Canadian Journal of Zoology
Revue canadienne de zoologie

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Manuscript ID	cjz-2016-0046.R2
Manuscript Type:	Article
Date Submitted by the Author:	21-Apr-2016
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Testing for a predicted decrease in body size in brown bears (*Ursus arctos*) based on a historical shift in diet

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25 **Testing for a predicted decrease in body size in brown bears (*Ursus arctos*) based on a**
26 **historical shift in diet**

27

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29

30 **Abstract**

31 A recent study found a historical decline in the proportion of meat in the diet of brown bears
32 (*Ursus arctos* (Linnaeus, 1758)) in the Hokkaido Islands, Japan. Because feeding habits are
33 strongly correlated with the body size of animals, the shift in diet should have led to a
34 decrease in the size of these bears. To predict the effects of this dietary shift on the skeletal
35 size in bears, we correlated the femur length in Hokkaido brown bears with the carbon and
36 nitrogen stable isotope values from bone samples and predicted the historical change in their
37 body size. The variation in the femur lengths of the male and female subpopulations was
38 positively correlated with their $\delta^{15}\text{N}$ values, but not with their $\delta^{13}\text{C}$ values, and the
39 explanatory power of the constructed model was higher in males than in females. Based on
40 the model and the $\delta^{15}\text{N}$ values for historic and modern bears, the skeletal size of bear
41 subpopulations in eastern Hokkaido was estimated to have decreased by 10-18% for males
42 and 8-9% for females. Our results suggest that a historical dietary shift caused the decrease in
43 the size of the Hokkaido brown bears.

44

45 **Keywords:** dietary shift, body size, brown bear, stable isotope, downsize, *Ursus arctos*

46

47 **Introduction**

48 The feeding habits of animals exert strong effects on their body size (Mahoney et al. 2001;
49 Eifler et al. 2003), and a positive correlation between dietary meat intake and body size of
50 brown bears has been demonstrated in several studies (Hilderbrand et al. 1999; Mowat and
51 Heard 2006; Zedrosser et al. 2007). In mammals, a larger body size influences various
52 ecological and physiological factors, including selection of available dietary resources
53 (McNab 1971), reproductive success (Andersson and Iwasa 1996), and population growth
54 and density (Atkinson and Ramsay 1995; Post et al. 1997; Laundré et al. 2007; Wauters et al.
55 2007). However, a human-induced shift in the diets of omnivorous bears has been reported in
56 many regions around the world (e.g., Peirce and Daele 2006; Kavčič et al. 2013; Hopkins III
57 et al. 2014). To better understand the effects of humans on wildlife, studies are required to
58 predict the physical and ecological adaptations of omnivorous species to changes in resource
59 availability.

60 In the Hokkaido Islands of Japan, a major shift has occurred in the diet of
61 omnivorous brown bears (*Ursus arctos*) over the last 200 years (Matsubayashi et al. 2015),
62 which has been characterized by a major decline in the consumption of meat, such as salmon
63 (*Oncorhynchus* spp. (Suckley, 1861)) and sika deer (*Cervus nippon* (Temminck, 1838)), due
64 to human activities. To our understanding, such a dietary shift from a carnivorous to a largely
65 herbivorous diet in omnivorous wild animals has not been reported previously elsewhere in

66 the world. Because the feeding habits of brown bears are strongly correlated with their body
67 size (e.g. Noyce and Garshelis 1994; Hilderbrand et al. 1999; Mowat and Heard 2006;
68 Zedrosser et al. 2007), the dietary shift in the Hokkaido population has potentially changed
69 the body size of individuals over time. For this reason, we predict that the change in the
70 feeding habits of the Hokkaido brown bears affected their body size.

