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8 **Echoes of the hunt? An inter-continental comparison of patterns of growth and determinants**
9 **of size of brown bears in Canada and Sweden.**

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24 ABSTRACT

25 Comparing life history traits among populations that have been separated genetically for several
26 hundred thousand years, but live in similar habitats on different continents, may help us understand
27 how ecological and anthropomorphic factors shape life histories. We compared patterns of growth
28 in body length and mass, and the influence of population density, habitat quality (NDVI), and
29 reproduction on age-specific length and mass of male and female brown bears between Alberta,
30 Canada, and Sweden. We found that Swedish females were significantly smaller in both length and
31 mass than Alberta females. Swedish females also reached primiparity earlier and at a smaller mass
32 and length. However, there were no continental differences in the patterns of growth in males. We
33 found strong positive effects of NDVI, but only weak negative effects of population density on
34 female mass and length in both areas. Generally, especially mass of Alberta females was more
35 strongly affected by NDVI and density than for Swedish females. Reproduction had stronger
36 negative effects on female mass in Alberta than in Sweden. We found no effects of NDVI and
37 population density on male mass and body length in both areas. The larger variation in female
38 growth and size between the areas, in contrast to males, may be related to differences in female
39 reproductive investment due to differences in population trends, i.e., earlier reproduction in
40 increasing populations or populations below carrying capacity, or to different selection pressures
41 in the past, potentially due to human persecution. Swedish females exhibited characteristics typical
42 of increasing populations, whereas Alberta females exhibited characteristics typical of stable or
43 decreasing populations. The difference in reproduction investment means that Swedish bears can
44 be harvested at higher rates, whereas Alberta bears must be managed more conservatively.

45 Key words: brown bear, Canada, length, mass, NDVI, reproduction, size dimorphism, Sweden,

46 *Ursus arctos*

47

48 INTRODUCTION

49 A species' life history is shaped by natural and sexual selection (Stearns 1992, Andersson
50 1994), but also human-caused selection (Coltman et al. 2003, Hutchings and Fraser 2008,
51 Darimont et al. 2009, Zedrosser et al. 2011). Body size is an important life-history trait influencing
52 an organism's anatomy, behavior, and physiology. Large individuals in relation to age tend to
53 reproduce earlier, survive better, and produce more and larger offspring with higher survival
54 (Stearns 1992, Robbins et al. 2012). Size and growth are affected by several ecological and
55 evolutionary constraints and individuals may trade growth later in life for earlier reproduction
56 (Stearns 1992). Quantifying and understanding the similarities and differences in determinants of
57 growth and size between and within populations enables us to understand different ecological and
58 evolutionary pressures and can result in better management of threatened or hunted populations
59 (Ruggetti and Festa-Bianchet 2011, Hamel et al. 2012).

60 Environmental and food conditions and their interactions with population density are major
61 selective forces affecting growth and body size in mammals (e.g. Hilderbrand et al. 1999, Coulson
62 et al. 2001, Martinez-Jauregui et al. 2009). However, the relative and absolute importance of these
63 factors can vary among populations of the same species, as has been found in mass variation in
64 adult female red deer (*Cervus elaphus*) in 3 countries in Europe (Martinez-Jauregui et al. 2009).
65 Human selection through targeted harvesting pressure can also cause differences in growth and
66 size among populations of the same species (Fenberg and Roy 2008, Servanty et al. 2011). For
67 example, selective phenotype-based harvest of high-quality bighorn sheep (*Ovis canadensis*) rams
68 over 5 generations resulted in selection against rapid early body and horn growth, and
69 consequently more males with smaller horns (Coltman et al. 2003).

70 Body size can vary considerably across a mammal's distributional range (e.g. Herfindal et al.
71 2006, Szuma 2008, McDonough and Christ 2012). Several studies have compared geographic

72 variations in a species' size, and growth (e.g. Swenson et al. 2007, Martinez-Jauregui et al. 2009,
73 McDonough and Christ 2012), although rarely between continents. Understanding factors affecting
74 life-history traits is fundamental in population and evolutionary ecology, as well as in conservation
75 biology (e.g., Festa-Bianchet and Apollonio 2003 and citations therein). Understanding the
76 differences, as well as the similarities, in life history traits, such as size, growth, and their
77 determinants among populations that have been separated genetically for several hundred thousand
78 years, but live in similar habitats on different continents, may help explain whether and how
79 ecological and anthropomorphic factors shape a species' life history and contribute to new
80 solutions for conservation problems (Carey 2005).

81 The brown bear (*Ursus arctos*) is a large terrestrial mammal with a Holarctic distribution
82 (Servheen et al. 1999). In brown bears, litter and offspring size are positively related to adult
83 female size (Hilderbrand et al. 1999, Dahle et al. 2006, Zedrosser et al. 2011), and reproductive
84 success in both sexes is positively related to adult size (Zedrosser et al. 2007, Zedrosser et al.
85 2013). Here we compare inter-population differences in age-specific body mass and size as well as
86 the patterns and determinants of mass and size of male and female brown bears in Alberta, Canada,
87 and Sweden. The populations live on unconnected continents, are genetically distinct, and have
88 been separated for several hundred thousand years (Taberlet and Bouvet 1994, Waits et al. 1998).
89 However, both populations are representative of interior (i.e., inland, not coastal) bear populations
90 (McLoughlin et al. 2000, McDonough and Christ 2012) and live under similar ecological
91 conditions (i.e., no access to salmon (*Oncorhynchus* spp., *Salmo* spp.); continental climate with
92 long and cold winters) in similar forested habitats, but with different persecution histories
93 (Zedrosser et al. 2011) and present population trends (i.e., increasing in Sweden, stable or
94 decreasing in Alberta, Canada; Alberta Sustainable Resource Development and Alberta
95 Conservation Association 2010, Kindberg et al. 2011). Because bears living on the same continent

96 in similar habitats have similar life histories (McLoughlin et al. 2000), we hypothesized 1) that
97 there are no differences in asymptotic body size (measured as asymptotic body mass and body
98 length; see Materials and Methods) of males and females. We further evaluated if ecological and
99 environmental factors affect the relationship between body mass and age, and body length and age
100 of male and female brown bears differently between continents/populations. We tested the null
101 hypotheses 2a) that there are no differences in the effects of population density on body size (i.e.,
102 mass and length; see Materials and Methods) of both sexes in Alberta and Sweden; 2b) that there
103 are no differences in the effects of habitat quality and productivity (using the Normalized
104 Difference Vegetation Index (NDVI) as a surrogate measure) on body size of both sexes in Alberta
105 and Sweden. Because production of offspring is generally costly (Stearns 1992), and female bears
106 may keep their offspring up to 5 years (Nawaz et al. 2008), and because average litter sizes in
107 brown bears are larger in Europe than in North America (Zedrosser et al. 2011), we hypothesized
108 2c) that the presence of dependent offspring has a more negative effect on female body size in
109 Sweden than in Alberta.

