained about twice as much grass in summer than in winter.

Sufficient diet samples for deer and elk were not available for summer. During winter, deer diets were composed largely of conifer (primarily *Juniperus communis*), with shrubs (*Salix* spp.) and forbs also being key forage resources (Table 4). Elk had relatively diverse winter diets, with their key forage resources being shrubs (primarily *Artemisia* spp. and *Salix* spp.), conifer (*Juniperus communis*), grasses (*Bromus* spp., *Poa* spp., *Festuca* spp., and *Calamagrostis purpurea*) and sedges and rushes.

Elevation Effects

Bison and moose were seasonally found at both high and low elevations, providing an opportunity to examine differences in diet based on elevation. Bison and moose diets generally did not differ during summer according to the elevation that the animals occurred (Table 6). However, for both bison and moose, some differences in diet were noted during winter between high and low elevations. During winter, bison consumed substantially less sedges and rushes and more grasses at high compared to low elevations (Tables 2 and 4). Bison diet diversity, evenness, and niche breadth was significantly greater at high elevations during winter (Table 6). Moose exhibited the opposite trend; their diet was more diverse and niche breadth was greater at low elevations (Table 6). Moose winter diets at high elevations were almost entirely composed of shrubs (Table 2). At low elevations, moose made significantly more use of sedges and rushes (Table 4).

Dietary Overlap

Diversity indices varied between the index used and ungulate species pairs (Table 7). Pianka's and the simplified Morisita's overlap indices produced values that were very similar, whereas Horn's overlap index generally indicated higher overlap than the others. Regardless, for the most part the indices were similar in indicating the relative dietary overlap among species pairs (Table 7). The lowest dietary overlap values were for bison and deer in winter (0.07–0.31), while the highest were for bison and sheep during summer (0.94–0.98).

Most species pairs found at high elevations had relatively high diet overlap during summer; however overlap was generally low ($\leq$0.25) between bison and moose and bison and caribou (Table 7). Bison and sheep had very high overlap values ($\geq$0.80), and bison and caribou, moose and caribou, and caribou and sheep also had high dietary overlap in the summer ($\geq$0.50). Most dietary overlap values for species pairs found at high elevations decreased during the winter (Table 7). Bison and sheep overlap remained very high ($\geq$0.80), however most other species pairs had moderate ($\leq$0.50) or low dietary overlap. Dietary overlap between moose and sheep increased substantially during winter (0.53–0.62).

At low elevations, dietary overlap was generally low to moderate for bison and moose and moose and horses, but very high (0.84–0.92) between bison and horses. During winter, dietary overlap generally increased between species pairs (Table 7). For example, winter diet overlap between bison and moose increased substantially (0.42–0.59). Overlap between bison and horses remained very high (0.97–0.98) and increased during winter. During winter, dietary overlap was generally low for deer and all other species except elk. For most other species pairs at low elevations during winter, dietary overlap was generally moderate ($\leq$ 0.50; Table 7).

DISCUSSION

Effect of Body Size on Dietary Overlap

Seasonal diets, niche breadth, and dietary overlap varied substantially within the ungulate community in southwestern Yukon. Gordon and Illius (1989) suggested that body size was the main predictor of dietary overlap among sympatric ungulates, with species pairs most similar in mass having the highest overlap values. Interestingly, we found that body mass appeared to be a key factor in determining the relative overlap in the diet of species pairs at low elevations, but not for the assemblage found at high elevations. At high elevations, the greatest diet overlap was between bison and sheep, the species pair with the greatest difference in body size. In contrast, the lowest diet overlap was between bison and moose, which were most similar in body mass. Both bison and sheep relied on sedges (*Carex* spp.) and grasses (*Calamagrostis purpurea*) during summer as key forage resources. In Patagonia, Vila et al. (2009) also reported the highest diet overlap values between cattle and domestic sheep, contrary to their predictions based on body mass similarity.

At lower elevations, dietary overlap was very high for bison and horse, the species most similar in body size, and lowest for bison and deer, which had the greatest difference in body size. Both bison and horses are primarily grazers (Hudson and Frank 1987, McInnis and Vavra 1987, Larter and Gates 1991); as such, they made extensive use of grasses and sedges and rushes during winter and summer.

Both species commonly used similar genera of sedges and rushes (*Carex* spp., *Juncus* spp., and *Eriophorum* spp.), but they differed in relation to the grass species used: bison predominately used *Calamagrostis purpurea* and *Poa* spp., whereas horses tended to use those species and also *Elymus trachycaulus*, *Bromus* spp., and *Festuca* spp. Horses broadened their diet in summer to include forbs as a key forage resource. Why body mass correlated with diet overlap at low, but not high, elevations is unknown. We believe that the difference likely was a result of the specific composition of the ungulate assemblages found at those elevations, which differed substantially in our study area. The functional foraging mode (i.e., browser-intermediate-grazer, *sensu* Hofmann 1989) among species at different elevations was independent of body size. At low elevations, the species pair with the most similarity in body size (bison and horses) were both grazers, whereas at high elevations the most similarly-sized species pair consisted of a grazer (bison) and a browser (moose). Bison and sheep, though quite different in body size, are both grazers, which likely explain their high diet overlap at high elevations. Intermediate species (*sensu* Hofmann 1989) included elk, deer, and caribou. None of these intermediate species had high diet overlap with another species; however they had relatively high diet diversity and moderately overlapped with most sympatric species. Our data suggests that diet overlap is primarily influenced by similarity in morphophysiological variations (i.e. functional foraging mode, Hofmann 1989), and secondarily by body size (Gordon and Illius 1989).

Seasonal Changes in Dietary Overlap

Contrary to our prediction that overlap would be greater in winter than summer, diet overlap between most species decreased somewhat in winter at high elevations. During winter, key forage resources for sheep changed, as they relied less on grasses and more on shrubs (*Artemisia frigida*). This change in diet resulted in less dietary overlap between bison and sheep in winter. However, the switch to shrubs in winter by sheep was accompanied by a substantial increase in diet overlap between moose and sheep. In this instance, the 2 species tended to use different species of shrubs, so diet overlap was overrepresented by our analyses at the forage-class level. Whereas sheep made extensive use of *Artemisia frigida* in winter, moose at high elevations used *Salix*, *Populus*, and *Betula glandulosa*. At low elevations, dietary overlap increased between most species pairs, as we had predicted *a priori*.

Dietary Overlap and Potential for Competition

Several authors (e.g., Kingery et al. 1996, Baldi et al. 2004, Vila et al. 2009) have concluded that the potential for competition for food among ungulates was positively correlated with dietary overlap. Overall, few species pairs in our study area had high (>0.80) diet overlap values; most diet overlap values were more moderate (0.40–0.80), and others were low (<0.40). The impetus for our study was to examine the dietary overlap and potential for competition between reintroduced bison and introduced elk on resident native ungulates, as a key action item from their respective Yukon management plans.

To the best of our knowledge, only Fischer and Gates (2005) have studied diet overlap between bison and 1 of our resident ungulate species (caribou), and their study was limited to winter. No studies have examined dietary overlap between bison and moose or sheep, or between bison and caribou during summer.

Singer and Norland (1994), however, examined diets of bison and bighorn sheep (*Ovis canadensis*) in Yellowstone National Park and reported low to moderate (0.31–0.53) dietary overlap. At the forage class scale, our study provided evidence that diets of reintroduced bison overlapped substantially (>0.80) with those of sheep and horses, and moderately so (0.42–0.65) with that of caribou during the summer and moose at low elevations during the winter. Overlap between caribou during winter, moose at high elevations and during the summer at low elevations, and all other species was low. Thus, the highest potential for competition for food by bison was with horses and sheep, which were also grazers (*sensu* Hofmann 1989) and used the same food resources as bison.

Dietary overlap suggested that potential competition between bison and caribou during summer, and moose at low elevations during winter, was moderate. Caribou diet diversity increased during summer, as did that for moose at low elevations during winter. In both instances, caribou and moose seasonally increased their use of sedges and rushes, which contributed to diet overlap with bison. Bison are bulk feeders (Reynolds et al. 1978, Larter and Gates 1991) and consume large quantities of sedges and rushes (primarily *Carex* spp.). Some competition between bison and moose and bison and caribou may seasonally occur, if those forage resources are limited. Unfortunately, we lacked data on forage availability.

Fischer and Gates (2005) studied diet overlap between bison and caribou during winter at our study area and found overlap values around 0.10, indicating low potential for competition. Their data, however, came from bison at low elevations and caribou at high elevations, so the species were spatially segregated. We ensured to contrast bison and caribou diets from the same elevation (high), but came to the same general conclusion of Fischer and Gates (2005) that diet overlap and the potential for competition between these species was low during winter.

We also provided evidence that the diverse winter diet of introduced elk moderately overlapped (0.44–0.72) with all other ungulates found at low elevations in our study area (bison, moose, horse, and deer). As intermediate foragers, the diet of elk was diverse, which likely contributed to the moderate overlap with all other ungulates at low elevations in our study area. Moose were the only resident native ungulate at low elevations, and of the most management interest. While several studies have examined diet overlap between elk and sympatric ungulates (e.g. Hansen and Reid 1975, Singer and Norland 1994, Kingery et al. 1996), to the best of our knowledge none have looked at similarities between elk and moose diets. Despite having a moderate diet overlap during winter, key forage resources varied substantially between elk and moose. During winter, elk used grasses, shrubs, sedges and rushes, and conifer as key forage resources, whereas moose used shrubs and sedges and rushes. While shrubs were important for both species at the forage class level, elk largely consumed *Artemisia frigida*, while moose mostly used *Salix* spp., *Betula glandulosa*, *Populus* spp., and *Alnus incana*. Thus, our dietary overlap values may over represent the potential for competition between elk and moose at lower elevations, during winter. Diet overlap between elk and horse, bison and deer was also moderate, similar to that reported in other studies (e.g. Hansen and Reid 1975, Olsen and Hansen 1977, Singer and Norland 1994, Kirchoff and Larsen 1998), indicating some potential for competition.

Information on dietary overlap can give an important indication of the potential for competition between species (e.g. Kirchoff and Larsen 1998, Baldi et al. 2004; Spitz et al. 2006, Hong-Jun et al. 2008, Li et al. 2008). However, dietary overlap alone is an insufficient measure for interspecific competition. For competition between species to occur, species must also overlap in habitat use and forage resources must be limited (de Boer and Prins 1990).

Some data on habitat overlap exist for our study area and it appears that bison, moose, caribou, and sheep, have low habitat overlap values (see Appendix B, Appendix C]). Moreover, limited data suggests that spatial overlap during late-winter for select species pairs in our community is also low, with only bison and sheep having a somewhat high degree of co-occurrence (see Appendix D). Most importantly, forage resources for most species are likely not limited in our study area. While we lack data on forage availability, ungulate densities are low and much of the study area likely maintains relatively high abundance of forage for species. Thus, while diet overlap may be substantial between bison and horse and bison and sheep, the actual potential for competition may be markedly lower, due to low habitat overlap and apparently abundant forage.

The only exception to our general conclusion may be the Takhini Valley, a small part of the study area that is largely aspen parkland and remnant grassland, and the core range for elk and horses in the study area. Strong et al. (2013) reported that forage resources in the Takhini Valley were limited and provided poor range for elk. In the Takhini Valley, where diet overlap between elk and other ungulates is moderate, the potential for competition may be higher than elsewhere in the study area because animal densities, and habitat and spatial overlap are somewhat higher, and forage availability is low.

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Table 1. Means and SE of percent diet composition of 7 broad forage classes and composite diet indices for an ungulate community occurring at high elevation (≥1000 m ASL) sites during summer (15 May – 14 October) in southwestern Yukon, Canada.

Forage Classes / Indices	Bison (*n* = 4)		Moose (*n* = 4)		Caribou (*n* = 4)		Sheep (*n* = 4)		Test Statistic [2]	
	x [1]	SE	x	SE	x	SE	x	SE	*H*	*P*
Forage Classes (%)										
Shrubs	5.2^A	1.5	91.2^B	3.5	23.3^C	6.9	9.1^A	2.6	11.681	0.009
Conifer	0	0	0	0	0	0	0	0	-	-
Forbs	2.1^A	0.3	0.8^A	0.3	4.5^A	1.3	6.1^A	1.9	11.554	0.009
Sedges and Rushes	61.0^A	2.0	3.8^B	1.0	22.7^C	4.8	47.0^D	8.6	12.640	0.005
Grasses	30.2^A	2.0	1.7^B	1.1	7.2^C	1.7	24.6^A	3.0	12.946	0.005
Lichens	0.1^A	0.1	2.4^A	1.4	30.5^B	9.5	6.4^A	2.1	11.750	0.008
Mosses	1.4^A	0.5	0.3^A	0.1	11.8^B	2.8	6.8^A	2.2	13.111	0.004
Indices										
Simpson's Diversity (1-*D*)	0.530^A	0.013	0.163^B	0.060	0.729^C	0.041	0.667^{AC}	0.072	11.404	0.010
Camargo's Evenness (*E'*)	0.293^A	0.006	0.191^B	0.023	0.533^C	0.052	0.469^{AC}	0.070	12.066	0.007
Levin's Niche Breadth (*B*)	0.200^A	0.018	0.036^B	0.015	0.487^C	0.089	0.397^{AC}	0.101	11.400	0.010

[1] Means in the same row followed by the same letter do not differ ($P \geq 0.05$), based on Conover-Inman post-hoc pairwise comparisons.
[2] Kruskal-Wallis test, all with 3 df.

Table 2. Means and SE of percent diet composition of 7 broad forage classes and composite diet indices for an ungulate community occurring at high elevation (≥1000 m ASL) sites during winter (15 October – 14 May) in southwestern Yukon, Canada.

Forage Classes / Indices	Bison (*n* = 4)		Moose (*n* = 4)		Caribou (*n* = 5)		Sheep (*n* = 3)		Test Statistic [2]	
	x [1]	SE	x	SE	x	SE	x	SE	*H*	*P*
Forage Classes (%)										
Shrubs	9.0^A	1.7	99.8^B	0.2	8.0^A	1.1	31.1^C	20.0	10.550	0.014
Conifer	0	0	0	0	0	0	0	0	-	-
Forbs	2.1^A	0.3	0^A	0	9.6^B	2.3	6.7^C	3.3	11.414	0.010
Sedges and Rushes	53.3^A	1.5	0.2^B	0.2	10.2^C	4.2	25.7^D	13.3	12.929	0.005
Grasses	30.7^A	2.5	0^B	0	2.8^B	0.7	27.8^A	2.8	13.534	0.004
Lichens	1.8^A	0.8	0^A	0	55.5^B	4.0	1.6^A	1.6	11.951	0.008
Mosses	3.1^A	1.0	0^A	0	13.8^B	2.4	7.2^C	6.9	10.648	0.014
Indices										
Simpson's Diversity (1-*D*)	0.608^A	0.014	0.013^B	0.001	0.627^A	0.030	0.622^A	0.108	8.695	0.034
Camargo's Evenness (*E*)	0.355^A	0.013	0.148^B	0.001	0.418^A	0.022	0.411^A	0.113	10.224	0.017
Levin's Niche Breadth (*B*)	0.260^A	0.014	0.002^B	0.001	0.294^A	0.042	0.356^A	0.152	8.956	0.033

[1] Means in the same row followed by the same letter do not differ ($P \geq 0.05$), based on Conover-Inman post-hoc pairwise comparisons.
[2] Kruskal-Wallis test, all with 3 df.

Table 3. Means and SE of percent diet composition of 7 broad forage classes and composite diet indices for an ungulate community occurring at low elevation (≤1000 m ASL) sites during summer (15 May – 14 October) in southwestern Yukon, Canada.

Forage Classes / Indices	Bison (*n* = 4)		Moose (*n* = 4)		Horse (*n* = 4)		Test Statistic[2]	
	x[1]	SE	x	SE	x	SE	*H*	*P*
Forage Classes (%)								
Shrubs	6.3 ^{A}	2.3	83.1 ^{B}	6.1	5.7 ^{A}	2.1	7.774	0.021
Conifer	0 ^{A}	0	0.2 ^{A}	0.2	0 ^{A}	0	2.250	0.325
Forbs	3.7 ^{A}	0.6	0.2 ^{B}	0.1	16.4 ^{C}	4.8	10.711	0.005
Sedges and Rushes	55.9 ^{A}	5.4	11.6 ^{B}	4.9	26.8 ^{C}	7.7	7.503	0.023
Grasses	32.9 ^{A}	3.4	3.7 ^{B}	1.6	50.5 ^{C}	5.7	9.613	0.008
Lichens	0.1 ^{A}	0.1	1.0 ^{B}	0.3	0 ^{A}	0	9.994	0.007
Mosses	1.1 ^{A}	0.6	0.3 ^{A}	0.2	0.6 ^{A}	0.4	1.068	0.586
Indices								
Simpson's Diversity (1-*D*)	0.560 ^{A}	0.044	0.276 ^{B}	0.090	0.596 ^{A}	0.026	7.045	0.030
Camargo's Evenness (*E*)	0.319 ^{A}	0.027	0.211 ^{B}	0.025	0.342 ^{A}	0.020	6.277	0.044
Levin's Niche Breadth (*B*)	0.223 ^{A}	0.035	0.074 ^{B}	0.029	0.252 ^{A}	0.025	7.026	0.030

[1] Means in the same row followed by the same letter do not differ ($P \geq 0.05$), based on Conover-Inman post-hoc pairwise comparisons.

