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Meeting caribou in the alpine: Do moose compete with caribou for food?



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ABSTRACT

The Atlantic-Gaspésie caribou (*Rangifer tarandus caribou*) is an endangered, isolated population that has been declining for decades in response to intensive logging. Timber harvesting has led to a significant increase in moose (*Alces americanus*) densities and has triggered numerical and functional predator responses. Moose are now frequently observed at higher altitudes in preferential caribou habitat. Despite extensive range overlap between these two species across Canada, few studies have precisely assessed the potential role of exploitative competition. We assessed the potential overlap between their diets during summer, a key period for energy and nutrient acquisition in cervids. We collected faeces from both species along an altitudinal gradient (200 m–1250 m asl) and used plant chloroplast barcoding sequence trnL to reconstruct diet at the species level. Plant species composition differed between caribou and moose samples, with cervid species explaining 40% of the variation in dissimilarity. We noted slight variations in dissimilarity between species between months and along an altitudinal gradient. Some species that are almost exclusively eaten by moose (speckled alder, wild redcurrant) or by caribou (common juniper, common horsetail) contributed the most to the dissimilarity between diets. The potential for food competition appears relatively low, even at increased moose densities, possibly as a result of past competition. This separation in food niche could also be explained by an imperfect segregation of species since the proportion of time spent in different strata of altitude is unequal. High moose densities thus appear to be more harmful to caribou due to shared predators, but a low level of competition for a few food items could contribute to the decline of this endangered population if some caribou are nutritionally stressed.

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1. Introduction

Exploitative competition is a key mechanism regulating interactions between large herbivores (Belovsky, 1986; Latham, 1999). It occurs when the three following conditions are met: 1) overlap in habitat use, 2) shared diet in the overlapping habitat and 3) limited shared resources (De Boer and Prins, 1990). Many studies on niche overlap have focused on interactions between native and human-introduced species, such as livestock (Baldi et al., 2004; Li et al., 2008). In contrast, species naturally co-occurring in sympatry are expected to demonstrate a stronger resource partitioning because they coevolved under higher competition pressure (Connell, 1980). For example, sympatric ungulates are known to use resources in a different way, as shown for grazing ungulates in the African savannah, which feed on different parts of the same plant species according to their nutrient requirements (Gwynne and Bell, 1968). In North America, Hodder et al. (2013) showed that the overlap in diet between three sympatric ungulates (mule deer *Odocoileus hemionus*, elk *Cervus canadensis* and moose *Alces americanus*) supported the theory that native sympatric herbivores display resource partitioning. However, the fragile equilibrium between sympatric species may have been recently disturbed by intensive anthropogenic activities such as cropping, forestry and urbanization. These activities have deeply modified the landscape structure and composition (St-Laurent et al., 2009) by mixing flora and fauna that were previously isolated (Vitousek et al., 1997). Those new situations of co-occurrence between species may cause rapid niche changes (over less than 100 years; Fitzpatrick et al., 2007), which may in turn represent a key factor in allowing successful invasion by new species (Pearman et al., 2008). For example, it has been shown that following the American mink (*Neovison vison*) invasion, the native European mink (*Mustela lutreola*) switched its diet considerably over the course of a few years to reduce the overlap in food niche (Sidorovich et al., 2010).

Caribou (*Rangifer tarandus caribou*) and moose are two ruminant cervids from northern regions. Despite the fact that these two species are sympatric in both forest and tundra biomes, they generally live in different habitats (Boer, 1998). In the boreal forest, caribou select areas found at higher elevations and with alpine shrubs while moose prefer mixed and early-seral habitats altered by anthropogenic disturbances like linear features and logging (Peters et al., 2013). Accordingly, the intensive forest management that occurred over the last decades has been beneficial to moose populations and has led to strong increases in their densities (Crête, 1988; Boan et al., 2011). This increase in moose abundance has in turn supported an increase in the densities of wolves (*Canis lupus*) and bears (*Ursus americanus*) (Wittmer et al., 2005), two common predators of both caribou and moose, linking these four large mammals in an apparent competition interaction (Holt, 1977, 1984), known to be detrimental to caribou (Kinley and Apps, 2001; Wittmer et al., 2007, 2010). In this multiple predator – multiple prey interaction, caribou populations are more vulnerable to decline, as they represent a less productive prey than moose (producing one calf annually while moose cows can have twins; Bergerud, 1974) and their preferential habitat is intensively altered (Fiesta-Bianchet et al., 2011; Environment Canada, 2012; Rudolph et al., 2017).

Moose densities found in Gaspésie (a region in eastern Québec, Canada) are among the highest in the province of Québec, with estimates ranging from 1.1 to 3.3 moose/km² in the surroundings of the Gaspésie National Park (Dorais and Lavergne, 2010; Lamoureux et al., 2012). In recent years, tourists and park rangers frequently reported observations of moose at higher altitudes in summer within the preferential habitat of caribou (i.e. alpine tundra, subalpine forests). Despite the fact that moose and caribou now appear to share the same summer habitat, no study, to our knowledge, has assessed the potential for exploitative competition between these two species (but see Jung et al., 2015). The direct or indirect interactions between these species and the difficulty of evaluating the final outcome of these interactions (positive or negative) in the natural environment were the basis of this study.

Studies conducted in Alaska and Newfoundland found that caribou mainly fed on deciduous shrubs like willow (*Salix* spp.; Boertje, 1984) and birch (*Betula* spp.; Bergerud, 1972) during the summer, but they also fed on terrestrial lichens, forbs and graminoids. Berries (*Vaccinium uliginosum*; Bergerud, 1972, and *V. vitis-idaea*; Boertje, 1984) were also found in their diet. In Ontario, Thompson et al. (2015) used remote video cameras to assess seasonal diet composition of woodland caribou. They found that caribou fed mainly on terrestrial lichens, even in spring and summer, and on graminoids. In contrast, the summer diet of moose living at high elevations in Colorado was largely composed of willow and, to a lesser extent, alder (*Alnus rugosa*), aspen (*Populus tremuloides*) and birch (Dungan and Wright, 2005). A study in south-central Norway found that moose fed mainly on birch, rowan (*Sorbus*), *Salix* spp., and aspen (*Populus*) in summer (Wam and Hjeljord, 2010). These previous studies were all based on microhistological faeces analyses, field observations and rumen content. These analyses can help estimate the proportion of the diet composed of various forage species (even if pooled into broader taxonomic groups), particularly when forage becomes senescent. However, they are also considered to be imprecise or unable to identify soft-tissue plants, and they do not have a high taxonomic resolution compared to DNA metabarcoding (Newmaster et al., 2013). This latter method consists in extracting DNA from an environmental sample, in this case faeces, and amplifying a target DNA fragment with a predefined pair of primers using polymerase chain reaction (PCR). Subsequently, the amplicons obtained are sequenced in order to identify the species to which they belong (Pompanon et al., 2011). In addition to its higher taxonomic resolution, DNA metabarcoding has the advantage of providing a rapid and automatable species identification in comparison to more traditional methods (Taberlet et al., 2007).

