BROWN BEARS IN ALBERTA AND SWEDEN
FINAL RESEARCH REPORT – PHASE 1 (2009-2011)

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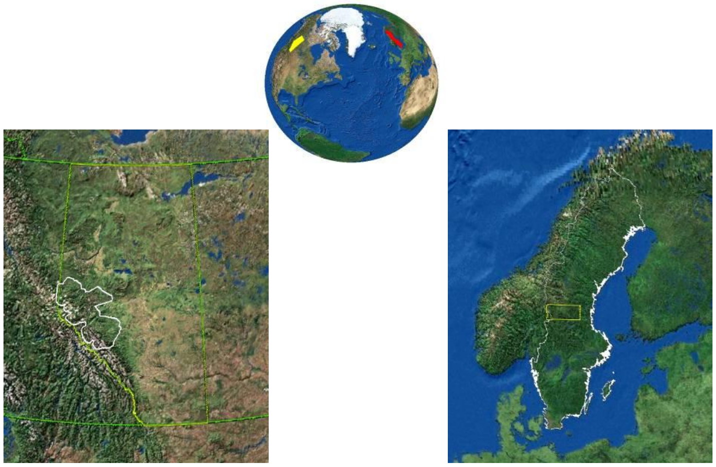

A COLLABORATIVE RESEARCH INITIATIVE BETWEEN THE

FOOTHILLS RESEARCH INSTITUTE (GRIZZLY BEAR PROGRAM),
THE
CANADIAN COOPERATIVE WILDLIFE HEALTH CENTRE,
THE
UNIVERSITY OF ALBERTA,
AND THE
SCANDINAVIAN BROWN BEAR RESEARCH PROGRAM

International Collaboration Background

With little more than 130 animals remaining, the brown bear in Scandinavia was almost exterminated in the 1930’s. Today, however, the species is believed to be thriving with over 3,300 animals estimated to inhabit boreal forest landscapes of Sweden and Norway. A well managed and sustainable hunt is part of the ongoing brown bear management program in Scandinavia. In contrast, the long-term persistence of brown bears in Alberta is a serious concern with approximately 700 bears estimated to remain in the province. The basis for these differences between jurisdictions is not obvious. Brown bears in both Scandinavia and Alberta occupy largely human-dominated boreal landscapes and appear to face similar pressures relating to human activities, e.g., urbanization, resource extraction, road development. It may be, however, that differences occur elsewhere relating to, for example, differences in climate and food abundance or differences in population density and resilience.

The Scandinavian Brown Bear Project has been underway since 1984 in study areas in both Sweden and Norway. During this time period there have been over a hundred scientific research papers published from the results of this project which has established both the credibility and scientific expertise of this research team. This group also has one of the longest term and unique data sets on brown bears anywhere in the world. The Foothills Research Institute Grizzly Bear Program is now in its 12th year of scientific study of grizzly bear populations in Alberta. Our research team is widely recognized, through scientific publications and conference presentations, as leaders in many aspects of grizzly bear science, ecology and health.

This international scientific collaboration was formed in 2009 to support the objectives of long term conservation and sustainability of brown bear populations in boreal forest landscapes in both Alberta and Scandinavia.. The participating research groups have been involved in long term research (12 years in Alberta and 25 years in Scandinavia) pertaining to brown (grizzly) bears in both Alberta and Scandinavia (Sweden and Norway), and have accumulated a great deal of new knowledge and expertise during this time. While each research team has focused on providing applied research findings to support management objectives for their location, the approaches taken and the data gathered by the researchers has at times been similar, and at other times quite different. In Scandinavia, managers have achieved remarkable success in brown (grizzly) bear population recovery and recolonization, while in Alberta, Canada, wildlife managers are now embarking on recovery efforts for this species. The FRI Grizzly Bear Program is highly regarded in the wildlife research community and our pioneering work in grizzly bear health, habitat mapping and modeling has garnered international recognition and interest. This collaboration is a unique opportunity for groups of internationally recognized scientists, from a wide range of disciplines, to work together to share knowledge, expertise, and experience conserving and managing brown (grizzly) bears in boreal forest and mountain ecosystems and to foster the exchange of skills, knowledge and expertise to advance each the program goals of each group and build upon the combined achievements.

Following a two-day planning workshop held in Edmonton, Alberta in March 2009, the research team members agreed on a mission statement for this scientific collaboration and to pursue a number of key research questions that are of common interest and are viewed as high research priorities within each research program.

Mission Statement and Purpose of this Scientific Collaboration

Mission statement: *A research collaboration to understand patterns of brown bear population viability in human-dominated boreal landscapes of Alberta-Scandinavia; applications towards conservation management.*

The purpose of this collaboration is to facilitate:

- The development of a working and ongoing research collaboration between scientists at the Foothills Research Institute Grizzly Bear Program, the Canadian Cooperative Wildlife Health Centre, and the Scandinavian Brown Bear Research Project.
- Exchange of knowledge, expertise, processes and techniques developed by each research group.
- Providing scientific data to aid managers with decisions relating to the long-term conservation of brown (grizzly) bears in each location.
- Communicating with stakeholders and research program partners on the achievements of the research groups and the benefits of this international collaboration.

Research Topics

We identified the following three primary research topics to form the first phase of our collaborative research effort.

1. Life History and Demographics – Growth patterns and reproductive rates are dynamic features of large mammal populations that may relate to genetic differences, temporal variations in food resources, human-caused environmental stressors, and density-dependent factors. In *Ursidae*, size-at-age curves and reproductive rates have been used to characterize life history patterns within a single population and to assess differences in life histories between populations. This research topic compared growth patterns in body length and mass and reproductive rates of brown bear populations in Scandinavia and Alberta. More specifically we evaluated: (i) the biological significance of any differences in life history patterns between the two areas, and (ii) how life history variations could relate to differences in population size and stability between the two areas.

2. Evaluation of long-term stress and stress-associated patterns in brown bears occupying human-dominated boreal landscapes of Scandinavia and Alberta - We believe that identifying and understanding possible health differences between brown bear populations in apparently similar, but distant, boreal forest landscapes will provide knowledge essential for the effective conservation of the species across its global distributional range. Within this research topic we investigated patterns and differences between the 2 populations in relation to human pressures and stress in bears. Within this research topic we examined: (i) hair cortisol stress levels in brown bears from Scandinavia and Alberta, (ii) associations between long-term stress, brown bear health (growth, reproduction, and behavior), and (iii) differences in stress levels and stress-associated patterns between brown bears from the two areas.

3. Effects of forestry on brown bears in boreal ecosystems: A comparison between Scandinavia and Alberta - Scandinavia and Alberta share a common landscape environment characterized by human-dominated boreal forests, both of which still contain populations of brown bear. Brown bears, however, are thriving in Scandinavia, while the long-term viability of Alberta populations is tenuous and perhaps more consistent with historic brown bear populations in Scandinavia. We suggest that much can be learned about the conservation of brown bears in human-altered boreal ecosystems by examining the factors that facilitated recovery of Scandinavian brown bear populations, the factors influencing Alberta's brown bear range, and applying recovery principles from Scandinavia to Alberta in order to help identify management actions for population recovery of a threatened population. This research undertaking will provide background on habitat and population responses of brown bears in boreal forest ecosystems.

In this research topic, we examined habitat and population factors to compliment research questions 1 and 2 above. For this habitat and population work, we focused efforts to: (i) map land cover and compile forestry information among the two research sites to evaluate and understand common patterns or causes in variations to behavioural (habitat selection/use, activity, etc.) and population characteristics of brown bears inhabiting some of the most exploited boreal forests in the world, with a goal of determining what forest management practices might influence range expansion and contraction of brown bear populations.

This report is presented in chapter format that corresponds to these three research questions and authorship of each chapter is identified. It is the intent of our research team that each of these chapters will be revised, edited, and submitted for publication in the scientific literature within the next 12 month period. All data and conclusions presented in this report should be viewed as preliminary until following the publication of these chapters in 2012.

Chapter 1.

One species, two populations, three patterns of growth; brown bears in Canada and Sweden.

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Abstract: Comparing life history traits of populations of a species living in similar habitats, but separated by great distance, may help us understand the evolutionary pressures a species is exposed to. We compared age-specific body size and mass, patterns of growth, and sexual size dimorphism (SSD) of male and female brown bears between Alberta, Canada and Sweden. We also compared the influence of population density, habitat quality and productivity (NDVI), and reproduction on size and mass between the areas. Females attained 90% asymptotic size and mass at the same age in both areas, but Alberta females were always significantly larger and heavier than Sweden females and were on average 11% longer and 17% heavier when reaching 90% asymptotic size and mass. The smaller Swedish females reproduced earlier (primiparous at 75% asymptotic mass) and had larger litters than Alberta females (primiparous at 84% asymptotic mass), perhaps due to differences in population trends (increasing in Sweden, stable or decreasing in Alberta) or long-term exploitation history. There was no statistical difference between the growth curves for male mass and only a trend towards a difference in size between the areas, resulting in a more pronounced SSD in Sweden than Alberta. NDVI was positively related to size and mass of both sexes in both areas. Reproduction was costly for females, because females with offspring were smaller than lone females. We found only limited effects of population density on size and mass. Our results suggest that the adaptive responses of a species to selective pressures vary between areas and populations, and may be shaped by habitat conditions, population status, as well as human pressure. This stresses the importance of population-specific knowledge for conservation and management.

