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Title

Dietary niche separation of three Late Pleistocene bear species from Vancouver Island, on the Pacific Northwest Coast of North America

Short Running Title

Diet of Late Pleistocene bears

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Abstract

Competition between taxa related to climate changes has been proposed as a possible factor in Pleistocene megafaunal extinctions, and here we present isotope evidence of the diets of three co-existing bear species (black bear (*Ursus americanus*), brown bear (*Ursus arctos*), and the now extinct short-faced bear (*Arctodus simus*)) from a locale in western North America dating to the Late (Terminal) Pleistocene (~14.5–11.7 ka). The three bear species were found at a number of sites on Vancouver Island, on the western coast of Canada. In order to examine the chronological overlap and niche partitioning between these species of bear, we used direct radiocarbon dating, stable isotope analysis, and ZooMS proteomic identification methods. Here we present new radiocarbon evidence from Terminal Pleistocene *U. americanus*, *U. arctos*, and *Arctodus simus* from several sites on the island, along with both bulk collagen and compound-specific isotope data for these species. Radiocarbon dates confirm the chronological overlap of *Arctodus* and both *Ursus* species in the montane regions of the island at the end of the Pleistocene. Stable isotope data reveal niche differentiation between these species, with *U. americanus* occupying a distinctly lower trophic position than the other two taxa.

Keywords

Pleistocene, Bears, *Arctodus*, amino acid, isotopes,

1. Introduction

At the terminus of the Pleistocene epoch, the final recession of the Cordilleran Ice Sheet following the Wisconsin glaciation opened previously ice-locked land masses to colonization by a variety of species. The maximum geographical extent of ice sheet coverage and exact timing of ice sheet recession from the northwest coast, and Vancouver Island in particular, remains an

48 area of study; however, a growing body of environmental proxy data is working to provide
49 insight on the specifics of these changes at local and regional scales (e.g., Al-Suwaidi et al. 2006,
50 Cosma et al. 2008, Howes 1983, James et al. 2000, Ward and Thomson 2004, Eamer et al. 2017,
51 McLaren et al. 2014). Pollen records from several sites on Vancouver Island indicate that glacial
52 recession and an initially treeless landscape was followed by the colonization of the region by
53 shade-intolerant Lodgepole Pine (*Pinus contorta*) and later by the establishment of increasingly
54 closed and shade-tolerant forests with the appearance of species such as Spruce (*Picea*),
55 Mountain Hemlock (*Tsuga mertensiana*), and Red Alder (*Alnus rubra*) (Hebda 1983, Al Suwaidi
56 et al. 2006, Lacourse 2005).

57 While both *Ursus americanus* and *Ursus arctos* were present elsewhere on the
58 Northwest Coast prior to the Last Glacial Maximum (LGM) (Heaton and Grady 2003), these
59 species have yet to be documented on Vancouver Island prior to the LGM. *Arctodus*, however,
60 was known to be present prior to the LGM on Vancouver Island (Steffen and Harington 2010).
61 The recolonization of the Northwest Coast by *Ursus* following deglaciation has been previously
62 documented by early post-glacial dates from Haida Gwaii (Ramsey et al. 2004) and Vancouver
63 Island (Steffen and Fulton, 2018). Examples of post-glacial *Arctodus* in the region are currently
64 limited to two specimens from Vancouver Island (Steffen and Fulton 2018).

65 *Ursus arctos* and *Arctodus* have been noted to co-occur in the paleontological record
66 elsewhere in North America (eg. Barnes et al. 2002, Matheus 1995, Davison et al. 2011).
67 Additionally, *U. americanus* and *U. arctos* were found to co-occur to the north on Haida Gwaii
68 during the Younger Dryas (12,900–11,500 cal YBP) (Fedje et al., 2011) and co-occur regionally in
69 several parts of North America to this day, including part of the northwest coast. Vancouver
70 Island presents a case of temporal overlap between not only two, but all three of these bear
71 species in the time period shortly preceding the extinction of the short-faced bear.

72

73 **1.1 Stable Isotope Analysis of Extinct Megafauna**

74 The dietary requirements of now-extinct *Arctodus simus* have been debated within
75 paleontological literature, with claims made for everything from an herbivorous to a hyper-
76 carnivorous diet based on morphological characteristics, microwear and paleopathological
77 analyses, and stable isotope analyses of skeletal remains (Figueirido et al. 2010, Kurtén 1967,
78 Emslie and Czaplewski 1985, Bocherens et al. 1995, Fox-Dobbs et al. 2008, Donohue et al 2013,
79 Figueirido et al. 2017). Existing stable isotope data for *Arctodus* is primarily limited to that of
80 more northerly specimens from the Yukon and Alaska, with only one specimen from pre-LGM
81 Vancouver Island (see Steffen and Harington 2010, Matheus 1995, Barnes et al., 2002,
82 Schwartz-Narbonne et al. 2015, Bocherens et al 1995, Fox-Dobbs et al. 2008), although recently
83 published data from a single Late Pleistocene specimen found on the California Channel Islands
84 contributes some insight into the diets of more southerly populations (Mychajliw et al. 2020).

85 It has been previously suggested by Steffen and Fulton (2018) that *U. Arctos* and
86 *Arctodus* may have exhibited territorial niche partitioning on the island, and that competition
87 should be considered as a factor in extinction. They proposed that future studies of the trophic
88 interactions of these species may reveal the influence of competition on resource availability
89 for *Arctodus* the end of the Pleistocene. Additionally, the influence of competition on *Arctodus*
90 diet has been suggested in recent explorations of *Arctodus* diet that consider regional variability
91 and the presence of other large carnivore species (Figueirido et al. 2017).

92 To better understand the diets of these three co-existing bear species in this region, we
93 used both bulk collagen stable isotope analysis as well as compound-specific stable isotope
94 analysis (CSIA) on a subset of specimens from all three species, as the latter technique offers a
95 high-resolution dietary analysis. A variety of contributing factors can influence the bulk collagen
96 carbon and nitrogen isotope composition of a consumer's tissues, including diet, environmental
97 and climatic conditions, and digestive physiology (DeNiro and Epstein 1978, DeNiro and Epstein
98 1981, Austin and Vitousek 1998, Craine et al. 2009, McMahon and McCarthy 2016). By
99 analyzing the carbon and nitrogen isotope ratios of individual amino acids within bone collagen,
100 it is possible to differentiate between some of the factors that contribute to the resulting
101 isotopic composition of consumer tissue. This is a relatively novel approach to isotope analysis
102 of paleontological materials; current challenges in the application of CSIA are summarized by
103 Whiteman et al. (2019).

104 While some amino acids in bone collagen closely reflect the isotopic composition of an
105 animal's diet, others experience higher magnitudes of trophic fractionation due to the isotopic
106 effects of amino acid synthesis and assimilation within the consumer's body. For the
107 investigation of carbon isotopes, CSIA allows for the distinction between the isotopic
108 compositions of essential and non-essential amino acids. Essential amino acids are those that
109 cannot be synthesized by the consumer; therefore, their carbon skeletons must be acquired
110 intact from dietary sources, and the carbon isotope composition of these amino acids in
111 consumer tissue closely reflects that of their dietary source. Non-essential amino acids, which
112 can be either directly acquired from dietary sources or synthesized within the body, reflect the
113 carbon isotope composition of dietary sources to different extents (Whiteman et al. 2018;
114 however, see Newsome et al. 2011 to consider the contribution of the gut microbiome to
115 essential amino acid isotope composition).

116 Because the nitrogen-containing amine group of each amino acid is affected by different
117 processes than its carbon skeleton, CSIA of nitrogen makes use of the distinction between
118 'source' and 'trophic' amino acids. Source amino acids are known to closely reflect the nitrogen
119 isotope composition of a dietary source, while trophic amino acids undergo significant
120 fractionation through the processes of deamination and transamination. The distinction
121 between these two groups has been well-established empirically across many food webs
122 (McClelland and Montoya 2002, Chikaraishi et al. 2009, Naito et al. 2010, Naito et al. 2013) and
123 more recently, metabolic explanations have been proposed to explain the fidelity of these
124 groupings (Chikaraishi et al. 2014, McMahon and McCarthy 2016, O'Connell 2017).