110

111 MATERIALS AND METHODS

112 *Study areas.* – The Swedish study area covered ~21,000 km² of intensively managed boreal
113 forest in a rolling landscape in south-central Sweden (61°N, 14°E), and mountainous national
114 parks and adjacent forested land in the north (67°N, 18°E), ca 600 km apart (Zedrosser et al.
115 2006). The forest is dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*).
116 Elevations range from 200 to 2,000 m, and timberline is located at 600-750 m. The climate is
117 continental with cold winters (January mean: -7°C in south, -13°C in north) and short, warm
118 summers (July mean: 15°C in south, 13°C in north). Snow cover lasts from late October until May,

119 the growing season is <130–180 days, and precipitation averages 500–1,000 mm annually
120 (Zedrosser et al. 2006).

121 The study area in Alberta, Canada (from now on referred to as Alberta), covered 132,000 km²,
122 mostly in and adjacent to the eastern slopes of the Rocky Mountains, from the American -
123 Canadian border (49°N, 113°W) to central Alberta (55°N, 118°W), a distance of 760 km.
124 Elevations range from 200 to 3,700 m, alpine meadows, rocky areas, and glaciers dominate the
125 highest elevations, and coniferous, deciduous, and mixed forests dominate the mountains and
126 foothills region. Lodgepole pine (*Pinus contorta*), spruces (*Picea engelmannii*, *P. glauca*, *P.*
127 *mariana*), and firs (*Abies lasiocarpa*, *A. balsamea*) are common conifers, and quaking aspen
128 (*Populus tremuloides*) is the most common deciduous species (Downing and Pettapiece 2006). The
129 continental climate has cold winters (January mean: -5°C in south, -15°C in north) and short, warm
130 summers (July mean: 17°C in south, 15°C in north). Snow cover lasts from late October until early
131 May, the growing season is <160–185 days, and average precipitation is 450-900 mm annually
132 (Downing and Pettapiece 2006).

133 Bear populations in both study areas live under similar ecological conditions and have similar
134 diets. Protein consumption is highest in spring and early summer, consisting of ungulate neonates
135 in Alberta (Munro et al. 2006), and ungulate neonates and insects (mainly ants (*Formica* spp.,
136 *Camponotus* spp.) in Sweden (Dahle et al. 1998). Summer and fall diets are dominated by
137 graminoids, herbs, and berries (mainly buffaloberry (*Shepherdia canadensis*) and mountain
138 huckleberry (*Vaccinium membranaceum*)) in Alberta, and mainly berries (especially bilberry (*V.*
139 *myrtillus*), crowberry (*Empetrum* spp.), and lingonberry (*V. vitis-idaea*)) in Sweden (Munro et al.
140 2006, Stenset et al. 2016). Neither study population has access to spawning salmon.

141 Brown bears in Alberta face interspecific competition with sympatric black bears (*Ursus*
142 *americanus*) (Mattson et al. 2005, Sawaya et al. 2012). The brown bear is the only bear species in
143 Europe.

144 Brown bears face resource extraction, agriculture, urbanization, and recreational activities in
145 both areas (Nielsen et al. 2004, Nellemann et al. 2007). In Sweden, however, brown bears have
146 increased from ~130 animals in the 1930s to >3,300 animals in 2008 (Kindberg et al. 2011), and
147 have been hunted since the 1940s (Swenson et al. 1994). In contrast, there are ~700 brown bears in
148 Alberta and the trend is unknown, although demographic information suggests that some
149 populations within the province may be declining (Alberta Sustainable Resource Development and
150 Alberta Conservation Association 2010). Regulated hunting was stopped in 2006 (Alberta
151 Sustainable Resource Development and Alberta Conservation Association 2010) and the
152 provincial status designation was changed to “threatened” in 2010.

153 *Capture and handling.* – Data were collected from bears captured between March and October
154 1988-2006 in Sweden, mostly during April and May (89% of 408 unique individuals; 90% of 960
155 total captures). In Alberta, bears were captured between April and October 1994-2009, mostly
156 during May-June (79% of 204 unique individuals; 76% of 323 total captures). Capture and
157 handling are described in Cattet et al. (2003) for Alberta, and Arnemo et al. (2011) for Sweden. A
158 premolar tooth was extracted from bears of unknown age for age determination (Matson et al.
159 1993). Bears were weighed in a sling suspended beneath a spring scale (Sweden) or a load scale
160 (Alberta). Contour body length was measured as the distance from tip of the nose to end of the last
161 tail vertebra with a measuring tape overlying the dorsal midline with the bear in sternal
162 recumbency. We used contour body length (the only measure of size available in both projects,
163 hereafter referred to as length) as a substitute measurement for skeletal size, and analyzed body
164 mass and length separately. All capture and handling were approved by the appropriate authorities

165 and ethical committees (Djuretiska nämnden i Uppsala, Sweden; Committee on Animal Care and
166 Supply, University of Saskatchewan, Canada; Alberta Sustainable Resource Development Animal
167 Care Committee, Canada).

168 *Statistical methods.* – We evaluated age-specific geometric growth using four different models
169 that have been used previously to describe bear growth (Kingsley et al. 1988, Derocher and
170 Stirling 1998a, Zedrosser et al. 2006, Swenson et al. 2007). These were the:

171 [1] von Bertalanffy growth curve for mass: $s(a) = S \cdot [1 - e^{(-k \cdot (a - A))}]^3$

172 [2] von Bertalanffy growth curve for length: $s(a) = S \cdot [1 - e^{(-k \cdot (a - A))}]$

173 [3] Gompertz growth curve: $s(a) = S \cdot e^{(-e^{(-k \cdot (a - A))})}$

174 [4] Logistic growth curve: $s(a) = S \cdot [e^{(-k \cdot (a - A))} + 1]^{-1}$

175 where $s(a)$ is mass (kg) or length (cm) at age a (years), S is asymptotic mass or length, k is the
176 growth-rate constant (year^{-1}), and A is either the theoretical age at which an animal would have
177 zero mass or length with the von Bertalanffy growth curves, or the age at the inflection point in
178 mass or length with the Gompertz and logistic growth curves (Zullinger et al. 1984).

179 Data for individuals from each study area were fitted to growth models, separately for each sex,
180 by using the iterative estimation algorithms in the SPSS nonlinear regression procedure (IBM
181 SPSS Statistics Version 20, IBM, Armonk, New York, USA). Julian day of capture was added as a
182 decimal value to age in years to incorporate time of the year when a bear was captured into the
183 calculation of the growth curves. We truncated the data to only those collected from captures
184 occurring prior to July 1st (Julian day <182) to minimize the influence of accelerated fat deposition
185 on mass, as occurs during the 2-3 months prior to hibernation. Because the data did not include
186 bears <1 year-of-age from either study area (too few captured in Alberta), we also constrained A to
187 ensure that the fitted curves for Sweden and Alberta closely approximated mass-at-birth (580 g)
188 and length-at-birth (25 cm) estimated as mid-range values from neonatal mass/length values

189 reported for European and North American brown bears (Farley and Robbins 1995, Tumanov
190 1998, Robbins et al. 2012). We used data collected from multiple captures of bears in Alberta (60
191 of 215 bears captured ≥ 2 times) and Sweden (195 of 407 bears captured ≥ 2 times). To determine
192 which of the three growth models described the data best, we compared the residual sum-of-
193 squares among models, separately for mass and length, and visually assessed scatterplots of the
194 residuals vs. age from each analysis (Zullinger et al. 1984). Parameter estimates between study
195 areas were judged to differ significantly if the 95% confidence intervals did not overlap.

