ARTICLE

Dietary niche partitioning among black bears, grizzly bears, and wolves in a multiprey ecosystem

Jerod A. Merkle, Jean L. Polfus, Jonathan J. Derbridge, and Kimberly S. Heinemeyer

Abstract: Identifying mechanisms that promote coexistence of sympatric species is important for predicting ecological effects of anthropogenic change. Many caribou (*Rangifer tarandus* (L., 1758)) populations are declining, and it is unclear to what extent sympatric predators consume caribou or how alternative prey affect caribou–predator relationships. We used stable isotope mixing models to estimate diets of black bear (*Ursus americanus* Pallas, 1780), grizzly bear (*Ursus arctos* L., 1758), and grey wolves (*Canis lupus* L., 1758) during early, middle, and late summer of 2009–2010 in northwestern British Columbia, Canada. Although we expected wolf diet to be primarily composed of moose (*Alces alces* (L., 1758)) — as they exist at twice the density of caribou — wolf diet consisted principally of caribou, and to a lesser extent moose and beaver (*Castor canadensis* Kuhl, 1820), with little change occurring throughout summer. Black bear diet consisted mainly of vegetation and moose, shifting from moose to vegetation through summer. Grizzly bear diet consisted primarily of vegetation and moose, and did not change throughout summer. Our results demonstrate the role of dietary niche partitioning in bear and wolf coexistence, and that caribou may be primary prey for wolves in an ecosystem with relatively high moose abundance and low human development.

Key words: black bear, grizzly bear, grey wolf, caribou, *Ursus americanus*, *Ursus arctos*, *Canis lupus*, *Rangifer tarandus*, predation, stable isotope analysis, carbon, nitrogen, niche, diet, trophic relations.

Résumé : La détermination des mécanismes qui favorisent la coexistence d'espèces sympatriques est importante pour la prédiction des effets écologiques de changements causés par les humains. De nombreuses populations de caribous (*Rangifer tarandus* (L., 1758)) sont en déclin, et l'ampleur de la consommation de caribous par des prédateurs sympatriques et l'incidence d'autres proies sur les relations caribous–prédateurs ne sont pas bien établies. Nous avons utilisé des modèles de mélange d'isotopes stables pour estimer les régimes alimentaires d'ours noirs (*Ursus americanus* Pallas, 1780), de grizzlis (*Ursus arctos* L., 1758) et de loups gris (*Canis lupus* L., 1758) au début, au milieu et à la fin des étés de 2009 et 2010 dans le nord-ouest de la Colombie-Britannique (Canada). Si nous nous attendions à ce que le régime alimentaire des loups soit principalement composé d'orignaux (*Alces alces* (L., 1758)), puisque ces derniers sont présents en densité deux fois plus grande que celle des caribous, le régime alimentaire des loups comprenait principalement des caribous et, dans une moindre mesure, des orignaux et des castors (*Castor canadensis* Kuhl, 1820), peu de changement étant observé au cours de l'été. Le régime alimentaire des ours noirs était principalement constitué de plantes et d'orignaux, un passage des orignaux aux plantes étant observé durant l'été. Le régime alimentaire des grizzlis était principalement constitué de plantes et d'orignaux et ne variait pas au cours de l'été. Nos résultats démontrent le rôle que joue la séparation des niches alimentaires dans la coexistence des ours et des loups et le fait que le caribou pourrait être la principale proie des loups dans un écosystème caractérisé par une abondance relativement grande d'orignaux et peu d'aménagements d'origine humaine. [Traduit par la Rédaction]

Mots-clés : ours noir, grizzli, loup gris, caribou, *Ursus americanus*, *Ursus arctos*, *Canis lupus*, *Rangifer tarandus*, prédation, analyse d'isotopes stables, carbone, azote, niche, régime alimentaire, relations trophiques.

Introduction

Identifying the mechanisms that promote coexistence of sympatric species at the same trophic level is essential to understanding and conserving biodiversity. As anthropogenic influences (including climate change) bring about alternative ecological states (Barnosky et al. 2012), interspecific dynamics will likely play an important role in ecosystem responses including whether a species is resilient or vulnerable to change (Post 2013). Although a number of mechanisms have been purported to explain coexistence among species within a trophic level (Schoener 1974), most research has focused on how species partition resources along

axes of diet, space, and time (Brown 1989). In general, coexistence appears to be driven by selection for one or more of the following traits: differential consumption of prey species and prey sizes (Karanth and Sunquist 1995), differential use of habitats and space (Palomares et al. 1996), and different temporal activity patterns (Fedriani et al. 1999).

A number of different methods exist to quantify resource partitioning (e.g., gut content, scat analysis), but noninvasive sampling methods coupled with innovative technologies have resulted in fruitful contributions to understanding trophic interactions. The analysis of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable

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isotopes based on hair and tissue samples is a robust method for determining the relative contribution of different foods to a consumer's diet (DeNiro and Epstein 1978, 1981). Notably, stable isotope analysis has been extended to assess how multiple species partition dietary resources (Hobson et al. 2000; Caut et al. 2006), as well as to understand predator–prey and other trophic relationships (Post 2002; Urton and Hobson 2005). For example, previous studies have determined grey wolf (*Canis lupus* L., 1758) diets in multiprey systems using stable isotope analysis of noninvasively collected guard hairs (Darimont and Reimchen 2002; Derbridge et al. 2012). Stable isotope analyses can also identify the suite of predators preying upon a given species and potentially how such predation is partitioned through time — providing important insight into prey species of conservation concern.