In this study, we aimed to assess the potential of exploitative competition between caribou and moose in the area of the Gaspésie National Park. We set the following four objectives: 1) describe the composition of moose and caribou diets and assess the similarity between them; 2) evaluate if the diet composition of caribou and moose changed over the summer (i.e. on a monthly basis, as a proxy of plant phenology) and along an altitudinal gradient; 3) if diets were different, determine which plant species distinguished caribou and moose diets and 4) apply metabarcoding for analysis of cervid diet.

2. Material and methods

2.1. Study area

This study was conducted in the Gaspésie National Park, at the center of the Gaspésie Peninsula, south of the St. Lawrence River (48°56'50.64" N, 66°07'20.49" W). Some of the highest peaks found in southern Quebec are located in this region. The climate is cold and humid, with an average rainfall of 1600 mm, of which 60% falls as snow (Boudreau, 1981), and annual average temperatures range from 2.1 °C at low altitudes to −4.0 °C on summits (Gagnon, 1970). The vegetation is typical of the boreal forest and belongs to the balsam fir (*Abies balsamea*) – white birch (*Betula papyrifera*) bioclimatic domain (Grandtner, 1966). The altitudinal-climatic gradient shapes the extent of three distinct vegetation belts: mountain (<900 m), subalpine (900–1050 m) and alpine (>1050 m) (Boudreau, 1981).

2.2. Sample collection

As the Atlantic-Gaspésie caribou is recognized as an endangered species under the Species at Risk Act (SARA) (Environment Canada, 2002), we used faecal analysis, a non-invasive sampling technique, to describe diet of both cervid species. Moose and caribou faeces were collected opportunistically in the caribou distribution range along an altitudinal gradient (ranging from 200 m to 1270 m asl). Only fresh faeces were collected to ensure that we based our analyses on samples that were a few hours or a few days old. Four sampling periods of 5 consecutive days each were conducted in June, July, August and September 2015. By spreading the sampling over a 4-month period along a considerable altitudinal gradient (>1000 m) in the 830 km² study area, we minimised the probability of pseudoreplication caused by sampling the same individual multiple times (see Fig. S1 for estimated monthly displacement). To maximise the time spent collecting samples during fieldwork sessions and given the low number of caribou in the study area (~70–80 during at the time of sample collection, divided in two subgroups on three mountain summits; Pelletier et al., 2019), we concentrated our sampling effort in core areas used by caribou (and delineated with the GPS data gathered on 43 collared individuals; see Lesmerises et al., 2017 for more details on telemetry tracking and Animal Welfare Certificates). On the other hand, since moose are very abundant in the area (Dorais and Lavergne, 2010; Lamoureux et al., 2012), it was much easier to find faeces. For each sample, we noted the date, location (GPS coordinates) and altitude. Samples were frozen as soon as possible while in the field, then transferred at −80 °C when back to the lab. We targeted a sample size of ~40 faecal pellet groups for each species for the entire summer, i.e. 10 pellet groups by species for each of the 4 sampling periods.

2.3. Genetic analyses of faecal samples

Faeces were freeze-dried for 48 h before being individually crushed with an ultra-centrifugal mill ZM 200 (Retsch®). Genomic DNA from 15 mg of each faeces was extracted with DNeasy Plant kit (Qiagen) according to manufacturer's instructions. DNA amplification, primer constructs, purification and sequencing were done as described in Bérubé et al. (2018; see for more details). We PCR-amplified the plant chloroplast barcoding sequence trnL UAA intron using Taberlet et al. (2007) primers *c* (CGAAATCGGTAGACGCTACG) and *d* (GGGGATAGAGGGACTTGAAC) located in exon 1 and 2 of the trnL gene. We used a two-step PCR method with fusion tagged primers developed for Illumina. In PCR-1, we amplified the trnL target region using the Illumina fusion primers. The amplicons obtained were reamplified in PCR-2 with Illumina Universal Indexed primer 1 and Illumina Indexed Primer 2 compatible with Illumina technology.

2.4. Bioinformatic

The amplicons obtained by trnL primers *c* and *d* were nearly as large as the assembled Illumina paired-end 300 bp forward and reverse sequences, producing a poor-quality overlap when assembled. We used only the forward Illumina sequence for the bioinformatics analyses since they were in the most informative portion of the gene. Sequence assembly was done using PANDASeq (Masella et al., 2012) and was then filtered and trimmed with Illumicut (Gagné and Bérubé, 2017a). Sequences with homopolymers longer than 9 bp were removed and HomopRemover (Gagné and Bérubé, 2017b) reads shorter than 120 bp were discarded. Dereplication on the full length of the set of sequences was performed before construction of clusters with MOTHUR v.1.28.0 (Schloss et al., 2009). The sequence set was then organized into clusters with USEARCH 64 bit (Edgar, 2010) with a sequence similarity threshold of 97% (Valentini et al., 2009) to agglomerate DNA reads and create the molecular operational taxonomic units (MOTU), our proxy for plant species eaten by cervids, the most abundant sequence types serving as cluster seeds. Representative sequences, which are the most frequent sequence in each MOTU, were extracted and then screened against Genbank databases using BLAST. Output Excel files were then organised by MOTU frequencies of occurrence (i.e. the number of pellet groups in which the MOTU was detected). MOTUs for which DNA reads were counted <300 times and those found in only one faeces sample were removed from subsequent analyses (Baamrane et al., 2012), as they represented incidental consumption of a food item. Additionally, a value of 0 was given to a MOTU found <10 times in one given sample, thus these MOTUs were not analysed.

2.5. Data analysis

We used sample-based rarefaction curves to determine if the sampling effort was high enough to be representative (Kartzinel et al., 2015; Gebremedhin et al., 2016). In order to visualize similarity between samples, we used non-metric multidimensional scaling (NMDS) on a presence – absence matrix using the Bray-Curtis distance, where a value of 0 means perfect similarity and a value of 1 means perfect dissimilarity (Bray and Curtis, 1957). We performed the NMDS using a presence – absence matrix as it offers a more conservative portrait of the diets than a frequency matrix of MOTUs' relative abundance (Gebremedhin et al., 2016). An NMDS was computed on the MOTUs encountered in more than 5 samples for each cervid species, resulting in a list of 18 MOTUs. These 18 food items represented 93% and 94% of the number of sequences read in the caribou and moose diets, respectively. We ran 50 iterations and the stress value was 0.18 ($k = 2$), which is relatively high, but still lower than 0.30, suggesting that the ordinations were not arbitrary and that the plots provide a realistic portrait of the original distances between caribou and moose samples (Legendre and Anderson, 1999). We tested for significant difference in MOTU composition between factors such as species (caribou/moose), sampling month, elevation at which samples were collected and the interaction between species and month and between species and elevation using the *adonis* function (Oksanen et al., 2016). We also tested for significant difference in MOTU composition between samples from each species according to months and elevation. *Adonis* performs an analysis of variance with distance matrices using permutations and can accommodate both categorical and continuous variables (Oksanen et al., 2016). The variable 'Elevation' represents the average elevation of all the pixels (size 50 m \times 50 m) found in a 1500-m radius buffer around each faeces collected. We tested different buffer sizes (500, 1000, 1500 and 2000-m radii) to compensate for the fact that animals did not forage exactly at the location where samples were collected and we ultimately used a 1500-m radius buffer (i.e. following an AIC model selection where candidate models had the same structure but differed in radius buffer size), as it explained the greatest proportion of variance in our analysis. We verified the assumption of homogeneous multivariate dispersion (Anderson, 2001) with the *betadisper* function from the *vegan* package (Oksanen et al., 2016). We conducted a similarity percentage (SIMPER) analysis (999 permutations) to discriminate MOTUs between caribou and moose samples; by doing so, we were able to determine which MOTU contributed the most to the overall Bray-Curtis dissimilarity between both species. We used R version 3.3.0 for all analyses (R Development Core Team, 2016).