196 We used generalized additive mixed models (GAMMs) (Wood 2006, Zuur et al. 2014) to
197 evaluate the relationships between mass and length at capture of males and females in Alberta and
198 Sweden, and several predictor variables. We defined 6 candidate models *a priori* (Table 2), based
199 on the hypotheses presented in the introduction, and selected the most parsimonious model based
200 on information theory (IT) and Akaike's Information Criteria (AIC)-based diagnostics (ΔAIC_c –
201 second order bias corrected AIC difference values, AIC_{cw} – second order bias corrected AIC
202 weights) (Burnham and Anderson 2002). We used model averaging if ΔAIC_c values between
203 candidate models were < 2 (Anderson 2008). We evaluated the relative importance of each model
204 term in the most parsimonious model by systematically in/excluding a specific term in the model
205 and recalculating the ΔAIC_c . For all analyses, we used a threshold level of 0.6 to identify
206 collinearity among model variables, and considered a model term informative (*sensu* Arnold 2010)
207 when a 95% confidence interval did not include 0. We included individual identity as a random
208 effect in all models. Based on the multiyear growth pattern of bears (Schwartz et al. 2003), we
209 expected age to be an important explanatory variable in all models. We therefore created a basic
210 model (Age model) with a cubic regression spline for age, and then evaluated the effect of other
211 explanatory variables (Table 2). The predictor variables available were study area (binomial,
212 Alberta = 0, Sweden = 1), the normalized difference vegetation index (NDVI, see below),

213 individual-based population density index (see below), Julian day of capture, presence/absence of
214 dependent offspring at capture (binomial, without cubs-of-the-year = 0, with cubs-of-the-year = 1),
215 and the interactions between NDVI * study area, population density index * study area,
216 presence/absence of dependent offspring * study area, and Julian day of capture * study area
217 (Table 2). The variables population density index and NDVI were standardized $((X - \bar{X})/SD)$ to
218 avoid potential differences in the scaling or calculation of these indices affecting the results. Model
219 fit was evaluated visually by plotting the normalized residuals against fitted values and model
220 covariates (Zuur et al. 2014).

221 *Calculation of individual population density index.* – In Sweden we estimated a population
222 density index within 17.84 km ($\sim 1000 \text{ km}^2$) of an individual based on the methods of Zedrosser et
223 al. (2006). We chose this radius/area because it approximates the median home range size of adult
224 males in both Alberta and Sweden (Table 1), and because the effect of neighboring females on
225 each other's probability to reproduce disappears beyond 20 km between the females' home range
226 centroids (Ordiz et al. 2008). In the southern portion of the Swedish study area, the population size
227 was estimated based on a DNA analysis of scats in 2001 and 2002. The temporally corrected
228 individual density index for radio-collared individuals was based on the location of individual
229 bears genetically identified by scat sampling (71% of the radio-collared bears were represented in
230 the scat samples) and the population growth rate (Zedrosser et al. 2006). No corresponding
231 population estimate was available for the northern portion of the study area, but virtually every
232 adult male and female, and all subadult female bears were radio-collared. We used the locations of
233 radio-collared bears, corrected to include subadult males, and growth rate of the population to
234 calculate an individual density index as in the south (Zedrosser et al. 2006).

235 To estimate an individual population density index in Alberta, we followed an approach similar
236 to that in southern Sweden with one exception; we used results from population inventories for 5
237 of 7 population units in Alberta, based on DNA analyses of barbwire-snagged hair collected from
238 2004-2008 (Boulanger et al. 2009).

239 *Calculation of Normalized Differential Vegetation Index (NDVI).* – The NDVI consistently
240 correlates with vegetation biomass and dynamics in various ecosystems, and we used NDVI in the
241 growing season as a predictor of habitat quality and productivity (Pettorelli et al. 2005b).
242 Vegetative conditions in spring and summer are regarded as decisive for the reproductive success
243 and the offspring condition of large herbivores (Pettorelli et al. 2006). NDVI tiles for Sweden were
244 downloaded from <http://glcf.umiacs.umd.edu/data/gimms/> (accessed September 2010). We
245 calculated an integrated NDVI within a radius of 17.84 km (this radius approximates an area of
246 1000 km²) around the center location of each individual for the months May-July (the capture and
247 growing season) in the year of capture with Erdas Imagine software (Leica Geosystems 2010). The
248 averaged NDVI grids were imported into ArcGIS 9.3.1 (ESRI). “NoData” was assigned to all open
249 water bodies. We then smoothed the averaged layer with a moving window approach to calculate
250 the mean NDVI for each pixel for each year within a radius of 17.84 km around a given pixel.

251 We downloaded NDVI tiles for Alberta from <http://glcf.umiacs.umd.edu/data/gimms/> (accessed
252 October 2010) and calculated a pixel-by-pixel mean for each grid of the months May-July 1999-
253 2006 using ArcGIS 9.2 (ESRI) Spatial Analyst Raster Calculator. For each individual bear we
254 calculated a mean home range center for May-July for each year. These home range centers were
255 buffered by a radius of 10,000 m using Arc View 3.2 Zonal Statistics tool, and every buffer was
256 then matched to the mean summer NVDI grid for that year.

257

258 RESULTS

259 *Growth curves.* – Age-specific mass and length for both sexes in both areas were best described
260 by the von Bertalanffy growth equation, because it had the lowest residual sum-of-squares and
261 provided the best fitting curve in relation to age-mass and age-length scatterplots (not included as
262 figures). The predicted mass- and length-at-age curves for female bears were approximately
263 parallel, with females from both areas attaining 90% of their asymptotic mass at 5.1-5.9 years and
264 90% of their asymptotic length at 3.2-3.3 years (Figure 1, Table 3). However, Alberta females
265 were significantly heavier at ages $\geq 90\%$ asymptotic mass (95% confidence interval and sample
266 size, Alberta: 97.8-107.4 kg, $n = 85$ vs. Sweden: 90.9-94.4 kg, $n = 199$) and longer at ages $\geq 90\%$
267 asymptotic length (Alberta: 168-172 cm, $n = 99$ vs. Sweden: 161-164 cm, $n = 333$). Alberta
268 females were also heavier and longer at primiparity (Figure 1, Table 3). Females in Sweden
269 reached primiparity at 84% of their asymptotic mass (or 79.5 kg) and 97% of their asymptotic
270 length (or 162 cm), whereas females in Alberta reached primiparity at 93% (96.7 kg) and 98%
271 (172 cm), respectively.

272 The predicted mass- and length-at-age curves for male bears were almost identical (Figure 2,
273 Table 3). Males from both areas attained 90% of their asymptotic mass at 8.7-8.8 years and 90% of
274 their asymptotic length at 4.2-4.5 years (Figure 2, Table 3). Alberta males and Sweden males were
275 also similar in mass at ages $\geq 90\%$ asymptotic mass (95% confidence interval and sample size,
276 Alberta: 180.0-216.7 kg, $n = 37$ vs. Sweden: 186.0-203.5 kg, $n = 63$) and length at ages $\geq 90\%$
277 asymptotic length (Alberta: 192-199 cm, $n = 79$ vs. Sweden: 188-192 cm, $n = 187$). The larger
278 confidence intervals for mass and length in Alberta males were likely due to the smaller sample
279 size than for Sweden males, because the coefficients of variation of male mass and length were
280 similar in data sets reduced to contain the same number of individuals from both study areas (see
281 Determinants of body mass and length).