[2] Kruskal-Wallis test, all with 2 df.

Table 4. Means and SE of percent diet composition of 7 broad forage classes and composite diet indices for an ungulate community occurring at low elevation (≤1000 m ASL) sites during winter (14 October – 15 May) in southwestern Yukon, Canada.

Forage Classes / Indices	Bison (*n* = 4)		Moose (*n* = 4)		Horse (*n* = 4)		Deer (*n* = 4)		Elk (*n* = 4)		Test Statistic[2]	
	x[1]	SE	x	SE	x	SE	x	SE	x	SE	*H*	*P*
Forage Classes (%)												
Shrubs	3.4 ^{A}	2.0	66.8 ^{B}	18.7	1.5 ^{A}	0.8	11.0 ^{C}	2.6	26.1 ^{D}	2.3	16.766	0.002
Conifer	0 ^{A}	0	1.8 ^{A}	1.5	0 ^{A}	0	65.7 ^{B}	13.6	14.4 ^{C}	6.4	17.667	0.001
Forbs	1.9 ^{A}	0.7	0 ^{A}	0	8.2 ^{B}	6.5	10.0 ^{B}	6.2	5.8 ^{B}	1.9	8.534	0.074
Sedges and Rushes	75.6 ^{A}	2.7	27.6 ^{B}	16.7	62.6 ^{A}	3.6	2.6 ^{C}	0.9	15.7 $_{B,C}$	10.3	14.790	0.005
Grasses	16.4 ^{A}	2.3	2.6 ^{B}	2.2	26.2 ^{C}	5.6	8.3 ^{A,B}	4.7	37.4 ^{C}	9.5	13.611	0.009
Lichens	0.4 ^{A}	0.2	1.3 ^{A}	1.0	0 ^{A}	0	1.3 ^{A}	0.8	0.2 ^{A}	0.1	3.713	0.446
Mosses	2.5 ^{A}	1.1	0 ^{A}	0	1.6 ^{A}	0.8	1.1 ^{A}	0.9	0.4 ^{A}	0.3	6.688	0.153
Indices												
Simpson's Diversity (1-*D*)	0.395 ^{A}	0.037	0.287 ^{A}	0.127	0.507 ^{B}	0.039	0.437 ^{AB}	0.109	0.670 ^{B}	0.025	8.681	0.047
Camargo's Evenness (*E*)	0.249 ^{A}	0.016	0.220 ^{A}	0.038	0.281 ^{B}	0.025	0.325 ^{AB}	0.069	0.417 ^{B}	0.030	8.631	0.041
Levin's Niche Breadth (*B*)	0.112 ^{A}	0.016	0.091 ^{A}	0.045	0.179 ^{AB}	0.031	0.202 ^{AB}	0.099	0.348 ^{B}	0.041	8.611	0.040

[1] Means in the same row followed by the same letter do not differ ($P \geq 0.05$), based on Conover-Inman post-hoc pairwise comparisons.
[2] Kruskal-Wallis test, all with 4 df.

Table 5. Test statistics for comparisons of forage classes and composite diet indices between seasons (summer and winter) for an ungulate community in southwestern Yukon, Canada. All Mann-Whitney U-tests are with 1 df. P-values ≤0.05 are in bold. Means ± SE are provided in Tables 1–4.

Forage Classes / Indices	Bison (*High*) [1]		Bison (*Low*)		Moose (*High*)		Moose (*Low*)		Caribou (*High*)		Sheep (*High*)		Horse (*Low*)	
	U	*P*	*U*	*P*	*U*	*P*	*U*	*P*	*U*	*P*	*U*	*P*	*U*	*P*
Forage Classes														
Shrubs	3.0	0.149	11.5	0.309	0.5	**0.018**	9.0	0.773	18.0	**0.050**	2.0	0.157	15.0	0.221
Conifer	-	-	-	-	-	-	5.0	0.321	-	-	-	-	-	-
Forbs	7.5	0.883	13.0	0.149	14.0	**0.046**	12.0	0.131	3.0	0.085	-	-	16.0	0.140
Sedges and Rushes	15.0	**0.043**	1.0	**0.043**	16.0	**0.018**	7.0	0.767	17.0	0.086	9.0	0.289	16.0	0.140
Grasses	8.0	1.000	16.0	**0.021**	14.0	**0.047**	10.0	0.561	18.0	**0.050**	4.5	0.593	19.0	0.027
Lichens	2.5	0.091	3.5	0.180	12.0	0.131	10.0	0.561	2.0	**0.050**	10.0	0.154	-	-
Mosses	3.0	0.149	4.5	0.309	12.0	0.127	12.0	0.131	7.5	0.537	8.0	0.480	6.0	0.319
Indices														
Simpson's Diversity (1-*D*)	0.5	**0.021**	15.0	**0.043**	16.0	**0.018**	7.0	0.773	18.0	**0.050**	7.0	0.724	16.0	0.140
Camargo's Evenness (*E'*)	0.5	**0.021**	14.0	0.083	16.0	**0.018**	7.0	0.773	17.5	0.065	8.0	0.480	16.0	0.140
Levin's Niche Breadth (*B*)	1.0	**0.043**	15.0	**0.043**	16.0	**0.018**	7.0	0.773	18.0	**0.050**	7.0	0.724	16.0	0.140

[1] "high" and "low" refer to the elevational treatment from which the tests were made. See Tables 1–4.

Table 6. Test statistics for comparisons of forage classes and composite diet indices between high (≥1000 m ASL) and low (≤1000 m ASL) elevations during summer and winter for bison and moose in southwestern Yukon, Canada. All Mann-Whitney U-tests are with 1 df. P-values ≤0.05 are in bold. Means ± SE are provided in Tables 1–4.

Forage Classes / Indices	Bison				Moose			
	Summer		Winter		Summer		Winter	
	U	*P*	*U*	*P*	*U*	*P*	*U*	*P*
Forage Classes								
Shrubs	8.0	1.000	14.0	0.083	11.5	0.309	15.0	0.038
Conifer	8.0	1.000	8.0	1.000	6.0	0.317	4.0	0.131
Forbs	2.0	0.083	7.5	0.885	13.0	0.137	8.0	1.000
Sedges and Rushes	11.0	0.386	16.0	**0.021**	4.0	0.248	2.0	**0.046**
Grasses	6.0	0.561	16.0	**0.021**	5.0	0.386	5.0	0.321
Lichens	6.5	0.617	12.5	0.191	8.0	1.000	4.0	0.131
Mosses	10.0	0.564	9.5	0.663	7.0	0.752	8.0	1.000
Indices								
Simpson's Diversity (1-*D*)	5.0	0.385	16.0	**0.021**	4.5	0.309	1.0	**0.038**
Camargo's Evenness (*E'*)	4.5	0.309	16.0	**0.021**	5.5	0.468	4.0	0.237
Levin's Niche Breadth (*B*)	6.0	0.564	16.0	**0.021**	4.5	0.309	1.0	**0.038**

Table 7. Dietary overlap index values for ungulate species pairs at high (≥1000 m ASL) and low (≤1000 m ASL) elevations during summer and winter in southwestern Yukon, Canada. Particularly high overlap values (≥0.80) are in bold. Index values range from 0–1, with 0 indicating no overlap and 1 representing complete overlap.

Elevation	Season	Species Pair	Pianka's Overlap Index	Morisita's Overlap Index	Horn's Overlap Index
High	Summer	Bison & Moose	0.12	0.12	0.32
		Bison & Caribou	0.55	0.51	0.65
		Bison & Sheep	**0.98**	**0.96**	**0.94**
		Moose & Caribou	0.54	0.44	0.62
		Moose & Sheep	0.21	0.19	0.43
		Caribou & Sheep	0.68	0.67	0.74
High	Winter	Bison & Moose	0.15	0.13	0.23
		Bison & Caribou	0.23	0.23	0.51
		Bison & Sheep	**0.82**	**0.80**	**0.90**
		Moose & Caribou	0.14	0.12	0.21
		Moose & Sheep	0.62	0.60	0.53
		Caribou & Sheep	0.28	0.28	0.60
Low	Summer	Bison & Moose	0.24	0.23	0.49
		Bison & Horse	**0.84**	**0.83**	**0.92**
		Moose & Horse	0.19	0.18	0.41
Low	Winter	Bison & Moose	0.42	0.42	0.59
		Bison & Horse	**0.98**	**0.97**	**0.97**
		Bison & Deer	0.08	0.07	0.31
		Bison & Elk	0.48	0.44	0.66
		Moose & Horse	0.38	0.38	0.52
		Moose & Deer	0.19	0.19	0.41
		Moose & Elk	0.63	0.59	0.72
		Horse & Deer	0.10	0.10	0.35
		Horse & Elk	0.59	0.57	0.71
		Deer & Elk	0.48	0.46	0.73

Appendix B:

Habitat Niche Breadth and Overlap between Reintroduced Wood Bison and Resident Woodland Caribou and Thinhorn Sheep in Northwestern Canada

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ABSTRACT: Wood Bison (*Bison bison athabascae*) were reintroduced to southwestern Yukon, Canada, in 1988–1992 as part of a national program to recovery the subspecies on its native range. The return of bison to the landscape, however, was a concern for local people because of the potential for competition between bison and culturally and economically important species such as woodland caribou (*Rangifer tarandus caribou*) and thinhorn sheep (*Ovis dalli dalli*). We used available geospatial data for bison, caribou, and sheep to conduct an ecological niche factor analysis (ENFA) for these species and determine seasonal habitat niche breadth and overlap through a subsequent discriminant analysis. For all 5 seasons examined, a general pattern emerged with sheep having the most restrictive niche, based on marginality scores (0.745–0.908), followed by caribou (0.517–1.321) and bison (0.461–0.792), indicating that sheep were most selective of habitat compared to caribou and bison. Consequently, sheep had the narrowest niche breadth. For bison and caribou, niche breadth varied seasonally, being wider in the winter than in other seasons. Habitat niche overlap was low for bison and caribou and bison and sheep, suggesting limited potential for competition for habitat. Our results are not surprising, given that bison were once a numerically dominant species in the region and likely co-evolved with caribou and sheep to partition resources and co-exist.

Keywords: *Bison bison*, ecological niche factor analysis, habitat use, interspecific competition, niche overlap, *Ovis dalli*, *Rangifer tarandus*, reintroduction, Yukon

INTRODUCTION

Species with similar ecological niches may compete for scarce resources, including food and habitat. For similar species to co-exist on a shared landscape they need to partition these resources in order to avoid interspecific competition (Sale 1974). Species that have been sympatric for sufficient time have likely co-evolved mechanisms to reduce interspecific competition and co-exist (Connell 1980). However, when new species are introduced into an extant species assemblage they may compete with resident species that share similar ecological niches.

With respect to ungulates, for example, much attention has been spent on examining potential niche overlap within communities (e.g., Jenkins and Wright 1988, Harris and Miller 1995, Redfern et al. 2006), and its concomitant impact on species (e.g. Forsyth and Hickling 1998). In particular, the introduction of new species to native ungulate ranges has been a long-standing concern to land and wildlife managers (e.g., Hansen and Reid 1975, Liu and Jiang 2009, Darmon et al. 2012). Much of the concern has focused on the potential for competition between native and non-native ungulate species (e.g., livestock such as cattle and domestic sheep), with the possibility of population declines of native species that are outcompeted by the non-natives (e.g. Voeten and Prins 1999, Baldi et al. 2004, Desbiewz et al. 2009).

By the turn of the 19th century, wood bison (*Bison bison athabascae*; hereafter, bison) in northwestern North America were on the brink of extinction, with population declines largely attributed to excessive hunting and habitat loss (Soper 1941, Sanderson et al. 2008). Extensive recovery efforts ensued in western Canada, beginning in the late 1950s, and in 1980 a program was initiated to re-establish bison in southwestern Yukon, Canada (Government of Yukon 2012). Subsequently, the bison population in southwestern Yukon grew rapidly post-reintroduction (*sensu* Larter et al. 2000; T. S. Jung, Environment Yukon, unpublished data), and produced unexpected management challenges. Despite formerly being indigenous to the region, local people had substantial concern over potential competition between reintroduced bison and resident ungulates, which they depended on culturally and economically. Consequently, a key management action arising from a community-based management plan for bison in the region was to better understand the potential impact of the bison reintroduction project on resident ungulates (Government of Yukon 2012).

Fischer and Gates (2005) studied resource partitioning between bison and woodland caribou (*Rangifer tarandus caribou*; hereafter, caribou) along several niche axes. They concluded that there was little potential for competition between bison and caribou; however their study was conducted only during winter, and at a time when these species were largely segregated by elevation. Since the work of Fischer and Gates (2005), bison in southwestern Yukon have seasonally shifted their distribution to include alpine sites (Environment Yukon, unpublished data), where they may be competing for food and habitat with alpine-dwelling species, such as caribou and thinhorn sheep (*Ovis dalli dalli*; hereafter sheep). Moreover, the bison population has more than doubled since the earlier study (Environment Yukon, unpublished data) and potentially limiting processes such as interference competition and exploitative competition (Birch 1957) may be density-dependent (e.g., Larter and Nagy 1997). Jung et al. (see Appendix A) studied the dietary overlap between bison and resident ungulates and found low diet overlap between bison and caribou and high diet overlap between bison and sheep, during both summer and winter. Thus, the question of the potential for competition between reintroduced bison and sympatric alpine-dwelling species remains only partially answered.

In this paper, we extend the work of Fischer and Gates (2005) and Jung et al. (see Appendix A) on the impact of reintroduced bison on resident caribou and sheep by examining the potential for competition along the niche dimension of habitat. We used available animal location data to examine habitat use, niche breadth, and overlap between bison and caribou and bison and sheep in southwestern Yukon, Canada. Our primary analysis procedure was an ecological niche factor analysis (ENFA), which requires the use of presence data only and avoids some of the pitfalls of presence/absence analyses (Hirzel et al. 2002).

ENFA has been used to conduct habitat suitability analyses for a variety of species, including several ungulates (e.g., Traill and Bigalke 2006; Acevedo et al. 2007*a*, Acevedo et al. 2007*b*; Acevedo and Cassinello 2009; Hansen et al. 2009; Singh et al. 2010; Arshad et al. 2012).

Bison were once a numerically-dominant member of the large mammal fauna of the region (Guthrie 1968). As such, we predicted that bison, caribou, and sheep would have co-evolved mechanisms (*sensu* Tilman 1987) to partition resources and minimize competition for habitat, allowing them to co-exist. Thus, we predicted that these species would use different habitats and that the potential for exploitive competition for habitat between species would be low.

METHODS

Study Area

Our study was conducted in a 19,710 km^2 area that approximated the range of the reintroduced Aishihik population (herd) of wood bison and the Aishihik population of woodland caribou in southwestern Yukon, Canada (see: Hayes et al. 2003, Hegel et al. 2012). The study area was in the Boreal Cordillera Ecozone (Yukon Ecoregions Working Group 2004), east of the village of Haines Junction (60.8°N, 137.5°W). Elevation ranges from 502–2345 meters above sea level (ASL). Much of the area is above treeline (approximately ≥1000 m ASL), with several mountain peaks ≥1600 m ASL and extensive alpine plateaus. Alpine areas are bisected by several large lakes, including Aishihik Lake and Taye Lake, and deeply incised river valleys. Vegetation at lower elevations and valley bottoms include open canopy black spruce (*Picea mariana*), white spruce (*P. glauca*) and trembling aspen (*Populus tremuloides*) forest, and dwarf willow (*Salix* spp.) and dwarf birch (*Betula nana*) shrublands, interspersed with mesic sedge (*Carex* spp.) meadows. Remnant boreal grasslands occur as small patches on south-facing slopes, also at low elevations. Alpine plant communities are dominated by willow and dwarf birch, graminoid species, and mosses (*Sphagnum* spp.). Climate is cold and semi-arid, with snow cover extending from early-October to mid-May.