3. Results

3.1. Diet description

Our sampling resulted in 40 and 39 faeces of caribou and moose, respectively. We had to remove two caribou samples and one moose sample because of low DNA sequence read, ending with 38 samples from each species. Sequencing yielded a total of 910 066 DNA reads after removing sequences that did not meet minimal distribution criteria (Table 1), clustered into 83 MOTUs of <300 reads. Only 29 MOTUs were left after deleting MOTUs with <10 reads per faeces. We were able to identify 27 MOTUs at the species level and one MOTU at the genus level (*Betula*), since it was impossible to differentiate *B. glandulosa* from *B. papyrifera*, using trnL sequence. Finally, 1 MOTU was identified at the family level (*Asteraceae*). Sample-based accumulation curves for both ungulate species approached asymptotes, meaning that more samples would not have improved the identification rate of MOTUs, suggesting that the sample sizes were sufficient to describe diet for the two cervid species (Fig. S2). Twenty-nine different MOTUs were identified in moose samples, while only 20 MOTUs were found in caribou faeces (Table 1). The number of MOTU per individual caribou sample ranged from 1 to 10 (mean = 4.84, variance = 3.87), and from 3 to 14 in individual moose samples (mean = 6.71, variance = 4.37) (see Fig. S3). We listed consumed MOTUs and marked those present in more than 5 samples for both species (Table 1). MOTUs most frequently found in caribou samples were *Juniperus communis*, *Abies balsamea*, *Betula* spp. and *Equisetum arvense*. These MOTUs have been identified respectively in 89%, 76%, 63% and 61% of the collected caribou faeces (Table 1). For moose, MOTUs most frequently found in faeces were *Betula* spp. (97%), *Alnus rugosa* (84%), *Ribes triste* (68%) and *A. balsamea* (53%; Fig. 1).

3.2. Similarity between diets

The NMDS suggests that two distinct groups exist in our dataset, representing caribou and moose samples (Fig. 2a). Species located near the origin of the NMDS plot (i.e. *Vaccinium vitis-idaea*, *Vaccinium uliginosum*, *A. balsamea* and *Betula* spp.) were the most represented species found in both caribou and moose samples. The assumption of homogeneous multivariate dispersion between groups was respected ($F_{(1)}=0.17$, n.perm = 99, $P=0.67$). MOTU composition differed between caribou and moose samples ($F_{(1)}=56.46$ $P<0.001$; see Table 2); the ungulate species explained 40% of variance of the Bray-Curtis distance in the presence – absence matrix of the samples. MOTU composition differed between months ($F_{(3)}=2.73$ $P=0.01$), but only explained 6% of the difference in sample composition. Diet composition changed slightly from June to September (Fig. 2). However, the interaction between species and months was only marginally significant ($F_{(3)}=1.93$, $P=0.045$) and explained a low portion of total variance ($R^2=0.04$). This suggests that dissimilarity between caribou and moose diet changed only slightly throughout summer months (see Fig. 2b, c, d and e). MOTU composition also differed along the altitudinal gradient ($F_{(1)}=3.82$; $P=0.02$), suggesting that samples collected at different elevations were more dissimilar than samples collected at comparable altitudes; still, this factor only explained 3% of the dissimilarity between species (Table 2). MOTU composition did not differ between

Table 1

List of plant species identified by best BLAST match from GenBank in the diet of caribou and moose in the Gaspésie National Park during summer 2015. Bolded characters are MOTUs found in more than 5 caribou faeces. Underlined MOTUs are present in more than 5 faeces of moose. Sorting is done according to frequency of occurrence in caribou faeces.

Best BLAST match	No. of sequence reads		Proportion of the number of sequences	
	caribou	moose	caribou	moose
<i>Juniperus communis</i>	133 684	140	0.45	0
<i>Abies balsamea</i>	8716	41 113	0.03	0.07
<i>Betula spp.</i>	29 321	375 286	0.1	0.62
<i>Equisetum arvense</i>	99 243	6468	0.33	0.01
<i>Ptilidium ciliare</i>	2758	112	0.01	0
<i>Vaccinium vitis-idaea</i>	1907	17 225	0.01	0.03
<i>Cornus canadensis</i>	506	4137	0	0.01
<i>Pleurozium schreberi</i>	313	1265	0	0
<i>Dicranum fuscescens</i>	258	614	0	0
<i>Vaccinium uliginosum</i>	1357	1468	0	0
<i>Asteraceae sp.</i>	152	436	0	0
<i>Equisetum hyemale</i>	6278	269	0.02	0
<i>Alnus rugosa</i>	4269	49 570	0.01	0.08
<i>Ribes triste</i>	3639	52 812	0.01	0.09
<i>Sorbus americana</i>	136	5982	0	0.01
<i>Picea glauca</i>	708	1707	0	0
<i>Equisetum sylvaticum</i>	2110	7831	0.01	0.01
<i>Ranunculus reptans</i>	227	140	0	0
<i>Salix Bebbiana</i>	28	2585	0	0
<i>Splachnum sphaericum</i>	4337	14 851	0.01	0.02
<i>Acer spicatum</i>	0	13 417	0	0.02
<i>Rubus idaeus</i>	0	1673	0	0
<i>Fragaria virginiana</i>	0	309	0	0
<i>Zea mays</i>	0	4858	0	0.01
<i>Trientalis borealis</i>	0	1597	0	0
<i>Sphagnum russowii</i>	0	417	0	0
<i>Epilobium angustifolium</i>	0	404	0	0
<i>Pinus strobus</i>	0	1615	0	0
<i>Tayloria serrata</i>	0	682	0	0

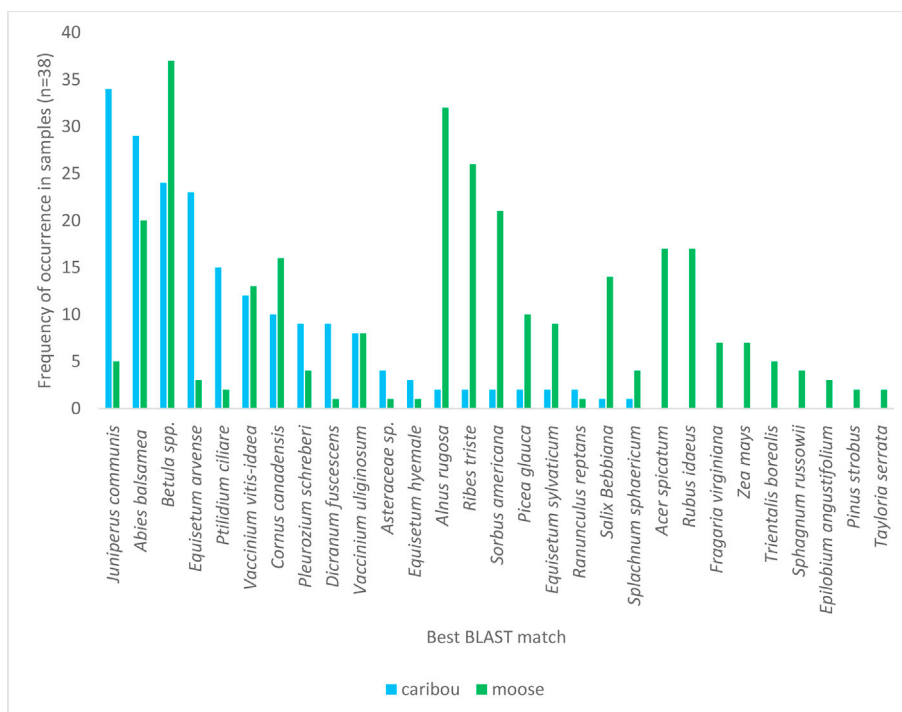


Fig. 1. Frequency of occurrence of the best BLAST from GenBank describing the diet of caribou and moose in the Gaspésie National Park during summer 2015.