Forest-dwelling caribou (*Rangifer tarandus* (L., 1758)) that occur in boreal forests and mountainous regions are experiencing significant population declines (Vors and Boyce 2009; Festa-Bianchet et al. 2011). Although the ultimate reason for the declines can be attributed to habitat alterations from resource extraction activities (Festa-Bianchet et al. 2011), the proximate mechanisms behind the declines can be indirect and complex. To reduce the risk of detection by predators, forest-dwelling caribou use an isolation strategy to spatially segregate themselves from other prey species and conspecifics (Stuart-Smith et al. 1997; James et al. 2004). Yet, evidence suggests that predation can significantly limit caribou populations (Stuart-Smith et al. 1997; Bergerud and Elliott 1998). Resource extraction activities can alter caribou–predator relationships by providing linear features (e.g., logging roads, seismic lines) that aid wolf movement (Wittmer et al. 2007; Peters et al. 2013; Losier et al. 2015). For example, in northeastern Alberta, James and Stuart-Smith (2000) found that caribou have higher risk of predation from wolves near linear features, which may have low human use, but are preferentially used by wolves, resulting in increased travel efficiency and caribou detections. Furthermore, an increase in young seral forests following human habitat alterations can enhance moose (*Alces alces* (L., 1758)) and wolf populations and increase caribou vulnerability to predation through the mechanism of apparent competition (Seip 1992; DeCesare et al. 2010). Even a small increase in predation through altered spatial relationships between caribou, alternative prey, and shared predators could lead to population-level effects in populations with low growth rates (Seip 1992; James et al. 2004; Hervieux et al. 2014).

The Northern Mountain caribou designatable unit (COSEWIC 2011) occurs in local populations throughout the Yukon, Northwest Territories, and northwestern British Columbia (BC), and was listed as a species of special concern in 2014 by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2014). Our current knowledge of why Northern Mountain caribou populations are declining is incomplete, mainly because a lack of information about the complex dynamics of multiprey, multipredator ecosystems (COSEWIC 2014). For instance, in east-central Yukon, Hayes et al. (2000) found that moose comprised 94% of the biomass of ungulates killed by wolves, and wolves did not prey heavily on caribou even when caribou outnumbered moose. Similarly, in the north Columbia Mountains of southeastern BC, Stotyn (2008) found that the relative proportion of caribou within wolf diet was not related to caribou density. Rather, caribou may use spatial or temporal refuges to avoid wolves, or wolves may preferentially kill moose and other prey items. In northeastern Alberta, Latham et al. (2013) found that during summer wolf selection for areas used by beaver (*Castor canadensis* Kuhl, 1820) led to an increase in spatial overlap with caribou. Furthermore, understanding predation on caribou is complicated by the presence of other predators (i.e., bears). It is well known that black bears (*Ursus americanus* Pallas, 1780) and grizzly bears (*Ursus arctos* L., 1758) can be important predators of neonatal ungulates (Zager

and Beecham 2006; Barber-Meyer et al. 2008), including caribou (Ballard 1992, 1994; Adams et al. 1995; Young and McCabe 1997).

In many populations of forest-dwelling caribou, it is still unclear which predators influence (or potentially limit) prey populations and how the levels of human development and alternative prey species affect these predator–prey interactions. In this study, we used Bayesian stable isotope mixing models to reconstruct the dietary differences and overlap of black bears, grizzly bears, and grey wolves during early, middle, and late summer in northwestern BC — an area characterized by relatively low levels of human development (including logging and resource extraction). We sampled hair from these predators and their potential prey species, as well as plant species important for bears. Based on previous literature, caribou are generally a secondary prey item because they are typically less numerous than moose. Our study area is no exception because there exists an estimated 777 caribou and 1971 moose (Taku River Tlingit First Nation and Province of British Columbia 2010; Marshall 2015; for details see the Study area section below). Thus, we expected that compared with moose, caribou would comprise relatively low proportions of predator diets. We also expected that bear diet would reflect predation on ungulate neonates in early summer and then shift to a primarily vegetarian diet during late summer when soft plant mast becomes available (Munro et al. 2006). Our study is unique as it provides a comprehensive analysis of the diets of three sympatric predators (i.e., a multipredator system) with a specific eye towards predation on caribou during the neonatal stage when bear predation is important.

Study area

This study took place within the traditional territory of the Taku River Tlingit First Nation in northwestern BC, extending into southern Yukon Territory (Fig. 1). The 11 594 km² study area primarily falls within the boreal mountains and plateaus ecoregion (Environment Canada 2005), characterized by high peaks, broad plateaus, and wide valleys with elevations ranging from 660 to 2000 m. Human development in the study area consists of the town of Atlin with approximately 350 residents, and a total of approximately 1250 km of roads (including approximately 100 km of paved roads, 400 km of unimproved gravel and dirt roads, and an additional 750 km of all-terrain vehicle trails; overall road density of 0.11 km/km²). All paved roads and most unimproved roads are disproportionately found at low elevations resulting from a long history of placer mining and mineral exploration in the region. Current mining activity is focused on stream drainages, which has been an important economic driver in the region for over 100 years (Taku River Tlingit First Nation and Province of British Columbia 2011). However, all-terrain vehicle trails provide access across the study area into higher elevation subalpine and alpine areas. There is no large-scale commercial logging; however, there is some small-scale local timber operations for home building and mine development (Taku River Tlingit First Nation and Province of British Columbia 2011).