A species' life history is shaped by natural and sexual selection (Andersson 1994, Stearns 1992), and sometimes human-caused selection (Coltman, et al. 2003, Darimont, et al. 2009). Understanding factors affecting life-history traits is fundamental in population and evolutionary ecology, and in conservation biology (Festa-Bianchet and Apollonio 2003). Body size is an important life history trait influencing an organism's anatomy, behavior, and physiology (Stearns 1992). For example, reproductive maturation in mammals occurs at 80-92% of threshold mass or size (Laws 1956). Sexual size dimorphism (SSD) is a result of different male and female growth strategies in relation to reproduction, reflecting sexual selection in males for access to females and competitive selection in females for access to food (Andersson 1994, Clutton-Brock, et al. 1988).

Environmental conditions and their interactions with population density are major selective forces for body size in mammals (e.g. Coulson, et al. 2001, Martinez-Jauregui, et al. 2009). However, their relative and absolute importance can vary among populations of the same species, as has been found in variation in mass in adult female red deer (*Cervus elaphus*) in three countries in Europe (Martinez-Jauregui, San Miguel-Ayanz, Mysterud, Rodriguez-Vigal, Clutton-Brock, Langvatn and Coulson 2009). Targeted harvesting pressure causes human selection and is important in influencing life history traits, such as body size. For example, experimental size-selective harvesting of fish populations shows evolutionary effects on somatic growth and population productivity (Conover and Munch 2002), and life-history traits of fish can change rapidly under strong selection (Reznick, et al. 1990). Selective phenotype-based harvest of high-quality bighorn sheep (*Ovis canadensis*) rams over five generations resulted in selection against rapid early body and horn growth and consequently more males with smaller horns (Coltman, O'Donoghue, Jorgenson, Hogg, Strobeck and Festa-Bianchet 2003).

Body size and size dimorphism vary considerably across a mammals' distributional range (e.g. Herfindal, et al. 2006). Several studies have compared size, growth, and SSD geographically (e.g. Martinez-Jauregui, San Miguel-Ayanz, Mysterud, Rodriguez-Vigal, Clutton-Brock, Langvatn and Coulson 2009, Swenson, et al. 2007), but rarely between continents. Comparing size, growth, and their determinants among populations in spatially separated, but similar, habitats may help explain whether and how ecological and anthropomorphic factors shape a species' life history, and contribute to new solutions for conservation problems (Carey 2005).

Few terrestrial large mammals have a complete Holarctic distribution; one example is the brown bear (*Ursus arctos*), the most widely distributed bear species (Servheen, et al. 1999). In western Eurasia, the brown bear's range once stretched from the Arctic Ocean to North Africa (Servheen, Herrero and Peyton 1999). The original distribution of brown bears in North America stretched from the Arctic Ocean to Mexico, with an eastern distributional limit at ~112º. It was exterminated in large parts of this range by direct human persecution (Servheen, Herrero and Peyton 1999). Today, brown bears are under severe pressure throughout Europe, Asia (except

Russia), and North America (except Alaska and northern-most Canada) by fragmentation and loss of habitat, and human-caused mortality (Servheen, Herrero and Peyton 1999).

In brown bears, female size is positively related to litter and offspring size (Dahle, et al. 2006, Hilderbrand, Jacoby, et al. 1999), and males size is positively related to reproductive success (Zedrosser, et al. 2007). Their body mass fluctuates seasonally, due to fat storage for hibernation and large inter-annual variations in food availability (Hilderbrand, Jenkins, et al. 1999). Therefore mass does not necessarily reflect skeletal size (hereafter referred to as size) in bears. We therefore analyze body mass and size separately.

Our goal is to compare age-specific body size and mass, patterns of growth, and patterns of size dimorphism of male and female brown bears in Canada (Alberta) and Sweden, separated by ~7,000 km. In addition we compared the influence of population density, habitat quality and productivity (using the Normalized Difference Vegetation Index (NDVI) as a surrogate measure), capture date, and reproduction on the relationship between body mass and age and body size and age of male and female brown bears between populations.

Material and methods

Study areas

The Swedish study area (Zedrosser, et al. 2006) covered ~21,000 km^2 of intensively managed boreal forest in a rolling landscape in south-central Sweden (61°N, 14°E) and mountainous national parks and adjacent forested land in the north (67°N, 18°E). The forest is dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). Elevations range from 200 to 2000 m, and the timberline is located at 600-750 m. The climate is continental with cold winters (January mean: -7°C in south, -13°C in north) and short, warm summers (July mean: 15°C in south, 13°C in north). Snow cover lasts from late October until May and the growing season is <130–180 days. Precipitation averages 500–1,000 mm annually. Bears are protected in the national parks, but intensively hunted in the rest of the area.

The study area in Alberta (Canada) covered 132,076 km^2, mostly in and adjacent to the eastern slopes of the Rocky Mountains, from northern Montana (49°N, 113°W) to the city of Grande Prairie (55°N, 118°W). Elevations range from 218 to 3,747 m, alpine meadows, rocky areas and glaciers dominate the highest elevations, and boreal coniferous, deciduous, and mixed forests dominate the mountains and foothills region. Lodgepole pine (*Pinus contorta*), spruces (*Picea englemanii*, *P. glauca*, *P. mariana*), and firs (*Abies lasiocarpa*, *A. balsamea*) are common conifers and quaking aspen (*Populus tremuloides*) is the most common deciduous species (Downing and Pettapiece 2006). The continental climate of cold winters (January mean: -5°C in south, -15°C in north) and short, warm summers (July mean: 17°C in south, 15°C in north) (Downing and Pettapiece 2006). Average precipitation is 450-900 mm annually. Snow cover lasts from late October until early May and the growing season is <160–185 days.

Population parameters and conservation status

Brown bears have comparable life-history parameters in both areas (Table 1), based on >25 years of research in Sweden and >16 years in Alberta. Both are arctic-interior populations, with similar ecological conditions, life-history traits (Ferguson and McLoughlin 2000), and diets (Dahle, et al. 1998, Munro, et al. 2006). Protein consumption is highest in spring and early summer, consisting of ungulate neonates in Canada (Munro, Nielsen, Price, Stenhouse and Boyce 2006) and ungulate neonates and insects (mainly ants (*Formica* spp., *Camponotus* spp.) in Sweden (Dahle, Sorensen, Wedul, Swenson and Sandegren 1998). Summer and fall diets are dominated by graminoids, herbs, and berries (mainly soopolallie (*Shepherdia canadensis*), mountain huckleberry (*Vaccinium membranaceum*)) in Canada, and mainly berries (especially blueberry (*V. myrtillus),* crowberry (*Epetrum* spp.), and lingonberry *(V. vitis-idaea*)) in Sweden. Neither study population has access to spawning salmon (*Oncorhynchus* spp., *Salmo* spp.).

In both areas, brown bears face resource extraction, agriculture, urbanization, and recreation (Nellemann, et al. 2007, Nielsen, et al. 2004). In Sweden, however, brown bears have increased from ~130 animals in the 1930s to >3,200 animals in 2008 (Kindberg, et al. 2009), and have been hunted since the 1940s (Swenson, et al. 1994). In contrast, they are designated as threatened in Alberta, with about 691 bears in the province (Alberta Sustainable Resource Development and Alberta Conservation Association 2010), within an area ~50% larger than that of Sweden (661,848 km^2 vs. 449,964 km^2). Forest harvesting and energy exploration and development (oil, gas, and coal) have led to recent and rapid changes in land use patterns, landscape characteristics, and human accessibility (Aumann, et al. 2007). Regulated hunting occurred until 2002, became increasingly restricted and was stopped in 2006 (Alberta Sustainable Resource Development and Alberta Conservation Association 2010).

Capture and handling

All bears were captured as a part of long-term research projects. Data were collected from bears captured between March and October 1988-2006 in Sweden, mostly during April and May (89% of 408 unique individuals; 90% of 960 total captures. In Alberta, bears were captured between April and October 1994-2009, mostly during May-June (79% of 204 unique individuals; 76% of 323 total captures). Bears were captured exclusively from a helicopter using a remote drug delivery system in Sweden (Arnemo, et al. 2011), whereas a variety of methods (leg-hold snares, remote drug delivery from helicopter, barrel traps) were used in Alberta (Cattet, Christison, et al. 2003). A premolar tooth was extracted from bears of unknown age for age determination (Matson, et al. 1993). Bears were weighed in a sling suspended beneath a spring scale (Sweden) or a load scale (Alberta). Contour body length was the distance from tip of nose to end of last tail vertebra with the measuring tape overlying the dorsal midline with the bear in sternal recumbency. Capture and handling are described in Cattet et al. (2003) for Alberta and Arnemo et al. (2011) for Sweden, and were approved by the appropriate authorities and ethical committees (Djuretiska nämden i Uppsala, Sweden; Committee on Animal Care and Supply, University of Saskatchewan, Canada; Alberta Sustainable Resource Development Animal Care Committee, Canada).

Statistical methods

We used the von Bertalanffy equation to describe the age- and sex-specific growth of bears, because it has been used previously to model bear growth (e.g. Kingsley, et al. 1988, Swenson, Adamic, Huber and Stokke 2007). We did not include one-year-old bears in the analysis, because few were captured in Alberta. In addition, yearling body size is correlated with maternal size (Dahle, Zedrosser and Swenson 2006), and thus it may be difficult to differentiate habitat effects and density dependency from maternal effects. We constrained the data in each model to include measurements from the last capture for individuals captured more than once. The mass-at-age equation was of the form: $m(a) = M[1 – e^{(-km(a – Am))}]^3$, where $m(a)$ is body mass (kg) at age a (years), M the asymptotic body mass (kg), k_m the mass growth rate constant (year^{-1}), A_m a fitting constant representing the theoretical age at which the animal would have zero mass, and e is the base of the natural logarithm.