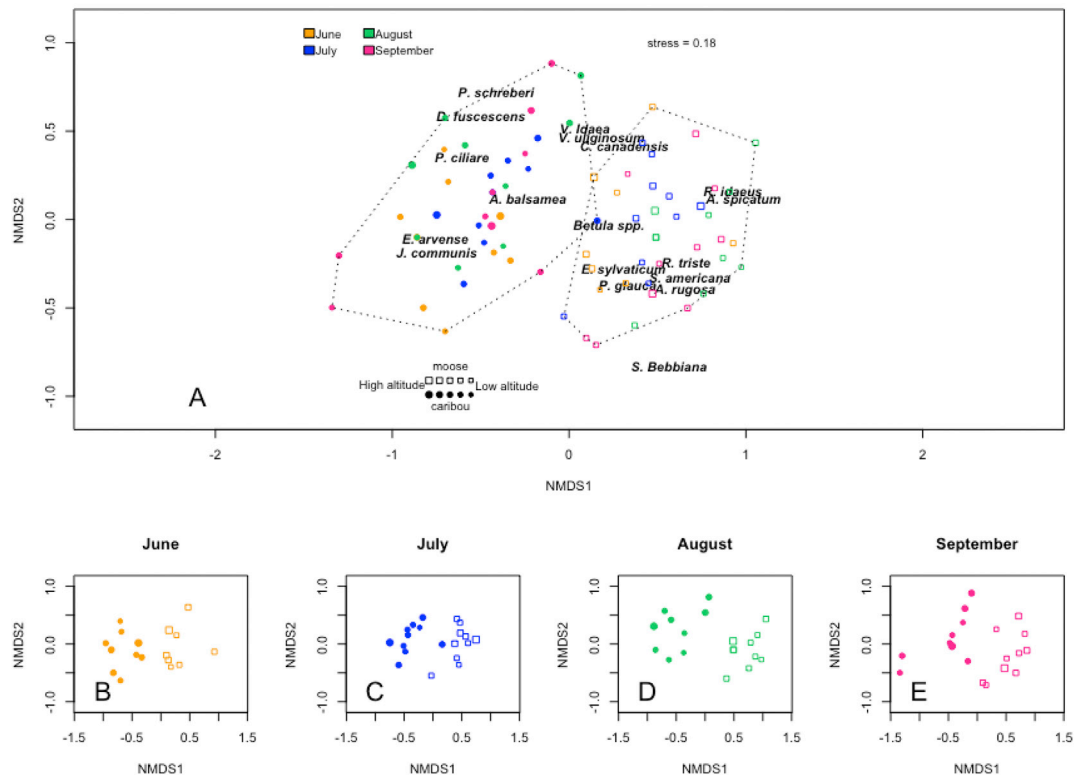


Fig. 2. The difference in the specific composition of the samples is illustrated by A) Non-metric multidimensional scaling (NMDS) using Bray-Curtis distance on a presence/absence matrix of the MOTUs found in more than five samples collected in the Gaspésie National Park during summer 2015 for both species (16 different MOTUs). In order to better visualize changes in dissimilarity between months, we plotted samples separately for each month: B) June, C) July, D) August and E) September. Note that some symbols overlap within a species.

Table 2

Results of the analysis of variance with distance matrices using permutations (*adonis* analysis) based on 999 permutations to compare MOTU composition between factors (species, month, altitude) and their interactions, based on faeces collected in the Gaspésie National Park during summer 2015. Degrees of freedom (df), F statistics, model fit (R^2) and P -values are shown.

Variables	df	F	R^2	P
Species	1	56.46	0.40	0.001
Month	3	2.73	0.06	0.010
Altitude	1	3.82	0.03	0.021
Species x months	3	1.93	0.04	0.052
Species x altitude	1	0.99	0.01	0.432
Residuals	66		0.47	
Total	75		1.00	

months and along the altitudinal gradient for caribou (months: $F_{(3)} = 1.55$, $P = 0.144$; altitude: $F_{(1)} = 0.21$, $P = 0.858$) (Table 3). However, the interaction between month and altitude was significant ($F_{(3)} = 2.67$, $P = 0.010$) (Table 3). For moose, we observed the opposite, as MOTU composition differed between months and along the altitudinal gradient (months: $F_{(3)} = 3.57$, $P < 0.001$; altitude: $F_{(1)} = 5.80$, $P < 0.001$) but the interaction between these variables was not significant ($F_{(3)} = 0.47$, $P = 0.900$) (Table 3).

Alnus rugosa, *J. communis*, *R. triste* and *E. arvense* drove the dissimilarity between caribou and moose diets ($P < 0.001$, accumulated dissimilarity contribution of 0.37) (Table 4). Other MOTUs such as *Sorbus americana*, *Acer spicatum*, *Betula spp.*, *Rubus idaeus* and *Salix bebbiana* also significantly contributed to the dissimilarity index, but their contribution was lower (Table 4). The overall Bray-Curtis dissimilarity index between caribou and moose samples yielded by the SIMPER analysis reached 0.72.

4. Discussion

We studied the summer diet of caribou and moose within the range of an endangered population of mountain caribou where moose are found at very high densities using a novel and efficient methodology that enables us to obtain an accurate,

Table 3

Results of the analysis of variance with distance matrices using permutations (*adonis* analysis) based on 999 permutations to compare MOTU composition of caribou and moose between month, altitude and their interactions, based on faeces collected in the Gaspésie National Park during summer 2015. Degrees of freedom (df), F statistics, model fit (R^2) and *P*-values are shown.

Caribou				
Variables	df	F	R^2	<i>P</i>
Month	3	1.55	0.11	0.144
Altitude	1	0.21	0.00	0.850
Month x altitude	3	2.67	0.19	0.010
Residuals	30		0.70	
Total	37		1.00	
Moose				
Variables	df	F	R^2	<i>P</i>
Month	3	3.57	0.22	0.010
Altitude	1	5.80	0.12	0.001
Month x altitude	1	0.47	0.03	0.900
Residuals	66		0.63	
Total	75		1.00	

rapid, automated and high-resolution description of diet. Consumed plant species composition differed between caribou and moose, explaining 40% of the variation in dissimilarity between samples. Slight variations in dissimilarity between species across different months and along an altitudinal gradient were observed, confirming distinction between both diets.