The climate is typified by long, cold winters and short, warm summers. The mean summer temperature is 10 °C and the mean winter temperature is –15 °C (Environment Canada 2005). Annual precipitation in the study area is approximately 33 cm, resulting in a mean late winter snow depth of 49.5 cm (Atlin snow station, 1964–2003). Low- to mid-elevation boreal forests include a mix of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex S. Watson), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), white spruce (*Picea glauca* (Moench) Voss), and black spruce (*Picea mariana* (Mill.) Britton, Sterns and Poggenb.). Deciduous stands of trembling aspen (*Populus tremuloides* Michx.), black cottonwood (*Populus balsamifera* ssp. *trichocarpa* (Torr. and A. Gray) Brayshaw), mountain alder (*Alnus incana* ssp. *tenuifolia* (Nutt.) Breitung), and willow (species of the genus *Salix* L.) occupy valley bottoms and riparian areas. The understory commonly consists of low shrubs and lichen species

Fig. 1. General location of the study area along with sampling locations within the traditional territory of the Taku River Tlingit First Nation (TRTFN) territory in northwestern British Columbia, Canada. Colour online.
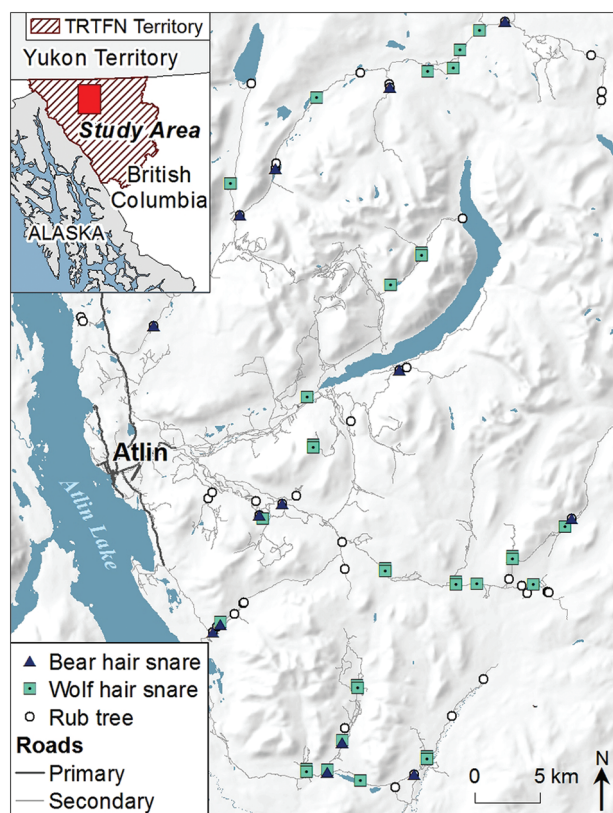
including various reindeer (*Cladonia* spp.), pixie-cup (*Cladonia* spp.), foam (*Stereocaulon* spp.), and Iceland (*Cetraria* spp.) lichens and numerous forbs and mosses. White spruce and subalpine firs dominate the subalpine from 850 to 1500 m transitioning at mid-elevations into krummholz where thick knee-high spreads of willow and dwarf birch (*Betula glandulosa* Michx.) dominate. Alpine zones (above 1500 m) consist of extensive areas of rolling alpine tundra characterized by sedge (species of the genus *Carex* L.) and altai fescue (*Festuca altaica* Trin.) dominated meadows. Mountain heather (species of the genus *Cassiope* D. Don), crowberry (*Empetrum nigrum* L.), mountain avens (species of the genus *Dryas* L.), and lichen communities are also common.

The Atlin Northern Mountain caribou population relies heavily on low-elevation mature lodgepole pine forests in the winter and high-elevation alpine and subalpine forest in the summer (Polfus et al. 2011; Polfus et al. 2014). Aerial surveys indicate that although the nearby Yukon caribou populations appear to be increasing in abundance (calf:female ratios for the Carcross and Yukon woodland caribou herds are 27:100 and 26:100, respectively; Hegel 2013), the Atlin population has maintained a stable or decreasing population with a low calf recruitment of 21 ± 3 calves : 100 females (Taku River Tlingit First Nation and Province of British Columbia 2010). The adjacent Carcross herd is hunted within its range in BC, but hunting is closed in the Yukon and voluntarily suspended by First Nations. British Columbia currently allows a limited entry hunt and guide-outfitter quota of 10 males/year in the Atlin population. There are an estimated 777 ± 132 caribou in the Atlin population (Taku River Tlingit First Nation and Province of British Columbia 2010) and 1971 ± 464 moose (estimated from a 2015 stratified random block survey of moose in the Atlin region yielding 0.17 ± 0.04 moose/km²; Marshall 2015). Other ungulates in the

area include mountain goats (*Oreamnos americanus* (Blainville, 1816)) and Stone's sheep (*Ovis dalli stonei* J.A. Allen, 1897) in alpine zones. Apart from grizzly bears, black bears, and wolves, the predator community relative to ungulates includes wolverines (*Gulo gulo* (L., 1758)) and lynx (*Lynx canadensis* Kerr, 1792).

Materials and methods

Sample collection

To estimate dietary differences and overlap between black bears, grizzly bears, and wolves, we collected hair samples using noninvasive hair snares set up throughout the study area during the summers (June–August) of 2009–2010. Wolves have one annual molt that begins in late spring when the old coat is shed and new hair grows until late fall (Darimont and Reimchen 2002). Bears begin molt in late spring after emerging from the den and continue into the fall (Jacoby et al. 1999; Stotyn et al. 2007). We collected wolf hair with noninvasive rub pads constructed following Ausband et al. (2011). The hair snares were scent-lured using Forsyth wolf call, Forsyth wolf gland, Forget's cachotier call (canine), freshwater fish oil, and commercial wolf urine purchased from Halford's (Edmonton, Alberta, Canada). We set up hair snares in areas identified as movement corridors based on field observations (tracks and scat) and on information from local hunters and trappers who had knowledge of animal locations.

We collected bear hair from rub trees and barbed wire corral stations with a nonreward scent lure following Boulanger and McLellan (2001). We placed corral stations near rub trees and along movement corridors that allowed repeated access over the course of the summer. Our lure was a mixture of salmon oil, beaver castor, and Forget's cachotier call (canine). We also opportunistically collected bear hair from rub trees that were encountered in the field. We set up rub pads and corral stations at the end of June and early July, and checked and re-lured the sites approximately every 10 days until mid-August.