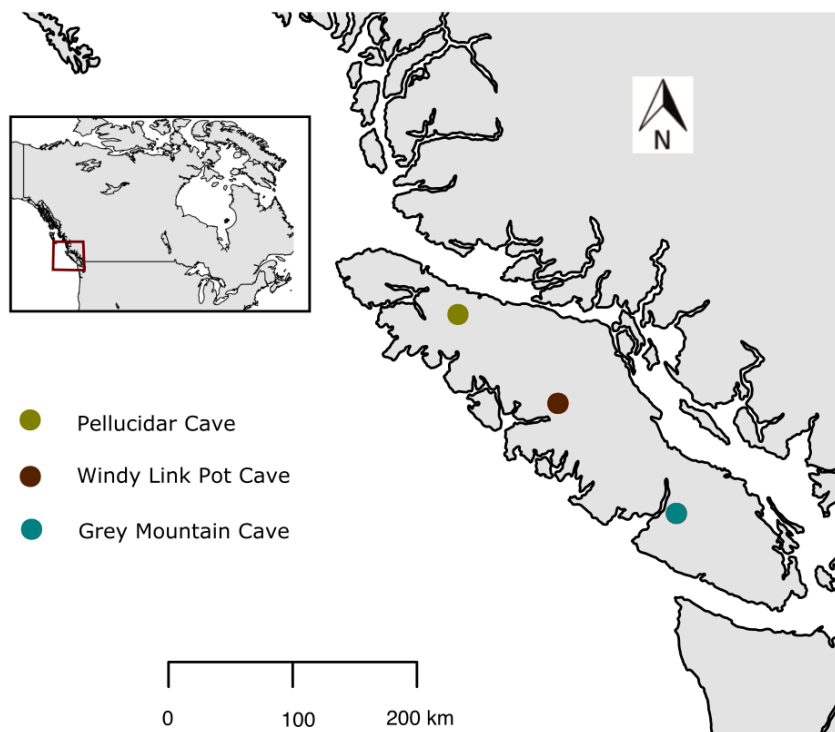
125 In this study, we aim to contribute to the small but growing body of individual amino
126 acid stable isotope data for extinct taxa and provide compound-specific collagen stable isotope
127 data for extant North American large mammal species—*Ursus americanus* and *Ursus arctos*. In
128 combination with direct radiocarbon dating and ZooMS proteomic identification, we use this
129 data to explore the ecological context of these three bear species on Vancouver Island at the
130 end of the Late Pleistocene.

131

132 **2. Materials**

133 A total of ten bone samples were analyzed in this study, consisting of three short-faced
134 bears (*Arctodus simus*) four brown bears (*Ursus arctos*), and three black bears (*Ursus*
135 *americanus*) from five locations on Vancouver Island, in British Columbia, Canada. All Terminal

136 Pleistocene material examined in this paper originates from montane cave sites. Limestone
137 solution caves can provide shelter for hibernating bears and sometimes act as traps for large
138 mammals, both situations resulting in the deposition of bones on cave floors. The specimens
139 examined in this study are housed at the Royal British Columbia Museum (RBCM) in Victoria,
140 B.C., Canada. The approximate geographic origins of the samples can be found in Figure 1.
141



142
143 Figure 1. Pleistocene bear recovery locations in this study.

144 S-SFU 269 and 270 come from Windy Link Pot Cave. The cave, with an entrance
145 elevation of approximately 900 m above sea level, is part of a large underground system
146 spanning nearly 10 km. The specimens used in this study were collected from the cave floor
147 surface at the base of the 78 m vertical drop cave entrance. They were identified as *Ursus*
148 *americanus* by Nagorsen et al. (1995), who report a detailed morphological description of their
149 identification. S-SFU 269 was sampled from a skull, and S-SFU 270 from a mandible, each
150 representing a different individual.

151 S-SFU 277–281 come from Pellucidar Cave. Pellucidar Cave is a large limestone cave
152 system with an underground stream elevated at approximately 480 m above sea level (Steffen
153 and McLaren 2008); it is described in detail by Nagorsen and Keddie (2000). The specimens in
154 this study were collected from the cave floor surface, approximately 60 m in from the cave
155 opening. The morphology and radiocarbon dates of these specimens are described in detail by
156 Steffen and Fulton (2018). The samples include an immature *Ursus arctos* humerus (S-SFU 277),
157 an *Arctodus simus* palatine (S-SFU 278), an *Arctodus simus* humerus (S-SFU 279), an *Ursus*
158 *arctos* femur (S-SFU 280), and an *Ursus arctos* humerus (S-SFU 281). It was noted by Steffen and
159 Fulton (2018) that the *Arctodus simus* palatine and humerus (S-SFU 278 and 279) are not
160 exclusive elements and could potentially represent the same individual.

161 S-SFU 272 was collected from Grey Mountain Cave in February 1990. The specimen is an
162 *Ursus arctos* juvenile femur.

163 S-SFU 276 comes from North Vancouver Island Cave (near Pellucidar cave) and was first
164 reported by Steffen and Fulton (2018). The specimen sampled is an *Ursus americanus* cranium.

165

166 **3. Methods**

167 3.1 ZooMS

168

169 Five samples (S-SFU-269, 278, 279, 280, 281) were processed for ZooMS collagen
170 peptide mass fingerprinting (Buckley et al. 2009). Approximately 50 mg bone chunk samples
171 were prepared and analyzed at the Manchester Institute of Biotechnology following the
172 procedure described by van der Sluis et al. (2014). In brief, this involved decalcification of ~25-
173 50 mg bone powder with 0.6 M hydrochloric acid for 18 hours, centrifugation at 12,400 rpm for
174 1 minute and the acid-soluble fraction ultrafiltered on a 10 kDa molecular weight cut-off
175 membrane (Vivaspin, UK). Following two washes in 50 mM ammonium bicarbonate (ABC), 100
176 μ L of retentate was removed and digested with 0.4 μ g sequencing grade trypsin (Promega, UK)
177 for 18 hours at 37 °C. Peptide solutions were then acidified to 0.1% trifluoroacetic acid (TFA;
178 Sigma, UK), and purified by C18 pipette tips (OMIX, UK) eluting with 50% acetonitrile
179 (ACN)/0.1% TFA, dried to completion and resuspended with 0.1% TFA. One tenth was then
180 spotted with an equal volume of 10 mg/mL alpha-cyano hydroxycinnamic acid in 50% ACN/0.1
181 % TFA onto a stainless steel Matrix Assisted Laser Desorption Ionization (MALDI) target plate
182 and allowed to air dry. Samples were then analysed using a Bruker Autoflex II MALDI time of
183 flight mass spectrometer with the m/z range 700-3,700 and resultant spectra compared with
184 reference materials (see Figure S4).

185

186 3.2 Radiocarbon Dating

187

188 Approximately 500 mg of bone powder was drilled from samples S-SFU-269, 270, 272,
189 and 276, and sent to the A.E. Lalonde AMS laboratory at the University of Ottawa for
190 radiocarbon age determination. Sample preparation included collagen extraction following a
191 modified version of the Longin (1971) method utilizing ultrafiltration of collagen through 30kDa
192 MWCO filters, the specific laboratory protocol for which is described as media code BU in Crann
193 et al. (2017). ^{14}C analysis was carried out by AMS on prepared graphite. Calibration of
194 radiocarbon determination to calendar year was performed using OxCal 4.4 software (Bronk
195 Ramsey 2009) according to the IntCal20 calibration curve (Reimer et al. 2020).

196

197 3.3 Bulk Collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ Stable Isotope Analysis

198

199 Samples S-SFU 277-281 were prepared for carbon and nitrogen bulk stable isotope
200 analysis (BSIA) following the protocol described in Müldner and Richards (2005) at the
201 Archaeology Isotope Laboratory, Department of Archaeology, Simon Fraser University. To
202 summarize, bone chunks (<1g) were demineralized in 0.5M HCl, rinsed with distilled water,
203 then gelatinized at 75 °C in pH3 HCl and filtered through 30kDa MWCO ultrafilters, with the

204 >30kDa fraction lyophilized for analysis. Duplicate samples were encapsulated in tin capsules
205 and sent to Iso Analytical, Crewe UK, where $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were measured in duplicate
206 by EA-IRMS.

207 Collagen quality standards required a collagen yield between 0.5 and 22%, C/N ratio of
208 2.9–3.6, %C of 15.3–47%, and %N between 5.5% and 17.3% (Ambrose 1990, DeNiro 1985, van
209 Klinken 1999). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values presented here are the average of duplicates, reported
210 as the ‰ difference from the international standards VPDB for carbon ($^{13}\text{C}/^{12}\text{C}$) and AIR for
211 nitrogen ($^{15}\text{N}/^{14}\text{N}$) (Coplen, 2011).