4.1. Niche breadth and similarity

Moose exhibited a broader food niche than caribou, with 29 MOTUs identified in moose samples vs. 20 in caribou samples, which reflects into a slightly higher species richness and diversity index for moose diet (Fig. S3). Moose are known to be a generalist herbivore (Belovsky, 1981). However, Jung et al. (2015) highlighted a wider niche breadth for caribou in Yukon. It has been shown that individuals could be forced to add alternative species to their diet when resources are scarce, a situation observed in Italy for Alpine chamois (*Rupicapra rupicapra*; La Morgia and Bassano, 2009) and in Africa for Black rhinoceros (*Diceros bicornis*; Landman et al., 2013). In our study area, *Betula* spp. (representing both white birch *Betula papyrifera* and American dwarf birch *B. glandulosa*) was the food item most frequently found in moose faecal samples, while the remaining consisted of deciduous browse such as *J. communis*. *Betula* was shown to be the main food item found in rumen collected in September in Sweden (Palo and Wallin, 1996) and was amongst the selected species in Norway in summer (Hjeljord et al., 1990). In contrast, moose did not favour *Betula* consumption during the summer in Colorado (Dungan and Wright, 2005), while Shipley et al. (1998) found that over 75% of moose diet consisted of Scots pine (*Pinus sylvestris*) and *Salix* in Sweden. This reflects how the selection of a specific food item can vary depending on its availability or the availability of other species (Vivas and Saether, 1987).

Juniperus communis and *E. arvense* were the most frequently found MOTU in our caribou samples. To our knowledge, we are the first to document *J. communis* in caribou summer diet; Bergerud (1969) observed a herd feeding mainly on this species in a wintering area disturbed by wildfire. Some studies on animal nutrition reported that *J. communis* is a highly caloric food item (Rolando and Laiolo, 1997; Rodríguez and Obeso, 2000), while another suggested that *E. arvense* was a notable source of sodium, potassium and calcium (Staaland et al., 1983). Our findings differ from observations made by Bergerud (1972), Boertje (1984) and Thompson et al. (2015) in Newfoundland, Alaska and Ontario respectively, who found that caribou summer diet was mainly focused on willow, birch and terrestrial lichens, and, to a lesser extent, on forbs and graminoids.

However, the availability of birch is likely to be reduced due to the narrow altitudinal forest belt in which birch can be found and the high moose densities in the area (Renecker and Schwartz, 1998). Moreover, balsam fir regeneration in fir stands of the mountain belt (<900 m) seems to be constrained by many factors, including overbrowsing by moose (Nadeau Fortin et al., 2016). Consequently, despite the fact that both cervids consume different food resources that may limit the competition intensity, we cannot exclude the relatively important potential for competition between caribou and moose for both balsam fir and white birch stems, two important food resources that support intensive browsing pressure in our study area.

The composition of summer diet differed between caribou and moose samples (but see the Limitations section below). Several studies demonstrated that such resource partitioning between sympatric species is a result of past competition (caribou and bison: Fischer and Gates, 2005; Alpine chamois and mouflon *Ovis gmelini musimon*: Darmon et al., 2012; mule deer, moose and elk *Cervus elaphus*: Hodder et al., 2013). The oldest fossils of caribou found in North America suggest that species occupancy is ~50 000 years old (Banfield, 1961), while there is no evidence of moose presence in North America >15 000 years ago (Hundertmark et al., 2002). Therefore, caribou and moose could have been living in sympatry on the same continent for the past ~15 000 years, suggesting they have coevolved to reduce exploitative competition. Our results suggest that this potential evolutionary differentiation in food niche remains observable despite the recent and important increases in moose densities in the range of Gaspésie caribou. Ben-David et al. (2001) compared caribou and moose summer diets in Alaska using stable isotopes and obtained similar results to ours. They showed that isotopic ratios were significantly different

Table 4

Results from the similarity percentage (SIMPER) analysis, showing the average contribution of each MOTU to overall Bray-Curtis dissimilarity between caribou and moose faecal samples collected in the Gaspésie National Park during summer 2015. Cumulative contribution (sum of average contribution to overall dissimilarity) and their associated *P*-values are also shown.

MOTU	Average contribution to overall dissimilarity (SD)	Proportion of caribou samples	Proportion of moose samples	Cumulative contribution	<i>P</i>
<i>Alnus rugosa</i>	0.07 (0.04)	0.05	0.84	0.10	<0.001
<i>Juniperus communis</i>	0.07 (0.04)	0.89	0.13	0.20	<0.001
<i>Ribes triste</i>	0.06 (0.04)	0.05	0.68	0.28	<0.001
<i>Equisetum arvense</i>	0.05 (0.05)	0.61	0.08	0.35	<0.001
<i>Abies balsamea</i>	0.05 (0.05)	0.76	0.53	0.42	0.070
<i>Sorbus americana</i>	0.05 (0.04)	0.05	0.55	0.48	<0.001
<i>Acer spicatum</i>	0.04 (0.05)	0.00	0.45	0.53	<0.001
<i>Cornus canadensis</i>	0.04 (0.04)	0.26	0.42	0.59	0.120
<i>Betula spp.</i>	0.04 (0.05)	0.63	0.97	0.64	<0.001
<i>Rubus idaeus</i>	0.04 (0.05)	0.00	0.45	0.69	<0.001
<i>Vaccinium Vitis.Idaea</i>	0.04 (0.04)	0.32	0.34	0.75	1.000
<i>Ptilidium ciliare</i>	0.03 (0.04)	0.39	0.05	0.79	0.020
<i>Salix Bebbiana</i>	0.03 (0.04)	0.03	0.37	0.84	<0.001
<i>Vaccinium uliginosum</i>	0.03 (0.04)	0.21	0.21	0.87	1.000
<i>Pleurozium schreberi</i>	0.02 (0.04)	0.24	0.11	0.91	1.000
<i>Picea glauca</i>	0.02 (0.04)	0.05	0.26	0.94	<0.001
<i>Equisetum sylvaticum</i>	0.02 (0.04)	0.05	0.24	0.97	0.010
<i>Dicranum fuscescens</i>	0.02 (0.04)	0.24	0.03	1.00	0.300

between caribou and moose, suggesting they had a different diet. According to their results, caribou mainly fed on herbaceous vegetation, while moose mostly fed on shrubs. However, in our case, caribou do not seem to use herbaceous vegetation. Indeed, it seems that mosses and horsetails, rather than herbaceous plants, contribute to the distinction of caribou and moose diets. However, the lack of information on the relative abundance of each item in faeces prevents the interpretation of competition intensity for each species identified in the samples.