The size-at-age equation was of the form $l(a) = L[1 – e^{(-kl(a – Al))}]$, where $l(a)$ is contour length (cm) at age a (years), L the asymptotic contour length (cm), k_l the length growth rate constant (year^{-1}), and A_l a fitting constant representing the theoretical age at which the animal would have zero size. We fitted the growth curves by using the iterative estimation algorithms in the SPSS non-linear regression procedure (SPSS Release 17.02., SPSS Inc., Chicago, Illinois, USA).

Both asymptotic mass (M) and length (L) are indices of the mean maximum body size attained by bears in a population. We corrected them for capture date. The median capture dates were 20 April in Sweden, 24 May in Alberta, and 11 May combined. We estimated the average daily change in mass (m) and length (l) by sex and area over the capture season by regressing size against Julian day-of-capture. Mass and length asymptotes were then corrected to a standard capture date of 11 May using the following adjustment for Sweden: $M_{corrected} = M + (21 \times m)$ and $L_{corrected} = L + (21 \times l)$, and for Alberta: $M_{corrected} = M - (13 \times m)$ and $L_{corrected} = L - (13 \times l)$.

To estimate SSD we calculated male-to-female body mass ratios using predicted body masses from mass-at-age equations across ages 2-22 years for Alberta bears and 2-24 years for Sweden bears. We used the same approach to estimate body size dimorphism with the predicted contour lengths from size-at-age equations for each area. Measuring size before the mating period, which starts in mid-May in both areas, may evaluate SSD best, because SSD is at its maximum, providing more power to detect intraspecific variation (Garel, et al. 2009).

We used general linear mixed models to evaluate the relationships between body mass (in kg) and body size (contour length in cm) of males and females in Alberta and Sweden and predictor variables. Based on the multiyear growth pattern of bears (Kingsley, Nagy and Reynolds 1988, Swenson, Adamic, Huber and Stokke 2007) and the calculated growth curves, we expected age to be an important explanatory variable in all models. We therefore created a base model with age (log-transformed) and then evaluated the effect of other explanatory variables. The best model was selected based on Akaike's Information Criterion (AIC) and we considered only models with ΔAIC values ≤2 to be most supported by the data (Burnham and Andersson 2002). The predictor variables available were age (log-transformed), study area (0 = Alberta, 1 = Sweden), individual-based population density index (see below), Julian day of capture, the normalized difference vegetation index (NDVI, see below), presence or absence of dependent offspring at capture, and meaningful interactions among these variables. The variables population density index and NDVI were centered. Individual identity was included as a random effect. Models based on AIC-selection may include uninformative parameter(s) which explain little variation in the model. They should not be interpreted as having ecological effects (Arnold 2010). We therefore discussed parameters with 85% confidence intervals (CI) including 0 very cautiously. The R^2 value of the best models was calculated with the method proposed by Kramer (2005). The software R 2.12.0 was used in all statistical analyses.

Variables used in evaluating the determinants of size and mass

Individual population density index In Sweden the population density within 17.84 km (~1000 km^2) of an individual was estimated based on the methods of Zedrosser et al. (2006). In the south, the population size was estimated based on a DNA analysis of scats in 2001 and 2002. The temporally corrected individual density index for radio collared individuals was based on the location of individual bears genetically identified by scat sampling (71% of the radio-collared bears were represented in the scat samples) and the population growth rate . No corresponding population estimate was available for the north, but virtually every adult male and female and all subadult female bears were radio-collared. We used the locations of radio-collared bears, corrected to include subadult males, and growth rate of the population to calculate an individual density index as in the south (Zedrosser, Dahle and Swenson 2006).

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

Normalized Differential Vegetation Index (NDVI) The NDVI consistently correlates with vegetation biomass and dynamics in various ecosystems, and we used NDVI in the growing season as a predictor of habitat quality and productivity (Pettorelli, et al. 2005). Vegetative conditions in spring and summer are regarded as decisive for the reproductive success and the offspring condition of large herbivores (Pettorelli, et al. 2006). The Global Land Cover Facility freely provides time series of NDVI, covering the entire world in biweekly and continental-wide mosaics since 1986. The spatial resolution (pixel size) of the NDVI tiles is 8x8 km. The data originates from imagery recorded by the Advanced Very High Resolution Radiometer Sensors on board of the National Oceanic and Atmospheric Administration satellites (Tucker, et al. 2005). NDVI tiles for Sweden were downloaded from http://glcf.umiacs.umd.edu/data/gimms/

(accessed September 2010). We calculated an integrated NDVI within a radius of 17.845 km around the center location of each individual for the months May-July (the growing and capture season) in the year of capture with Erdas Imagine software. The averaged NDVI grids were imported into ArcGIS 9.3.1 and in further processing "NoData" was assigned to all water to avoid bias, because of its default value. We then smoothed the grids to obtain the mean NDVI for each cell.

NDVI tiles for Alberta were downloaded from http://glcf.umiacs.umd.edu/data/gimms/ (accessed October 2010). A pixel-by-pixel mean value for the six grids for May-July for each year 1999-2006 was calculated using ArcGIS 9.2 Spatial Analyst Raster Calculator. The weekly mean of all bear positions, excluding dens, was calculated and an annual mean of weekly positions was obtained for each individual. The home range centers were buffered by 10,000 m. Buffers for each year 1999-2006 were matched to the mean summer NVDI grid for that year (buffers for 2007-2010 were matched with the 2006 grid). A mean NDVI value for each buffer was calculated with ArcView 3.2 Zonal Statistics tool (Spatial Analyst extension).

Results

Growth curves and size dimorphism

The predicted mass- and size-at-age curves for female bears were approximately parallel, but Alberta females were significantly heavier ($F = 14.405$, $P < 0.001$) and longer ($F = 28.496$, $P < 0.001$) at a given age (Fig. 1). Females from both areas attained 90% of their asymptotic size at 3.7 years and 90% asymptotic mass at 7.5-7.6 years (Table 2). However, at these ages Alberta females averaged 11% longer (179 cm vs. 161 cm) and 17% heavier (108.6 kg vs. 92.9 kg) than Sweden females. Alberta females were also longer and heavier at primiparity (Fig. 1). Females in Sweden reached primiparity at 75% of their asymptotic mass (or 69.8 kg) and 95% of their asymptotic size (or 153.5 cm), whereas females in Alberta reached primiparity at 84% (91.4 kg) and 94% (168.5 cm), respectively.

The predicted mass- and size-at-age curves for male bears overlapped considerably (Fig. 1). Alberta males were suggestively longer ($F = 3.380$, $P = 0.070$), however the growth curves of mass did not differ between areas ($F = 1.946$, $P = 0.164$). Alberta males attained 90% asymptotic mass 3.1 years later and 90% asymptotic size 2.9 years later than Sweden males (Table 2). When Swedish males reached 90% asymptotic mass (8.6 years, Table 2) and size (4.3 years, Table 2), Alberta males had reached 88% of 90% asymptotic mass and 64% of 90% asymptotic size.

Variance in mass and size was approximately twice as large for Alberta bears (Coefficient of variation (CV) – Mass: $CV_{Alberta} = 81\%$ vs. $CV_{Sweden} = 35\%$; Size: $CV_{Alberta} = 24\%$ vs. $CV_{Sweden} = 12\%$). Sexual size dimorphism (SSD) was more pronounced for both mass and size in Sweden. At 90% asymptotic mass, the male-to-female mass ratio was 2.17 in Sweden and 2.03 in Alberta (Fig 1). At 90% asymptotic size, it was 1.22 in Sweden and 1.14 in Alberta (Fig. 1).

Determinants of body size and mass

The ΔAIC between the best and second-best model explaining female mass was 1.942 (Table 3). Therefore both models were considered for interpretation, and both explained 73% of the total variation in female mass. The best model suggested that females in Sweden weighed less than females in Alberta (*β*=-26.810±3.198 SE). Body mass of female brown bears increased with age (27.772±1.347), and increasing NDVI (61.281±14.233). The negative interaction between NDVI and study area suggests that females in Sweden weigh less at higher NDVI values than in Alberta (-39.396±15.565). Females with offspring may have weighed less than lone females (-4.495±3.903), but the 85% CI of this parameter included 0. An interaction between the absence or presence of offspring and NDVI suggests that a female with offspring was heavier than a lone female at high NDVI values (26.024±8.995). The interaction between the presence/absence of offspring and study area suggested that females accompanied by offspring may have weighed more in Sweden than in Alberta (5.126±3.784), however the 85% CI of this interaction included 0. A weak positive effect of population density on female body mass was present in the model (0.058±0.150), however the 85% CI of this interaction included 0. An interaction between body mass and study area suggested that female body mass decreased more with increasing density in Sweden than in Alberta (-0.302±0.161). The parameters and their estimates in the second-best model are not presented because they were so similar to the best model, except for an additional interaction between NDVI and population density in the second-best model, which suggested that female body mass increased with decreasing NDVI values and increasing density values (-0.177±0.366), however the 85% CI of this interaction included 0.