212 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were calibrated to VPDB and AIR using the standard IA-RO68 (soy
213 protein, $\delta^{13}\text{C} = -25.22$ ‰, $\delta^{15}\text{N} = 0.99$ ‰). Check standards included IA-R038 (L-alanine, $\delta^{13}\text{C} = -$
214 24.99 ‰, $\delta^{15}\text{N} = -0.65$ ‰), IA-R069 (tuna protein, $\delta^{13}\text{C} = -18.88$ ‰, $\delta^{15}\text{N} = 11.60$ ‰) and a
215 mixture of IAEA-C7 (oxalic acid, $\delta^{13}\text{C} = -14.48$ ‰) and IA-R046 (ammonium sulfate, $\delta^{15}\text{N} = 22.04$
216 ‰). Average observed values of these check standards during analysis were $\delta^{13}\text{C} = -25.05$ ‰,
217 $\delta^{15}\text{N} = -0.47$ ‰ (IA-R038, $n = 2$); $\delta^{13}\text{C} = -18.85$ ‰, $\delta^{15}\text{N} = 11.72$ ‰ (IA-R069, $n = 2$); and $\delta^{13}\text{C} = -$
218 14.57 ‰, $\delta^{15}\text{N} = 21.97$ ‰ (IAEA-C7 and IA-R046, $n = 2$).

219 Samples 269, 270, 272, and 276 were prepared and analyzed at the University of Ottawa
220 G.G. Hatch stable isotope laboratory, where a subsample of the lyophilized collagen prepared
221 for radiocarbon dating was analyzed in duplicate by EA-IRMS for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. $\delta^{13}\text{C}$ and
222 $\delta^{15}\text{N}$ values were calibrated to VPDB and AIR using internal standards calibrated to the
223 international standards IAEA-N1 (+0.4‰), IAEA-N2 (+20.3‰), USGS-40 (-4.52‰) and USGS-41
224 (47.55‰) for nitrogen and IAEA-CH-6 (-10.4‰), NBS-22 (-29.91‰), USGS-40 (-26.39‰) and
225 USGS-41 (36.55‰) for carbon. Analytical precision was determined based on the results of the
226 internal check standard C-55 glutamic acid (expected value: $\delta^{15}\text{N} = -3.98$, $\delta^{13}\text{C} = -28.53$;
227 measured value = $\delta^{15}\text{N} = -4.0$, $\delta^{13}\text{C} = -28.4$).

228

229 3.4 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ Analysis of Individual Amino Acids

230

231 Extracted collagen was prepared and analysed for CSIA-AA at the Memorial Applied
232 Archaeological Science (MAAS) laboratory and Biogeochemistry of Boreal Ecosystems
233 Laboratory at Memorial University (S-SFU-269, 276, 278, and 279) and at the Archaeology
234 Isotope Laboratory, Department of Archaeology, Simon Fraser University (S-SFU 272, 277, and
235 281), with the same preparation protocol followed at both labs. For each sample, 1 mg of
236 lyophilized collagen was hydrolyzed in 6M HCl at 110 °C for 20 hours, blown down at 60°C
237 under a gentle stream of pure nitrogen, and re-dissolved in 0.1M HCl. An internal standard (nor-
238 leucine) was added to each sample prior to derivatization. Due to the amide to carboxylic group
239 conversion during acid hydrolysis, glutamine (Gln) and asparagine (Asn) are respectively
240 converted to glutamic acid (Glu) and aspartic acid (Asp), and their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values reflect
241 the combined contributions; these are hereafter notated as Glx and Asx (Fountoulakis and
242 Lahm 1998).

243 A standard, AAmix, was prepared and derivatized along with the samples containing
244 each of the analyzed amino acids—alanine (Ala), glycine (Gly – USGS65), valine (Val – USGS74),
245 leucine (Leu), threonine (Thr), serine (Ser), proline (Pro), aspartic acid (Asp), glutamic acid (Glu),
246 hydroxyproline (Hyp), phenylalanine (Phe), and lysine (Lys). EA-IRMS was used to determine the
247 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the individual amino acids in the standard mixture prior to their

248 combination, except for Gly and Val, which had certified values. A quality control sample,
249 QCmix, contained only Gly, Val, Pro and Glu. The free amino acids in the standards and samples
250 were derivatized into N-acetyl isopropyl (NAIP) esters following the procedure described in Corr
251 et al. (2007).

252 GC-C-IRMS analysis for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of derivatized amino acids was performed
253 at the CREAT - Stable Isotope Laboratory at Memorial University using an Agilent 6890N gas
254 chromatograph coupled via a GC Combustion III interface to a Delta V Plus isotope ratio mass
255 spectrometer (GC-C-IRMS). For $\delta^{13}\text{C}$ analysis, a GC-PAL autosampler (CTC Analytics) injected
256 samples at 250 °C onto a VF-23ms GC column (60 m x 0.32 mm x 0.15 μm ; Agilent Technologies)
257 following an oven temperature program of 70 °C for 0.5 min; to 120 °C at 15 °C/min; to 180 °C
258 at 2 °C/min; to 255 °C at 5 °C/min; hold 16 min. Separated gases then entered a Cu, Ni, and Pt
259 wire oxidation reactor held at 940 °C, followed by a reduction reactor at 640 °C at a flow rate of
260 1.5mL/min. Samples were analyzed in triplicate in a sequence with an amino acid standard and
261 quality control (QC) sample. Each sample and standard was then blown down under nitrogen by
262 a factor of approximately 5 for $\delta^{15}\text{N}$ analysis. Samples were injected onto a VF-23 ms GC
263 column (60 m x 0.32 mm x 0.50 μm ; Agilent Technologies) at 250 °C and subjected to an oven
264 temperature program of 70 °C for 0.5 min; to 130 °C at 15 °C/min; to 255 °C at 6 °C/min; hold
265 11 min. A liquid nitrogen trap was used to capture CO_2 and prevent its entry into the IRMS.

266 At the Archaeology Isotope Laboratory, Department of Archaeology, Simon Fraser
267 University, CSIA-AA measurements followed a similar protocol, with modifications made for
268 differences in instrument specifications. Amino acid derivatives were analyzed on a Trace 1310
269 gas chromatograph coupled to a GC Isolink II combustion system and a Delta V Plus mass
270 spectrometer (GC-C-IRMS; all Thermo Scientific). Separated amino acids passed through a
271 combustion reactor (1000°C) consisting of a NiO tube containing CuO, NiO, and Pt wires, which
272 provides quantitative oxidation and reduction of N_2 . An AS 1310 autosampler (Thermo
273 Scientific) was used to inject 1.0 μL for both ^{13}C and ^{15}N measurements. For $\delta^{13}\text{C}$ analysis, the
274 same GC column specifications and oven temperature program as described above were utilized,
275 with the exception that the final temperature of 255 °C was held for 21 minutes. Samples were
276 analyzed in triplicate with the AAmix and QCmix standards interspersed throughout the
277 sequence. Following C isotope analysis, samples and standards were concentrated under a
278 gentle flow of nitrogen by a factor of ~5 for N isotope analysis. Samples were injected onto an
279 Agilent DB-35 GC column (60 m x 0.32 mm x 0.5 μm) at 240 °C with a 3.5 second pre-injection
280 dwell time following a short (12 sec) seed oxidation prior to each analysis. Samples S-SFU 277
281 and 281 were analyzed with the following GC oven program with a flow rate of 1.4 ml/min: 50
282 °C for 2 min, to 140 °C at a rate of 13 °C/min, to 195 °C at 3°C/min and held for 7 mins, to 245°C
283 at 8°C/min and held for 11 mins, to 280°C at 15 °C/min; this final temperature was held for 8
284 minutes. Sample S-SFU 272 was analyzed with the following GC oven program with a flow rate
285 of 1.3 ml/min: 40 °C for 5 min, to 120 °C at a rate of 15 °C/min, to 180 °C at 3 °C/min, to 210 °C
286 at 1.5 °C/min, and finally to 280 °C at 5 °C/min, where this final temperature was held for 8.8
287 minutes. A liquid nitrogen trap was used to capture CO_2 and prevent its entry in to the IRMS.

288 $\delta^{13}\text{C}$ values were corrected for the carbon added during derivatization by applying a
289 correction factor following Silfer et al. (1991) to the measured values. For $\delta^{15}\text{N}$ analysis, GC-C-
290 IRMS-measured values of the AAmix were plotted against EA-IRMS-measured values for each
291 amino acid, and the linear relationship was used to correct measured values in samples.

292 Matrix-matched quality Control (QC) samples were also derivatized and analyzed
293 alongside the samples. At Memorial University, this included a bovine gelatin (BGEL) standard,
294 for which long-term data on $\delta^{13}\text{C}$ means and standard deviations are available (Table S1).
295 Longterm data on the $\delta^{15}\text{N}$ values of the amino acids in these QCs are not available yet;
296 standard deviations of measurements within runs are presented alongside $\delta^{15}\text{N}$ data. At Simon
297 Fraser University, both seal collagen (SRM-1) and deer collagen (SRM-2) QC samples were used;
298 data on the $\delta^{13}\text{C}$ means and standard deviations are presented in Table S2, and the $\delta^{15}\text{N}$ means
299 and standard deviations are presented in Table S3. These QC standards allow for the evaluation
300 of the quality of derivatization and GC-C-IRMS analysis.