71 Based on samples and data collected from modern brown bears on Hokkaido from
72 1996 to 2011, we used the relationship between skeletal size and diet quality to predict the
73 change in body size due to the dietary shift. Femur length was used as an indicator of total
74 skeletal size, and we used the ratios of the stable carbon and nitrogen isotopes in collagen
75 extracted from the femurs to indicate food quality. The stable nitrogen isotope ratios in
76 animal tissues reflect the trophic level of the organism (DeNiro and Epstein 1981), and the
77 stable carbon isotope ratios reflect the contribution of C₃ and C₄ plant-based food webs to the
78 diet of the target species (O'Leary 1981). The collagen in the human femoral bone
79 isotopically reflects the diet of an individual for a period of more than 10 years (Hedges et al.
80 2007), so analyzing the ratios of the stable carbon and nitrogen isotopes in bear bone collagen
81 will approximate the food habits of the bears over their lifetimes.

82 The predicted shift in skeletal size related to the change in diet was performed in the
83 following steps: (i) determine the age at which the femur length reached 95% of the
84 asymptotic size (maturity), (ii) measure the stable carbon and nitrogen isotope values of the

85 bone collagen of bears that reached maturity, (ii) test the relationship between femur length
86 and isotope values at the individual and subpopulation scales (i.e., intra- and
87 inter-subpopulation scale), and (iv) predict the femur length of historical brown bears using
88 stable isotope values of historic samples. These analyses were performed separately for each
89 sex, because several previous studies have suggested that male and female growth patterns
90 are different in brown bears (Bershinikov et al. 2004; Mowat and Heard 2006). Finally, we
91 predicted the differences in body sizes between modern and historical bears using the isotopic
92 values for each as reported in Matsubayashi et al. (2015).

93

94 **Materials and methods**

95 *Study site*

96 This study was performed on Hokkaido Islands, which is located at the northern tip of Japan
97 (41°21'–45°33' N, 139°20'–148°53' E) (Fig. 1). Its total area is 83,456 km², and the mean
98 annual temperature and precipitation are, respectively, 9.1 °C and 1151.7 mm in Hakodate
99 City, 8.9 °C and 1106.5 mm in Sapporo City, 6.9 °C and 1042.7 mm in Asahikawa City and
100 6.5 °C and 787.6 mm in Abashiri City (Fig. 1). Generally, a subpopulation is defined as a
101 spatially delimited subset of individuals from within a population (Wells and Richmond
102 1995). For this study, we used the 12 bear subpopulations defined by the Hokkaido Institute
103 of Environmental Sciences (HIES); initially, 5 brown bear populations have been defined

104 considering their distribution range in Hokkaido (Hokkaido Government 1986), and then, the
105 populations have been divided into 12 subpopulations based on their distribution connectivity
106 and administrative boundaries (HIES 2000; Fig. 1). The major components of the diet of the
107 Hokkaido brown bears are C_3 herbs, C_3 fruits, agricultural crops, insects, sika deer and
108 salmon (Sato et al. 2005; Matsubayashi et al. 2014), although salmon consumption occurs in
109 a limited zone in eastern Hokkaido (Ohdachi and Aoi 1987; Sato et al. 2005; Matsubayashi et
110 al. 2014). Corn (*Zea mays* L.) is the only C_4 plant consumed by the bears, and it is the most
111 frequently eaten agricultural crop (Sato et al. 2005). Therefore, the stable carbon isotope
112 ratios of corn can be used to indicate agricultural crop consumption.

113 *Growth curve construction*

114 To estimate the age at which femur growth slows, we constructed a von Bertalanffy-based
115 growth curve (Von Bertalanffy 1938). The HIES collected femur samples from brown bears
116 killed on the Hokkaido Islands from 1991 to present, as well as data on the age, sex, location
117 of kill and kill date. The age of each bear is determined by counting the cementum annuli
118 from an extracted tooth (Mundy and Fuller 1964; Yoneda 1976). In this study, the femur
119 length represented the total length (mm), as measured from the femoral head to the medial
120 condyle. First, we estimated the growth curve for each sex to correct for the differences in
121 femur growth with age using femur length data for 1148 males and 548 females for the
122 calculations. According to Friebe et al. (2014), we assumed that all bears were born on

February 1, and the estimated age was corrected by counting the tooth annuli to the second decimal place and adjusting for the period from February 1 to the kill date of each bear. The von Bertalanffy growth curve was fitted because it is optimal for expressing growth in bear species (Bartareau et al. 2011) as follows:

Eq. 1
$$A(t) = A_{\infty} \cdot [1 - e^{-K(t-T)}],$$

where A is the femur length (mm) at age t (years); A_{∞} is the mean asymptotic femur length of the sampled population; K is the rate at which the asymptotic femur length is reached (years^{-1}); and T is a fitting constant, which is interpreted as the hypothetical age of an individual at zero femur length assuming the equation to be valid for all ages (years). We calculated the femur length of all bears for the age at which the expected femur length reached 95% of the asymptotic size using the growth curve. Then, we estimated the age at which the expected thighbone length reached 95%, which was assumed to represent maturity.

Sample preparation and stable isotope analyses

In addition to the age, sex, location of kill and kill date, as well as the femur length data from the HIES, we obtained bone samples from 201 males and 178 adult females for the analysis of stable isotopes (Table 1, Fig. S1). The bear femurs were powdered using an electric drill, and the collagen was extracted following the methods of Schoeninger and DeNiro (1984); approximately 0.4 mg of extracted collagen from each sample was used for the analysis. We expressed carbon and nitrogen isotope ratios in δ notation based on the international standard

142 scale as follows:

143 Eq. 2
$$\delta X = (R_{\text{sample}} / R_{\text{standard}}) - 1,$$

144 where X is ^{13}C or ^{15}N ; R_{sample} corresponds to the $^{13}\text{C}/^{12}\text{C}$ or the $^{15}\text{N}/^{14}\text{N}$ ratio of the measured
145 samples; and R_{standard} is the $^{13}\text{C}/^{12}\text{C}$ of the Vienna Pee Dee Belemnite (VPDB) or the $^{15}\text{N}/^{14}\text{N}$
146 of atmospheric nitrogen.

147 The stable carbon and nitrogen isotope ratios were measured with commercial
148 equipment (ANCA-IRMS; Europa Scientific Integra, UK) at the University of California,
149 Davis, and the overall estimated measurement error was $< 0.1\text{‰}$ for $\delta^{13}\text{C}$ and $< 0.2\text{‰}$ for
150 $\delta^{15}\text{N}$. The stable carbon and nitrogen isotope data for the bears in subpopulation No. 8, which
151 were measured using a Finnigan MAT 252 mass spectrometer (Finnigan MAT, Bremen,
152 Germany) connected to a Fisons NA1500 elemental analyzer at Hokkaido University, were
153 obtained from Matsubayashi et al. (2014). The estimated measurement error was $< 0.1\text{‰}$ for
154 $\delta^{13}\text{C}$ and $< 0.2\text{‰}$ for $\delta^{15}\text{N}$.

155 *Statistical analyses*

156 The differences between the stable isotope values of the male and female bears were tested
157 using a Wilcoxon signed-rank test ($P < 0.05$). Then, to examine the relationship between
158 femur length and the stable isotope values, we used GLMM for the individual-scale analysis
159 and a weighted least squares regression model for the subpopulation-scale analysis. In the
160 individual-level model, the femur length for the individual bears was explained by their $\delta^{13}\text{C}$

161 and $\delta^{15}\text{N}$ values, and the subpopulation No. was used as a random effect. In the
162 subpopulation-level model, the mean femur length for each subpopulation was explained by
163 the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of each subpopulation, and the sample size of each subpopulation
164 was used as the weighting factor. We assumed a normal distribution with an identity link
165 function. Then, we tested several candidate models with 1 or more explanatory variables and
166 performed model selection based on the Akaike information criterion with a correction for the
167 sample bias (AICc) (Akaike 1973; Sugiura 1978; Hurvich and Tsai 1989). These modeling
168 procedures were conducted separately for the males and females, and all statistical analyses
169 were performed using the R statistical software package (R Core Team 2014).