282 *Determinants of body mass and length.* – In general, body mass was informative and increased
283 and nonlinearly with age in all models evaluating the determinants of male and female body size in
284 Alberta and Sweden (Figures 3A-D, Figure 4A-E).

285 Female age distribution was not significantly different between the study areas in either the
286 mass data set (mean age Alberta: 7.6 ± 4.7 years, $N = 70$; Sweden: 7.0 ± 4.8 years, $N = 397$; two-
287 sample t-test: $t = 1.014$, $p = 0.314$) or the length data set (mean age Alberta: 7.6 ± 4.7 years, $N =$
288 59 ; Sweden: 7.0 ± 4.8 years, $N = 388$; two-sample t-test: $t = 0.837$, $p = 0.406$) (Figure 3A-B). The
289 coefficients of variation (CV) of mass and length in Alberta were 19.8% and 6.4%, respectively,
290 and 27.3% and 9.2%, respectively, in Sweden.

291 Variation in female mass between the study areas was best described by the
292 habitat/reproduction model ($AIC_{cw} = 0.76$; Table 4, Figure 4A), which explained 68% (R^2) of the
293 variation in female mass. The second-order bias-corrected AIC weights of specific model terms
294 and their interactions in the habitat/reproduction model were, in order of relevance, the variable
295 ‘area’ and its interactions ‘area*NDVI’, ‘area*population density’, and ‘area*presence of cubs’
296 ($\Delta AIC_c = 56.98$); ‘NDVI’ and its interaction ‘area*NDVI’ ($\Delta AIC_c = 36.42$); ‘population density’
297 and ‘area*population density’ ($\Delta AIC_c = 9.86$); and the ‘presence of cubs’ and ‘area*presence of
298 cubs’ ($\Delta AIC_c = 4.59$). Females in Sweden weighed less than in Alberta (Table 5A). Female body
299 mass increased with higher NDVI values, but this increase was lower in Sweden than in Alberta.
300 Females accompanied by dependent offspring weighed less than lone females. The most
301 parsimonious model also contained effects of population density and its interaction with study
302 area, as well as the interaction between absence/presence of dependent offspring and study area,
303 however, the CI’s of these variables and interactions contained 0 (Table 5A).

304 Two models comparing the determinants of female length between Alberta and Sweden were
305 within a $\Delta AIC_c < 2$ (Table 4, Figure 4B-C). The most parsimonious model was the habitat model

306 (AICcw = 0.52), which explained 53% of the variation in female length. The second-order bias-
307 corrected AIC weights of specific model terms and their interactions in the habitat model were, in
308 order of relevance, the variable 'area' and its interactions 'area*NDVI' and 'area*population
309 density' ($\Delta\text{AICc} = 24.34$); 'NDVI' and 'area*NDVI' ($\Delta\text{AICc} = 8.22$); and 'population density' and
310 'area*population density' ($\Delta\text{AICc} = -3.24$). The habitat/reproduction model was the second-most
311 parsimonious model ($\Delta\text{AICc} = 0.39$; AICcw = 0.42) and explained 54% of the variation in female
312 length. The second-order bias-corrected AIC weights of specific model terms were the variable
313 'area' and its interactions 'area*NDVI', 'area*population density', and 'area*presence of cubs'
314 ($\Delta\text{AICc} = 25.91$); 'NDVI' and 'area*NDVI' ($\Delta\text{AICc} = 7.81$); the 'presence of cubs' and
315 'area*presence of cubs' ($\Delta\text{AICc} = -0.39$); and 'population density' and 'area*population density'
316 ($\Delta\text{AICc} = -2.53$). We performed model averaging on the parameter estimates of the habitat and the
317 habitat/reproduction models (Table 5B). Females were smaller in Sweden. The averaged model
318 also contained effects of NDVI and its interaction with area, population density and its interaction
319 with area, as well as the absence/presence of dependent offspring and its interaction with study
320 area, however, the CI's of all of these parameters and interactions contained 0 (Table 5B).

321 Male age distribution differed significantly between the study areas for both the mass data set
322 (mean age Alberta: 8.0 ± 4.8 years, Sweden: 6.2 ± 4.5 years; two-sample t-test: $t = 2.668$, $p = 0.009$)
323 and the length data set (mean age Alberta: 8.4 ± 5.0 years, Sweden: 6.2 ± 4.5 years; two-sample t-
324 test: $t = 3.089$, $p = 0.003$). Due to the multiyear growth pattern of bears (Schwartz et al. 2003), to
325 avoid that age differences affecting the results, and to fulfill model assumptions of homogeneity,
326 we truncated the larger Swedish data sets to obtain data sets with similar male age distribution by
327 randomly selecting the same number of bears per age class as in the Alberta data set (Figure 2D-
328 E). The CV of mass and length were 37.1% and 10.0%, respectively, in Alberta, and 37.8% and
329 8.7%, respectively, in the truncated data set in Sweden.

330 The capture model was the most parsimonious model ($AIC_{cw} = 0.63$, Figure 4D) to explain
331 variation in male mass between the study areas (Table 4) and explained 69% of the variation in
332 male mass. The second-order bias-corrected AIC weights of specific model terms and their
333 interactions in the capture model were, in order of relevance, the variable 'area' and its interaction
334 'area*Julian day of capture' ($\Delta AIC_c = 0.461$); and the variable 'Julian day of capture' and its
335 interaction 'area*Julian day of capture' ($\Delta AIC_c = 0.310$). Body mass increased non-linearly with
336 age, and males captured later in the year were heavier (Table 6). The interaction 'area*Julian day
337 of capture' suggested that males in Sweden may have been lighter, because they were captured
338 earlier in the year than males in Alberta, however the CI contained 0. Males in Sweden were
339 captured on average on Julian day 122 ± 20 days (May 2 in nonleap years), whereas males in
340 Alberta were captured on average on Julian day 139 ± 16 days (May 19 in nonleap years); the
341 difference in capture dates was significant when evaluated with a two-sample t-test ($t = 4.371$, $p <$
342 0.001).

343 The age model was the most parsimonious model ($AIC_{cw} = 0.89$, Figure 4E) to explain male
344 body length (Table 4) and explained 89% of the variation in length. The age model contained only
345 the nonlinear effect of age, i.e., body length increased nonlinearly with age.