Bison are common in both alpine and lowland habitats, and occur predominately in the eastern part of the study area (Figure 1). Caribou and sheep are also common, but patchily distributed, and found predominately in alpine habitats. Caribou occur largely in the western portion of the study area (Figure 1, Fischer and Gates 2005). Bison, caribou and sheep occur at low densities; however populations of bison and caribou were increasing during our study (Hegel et al. 2012). Current abundance trends for sheep is unknown, but presumed stable. Other larger mammals in the study area included moose (*Alces americanus*), mountain goats (*Oreamnos americanus*), mule deer (*Odocoileus virginianus*), elk (*Cervus canadensis*), semi-feral horses (*Equus ferus caballus*), wolves (*Canis lupus*), coyotes (*Canis latrans*), lynx (*Lynx canadensis*), wolverine (*Gulo gulo*), grizzly bears (*Ursus arctos*) and black bears (*Ursus americanus*; Hayes et al. 2003, Appendix A).

Ungulate Data

Our ENFA modeling procedures required spatial data of animal locations, which we obtained from available sources. Briefly, spatial data for bison ($n = 2951$ geo-referenced locations) were obtained from global position system (GPS) collars (Lotek Engineering Ltd., Newmarket, Ontario) affixed to 12 adult bison during 2005–2007 (Environment Yukon, unpublished data). GPS collars collected a daily location for each bison, which was stored on a memory chip within the collars and subsequently downloaded upon retrieval of the collars (T. S. Jung and K. Kuba, Environment Yukon, unpublished report). Caribou spatial data ($n = 1961$ geo-referenced locations) was collected from caribou surveys and relocations of 53 adult caribou equipped with very high frequency (VHF) collars (Telonics, Mesa, Arizona) during 1997-2007 (Hayes et al. 2003; Environment Yukon, unpublished data; Figure 1). Radio-collared caribou were located during 41 aerial surveys, conducted from a small fixed-wing aircraft to obtain geo-referenced locations. We considered groups of animals a single location. Spatial accuracy of GPS and VHF collar locations were estimated at ≤30 m and ≤100 m for bison and caribou, respectively. For sheep, the best available information was spatially distinct polygons depicting known seasonal ranges from the Yukon Department of Environment's Wildlife Key Areas database, which is based on aerial surveys of sheep distribution and abundance (Hayes et al. 2003; T. M. Hegel, Environment Yukon, unpublished data; Figure 1).

Ecogeographical Variables (EGVs)

The study area was delineated by creating a rectangle encompassing all bison locations. Ecogeographical variables of interest were mapped within a GIS (Table 1) and made overlayable (identical in extent and cell size) to use in an ENFA implemented in Biomapper (ver 4.0). Vegetation maps were generated from Earth Observation for Sustainable Development of Forests (EOSD) base layers, which were based on LandSat-7 Enhanced Thematic Mapper Plus (ETM+) images, circa 2000 (Wulder et al. 2008). For maps to be compatible with the Biomapper 4.0, they must be continuous or frequency rasters. Therefore, habitat types of interest were extracted to create binary rasters for each habitat type. Vegetation types considered in the analysis included the percent of shrub, wetland, herbs (i.e., vascular plants such as grasses and forbs), and conifer and deciduous forest cover. A moving window analysis was used at the 100 m and 1 km radius scales to produce rasters where each pixel represents the percent of the habitat type of interest within the specified buffer. Therefore, 10 individual habitat maps were generated for preliminary analysis (Table 1). In addition, map layers depicting the distance to water sources were generated at the large (1:250,000) and small (1:50,000) scales by extracting river and lake layers from digitized topographic NTS (National Topographic Series) maps. Maps were rasterized to 25 m x 25 m pixels to match the pixel size of EOSD maps and the Euclidean distance from each cell to the nearest water source was calculated. Digital Elevation Maps (DEMs; geogratis.com) were merged and resampled (from 30 m x 30 m to 25 m x 25 m) also to match other EGV maps. This layer was used to generate a terrain ruggedness map using a vector ruggedness measure that quantifies local variation in terrain, as per Sappington et al. (2007).

Ecological Niche Factor Analysis

We used ecological niche factor analysis (ENFA) and discriminant analysis (DA) to quantify and compare the seasonal habitat use of bison with that of caribou and sheep. This analysis is based on the concept of ecological niche and implemented in Biomapper (ver. 4.0) (Hirzel et al. 2002, Hirzel et al. 2006; Hirzel and Le Lay 2008). One of the main advantages of this approach is that it does not require any information on absences. ENFA is an approach that requires only presence data for model paramatization (Hirzel et al. 2002), which was critical for comparing niches of species for which data sources are disparate. ENFA is based on ordination of data and estimates suitability functions by comparing the distribution of species in predetermined EGVs.

ENFA is based on the computation of marginality (M) and specialization (S) factors that explain the realized niche of a species within the available niche space (Hirzel et al. 2002, Hirzel et al. 2006). These factors are uncorrelated and have biological significance. The marginality factor (the first factor), the absolute difference between the global mean and species mean divided by 1.96 standard deviations, describes how far the species optimum is from the mean global distribution of EGV describing the study area (Hirzel et al. 2002). M close to 1 indicates that the species habitat differs from the mean conditions in the study area. The specialization factors, the ratio of the standard deviation of the global distribution to that of the focal species, describe how specialized the species is with regard to the available covariates in the study area (Hirzel et al. 2002, Hirzel et al. 2006). When S is greater than 1 it indicates that there is some degree of specialization.

Biomapper requires that species information be provided in binary raster format so that it is compatible with EGV maps. Bison and caribou locations were thus converted into 25 m x 25m rasters where a pixel was either occupied (1) or not (0) by the species. Seasonal sheep polygons were similarly converted to rasters and all pixels overlapping range polygons were considered occupied.

The median algorithm based on the first factors obtained in the ENFA was used to calculate habitat suitability maps. The number of factors included was based on a comparison of the factors' eigenvalues using MacArthur's broken-stick distribution (Hirzel et al. 2002, Hirzel et al. 2006). Overall habitat suitability for each cell is calculated by combing the score for each factor. Overall habitat suitability varied from 0 (least suitable) to 100 (most suitable) and indicated how the EGV of each cell suited the niche requirements of the focal species.

Niche Differentiation

We used discriminant analysis to compare the ecological niches of bison with caribou and sheep. This technique is a multivariate analysis that computes factors that maximize the interspecific variance and minimize the intraspecific variance. In Biomapper, these discriminant factors are used to compute indices quantifying niches breadth and overlap. We used the Hurlbert index (B') to measure niche breadth (Hurlbert 1978). B' may range from 0 (corresponding to specialized species) to 1 (corresponding to generalist species). Lloyd's asymmetric overlap index (Z) was computed on the discriminant factor and used to assess how much the niches of the species overlapped (Sattler et al. 2007, Praca and Gannier 2008). Larger Z values, and smaller associated reciprocals, signify greater niche overlap (Hulbert 1978).

RESULTS

Ecological Niche Factor Analysis

Spring. – All species used habitats different from the mean available in the study area. Based on marginality values, sheep had the most restrictive spring habitat niche ($M = 0.908$) followed by caribou ($M = 0.859$) and bison ($M = 0.700$; Table 2). Bison had the highest specialization value ($S = 2.680$) probably because the marginality and specialization factorial axes indicated a strong relationship with valley bottoms (Elevation coefficient F1 = -0.55 and F2 = 0.94; Table 3).

Bison were also associated with avoidance of shrub areas (-0.42), proximity to water (-0.41), and selection for meadows (0.39). Caribou and sheep had similar specialization values (1.633 and 1.575, respectively) and showed selection for high elevation (0.66 and 0.71, respectively) and alpine meadows (0.59 and 0.53, respectively). However, the marginality factor for sheep accounted for 43% of the total specialization whereas the caribou marginality factor was only 16% suggesting that sheep display a more restricted range on those conditions for which they mostly differ from the mean conditions in our study area.

Summer. – Caribou were more specific than bison in terms of how specialized they were on the landscape based on their global marginality (1.321 and 0.516, respectively) and specialization (3.810 and 1.280, respectively) factors. Marginality coefficients in summer showed that caribou are linked to high elevation (0.65) and meadow habitat (0.62; Table 3). In particular, the specialization axis highlights a strong relationship of caribou with higher elevations (0.95) with 79% of the total specialization accounted for by the marginality factor. In summer, bison were most associated with avoidance of shrub habitat based on the marginality (-0.56) and specialization (0.92) axes. Elevation was not an important covariate in summer (-0.15) and the marginality factor only accounted for 16% of the total specialization meaning that bison niche is quite wide. The bison marginality factorial axis indicated a strong relationship with proximity to water bodies (-0.50), meadows (0.37) and conifer habitat (0.34). No sheep data was available for the summer season.

Fall. – Based on global marginality values, caribou had the most restrictive niche ($M = 1.036$) followed by sheep ($M = 0.846$) and then bison ($M = 0.792$; Table 2). Bison marginality factor accounted for only 11% of the total specialization meaning that they have quite a wide range on those conditions that differ from the mean conditions of the study area (Table 3). Marginality coefficients showed that, in fall, bison are linked to low elevation (-0.62), conifer forests (0.44), proximity to water (-0.41) and avoidance of shrub habitats (-0.40). Caribou and sheep marginality coefficients were similar in importance and direction. For caribou and sheep, both species selected for higher elevation (0.63 and 0.71, respectively) and meadow habitat (0.62 and 0.51, respectively), and avoided spruce habitats (-0.43 and -0.43, respectively). However, the caribou marginality factor (47%) accounted for more of the total specialization than the sheep marginality factor (27%) suggesting that caribou had a more restricted range on these coefficients.

Early-winter. – Based on global marginality values, sheep had the most restrictive niche ($M = 0.745$), followed by bison ($M = 0.632$) and then caribou ($M = 0.591$; Table 2). The bison marginality factor accounted for more specialization (40%) than the caribou (18%) or sheep (27%) marginality factors indicating that bison displayed a more restrictive range than the other species on those conditions for which they differed compared to the mean of the study area (Table 3).

Specifically, bison were associated with proximity to water (-0.63), lower elevations (-0.49), avoidance of deciduous (-0.33) and shrub (-0.30) habitat, and selection for conifer habitat (0.29) in rugged terrain (0.27). Caribou and sheep were relatively similar in their most important marginality covariates and selected for high elevations (0.47 and 0.64, respectively), meadows (0.60 and 0.52, respectively), and avoided conifer habitats (-0.52 and -0.45, respectively). The main difference in their early-winter habitat associations was that the caribou marginality axis showed an association with shrub habitat (0.29) whereas no such association was detected in sheep (0.08; Table 3).

Late-winter. –Based on global marginality values, sheep had a more restrictive niche ($M = 0.745$) than either caribou ($M = 0.517$) or bison ($M = 461$; Table 2). Bison were associated with proximity to water (-0.69), lower elevations (-0.52), and avoidance of deciduous habitat (-0.39; Table 3). Caribou and sheep marginality coefficients showed that they were linked to higher elevations (0.50 and 0.64, respectively) and meadows (0.62 and 0.52, respectively).

Niche Differentiation and Overlap

We used the first discriminate factor to visually represent niche differentiation on the landscape (Figure 3, – 4). Hurlbert's niche breadth index indicates that bison and caribou are more of a "generalist" species in the winter than throughout the rest of the year (Table 4). This is consistent with Lloyd's asymmetrical overlap index where the most significant overlap of caribou niche by bison occurs in early- and late-winter (Table 5). There also was another peak in overlap in the summer (Table 5). The least amount of niche overlap between bison and caribou occurred in spring and fall (Table 5) when the difference in mean elevation used was greatest (Figure 2). Based on the coefficients of the first discriminant factor, in spring the EGVs that were most responsible for niche separation between bison and caribou other than elevation were conifer (0.40) and deciduous (-0.49) habitats (Table 6). In fall, the influence of shrub habitat (-0.58) was an influential coefficient of the first discriminant factor (Table 6). Sheep niche breadth was extremely specialized (Table 4) and no niche overlap was detected with bison based on Lloyd's asymmetrical overlap index (Table 5).

DISCUSSION

Bison are the largest living land mammal in North America, with some individuals weighing up to 1000 kg. Given their large body size and that they may occur in large seasonal congregations of up to 100 animals (T. S. Jung, Environment Yukon, unpublished data), it is reasonable that local people would be concerned about the potential for competition between reintroduced bison and resident caribou and sheep (Government of Yukon 2012). In response to this concern, we determined the habitat niche breadth and niche overlap between bison and caribou and bison and sheep.

The habitat niche of bison somewhat overlapped that of caribou in summer. However, the mean elevations used by each species were substantially different, with caribou located at higher elevations. Interestingly, the variance in bison elevation during the summer period is greater than during any other time of the year whereas seasonal variance for caribou elevation remains relatively consistent. This suggests that bison use a wider range of elevations than sheep.

Furthermore, the bison summer marginality factor only explained 16% of the total specialization whereas caribou niche marginality was 79% and animals were most linked to alpine meadows. These results are consistent with ENFA analyses where bison global specialization values were lowest, whereas caribou values were greatest in summer compared to other seasons indicating that the overlap was an effect of increased niche breadth by bison. Niche overlap analyses revealed that bison overlapped caribou habitat most in early and late winter. This overlap was largely an effect of both species utilizing habitats at similar elevations. However, caribou were associated with alpine meadow habitat whereas bison were more linked with conifer. These results are consistent with previous winter analyses where bison fed almost exclusively on graminoids whereas caribou predominantly consumed terrestrial lichens (Fischer and Gates 2005, Appendix A). The conifer forest in our study area is interspersed with small lakes and meadows which are a source of graminoids for bison but would not be detected after the 1km moving window analysis used to generate habitat layers. Habitat niche overlap between bison and caribou during spring and fall was low. Therefore, although overlap indices show the greatest amount of overlap during winter, and a proportion of animals of each species can be found at similar elevations, our results suggest that bison and caribou are associated with different habitat types and therefore do not show strong evidence of potential interspecific competition for habitat during any season.

We did not detect niche overlap between bison and sheep during any season. However, this result should be interpreted with caution given the specialized niche exhibited by sheep and the wide breadth of habitats used by bison in summer. Specifically, winter range (with graminoid cover) is critical in the welfare of sheep (Oldemeyer et al. 1971) and heavy use of these areas by bison may result in changes in graminoid cover from grazing, trampling, and wallowing (Knapp et al. 1999). Although our results do not provide evidence for resource competition, the wide summer niche breadth of bison could have a time-lag effect on the quality of sheep winter range, either positively or detrimentally. Addressing this question will require information beyond habitat use data whereby the direct effects of bison on vegetation would be measured. Moreover, we lacked data for sheep habitat use during summer, the season when bison occurred at the highest elevations and may have the highest potential for competition for habitat with sheep. Jung et al. (see Appendix D) provided evidence of a weak positive association in the co-occurrence of bison and sheep in winter. Given high dietary overlap between bison and sheep (see Appendix A) in summer and winter, and a weak positive co-occurrence between the species in late-winter, an examination of habitat overlap by these species in summer would be of interest.

While several studies have examined habitat overlap between introduced and indigenous ungulates (e.g. Baldi et al. 2004; Acevedo et al. 2007*a*, Acevedo et al. 2007*b*), to the best of our knowledge our study was the first to assess the impact of a reintroduced species on resident ungulates. Generally, we found that bison and caribou exhibited more similar seasonal niche characteristics than did bison and sheep. However, we lack data on sheep habitat use in summer; bison use of sheep range may result in lowered productivity of those ranges, which may have direct effects on the fitness of sheep. Our results are not surprising, given that bison were once a numerically dominant species in the region and likely co-evolved with caribou and sheep to partition resources and co-exist.

Niche overlap is often used as an indicator of the potential for interspecific competition between species (Holt 1987, Hopf et al. 1993). However, it is important to note that studies such as ours can only infer a potential for competition based on niche partitioning (Sinclair 1985, Jenkins and Wright 1988, Fischer and Gates 2005). We concur with these authors that evidence for competition requires demonstrating a deleterious impact resulting from overlapping resource use, which is difficult to do with free-ranging individuals in a natural environment (Mishra et al. 2004, Ritchie et al. 2009). Our results should be interpreted with the caveat that niche overlap does not imply competition; it demonstrates an association and the possibility of competition. Moreover, to infer competition between species a multi-dimensional approach along several niche axes, as well as an assessment of resource availability, is necessary (Holt et al. 1987, de Boer and Prins 1990). Truly, only an experimental approach can determine a cause and effect relationship between species. Nonetheless, our ENFA models are an important tool for determining if further resources should be concentrated to determine if exploitative competition is occurring between reintroduced bison and resident caribou and sheep, and where and when to focus those efforts.