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4. Results

A summary of results discussed within the text are presented in Table 1 and Table 2.

Table 1. ZooMS identification and Radiocarbon results. ** = ¹⁴C age reported by Steffen and Fulton (2018); All other dates listed are from this study.

S-SFU	Taxon	Skeletal Element	Context	ZooMS ID	¹⁴ C Lab Designation	¹⁴ C a BP	Calibrated μ	Median	68.3% range cal a BP
269	<i>Ursus americanus</i>	skull	Windy Link Pot Cave	Ursus	UOC-4529	11,202±49	13125	13124	13,160-13,094
270	<i>Ursus americanus</i>	mandible	Windy Link Pot Cave	N/A	UOC-4530	11,219±49	13135	13134	13,161-13,100
272	<i>Ursus arctos</i>	femur	Grey Mtn Cave	N/A	UOC-4532	11,830±49	13682	13684	13,758-13,609
276	<i>Ursus americanus</i>	cranium	North V. l. Cave	N/A	UOC-4535	11,913±49	13778	13773	13,981-13,611
277	<i>Ursus arctos</i>	humerus	Pellucidar Cave	N/A	UCIAMS-41052**	11,110±30	13033	13042	13,097-12,998
278	<i>Arctodus simus</i>	palatine	Pellucidar Cave	Arctodus	UCIAMS-41049**	11,615±30	13484	13480	13,571-13,453
279	<i>Arctodus simus</i>	humerus	Pellucidar Cave	Arctodus	UCIAMS-41048**	11,775±30	13637	13638	13,741-13,520
280	<i>Ursus arctos</i>	femur	Pellucidar Cave	Ursus	UCIAMS-41050**	12,425±3	14569	14545	14,830-14,337
281	<i>Ursus arctos</i>	humerus	Pellucidar Cave	Ursus	UCIAMS-41051**	12,440±35	14599	14583	14,845-14,366

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Table 2. Summary of discussed stable isotope results reported in ‰ with measurement uncertainties for duplicate and triplicate injections. Long-term uncertainties presented in supplementary tables 1-3.

S-SFU	Taxon	Bulk collagen $\delta^{13}\text{C}$	Bulk collagen $\delta^{15}\text{N}$	$\delta^{15}\text{N}_{\text{Glx}}$	$\delta^{15}\text{N}_{\text{Phe}}$	$\delta^{15}\text{N}_{\text{Thr}}$	$\delta^{13}\text{C}_{\text{Phe}}$	$\delta^{13}\text{C}_{\text{Gly}}$
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269	<i>Ursus americanus</i>	-19.5	1.7	10.4 (±0.2)	11.9 (±0.3)	-11.2 (±1.4)	-25.8 (± 0.9)	-16.7 (± 0.1)
270	<i>Ursus americanus</i>	-19.9	0.6	----	----	---	---	---
272	<i>Ursus arctos</i>	-17.1	10.2	11.0 (±0.4)	7.6 (±0.6)	-13.9 (±0.3)	-24.6	-18.3
276	<i>Ursus americanus</i>	-20.8	1.7	6.4 (±0.1)	7.7 (±0.2)	-12.5 (±0.2)	-25.8 (±0.2)	-14.9 (±0.1)
277	<i>Ursus arctos</i>	-19.6	6.2	8.1 (±0.8)	---*	-13.8**	-25.9 (±0.1)	-19.9 (± 0.1)
278	<i>Arctodus simus</i>	-19.0	5.3	12.0 (±0.0)	7.1 (±1.1)	-25.6 (±0.8)	-23.4 (±0.7)	-11.3 (± 0.2)
279	<i>Arctodus simus</i>	-19.0	5.5	11.8 (±0.8)	5.6 (±1.6)	-24.9 (±1.6)	-25.1 (± 0.3)	-13.3 (± 0.0)
280	<i>Ursus arctos</i>	-19.2	7.3	----	----	----	----	---
281	<i>Ursus arctos</i>	-18.3	9.4	13.0 (±0.2)	5.8 (±0.5)	-15.2 (±0.8)	-26.4 (± 0.4)	-13.2 (± 0.3)

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* excluded due to co-elution

**measurement uncertainty unknown; first injection caused co-elution (no duplicate injection)

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4.1 ZooMS Identifications

Due to variations in morphological characteristics through time and between populations, distinguishing between different bear taxa in fragmentary Pleistocene remains based on skeletal morphology alone can present difficulties (e.g. Richards et al. 1996, Steffen and Fulton 2018). The task of distinguishing *Ursus arctos* from *Ursus americanus* can present particular challenges when considering Pleistocene remains. Although modern grizzly bears are generally larger than modern black bears, these bears may have been more similar in size during parts of the Pleistocene (Gordon 1986, Wolverton and Lyman 1998), with *U. americanus* adults significantly overlapping in cranial size with immature *U. arctos* (Nagorsen et al. 1995). The comparatively large size of Pleistocene *U. americanus* has been proposed as an explanation for why some relatively isolated populations of *U. americanus*, such as those found on Pacific northwest islands today (including Vancouver Island), are unusually large (Gordon 1986), featuring larger teeth and broader skulls. Vancouver Island's modern black bears feature such distinctly large skulls that they have been sometimes referred to as the separate subspecies *Ursus americanus vancouveri* (Hall 1928:231). Molar size criteria have been developed to distinguish between these species (Gordon 1977); however, molars are not always available for Pleistocene specimens consisting of only one or a few skeletal elements. More recently, geometric morphometric analyses of Pleistocene *Ursus* specimens has sought to reclassify several previously misidentified specimens (Kantelis 2017).

Biomolecular identification methods had been previously attempted on some of the samples included in this study, with mixed results. One sample in the current study (SFU-277) was originally reported as *U. americanus* for radiocarbon dating (Steffen and McLaren 2008) but was later identified using aDNA as *U. arctos* (Steffen and Fulton 2018). Although ancient DNA analysis of S-SFU 279 was also attempted by Steffen and Fulton (2018), no endogenous DNA was recovered, and its identification as *Arctodus* remained solely morphological. However, the potential for collagen to survive longer in a burial environment than DNA (Nielsen-Marsh 2002, Buckley and Collins 2011) made this sample a good potential candidate for ZooMS identification, as this technique allows identification to the genus level and therefore differentiation between *Arctodus* and *Ursus* spp. Preserved collagen peptide sequences from five of our samples confirmed S-SFU-278 and 279 as *Arctodus*, and SFU-269, 280, and 281 as *Ursus*.

4.2 Radiocarbon Chronology

Radiocarbon dating was carried out on all specimens of unknown age and those lacking direct radiocarbon dates. We report new direct AMS dates on three Late Pleistocene *Ursus* individuals (S-SFU-269; S-SFU 270; S-SFU-272) along with a corroborating radiocarbon date for S-SFU-276, which is in close agreement with the radiocarbon date for this specimen recently reported by Steffen and Fulton (2018) of 11935 +/- 40 (UCIAMS 56479). Figure 2 shows calibrated radiocarbon date distributions for the bears analyzed in this study.