346

347 DISCUSSION

348 We found support for hypothesis 1a (no differences between the study areas in mass and length)
349 for males but not for females; Swedish females were significantly smaller than Alberta females.
350 Females in Sweden also reached primiparity earlier and at a smaller mass and length than females
351 in Alberta, although there were no differences in the patterns of growth in males. We evaluated
352 factors affecting size in both areas, and confirmed the null hypothesis of no differences in the
353 effects of population density between the areas (i.e., hypothesis 2a) for males; however, we found

354 weak support (i.e., non-informative interactions, because the 95% CI contained 0, although it was
355 retained in the most parsimonious model) for a stronger effect of density on female mass and
356 length in Alberta than in Sweden. We did not find study area effects of NDVI on mass and length
357 (e.g., confirmation of hypothesis 2b) for males, but mass of Alberta females increased more with
358 higher NDVI values than for Sweden females, and there was weak support for the same pattern in
359 female length. We found negative effects of the presence of dependent offspring on female mass,
360 but only weak effects on female length. These negative effects were stronger on female mass in
361 Alberta than in Sweden (i.e., contrary to our expectations in hypothesis 2c), but there was only
362 weak support for stronger negative effects of dependent offspring on female length in Alberta than
363 in Sweden.

364 Brown bears grew faster in length than in mass in both areas, because both sexes reached
365 asymptotic length before asymptotic mass. The area differences in asymptotic length and mass
366 were pronounced in females (smaller and lighter in Sweden), but there was no difference in males.
367 Male reproductive success in polygynous, sexually dimorphic species is dependent on body size
368 (Andersson 1994), and males probably have been selected to maximize growth rate (Clutton-Brock
369 1988). Similar environmental conditions should lead to similar life history traits, which has been
370 suggested for female bears (Ferguson and McLoughlin 2000). Males in Alberta and Sweden
371 reached 90% asymptotic size and length at the same age (Fig. 1, Table 2). The similarities in male
372 size suggest that similar environmental conditions and energy availability are operating in the
373 study areas and continents.

374 In contrast to males, females do not grow as fast and may trade growth for reproduction
375 (Clutton-Brock et al. 1988, Festa-Bianchet et al. 1994). Female brown bears in both study areas
376 attained 90% asymptotic length and mass at very similar ages (Figure 1, Table 2). However,
377 Alberta females were significantly larger (5%, 8 cm) and heavier (9%, 8 kg) at 90% asymptotic

378 length and mass than females in Sweden. In mammals, female sexual maturity depends on
379 reaching a threshold body mass, after which energy is allocated primarily to reproduction; age at
380 primiparity in ungulates corresponds to the age when females reach ~80% of their adult mass
381 (Gaillard et al. 2000). In general, bears seem to reach primiparity when relatively larger than
382 ungulates, because females reached primiparity at 93% and 84% of asymptotic mass in Alberta
383 and Sweden, respectively. A trade-off between growth, reproduction, and hibernation may be
384 responsible for this relatively larger threshold in bears. Brown bears may also keep their offspring
385 for up to 5 years (Nawaz et al. 2008), which involves higher costs of lactation and maternal care,
386 compared to ungulates, which usually wean their offspring at age 1. Female fecundity is strongly
387 influenced by body mass in both ungulates (e.g. Garel et al. 2005) and bears (Hilderbrand et al.
388 1999, Zedrosser et al. 2011), with larger individuals generally reproducing earlier and producing
389 more offspring of better quality (Clutton-Brock et al. 1988, Stearns 1992, Derocher and Stirling
390 1998b, Robbins et al. 2012). Females in Sweden and Alberta are both in the group of interior bears
391 (Ferguson and McLoughlin 2000), with similar growth rates, despite geographic and genetic
392 separation. Nevertheless, our data showed that the smaller and lighter Swedish females reproduced
393 earlier, had larger litters, and had higher proportions of litters with 3 and 4 cubs than the larger and
394 heavier Alberta females (Fig. 1, Table 1) and females in other North American interior brown bear
395 populations (mean age primiparity: 6.2 years, range 5.5-8 years; mean litter size: 2.0, range: 1.8-
396 2.2) (McLoughlin et al. 2000, Zedrosser et al. 2011, Steyaert et al. 2012). It is a general pattern
397 that female European brown bears produce larger litters in relation to body mass than females in
398 North America (Zedrosser et al. 2011).

399 The continental differences we found in female reproductive investment may be caused by
400 differences in carrying capacity and population trends (i.e., increasing, decreasing, stable). Both
401 populations were likely below carrying capacity, although they were increasing in Sweden

402 (Kindberg et al. 2011), and maybe were locally decreasing in Alberta (Boulanger et al. 2009),
403 which may contribute to differences in female reproductive investment. Another potential
404 explanation for the size similarities in males and the differences in female size and reproductive
405 investment is differences in persecution history (Zedrosser et al. 2011). Europeans conducted
406 extermination campaigns for centuries with primitive weapons and traps; thus the mortality was
407 likely nonselective and populations declined relatively slowly until effective firearms became
408 available in the 1800s (Curry-Lindahl 1972, Swenson et al. 2000, Zedrosser et al. 2011). In much
409 of northern North America, settlers arrived later and in smaller numbers, and brown bear
410 populations have remained large over vast areas (Servheen et al. 1999). There is evidence of
411 human-induced selection on morphology (Hendry et al. 2008) and life-history traits (Darimont et
412 al. 2009) of wild animal populations, the latter especially from commercially exploited fish
413 populations (Hutchings and Fraser 2008). Modeling suggests that random harvest also alters
414 female reproductive strategies, with higher harvest rates causing lower body mass at primiparity
415 (Proaktor et al. 2007). Thus, differences in long-term human selection pressure may have selected
416 for earlier and higher reproductive investment in Swedish than Alberta bears (Zedrosser et al.
417 2011).

418 We investigated the influence of habitat productivity (NDVI), population density, presence of
419 offspring, and capture date on the relationships between age and both mass and length by sex and
420 area. The variance in length and mass was similar for both sexes in both areas.

421 Environmental conditions, i.e., NDVI, and its interactions with study area, were always part of
422 the most parsimonious models and positively affected female mass and length (e.g. Martinez-
423 Jauregui et al. 2009). Recent ecological studies have highlighted NDVI as an index linking
424 vegetation to animal performance (Pettorelli et al. 2005a). Correlations between plant phenology
425 and carnivore life history traits likely operate indirectly, through prey abundance (Melis et al.

426 2010); however, brown bears are omnivorous, not true carnivores. We used NDVI values during
427 the growing season to reflect plant growth and fruit production, and thus food availability and
428 quality, because available nutrition is probably the most important factor affecting growth (Laws
429 1956). In contrast to other large mammals, bears partition their physical resources into growth and
430 fat accumulation for hibernation. Bears depend upon various plants, especially berries, for fat
431 accumulation in both Alberta and Sweden (Dahle et al. 1998, Munro et al. 2006). Although there
432 may be no general *a priori* reason to expect conspecific populations in different areas to respond
433 similarly to climate, as limiting factors may operate at different times of the year and the forms of
434 regulation may differ (Martinez-Jauregui et al. 2009), bear populations in our study lived in
435 comparable habitat, which has been suggested to cause similar life history responses in brown
436 bears (Ferguson and McLoughlin 2000, McLoughlin et al. 2000). Nevertheless, the strength of the
437 relationship between NDVI and body mass differed between areas. Swedish females weighed less
438 with increasing NDVI than Alberta females, perhaps due to longer hibernation in Sweden (Table
439 1), or alternatively, because bears in Sweden were closer to carrying capacity. The earlier and
440 higher reproductive investment of Swedish bears may be related to the different population status
441 of bears in the study populations (see above), or nutritional landscape characteristics that differed
442 between areas.