The best model explaining female size (Table 3) suggested that females in Sweden were smaller (-12.508±2.118). Body size of female brown bears increased with age (*β*=14.433±2.629), and increasing NDVI (4.628±12.407) (the 85% CI of this parameter included 0), but the effect of NDVI was stronger in Sweden (14.433±2.629). Having offspring was costly, because females with offspring were smaller than lone females (-5.610±3.213), however the interaction between study area and the presence of offspring showed that Sweden females with offspring were larger (7.183±3.356). There was a weak interaction between the absence/presence of offspring and NDVI, suggesting that a female with offspring was larger with increasing NDVI values (1.832±7.636), but the 85% CI of this parameter included 0. This model explained 58% of the variation in female size.

The best model explaining male mass (Table 3) suggested that Sweden males weighed less than Alberta males (-12.103±5.509). Male mass increased with increasing age (86.675±2.741) and NDVI (108.093±34.237). The negative interaction between NDVI and area suggested that Sweden males may weigh less at higher NDVI (-127.950±38.449). This model explained 86% of the variation in male mass.

The best model explaining male size (Table 3) suggested that Sweden males were smaller (-1.256±2.350), but the 85% CI of this parameter included 0. Body size of males increased with age (31.863±1.258) and increasing NDVI (41.281±19.605). The negative interaction between NDVI and area suggested that Sweden males were smaller at higher NDVI (-42.205±21.066). This model explained 77% of the variation in male size.

Discussion

Brown bears grew faster in size than in mass, because both sexes reached asymptotic size before reaching asymptotic mass in both areas. The area differences in asymptotic size and mass were more pronounced in females (smaller and lighter in Sweden) than in males. In polygynous, sexually dimorphic species, the sexes show different growth patterns and energy expenditure (Clutton-Brock, Albon and Guinness 1988). Differences in growth in brown bears are likely a response to sexual selection; males grow as fast as possible to achieve large size, which is associated with high reproductive success (Zedrosser, Bellemain, Taberlet and Swenson 2007), whereas females trade growth for early sexual maturity and reproduction (Clutton-Brock, Albon and Guinness 1988).

Female brown bears attained 90% asymptotic size and mass at the same age in both areas (Table 2), similar to 3 brown bear populations in comparable taiga/tundra habitat without access to spawning salmon, where females reached 90% asymptotic mass at 7.2-7.9 years and 90% asymptotic size at 3.8-4.8 years (Kingsley, Nagy and Reynolds 1988). Females in our study areas therefore grow at approximately the same rate. However, Alberta females were always significantly larger and heavier, on average 11% longer and 17% heavier when reaching 90% asymptotic size and mass. Due to lack of data we were not able to evaluate if the area differences in absolute female asymptotic size and mass were present in cubs and yearlings. Alberta females were on average 4-9% larger and 1-14% heavier and Sweden females were 1-7% shorter and 0-16% lighter than females from other North American populations (Kingsley, Nagy and Reynolds 1988). This suggests that Alberta females are relatively large in comparison to females in other interior, boreal forest populations, whereas Swedish females were the smallest yet recorded in such habitat.

Female sexual maturity depends on reaching a threshold body mass, after which energy is allocated primarily to reproduction; age at primiparity in ungulates corresponds to the age when females reach ~80% of their adult mass (Gaillard, et al. 2000). Females in Alberta reached primiparity at 84% asymptotic mass, whereas females in Sweden apparently traded growth for earlier reproduction and reached primiparity at 75% asymptotic mass. Female fecundity is strongly influenced by mass in ungulates (e.g. Garel, et al. 2005) and bears (Hilderbrand, Jacoby, Schwartz, Arthur, Robbins, Hanley and Servheen 1999); larger individuals reproduce earlier and produce more offspring of better quality (Stearns 1992). However, our data show that the smaller and lighter Swedish females reproduced earlier and had larger litters than the larger and heavier Alberta females (Fig. 1, Table 1). Both populations are likely below carrying capacity, however populations are increasing in Sweden (Kindberg, Swenson and Ericsson 2009), and may be locally decreasing in Alberta (Boulanger, Minifie, Stenhouse, Paetkau, Cranston, Proctor, MacHutchon and Himmer 2009), which may contribute to differences in female reproductive investment.

The growth curves for mass and size were more similar between the areas for males than females; there was no statistical difference for male mass and only a trend towards a difference in size. However, males in Sweden reached 90% asymptotic mass 3.1 years earlier and 90% asymptotic size 2.9 years earlier than Alberta males (Table 2); when Swedish males reached 90% asymptotic size and mass, Alberta males had only reached 72% asymptotic size and mass. In general, the pattern of brown bear growth seems to vary more in males than females, because males in 3 populations from interior North America reached asymptotic size at 4.5-6.5 years, and asymptotic mass at 10.6-12.7 years (Kingsley, Nagy and Reynolds 1988). In contrast to Sweden and other North American interior boreal populations (Kingsley, Nagy and Reynolds 1988), Alberta males reached the largest asymptotic size and mass, but showed the slowest growth in size, although their growth in mass was comparable to other populations (Kingsley, Nagy and Reynolds 1988).

For males in polygynous size-dimorphic species, access to females depends on intrasexual competition (Andersson 1994) and body size positively influences male reproductive success (e.g. Clutton-Brock, Albon and Guinness 1988, Zedrosser, Bellemain, Taberlet and Swenson 2007). Males in such species, as brown bears, should therefore be selected for growth patterns that benefit them in male-male competition (Weckerly 1998). In social systems with intrasexual competition for mates (Weckerly 1998), males may delay maturity, because early reproduction may reduce subsequent growth (e.g. Garel, Loison, Jullien, Dubray, Maillard and Gaillard 2009, Mysterud, et al. 2003). The earliest observed ages of first successful male reproduction in Alberta were 5 and 6 years (G. Stenhouse, unpublished data), compared with 3 years in Sweden (Zedrosser, Bellemain, Taberlet and Swenson 2007). Growth patterns co-vary with mortality patterns (Stearns and Koella 1986) independently of body size (Pontier, et al. 1993), and are thus expected to reflect selective pressures (Garel, Loison, Jullien, Dubray, Maillard and Gaillard 2009). The faster growth of males in Sweden may be related to heavy hunting pressure, where most adult bear mortality is human caused and a male bear dies on average at 4.8 years (Bischof, et al. 2008).

Divergent growth tactics between sexes in relation to reproduction generally leads to marked SSD in polygynous species (Andersson 1994). SSD in our study was due to a longer growth period in males than females, as in polar bears (*Ursus maritimus*) (Derocher, et al. 2005). However, in contrast to polar bears, SSD in brown bears was greater for length than mass (Figure 3). Most sexually dimorphic mammals have mass dimorphism ratios of 1.2 to 1.8 (Weckerly 1998); brown bears in our study showed mass ratios of 2.03-2.14. Patterns of SSD can vary among populations of the same species, including bears (e.g. Derocher and Wiig 2002, Swenson, Adamic, Huber and Stokke 2007). SSD ratios in Alberta were within the range reported in 3 other North American populations in similar habitat (Kingsley, Nagy and Reynolds

1988); ratios of 1.11-1.15 for size and 1.78-2.02 for mass. In comparison, SSD ratios in Sweden were higher; 1.22 for size and 2.17 for mass. A SSD mass ratio of 2.16 was found in brown bears in southeastern Europe (Swenson, Adamic, Huber and Stokke 2007). This suggests that SSD in brown bears is larger in Europe than in North America. The degree of SSD in ungulates depends strongly on growth and size of males (Clutton-Brock, et al. 1982, Pepin, et al. 1996), however our results suggest that also the growth of females may be important, at least in one large carnivore.

Male-biased hunting decreases the proportion of adult males in a population, with several potential life history consequences (e.g. Garel, et al. 2006). Young males may increase their reproductive investment during the mating season, due to reduced competition from older males (e.g. Mysterud, Holand, Roed, Gjostein, Kumpula and Nieminen 2003), which may reduce their body growth due to the high energetic expenses involved (e.g. Garel, Solberg, Sæther, Herfindal and Hogda 2006). However, a female-biased sex ratio likely did not cause the area difference in SSD (see also Weckerly 1998), as hunting of bears of both sexes (with the exception of females accompanied by offspring) occurred in Sweden (Bischof, Fujita, Zedrosser, Soderberg and Swenson 2008) and Alberta (before full protection in 2006) (Kansas 2002). Sexually selected infanticide may be an important factor for cub mortality in European brown bears (Swenson, et al. 1997), but not in North America (e.g. McLellan 2005). Females may less effectively defend their cubs in Europe, with larger SSD, resulting in more infanticide there.

We investigated the influence of habitat productivity (NDVI), population density, presence of offspring, and capture date on the relationships between age and both mass and size by sex and area. We found a greater variance in size and mass in Alberta bears, which may be caused by larger variation in habitat productivity and elevations there. We did not investigate clinal changes consistent with Bergmann's rule, because such a pattern likely does not exist in brown bears (Kojola and Laitala 2001).

The analysis of the age-related determinants of size and mass showed a clearer difference between the areas than size and mass based on growth curves only. Females were smaller and weighed less and males weighed less in Sweden than in Alberta, when controlling for the effect of other variables. Also male size tended to be smaller in Sweden, when controlling for the effect of other variables, although the CI of this parameter included 0 and must therefore be interpreted cautiously. Habitat productivity was positively related to size and mass in both sexes. We did not find any effect of capture date, likely because capture occurred within a short time period. The ultimate reasons for the differences we found, discussed above, are likely related to earlier reproduction in both sexes in Sweden. An additional factor may be differing population trends (increasing with higher densities in Sweden, decreasing in Alberta).