During summers of 2009–2010, we also opportunistically collected hair from prey species at predator kill sites found in the field, from the ground near hunting camps, and from local hunters and trappers. We collected guard hairs with tweezers and placed them in manila envelopes, which we then placed in plastic bags with desiccant beads to prevent moisture build-up. The Kluane Ecological Monitoring Project in the Yukon provided snowshoe hare (*Lepus americanus* Erxleben, 1777) hair samples collected during annual monitoring efforts. The Museum of Southwestern Biology at the University of New Mexico provided small-mammal hair samples from least chipmunk (*Tamias minimus* Bachman, 1839) and northern red-backed voles (*Myodes rutilus* (Pallas, 1779)) collected within or immediately adjacent to our study area.

We also collected samples from 13 plant species known to be important to bear diet (Fuhr and Demarchii 1990; Nielsen et al. 2004). We collected aboveground foliage from horsetail (species of the genus *Equisetum* L.), dandelion (species of the genus *Taraxacum* F.H. Wigg.), clover (species of the genus *Trifolium* L.), sedges (*Carex* spp.), fescue (species of the genus *Festuca* L.), cow parsnip (*Heracleum lanatum* Michx. = *Heracleum sphondylium* ssp. *montanum* (Schleich. ex Gaudin) Briq.), lupine (species of the genus *Lupinus* L.), rose (species of the genus *Rosa* L.), arrowleaf (*Senecio triangularis* Hook.), and berries from kinnikinnick (*Arctostaphylos uva-ursi* (L.) Spreng.), soapberry (*Shepherdia canadensis* (L.) Nutt.), blueberry (*Vaccinium cespitosum* Michx.), and black crowberry (*Empetrum nigrum* L.). Vegetation samples were desiccated in a drying oven and ground into a fine powder for stable isotope analysis.

Stable isotope analysis

We cleaned all hair samples of surface oils in a 2:1 chloroform: methanol solution for 24 h and dried them at low heat for 24 h. Predator guard hairs were cut into three sections (root, middle, and tip sections) representative of different seasons during hair

growth (Milakovic and Parker 2011): root section reflects most recent growth (hereafter termed late summer), the middle section reflects earlier growth (hereafter termed mid-summer), and the tip section reflects earliest hair growth (hereafter termed early summer). The rate and timing of hair growth is expected to differ between individual bears (B. Milakovic, personal communication). Thus, we split bear and wolf hairs into three equal sections based on each guard hair length so that each section was representative of a specific time period relative to each individual.

Hair and vegetation samples were sent to the Stable Isotope Facility at the University of California Davis where stable isotope ratios of carbon and nitrogen were measured on a continuous flow isotope-ratio mass spectrometer. When enough hair was available, replicates were included approximately every 8–12 samples to check instrument precision. Stable isotopes are expressed in delta notation (δ) in parts per thousand (‰) following standard methods (Post 2002). Based on repeated internal standards, precision was better than ±0.10 for $\delta^{13}C$ and ±0.2 for $\delta^{15}N$.

DNA analysis

Prior to stable isotope analyses, a subsample of hairs from each predator sample was sent to the U.S. Forest Service Rocky Mountain Research Station (Missoula, Montana) to identify species (mtDNA) and individuals (microsatellites). We used a previously developed panel of nine variable loci for bears and eight variable loci for wolves. To avoid pseudoreplication within our sample, subsequent stable isotope analyses were only conducted on a single sample from each unique individual sampled during the study. When individuals were identified more than once during the study, we randomly selected one of the samples for analysis.

Stable isotope mixing models

We used a Bayesian mixing model approach (Phillips 2012) to determine the proportions of prey in the diets of black bears, grizzly bears, and wolves for each of the three seasons (early, middle, and late summer). Mixing models estimate the proportion p of each food source s (from 1 to k different sources) in the diet of each consumer X (from 1 to i individual consumers), based on fractionation values c for each isotope of interest (from 1 to j different isotopes). As formulated by Jackson et al. (2009), the form of the mixing model was

$$X_{ij} = \sum_{k=1}^{k} p_k(s_{jk} + c_{jk}) + \varepsilon_{ij}$$

where X_{ij} was the observed isotope value j of individual consumer i based on k sources. The residual error ε_{ij} described additional interobservation variance not described by the model (Jackson et al. 2009). The model distributions were $s_{jk} \sim \text{Normal}(\mu_{jk}, \omega_{jk}^2)$, $c_{jk} \sim \text{Normal}(\lambda_{jk}, \tau_{jk}^2)$, $\varepsilon_{ij} \sim \text{Normal}(0, \sigma_j^2)$. Because there was no previous literature documenting diets of all three predator species within the same predator–prey complex as in our study area, we specified uninformative priors (i.e., a Dirichlet distribution with all α_k in each analysis equal to 1) for all analyses.

We estimated proportions of each food source p_k using standard Markov chain Monte Carlo simulations with a burn-in of 50 000 iterations. We generated posterior samples using 15 000 iterations of the model and a thinning rate of 15. We chose the number of iterations by calculating the Gelman and Rubin convergence diagnostic (Brooks and Gelman 1998) and increasing the number of iterations until the statistic was <1.1. Parameterization of the mixing model was conducted in R version 3.2 (R Core Team 2014) and JAGS (Plummer 2003).

For wolves, we used fractionation values developed by Derbridge et al. (2015) on captive wolves that were fed a known diet (mean ± SD; $\Delta^{13}C = 1.972$‰ ± 0.705‰, $\Delta^{15}N = 3.04$‰ ± 0.313‰). For bears, we used fractionation values for nitrogen ($\Delta^{15}N = 4.76$‰ ± 0.45‰ for vegetation and 4.5‰ ± 0.45‰ for meat) from Hilderbrand et al. (1996), and for carbon ($\Delta^{13}C = 2$‰ ± 1‰) from Mowat and Heard (2006) and Ben-David et al. (2004), as used on other stable isotope diet studies of bears (e.g., Merkle et al. 2011).