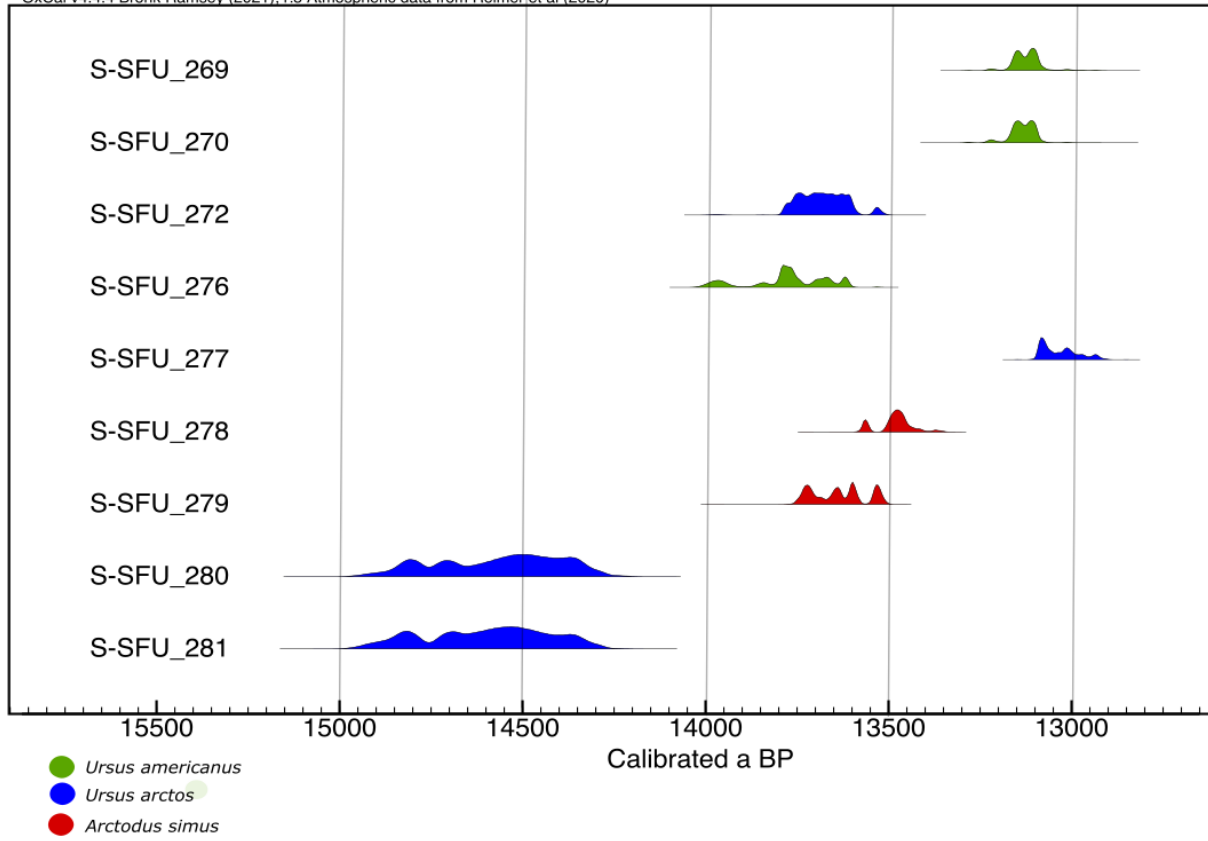


Figure 2. Calibrated radiocarbon age distributions

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356 Previously, a composite sample of post-cranial fragments from an immature individual found on
 357 the surface of the cave floor near S-SFU 269 and 270 was radiocarbon dated to 9,760 +/- 140
 358 ¹⁴C a BP (Nagorsen et al. 1995). S-SFU 269 and 270 represent mature individuals, and this
 359 composite date cannot be directly applied to other materials on the cave floor surface, as their
 360 association is unknown. The new dates given here of 13,160–13,094 cal a BP for S-SFU 269
 361 (11,202 +/- 49 ¹⁴C a BP) and 13,161-13100 cal a BP for S-SFU 270 (11219 +/- 49 ¹⁴C YBP) show
 362 that *Ursus americanus* was present on Vancouver Island during the Late Pleistocene at Windy
 363 Link Cave, significantly earlier than the initial date reported in association with these
 364 specimens.

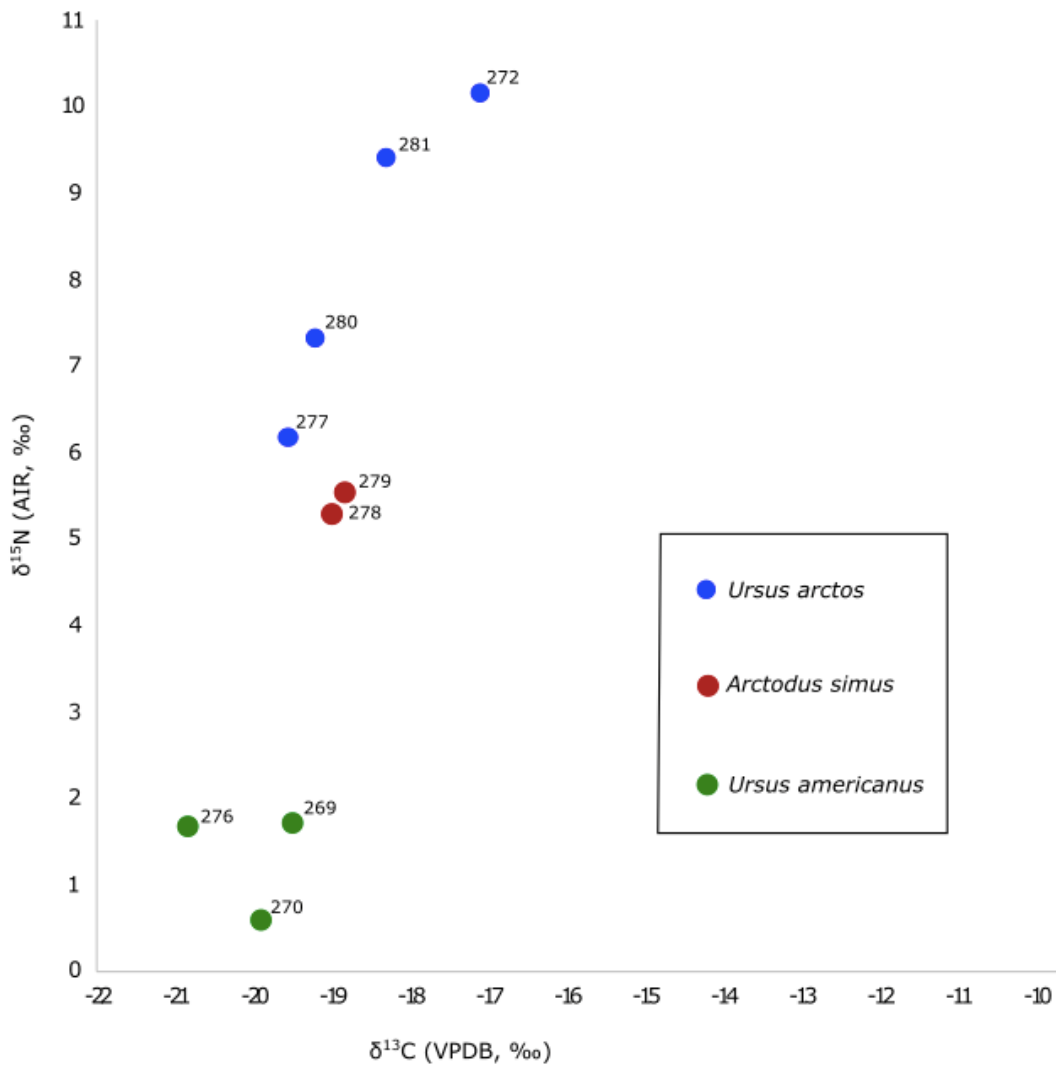
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366 **4.3 Bulk Collagen Stable Isotope Analysis**

367 Carbon and nitrogen stable isotope analysis has been used to investigate the diet of
 368 extinct and extant species of bears in both modern and paleontological or archaeological
 369 contexts (e.g., Hildebrand et al. 1996, Barnes et al. 2002, Dykstra 2015, Richards et al. 2008,
 370 Hopkins et al. 2017). Hildebrand et al. (1996) conducted experiments on bears in the modern
 371 Pacific Northwest to determine the relationship between the stable carbon and nitrogen
 372 composition of bear tissues and their observed dietary inputs. The $\delta^{13}\text{C}$ values of bear bone
 373 collagen has been observed to indicate the amount of marine versus terrestrial carbon
 374 contributed via protein ingestion (Hildebrand et al. 1996). However, such values can also be

375 influenced by trophic level fractionation and the consumption of plants with different pathways
376 of carbon metabolism (DeNiro and Epstein 1978). Nitrogen stable isotope composition can help
377 determine the bear's trophic level (Hildebrand et al. 1996, DeNiro and Epstein 1981) due to the
378 significant enrichment in ^{15}N that occurs with increasing trophic levels within a food web.
379 However, $\delta^{15}\text{N}$ values can also be affected by fluctuations in climate, such as relative aridity
380 (Austin and Vitousek 1998, Craine et al. 2009), and the difference in climatic context between
381 specimens of different ages should be considered when comparing these bulk tissue stable
382 isotope results. A summary of bulk collagen carbon and nitrogen stable isotope data from the
383 bears investigated in this study is presented in Figure 3.

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Figure 3. Bulk collagen carbon versus nitrogen isotope compositions of the bear specimens

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389 In the case of bears, anadromous fish such as salmon are a likely marine source that would
390 elevate $\delta^{13}\text{C}$ values (Hildebrand et al. 1996). In these Pleistocene Vancouver Island samples,
391 $\delta^{13}\text{C}$ values appear to increase stepwise with $\delta^{15}\text{N}$ values, indicating a trophic level diet-tissue

392 offset rather than a significant contribution of anadromous fish; however, there is some spread
393 within both the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *U. arctos*. While the carbon and nitrogen stable isotope
394 ratios of *U. americanus* converge around the expected values for a terrestrial diet at a low
395 trophic level, the *U. arctos* values have a much wider range of values.