Recent ecological studies have highlighted NDVI as an index linking vegetation to animal performance (Pettorelli, Vik, Mysterud, Gaillard, Tucker and Stenseth 2005). Both size and mass of male and female bears were positively related to NDVI values in both areas, as has been found in ungulates (e.g. Martinez-Jauregui, San Miguel-Ayanz, Mysterud, Rodriguez-Vigal, Clutton-Brock, Langvatn and Coulson 2009). Correlations between plant phenology and carnivore life history traits likely operate more indirectly, through prey abundance (Melis, et al. 2010), however brown bears are omnivorous, not true carnivores. We used NDVI values during the growing season to reflect plant growth and fruit production, and thus food availability and quality, because available nutrition is probably the most important factor affecting growth (Laws 1956). In contrast to other large mammals, bears partition their physical resources into growth and fat accumulation for hibernation. Bears dependent upon various plants, especially berries, for fat accumulation in both Alberta and Sweden (Dahle, Sorensen, Wedul, Swenson and Sandegren 1998, Munro, Nielsen, Price, Stenhouse and Boyce 2006). Based on our results, environmental productivity and food conditions, as reflected by NDVI, are good predictors of variation in life history variables in brown bears (see also Ferguson and McLoughlin 2000).

There may be no *a priori* reason to expect conspecific populations in different areas to respond similarly to climate, as limiting factors may operate at different times of the year and the forms of regulation may differ (Martinez-Jauregui, San Miguel-Ayanz, Mysterud, Rodriguez-Vigal, Clutton-Brock, Langvatn and Coulson 2009). Bear populations in our study lived on different continents, but in similar habitat (i.e. high latitude and altitude populations in boreal forest ecosystems), which has been suggested to cause similar life history responses in brown bears (Ferguson and McLoughlin 2000). The strength of the relationship between NDVI and size and mass differed between the areas, however, with bears in Sweden more positively influenced by NDVI, perhaps related to longer winters and longer hibernation in Sweden. Harsher climatic conditions should result in smaller size, slower growth, and later reproduction, however we found the opposite. The earlier and higher reproductive investment of Swedish bears may be related to the different population status of bears in the study populations (see above), or nutritional landscape characteristics that differ between areas.

Density-dependent relationships for body size and body mass have been reported in large mammals, especially ungulates (e.g. Hjeljord and Histol 1999), but also bears (Zedrosser, Dahle and Swenson 2006). In general, an increase in population density increases competition for food, often decreasing body size and mass. Contrary to the expectations, we found that population density had a weak but positive effect on female body mass; however the CI of the interaction included 0 and it may therefore have only limited biological meaning (Arnold 2010). An interaction between area and density suggests that female mass decreased more with increasing density in Sweden than in Alberta, suggesting that bear populations may be closer to carrying capacity in Sweden. This is supported by the general increase of bears in Sweden and the possibly local decrease of brown bears in Alberta (Boulanger, Minifie, Stenhouse, Paetkau, Cranston, Proctor, MacHutchon and Himmer 2009, Kindberg, Swenson and Ericsson 2009). Due to the sex differences in the growth patterns of size dimorphic species in relation to reproduction, female body mass may be most affected by density of the life history traits we studied.

Life history theory predicts a trade-off between mass and reproduction when resources are limited (Stearns 1992) and reproduction and maternal care seem to be costly for females (e.g. Pelabon, et al. 1995). Female brown bears with offspring were smaller than lone females in both areas and perhaps lighter, but the CI of this variable included 0. Brown bears are typical capital breeders and primiparous females have smaller litters and a higher probability of litter loss, however there is no evidence of a cost of maternal care such as longer interlitter intervals or smaller subsequent litters (Zedrosser, et al. 2009). Our results suggest that decreased size is a cost of reproduction and maternal care incurred by female brown bears. The long interlitter intervals (≥2years, Table 1) may help reduce or balance incurred costs, because dependent young start feeding by themselves during their first year and suckling bouts become less frequent, especially during the second year of maternal care. In addition, bears have delayed implantation during hibernation (Schwartz, et al. 2003), and thus females incur little costs of pregnancy before hibernation. Habitat productivity may buffer the negative effects of maternal care on the size of female bears, because females with offspring may be larger following years with high NDVI values. This suggests that female bears invest surplus energy into skeletal size rather than mass. An interaction between the presence/absence of offspring and area suggests that females with offspring weighed more in Sweden, however the 85% CI of the interaction included 0 and it may therefore have only limited biological meaning (Arnold 2010).

Interspecific competition by American black bears (*Ursus americanus*) may affect brown bear life history in Alberta. Black bears are not present in Sweden. Mattson et al. (2005) suggested that the primary impact of black bears on brown bears would be through reduced reproduction and recruitment caused by exploitation competition, even though brown bears dominate black bears during confrontations. Such competition may have selected for larger brown bear size in Alberta, but not the earlier primiparity in relation to size and mass of females in Sweden and the very similar size and mass of males in both study areas.

Implications for population dynamics, management and conservation

Bears may be more affected by climate change than other carnivores, because they rely largely on vegetation for growth and especially the accumulation of fat reserves necessary for hibernation. Further work is needed to determine how environmental and climatic factors may influence of mass and size in brown bears in different populations and different habitats to help understand variation of life-history traits in relation to climate change (Martinez-Jauregui, San Miguel-Ayanz, Mysterud, Rodriguez-Vigal, Clutton-Brock, Langvatn and Coulson 2009).

Individual differences in body mass and size exert a major influence on mammalian life-history traits. Despite smaller body size and mass, Sweden females invest more and earlier into reproduction and have larger litters and shorter interlitter intervals than Alberta females. Males in both areas maximize growth, however Sweden males select a more risky strategy by growing faster and reaching asymptotic mass and size earlier than Alberta males. We believe that these differences are likely related to differences in population status, with Swedish brown bears exhibiting characteristics typical of increasing populations, whereas Alberta bears exhibit characteristics typical of stable or decreasing populations. How fast such a switch in life-history strategies can occur in a large mammal with slow reproduction is unknown, however it likely takes several generations. There is evidence of human-induced selection on morphology and life-history traits in wild animal populations (Coltman, O'Donoghue, Jorgenson, Hogg, Strobeck and Festa-Bianchet 2003, Darimont, Carlson, Kinnison, Paquet, Reimchen and Wilmers 2009). In large mammals, effects of selective harvest on morphological traits have been documented (Coltman, O'Donoghue, Jorgenson, Hogg, Strobeck and Festa-Bianchet 2003), and in red deer (*Cervus elaphus*), modeling suggested that random harvest also alters female reproductive strategies, with higher harvest rates causing lower body mass at primiparity (Proaktor, et al. 2007). Swedish brown bears have been hunted since the Middle Ages, with the goal of species extinction (Swenson, Sandegren, Bjarvall, Soderberg, Wabakken and Franzen 1994). After several centuries of persecution, the brown bear was almost extinct in Sweden at the beginning of the 20th century, when it was protected and populations started to increase (Swenson, Sandegren, Bjarvall, Soderberg, Wabakken and Franzen 1994). In comparison, brown bear populations in Alberta did not decline until European settlers arrived in the late 19th and early 20th century. Populations were reduced within a century and some may now be in decline (Boulanger, Minifie, Stenhouse, Paetkau, Cranston, Proctor, MacHutchon and Himmer 2009). These differences in long-term human selection pressure may have selected Swedish brown bears for earlier and higher reproductive investment than Alberta bears. For the manager and conservationist this means that bears in Sweden can be harvested at higher rates and are likely more resilient towards fluctuations in the environment, whereas in Alberta bears must be managed more conservatively, climate change may have a stronger influence, and stronger protective measures are needed to promote population increase.

In conclusion, our results suggest that the adaptive responses of a species to selective pressures vary among areas and populations, and may be shaped by habitat conditions as well as human pressure. This stresses the importance of population-specific knowledge for conservation and management. Habitat conditions and density dependency may affect the sexes and populations differently. Due to this complexity, the effects of climatic change on bears may take a long time to become evident (Pepin, Faivre and Menaut 1996) and difficult to predict. Climatic effects may be especially severe if they influence the major food sources necessary for fat accumulation for hibernation, i.e. berries. Potential population-level effects can only be detected with long-term individual-based studies and a well designed monitoring program (Martinez-Jauregui, San Miguel-Ayanz, Mysterud, Rodriguez-Vigal, Clutton-Brock, Langvatn and Coulson 2009).

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Figure 1. Predicted body mass and sexual mass dimorphism at age (left side of panel) as well a predicted body size and sexual size dimorphism at age for brown bears in Alberta (Canada) and Sweden. Predicted values were calculated from data collected at last capture and adjusted for date of capture. Lines represent predicted mass or size ⍰ 95% confidence interval.