Prior to fitting mixing models, we reduced our suite of prey in the models to (i) focus on prey species that we were interested in making inference about and (ii) because each prey item must have isotopically distinct stable isotope values when reconstructing animal diets (Phillips 2012). We tested for isotopically distinct stable isotope values among our prey items using Welch's two-sided t tests and two-sided Wilcoxon rank sum test with continuity correction for carbon and nitrogen isotopes separately, and a multiple analysis of variance (MANOVA) for carbon and nitrogen isotopes simultaneously (for results see Supplementary Table S1).[1]

Our intent was to identify the main components of bear and wolf diets, while also being able to compare across the three predators. Thus, we only focused on large mammals and did not include any potential prey smaller than beaver. Indeed, little to no mammals smaller than beaver were found in wolf scats in a nearby study area (Milakovic and Parker 2011), and wolf diet is known to be mainly composed of large mammals (Merkle et al. 2009; Derbridge et al. 2012). Additionally, when bear diet during summer includes meat, it is often from neonatal ungulates (Mowat and Heard 2006).

We included moose and beaver as potential dietary sources because moose are common in the study area and beaver can be an important diet component for wolves (Potvin et al. 1988). Because we were interested in quantifying the proportion of caribou in predator diet, caribou was also included as a prey item in our mixing models for all three predator species. The isotope signature of caribou was significantly different from all other species, except for Stone's sheep. We assumed that Stone's sheep were rarely depredated by wolves and bears given the low density of the local population (approximately 80 in the study area; Taku River Tlingit First Nation and Province of British Columbia 2010), and Stone's sheep generally avoid areas where wolves and bears are found during summer and fall (Walker et al. 2007). Thus, we did not include Stone's sheep, nor combine their isotope values with caribou, in the stable isotope analysis. Nonetheless, we note that it does appear that wolf predation is a leading cause of mortality in some Stone's sheep populations (Bergerud and Elliott 1998), and by excluding Stone's sheep, a small proportion of predator diet attributed to caribou may be due to predation on the isotopically similar Stone's sheep. We also excluded mountain goats from the analysis because of their relatively low density in our study area (Environment Yukon 2011) and because no study to our knowledge has suggested that mountain goats are an important dietary component of wolves or bears. Finally, for black bear and grizzly bear diets, we also included vegetation (Hobson et al. 2000; Mowat and Heard 2006). There was considerable overlap in $\delta^{13}C$ and $\delta^{15}N$ of the 13 plant species that we sampled, so we subsampled four random plant isotope values from each plant type and estimated a general vegetation baseline for the study area by calculating the mean and SD of all of the combined vegetation isotope values.

Results

DNA analysis

During summers of 2009–2010, we collected 127 bear and 41 wolf hair samples. Due to sample quantity and quality, only the largest

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Fig. 2. Mean (with SD bars in black) prey carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values from tissue samples (guard hair for mammals and aboveground tissue for plants) collected in the traditional territory of the Taku River Tlingit First Nation in northwestern British Columbia, Canada, 2009–2010. For statistical tests of differences among the mammalian prey items see Supplementary Table S1.[1]
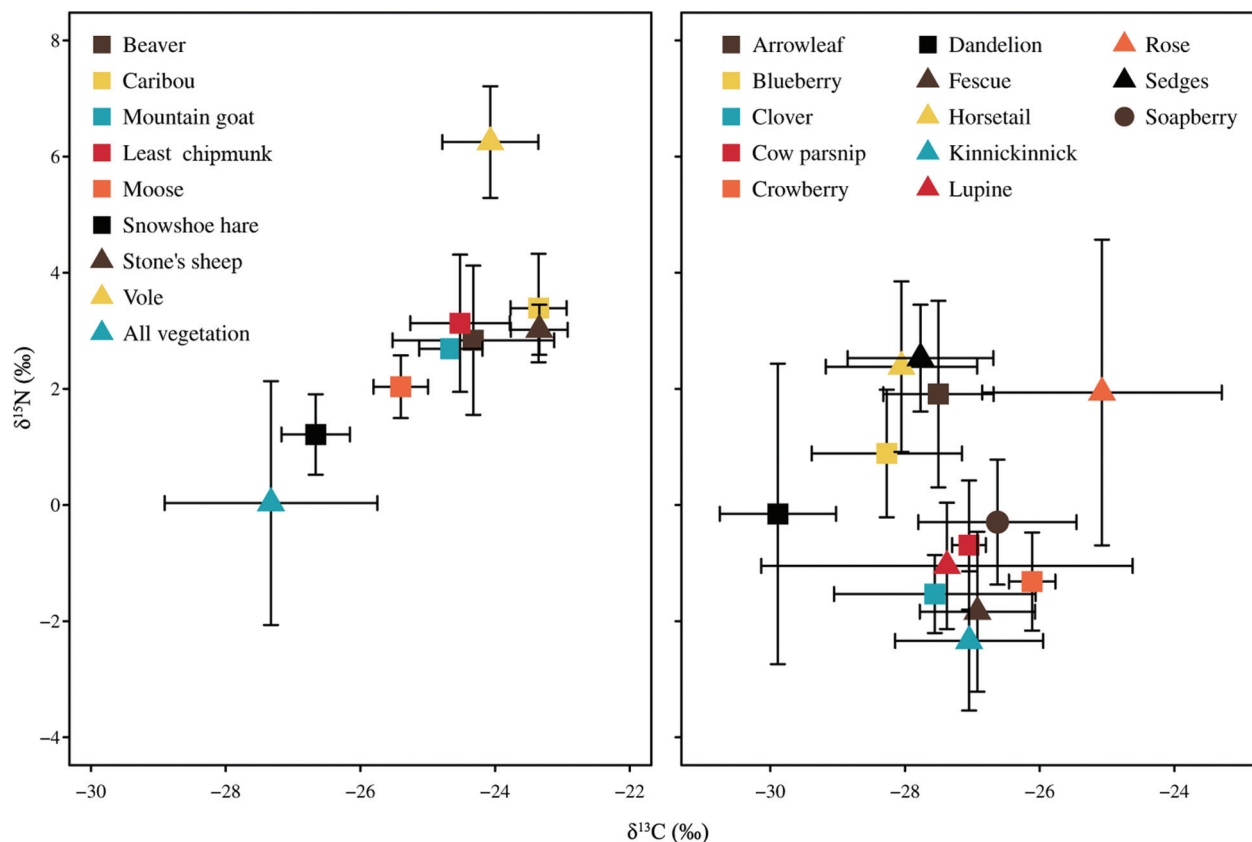