396 Considering that bone collagen provides a signal reflective of the dietary intake across
397 several years of an animal's life (Stenhouse and Baxter 1979), small contributions of
398 anadromous fish to the diets of *U. arctos* could be obscured in the bulk collagen isotopic signal
399 by the consumption of ^{13}C -depleted resources. Smaller contributions of such resources to the
400 diet are especially obscured when overall lower quantities of protein are consumed, causing
401 collagen formation that routes a higher percentage of carbon from non-protein (lipid and
402 carbohydrate) sources (Howland et al. 2003).

403 404 **4.4 Carbon compound specific isotope analysis (CSIA)**

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406 Due to the low availability of contemporary comparative paleontological samples from these
407 contexts on Vancouver Island, it was not possible to employ the CSIA carbon isotope
408 fingerprinting technique used by other researchers which uses different species to reconstruct
409 food-webs and diets (e.g. Larsen et al. 2009, Corr et al. 2007, Larsen et al. 2013, Jarman et al.
410 2017). However, several trends in individual amino acid carbon isotope composition have been
411 observed across a variety of ecosystems and time periods, and syntheses of published CSIA
412 carbon data (eg. Corr et al. 2005, Honch et al. 2012, Webb et al 2018) allow for broad
413 comparisons with these trends.

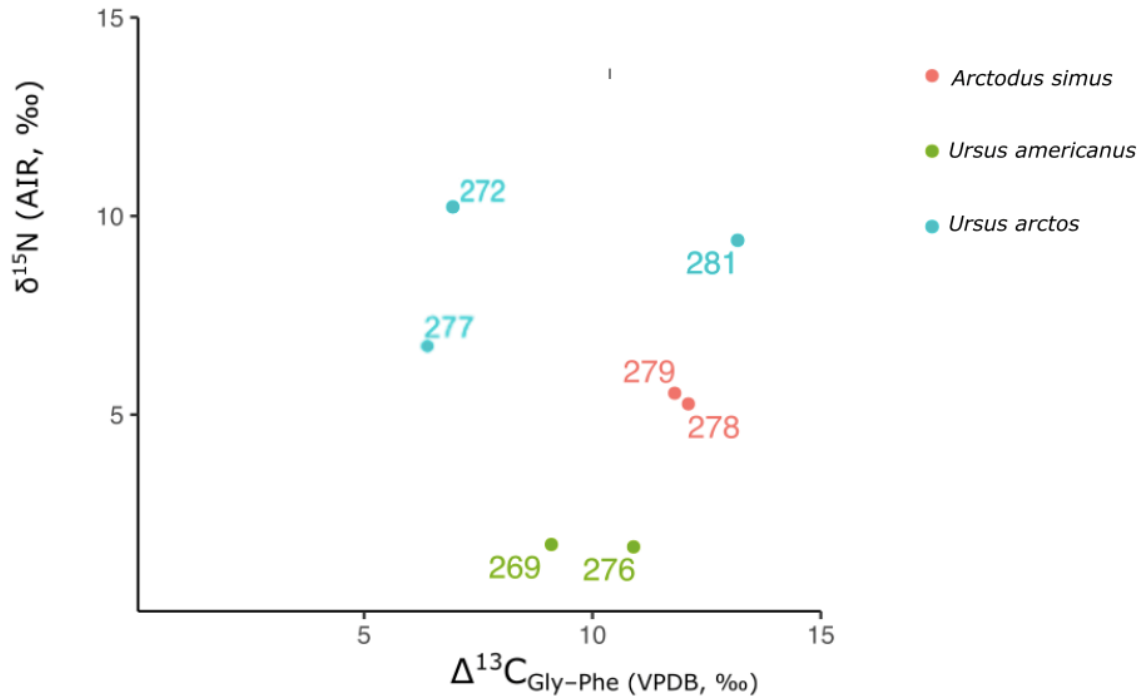
414 The difference between the $\delta^{13}\text{C}$ values of the nonessential amino acid Gly and the
415 essential amino acid Phe the ($\Delta^{13}\text{C}_{\text{Gly-Phe}}$) has been used as a proxy for aquatic (marine and
416 freshwater) versus terrestrial protein consumption, with higher $\Delta^{13}\text{C}_{\text{Gly-Phe}}$ values indicating
417 higher contributions of aquatic resources and lower $\Delta^{13}\text{C}_{\text{Gly-Phe}}$ values indicating relatively lower
418 contributions of such resources (Webb et al 2018:6).

419 The $\Delta^{13}\text{C}_{\text{Gly-Phe}}$ values do not appear to vary greatly between the difference bear species
420 investigated here, and all samples fall below the values expected for high aquatic protein
421 consumers (Figure 4; see Webb et al. 2018:6). Furthermore, bulk collagen $\delta^{13}\text{C}$ values and
422 nitrogen CSIA data (discussed below) further suggest that heavy reliance on aquatic resources
423 was unlikely for any of these bears.

424 It is possible that the *U. arctos* shown here consumed some amount of anadromous fish;
425 however, it does not appear to have been a significant protein source. The *U. americanus*
426 shown here appear to have consumed a year-round terrestrial diet at a significantly lower
427 trophic level. The *Arctodus* appear to occupy a middling position between *U. americanus* and *U.*
428 *arctos*.

429 Despite popular depictions of *U. arctos* consuming salmon, fish are not essential to the
430 survival of *U. arctos*, and when resources such as salmon are not available the bears rely on
431 terrestrial vegetation, insects, freshwater fish, and mammals (Davis 1996). Furthermore, *U.*
432 *arctos* can, as observed in some modern ecosystems, subsist on a completely vegetarian diet;
433 some populations of *U. arctos* have been observed to subsist solely on vegetation across
434 multiple years, despite the availability of other resources such as fish (Rode et al. 2001,
435 Mychajliw 2020).

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439 Figure 4. Comparison of $\Delta^{13}\text{C}_{\text{Gly-Phe}}$ values versus bulk $\delta^{15}\text{N}$ values of the Vancouver Island bears.

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441 **4.5 Nitrogen compound-specific isotope analysis**
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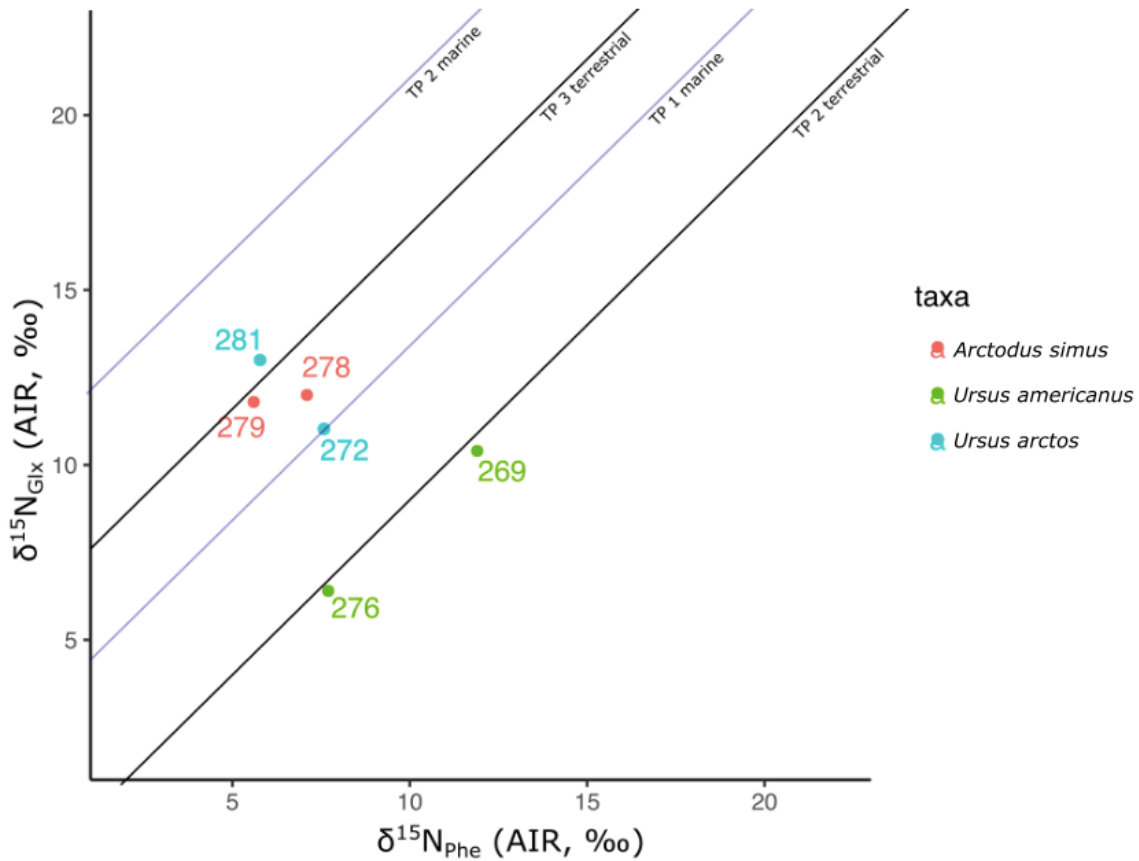
443 Nitrogen CSIA was undertaken to further distinguish the trophic positions of these
444 bears, as such data can provide a more informative comparison between individuals from
445 different time periods or that consume foods with different environmental baseline nitrogen
446 isotopic compositions. The difference in ^{15}N enrichment between source and trophic amino
447 acids has been attributed to the amino acid's participation or lack thereof in deamination or
448 transamination reactions as the protein from food is incorporated into consumer tissue
449 (McMahon and McCarthy 2016, O'Connell 2017, Whiteman et al. 2019). Therefore, animals
450 occupying higher trophic positions display a larger internal spacing between their Phe (source
451 AA) and Glx (trophic) AA $\delta^{15}\text{N}$ values, regardless of the level of ^{15}N enrichment at the base of
452 the food chain.