170 *Prediction of the historical shift in body size*

171 Stable isotope data for the brown bears that lived in the Hokkaido Islands before human
172 colonization (from BC 4000 to the late 19th century) were obtained from Matsubayashi et al.
173 (2015) (Table S1). Growth stage and sex data were also available for most of the historical
174 brown bears of the eastern region (subpopulations No. 7, 8, 9, 10; Fig. 1; Matsubayashi et al.
175 2015), so we used the stable isotope data of these bears to predict their body size. The $\delta^{13}\text{C}$
176 and $\delta^{15}\text{N}$ values of the historical brown bears were $-18.4 \pm 1.4\text{‰}$ (mean $\pm$ SD) and $9.4 \pm$
177 2.7‰ for eastern males ($n = 14$) and $-20.0 \pm 1.1\text{‰}$ and $6.7 \pm 2.5\text{‰}$ for eastern females ($n =$
178 13). We estimated the change in the femur length of the Hokkaido brown bears using the
179 isotopic values of the historical bears in the top-ranking model constructed with the isotopic

180 data from modern bears.

181 **Results**

182 The asymptotic femur lengths estimated from the growth curves were 418.93 mm for male
183 and 342.39 mm for female bears (Fig. 2), and the ages at which the femurs reached 95% of
184 the asymptotic length (maturity) were 5.67 years for males and 3.31 years for females.

185 Therefore, male bears older than 6 years and female bears older than 4 years were used for
186 the stable isotope measurements and the subsequent statistical analysis. There were 12
187 subpopulations, but there were no samples for 1 subpopulation (Table 1, Fig. 1). The mean
188 ($\pm$ SD) stable isotope ratios of male brown bears were -21.5 ± 1.7 ‰ for $\delta^{13}\text{C}$ and 3.8 ± 2.0 ‰
189 for $\delta^{15}\text{N}$, and those of female bears were -22.1 ± 1.24 ‰ for $\delta^{13}\text{C}$ and 3.1 ± 1.6 ‰ for $\delta^{15}\text{N}$.
190 Significant differences between sexes were detected in both the $\delta^{13}\text{C}$ (Wilcoxon test, $w =$
191 34172.5 , $P < 0.001$) and $\delta^{15}\text{N}$ values ($w = 34042.0$, $P < 0.001$). In the individual-scale
192 analysis, both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were correlated with the body size of both male and
193 female bears (Table 2), although the percentage of deviance explained was very low in every
194 model (less than 1%; Table 2). In the subpopulation-scale analysis, a positive relationship
195 between femur length and the $\delta^{15}\text{N}$ values for the male and female subpopulations was
196 supported by the top-ranking model (Figure 3), whereas the $\delta^{13}\text{C}$ value did not have a strong
197 effect on femur length (Table 2). The relationship between femur length and $\delta^{15}\text{N}$ values in
198 the female subpopulations was relatively weak, based on the ΔAICc , and the deviance

199 explained ($\Delta\text{AICc}_{\text{Best} - \text{null model}} = 2.70$; deviance explained = 45.26%) compared to the male
200 subpopulations ($\Delta\text{AICc}_{\text{Best} - \text{null model}} = 18.51$; deviance explained = 87.00%) (Table 2). The
201 historical change in the femur length of the Hokkaido brown bear subpopulations was
202 predicted using the equation of the top-ranking model (Table 3) and was estimated to have
203 shifted from 524.2 mm to 428.7 mm (10-18%) in males and from 366.1 mm to 337.3 mm
204 (8-9%) in females in the eastern region.

205 Discussion

206 Our results showed that the carbon and nitrogen stable isotope values were correlated with
207 skeletal size of individual bears, but the predictive ability of the stable isotope ratios was poor.
208 Presumably, other factors, such as inheritance, nutritional condition at birth and birth mass,
209 are stronger determinants of individual body size than nutritional condition during life. As a
210 result, we were not able to predict the historical shift in the body size of Hokkaido brown
211 bears at the individual scale.