samples of complete wolf and bear hairs were sent to the laboratory for genetic analysis. DNA extractions were performed on 42 bear hair samples and 18 wolf hair samples from 2009, and 22 bear hair samples and 13 wolf hair samples from 2010. We obtained mtDNA for species identification from 47 of the 64 suspected bear samples (73%); 30 samples were from grizzly bear, 16 samples were from black bear, and 1 sample was a mix of grizzly and black bear. We obtained mtDNA for species identification from 29 of the 31 wolf samples (94%); all were identified as *C. lupus*.

After obtaining high-quality DNA that allowed for individual identification using the microsatellite panel, we identified 13 individual grizzly bears in 2009 and 4 individual grizzly bears in 2010. One grizzly bear was identified in both 2009 and 2010. We identified six individual black bears in 2009 and seven in 2010. One black bear was identified in both 2009 and 2010. We identified 10 individual wolves in 2009 and 5 individual wolves in 2010. Three individual wolves were identified in both 2009 and 2010.

Stable isotope mixing models

We obtained $\delta^{13}C$ and $\delta^{15}N$ estimates for the 12 known black bear samples, 16 known grizzly bear samples, and 12 known grey wolf samples (sample sizes do not include individuals captured in both 2009 and 2010). For prey species, stable isotope estimates were derived from moose, caribou, mountain goat, Stone's sheep, beaver, snowshoe hare, least chipmunks, northern red-backed voles, and 13 plant species (Fig. 2, Supplementary Table S2[1]). Our replicate analysis (*n* = 7) suggested that instrument precision at the stable isotope facility was relatively high and that there was little to no measurement or calculation error associated with estimating $\delta^{13}C$ and $\delta^{15}N$ (Supplementary Figs. S1*a* and S1*b*).[1]

In general, compared with both bear species, the diet of wolves was more enriched in both nitrogen and carbon. Black bear and

grizzly bear $\delta^{13}C$ and $\delta^{15}N$ were relatively similar to each other. Furthermore, $\delta^{13}C$ and $\delta^{15}N$ for all predators were similar across early, middle, and late summer, except for the root section of black bear hair (representing late summer diet), which was more depleted in nitrogen compared with other periods of black bear and grizzly bear diet (Figs. 3*a*–3*c*).

Based on Bayesian stable isotope mixture models, wolf diet consisted principally of caribou (mean (±SD) of 50% ± 0.10% of diet), and to a lesser extent beaver (21% ± 0.12%) and moose (29% ± 0.09%), with little change occurring over the course of the summer (Fig. 4). Black bear diet consisted mainly of vegetation (43% ± 0.10%) and moose (31% ± 0.16%), and to a lesser extent beaver (14% ± 0.10%) and caribou (12% ± 0.09%), with a clear shift from a diet of moose and vegetation in early summer to a diet of mostly vegetation in late summer (Fig. 4). Similar to black bear, grizzly bear diet consisted mainly of vegetation (42% ± 0.08%) and moose (28% ± 0.16%), and to a lesser extent beaver (16% ± 0.11%) and caribou (15% ± 0.10%); however, we observed little change in diet occurring over the course of the summer (Fig. 4).

Discussion

We quantified diet of three sympatric predators in a multiprey ecosystem over the course of the summer. As expected, both bear species primarily consumed vegetation and moose (the most abundant large mammalian prey in our study area), and to a lesser extent caribou and beaver. As expected, over the course of the summer, black bears shifted from a diet consisting of meat and vegetation to a diet mainly consisting of vegetation. This was not the case for grizzly bears, where moose and vegetation were consistently consumed throughout the summer. Unexpectedly, our results suggest that wolves primarily consumed caribou, and to a