453 In determining trophic positions for these samples by comparing their $\delta^{15}\text{N}_{\text{Phe}}$ and
454 $\delta^{15}\text{N}_{\text{Glx}}$ values, some additional dietary factors should be considered. As a food source is
455 consumed and its amino acids are incorporated into a consumer's tissues, the difference
456 between the value by which the source amino acid is enriched and the value by which the
457 trophic amino acid is enriched is deemed the trophic discrimination factor (TDF). Therefore, the
458 TDF describes the expected increase in spacing between source and trophic amino acid $\delta^{15}\text{N}$
459 values with each increase in trophic position. Because the TDF of Glx-Phe has been found to
460 vary with quality and quantity of protein in the diet among other factors (Germain et al. 2013,
461 Chikaraishi et al. 2014, McMahon et al., 2015, McMahon and McCarthy 2016, Fuller and Petzke.

462 2017), exact values for trophic position are not presented. Threonine $\delta^{15}\text{N}$ values have be
463 explored as an indicator for level of protein consumption (Styring et al. 2010). High dietary
464 protein concentrations are thought to cause increased enzymatic activity of threonine
465 ammonia-lyase in mammals (Hare et al. 1991, Fuller and Petzke 2017), which preferentially
466 removes ^{15}N over ^{14}N and thus causes a decrease in the $\delta^{15}\text{N}$ values of Threonine. Therefore,
467 lower $\delta^{15}\text{N}$ values of threonine have been proposed as a biomarker for protein consumption. As
468 shown in table 2, the *U. americanus* display moderately low $\delta^{15}\text{N}_{\text{Thr}}$ values (-11.2‰ and -
469 12.5‰); *U. arctos* show similar (albeit slightly lower) $\delta^{15}\text{N}_{\text{Thr}}$ values compared to *U. americanus*
470 (-13.9‰ and -15.2‰); and *Arctodus* display significantly lower $\delta^{15}\text{N}_{\text{Thr}}$ values than the other
471 two taxa (-24.9‰ and -25.6‰). This may indicate significantly higher levels of protein
472 consumption by *Arctodus* compared to the other two taxa. Previous research indicates that as
473 dietary protein quality increases, the TDF between source and trophic amino acids tends to
474 decrease (McMahon and McCarthy 2016). Therefore, if higher levels of protein are being
475 consumed by *Arctodus* compared to the other taxa examined here, a lower TDF is likely more
476 appropriate for determining their trophic positions. If the TDF value being applied universally to
477 all taxa here is higher than the appropriate value for the *Arctodus* samples, the trophic
478 positions of *Arctodus* will be underestimated in this comparison.

479 Although a custom TDF could not be calculated for these ancient samples due to a lack
480 of direct information on protein quality, the limits of the trophic levels defined using a $\text{TDF}_{\text{Glx-Phe}}$
481 of 7.6 ‰ (Chikaraishi et al., 2014) were considered consistent enough as used in other studies
482 on ancient bone collagen (e.g. Chikaraishi et al 2014, Ogawa et al. 2013, Naito et al. 2010, Naito
483 et al. 2013) to usefully inform broad comparisons in a visual aid, while keeping in mind the
484 potential underestimation of TP for the *Arctodus* samples (Figure 5). Because the results of both
485 carbon CSIA and bulk collagen SIA indicate that none of the bears considered in this study show
486 a high marine protein signal, trophic level can be considered by employing the β value (which
487 represents the initial estimated spacing between the $\delta^{15}\text{N}$ values of Glu and Phe at the base of
488 the food chain) for terrestrial ecosystems. For the sake of comparison, the β value as previously
489 determined for marine ecosystems (Chikaraishi et al., 2014) is also shown in figure 5. The
490 unrealistically low marine trophic position that the bears would have occupied while displaying
491 these values (< TP2) is further indication that terrestrial resources were instead the main
492 protein source for all taxa examined here.

493



494
 495 Figure 5. Comparison of $\delta^{15}\text{N}$ values for Glx and Phe. Estimated trophic position delineations for
 496 both marine and terrestrial consumers are defined following the equation and graphing
 497 procedure outlined by Chikaraishi et al. (2014) following a trophic discrimination factor of 7.6
 498 ‰, β value of -3.4‰ for marine, β value of 8.4‰ for terrestrial.
 499

500 A comparison of trophic positions using $\delta^{15}\text{N}$ values of Glu and Phe reveals that *U.*
 501 *americanus* occupied a distinctly lower trophic level than the other taxa, while *U. arctos* and
 502 *Arctodus* show some overlap in their trophic positions, with a potential underestimation of
 503 *Arctodus* trophic position as discussed above (see Figure 5).

504 An additional noteworthy source of variation in the nitrogen isotope composition of
 505 bear tissue may be sex or size. Although we were unable to reliably determine the sex of the
 506 specimens in this study based on the morphological characteristics of the fragmentary remains,
 507 Hobson et al. (2000) observe a significant difference in the $\delta^{15}\text{N}$ values of modern female *U.*
 508 *arctos* compared to their male counterparts in areas where they coexist with *U. americanus*.
 509 This could be due to the female bears' smaller range, and thus lower access to higher trophic-
 510 level resources (Hobson et al. 2000). Additionally, it has been suggested via bite size ecology
 511 studies that smaller *U. arctos* can sustain their energy on a vegetarian diet, but very large bears
 512 cannot (Rode et al. 2001). This, considered with the sexual dimorphism of the species, could
 513 explain the sex-patterned difference in $\delta^{15}\text{N}$ values of bear collagen, and could indicate size as a
 514 constraint on the level of herbivory possible for short-faced bears. The *Arctodus* specimens
 515 analyzed here were noted by Steffen et al. (2018) to be possibly female, based on their size. If

516 not conclusively female, they were at least noted to be relatively small in comparison with
517 other *Arctodus* specimens. Considering the small sample size compared here and potential size
518 and sex influences on bear diet, conclusions drawn regarding trophic position and resource
519 specialization should be taken as contributors to understanding *Arctodus* diet in a particular
520 context, and not as representative of an entire extinct species.

521

522 **6. DISCUSSION**

523

524 **6.1 Late Pleistocene Bear Sympatry**

525 As evidenced by the radiocarbon dates presented here, *Ursus arctos*, *Ursus americanus*, and
526 *Arctodus simus* were present on Vancouver Island in the Terminal Late Pleistocene, with all
527 three bear species present with the approximate range of ~13,800–13,500 cal a BP. When
528 contemporaneous in the same area, *U. americanus* have been observed to occupy ranges of up
529 to 40 km, while *U. arctos* have been seen to occupy ranges up to 111 km (Mowat et al. 2005);
530 therefore, range overlap between these site locations is feasible. We surmise that these three
531 bear species could have lived within overlapping territories during the Terminal Late
532 Pleistocene on Vancouver Island.