443 Density-dependent relationships for body size and body mass have been reported in large
444 mammals, especially ungulates (e.g., Clutton-Brock and Pemberton 2004), but also bears
445 (Zedrosser et al. 2006). The effects of density and its interactions with study area were retained in
446 the most parsimonious models explaining female mass and length, albeit never informative.
447 Investigations on a more local/intra-population scale may reveal more pronounced effects of
448 density on female life history traits, as has been suggested for Sweden (Zedrosser et al. 2006).

449 Life history theory predicts a trade-off between mass and reproduction when resources are
450 limited (Stearns 1992), and reproduction and maternal care are costly for females (e.g. Pelabon et
451 al. 1995). Female brown bears with dependent offspring weighed less than lone females in both
452 areas, a pattern that has been found in several other mammals (e.g. Sand 1998, Pomeroy et al.
453 1999). Noninformative interactions between the absence/presence of dependent offspring and
454 study area suggested area differences in the costs of reproduction. More data, especially from
455 Alberta, may be needed to better understand these differences.

456 The only informative variable explaining the differences in the determinants of mass and length
457 of male bears in Alberta and Sweden was the positive effect of Julian day of capture on body mass.
458 Males in Alberta were captured later in the year on average than in Sweden, which, together with a
459 shorter denning period (Table 1), may be sufficient to explain differences in mass. Swenson et al.
460 (2007) investigated the differences on body mass between brown bear populations in northern and
461 southern Europe, and found that northern bears gained and southern bears lost mass during the
462 spring, perhaps due to the greater availability and use of protein-rich food in spring in the north.
463 Our results suggest that male bears in Alberta also follow the northern European pattern of a
464 relatively rapid increase in body mass after hibernation.

465 Mattson et al. (2005) suggested that black bears could affect brown bears through reduced
466 reproduction and recruitment caused by exploitation competition. Interspecific competition by
467 American black bears therefore could affect brown bear life history in North America, potentially
468 by causing smaller litter sizes and larger female body size in brown bears. However, we found no
469 evidence of such an effect in our results. Also, an analysis of the presence/absence effect of black
470 bears on mean litter size in relation to mean adult female body mass in 19 brown bear populations
471 suggested no such effect (Zedrosser et al. 2011). Black bears are not present in Europe.

472 Many bear biologists and managers considered it a “commonly known fact” that brown bears
473 are larger in North America than in Europe. However, our results suggest that, in comparable
474 habitats and at the densities present in this study, at least males reach similar sizes. Although
475 habitat and population density also affect female size and mass, the larger variation in female
476 growth and size may be related to differences in female reproductive investment (see also
477 Hilderbrand et al. 1999, Zedrosser et al. 2011), due to differences in population trends, i.e., earlier
478 reproduction in increasing populations or populations below carrying capacity, or to different
479 selection pressures in the past, potentially due to human persecution (Zedrosser et al. 2011).
480 Swedish brown bears exhibited characteristics typical of increasing populations, whereas Alberta
481 bears exhibited characteristics typical of stable or decreasing populations. How fast such a switch
482 in life-history strategies can occur in a large mammal with slow reproduction is unknown;
483 however, it likely takes several generations (Zedrosser et al. 2011). For the manager and
484 conservationist, the difference in reproduction investment means that bears in Sweden can be
485 harvested at higher rates (Bischof and Swenson 2009, Bischof et al. 2009), whereas in Alberta
486 bears must be managed more conservatively and stronger protective measures are needed to
487 promote population increase.

488

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501

502 **Data Accessibility Statement**

503 The data used in this manuscript will be deposited in FigShare.

504

505 **Author Contributions**

506 This manuscript is based on an idea developed commonly during a cooperation meeting of the 4 coauthors. The study
507 design was developed by all four co-authors, data selection and analysis were carried out by A. Zedrosser and M.
508 Cattet. The manuscript was prepared mainly by A. Zedrosser and M. Cattet, and all co-authors have provided
509 substantial comments and feedback to the manuscript. All co-authors have approved the final version of the
510 manuscript before submission.

511

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714

715 FIGURE LEGENDS

716 **Figure 1.** Predicted body mass (upper figure) and length (contour body length; lower figure) at age
717 for female brown bears in Alberta and Sweden. Predicted values were calculated from data
718 collected at last capture and adjusted for date of capture. Lines represent predicted mass or size \pm
719 95% confidence interval.

720

721 **Figure 2.** Predicted body mass (upper figure) and length (contour body length; lower figure) at age
722 for male brown bears in Alberta and Sweden. Predicted values were calculated from data collected
723 at last capture and adjusted for date of capture. Lines represent predicted mass or size \pm 95%
724 confidence interval.

725

726 **Figure 3.** Body mass and length (contour body length) in relation to age of brown bears in Alberta,
727 Canada (symbol: Δ), and Sweden (symbol: +). These data were used to evaluate the factors
728 affecting growth in both study areas. A) Female body mass (N = 449); B) female body length (N =
729 439); C) male body mass (truncated, N = 98); D) male body length (truncated, N = 94). Due to
730 significant differences in age distribution between the study areas, the datasets on male mass and
731 length were truncated to contain the same number of individuals in all age classes.

732

733 **Figure 4.** Plots of the smoother functions for age obtained by the most parsimonious generalized
734 additive mixed effect models analyzing the determinants of body mass and length (contour body
735 length) of male and female brown bears in Alberta, Canada and Sweden. A) Female body mass (N

736 = 449); B) and C) female body length (N = 439); D) male body mass (N = 98); E) male body
737 length (N = 94). For female body length two models had $\Delta\text{AICc} \leq 2$, therefore the smoothed
738 functions for both models are shown.
739

740 **Table 1.** Brown bear life-history parameters in Alberta, Canada, and Sweden.

Life history parameter	Alberta	Sweden
Age at primiparity (years)	5.8 (13) ^a	5.0 (59) ^b
Litter size, mean \pm SD/median, range	1.79 \pm 0.52/2, 1-3 (39) ^a	2.34 \pm 0.80/2, 1-4 (211) ^c
Proportion of litters with 1, 2, 3, 4 cubs	26/69/5/0 ^a	16/40/40/5 ^c
Interval between successful litters (years)	2.5 (10) ^a	2.3 (124) ^b
Mean mass (kg) at primiparity	91.3 (13) ^d	69.9 (59) ^d
Mean body length (cm) at primiparity	168 (13) ^d	154 (59) ^d
Median adult male home range size (km ²)	899 (22) ^a	833-1055 (36) ^e
Median adult female (without dependent offspring) home range size (km ²)	273 (39) ^a	217-280 (52) ^e
Mean date of den entry		
Adult male	Nov. 22 (15) ^a	Oct. 27 (33) ^f
Adult female without dependent offspring	Nov. 9 (41) ^a	October 25 (43) ^g
Mean date of den exit		
Adult male	April 4 (13) ^a	April 4 (33) ^g
Adult female without dependent offspring	April 11 (24) ^a	April 13 (13) ^g

741 The number of individuals a parameter estimate is based upon is given in parenthesis. ^aG. Stenhouse, unpublished
742 data; ^bdata updated from A. Zedrosser, unpublished et al. (2009); ^cA. Zedrosser, unpublished; ^ddata are results of the
743 present study; ^e Dahle and Swenson (2003); ^f Manchi and Swenson (Manchi and Swenson 2005); ^g Friebe et al. (2001).