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Table 1. Ecogeographical variables used for model selection and seasonal Ecological Niche Factor Analysis (ENFA).**Error! Bookmark not defined.**

Variable	Used	Description	Variable type
Dist. Water sm.	Y	Distance to nearest lake or river based on 1:50,000 topographic maps	Continuous
Dist. Water lg.	N	Distance to nearest lake or river based on 1:250,000 topographic maps	Continuous
Elevation	Y	Elevation based on Digital Elevation Maps (DEMs)	Continuous
Ruggedness	Y	Terrain ruggedness index uncorrelated to elevation	0–1
% Shrub sm.	N	% area covered by shrub within a 100 meter radius	0–1
% Shrub lg.	Y	% area covered by shrub within a 1 km radius	0–1
% Herb sm.	N	% grass, forb, graminoid within a 100 meter radius	0–1
% Herb lg.	Y	% grass, forb, graminoid within a 1 km meter radius	0–1
% Decid. sm.	N	% area covered by deciduous trees within a 100 meter radius	0–1
% Decid. lg.	Y	% area covered by deciduous trees within a 1 km radius	0–1
% Conif. sm.	N	% area covered by coniferous trees within a 100 meter radius	0–1
% Conif lg.	Y	% area covered by coniferous trees within a 1 km radius	0–1
% Wetland sm.	N	% area covered by wetlands within a 100 meter radius	0–1
% Wetland lg.	N	% area covered by wetlands within a 1 km radius	0–1

Habitat Niche Breadth and Overlap between Reintroduced Wood Bison and
Resident Woodland Caribou and Thinhorn Sheep in Northwest Canada Appendix B

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Table 2. Seasonal marginality (*M*) and specialization (*S*) values for bison, caribou, and sheep in southwestern Yukon, Canada. Marginality represents how much a species habitat differs from the mean available conditions, with increasing *M* indicating increasing marginality. Specialization is the breadth of ecological niche, with *S* >1 indicating some degree of specialization. No habitat use data was available for sheep in summer.

Season	Bison		Caribou		Sheep	
	M	*S*	*M*	*S*	*M*	*S*
Spring	0.700	2.680	0.859	1.633	0.908	1.575
Summer	0.516	1.280	1.321	3.810	-	-
Fall	0.792	2.080	1.036	1.985	0.846	1.412
Early winter	0.632	2.458	0.591	1.535	0.745	1.284
Late winter	0.461	1.858	0.517	1.323	0.745	1.284

Table 3. Relevant axes (with their eigenvalues) and the EGV coefficients of bison, caribou, and sheep used in the ENFA for 5 seasons in southwestern, Yukon, Canada. The positive or negative sign is relevant for the first axis coefficients, but in the following axes only the absolute value of coefficients is considered. The percentages in parentheses are the amount of specialization accounted for by the factor. No sheep data was available for the summer.

a) SPRING MODELS

EGV [1]	Bison			Caribou			Sheep		
	Factor 1 (43%)	Factor 2 (32%)	Factor 3 (12%)	Factor 1 (16%)	Factor 2 (30%)	Factor 3 (21%)	Factor 1 (43%)	Factor 2 (21%)	Factor 3 (11%)
Dist. Water	-0.41	0.18	0.35	0.00	0.04	-0.05	0.04	0.04	0.02
Elevation	-0.55	0.94	0.65	0.66	0.82	0.90	0.71	-0.86	0.87
Decid.	-0.32	-0.12	0.05	-0.08	0.06	0.07	0.14	-0.11	-0.10
Ruggedness	0.14	0.00	0.00	-0.17	0.09	0.08	-0.11	0.08	0.08
Conif.	0.28	-0.12	-0.02	-0.44	0.29	0.13	-0.43	-0.11	-0.25
Herb	0.39	0.13	0.26	0.59	0.48	0.40	0.53	-0.47	-0.41
Shrub	-0.42	-0.19	-0.62	0.01	0.06	-0.05	-0.07	-0.06	0.02

b) SUMMER MODELS

EGV [1]	Bison			Caribou			Sheep		
	Factor 1 (16%)	Factor 2 (25%)	Factor 3 (23%)	Factor 1 (79%)	Factor 2 (11%)	Factor 3 (5%)	-	-	-
Dist. Water	-0.50	0.28	0.60	0.12	0.04	0.06	-	-	-
Elevation	-0.15	0.02	0.00	0.65	-0.95	-0.82	-	-	-
Decid.	-0.24	0.02	0.05	-0.09	0.02	0.01	-	-	-
Ruggedness	0.32	0.09	0.09	-0.10	-0.03	0.04	-	-	-
Conif.	0.34	-0.14	-0.18	-0.36	0.20	-0.16	-	-	-
Herb	0.37	0.22	0.45	0.62	0.22	-0.53	-	-	-
Shrub	-0.56	-0.92	0.63	-0.17	0.06	-0.16	-	-	-

Table 3 continued

c) FALL MODELS

EGV [1]	Bison			Caribou			Sheep		
	Factor 1 (11%)	Factor 2 (39%)	Factor 3 (29%)	Factor 1 (47%)	Factor 2 (22%)	Factor 3 (14%)	Factor 1 (27%)	Factor 2 (32%)	Factor 3 (13%)
Dist. Water	-0.41	-0.35	-0.43	0.04	-0.01	-0.01	0.07	0.04	-0.02
Elevation	-0.62	0.79	-0.59	0.63	0.64	0.77	0.71	0.85	-0.91
Decid.	-0.24	0.21	-0.14	-0.05	-0.08	0.10	0.18	0.10	0.10
Ruggedness	0.21	0.19	-0.10	-0.13	0.27	0.20	-0.09	-0.09	-0.05
Conif.	0.44	0.35	0.52	-0.43	0.39	0.39	-0.43	0.23	0.24
Herb	-0.03	-0.01	0.02	0.62	-0.60	0.44	0.51	0.45	0.32
Shrub	-0.40	-0.21	0.41	0.04	-0.04	-0.06	-0.02	0.02	-0.02

d) EARLY-WINTER MODELS

EGV [1]	Bison			Caribou			Sheep		
	Factor 1 (40%)	Factor 2 (38%)	Factor 3 (12%)	Factor 1 (18%)	Factor 2 (26%)	Factor 3 (18%)	Factor 1 (27%)	Factor 2 (27%)	Factor 3 (15%)
Dist. Water	-0.63	0.91	-0.77	-0.12	-0.03	-0.05	0.20	-0.11	0.12
Elevation	-0.49	-0.38	0.45	0.47	0.39	0.42	0.64	-0.86	-0.93
Decid.	-0.33	0.14	0.30	-0.12	0.06	-0.09	0.24	-0.21	-0.13
Ruggedness	0.27	0.01	0.06	-0.18	0.14	0.12	-0.10	0.05	-0.10
Conif.	0.29	0.05	0.14	-0.52	-0.51	0.56	-0.45	-0.26	-0.19
Herb	0.03	-0.01	-0.04	0.60	0.73	0.67	0.52	-0.36	-0.21
Shrub	-0.30	-0.12	-0.29	0.29	-0.16	0.17	0.08	0.02	0.10

Table 3 continued

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e) LATE-WINTER MODELS

EGV [1]	Bison			Caribou			Sheep		
	Factor 1 (37%)	Factor 2 (28%)	Factor 3 (19%)	Factor 1 (20%)	Factor 2 (24%)	Factor 3 (16%)	Factor 1 (27%)	Factor 2 (27%)	Factor 3 (15%)
Dist. Water	-0.69	-0.91	-0.68	-0.17	-0.05	0.10	0.20	-0.11	0.12
Elevation	-0.52	0.34	0.56	0.50	0.26	-0.28	0.64	-0.86	-0.93
Decid.	-0.39	0.22	-0.34	-0.17	-0.16	-0.19	0.24	-0.21	-0.13
Ruggedness	0.31	-0.05	0.30	-0.20	-0.20	0.20	-0.10	0.05	-0.10
Conif.	0.10	-0.02	-0.11	-0.51	0.66	-0.62	-0.45	-0.26	-0.19
Herb	-0.01	0.01	-0.09	0.62	-0.66	-0.67	0.52	-0.36	-0.21
Shrub	0.01	0.00	0.02	0.06	0.00	0.02	0.08	0.02	0.10

[1] see Table 1 for a description of the EGVs

Table 4. Seasonal Hurlbert's niche breadth index (B') for bison, caribou, and sheep. B' may range from 0–1, with 0 and 1 corresponding to specialized and generalist species, respectively. No data were available for sheep during the summer.

Species	Spring	Summer	Fall	Early-Winter	Late-Winter
Bison	0.423	0.513	0.447	0.612	0.712
Caribou	0.510	0.311	0.453	0.674	0.689
Sheep	0.000	-	0.000	0.000	0.000

Table 5. Lloyd's asymmetrical overlap indices (Z) for the seasonal niches of bison and caribou and bison and sheep, and their reciprocal, in southwestern Yukon, Canada. Larger Z values, and smaller associated reciprocals, signify greater niche overlap by bison. No summer habitat data was available for sheep

Season	Bison and Caribou		Bison and Sheep	
	Z	**Reciprocal**	**Z**	**Reciprocal**
Spring	3.841	0.889		
Summer	13.590	5.653	-	-
Fall	2.131	3.944		
Early winter	27.345	3.716		
Late winter	24.375	15.516		

Table 6. Coefficients of the modeled ecogeographical variables (EGV) along the first discriminant factor for seasonal pairwise comparisons of bison and sheep and bison and caribou in southwestern Yukon, Canada. No summer data were available for sheep. Coefficients are from discriminant function analyses for species pairs (see text for details).

EGV [1]	Spring		Summer	Fall		Early-Winter		Late-Winter	
	Bison & Caribou	Bison & Sheep	Bison & Caribou	Bison & Caribou	Bison & Sheep	Bison & Caribou	Bison & Sheep	Bison & Caribou	Bison & Sheep
Dist. Water	-0.44	-0.21	-0.371	-0.247	0.204	-0.501	-0.367	-0.354	-0.383
Elevation	-0.60	-0.46	-0.444	-0.462	0.429	-0.503	-0.401	-0.525	-0.408
Herb	0.20	0.21	-0.356	-0.328	0.028	-0.207	-0.095	-0.427	-0.146
Conif.	0.40	0.52	0.528	0.373	-0.483	0.110	0.455	0.144	0.430
Decid.	-0.49	-0.36	-0.233	-0.298	0.334	-0.494	-0.331	-0.402	-0.437
Shrub	0.02	-0.53	-0.107	-0.581	0.639	-0.320	-0.523	0.256	-0.377
Ruggedness	0.13	0.15	0.440	0.228	-0.143	0.307	0.325	0.411	0.384

[1] see Table 1 for a description of the EGVs
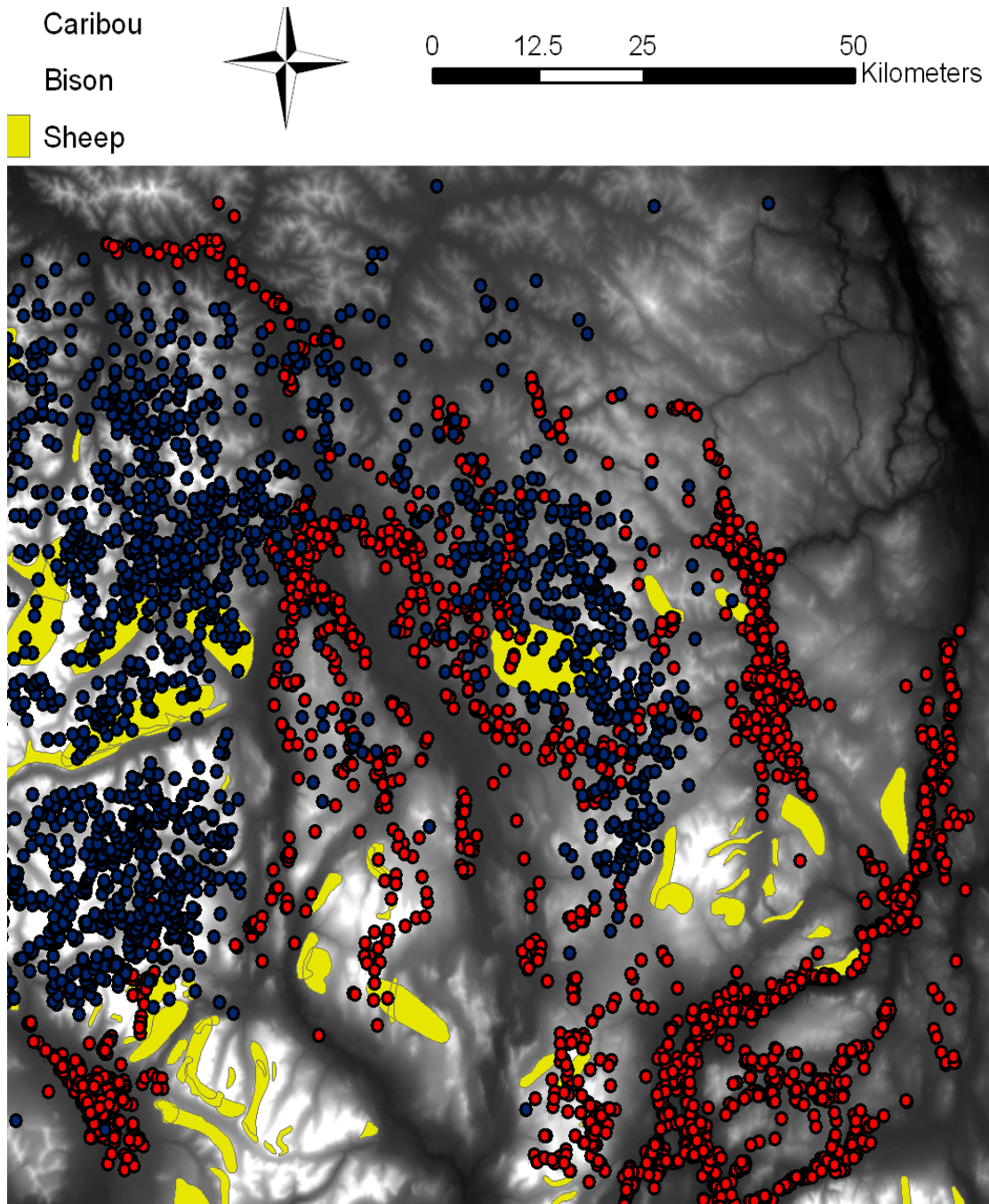
Figure 1. All Bison, caribou, and sheep data used in Ecological Niche Factor Analysis (ENFA)
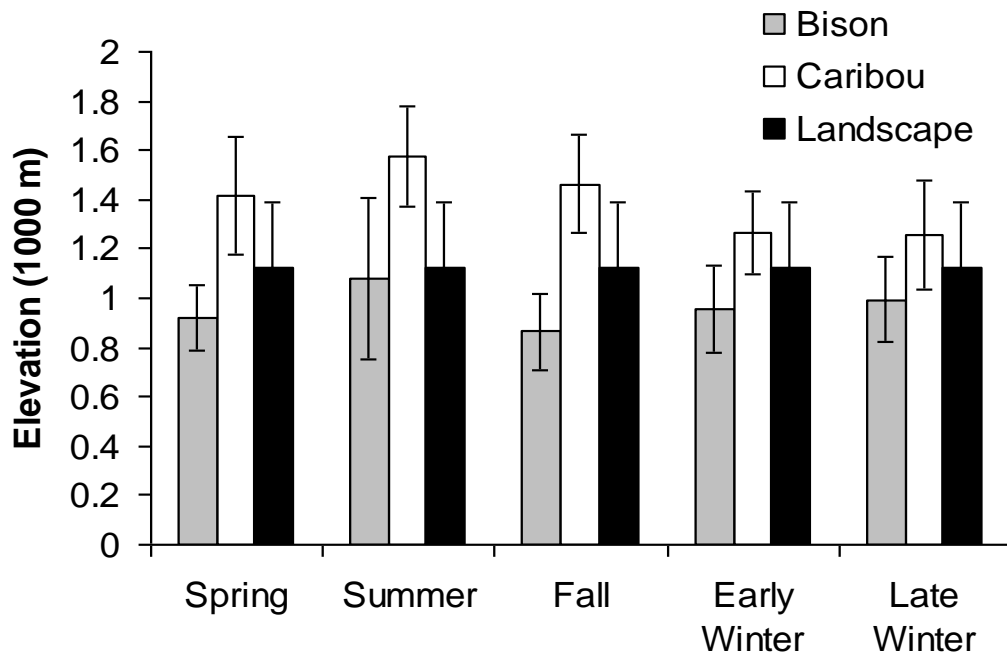
Figure 2. Seasonal elevation values for bison, caribou, and the landscape. Species data generated from telemetry locations within the study area. Error bars are standard deviations for all raster 25m x 25m pixels
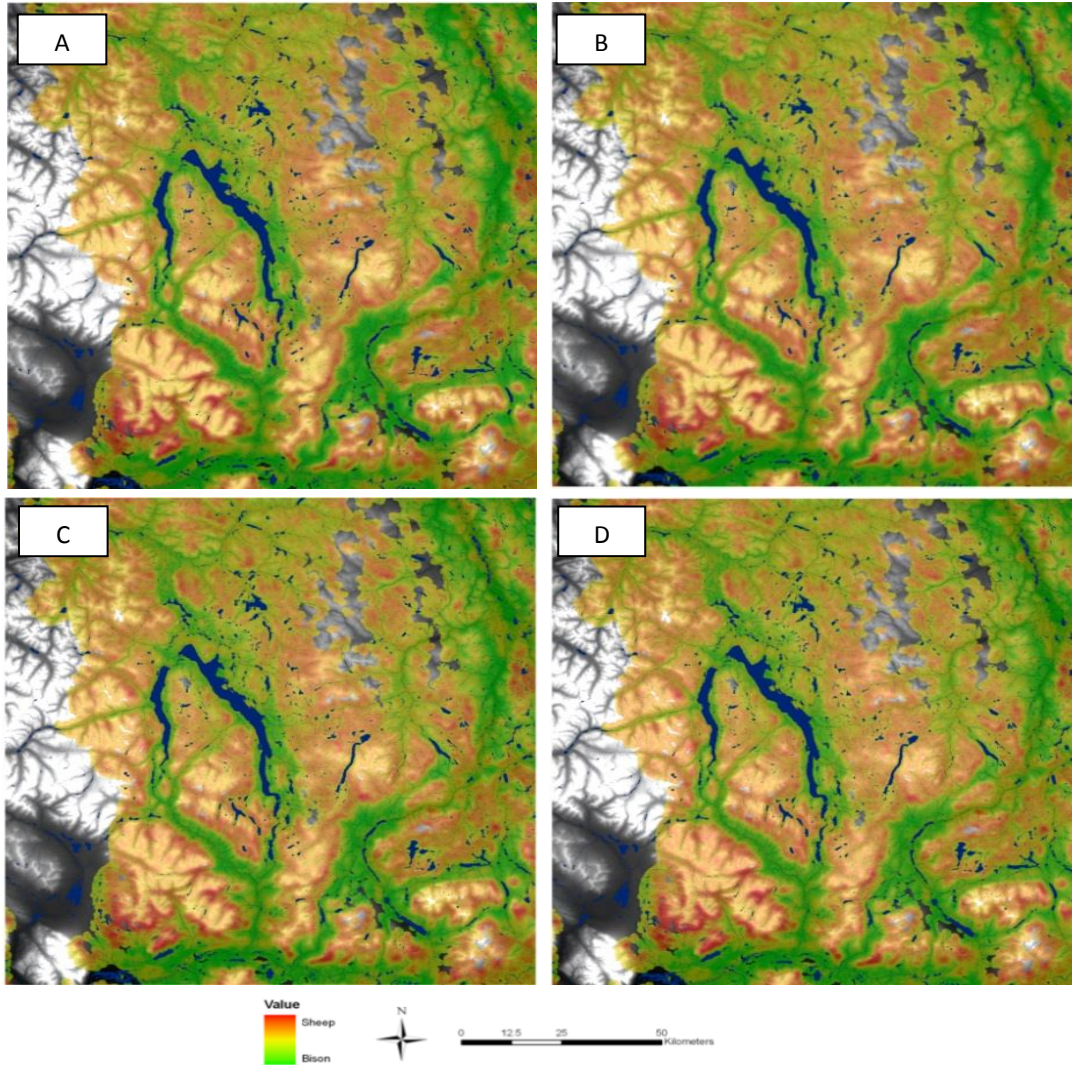
Figure 3. Niche differentiation map between bison and sheep for A) spring, B) fall, C) early-winter, and D) late-winter. Green areas represent conditions favouring bison whereas red areas represent environmental conditions favouring sheep. No sheep data was available for summer.