533 Examples of two bear species occupying the same region can be found in both modern
534 and past environments, and may provide insight into the competitive pressures that could have
535 arisen when the three species examined here were alive. *U. americanus* have been present in
536 North America since at least the Middle Pleistocene and currently overlap geographically with
537 *U. arctos* in certain regions, with competition sometimes causing seasonal displacement of
538 *Ursus americanus* (Herrero 1972, Belant et al. 2010). It is thought that these species overlapped
539 south of the Cordilleran and Laurentide ice sheets as early as 31,000 cal BP (Davison et al.
540 2011). The ranges of these two species heavily overlapped through the Holocene prior to
541 European arrival in North America (Herrero 1972). *U. americanus* tend to have much lower
542 population densities in areas where *U. arctos* are also present (Miller et al. 1997, Mowat et al.
543 2005). In locations where these two species coexist today, *U. americanus* territorial ranges are
544 much smaller than the ranges of sympatric *U. arctos* (Mowat et al. 2005).

545 *U. arctos* and *A. simus* have been found to co-occur elsewhere during the Pleistocene,
546 including their overlap in eastern Beringia approximately 45–35 ka (Barnes et al. 2002). Barnes
547 et al. (2002) noted an inverse correlation between the radiocarbon dates of *Arctodus* and *Ursus*
548 in Eastern Beringia, suggesting that higher populations of *Arctodus* in the region from 35–21 ka
549 had temporarily excluded large populations of *Ursus* from the area. More recently, Steffen and
550 Fulton (2018) have proposed a similar effect at Pellucidar Cave on Vancouver Island, where an
551 approximately 1300-year gap between *U. arctos* radiocarbon dates is bridged by two *Arctodus*
552 dates (here referred to as S-SFU 278 & 279). However, incorporating new radiocarbon evidence
553 from other montane sites on the island, it appears that the presence of *A. simus* did not act to
554 exclude *Ursus* from the region. Despite the limited number of individuals recovered for any
555 bear species on Vancouver Island from this time, both *U. americanus* (S-SFU 276 at 13,981–
556 13,611 cal BP) and *U. arctos* (S-SFU 272 at 13,758–13,609 cal BP) appear in close chronological
557 association with each other and with *A. simus* (S-SFU 279 at 13741–13520 YBP) (see Figure 2).

558

559 **6.2 Pacific Northwest Coast Late Pleistocene Paleoenvironment**

560 The geographic and temporal specifics of the Cordilleran ice sheet's extent on
561 Vancouver Island, as well as associated sea-level changes, are still being revealed through the
562 accumulation of local paleofauna, paleoflora, and sedimentological data, and the presence of
563 glacial refugia in the region has been explored. Based on a composite date from an associated
564 juvenile specimen, Nagorsen et al. (1995) had previously reported that the bear specimens
565 from Windy Link Pot Cave (S-SFU 269 and 270) were too young to provide insight into the
566 Pleistocene refugium hypothesis. However, the new direct dates on these specimens reveal
567 that they are several thousand years older than originally believed, placing them at the end of
568 the Pleistocene. These dates add to a growing body of radiocarbon evidence for ice-free
569 environments on Vancouver Island that were able support a variety of large terrestrial
570 mammals, including these three species of bear, from as early as 14,000 years ago (e.g.
571 McLaren et al. 2014, Nagorsen and Keddie 2000, Al-Suwaidi et al. 2006, Harington 2011, Steffen
572 and Fulton 2018).

573 **6.3 Competition and Partitioning**

574 Considering the potential range overlap for some of these samples, and with their
575 temporal overlap now confirmed through radiocarbon dating, it appears that inter-species
576 niche partitioning within a shared geographical area, rather than long-term competitive
577 geographical displacement, occurred on the island.

578 The partitioning of resources between bear species in shared geographical areas has
579 been observed in modern case studies. Observational studies (Belant et al. 2010) and isotopic
580 investigations (Jacoby et al. 1999) have found that although *U. americanus* may consume large
581 amounts of salmon and other higher trophic-level resources in environments where *U. arctos*
582 are rare or absent, competition with *U. arctos* will influence the nature of their resource intake.
583 In environments where these two bear species overlap, *U. arctos* are observed to take over the
584 higher trophic niche, create avoidance at the population level, and seasonally displace the local
585 *U. americanus*.

586 Such a pattern of niche partitioning seems apparent in the isotopic evidence reported
587 by Fedje et al. (2011) from the most temporally and geographically similar data from *U.*
588 *americanus* and *U. arctos*—an assemblage from Haida Gwaii, a large island to the north of
589 Vancouver Island, dated to ~1000-2000 years later than the bears studied here. The bears from
590 the Younger Dryas interval on Haida Gwaii show very distinct differentiation in the carbon and
591 nitrogen isotope composition of *U. americanus* and *U. arctos* collagen, with *U. arctos* displaying
592 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values up to 5.2 and 17.5 ‰ higher, respectively, than those of *U. americanus*.
593 This can likely be attributed to differences in salmon consumption, and the isotopic
594 composition of contextually associated salmon remains from the site supports this attribution
595 (Fedje et al. 2011).

596 Compared to this data, our Vancouver Island *Ursus* specimens show much less
597 differentiation. Although the smaller sample size in the current dataset should not be ignored,
598 the largest differences between bulk collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of our samples are 3.7‰
599 and 10.0 ‰, respectively, showing a much narrower difference between these species.

600 However, results of CSIA do suggest that *U. americanus* occupied a distinctly lower trophic level
601 than both *U. arctos* and *Arctodus*, and the smaller range of isotopic values could be due to the
602 lack of aquatic resource consumption by the higher trophic level taxa.

603 Although these samples show potential range overlap between species, it is possible
604 that the different taxa were specialized to different environmental settings, which vary greatly
605 across small geographical areas on the mountainous island. It has been noted that *U. arctos* are
606 more open-adapted, while *U. americanus* are forest-adapted (Herrero 1972); however, this
607 distinction may have been complicated by competition from *A. simus*, another potentially
608 open-adapted species.

609 In a comparison of the bulk collagen carbon and nitrogen isotopes of *Arctodus* and *U.*
610 *arctos* from sympatric contexts in Beringia, Matheus (1995) found that *Arctodus* in the Yukon
611 and Alaska cluster tightly in terms of their high $\delta^{15}\text{N}$ values, while *U. arctos* display a broader
612 range of values. They suggest that the *U. arctos* out-competed *Arctodus* because they were able
613 to be more flexible and use vegetation supplements, while *Arctodus* could not. They also argue
614 that their data supports *Arctodus* as being strict carnivores in Beringia, and that morphological
615 data suggest that they were specialized scavengers of large mammal carcasses (such as
616 mammoths), while *U. arctos* were more generalized consumers. However, Hobson et al. (2000)
617 caution against interpreting high $\delta^{15}\text{N}$ values in bears as the consumption of large terrestrial
618 mammal prey, because modern studies utilizing bulk CN measurements have shown that bears
619 that feed heavily on insect prey (such as ants) are isotopically indistinguishable from bears that
620 gain most of their protein from large ungulates. On Vancouver Island, similar trophic positions
621 are indicated for *U. arctos* and *Arctodus*; however, the resources exploited by the two taxa
622 likely differed in protein content (as indicated by the difference in $\delta^{15}\text{N}_{\text{Thr}}$), indicating a
623 differentiation in prey choice within the same trophic level (i.e. insects versus terrestrial, plant-
624 consuming mammals).

625 Considering the potential effects of competition on the resource exploitation patterns of
626 all coterminous bear taxa, rather than simply assigning designations such as “specialized
627 scavenger” to an extinct taxon like *Arctodus*, may provide a more context-specific
628 understanding of the ecological roles of these taxa. For example, Barnes et al. (2002) report
629 bulk collagen stable isotope data from *Arctodus* and *U. arctos* in Beringia that show an increase
630 in $\delta^{15}\text{N}$ values for *U. arctos* after the extirpation of *Arctodus* from the region, demonstrating the
631 effects of competition between the taxa on their diets. In addition, recent isotopic data from
632 *Arctodus* from a specimen found on the California Channel Islands points to a greater degree of
633 omnivory than previously seen in isotopic data for the taxon, which the authors suggest may
634 have been caused by inter-species competition (Mychajliw et al. 2020).

635

636 **7. Conclusions**

637

638 We have measured the isotope values to determine diet of three temporally overlapping bear
639 species—*Ursus americanus*, *Ursus arctos*, and *Arctodus simus*—from Terminal Pleistocene
640 Canada (Vancouver Island). The island was sufficiently deglaciated by approximately 14,500
641 years ago to have a diverse and productive environment that could support populations of
642 several large, omnivorous taxa. According to our bulk collagen and compound-specific isotope
643 analysis results, these bear species appear to occupy distinct ecological niches on the island,

644 with *U. americanus* occupying a distinctly lower trophic position, and *U. arctos* and *A. simus*
645 occupying higher trophic positions with contributions of different specialized resources. As the
646 body of CSIA data on extinct Pleistocene species grows, additional high-resolution dietary
647 comparisons across different regions and time periods will add to our understanding of how
648 these animals lived and interacted.

649

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654

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