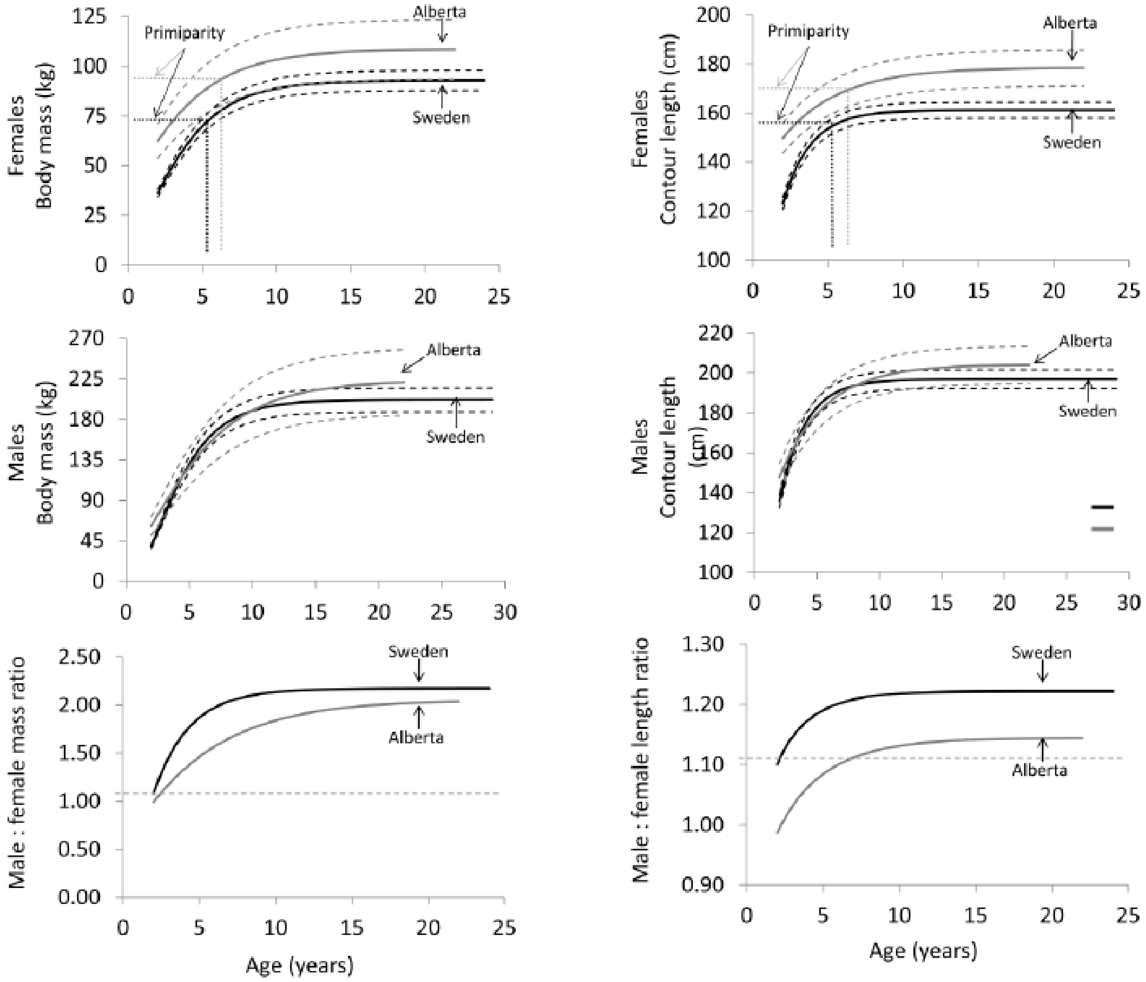

Table 1. Brown bear life-history parameters in Canada (Alberta) and Sweden. The number of individuals a parameter estimate is based upon is given in parenthesis.

Life history parameter	Alberta	Sweden
Age (years) at primiparity	5.8 (13)	5.0 (59)[1]
Mean litter size	2.07 (30)	2.34 (83)[1]
Interlitter interval (years, between successful litters)	2.5 (10)	2.3 (124)[1]
Mean mass (kg) at primiparity	91.3 (13)	69.9 (59)
Mean body length (cm) at primiparity	168 (13)	154 (59)
Mean date of den entry		
Adult male	Nov. 22 (15)	Oct. 27 (33)[2]
Adult female without dependent offspring	Nov. 9 (41)	October 25 (43)[3]
Mean date of den exit		
Adult male	April 4 (13)	April 4 (33)[2]
Adult female without dependent offspring	April 11 (24)	April 13 (13)[3]
Adult female with cubs of the year	April 17 (11)	May 7 (21)[3]
Timing of breeding season	~May 15-July 31[5]	~May 15-July 7
Median adult male home range size (km^2)	899 (22)	833-1055 (36)[4]
Median adult female (without dependent offspring) home range size (km^2)	273 (39)	217-280 (52)[4]

[1] data updated from Zedrosser et al. (2009), [2] Manchi and Swenson (2005), [3] Friebe et al. (2001) [4] Dahle and Swenson (2003), [5] Stenhouse et al. (2004)

Table 2. Parameter estimates (±SE) for the von Bertalanffy size/mass-at-age curves for male and female brown bears in Canada (Alberta) and Sweden. S is the asymptomatic measurement (body mass in kg, contour body size in cm) corrected for capture date = May 11, k is the size growth constant, A is the theoretical age (in years) at which the animal would have size 0, and 90% A is the age (in years) at which an animal reaches 90% of its asymptotic mass or size, and N is the sample size. Parameter estimates are based on measurements recorded from bears >1-year old at the last capture, if the bear had been captured more than once.

Measurement	Area	S	K	A	90% A	*N*
Females						
Body mass	Alberta	108.6 ± 7.54	0.290 ± 0.165	-4.15 ± 4.02	7.5	71
	Sweden	92.9 ± 2.52	0.364 ± 0.061	-1.60 ± 0.83	7.6	129
Body size	Alberta	179 ± 3.7	0.266 ± 0.126	-4.87 ± 3.55	3.7	67
	Sweden	161 ± 1.6	0.540 ± 0.133	-0.68 ± 0.88	3.7	129
Males						
Body mass	Alberta	222.8 ± 18.48	0.238 ± 0.070	-2.44 ± 1.59	11.7	92
	Sweden	201.8 ± 6.73	0.379 ± 0.047	-0.28 ± 0.43	8.6	120
Body size	Alberta	204 ± 4.6	0.275 ± 0.079	-2.68 ± 1.51	7.2	94
	Sweden	197 ± 2.4	0.491 ± 0.077	-0.38 ± 0.46	4.3	120

Table 3. Akaike Information Criterion (AIC)-based rank of the 5 best generalized linear mixed models explaining body mass and size of female and brown bears in Alberta/Canada and Sweden. The response variables were body mass (kg) and body size (contour length in cm). The predictor variables available were study area (SA; Alberta and Sweden), population density (PD), the normalized difference vegetation index (NDVI), age (A; log-transformed), Julian day of capture (JDC), and for females presence/absence of offspring (DO). N is the sample size, number of groups is the number of individual identities included as a random effect, *w* is the AIC-weight, *K* is the number of estimable parameters in a model, and R^2 ss the amount of variation explained by all models with a ΔAIC≤2.

Model		AIC	*Δ*AIC	*w*	*K*	R^2
Female Mass (N = 449, number of groups = 175)						
1	A+NDVI+SA+PD+DO+SA*NDVI+SA*PD+DO*NDVI+ DO*SA	3517.947	0.000	0.588	9	0.73
2	A+NDVI+SA+PD+DO+SA*NDVI+SA*PD+DO*NDVI+ DO*SA+PD*NDVI	3519.889	1.942	0.223	10	0.73
3	A+NDVI+SA+PD+DO+SA*NDVI+SA*PD+DO*NDVI	3522.251	4.304	0.068	8	
4	A+NDVI+SA+PD+DO+SA*NDVI+SA*PD+DO*NDVI+ DO*SA+DO*PD	3522.794	4.847	0.052	10	
5	A+NDVI+SA+PD+DO+SA*NDVI+SA*PD+DO*NDVI+ DO*SA+JDC	3523.826	5.879	0.031	10	
Female Size (N = 439, number of groups = 174)						
1	A+NDVI+SA+DO+SA*NDVI+DO*NDVI+DO*SA	3261.792	0.000	0.644	7	0.58
2	A+NDVI+SA+PD+DO+SA*NDVI+DO*NDVI+DO*SA	3263.943	2.151	0.220	8	
3	A+NDVI+SA+DO+SA*NDVI+DO*SA	3265.752	3.960	0.089	6	
4	A+NDVI+SA+DO+SA*NDVI+DO*NDVI	3268.568	6.776	0.022	6	
5	A+NDVI+SA+DO+JDC+SA*NDVI+DO*NDVI+DO*SA	3268.640	6.848	0.021	8	

Male Mass (N = 317, number of groups = 155)						
1	A+NDVI+SA+SA*NDVI	2955.241	0.000	0.663	4	0.86
2	A+NDVI+SA+PD+SA*NDVI	2958.781	3.540	0.113	5	
3	A+NDVI+SA+PD+SA*NDVI+PD*NDVI	2958.862	3.621	0.108	6	
4	A+NDVI+SA+JDC+SA*NDVI	2960.163	4.922	0.057	5	
5	A+NDVI+SA+PD+SA*NDVI+SA*PD+PD*NDVI	2961.184	5.943	0.034	7	
Male Size (N = 318, number of groups = 157)						
1	A+NDVI+SA+SA*NDVI	2484.931	0.000	0.806	4	0.77
2	A+NDVI+SA+PD +SA*NDVI	2489.230	4.299	0.094	5	
3	A+NDVI+SA+JDC+SA*NDVI	2490.817	5.886	0.043	5	
4	A+NDVI+SA+PD+SA*NDVI+PD*NDVI	2491.186	6.255	0.035	6	
5	A+NDVI+SA+PD+SA*NDVI+SA*PD	2494.122	9.191	0.008	6	

Chapter 2.