Figure 4. Niche differentiation map between bison and caribou for A) spring, B) summer, C) fall, D) early-winter, and E) late-winter. Green areas represent conditions favouring bison whereas red areas represent environmental conditions favouring caribou.

Appendix C:

Winter Habitat Overlap by Moose (*Alces americanus*) and Reintroduced Bison (*Bison bison*) in Southwestern Yukon, Canada
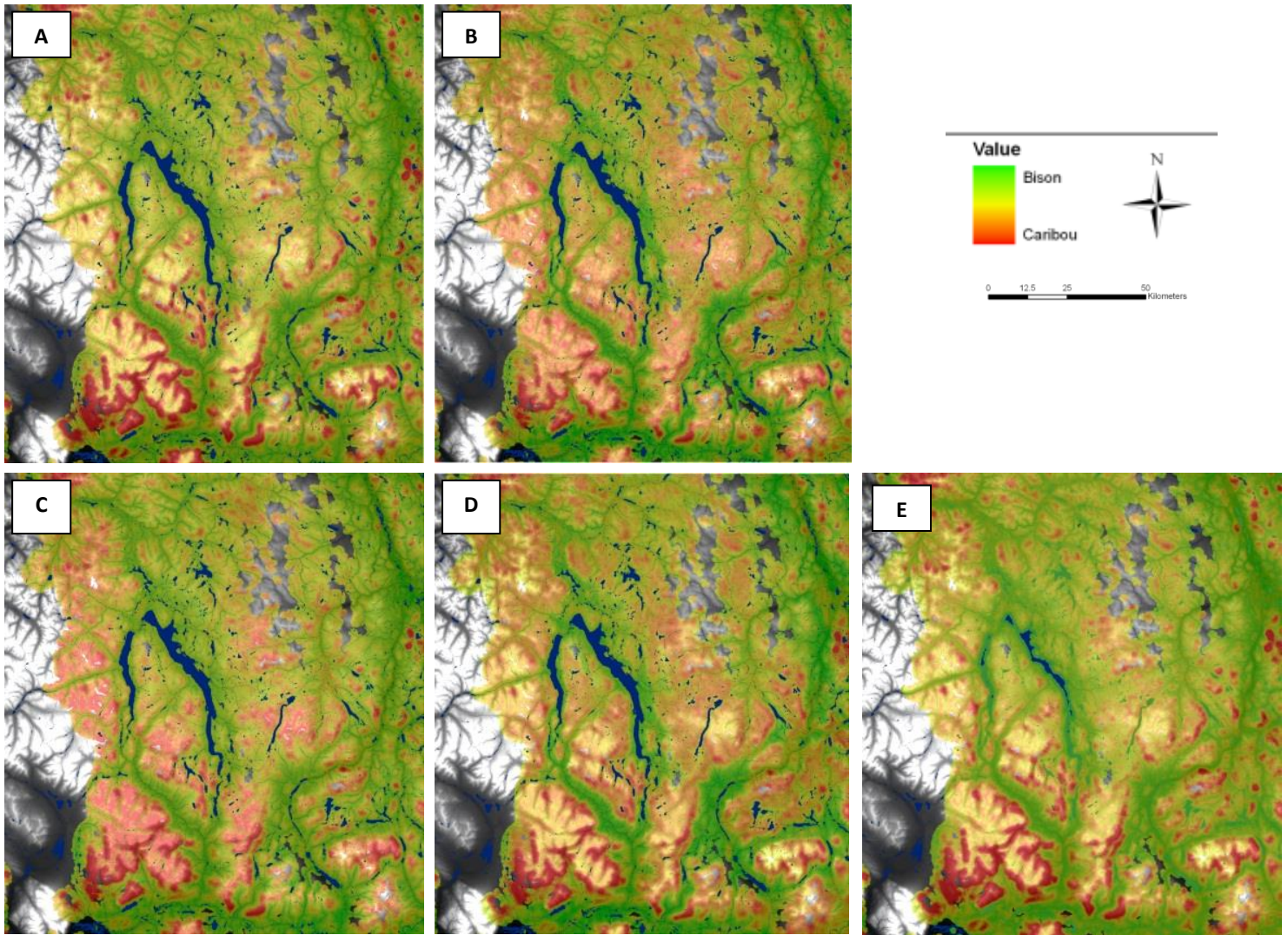
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ABSTRACT: Despite moose (*Alces americanus*) being a cultural and ecological keystone species in the North American boreal forest, only a handful of studies have examined the potential for interspecific competition between moose and other ungulates. In response to local concerns about the potential for competition between moose and reintroduced bison (*Bison bison*), we investigated winter habitat overlap between the 2 species in southwestern Yukon, Canada. We used available geo-referenced data of animal locations, and associated habitat covariates, to develop resource selection probability function (RSPF) models of early-winter and late-winter habitat selection by moose and bison. Candidate models were assessed using Akaike information criteria (AIC) and associated statistics. In both early-winter and late-winter, bison and moose selected for very different habitat types. Given observed differences in seasonal habitat use between moose and bison, these species are predicted to overlap on only 0.5% and 6.6% of the study area during early-winter and late-winter, respectively. The lack of demonstrated winter habitat overlap, coupled with low diet overlap, between moose and reintroduced bison points to an overall low potential for exploitative competition between these species. Diet specialization likely results in resource partitioning between moose and bison, allowing them to coexist on a shared landscape.

Keywords: *Alces americanus*, bison, *Bison bison*, competition, habitat, niche overlap, moose, resource selection probability function

INTRODUCTION

Moose (*Alces americanus*) are perhaps the most valued wildlife resource by local people throughout the North American boreal forest. They are primarily a key food resource for local people, but also provide an important basis for spiritual and cultural, recreational, and economic benefits to many northern communities (reviewed by Timmerman and Rodgers 2005). In addition, they are likely a keystone species in the ecology of boreal forests (e.g., Pastor et al. 1988, Molvar et al. 1993).

As such, factors that may potentially limit or regulate their abundance have received considerable scientific attention, with research focused on predation (e.g., Gasaway et al. 1992, Messier 1994, James et al. 2004), climate change (e.g., Lowe et al. 2010, Broders et al. 2012), modifications to the landscape and habitat (e.g., Rempel et al. 1997, Collins and Schwartz 1998, Bowman et al. 2010), harvest sustainability (e.g., Crête et al. 1981, Sæther et al. 2001), and human disturbance (Colescott and Gillingham 1998, Lykkja et al. 2009). Interspecific competition between moose and other herbivores, however, has received relatively cursory attention by researchers. Several investigations on the potential for exploitative competition between moose and hare (*Lepus* spp.) have commonly reported a high potential for competition for food resources (Dodds 1960, Wood 1974, Wolff 1980, Belovsky 1984). Surprisingly, less work has been done on the potential for competition for food or habitat between moose and other indigenous ungulates (but see: Telfer 1970, Jenkins and Wright 1988, Messier 1991, Cumming et al. 1996).

We investigated the potential for competition between moose and reintroduced wood bison (*Bison bison athabascae*, hereafter bison) for habitat on a shared winter range in southwestern Yukon, Canada. Bison were extirpated from much of northwestern North America by the turn of the 19th century (Soper 1941, Sanderson et al. 2009). Extensive recovery efforts ensued in western Canada, beginning in the late 1950s, and in 1980 a program was initiated to re-establish bison in southwestern Yukon, Canada (Government of Yukon 2012). Subsequently, the bison population in southwestern Yukon grew rapidly post-reintroduction (Environment Yukon unpublished data), and produced unexpected management challenges. Despite formerly being indigenous to the region, local people had substantial concern over potential competition between reintroduced bison and moose, which they depended on culturally and economically as a cultural keystone species (*sensu* Garibaldi and Turner 2004). Consequently, a key management action arising from a community-based management plan for bison in the region was to better understand the potential impact of the reintroduced bison on resident moose (Government of Yukon 2012).

In a concurrent study, Jung et al. (see Appendix A) investigated dietary overlap between moose and bison during winter in our study area. As reported from elsewhere by others (e.g. Risenhoover 1989), moose in our study area were shrub specialists, with 99.8% of their winter diet at high elevations consisting of shrubs, predominately *Salix* spp. and *Betula* spp. While bison, on the other hand, had much more diverse winter diets that were largely composed of sedges (*Carex* spp.) and rushes, at both high and low elevations (53.3%–75.6%, respectively; Appendix A). Consequently, winter dietary overlap between reintroduced bison and moose was found to be low to moderate (13%–42% ; Appendix A).

In this study, we extend our work on the potential for competition between moose and reintroduced bison by examining habitat overlap between resident moose and reintroduced bison. We used available datasets of geo-referenced locations of bison and moose to develop habitat selection models and calculate habitat suitability maps for each species. These maps were overlaid upon one another to identify areas of overlap. While much work has been done on winter habitat selection by moose (e.g., Clyde 2005, Poole and Stuart-Smith 2006, Jung et al. 2009, Lenarz et al. 2011) and bison (e.g. Larter and Gates 1991) in northwestern North America, how these species partitioned resources on a shared winter range remained unknown and was a source of angst for managers and local people (Government of Yukon 2012).

We focused our analyses during winter, a time when food resources are most limiting and niche overlap for northern ungulates may be greatest (Jenkins and Wright 1987). The current work is based on the theoretical premise that a lack of resource partitioning between similar species will result in interspecific competition and a potential inability for both species to coexist without differentiation along ≥1 other niche axes (Birch 1957, Sale 1974, de Boer et al. 1990, Hopf et al. 1993). Given that moose and reintroduced bison had dissimilar winter diets in our study area (see Appendix A) we predicted that they would also use different winter habitats, where each would find preferred forage.

METHODS

Study Area

Our study area was located in the Boreal Cordillera Ecozone (Yukon Ecoregions Working Group 2004, east of the village of Haines Junction, Yukon, Canada (60.8°N, 137.5°W). We defined our study area (12,818 km^2) by generating a 100% minimum convex polygon (MCP) around locations of radio-collared bison (see below) in a geographic information system (GIS) and buffering the area by 10 km. Elevation ranged from 502–2345 meters above sea level (ASL). Much of the area was above treeline (approximately ≥1000 m ASL), with several mountain peaks ≥1600 m ASL and extensive alpine plateaus. Alpine areas were bisected by several large lakes, including Aishihik Lake and Taye Lake, and deeply incised river valleys. Vegetation at lower elevations and valley bottoms included open canopy black spruce (*Picea mariana*), white spruce (*P. glauca*) and trembling aspen (*Populus tremuloides*) forest, and dwarf willow (*Salix* spp.) and dwarf birch (*Betula nana*) shrublands, interspersed with mesic sedge (*Carex* spp.) meadows. Remnant boreal grasslands occurred as small patches on south-facing slopes, also at low elevations. Alpine plant communities were dominated by willow and dwarf birch, graminoid species, and mosses (*Sphagnum* spp.; Hayes et al. 2003). Climate was cold and semi-arid, with snow cover extending from early-October to mid-May.

Bison and moose were common in both alpine and lowland habitats. Bison and moose occurred at low densities; however populations of bison were increasing during our study and moose were presumably stable (Environment Yukon, unpublished data). Other larger mammals in the study area included woodland caribou (*Rangifer tarandus caribou*), thinhorn sheep (*Ovis dalli dalli*), mule deer (*Odocoileus virginianus*), elk (*Cervus canadensis*), semi-feral horses (*Equus ferus caballus*), wolves (*Canis lupus*), coyotes (*Canis latrans*), Canada lynx (*Lynx canadensis*), wolverine (*Gulo gulo*), grizzly bears (*Ursus arctos*) and black bears (*Ursus americanus*).

Ungulate Data

Bison spatial data was obtained from 16 animals equipped with global positioning system (GPS) collars from November 2005 to November 2009. Locations were collected hourly for GPS-collared bison. We excluded the first 3 days post-capture to negate potentially abnormal movement behaviour and habitat choices that may have been a result of capture effects (*sensu* Morellet et al. 2009, Neumann et al. 2011). We calculated the movement rate between locations and found that only 1% of movement bouts were >1.7 km/h.

We visually inspected all locations above this cutoff to assess inclusion in the final dataset. Bison were not faithful to specific areas between years (T. S. Jung, Environment Yukon, unpublished data), therefore; we included multiple years of locations for individual bison where the data was available. However, we restricted inclusion of a bison/season if locations were not available for ≥80% of the length of the season. The remaining dataset consisted of 106,203 winter (mid-November to mid-May) locations. We estimated telemetry error rates to be ≤30 m and ≤100 m for bison and moose, respectively.

Geo-referenced locations of moose in our study area were obtained from various aerial surveys (Environment Yukon, unpublished data). Specifically, we used early winter census data from surveys conducted in 1990, 1992, and 1998 ($n = 393$). For the late winter, we used annual recruitment survey data from 1993 to 1999 and locations from a 2011 census ($n = 672$) Because of the minimum sample requirements for model estimation, we combined all sex/age classes to describe general moose habitat selection patterns.