4.2. Factors influencing dissimilarity

MOTU composition of moose and caribou samples slightly changed throughout the summer and according to elevation. Thomas et al. (1996) found that the diet composition of mountain caribou changed between summer months, reflecting changing preferences. Indeed, they reported that the proportions of fragments of terrestrial lichens, *Salix* and graminoids changed over the months of June to August (Thomas et al., 1996). Dungan and Wright (2005) obtained similar results for moose, with the proportion of major plant species consumed changing over time during summer. Plant availability is known to change according to phenology (Klein, 1990) and altitude (Hebblewhite et al., 2008). However, we found that the species x month interaction and the species x elevation interaction were marginally significant. These results suggest that resource partitioning between caribou and moose is strong enough to persist even when resource availability changes through summer or along the altitudinal gradient. The overall dissimilarity between caribou and moose diet was relatively high (close to 1). As a comparison, Krüger et al. (2014), who studied the diet of insectivorous bats during autumn migration and summer residence, obtained a Bray-Curtis index value of 0.84 and thus concluded that the similarity between the two diets was quite low. According to our results, *Alnus rugosa*, *J. communis*, *R. triste* and *E. arvense* contributed the most to that dissimilarity. *Alnus rugosa* and *R. triste* were almost exclusively consumed by moose, while *J. communis* and *E. arvense* were mainly eaten by caribou. Dissimilarity between caribou and moose diets could be explained by the differences in digestive physiology between these two cervid species. Indeed, caribou are classified as grazers, an “intermediate type” of herbivore, while moose are recognized as browsers, i.e. “concentrate selectors” (Hofmann, 1989). Differences in anatomy imply some specialization of the digestive tract, which could allow a better extraction of nutrients from the vegetation ingested, and preferred forage items could also differ between the two species; as browsers, moose feed mostly on forbs, shrub leaves and stems while caribou, as grazers, tend to feed mainly on grasses (Hofmann and Stewart, 1972; Jarman, 1974). Moreover, this separation in food niche could also be explained by the segregation of species since the proportion of time spent in different strata of altitude is unequal. Even if moose observations are now more frequently made in the alpine zone, their optimal habitat is still found at lower elevations compared to caribou, which use relatively higher elevations.

4.3. Limitations

Here we studied the potential competition for forage resources between two sympatric cervid species during summer, a period of higher forage availability. As explained above, the resource partitioning between caribou and moose persisted along the altitudinal gradient (i.e. along a decreasing forage availability gradient), providing support to niche separation even at a lower abundance of food resources. We performed our statistical analysis on MOTU occurrence (presence/absence) to ensure a conservative evaluation of the species consumed by caribou and moose (Gebremedhin et al., 2016), considering that the abundance of MOTUs in faeces can be influenced by the animal's digestion and the sequencing process. However, we recognize that not accounting for the abundance of plant species in samples limits our interpretation of their relative importance in species diets. Moreover, since pseudoreplication of individual animals in our samples remains possible despite the extensive distribution of our sampling over space and time and the low abundance of caribou, the niche breadth of caribou and moose from our study area could be larger than suggested by our results, although an asymptote was noted in the sample-based accumulation curves for both species. We also consider that the inclusion of some critical variables such as sex and age could have added more precision to our model.

4.4. Conservation implications

In this study, we wanted to assess if high moose densities could exert pressure on an endangered caribou population by competing for food resources. Our findings showed that the potential for food competition appears to be low, as only a few food items are shared between the two diets. The high moose densities in the area are thus probably more detrimental to caribou due to the fact these two species share common predators (coyotes *Canis latrans* and bears; see Frenette, 2017), rather than intensively competing for food resources. Nonetheless, it would be interesting to proceed to further analyses and compare diet quality, since it can relate to body condition (Tollefson et al., 2010) and therefore population density (Couturier et al., 2009; Gaidet and Gaillard, 2008). As body condition was shown to be quite variable among caribou in this population (Turgeon et al., 2018), even a low level of competition for a few food items found in both diets could contribute to the decline of this endangered caribou population, compromising the survival of some individuals that may be nutritionally stressed.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2019.e00733>.

References

- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecol.* 26, 32–46.
- Baamrane, M.A.A., Shehzad, W., Ouhammou, A., Abbad, A., Naimi, M., Coissac, E., Taberlet, P., Znari, M., 2012. Assessment of the food habits of the Moroccan dorcas gazelle in M'Sabih Talaa, West Central Morocco, using the trnL approach. *PLoS One* 74, e35643.
- Baldi, R., Pelliza-Sbriller, A., Elston, D., Albon, S., 2004. High potential for competition between guanacos and sheep in Patagonia. *J. Wildl. Manag.* 68, 924–938.
- Banfield, A.W.F., 1961. A Revision of the Reindeer and Caribou Genus Rangifer. Bulletin 177, Biological Series 66. National Museum of Canada, Ottawa, Ontario, Canada.
- Belovsky, G.E., 1981. Food plant selection by a generalist herbivore: the moose. *Ecology* 62, 1020–1030.
- Belovsky, G.E., 1986. Generalist herbivore foraging and its role in competitive interactions. *Am. Zool.* 26, 51–69.
- Ben-David, M., Shochat, E., Adams, L.G., 2001. Utility of stable isotope analysis in studying foraging ecology of herbivores: examples from moose and caribou. *Alces* 37, 421–435.
- Bergerud, A.T., 1969. The caribou have returned. *Ecology* 50, 940–941.
- Bergerud, A.T., 1972. Food habits of Newfoundland caribou. *J. Wildl. Manag.* 36, 913–923.
- Bergerud, A.T., 1974. Decline of caribou in North America following settlement. *J. Wildl. Manag.* 38, 757–770.
- Bérubé, J.A., Gagné, P.N., Ponchart, J.P., Tremblay, E.D., Bilodeau, G.J., 2018. Detection of *Diplodia corticola* spores in Ontario and Québec based on high throughput sequencing (HTS) methods. *Can. J. Plant Pathol.* 40, 378–386.
- Boan, J.J., McLaren, B.E., Malcolm, J.R., 2011. Influence of post-harvest silviculture on understory vegetation: implications for forage in a multi-ungulate system. *For. Ecol. Manag.* 262, 1704–1712.
- Boer, A.H., 1998. Interspecific relationships. In: Schwartz, C.C., Franzmann, A.W., McCabe, R.E. (Eds.), *Ecology and Management of the North American Moose*. Smithsonian Institution, Washington DC, USA, pp. 337–349.
- Boertje, R.D., 1984. Seasonal diets of the Denali caribou herd, Alaska. *Arctic* 37, 161–165.