212 The femur lengths of males at the subpopulation level were positively correlated
213 with the $\delta^{15}\text{N}$ values, and because $\delta^{15}\text{N}$ values are higher at the predator trophic level (DeNiro
214 and Epstein 1981; Minagawa and Wada 1984), the mean skeletal size of the male bear
215 subpopulations was strongly correlated with their trophic status, which is consistent with
216 other studies from North America (Hilderbrand et al. 1999; Mowat and Heard 2006). The
217 result suggests that the body size of male bears is adapted to regional nutrient availability

218 over several generations but not within a generation, and the geographical variation in diets
219 causes the geographical variation in the body size of brown bear subpopulations. Generally, a
220 larger size is advantageous when in competition for mates, so male body size should be
221 related to reproductive success (McLellan 1994; Schwartz et al. 2003; Zedrosser et al. 2007;
222 Costello et al. 2009). Therefore, size should be an adaptive characteristic of male bears, and
223 they should exhibit larger overall sizes when the available nutrients are plentiful.

224 A positive relationship between femur length and $\delta^{15}\text{N}$ values was also detected in the
225 female subpopulations, but given that the difference in the AICc between the null model and
226 the top-ranking model was small, whether feeding habits have a strong effect on female body
227 size remains inconclusive. A larger body size also increases the reproductive success of
228 female bears (Hilderbrand et al. 1999; Zedrosser et al. 2007; Stringham 1990), but a larger
229 size is not always adaptive for females due to the important role of caring for the offspring.
230 Because female bears with cubs sometimes face the risk of infanticide by male bears (Dahle
231 2003; Ben-David et al. 2004; McLellan 2005), larger females should be better at defending
232 their offspring, as they are likely stronger than small females. However, compared to larger
233 females, small females may cope better with poor nutritive conditions and thus experience
234 less stress by avoiding males spatiotemporally (Steyaert et al. 2013a; b). Many previous
235 studies have shown that females with cubs change their habits to reside in safer areas that are
236 less frequently occupied by male bears (Dahle 2003; Rode et al. 2006; Steyaert et al. 2013a)

237 and meet their maintenance requirements by feeding on a lower quality diet (Matsubayashi et
238 al. 2014; Ben-David et al. 2004; Steyaert et al. 2013b). Thus, the trade-off between growth
239 and the risk of infanticide should affect the relationship between body size and diet quality in
240 female subpopulations. This may explain why the relationship between body size and diet
241 among female subpopulations was weaker than among the male subpopulations. Conversely,
242 a larger skull size of the female brown bears on Etorofu Island, which is a neighboring island
243 of Hokkaido, was recently reported (Matsubayashi et al. 2016). The larger skeletal size may
244 be attributed to a larger amount of dietary salmon consumed by Etorofu brown bears than
245 bears from the Hokkaido Islands (Matsubayashi et al. 2016). Presumably, more data is
246 needed to understand the true relationship between body size and diet of female populations.

247 According to the model relating the femur length of male bears to the $\delta^{15}\text{N}$ values, we
248 predicted that the historical shift in diet decreased the body size of male bear subpopulations
249 by about 10% in the eastern region of Hokkaido. Although such downsizing was also
250 predicted for female bears, the relationship between body size and diet was too weak to reach
251 a conclusion. The estimated femur length of the historical male bears in the eastern region
252 may have been overestimated, because the $\delta^{15}\text{N}$ values (mean $\pm$ SD: $9.4 \pm 2.7\text{‰}$) were out of
253 the range of the values for modern male subpopulations (Fig. 3). For cases in which the femur
254 lengths of the male subpopulations were nonlinearly correlated with the $\delta^{15}\text{N}$ values, our
255 estimates for the bears in the past are unreliable. Although some uncertainty remains in the

prediction, our results suggest that the historical shift in diet resulted in a decrease in the size of male Hokkaido brown bears.

The survival of a predator species in a changing environment is strongly affected by the flexibility in prey choice (Yeakel et al. 2013), and in previous studies, the feeding habits of Hokkaido brown bears were shown to be highly flexible (Sato et al. 2004; McDonough and Christ 2012,). In addition, our data suggested that brown bears have adapted their body size over several generations in response to nutrient availability. With this physical and ecological flexibility, bear populations and the species have been sustained for a long period of time even in the face of drastic environmental change. Nevertheless, the historical decrease in body size has likely influenced population dynamics because body size is correlated with many population parameters, including population density, productivity and persistence (Andersson and Iwasa 1996; Atkinson and Ramsay 1995; Post et al. 1997; Laundré et al. 2007; Wauters et al. 2007). The major historical dietary shift in Hokkaido brown bears is likely the result of human activities, such as salmon fishing and dam construction (Matsubayashi et al. 2015). If this is the case, our results suggest that human activities not only caused the historical shift in diet, but also contributed to the downsizing of Hokkaido brown bears (Robbins et al. 2004).