Habitat Covariates

Habitat covariates of interest were extracted and mapped as layers within a geographic information system (GIS), using available data sources (Table 1). Vegetation maps were generated from Earth Observation for Sustainable Development of Forests (EOSD) base layers, which were based on LandSat-7 Enhanced Thematic Mapper Plus (ETM+) images, circa 2000 (Wulder et al. 2008). Vegetation types considered in the analysis included the percent of shrub, wetland, herbs (i.e., vascular plants such as grasses and forbs), and conifer and deciduous forest cover. A moving window analysis was used at the 100 m and 1 km radius scales to produce rasters where each 25 m x 25 m pixel represented the percent of the habitat type of interest within the specified buffer. Therefore, 10 individual habitat maps were generated for preliminary analysis (Table 1). In addition, map layers depicting the distance to water sources were generated by extracting river and lake layers from digitized topographic NTS (National Topographic Series) maps. Maps were rasterized to 25 m x 25 m pixels to match the pixel size of EOSD maps and the Euclidean distance from each cell to the nearest water source was calculated. Digital Elevation Maps (DEMs; geogratis.com) were merged and resampled (from 30 m x 30 m to 25 m x 25 m) also to match other habitat maps. This layer was used to generate slope, aspect, and terrain ruggedness maps. Terrain ruggedness was calculated using a vector ruggedness measure that quantifies local variation in terrain, as per Sappington et al. (2007). We generated 20,000 random points within the study area (approx. 1.5 points/km^2) to represent available habitat.

Habitat Selection Models

We used weighted distributions to estimate resource selection probability functions (RSPFs) in the case of the use-available design (Lele and Keim 2006, Lele 2009). An RSPF is a function that describes the probability that a particular resource, as described by a series of environmental covariates, will be selected by an individual animal (Manly et al. 2002). Recent advances in computational algorithms make it possible to estimate probability of selection with logistic regression models (Hosmer and Lemeshow 2000). These models provide stronger inferences compared to commonly used exponential models that often are not an accurate representation of natural processes and can result in biased probability maps. These models represent the "mean" habitat selection observed.

We divided the bison and moose datasets into two biologically relevant seasons, based on bison movement rates (S. M. Czetwertynski and T. S. Jung, Environment Yukon, unpublished data), including: early-winter (11 November – 31 January) and late-winter (1 February – 13 May). In addition, the selection for elevation in each season was bimodal and would require a third order covariate. Moreover, bison exhibited different selection patterns at high and low elevations (this study). Therefore, we generated bison models separately for high ($\geq$ 1,200 m ASL) and low (< 1,200 m ASL) elevations. The number of moose locations was insufficient for developing separate models for high and low elevations.

We used a manual stepwise model building procedure whereby covariates were individually visually screened and only those covariates with biologically relevant selection relationships were considered as potential covariates in seasonal models. Model selection was based on forward stepwise inclusion where pre-screened covariates were added sequentially in order of their strength in explaining the data based on Akaike information criterion (AIC; Burnham and Anderson 2002) and visual inspection. We considered this approach appropriate as models would be used for predictive purposes. RSPF estimation requires at least 1 continuous covariate; therefore, seasons where the best 2 covariates were categorical required the addition of a subsequent covariate to be estimated. This would only be an issue if more complex models do not improve fit. When covariates were highly correlated ($r > 0.6$), we only considered the variable that provided the better fit to avoid collinearity issues (Hosmer and Lemeshow 2000). However, we also considered models with the second best covariate when there was high multicollinearity between variables and similar predictive value. When biologically appropriate, we also tested the fit of second order transformations. This pluralistic approach incorporates advantages of hypothesis testing and information theory (Stephens et al. 2005, 2007).

We identified the most parsimonious models based on AIC using the cutoff of 10 for distinguishing differences in models (Burnham and Anderson 2002), area under the receiver operating characteristic curve (AUC), and variance inflation factors (VIF) statistics. Models with the lowest AIC score and highest AUC are considered the best fit to the data. We used AUC to measure the discrimination of the model. Specifically, AUC graphs plots true positives (sensitivity) vs. false positives (1-specificity) for a binary classifier system as its discrimination threshold is varied. Therefore, a model with no discriminating power would have an AUC value of 0.5. Generally, AUC values between 0.7 and 0.8 are considered to have acceptable discrimination and values above 0.8 are considered to be excellent (Hosmer and Lemeshow 2000). Variance Inflation Factors provide information on the level of correlation between predictors, with VIF values below 5.0 being considered acceptable.

Habitat Selection Overlap

We assumed that areas of high selection were biologically important (Railsback et al. 2003) and identified high quality habitats based on RSPF models. We generated the study area into 3 equal-sized bins, representing low, medium, and high selection areas for bison and moose. Our bins were based on an equal area classification. Early-winter and late-winter habitat suitability maps were generated for bison and moose using the most supported RSPF model. To quantify the percent of overlap between bison and moose, we identified areas with a high probability of habitat selection for both species overlapped.

RESULTS

Early-Winter Habitat Selection and Overlap

During the early winter season, bison spent most of their time (96.4% of locations) at lower elevations between 600 and 900 m ASL on flat terrain. Our most parsimonious habitat selection model for bison during early-winter at low elevations (M4, Table 2a) had excellent discrimination (AUC = 0.83) and low VIF levels (1.7, Table 2a). During this season, bison selected for wetland-conifer complexes and more specifically areas close to water (Table 3). Bison avoided patches with more than 40% shrub cover at the 1 km scale.

Only a small percentage (3.6%) of bison locations in early-winter was at high elevations. Model M4 (Table 2b) was the most parsimonious representation of bison habitat selection during early-winter. This model also had excellent discrimination (AUC = 0.87) and low VIF levels (1.7). During early-winter, bison at high elevations selected predominantly for areas between 1000–1300 m ASL, on flat terrain close to lakes with only slight selection for south facing slopes (Table 3). Bison also selected for increasing terrain ruggedness.

The most parsimonious habitat selection model (M1, Table 2c) for moose in our study area during early-winter had excellent discrimination power (AUC = 0.82) and low VIF levels (1.1). During this season, moose selected shrub habitats 1200–1500 m ASL and avoided conifer forests. Moose selected for slopes of 5–20° and did not show selection for any aspect (Table 3).

Late-Winter Habitat Selection and Overlap

During the late winter season, bison spent most of their time (89.7% of locations) at lower elevations (700–900 m ASL). The most parsimonious habitat selection model for bison at low elevations during late winter (M5, Table 4a) had adequate discrimination (AUC = 0.79) and acceptable VIF level (2.7). During this season, bison at low elevations selected predominantly for areas rich in forbs and graminoids on south-facing slopes of approximately 15–25°. Secondly, bison also selected for flat areas near lakes in wetland/conifer mosaics and avoided deciduous forests (Table 5).

More bison locations were at high elevations in late-winter than early-winter, however the overall percentage of bison locations at high elevations remained low (10.3%). The most parsimonious model of bison habitat selection at high elevation in late-winter in our analysis (M3, Table 4b) had adequate discrimination (AUC = 0.79) and an acceptable VIF level (2.1). During this season, bison at high elevations selected primarily for south facing slopes in areas up to 1,500 m ASL (Table 5). Secondly, bison selected for flat terrain close to lakes.

Moose habitat selection was less specific during late-winter than during the early winter. Our best moose habitat selection model for late-winter (M4, Table 4c) had somewhat poor discrimination (0.68), but an acceptable VIF level (1.1). Moose selection was greatest for areas with a high proportion of deciduous forest at the 1 km scale and close to rivers. Moose selected for a wide range of elevations between 1000 and 1500 m ASL. Moose also selected for areas with greater than 20% shrub cover at the 1 km scale and avoided areas where coniferous forest cover was greater than 20% at the 1 km scale (Table 5).

Habitat Overlap

In both early-winter and late-winter, bison and moose selected for very different habitat types. In early-winter, bison largely used areas that were below 900 m ASL and avoided sites with more than 40% shrub cover. In contrast, moose selected shrub habitats between 1000 and 1500 m ASL (Table 3). In late-winter, bison generally avoided deciduous forest areas whereas this habitat type was the strongest predictor of moose habitat selection (Table 5). Given these differences in seasonal habitat use between moose and bison, these species are predicted to overlap on only 0.5% and 6.6% of the study area during early-winter and late-winter, respectively, based on the most highly selected third of the study area by each species (Figure 1).

DISCUSSION

Despite moose being a cultural and ecological keystone species in the North American boreal forest, this study is one of a few that has examined the potential for exploitative competition between moose and other ungulates. Our main finding is that we failed to find much evidence of habitat overlap between moose and reintroduced bison in southwestern Yukon during either early- or late-winter. Our habitat suitability maps predicted that there was ≤ 6.6% of the landscape where moose and bison may both find highly suitable winter habitat.

Winter habitat selection choices made by moose and bison in our study were in general agreement with autoecological studies of moose (e.g. Molvar and Bowyer 1994, Clyde 2005) and bison (e.g., Larter and Gates 1991) in northwestern Canada and Alaska. Our RSPF models demonstrated that moose and bison were spatially segregated on the landscape along 2 primary axes: elevation and habitat type. Most bison locations were below the treeline and in mesic areas, whereas moose were most often above treeline in vast alpine shrublands. These species-specific habitat choices are in keeping with the forage preferences of moose and bison, with moose preferring shrubs and bison preferring sedges (Risenhoover 1989, Larter and Gates 1991, Appendix A). Clearly, moose and bison were selecting habitats that provided access to sufficient forage, and differences in their diets resulted in different habitat choices by the 2 species.

Our lack of finding substantial habitat overlap is consistent with studies that examined habitat use by sympatric moose and other indigenous ungulates; for example, woodland caribou (*Rangifer tarandus caribou*; Cummings et al.1996), white-tailed deer (*Odocoileus virginianus*; Telfer 1970), and elk (*Cervus canadensis*; Jenkins and Wright 1988). None of these studies reported substantial winter habitat overlap between those indigenous ungulates and moose. For instance, Telfer (1970) reported that moose and white-tailed deer were exclusive of their winter habitat in New Brunswick, sharing only 1% of his study area.

Some workers have suggested that similar-sized ungulates may partition resources the least, compared to other species pairs (Jenkins and Wright 1988, Gordon and Illius 1989). Moose and bison are the largest land mammals in the region, and similar in body size. Thus, the lack of resource overlap between these species in our study is in disagreement with the "similar body size" hypothesis. Rather, a lack in resource overlap between moose and bison is consistent with the hypothesis that similarity in ecophysiological characteristics (e.g., functional foraging mode, Hofmann 1989) is the primary predictor of competition among sympatric ungulates. As a shrub specialist (e.g., Risenhoover 1989, Appendix A), moose are an extreme browser on the grazer-intermediate-browser scale (Hofmann 1989), while bison are primarily a grazer (Larter and Gates 1991, Appendix A).

Given differences on where they lay on the ecophysiological scale of Hofmann (1989), it is not too surprising that moose in bison select different habitats. Most other ungulates in the region are intermediate feeders, and might be expected to overlap the niche of moose more so than a grazer such as bison.

In conclusion, for interspecific competition between species to occur, they must overlap along several niche dimensions, including food and habitat, and those resources must be limited (Holt 1987, de Boer and Prins 1990). The lack of demonstrated winter habitat overlap, coupled with low diet overlap (Appendix A), between moose and reintroduced bison points to an overall low potential for exploitative competition between these species. Diet specialization by moose likely results in resource partitioning with sympatric ungulates, allowing them to coexist in a shared landscape. In fact, probably the greatest potential competitor for food and habitat resources with moose in our study area are snowshoe hare (*Lepus americana*), given that both species are shrub specialists in winter (Dodds 1960, Wolff 1980, Belovsky 1984).

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Table 1. Habitat covariates used in seasonal resource selection probability function (RSPF) models of bison and moose winter habitat selection in southwestern Yukon, Canada. The "used" column refers to if the variable was used in RSPF models, after controlling for multicollinearity among covariates.

Covariate	Used	Description	Covariate Type
Dist. Water sm.	Yes	Distance to nearest lake or river based on 1:50,000 topographic maps	Continuous
Dist. Water lg.	No	Distance to nearest lake or river based on 1:250,000 topographic maps	Continuous
Elevation	Yes	Elevation based on Digital Elevation Maps (DEMs)	Continuous
Slope	Yes	Slope based on 4 categories, from DEM	Categorical
Aspect	Yes	Aspect based on 4 categories, from DEM	Categorical
Ruggedness	Yes	Terrain ruggedness index uncorrelated to elevation	0–1
% Shrub sm.	No	% area covered by shrub within a 100 meter radius	0–1
% Shrub lg.	Yes	% area covered by shrub within a 1 km radius	0–1
% Herb sm.	No	% grass, forb, graminoid within a 100 meter radius	0–1
% Herb lg.	Yes	% grass, forb, graminoid within a 1 km meter radius	0–1
% Decid. sm.	No	% area covered by deciduous trees within a 100 meter radius	0–1
% Decid. lg.	Yes	% area covered by deciduous trees within a 1 km radius	0–1
% Conif. sm.	No	% area covered by coniferous trees within a 100 meter radius	0–1
% Conif lg.	Yes	% area covered by coniferous trees within a 1 km radius	0–1
% Wetland sm.	No	% area covered by wetlands within a 100 meter radius	0–1
% Wetland lg.	No	% area covered by wetlands within a 1 km radius	0–1

Table 2. RSPF models of the relative explanatory power of covariates related to early-winter habitat selection by bison (tables *a* and *b*) and moose (table *c*) in southwestern Yukon, Canada. RSPF models were based on forward stepwise procedures. Covariates are listed in order of their explanatory strength. The best model (lowest AIC score) is shaded. AIC, AUC, and maximum VIF are test values used to assess the relative strength of each model.

a) Bison low elevation models

Model	Distance to Water (m)	Wetland 100 m (%)	Slope (°)	Elevation (m)	Conifer 100 m (%)	Shrubs 1 km (%)	Aspect	AIC	AUC	Max.VIF
M1	X	X	X					-64870	0.82	1.1
M2	X	X	X	X				-65443	0.82	1.2
M3	X	X	X	X	X			-65987	0.82	1.4
M4	X	X	X	X	X	X		-67288	0.83	1.7
M5	X	X	X	X	X	X	X	-67099	0.83	1.8

b) Bison high elevation models

Model	Distance to Lakes (m)	Slope (°)	Elevation (m)	Aspect	Green-ness	Terrain Rugged-ness	Herbs 1 Km (%)	AIC	AUC	Max.VIF
M1	X	X	X					-2808	0.83	1.2
M2	X	X	X	X				-3134	0.86	1.7
M3	X	X	X	X	X			-3372	0.87	1.7
M4	X	X	X	X	X	X		-3437	0.87	1.7
M5	X	X		X	X	X	X	-3015	0.85	1.7

c) Moose models

Model	Elevation (m)	Shrubs 100 m (%)	Conifer 1 km (%)	Slope (°)	AIC	AUC	Max.VIF
M1	X	X			-557	0.82	1.1
M2	X		X		-453	0.79	2.3
M3	X	X	X		-557	0.82	2.3
M4	X	X		X	-566	0.82	2.3
M5	X		X	X	-472	0.80	2.6

Table 3. Coefficients (estimates), standard errors (SE) and test statistics (z and Pr values) for covariates in the highest ranked (shaded in Table 2) early-winter RSPF models of bison and moose habitat selection in southwestern Yukon, Canada.