744

745 **Table 2.** Candidate general additive mixed models explaining body mass and body length (contour
746 body length) of brown bears in Alberta, Canada and Sweden. Check marks indicate inclusion of
747 variables in a certain model. All models were executed for males and females separately. Bear ‘ID’
748 was included as random component, and ‘age’ was included as regression spline into all models.
749 Whenever one of the variables Julian day of capture, normalized difference vegetation index
750 (NDVI), population density, or absence/presence of offspring was included into a model, an
751 interaction term with the binomial variable area (Alberta = 0, Sweden = 1) was included as well.

Hypotheses	Age	Area	Julian day of capture	NDVI	Population density	Absence/presence of offspring
Full	✓	✓	✓	✓	✓	✓
Age	✓					
Habitat	✓	✓		✓	✓	
Reproduction	✓	✓				✓
Habitat/reproduction	✓	✓		✓	✓	✓
Capture	✓	✓	✓			

752

753 **Table 3.** Parameter estimates (\pm SE) for the von Bertalanffy mass-at-age and length-at-age curves
 754 for female and male brown bears in Canada (Alberta) and Sweden.

Sex	Measurement	Area	S	k	A	90% A	N
Female	Body mass	Alberta	104 \pm 3.04	0.626 \pm 0.157	-0.313	5.1	126
		Sweden	95 \pm 0.98	0.536 \pm 0.022	-0.377	5.9	541
	Body length	Alberta	175 \pm 1.4	0.664 \pm 0.050	-0.235	3.2	105
		Sweden	167 \pm 0.8	0.660 \pm 0.031	-0.250	3.3	541
Male	Body mass	Alberta	204 \pm 10.01	0.370 \pm 0.076	-0.415	8.7	125
		Sweden	203 \pm 3.62	0.364 \pm 0.017	-0.420	8.8	401
	Body length	Alberta	199 \pm 2.2	0.490 \pm 0.041	-0.275	4.5	124
		Sweden	197 \pm 1.2	0.517 \pm 0.023	-0.263	4.2	401

755 S is the asymptomatic body mass (kg) or contour body length (cm), k is the growth-rate constant (year⁻¹), A is the
 756 theoretical age at which the animal would have mass or length 0, 90% A is the age at which an animal reaches 90% of
 757 its asymptotic mass or length, and N is the sample size.

758

759 **Table 4.** Model selection diagnostics of 6 *a priori* models to explain body mass and body length
760 (contour body length) of female and male brown bears in Alberta, Canada, and Sweden. Rank
761 indicates the model rank, $\Delta AICc$ and $AICcw$ indicate the second-order bias-corrected Akaike's
762 Information Criteria difference values, respectively.

Hypotheses	Females						Males					
	Mass			Length			Mass			Length		
	Rank	$\Delta AICc$	$AICcw$	Rank	$\Delta AICc$	$AICcw$	Rank	$\Delta AICc$	$AICcw$	Rank	$\Delta AICc$	$AICcw$
Full	2	3.11	0.161	3	4.27	0.061	4	5.66	0.037	4	11.96	0.002
Age	6	89.18	0	6	93.57	0	3	3.28	0.122	1	0.00	0.891
Habitat	3	4.59	0.077	1	0	0.515	2	2.16	0.213	3	9.95	0.06
Reproduction	4	36.89	0	4	62.65	0		-	-		-	-
Habitat/reproduction	1	0	0.762	2	0.39	0.424		-	-		-	-
Capture	5	42.92	0	5	66.80	0	1	0	0.628	2	4.36	0.101

763

764 **Table 5.** Model output of A) the most parsimonious model (habitat/reproduction model, AICcw =
765 0.76) of 6 *a priori* defined candidate models to explain body mass (N = 449), and B) model
766 averaged output of the two most parsimonious models (habitat model, AICcw = 0.515;
767 habitat/reproduction model, AICcw = 0.424; Δ AICc = 0.39) to explain body length (contour body
768 length; N = 439) of female brown bears in Alberta, Canada, and Sweden. β 's indicate parameter
769 estimates, SE = standard error, LCI = lower limit of the 95% confidence interval, UCI = upper
770 limit of the 95% confidence interval.

Model terms	β	SE	LCI	UCI
A) Female mass				
Area	-16.201	2.374	-20.854	-11.548
NDVI	10.024	1.896	6.308	13.740
NDVI * Area	-6.295	2.121	-10.452	-1.138
Population density	0.007	1.819	-3.558	3.572
Population density * Area	-3.622	2.067	-0.389	7.713
Absence/presence offspring	-6.859	3.250	-13.229	-0.489
Absence/presence offspring * Area	2.833	3.355	-3.743	9.409
B) Female length				
Area	-10.562	2.203	-6.244	-14.880
NDVI	0.939	1.636	-2.268	4.146
NDVI * Area	1.775	1.809	-1.771	5.321
Population density	-1.170	1.563	-4.233	1.893
Population density * Area	0.559	1.750	-2.871	3.989
Absence/presence offspring	-4.825	3.009	-10.723	1.073
Absence/presence offspring * Area	5.986	3.103	-0.096	12.068

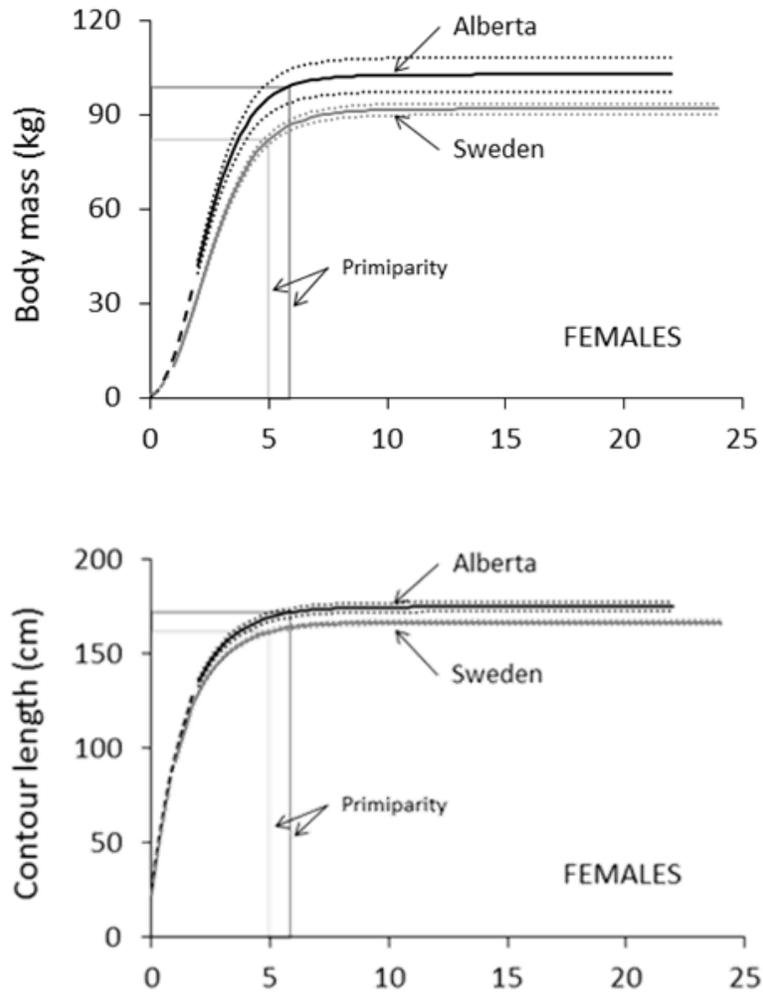
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772 **Table 6.** Model output of A) the most parsimonious model (capture model, AICcw = 0.63) of 6 *a*
 773 *priori* defined candidate models to explain body mass (N = 98) of male brown bears in Alberta,
 774 Canada, and Sweden. β 's indicate parameter estimates, SE = standard error, LCI = lower limit of
 775 the 95% confidence interval, UCI = upper limit of the 95% confidence interval.