Acknowledgments

275 We thank Y. Osada and S. Fujinaga for their support. We would also like to thank the
276 anonymous reviewers for their helpful comments on the manuscript drafts. This work was
277 partially funded by a Grant for Environmental Research Projects from the Sumitomo
278 Foundation (103406); a Grant-in-Aid for Scientific Research from the Japanese Ministry of
279 Education, Science, Sports and Culture (50338208, 25291101, 16K18627); and a
280 Grant-in-Aid for JSPS Fellows (24*2469) from the Ministry of Education, Culture, Sports,
281 Science and Technology of the Japanese Government.

Draft

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441 **Figure Legends**

442 **Fig. 1.** Brown bear (*Ursus arctos* (Linnaeus, 1758)) locations of kills (5-km quadrat) and the
443 area classifications of the Hokkaido brown bear subpopulations with the subpopulation IDs
444 denoted as 1–12.

445

446 **Fig. 2.** Femur and age relationship for male (blue, ○) and female (red, Δ) Hokkaido brown
447 bears (*Ursus arctos* (Linnaeus, 1758)). The vertical axis shows the femur lengths of the bears,
448 and the horizontal axis shows the ages. The fitted lines and the equations in the graph
449 represent the von Bertalanffy growth curves.

450

451 **Fig. 3.** Femur length and $\delta^{15}\text{N}$ relationship of the male (A) and female (B) Hokkaido brown
452 bear (*Ursus arctos* (Linnaeus, 1758)) subpopulations. The regression line and the equation are
453 shown for both males and females. The numbers in the graph indicate the subpopulation IDs.

454 **Table 1.** Femur lengths and isotopic data for the brown bear subpopulations. Sex,
455 subpopulation number (No.), sample size (*n*), mean and SD of femur length, and the carbon
456 ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios are shown.

Subpopulation			Femur length (mm)		$\delta^{13}\text{C}$ (‰)		$\delta^{15}\text{N}$ (‰)	
Sex	No.	<i>n</i>	Mean	SD	Mean	SD	Mean	SD
Male	1	53	395.62	21.83	-21.8	1.6	2.2	1.3
	2	12	430.77	19.43	-21.8	0.8	3.5	1.2
	4	5	438.90	15.11	-22.9	0.5	4.8	1.1
	5	29	440.49	23.98	-21.4	2.2	4.0	0.9
	6	18	421.71	32.41	-20.9	1.8	3.6	1.3
	7	1	452.00	-	-18.0	-	5.2	-
	8	23	438.46	28.13	-21.0	1.2	4.9	2.2
	9	1	450.80	-	-22.2	-	6.8	-
	10	6	451.51	14.79	-21.0	1.0	5.4	1.0
	11	48	426.94	28.81	-22.1	2.0	3.4	1.2
	12	5	432.14	15.43	-22.8	0.6	3.5	0.3
Female	1	55	328.99	16.34	-22.4	0.4	2.4	1.1
	2	4	350.24	6.18	-22.1	1.8	2.8	1.2
	4	2	332.43	36.43	-23.0	1.9	4.1	0.3
	5	16	360.77	17.57	-21.6	1.6	3.9	0.9
	6	10	356.86	17.49	-20.9	1.2	2.9	1.4
	7	1	354.20	-	-19.9	-	4.3	-
	8	27	356.17	13.83	-21.1	0.9	3.6	2.6
	9	1	346.50	-	-22.5	-	5.3	-
	10	9	355.78	19.02	-21.8	0.3	4.8	0.7
	11	45	348.07	16.71	-23.3	1.2	2.8	1.3
	12	8	335.68	27.97	-21.2	1.6	3.7	0.6

1 **Table 2.** Model selection results using weighted least squares regression of brown bear femur lengths. Sex, model structure, degrees of freedom
2 (df), Akaike information criterion (AIC), a second-order corrected AIC (AICc) and the deviance explained are given for each model. ΔAICc
3 denotes the differences in the AICc values from the top-ranking model.