Bison Low Elevation Model					Bison High Elevation Model					Moose Model				
Covariate	Estimate	SE	z value	Pr(>|z|)	Covariate	Estimate	SE	z value	Pr(>|z|)	Covariate	Estimate	SE	z value	Pr(>|z|)
(Intercept)	1.519	0.052	29.5	<0.001	(Intercept)	6.382	0.478	13.3	<0.001	(Intercept)	-53.470	7.354	-7.3	<0.001
Dist. Water	-1.332	0.024	-55.8	<0.001	Dist. Lakes	-0.586	0.025	-23.5	<0.001	Elevation	55.767	5.925	9.4	<0.001
%Wetland 100m	108.197	2.258	47.9	<0.001	Slope	-0.060	0.005	-12.5	<0.001	Elevation^2	-19.242	2.161	-8.9	<0.001
Slope	-0.124	0.003	-46.3	<0.001	Elevation	-5.834	0.270	-21.6	<0.001	%Shrub 100m	1.902	0.220	8.6	<0.001
Elevation	-2.436	0.048	-50.7	<0.001	Aspect East	0.182	0.118	1.5	0.123					
%Conifer 100m	4.498	0.082	54.8	<0.001	Aspect South	1.981	0.106	18.6	<0.001					
(%Conifer 100m)^2	-5.684	0.090	-63.3	<0.001	Aspect West	0.906	0.085	10.7	<0.001					
%Shrub 1km	-1.888	0.042	-45.3	<0.001	Aspect Flat	1.325	0.263	5.0	<0.001					
					Greenness	-4.542	0.333	-13.6	<0.001					
					Terrain Rugged	3.767	0.478	7.9	<0.001					

Table 4. RSPF models of the relative explanatory power of covariates related to late-winter habitat selection by bison (tables *a* and *b*) and moose (table *c*) in southwestern Yukon, Canada. RSPF models were based on forward stepwise procedures. Covariates are listed in order of their explanatory strength. The best model (lowest AIC score) is shaded. AIC, AUC, and maximum VIF are test values used to assess the relative strength of each model.

a) Bison low elevation models

Model	Herbs 100 m (%)	Distance to Lakes (m)	Wetland 100 m (%)	Aspect	Green-ness	Shrubs 100 m (%)	Slope	AIC	AUC	Max.VIF
M1	X	X	X					-54664	0.77	1.1
M2	X	X	X	X				-57918	0.77	2.6
M3	X	X	X	X	X			-63641	0.79	2.6
M4	X	X	X	X		X		-59441	0.78	2.6
M5	X	X	X	X	X		X	-63732	0.79	2.7

b) Bison high elevation models

Model	Aspect	Elevation (m)	Distance to Lakes (m)	Herbs 100 m (%)	Green-ness	Slope	AIC	AUC	Max.VIF
M1	X	X	X				-6088	0.77	2.1
M2	X	X	X		X		-7222	0.79	2.1
M3	X	X	X		X	X	-7902	0.79	2.1
M4	X		X	X			-4848	0.74	2.1
M5	X		X	X		X	-5240	0.75	2.1

c) Moose models

Model	Deciduous 1 km (%)	Conifer 1 km (%)	Distance to Rivers (m)	Shrubs 1 km (%)	AIC	AUC	Max.VIF
M1	X	X			-245	0.65	1.1
M2	X		X		-215	0.63	1.0
M3	X			X	-155	0.60	1.1
M4	X	X	X		-326	0.68	1.1
M5	X	X		X	-243	0.65	1.2

Table 5. Coefficients (estimates), standard errors (SE) and test statistics (z and Pr values) for covariates in the highest ranked (shaded in Table 4) late-winter RSPF models of bison and moose habitat selection in southwestern Yukon, Canada.

	Bison Low Elevation Model					Bison High Elevation Model					Moose Model			
Covariate	Estimate	SE	z value	Pr(>|z|)	Covariate	Estimate	SE	z value	Pr(>|z|)	Covariate	Estimate	SE	z value	Pr(>|z|)
(Intercept)	-2.002	0.139	-14.3	<0.001	(Intercept)	5.1418	1.728	3.0	0.003	(Intercept)	-3.440	3.823	-0.9	0.368
%Herb 100m	5.882	0.345	17.1	<0.001	Aspect East	0.9657	0.175	5.5	<0.001	%Decid. 1km	4.686	0.696	6.7	<0.001
Dist. Lakes	-0.225	0.014	-16.3	<0.001	Aspect South	2.6350	0.200	13.2	<0.001	%Conifer 1km	-2.214	0.218	-10.1	<0.001
%Wetland 100m	9.851	9.633	1.0	0.307	Aspect West	1.8614	0.176	10.6	<0.001	Dist. Rivers	-0.678	0.084	-8.1	<0.001
Aspect East	0.509	0.105	4.9	<0.001	Aspect Flat	2.4484	0.462	5.3	<0.001					
Aspect South	1.335	0.105	12.7	<0.001	Elevation	-5.7964	0.359	-16.1	<0.001					
Aspect West	1.174	0.122	9.6	<0.001	Dist. Lakes	-0.2335	0.016	-14.8	<0.001					
Aspect Flat	0.653	0.179	3.6	<0.001	Greenness	-3.5343	0.315	-11.2	<0.001					
Greenness	-4.075	0.434	-9.4	<0.001	Slope Low	-0.0035	0.071	-0.1	0.960					
Slope Low	-0.292	0.044	-6.7	<0.001	Slope Med	0.8236	0.074	11.1	<0.001					
Slope Med	0.240	0.078	3.1	0.002	Slope Steep	0.2287	0.099	2.3	0.020					
Slope Steep	-0.307	0.210	-1.5	0.144										

Table 5 Continued

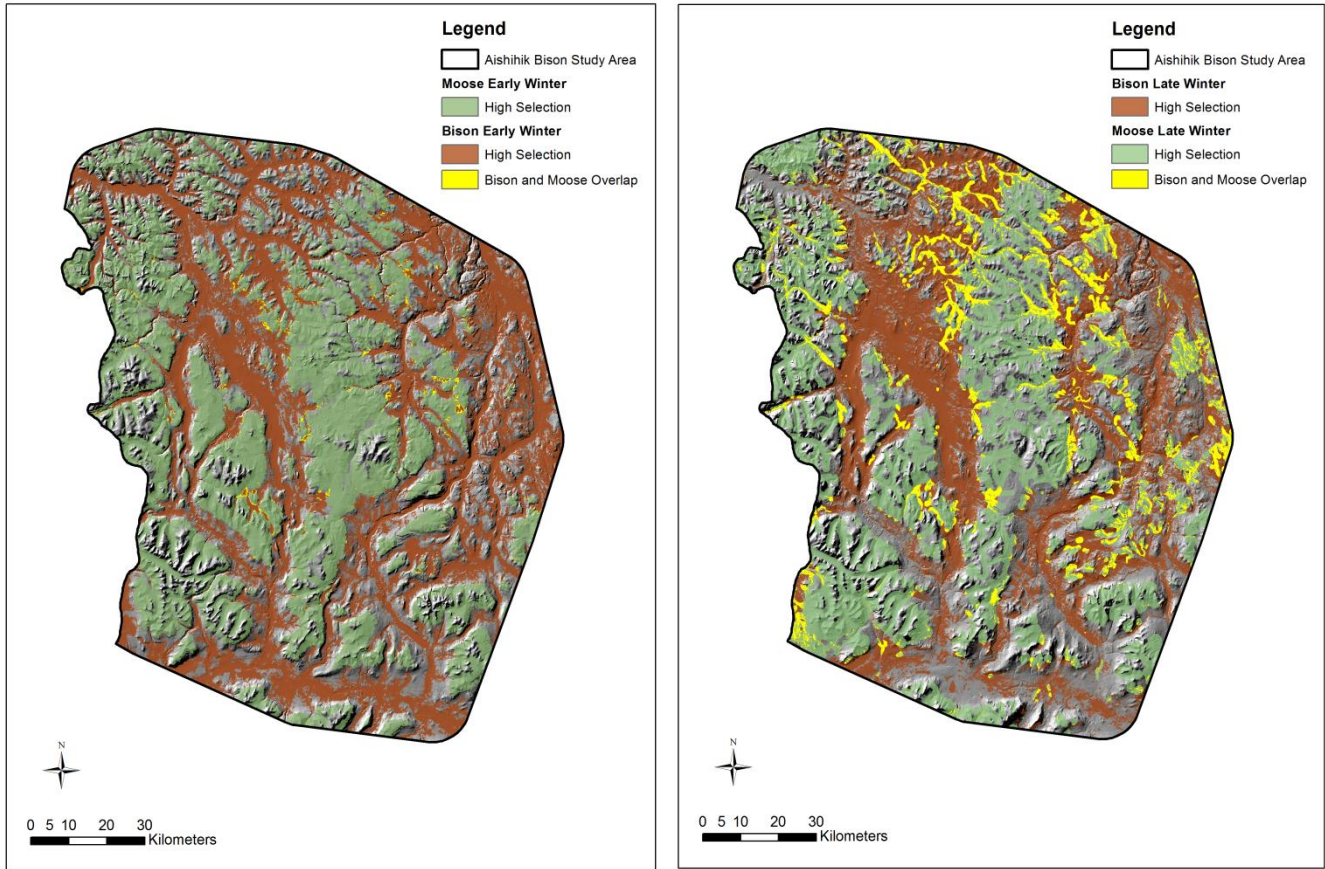|	Bison Low Elevation Model					Bison High Elevation Model					Moose Model			
Covariate	Estimate	SE	z value	Pr(>|z|)		Covariate	Estimate	SE	z value	Pr(>|z|)	Covariate	Estimate	SE	z value	Pr(>|z|)
(Intercept)	-2.002	0.139	-14.3	<0.001		(Intercept)	5.1418	1.728	3.0	0.003	(Intercept)	-3.440	3.823	-0.9	0.368
%Herb 100m	5.882	0.345	17.1	<0.001		Aspect East	0.9657	0.175	5.5	<0.001	%Decid. 1km	4.686	0.696	6.7	<0.001
Dist. Lakes	-0.225	0.014	-16.3	<0.001		Aspect South	2.6350	0.200	13.2	<0.001	%Conifer 1km	-2.214	0.218	-10.1	<0.001
%Wetland 100m	9.851	9.633	1.0	0.307		Aspect West	1.8614	0.176	10.6	<0.001	Dist. Rivers	-0.678	0.084	-8.1	<0.001
Aspect East	0.509	0.105	4.9	<0.001		Aspect Flat	2.4484	0.462	5.3	<0.001					
Aspect South	1.335	0.105	12.7	<0.001		Elevation	-5.7964	0.359	-16.1	<0.001					
Aspect West	1.174	0.122	9.6	<0.001		Dist. Lakes	-0.2335	0.016	-14.8	<0.001					
Aspect Flat	0.653	0.179	3.6	<0.001		Greenness	-3.5343	0.315	-11.2	<0.001					
Greenness	-4.075	0.434	-9.4	<0.001		Slope Low	-0.0035	0.071	-0.1	0.960					
Slope Low	-0.292	0.044	-6.7	<0.001		Slope Med	0.8236	0.074	11.1	<0.001					
Slope Med	0.240	0.078	3.1	0.002		Slope Steep	0.2287	0.099	2.3	0.020					
Slope Steep	-0.307	0.210	-1.5	0.144											

Figure 1. Areas of predicted high habitat selection for bison (brown shading) and moose (green shading) and their overlap (yellow shading) during early-winter (left panel) and late-winter (right panel) in southwestern Yukon, Canada. Grey areas were not predicted to be highly suitable habitat for either species. Areas of predicted high habitat selection were based on 3 equal sized bins from the RSPF model, see text for details.

Appendix D:

Co-occurrence of Reintroduced and Resident Ungulates on a Shared Winter Range in Southwestern Yukon, Canada

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ABSTRACT: It is generally believed that for competition to occur, species must use the same resources (food, habitat) *and* overlap in time and space. Bison (*Bison bison*) were reintroduced to southwestern Yukon, Canada, where they are sympatric with resident caribou (*Rangifer tarandus*), moose (*Alces americanus*), and thinhorn sheep (*Ovis dalli*). Local concerns regarding potential competition between reintroduced bison and resident ungulates prompted us to test their spatial distribution for co-occurrence. We conducted multiple aerial surveys ($n = 11$) to develop a presence/absence matrix (4 species x 779 cells) of ungulates. Randomization procedures were used to conduct a null model analysis of co-occurrence. *C*-scores and *V*-ratios indicated that species were neither negatively nor positively associated with one another; rather their spatial distribution suggested neutral interactions between these species. The most co-occurrence, however, was between bison and sheep, suggesting that there may be a weak positive association between these species. We conclude that the overall potential for competition between reintroduced bison and resident ungulates during winter is low, based on spatial overlap. Even though bison are reintroduced, these species had interacted for thousands of years and have likely co-evolved mechanisms to partition resources and co-exist.

Key words: *Alces americanus*, bison, *Bison bison*, caribou, competition, co-occurrence, C-score, moose, *Ovis dalli*, null model analyses, range overlap, Rangifer tarandus, thinhorn sheep

INTRODUCTION

Understanding patterns in the spatial distribution of co-occurring species has long been a fundamental pursuit of ecologists. Where species with similar niches are sympatric, there is the potential for interspecific competition (Conner and Simberloff 1979, Hopf et al. 1993). Competition among species filling similar niches may lead to competitive exclusion, resulting in the classic "checkerboard" distribution whereby species separate themselves spatially to avoid competition (Diamond and Gilpin 1982, Stone and Roberts 1990). The question then remains whether species communities are spatially structured based on competition or chance (Conner and Simberloff 1979). Quantifying interspecific competition, however, is problematic (Mishra et al. 2004, Ritchie et al. 2009).

Even when changes in density and abundance are apparent, it is often difficult to demonstrate a definitive causal relationship between a species and the survival and fitness of another (Forsyth and Hickling 1998). It is generally believed that for competition to occur, the species pair must use the same resources (food, habitat) *and* occur in the same areas at the same time (de Boer and Prins 1990).

One proposed measure of potential competition among sympatric species is co-occurrence (Stone and Roberts 1990, Gotelli 2000). Co-occurrence measures the niche dimension of space. Simply put, do species co-occur in the same place? Species assemblages may be structured at random (neutral interaction); alternatively, they may be either positively or negatively (avoidance) associated, which may indicate the potential for, or consequences of, interspecific competition, respectively.

With respect to ungulates, several studies have examined co-occurrence of potentially competing species (e.g. Whitlaw and Lankester 1994, Bagchi et al. 2004, Namgail et al. 2010, Acebes et al. 2012, Darmon et al. 2012). In this study, we test the spatial distribution of an ungulate community in southwestern Yukon, Canada, for co-occurrence. The ungulate community in this region has undergone considerable change in the past few decades (Jung et al. in review). Eight species, with varied histories, currently make up the ungulate community. Woodland caribou (*Rangifer tarandus caribou*, hereafter caribou), moose (*Alces americanus gigas*), thinhorn sheep (*Ovis dalli dalli*, hereafter sheep), and mountain goats (*Oreamnos americanus*; hereafter goats) are native resident species that have been extant in the region for ≥200 years (Slough and Jung 2007). Wood bison (*Bison bison athabascae*; hereafter, bison) were extirpated from the region ≥350 years ago, but were reintroduced in 1988–1992 as part of a national recovery program (Government of Yukon 2012). Elk (*Cervus canadensis manitobensis*) were introduced into the study area in the 1950s (population augmentations occurred in the 1990s) with the aim of providing another ungulate species to local area hunters (Strong et al. 2013). Mule deer (*Odocoileus hemionus hemionus*; hereafter deer) have been naturally colonizing the region over the last few decades; there were no records of deer prior to the 1940s in the region (Hoefs 2001). Semi-feral horses (*Equus ferus caballus*) have been free-ranging in portions of the study area for probably ≥125 years. Thus, 4 species were considered native residents (caribou, moose, sheep, and goats), 2 were introduced (elk and horses), 1 was naturally colonizing (deer) and another was reintroduced (bison). Populations of some of the "new" species (bison, elk, deer) had been increasing in the past 20 years (Environment Yukon, unpublished data), while those of native resident species (caribou, moose, and sheep) were the focus of substantial population recovery efforts (Hayes et al. 2003). Local populations of bison and caribou were listed as species at risk in Canada's *Species at Risk Act*.

Native resident ungulates are often of high societal value to local people (e.g., Hayes et al. 2003) and factors that may compromise their conservation status are likely to be a cause for concern. Local people have expressed considerable concern that reintroduced bison may compete with native resident species and cause their populations to decline. Theoretically, the introduction of a new species to a presumably stable species assemblage may culminate in interspecific competition because of a potential lack of resource partitioning and high niche overlap with ≥1 resident species. This has been repeatedly demonstrated when livestock, for example, are introduced on to native ungulate range (e.g., Voeten and Prins 1999, Shrestha and Wegge 2008, Acebes et al. 2012).

As such, the aim of our study was to examine the potential for competition between reintroduced bison and resident native ungulates, as a key action item arising from the management plan for bison in Yukon (Government of Yukon 2012). To the best of our knowledge, this is the first study to assess the impact of a reintroduced ungulate on the spatial distribution of resident native species.

We took a null model (randomization) approach to examine co-occurrence patterns in the ungulate community in southwestern Yukon (*sensu* Gotelli 2000). We focused our effort during late-winter, a time when food resources are most limiting and niche overlap for northern ungulates may be greatest (Jenkins and Wright 1987). Our null hypothesis (H_0) was that ungulate species were randomly distributed with respect to each other. That is, there was neither a positive nor a negative association (neutral interaction) between species pairs, including those with bison. Alternate hypotheses included: H_1 = species were more likely to be found with each other (positive association), or H_2 = species were more likely to not be found together (negative association). In communities structured by competition, co-occurrence should be decreased (negative association) Conner and Simberloff 1979, Diamond and Gilpin 1982). Jung et al. (see Appendix A) examined winter diet overlap between this population of reintroduced bison and native resident species and have concluded that the potential for competition over food resources between bison and caribou (also see: Fischer and Gates 2005) and bison and moose was low, but high for bison and sheep, because both are grazers (*sensu* Hofmann 1989). As such, we predicted that bison and sheep would have either a negative (i.e., high co-occurrence) or positive (i.e., low co-occurrence) association, given the similarity in their winter diets; whereas bison and moose, and bison and caribou would be distributed at random (neutral interaction) during winter because the potential for competition for food between these species is low during winter.