Advancements in the development of hair cortisol concentration as an indicator of long-term stress in brown bears

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EXECUTIVE SUMMARY

Measurement of the concentration of cortisol in hair has recently emerged as a promising indicator of long-term stress across a suite of mammals that includes humans, domestic and laboratory animals, and captive and free-ranging wildlife. Despite a spate of publications on the application of HCC, few report on its validation which includes the identification of variables that could compromise its soundness as an indicator of long-term stress. In this study, we extend previous developmental research to investigate what factors influence HCC at the level of individual brown bears[1] (*Ursus arctos*), with the aim of eventually employing HCC at the population level as a wildlife conservation tool. We compared HCC values from 785 brown bear hair samples collected by various methods (hair snag, live-capture, hunter-kill) over 16 years and representing four geographic areas (Alberta, Sweden, Nunavut, and Mongolia) across the species' Holarctic distribution, and found a four-fold difference between the highest (Alberta live-capture: 2.90 pg/mg) and lowest median HCC (Mongolia hair snag: 0.77 pg/mg). HCC was influenced by sex and age, as well as physical attributes (body mass and body length), but not in a consistent manner across populations. Through a detailed analysis of data from live-captured bears in Alberta, we also identified body condition, season of hair collection, and several capture-related factors that influence HCC, including the presence of radio-telemetry devices (radio-collars and/or radio ear-tags. In general, we found no evidence to discount HCC as a reliable indicator of long-term stress in individual bears, and suggest the next step is to widen the application of HCC to ascertain its effectiveness at the population level. We provide two examples of how this might be done using HCC values from five bear management units in Alberta. The first applied HCC as a direct measure of long-term stress and underscores the need to confirm associations between HCC and fitness parameters to firmly establish the value of HCC for monitoring of long-term stress in populations. The second applies HCC as an indirect marker of body condition status to show there may be some value in using HCC to monitor body condition trends, especially in food-limited environments.

INTRODUCTION

Long-term stress is increasingly recognized as a primary determinant of the health of individual animals. This trend is evident across several fields of knowledge, including human medicine (Juster *et al*. 2010, Kudielka and Wüst 2010), animal science (Korte *et al*. 2009, Riondato *et al*. 2008), laboratory animal medicine (Konkle *et al*. 2010, Laber *et al*. 2008), veterinary medicine (Accorsi *et al*. 2008, Smith *et al*. 2010), and wildlife conservation (Busch and Hayward 2009, Johnstone *et al*. 2012). Whereas the physiological stress response when elicited over seconds or minutes is generally beneficial to an individual, this same response when sustained or repeated

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[1] Brown bear and grizzly bear refer to the same species, *Ursus arctos*, with "brown bear" being the more general term applied to the species across its Holarctic distribution. To avoid confusion within this report, we use brown bear in reference to all populations.

frequently over days or weeks becomes detrimental to health and fitness (Romero 2004, Wingfield *et al*. 1998). A prolonged state of elevated stress, widely accepted as a measurable increase in hypothalamus-pituitary-adrenal (HPA-) axis activation, can suppress immune function, growth, tissue maintenance, and reproduction; promote protein loss, deposition of fat, and hypertension; disrupt second messenger systems and signal transduction cascades; and initiate neuronal cell death (reviews in Busch and Hayward 2009, McEwen 2008).

Populations rather than individuals provide the context for interest in long-term stress in the field of wildlife conservation (Busch and Hayward 2009, Ellis *et al*. 2012). For example, how does stress influence population regulation and spatial patterns of animal distribution, particularly in the face of anthropogenic environmental degradation and habitat fragmentation? Can monitoring population stress provide early warning capability and opportunity to mitigate stressors before negative consequences begin to manifest? However, despite these significant questions, the importance of understanding how stress also operates at the individual level cannot be understated. The impact of stressors is manifest on individuals at a physiological level before negative consequences are expressed and observed at a population level (Ellis *et al*. 2012). If long-term stress is localized and affecting few animals or wide-spread and affecting many, if it is sex- or age-biased, or if it affects reproduction and/or survival, will all influence if and how it manifests at the population level. Furthermore, the likelihood of detecting long-term stress is much greater at the level of individuals than populations. So, increased attention toward sampling or measuring of stress in individual animals has potential to provide early warning of population-level effects and opportunity to take preventative action.

Although quantifiable, physiological measurements to estimate HPA-axis activation in vertebrates are numerous, many are sensitive to short-term (acute) stress or both short- and long-term (chronic) stress (Johnstone *et al*. 2012). Few if any are sensitive only to long-term stress, but a measure that has emerged as a promising long-term stress index is the glucocorticoid concentration of keratinous tissue, such as hair (fur) and feathers (Bortolotti *et al*. 2008, Gow *et al*. 2010, Sheriff *et al*. 2011). In contrast to other biological media (blood, saliva, urine, feces), keratinous tissues are relatively stable media known to incorporate blood-borne hormones and xenobiotics during periods of growth (Bortolotti *et al*. 2010, Pragst and Balikova 2006). The quantification of cortisol in hair (or corticosterone in feathers) represents an integration of HPA activity over a period of weeks to months (Bortolotti *et al*. 2008, Davenport et al. 2006, Russell *et al*. 2012), thus making it a particularly appropriate measurement for evaluating long-term stress in wildlife populations (Koren *et al*. 2002, Macbeth *et al*. 2010, Sheriff *et al*. 2011). Further, hair can be collected non-intrusively without capture or restraint (Macbeth *et al*. 2010), it can be transported and stored at ambient temperature, and under optimal conditions, cortisol and other molecules incorporated into hair may remain detectable for years to centuries (Kintz 2004, Webb 2010).

We recently adapted a technique for the measurement of cortisol in rhesus macaque (*Macaca mulatta*) hair (Davenport *et al*. 2006) and refined it for application to brown bear (*Ursus arctos*) hair (Macbeth *et al*. 2010). Beyond working out the procedures for hair preparation and cortisol analysis, and the accuracy and precision of the measurement, Macbeth *et al*. (2010) also sought to determine how a range of factors, including hair colour, exposure to inclement weather for 18 days, and laboratory storage for more than one year affect the hair cortisol concentration. The intent behind this work was to establish the robustness of the measurement and, by extension, build its utility as a wildlife conservation tool.

In this report, we build on the foundation study of Macbeth *et al*. (2010) to investigate what factors influence the hair cortisol concentration (HCC) at the level of individual bears, again with the intent of developing HCC as a wildlife conservation tool. Our approach is both opportunistic and stepwise. It is opportunistic in the sense that we make use of HCC data collected by several different projects, all focused on brown bears but involving different populations, different research objectives, and different methods of hair collection. It is stepwise in the sense that we start with a broad comparison of HCC levels across projects and then ask whether differences between projects correctly reflect differences in long-term stress or are there confounding factors at play. Controlling for appropriate covariates, such as sex, life-history stage, and season is essential to the interpretation of HCC data (Busch *et al*. 2009). What follows is essentially a series of questions with each subsequent step in our analysis determined by the outcome of the previous step. In the end, we demonstrate two ways in which HCC can be applied as a monitoring tool for populations.

MATERIALS AND METHODS

Sources of brown bear hair

We obtained 785 brown bear hair samples from six different projects representing four geographic areas across the species' Holarctic distribution (Table 1). Although hair collection methods varied by project, hair samples were handled similarly in that they were air-dried and stored in a paper envelope under low light at room temperature (~20°C) until the time of laboratory analysis. Details of each project follow with the circumstances around hair collection and availability of supplementary data summarized in Table 1.

1. *Alberta Grizzly Bear DNA Inventory for Population and Density Estimates (Alberta, 2004-2008):* As part of grizzly bear management and recovery in Alberta (Canada), the provincial government conducted DNA inventories from 2004-2008 to estimate population size and density for five bear management units (Alberta SRD 2010). The total area covered approximately 132,000 km^2, mostly in and adjacent to the eastern slopes of the Rocky Mountains, from northern Montana (49°N, 113°W) to the city of Grande Prairie (55°N, 118°W). Hair was collected by barbwire snag during June and July of each year with study

design details provided in a series of technical reports (Boulanger *et al*. 2005a, 2005b, 2007, 2008). Absolute locations were determined for all samples by Global Positioning System (GPS) receiver and suitable samples were genotyped to confirm species, sex, and individual identity (Paetkau 2003).

2. *Eastern Slopes Grizzly Bear Project (Alberta, 1994-2002):* The Eastern Slopes Grizzly Bear Project was conducted over a 9-year period with the goal of contributing toward a scientific understanding of grizzly bear biology, ecology, and demography in an area of west-central Alberta and east-central British Columbia known as the Central Canadian Rocky Mountain Ecosystem (50-52°N, 114-117°W) (Herrero 2005). Hair samples were collected from live-captured bears with details on capture and handling procedures provided in Garshelis *et al*. (2005). In addition to hair samples, we also were provided with supplementary data that included the identification, sex, age, location, body mass, morphometric measurements, and capture history for each bear sampled.
3. *Foothills Research Institute Grizzly Bear Program (Alberta, 1999-present):* The Foothills Research Institute Grizzly Bear Program, now in its 13th year, was initiated in 1999 to provide knowledge and planning tools to land and resource managers to ensure the long-term conservation of grizzly bears in Alberta (Stenhouse and Graham 2011). The study area encompasses the entire distributional range of grizzly bears within the province (49-58°N, 113-120°W) with yearly research effort typically targeted toward one or two bear management units. Hair samples were collected from live-captured bears with details on capture and handling procedures provided in Cattet *et al*. (2008). In addition to hair samples, we also have an extensive sum of data for each bear that includes its identification, sex, age, location, body mass, morphometric measurements, and capture history.
4. *Scandinavia Brown Bear Research Project (Sweden, 1984-present):* The Scandinavian Brown Bear Research Project (SBBRP) was initiated in 1984 with the primary goals to (i) document the basic ecology of the Scandinavian brown bear, (ii) provide management authorities with data and interpretations of the results to help meet bear management objectives, and (iii) provide information about brown bears to the general public. The Swedish study area (Zedrosser *et al*. 2006) covers approximately 21,000 km^2 of intensively managed boreal forest in a rolling landscape in south-central Sweden (61°N, 14°E), and mountainous national parks and adjacent forested land in the north (67°N, 18°E). Under SBBRP coordination, hair samples were collected by hunters from harvested brown bears in Sweden from August to October, 2008. By law, successful brown bear hunters are required to present bear carcasses to an officially appointed inspector on the day of the harvest and to provide information about harvest methods, sex of harvested bears, body mass, and harvest location to the Swedish Hunters Association and the National Veterinary Institute of Sweden (Bischoff *et al*. 2008). The information and samples are archived by the National Veterinary Institute of Sweden.
5. *Western Kitikmeot Grizzly Bear Project (Nunavut, 2004-present):* The major goal of the Western Kitikmeot Grizzly Bear Project is to assess the status of grizzly bear populations in