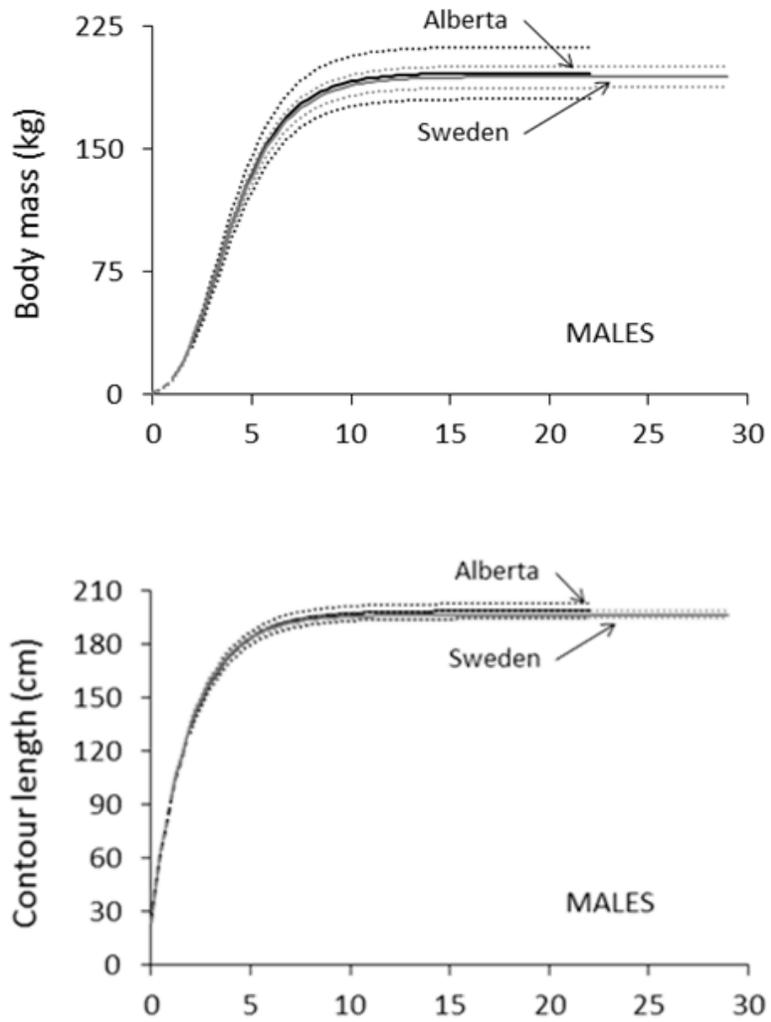
Model terms	β	SE	LCI	UCI
A) Body mass				
Area	67.866	46.270	-22.829	158.549
Day of capture	0.596	0.256	0.094	1.098
Day of capture* Area	-0.602	0.346	-1.280	0.076

776

777 **Figure 1.**



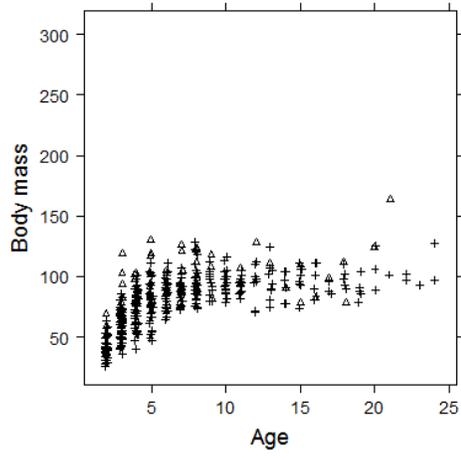
778 **Figure 2.**



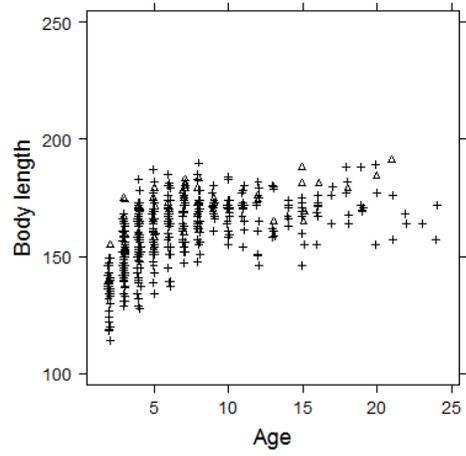
779 **Figure 3.**

780

A) Females

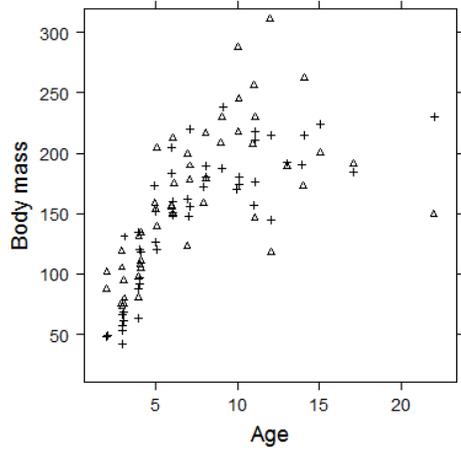


B) Females

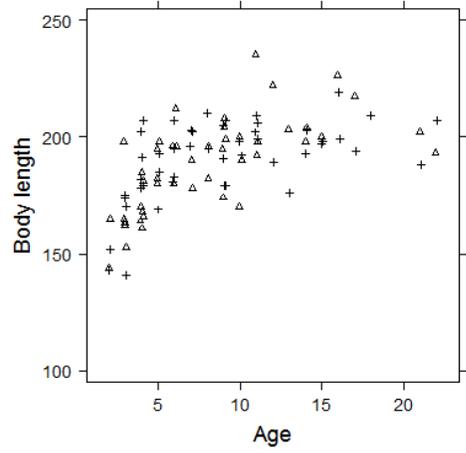


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C) Males



D) Males



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783

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