Fig. 3. Mean (with SD bars in black) predator carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values based on samples of grey wolf (*Canis lupus*; *a*), black bear (*Ursus americanus*; *b*), and grizzly bear (*Ursus arctos*; *c*) guard hairs representing early (tip section), mid- (middle section), and late (root section) summer growth. Hair samples were collected in the traditional territory of the Taku River Tlingit First Nation in northwestern British Columbia, Canada, 2009–2010. Colour online.
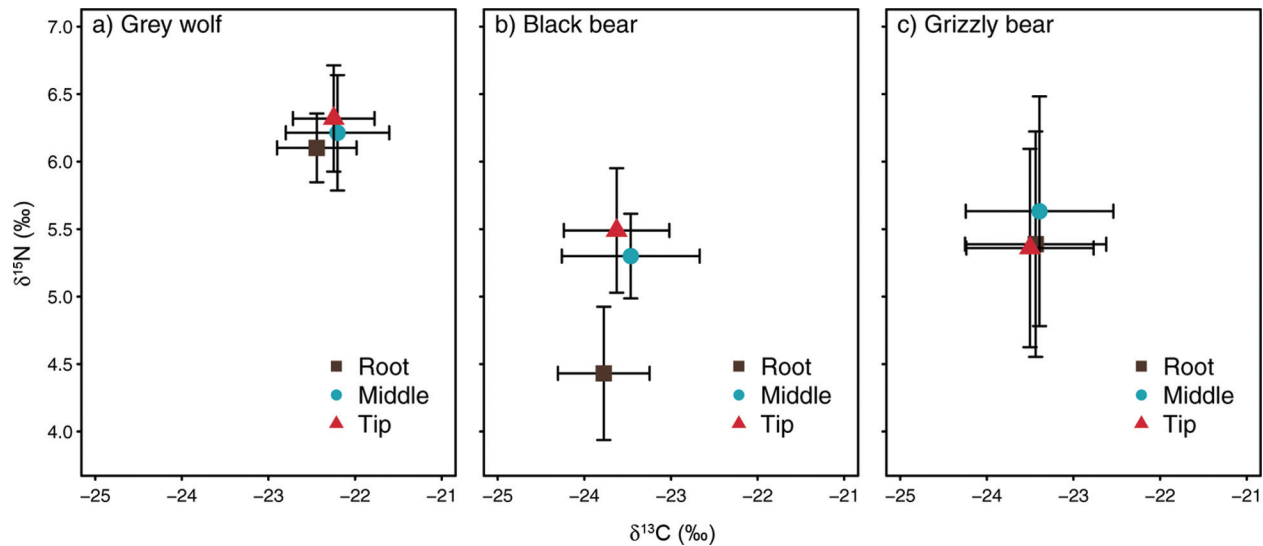
Fig. 4. Mean posterior distributions (with SD bars in black) of the proportional contribution of caribou (*Rangifer tarandus*), beaver (*Castor canadensis*), moose (*Alces alces*), and vegetation in the diets of grey wolves (*Canis lupus*), black bears (*Ursus americanus*), and grizzly bears (*Ursus arctos*) in early, middle, and late summer of 2009–2010 in the traditional territory of the Taku River Tlingit First Nation in northwestern British Columbia, Canada. Distributions calculated from a Bayesian *n*-mixture model of carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values derived from guard hairs (mammals) and aboveground whole tissue (vegetation). Colour online.
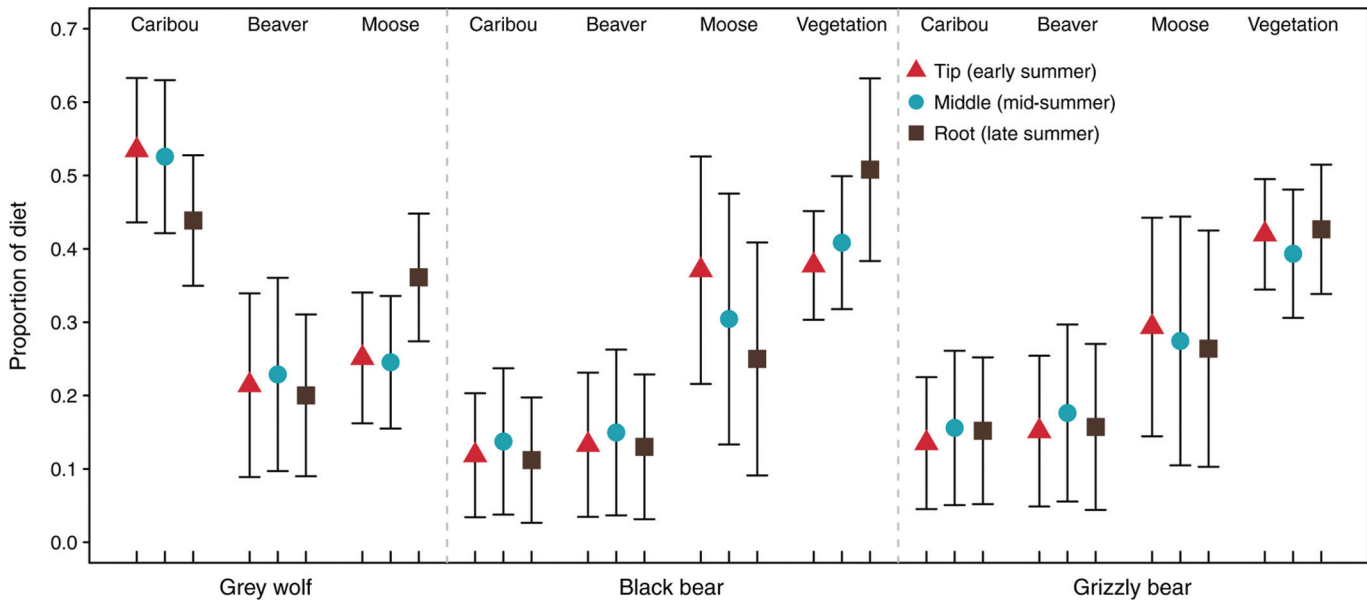
lesser extent beaver and moose, even though caribou density is approximately half that of moose density in our study area (Taku River Tlingit First Nation and Province of British Columbia 2010). Our results demonstrate that black bear, grizzly bear, and wolf coexistence is driven in part by strong dietary niche partitioning, and that wolves may be consuming more caribou than expected based on availability of prey.

The partitioning of diet among black bears, grizzly bears, and wolves may not be solely driven by diet selection, but also by spatial separation (Hobson et al. 2000). During summer, caribou select for high-elevation, broad mountain plateaus (Polfus et al. 2011; Polfus et al. 2014), whereas moose select valley bottoms consisting of deciduous and riparian vegetation (Peters et al. 2013). It

is plausible that the underlying diet differences between bears and wolves that we observed was because wolves spent significant time in high-elevation areas, whereas bears spent significant time in low-elevation areas. Indeed, Whittington et al. (2011) found that in Banff and Jasper national parks, wolves spend the most time at high elevations resulting in the highest encounter risk for caribou. In Quebec, caribou that avoided areas used by wolves tended to select areas where black bears occurred, consequently exposing themselves to higher predation by bears (Leblond et al. 2016). Whether driven by space use or not, diet partitioning appears to allow these sympatric predators to minimize competition and coexist in a multipredator, multiprey ecosystem.