- Boudreau, F., 1981. Écologie des étages alpins et subalpins du Mont Jacques-Cartier, Parc de la Gaspésie, Québec. MSc Thesis, Université Laval, Québec, Québec, Canada.
- Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27, 325–349.
- Connell, J.H., 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35, 131–138.
- Couturier, S., Côté, S.D., Huot, J., Otto, R.D., 2009. Body-condition dynamics in a northern ungulate gaining fat in winter. *Can. J. Zool.* 87, 367–378.
- Crête, M., 1988. Forestry practices in Québec and Ontario in relation to moose population dynamics. *For. Chron.* 64, 246–250.
- Darmon, G., Calenge, C., Loison, A., Jullien, J.M., Maillard, D., Lopez, J.F., 2012. Spatial distribution and habitat selection in coexisting species of mountain ungulates. *Ecography* 35, 44–53.
- De Boer, W.D., Prins, H.H.T., 1990. Large herbivores that strive mightily but eat and drink as friends. *Oecologia* 82, 264–274.
- Dorais, M., Lavergne, D., 2010. Inventaire aérien de l'original dans la réserve faunique des Chic-Chocs à l'hiver 2010. Ministère des Ressources naturelles et de la Faune, Direction de l'expertise (Énergie, Faune, Forêts, Mines, Territoire) de la Gaspésie—Îles-de-la-Madeleine, Caplan, Québec, Canada.
- Dungan, J.D., Wright, R.G., 2005. Summer diet composition of moose in rocky mountain national park, Colorado. *Alces* 41, 139–146.
- Edgar, R.C., 2010. Search and clustering orders of magnitude faster than BLAST. *Bioinformatics* 26, 2460–2461.
- Environment Canada, 2002. Species at Risk Act (Appendix 1). <http://lois.justice.gc.ca/PDF/S-15.3.pdf>.
- Environment Canada, 2012. Gaspésie Woodland Caribou Recovery Plan (2002–2012) (*Rangifer tarandus Caribou*). http://www.registrelep-sararegistry.gc.ca/document/default_e.cfm?documentID=930.
- Festa-Bianchet, M., Ray, J.C., Boutin, S., Côté, S.D., Gunn, A., 2011. Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. *Can. J. Zool.* 89, 419–434.
- Fischer, L.A., Gates, C.C., 2005. Competition potential between sympatric woodland caribou and wood bison in southwestern Yukon, Canada. *Can. J. Zool.* 83, 1162–1173.
- Fitzpatrick, M.C., Weltzin, J.F., Sanders, N.J., Dunn, R.R., 2007. The biogeography of prediction error: why does the introduced range of the fire ant over-predict its native range? *Glob. Ecol. Biogeogr.* 16, 24–33.
- Frenette, J., 2017. Démographie et viabilité de la population de caribous de la Gaspésie-Atlantique. Master Thesis. Université du Québec à Rimouski, Rimouski, p. 119.
- Gagné, P.N., Bérubé, J., 2017a. Illumicut. GitHub Repository. <https://github.com/Patg13/Illumicut>.
- Gagné, P.N., Bérubé, J., 2017b. HomopRemover. GitHub Repository. <https://github.com/Patg13/HomopRemover>.
- Gagnon, R.-M., 1970. Climat des Chic-Chocs. Ministère des richesses naturelles, Direction générale des eaux, Service de la météorologie. Québec, Québec, Canada.
- Gaidet, N., Gaillard, J.M., 2008. Density-dependent body condition and recruitment in a tropical ungulate. *Can. J. Zool.* 86, 24–32.
- Gebremedhin, B., Flagstad, Ø., Bekele, A., Chala, D., Bakkestuen, V., Boessenkool, S., Popp, M., Gussarova, G., Schroden-Nielsen, A., Nemomissa, S., Stenseth, N.-C., Epp, L.S., Brochmann, C., 2016. DNA metabarcoding reveals diet overlap between the endangered walia ibex and domestic goats: implications for conservation. *PLoS One* 11, e0159133.
- Grandtner, M.M., 1966. La végétation forestière du Québec méridional. Presses de l'Université Laval, Québec, Québec, Canada.
- Gwynne, M.D., Bell, R.H.V., 1968. Selection of vegetation components by grazing ungulates in the Serengeti National Park. *Nature* 220, 390–393.
- Hebblewhite, M., Merrill, E., McDermid, G., 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecol. Monogr.* 78, 141–166.
- Hjeljord, O., Hövik, N., Pedersen, H.B., 1990. Choice of feeding sites by moose during summer, the influence of forest structure and plant phenology. *Ecography* 13, 281–292.
- Hodder, D.P., Rea, R.V., Crowley, S., 2013. Diet content and overlap of sympatric mule deer (*Odocoileus hemionus*), moose (*Alces alces*), and elk (*Cervus elaphus*) during a deep snow winter in north-central British Columbia, Canada. *Can. Wildl. Biol. Manag.* 2, 43–50.
- Hofmann, R.R., 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* 78, 443–457.
- Hofmann, R.R., Stewart, D.R.M., 1972. Grazer or browser: a classification based on the stomach structure and feeding habits of East African ruminants. *Mammalia* 36, 226–240.
- Holt, R.D., 1977. Predation, apparent competition, and the structure of prey communities. *Theor. Popul. Biol.* 12, 197–229.
- Holt, R.D., 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *Am. Nat.* 124, 377–406.
- Hundertmark, K.J., Shields, G.F., Udina, I.G., Bowyer, R.T., Daniilkin, A.A., Schwartz, C.C., 2002. Mitochondrial phylogeography of moose (*Alces alces*): late Pleistocene divergence and population expansion. *Mol. Phylogenetics Evol.* 22, 375–387.
- Jarman, P.J., 1974. The social organization of antelope in relation to their ecology. *Behaviour* 48, 215–267.
- Jung, T.S., Stotyn, S.A., Czetwertynski, S.M., 2015. Dietary overlap and potential competition in a dynamic ungulate community in northwestern Canada. *J. Wildl. Manag.* 79, 1277–1285.
- Kartzinel, T.R., Chen, P.A., Coverdale, T.C., Erickson, D.L., Kress, W.J., Kuzmina, M.L., Rubenstein, D.I., Wang, W., Pringle, R.M., 2015. DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. *Proc. Natl. Acad. Sci.* 112, 8019–8024.
- Kinley, T.A., Apps, C.D., 2001. Mortality patterns in a subpopulation of endangered mountain caribou. *Wildl. Soc. Bull.* 29, 158–164.
- Klein, D.R., 1990. Variation in quality of caribou and reindeer forage plants associated with season, plant part, and phenology. *Rangifer* 10, 123–130.
- Krüger, F., Clare, E.L., Symondson, W.O., Keiss, O., Petersons, G., 2014. Diet of the insectivorous bat *Pipistrellus nathusii* during autumn migration and summer residence. *Mol. Ecol.* 23, 3672–3683.
- La Morgia, V., Bassano, B., 2009. Feeding habits, forage selection, and diet overlap in Alpine chamois (*Rupicapra rupicapra* L.) and domestic sheep. *Ecol. Res.* 24, 1043–1050.
- Lamoureux, J., Bélanger, M., Larocque, C., 2012. Inventaire aérien de l'original dans les réserves fauniques de Matane et de Dunière, à l'hiver 2012. Ministère des Ressources naturelles et de la Faune, Direction de l'expertise Faune-Forêts-Territoire du Bas-Saint-Laurent, Rimouski, Québec, Canada.
- Landman, M., Schoeman, D.S., Kerley, G.I., 2013. Shift in black rhinoceros diet in the presence of elephant: evidence for competition? *PLoS One* 8, e69771.
- Latham, J., 1999. Interspecific interactions of ungulates in European forests: an overview. *For. Ecol. Manag.* 120, 13–21.
- Legendre, P., Anderson, M.J., 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecol. Monogr.* 69, 1–24.
- Lesmerises, F., Johnson, C.J., St-Laurent, M.-H., 2017. Refuge or predation risk? Alternate ways to perceive hiker disturbance based on maternal state of female caribou. *Ecol. Evol.* 7, 845–854.
- Li, Z., Jiang, Z., Li, C., 2008. Dietary overlap of przewalski's gazelle, Tibetan gazelle, and Tibetan sheep on the qinghai-tibet plateau. *J. Wildl. Manag.* 72, 944–948.
- Masella, A.P., Bartram, A.K., Truszkowski, J.M., Brown, D.G., Neufeld, J.D., 2012. PANDAseq: paired-end assembler for illumina sequences. *BMC Bioinf.* 13, 31.
- Nadeau Fortin, M.-A., Sirois, L., St-Laurent, M.-H., 2016. Extensive forest management contributes to maintain suitable habitat characteristics for the endangered Atlantic-Gaspésie caribou. *Can. J. For. Res.* 46, 933–942.
- Newmaster, S.G., Thompson, I.D., Steeves, R.A., Rodgers, A.R., Fazekas, A.J., Maloles, J.R., McMullin, R.T., Fryxell, J.M., 2013. Examination of two new technologies to assess the diet of woodland caribou: video recorders attached to collars and DNA barcoding. *Can. J. For. Res.* 43, 897–900.
- Oksanen, J., Blanchet, G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, G., Henry, M., Stevens, H., Wagner, H., 2016. Vegan: community ecology package. R package version 2.3-5. <https://CRAN.R-project.org/package=vegan>.
- Palo, R.T., Wallin, K., 1996. Variability in diet composition and dynamics of radiocaesium in moose. *J. Appl. Ecol.* 33, 1077–1084.
- Pearman, P.B., Guisan, A., Broennimann, O., Randin, C.F., 2008. Niche dynamics in space and time. *Trends Ecol. Evol.* 23, 149–158.