Scale	Sex	Model structure	df	AIC	AICc	ΔAICc	Deviance explained (%)
Individual	Male	$\delta^{13}\text{C} + \delta^{15}\text{N}$	5	1909.84	1920.4	0.00	0.76
		$\delta^{13}\text{C}$	4	1910.98	1918.4	1.14	0.75
		$\delta^{15}\text{N}$	4	1920.63	1928.3	10.79	0.24
		Null	3	1925.42	1930.7	15.58	0.00
	Female	$\delta^{13}\text{C} + \delta^{15}\text{N}$	5	1534.20	1543.0	0.00	0.65
		$\delta^{13}\text{C}$	4	1534.44	1541.3	0.25	0.63
		$\delta^{15}\text{N}$	4	1540.60	1546.8	6.40	0.00
		Null	3	1544.23	1548.9	10.03	0.27
Subpopulation	Male	$\delta^{15}\text{N}$	9	85.36	88.79	0.00	87.00
		$\delta^{13}\text{C} + \delta^{15}\text{N}$	8	86.21	92.87	4.09	88.29
		Null	10	105.80	107.30	18.51	0.00
		$\delta^{13}\text{C}$	8	107.02	110.45	21.66	6.86
	Female	$\delta^{15}\text{N}$	9	93.29	96.72	0.00	45.26

Null	10	95.28	99.42	2.70	0.00
$\delta^{13}\text{C}$	9	97.92	101.77	5.05	13.33
$\delta^{13}\text{C} + \delta^{15}\text{N}$	8	98.34	101.95	5.23	45.30

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Table 3. Summary of the model parameters for the top-ranking model. A weighted least squares regression was used to predict the relationship between the femur length and the isotopic values for the male and female brown bear subpopulations. The estimated coefficients (Coef.), standard errors (Std. error), and the *t*-values for each variable used in the model are shown.

Scale	Sex	Variable	Coef.	Std. error	<i>t</i>
Individual	Male	Intercept	533.670	35.494	15.035
		$\delta^{13}\text{C}$	4.687	1.407	3.332
		$\delta^{15}\text{N}$	-0.833	1.732	-0.481
	Female	Intercept	421.510	33.094	12.737
		$\delta^{13}\text{C}$	3.465	1.422	2.436
		$\delta^{15}\text{N}$	0.638	1.003	0.636
Subpopulation	Male	Intercept	363.772	7.949	45.761
		$\delta^{15}\text{N}$	17.005	2.191	7.761
	Female	Intercept	309.058	13.420	23.030
		$\delta^{15}\text{N}$	11.565	4.239	2.728

6

Brown bear (*Ursus arctos* (Linnaeus, 1758)) locations of kills (5-km quadrat) and the area classifications of the Hokkaido brown bear subpopulations with the subpopulation IDs denoted as 1–12.
202x169mm (300 x 300 DPI)

Femur and age relationship for male (blue, ○) and female (red, Δ) Hokkaido brown bears (*Ursus arctos* (Linnaeus, 1758)). The vertical axis shows the femur lengths of the bears, and the horizontal axis shows the ages. The fitted lines and the equations in the graph represent the von Bertalanffy growth curves.
286x226mm (300 x 300 DPI)

Femur length and $\delta^{15}\text{N}$ relationship of the male (A) and female (B) Hokkaido brown bear (*Ursus arctos* (Linnaeus, 1758)) subpopulations. The regression line and the equation are shown for both males and females. The numbers in the graph indicate the subpopulation IDs.