Our results confirm that ungulates are an important component of bear diet in early summer. As summer progresses, however, both bear species typically consume relatively large amounts of vegetation, especially as soft mass becomes available in late summer (Raine and Kansas 1990; McLellan and Hovey 1995; Munro et al. 2006). We observed this typical shift from meat to vegetation in the diet of black bears, which matched high relative availability of soft mast later in summer in our study area. However, our results indicated that grizzly bears foraged on both meat and vegetation throughout the summer. Milakovic and Parker (2013) reported that meat was a significant part of the grizzly bear diet in northern BC throughout the summer, and even noted a relative increase in meat consumption compared with vegetation from early to late summer. They attributed the result to increased consumption of elk — a species that does not exist in our study area (Milakovic and Parker 2013). In accordance with our results, Fortin et al. (2013) found that black bears indeed consumed less meat than grizzly bears in Yellowstone National Park. Decreased black bear predation on moose likely occurs as moose calves become too large and fast to capture as summer progresses. Furthermore, grizzly bears may be more effective than black bears at obtaining and competing for ungulate carcasses killed by wolves over the course of the summer (Smith et al. 2003). Both reasons suggest mechanisms behind dietary niche portioning among the three predators.

Caribou were the most important prey item for wolves throughout the summer. This result is somewhat surprising, as it suggests that wolves are selecting for caribou even though moose density is twice that of caribou in our study area. Previous studies have suggested that in multipredator prey systems, moose are generally the primary prey of wolves and caribou are more likely to be an opportunistic or alternative prey (Wittmer et al. 2005, 2007). However, it has also been shown that availability alone may not determine primary prey of wolves, which sometimes exhibit preference for particular prey species (Huggard 1993; Dale et al. 1995). Prey switching can also occur, as prey abundance varies over time (Garrott et al. 2007), and variation in diet among packs within a population has been reported (Kunkel et al. 2004; Derbridge et al. 2012). Regardless of prey species, vulnerability to predation is the most consistent factor determining wolf predation (Mech and Peterson 2003). Since wolves are more likely to be found alone, in pairs, or in small groups during the summer (Fuller et al. 2003), caribou may be a more vulnerable or profitable prey item (in terms of energy/handling time) than moose, which are generally 2–3 times larger than caribou. This greater profitability was noted by Dale et al. (1995) who suggested relative vulnerability of caribou explained why they were selected by wolves even when moose were more abundant in Alaska. We also note that our results provide some evidence that 5 of the 12 individual wolves that we sampled likely preyed mainly on caribou (i.e., their isotope signatures fall exactly on top of the isotopic signature of caribou; see Supplementary Fig. S2[1]), whereas isotopic signatures of the other wolves were closer to the signatures of moose and beaver — potentially explaining how the overall average consumption of caribou was so high.

Predation rates, predator preferences, and mortality risks for prey may be strongly impacted by the level of habitat modification in a landscape (Schlaepfer et al. 2002). For example, in Alberta and Quebec, anthropogenic conversion of habitats that favor moose appears to result in larger wolf populations and increased wolf predation risk on caribou via apparent competition (Seip 1992; DeCesare et al. 2010; Losier et al. 2015). Furthermore, as human development increases, the spatial overlap of caribou and moose, as well as caribou mortality from wolves, tends to increase (Peters et al. 2013). Our study system, on the other hand, has not experienced extensive habitat conversion (e.g., no significant logging) that impacts other regions which support caribou–moose–wolf dynamics (Johnson et al. 2015; Losier et al. 2015). The

predominant human disturbance in the Atlin area is placer mining along creek bottoms of two drainage systems within the study area. The study area has only one main road (Highway 7) that connects Atlin to the Alaska Highway and the city of Whitehorse in the Yukon Territory. However, because of historical prospecting, our study area does have a rather high density of low-use roads. There are approximately 100 km of paved roads, 400 km of unimproved gravel and dirt roads, and an additional 750 km of all-terrain vehicle trails in the study area. These roads likely provide wolves with easy access to alpine plateaus and caribou summer habitats. If wolf predation is enhanced by linear features on the landscape (Whittington et al. 2011), then it is likely that wolf predation rates on caribou would be increased by even moderate levels of linear features. Furthermore, caribou have been shown to avoid linear developments (and other human landscape alterations including placer mines and cabin sites) in our study area during the summer, even though human presence on the road network is relatively low (Polfus et al. 2011). Therefore, as others have suggested (e.g., Whittington et al. 2011), decommissioning roads and other habitat restoration projects may be a future management strategy to help minimize declines in woodland caribou populations.

It is important to note that the results of our stable isotope analysis cannot be projected during winter months when bears are inactive, as it is unknown in our study area whether wolves switch to moose as their main prey during winter. Such seasonal variation in predation by wolves on moose and caribou must be taken into account when determining the total influence of multiple predators on prey populations. For example, Metz et al. (2012) found that the species composition of wolf predation events varies by season in Yellowstone National Park, and Peters et al. (2013) found that the strength of resource separation between moose and caribou in Alberta depends on season.

Wolves, grizzly bears, and black bears have coexisted, along with a suite of large ungulate prey (that includes caribou), for thousands of years in North America. Our study sheds light on how these three predators partition resources to coexist, suggesting that bears consume mainly moose and vegetation, whereas wolves consume mainly caribou during summer. Our study also reveals that caribou are the primary prey for wolves during summer in an ecosystem where moose are more abundant than caribou and relatively little human development has occurred compared with the habitat of other forest-dwelling caribou populations across their range. Together these findings suggest that dietary niche partitioning allows for these multiprey, multipredator ecosystems to exist, and that these ecosystems are challenging to understand with processes such as apparent competition, prey selectivity, and redundancy among interspecific interactions all at play. No single management strategy (e.g., habitat enhancements, decrease density of a single predator, or preferred prey of a predator) will likely result in significant, long-term changes to these communities and it appears successful caribou conservation will require a multifaceted approach that includes curbing human development and native habitat restoration.

Acknowledgements

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