- Pelletier, F., Turgeon, G., Bourret, A., Garant, D., St-Laurent, M.-H., 2019. Genetic structure and effective size of an endangered population of woodland caribou. *Conserv. Genet.* 20, 203–213.
- Peters, W., Hebblewhite, M., DeCesare, N., Cagnacci, F., Musiani, M., 2013. Resource separation analysis with moose indicates threats to caribou in human altered landscapes. *Ecography* 36, 487–498.
- Pompanon, F., Coissac, E., Taberlet, P., 2011. Metabarcoding, une nouvelle façon d'analyser la biodiversité. *Biofutur* 319, 30–32.
- R Development Core Team, 2016. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Renecker, L.A., Schwartz, C.C., 1998. Food habits and feeding behavior. In: Schwartz, C.C., Franzmann, A.W., McCabe, R.E. (Eds.), *Ecology and Management of the North American Moose*. Smithsonian Institution Press, Washington DC, USA, pp. 403–440.
- Rodríguez, A.E., Obeso, J.R., 2000. Diet of the Cantabrian capercaillie: geographic variation and energetic content. *ARDEOLA* 47, 77–83.
- Rolando, A., Laiolo, P., 1997. A comparative analysis of the diets of the chough *Pyrrhocorax pyrrhocorax* and the alpine chough *Pyrrhocorax graculus* coexisting in the Alps. *Ibis* 139, 388–395.
- Rudolph, T.D., Drapeau, P., Imbeau, L., Brodeur, V., Légaré, S., St-Laurent, M.-H., 2017. Demographic responses of boreal caribou to cumulative disturbances highlight elasticity of range-specific tolerance thresholds. *Biodivers. Conserv.* 26, 1179–1198.
- Shipley, L.A., Blomquist, S., Danell, K., 1998. Diet choices made by free-ranging moose in northern Sweden in relation to plant distribution, chemistry, and morphology. *Can. J. Zool.* 76, 1722–1733.
- Schloss, P.D., Westcott, S.L., Ryabin, T., Hall, J.R., Hartmann, M., Hollister, E.B., Lesniewski, R.A., Oakley, B.B., Parks, D.H., Robinson, C.J., Sahl, J.W., Stres, B., Thallinger, G.G., Van Horn, D.J., Weber, C.F., 2009. Introducing mothur: open-source, platform-independent, community-supported software for describing and comparing microbial communities. *Appl. Environ. Microbiol.* 75, 7537–7541.
- Sidorovich, V.E., Polozov, A.G., Zalewski, A., 2010. Food niche variation of European and American mink during the American mink invasion in north-eastern Belarus. *Biol. Invasions* 12, 2207–2217.
- Staaland, H., Brattbakk, I., Ekern, K., Kildemo, K., 1983. Chemical composition of reindeer forage plants in Svalbard and Norway. *Ecography* 6, 109–122.
- St-Laurent, M.-H., Dussault, C., Ferron, J., Gagnon, R., 2009. Dissecting habitat loss and fragmentation effects following logging in boreal forest: conservation perspectives from landscape simulations. *Biol. Conserv.* 142, 2240–2249.
- Taberlet, P., Coissac, E., Pompanon, F., Gielly, L., Miquel, C., Valentini, A., Vermet, T., Corthier, G., Brochman, C., Willerslev, E., 2007. Power and limitations of the chloroplast trnL (UAA) intron for plant DNA barcoding. *Nucleic Acids Res.* 35 (2–8), e14.
- Thomas, D.C., Edmonds, E.J., Brown, W.K., 1996. The diet of woodland caribou populations in west-central Alberta. *Rangifer* 16, 337–342.
- Thompson, I.D., Wiebe, P.A., Mallon, E., Rodgers, A.R., J.M., Fryxell, J.A., Baker, J.A., Reid, D., 2015. Factors influencing the seasonal diet selection by woodland caribou (*Rangifer tarandus tarandus*) in boreal forests in Ontario. *Can. J. Zool.* 93, 87–98.
- Tollefson, T.N., Shipley, L.A., Myers, W.L., Keisler, D.H., Dasgupta, N., 2010. Influence of summer and autumn nutrition on body condition and reproduction in lactating mule deer. *J. Wildl. Manag.* 74, 974–986.
- Turgeon, G., Kutz, S.J., Lejeune, M., St-Laurent, M.-H., Pelletier, F., 2018. Parasite prevalence, infection intensity and richness in an endangered population, the Atlantic-Gaspésie caribou. *Int. J. Parasitol. Parasites Wildl.* 7, 90–94.
- Valentini, A., Miquel, C., Nawaz, M.A., Bellemain, E.V.A., Coissac, E., Pompanon, F., Gielly, L., Cruaud, C., Nascetti, G., Wincker, P., Swensen, J.E., Taberlet, P., 2009. New perspectives in diet analysis based on DNA barcoding and parallel pyrosequencing: the trnL approach. *Mol. Ecol. Resour.* 9, 51–60.
- Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of Earth's ecosystems. *Science* 277, 494–499.
- Vivas, H.J., Saether, B.E., 1987. Interactions between a generalist herbivore, the moose *Alces alces*, and its food resources: an experimental study of winter foraging behaviour in relation to browse availability. *J. Anim. Ecol.* 56, 509–520.
- Wam, H.K., Hjeljord, O., 2010. Moose summer and winter diets along a large-scale gradient of forage availability in southern Norway. *Eur. J. Wildl. Res.* 56, 745–755.
- Wittmer, H.U., Sinclair, A.R.E., McLellan, B.N., 2005. The role of predation in the decline and extirpation of woodland caribou. *Oecologia* 144, 257–267.
- Wittmer, H.U., McLellan, B.N., Serrouya, R., Apps, C.D., 2007. Changes in landscape composition influence the decline of a threatened woodland caribou population. *J. Anim. Ecol.* 76, 568–579.
- Wittmer, H.U., Ahrens, R.N.M., McLellan, B.N., 2010. Viability of mountain caribou in British Columbia, Canada: effects of habitat change and population density. *Biol. Conserv.* 143, 86–93.