114x51mm (300 x 300 DPI)

1 **Testing for a predicted decrease in body size in brown bears (*Ursus arctos*) based**
2 **on a historical shift in diet**

3
4 Jun Matsubayashi, Ichiro Tayasu, Junko O. Morimoto, Tsutomu Mano

5
6 **Supplementary materials:**

7 1. Figure S1

8 2. Table S1

9 3. Reference

10

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11 **Figure S1.** The relationships between the femur length and the isotopic values of
12 individual brown bears (*Ursus arctos*). The vertical axis shows the femur length, and the
13 horizontal axis shows the carbon (A) and nitrogen (B) stable isotope ratios.

14

15 **Table S1.** Stable isotope and sampling data for historical brown bears (*Ursus arctos*). The carbon and nitrogen concentrations (C and N),
16 the carbon to nitrogen ratios (C/N), the carbon and nitrogen stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), and other information of the historical
17 brown bear samples are given. The data were obtained from Matsubayashi et al. (2015).

Sample ID	Site	Piece	Sex	Age	% collagen yield	C(%)	N(%)	C/N	$\delta^{13}\text{C}(\text{‰})$	$\delta^{15}\text{N}(\text{‰})$
IKS1	Eastern	Skull	Male	Adult	6.5	43.79	14.90	3.43	-16.0	13.3
IKS2	Eastern	Skull	Male	Adult	7.0	43.21	14.61	3.45	-16.0	13.5
IKS4	Eastern	Skull	Male	Adult	4.6	44.17	14.64	3.52	-17.8	9.8
IKS5	Eastern	Skull	Male	Adult	5.4	44.10	14.31	3.59	-18.4	10.6
IKS7	Eastern	Skull	Male	Adult	5.2	45.30	15.25	3.46	-16.9	12.0
NJB2R	Eastern	Mandible	Female	Adult	4.1	40.41	14.25	3.31	-18.7	8.9
NJB4	Eastern	Mandible	Female	Adult	7.3	42.57	14.14	3.51	-21.7	4.6
NJB9	Eastern	Mandible	Male	Adult	7.0	42.78	14.72	3.39	-18.7	8.9
NJB17	Eastern	Mandible	Male	Adult	7.7	41.78	14.41	3.38	-17.9	10.3
NJB18	Eastern	Mandible	Female	Adult	5.7	31.94	11.06	3.37	-21.0	5.7
NJB42	Eastern	Mandible	Female	Adult	11.0	45.60	16.17	3.29	-19.0	7.2
NJB45	Eastern	Mandible	Female	Adult	9.3	45.26	15.81	3.34	-20.6	6.6
NJB60	Eastern	Mandible	Male	Adult	8.6	43.61	15.34	3.32	-17.8	10.2
NJB61	Eastern	Mandible	Female	Adult	4.7	42.50	14.33	3.46	-20.1	5.7
NJB84	Eastern	Mandible	Male	Adult	4.7	44.15	14.78	3.48	-18.4	10.8

NJB87	Eastern	Mandible	Male	Adult	7.8	46.78	16.61	3.28	-19.4	7.6
NJB88	Eastern	Mandible	Female	Adult	9.9	44.89	15.81	3.31	-20.6	5.4
NJB89	Eastern	Mandible	Male	Adult	7.9	45.68	16.41	3.25	-20.4	5.2
NJB99	Eastern	Mandible	Male	Adult	7.0	45.57	15.21	3.50	-19.4	8.7
NJB111	Eastern	Mandible	Female	Adult	5.4	43.23	15.17	3.32	-19.7	5.7
NJB117	Eastern	Mandible	Female	Adult	12.9	46.02	16.21	3.31	-22.0	1.1
NJB118	Eastern	Mandible	Male	Adult	7.8	44.15	15.43	3.34	-21.2	4.2
NJB146	Eastern	Mandible	Female	Adult	7.7	43.49	14.88	3.41	-18.9	9.6
TS37	Eastern	Mandible	Female	Adult	6.9	43.18	14.65	3.44	-20.2	7.5
TS159	Eastern	Mandible	Female	Adult	3.3	43.63	14.85	3.43	-19.6	7.5
TS167	Eastern	Mandible	Male	Adult	3.1	41.28	13.96	3.45	-19.4	6.8
TS235	Eastern	Mandible	Female	Adult	3.6	42.67	14.32	3.48	-18.0	11.7

18 Reference

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