Methods

Study Area

Our study was conducted in a roughly 8,000 km^2 area that approximated the winter range of reintroduced wood bison in southwestern Yukon, Canada. The study area was in the Boreal Cordillera Ecozone (Yukon Ecoregions Working Group 2004), east of the Village of Haines Junction (60.8°N, 137.5°W). Much of the area is above treeline (approximately ≥1000 m ASL), with several mountain peaks ≥1600 m ASL and extensive alpine plateaus. Alpine areas are bisected by several large lakes, including Aishihik Lake and Taye Lake, and deeply incised river valleys. Lowland areas are largely open canopied forest, dominated by either white spruce (*Picea glauca*) or trembling aspen (*Populus tremuloides*). Small areas of wet sedge meadows and wet shrub meadows occur at low elevations. Remnant boreal grasslands occur as small patches on south-facing slopes, also at low elevations. Climate is cold and semi-arid, with snow cover extending from October to May. Bison and moose are common and occur throughout the study area, in both alpine and lowland habitats. Caribou and sheep are also common, but patchily distributed throughout the study area, and found predominately in alpine habitats.

Aerial Surveys

We divided the study area into a regular tessellation comprised of 779 hexagonal cells that were each 12 km^2 (Figure 1). Cell size was based on the approximate daily travel distance of bison in our study area during late-winter (T. S. Jung, Environment Yukon, unpublished data).

Occurrence of bison, moose, caribou, and sheep was determined through the observation of animals or their tracks in the snow (e.g. Jenkins and Wright 1988, Jung et al. 2009, Bowman et al. 2010) during aerial surveys ($n = 11$) conducted 10–31 March 2010. Aerial surveys were completed in a Maule M-7-235 "Super Rocket" (Maule Air, Moultrie, Georgia, USA), which is a small, manoeuvrable fixed-wing aircraft that has a low stall speed and a tight turning radius. A crew consisting of the pilot and 1or 2 experienced observers flew through the approximate center of each grid cell (*sensu* Bowman et al. 2010) at an altitude of approximately 150–300 m ASL and an approximate ground speed of 90–120 km/hr. The open nature of most of the habitat in our study area permitted observation distances of ≥500 m on either side of the aircraft. When animals or their tracks in the snow were observed we broke our flight path and investigated to obtain a positive species identification. All observers and the pilot were experienced in identifying fresh ungulate tracks in the snow. The 4 primary species in our study area (bison, caribou, moose, sheep) left distinctive tracks in the snow that were readily recognizable to experienced observers. Regardless, to reduce observation bias in the identification of animal tracks in the snow an experienced observer (T. S. Jung) conducted 82% (9 of 11) of the aerial surveys. We surveyed 92–265 ($\bar{x} = 183.3 \pm 69.5$ *SD*) cells per survey. Each cell was surveyed 1–5 times ($\bar{x} = 2.6 \pm 0.8$ *SD*) to increase our confidence in determining species presence (Bowman et al. 2010). With each subsequent survey we strived to enter and exit cells from a different angle, increasing our spatial coverage of each cell.

Data Analyses

We used ArcGIS (ver. 10.1) to calculate the number of observed cells occupied by a species, as well as the number and percentage of cells where bison and each of the other species co-occurred. Co-occurrence was assessed through a null model analysis (Gotelli 2000, Ulrich and Gotelli 2013), using EcoSim Professional (ver. 1.2d). Data were organized in a 4 x 779 presence-absence matrix with rows as species ($n = 4$) and columns as sites (cells; $n = 779$). We calculated the *C*-score (Stone and Roberts 1990) and *V*-ratio (Schluter 1984) indices of co-occurrence, both of which are based on the checkerboard distribution (Conner and Simberloff 1979, Diamond and Gilpin 1982). The *C*-Score is the average number of checkerboards between all possible species pairs. The *V*-ratio is the ratio of the variance of the column (cells) sums to that of the row (species) sums. Higher *C*-score values indicate less co-occurrence of species; conversely, the smaller *V*-ratio values indicate greater co-occurrence of species. In a community structured by competition, the *C*-score should be significantly greater, and the *V*-ratio significantly smaller, than by chance (Gotelli 2000). *C*-scores and *V*-ratios were calculated by comparing our observed ungulate community structure with simulated communities, using fixed randomization algorithms for both row and columns, and a Random Knight's Tour swapping algorithm, as model settings in EcoSim Professional. Our Monte Carlo simulations used 50,000 simulated communities to combat potentially high Type 1 and Type 2 error rates (Fayle and Manica 2010). Ulrich and Gotelli (2007, 2013) concluded that fixed-fixed randomization algorithms have become "a standard method for testing for patterns of species co-occurrence" because of their power "to detect checkerboard pairs embedded in noisy data matrices", compared to equiprobable or proportional randomization algorithms.

The observed *C*-score was considered significantly less than expected by chance when $P_{(observed \geq expected)} < 0.05$ and significantly greater when $P_{(observed \leq expected)} < 0.05$. Conversely, *V*-ratios were significantly greater than random when $P_{(observed \geq expected)} < 0.05$ and lesser when $P_{(observed \leq expected)} < 0.05$.

RESULTS

Of the 779 hexagonal cells we surveyed, 676 (86.8%) cells were surveyed ≥2 times, 501 (64.3%) were surveyed ≥3 times, and 56 (7.2%) were surveyed 4–5 times. Altogether we flew 7,670 km during 73.5 hours of aerial survey. We observed bison, moose, caribou, and sheep (or their tracks in the snow) in a sufficient number of cells to permit analyses. Horses, elk, and deer were observed in only a few (≤10) cells clustered in the southern edge of the study area; thus, we excluded them from our analyses. We observed no mountain goats during our aerial surveys.

No evidence of ungulate occurrence was observed in 119 (15.3%) of the cells. Only 1 species of ungulate was observed in 313 (40.2%) of the cells, whereas 309 (39.7%) and 38 (4.9%) cells had evidence of 2 and 3 species of ungulates, respectively. We did not observe evidence of all 4 ungulate species present in any cells during our survey period.

Moose were observed in the largest percentage of cells surveyed (66%), followed by bison (54%), caribou (12%), and sheep (4%). Bison, moose, and sheep were distributed throughout the study area, whereas caribou were absent from the eastern third (Figure 1). Moose were found in a much higher percentage of cells (28%) without bison than caribou (4%) or sheep (2%; Table 1). However, the percentage of cells that were occupied by moose, caribou, and sheep, but not bison, was similar among species (37–43%; Table 1; Figure 1).

The ungulate community in southwestern Yukon was distributed at random with respect to each other, based on the statistical significance of the *C*-score (11,890.5; $P_{(observed \leq expected)} = 0.66144$, $P_{(observed \geq expected)} = 0.33894$) and *V*-ratio (0.68907, $P_{(observed \leq expected)} = 1.0$, $P_{(observed \geq expected)} = 1.0$). Thus, at the community level, the null hypothesis was supported. *C*-scores and *V*-ratios provided similar (but not identical) rank orders of comparisons among species pairs (Table 2). Caribou and sheep, and bison and sheep, had the greatest co-occurrence of our species pairs, indicating a somewhat positive association. Conversely, bison and moose, and bison and caribou had the lowest co-occurrence, indicating an association that tended to be negative (Table 2). The difference in *C*-scores between bison and sheep and bison and moose was over 5-fold (3,135 v. 27,750, respectively). None of the pairwise comparisons, however, were significant (all *P* values ≥ 0.2486), suggesting that all of the species pairs were distributed at random with respect to one another. The null hypothesis was supported for all species pairs in our study area.

DISCUSSION

Species Co-occurrence

The main finding of our study is that we did not find evidence that the late-winter spatial distribution of reintroduced bison impacted that of resident caribou, moose, or sheep. The ungulate community in our study area was randomly distributed (i.e., neutral interaction; Darmon et al. 2012) with respect to interactions between its member species; our null hypotheses was supported at the community level and for all subsequent pairwise comparisons.

Our results are contrary to a meta-analysis of 96 ecological communities conducted by Gotelli and McCabe (2002). They reported that co-occurrence was significantly less in most of the plant and animal communities they investigated, suggesting that competition played a role in structuring those communities. However, results for ungulate communities tend to be more mixed. This is consistent with a review by Hopf et al. (1993), who found that "some [terrestrial vertebrate communities] exhibited strong assortment patterns while others showed no evidence of such patterns". Many studies provided evidence for a spatial structure among ungulate species based on negative associations, indicating communities structured by competition (e.g., Voeten and Prins 1999, Namgail et al. 2010, Acebes et al. 2012); yet, others reported spatial distributions that were based on positive associations among species pairs that were centered on areas rich in forage (e.g., Stewart et al. 2002, Redfern et al. 2006, Shrestha and Wegge 2008, Darmon et al. 2012). Few studies provided evidence for a neutral interaction among ungulate species pairs, such as we observed.

Perhaps our failure to detect spatial structure in the ungulate community of southwestern Yukon, may be a result of the spatial scale we chose. Multi-scale approaches of the spatial structure of ungulate communities appear to be rare. For example, Namgail et al. (2010) observed that the co-occurrence of urial (*Ovis orientalis*) and blue sheep (*Pseudois nayaur*) was neutral at the coarse regional scale, but there was a negative association at a finer landscape scale. Our survey cells were of moderate size (12 km^2), and it is possible that smaller cells would have resulted in us more readily observing negative associations and larger cells would have likely led to observable positive associations. Smaller cells surveyed frequently may have also allowed an opportunity to observe any competitive displacement between species pairs (e.g., Stewart et al. 2002), but that was beyond the scope of our study. Nevertheless, it seems reasonable that the detection of co-occurrence is scale-dependent; however we are not aware of any formal tests of this. Regardless, our cell size, based on the approximate daily movement rate of ungulates in our study area, seemed *a priori* like a reasonable size for surveying a large area at an appropriate scale. The fact that 55.5% of the cells we surveyed had evidence of ≤1 ungulate species present suggests that our cell size was small enough to detect a checkerboard pattern (negative association) among species pairs, if one had existed.

Potential for Competition

While none of our species pairs were statistically associated with one another, bison and sheep were substantially more positively associated then were bison and caribou or bison and moose. This suggests that there may be the potential for interspecific competition between bison and sheep, given that they are similarly distributed across the landscape, even though that association is weak. Conversely, our data suggest that the potential for competition between bison and caribou and bison and moose is low, given that, during late-winter, they do not co-occur on the landscape. Winter co-occurrence patterns we observed between bison and resident ungulates mirror those of diet overlap. Jung et al. (see Appendix A) reported high dietary overlap between bison and sheep and low overlap between bison and moose and bison and caribou, during winter. Given high dietary overlap and weak co-occurrence, there may be some (low) potential for competition between bison and sheep in winter.

Pointedly, while the potential for competition may be a cause for concern because of the insertion of a large ungulate (bison) into an existing species assemblage by humans (Voeten and Prins 1999, Mishra et al. 2004), our finding that the spatial distribution of these species is neutral (random) is consistent with the theory of the "ghost of competition past" (Connell 1980). While bison have been absent from our ungulate community for ≥350 years, they were once a numerically dominant species in northwestern North America that coexisted with caribou, moose, and sheep (Guthrie 1968). For these species to have coexisted on a shared range for thousands of years during the late Pleistocene and early Holocene they would have likely mutually evolved mechanisms to partition resources along various niche axes (Connell 1980, Hopf et al. 1993). Ecological niches filled by caribou, moose, and sheep in our study area had perhaps already co-evolved such that spatial or temporal segregation, or sharing of resources (food and habitat), was not incompatible with respect to bison. In this sense, it is plausible that bison reintroduced to this species assemblage may in fact be filling an ecological niche that has been largely vacated since they were locally extirpated.

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Table 1. Summary counts of the presence/absence of reintroduced bison and resident ungulates (moose, caribou, and sheep) in 12.2 km^2 cells (n = 779) surveyed in southwestern Yukon, Canada, during March 2010.

	Bison-Moose		Bison-Caribou		Bison-Sheep	
	Number	%[1]	Number	%[1]	Number	%[1]
Cells with bison only	125	16	357	46	397	51
Cells with the resident species only	222	28	35	4	13	2
Cells with both species	292	37	60	8	20	3
Occupied cells without bison [2]	222	43	35	37	13	39

[1] does not add to 100% because some cells had neither species present.
[2] the number and percent of cells occupied by the other species that were not occupied by bison.

Table 2. Co-occurrence index values for ungulate species pairs on a shared winter range in southwestern Yukon, Canada. *C*-scores are above the dotted line, whereas *V*-ratios are provided below the dotted line. Smaller *C*-score values, and larger *V*-ratios, indicate greater co-occurrence of species pairs than expected by random. Co-occurrence indices calculated via null model analyses using 50,000 Monte Carlo simulations (randomizations) each. All *P* values ≥ 0.2846.

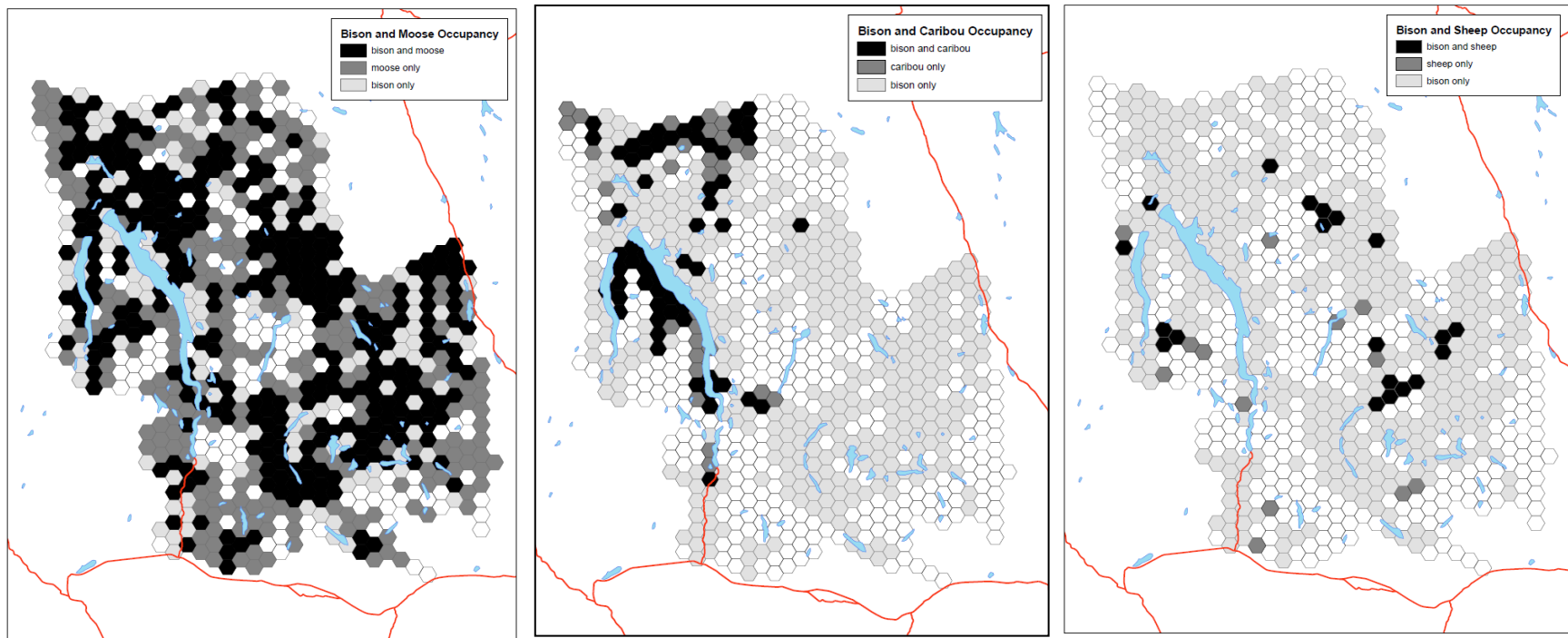| SPECIES	Bison	Caribou	Moose	Sheep
Bison		12,485	27,750	5,161
Caribou	0.859		16,380	3,135
Moose	0.730	0.469		6,422
Sheep	0.936	0.930	0.441	

Figure 1. Late-winter occurrence of A) bison and moose, B) bison and caribou, and C) bison and sheep in 12 km^2 hexagon cells ($n = 779$) in southwestern Yukon, Canada. Occurrence was determined by observations of animals or their tracks in snow as seen during 11 aerial surveys in March 2010.