the Western Kitikmeot region of Nunavut (Canada) using genetic information extracted from hair trapped by barbwire snag on an annual basis since 2005 (Dumond *et al*. 2011). The study area covers approximately 40,000 km^2 in western Nunavut (66.7-69.0°N, 112.7-113.5°W). We received hair samples collected from May to August 2008, as well as absolute locations and confirmation of species, sex, and individual identity for each sample (Paetkau 2003).

6. *Mongolian Gobi Bear Research Project (Mongolia, 2006-present):* The primary objectives of the Mongolian Gobi Bear Research Project are to: (i) determine population size and assess potential limiting factors, (ii) determine habitat use and movement patterns between and within the three oasis complexes, (iii) determine genetic status, (iv) train and enhance capacity of Mongolian bear specialists in techniques for bear capture, handling, and data analysis, and (v) provide training on data collection and monitoring for rangers of the Great Gobi Strictly Protected Area (Tumendemberel *et al*. 2011). The study area is the Great Gobi Strictly Protected Area of southwestern Mongolia (42-44°N, 95-98°E). A DNA-based population inventory was conducted in 2008 and 2009 to estimate the population, ascertain sex ratio, document inter-oases movements of individual bears, and explore genetic variability of Gobi bears (Proctor *et al*. 2010). We received hair samples trapped by barbwire snag during this effort, as well as absolute locations and confirmation of species, sex, and individual identity for each sample (Paetkau 2003).

Table 1. Source, sampling situation, and supplementary data for brown bear hair samples provided to this study for the determination of hair cortisol concentration as a marker of long-term stress.

Source	Year(s)	Sample (*N*)	Sampling situation	Supplementary data
Alberta	2004-2008	350	barbwire snag	Individual identification, sex, location
Alberta	1994-2010	192	live-capture	Individual identification, sex, age, location, body mass, morphometric measurements, capture history
Sweden	2008	149	hunter-kill	Individual identification, sex, age, location, body mass, morphometric measurements
Nunavut	2008	84	barbwire snag	Individual identification, sex, location
Mongolia	2008-2009	10	barbwire snag	Individual identification, sex, location

Laboratory analysis of hair cortisol concentration

We used only guard hairs for the determination of hair cortisol concentration as recommended by Macbeth *et al*. (2010). Surface contamination was removed by washing hairs with methanol as described in detail elsewhere (Macbeth *et al*. 2010). Following decontamination, hair was dried and then ground to a fine powder using a ball mill. Ground hair samples were immersed in 0.5 ml of high resolution gas chromatography grade methanol, gently swirled (10 s), and placed on a slowly-spinning rotator to extract for 24 hours. The hair extract was dried under nitrogen gas (38°C), concentrated, reconstituted in phosphate buffer (0.2 ml), and analyzed on a commercially available enzyme linked immunoassay kit (Oxford EA-65 Cortisol EIA kit, Oxford Biomedical, Lansing, MI, USA). Any remaining guard hairs, as well as undercoat hair, was stored at room temperature in the dark and surplus reconstituted hair extract was stored at -80°C.

Statistical analysis

We analyzed data using IBM-SPSS version 19.0.0 (IBM Corporation, Armonk, New York, United States) with the significance level (α) set at ≥ 0.95 and power ($1 - \beta$) set at ≥ 0.80 for statistical tests. Before performing tests though, all variables were assessed for normality and the need to remove influential outliers and/or apply natural log-transformations. Consequently, sample size varied to some degree between tests.

To compare mean hair cortisol concentration between sources, we performed a univariate analysis of variance (ANOVA) with source as the factor, including the separation of Alberta bears into two sources based on the circumstances around hair collection, live-capture or barbwire snag. For any bears sampled more than once within the same cycle of hair growth (August to May), we used only the HCC value recorded for the first sampling. HCC values for bears sampled more than once, but in different years (different hair cycles), were treated as individual observations. We used Tukey's b-test for a *post-hoc* comparison of means. Mongolia data was excluded from this and subsequent analyses due to small sample size (n = 10).

We also calculated median values for the HCC given that its distribution is likely to always be positively skewed (skewed to the right) with the minimum possible value set at 0.16 pg/mg cortisol, which is half the limit of detection of the assay (Macbeth *et al*. 2010). Median values were compared between sources using an independent samples median test with identification of homogeneous subsets based on all pair-wise comparisons.

We compared mean and median HCC values between female and male brown bears from each source (except Mongolia) using a *t*-test for comparison of means and an independent samples median test, respectively.

The availability of supplementary data for live-captured bears from Alberta and hunter-killed bears from Sweden allowed us to compare between sources the influence of a common set of potential predictor variables (sex, age, body mass, chest girth, and contour length) on the HCC. For this, we used generalized linear models in SPSS with the Wald χ^2-statistic to describe model effects and the adjusted-R^2 (also called pseudo-R^2) value to quantify the proportion of variation in HCC explained by the complete model. We also repeated the same procedures for live-captured bears from Alberta, but expanded the range of potential predictor variables to include:

(i) Body condition status – categorized as 'normal' or 'poor'
(ii) Season of capture – categorized as 'hypophagia' (den emergence to June 14), 'early hyperphagia' (June 15 to August 7), or 'late hyperhagia' (August 8 to den entry)
(iii) Capture method – categorized as 'by culvert trap' or 'by other methods', i.e., by leg-hold snare or by remote drug delivery from helicopter
(iv) Radio-telemetry – categorized as 'not wearing a radio-collar and/or radio-ear tag prior to capture' or 'wearing a radio-collar and/or radio-ear tag prior to capture'
(v) Capture number – number of times captured previously + 1

The categorization of body condition was based on the body condition index (BCI) value for each bear as described by Cattet *et al*. (2002). We assigned bears as 'normal' or 'poor' by using the 25th percentile BCI value by sex and capture season as the cut-off value. Female brown bears (n = 162) in poor condition had BCI values of ≤ -0.66 during hypophagia, ≤ +0.02 during early hyperphagia, and ≤ +1.28 during late hyperphagia. Male brown bears (n = 147) in poor condition had BCI values of ≤ +0.04 during hypophagia, ≤ -0.26 during early hyperphagia, and ≤ +0.93 during late hyperphagia.

We also performed several smaller analyses that were directed at three specific questions arising from the analyses described above. First, to determine if physical injury was greater than expected in bears wearing radio-telemetry devices (radio-collar and/or radio-ear tag), we used a Pearson χ^2-test to compare the frequency of physical injury observed for bears wearing radio-telemetry devices versus that for bears without these devices.

Second, to determine if there was any evidence to show that sudden death can cause an immediate rise in HCC (acute effect), we compared mean and median HCC values using a t-test for two independent samples and an independent samples median test, respectively, between a select group of "normal-health" Alberta live-capture bears and twelve Alberta bears that had died suddenly as a consequence of research (n = 4), management (n = 6), or hit-by-vehicle (n = 2). The normal-health group comprised twenty bears that met the following criteria: (i) HCC values were measured, (ii) no physical injuries were recorded, (iii) no complete blood count abnormalities were identified, (iv) no serum biochemistry abnormalities were identified, (v) and the bear had not been captured previously.

Third, to determine if capture effects alone could explain differences in median HCC values between bears that were sampled following live-capture and bears that were sampled by barbwire snag, we divided bears from Alberta that were sampled by barbwire snag into three groups as follows: (i) bears that had never been captured (*n* = 299), (ii) bears that were captured previously, but during a different cycle of hair growth (*n* = 41), and (iii) bears that were captured previously, but during the same cycle of hair growth (*n* = 10). We then compared the three groups using an independent samples median test followed by pair-wise comparisons for homogeneous subsets.

The final facet of our analysis was focused on determining ways in which the HCC could be applied as a conservation tool to monitor long-term stress at the population level. For this analysis, we used the HCC values for bears from Alberta that were sampled by barbwire snag across five bear management units (*n* = 350; Fig. 1). In the first approach, we considered using the HCC as a direct measure of long-term stress, calculated median HCC values for each bear management area (population), and then compared between populations using an independent samples median test followed by pair-wise comparisons for homogeneous subsets.

In the second approach, we considered using the HCC as an indirect measure of body condition. For this, we selected a subset of Alberta live-captured bears that had not been captured previously and were not captured by culvert trap when sampled (*n* = 76). We divided these bears into two groups, bears with poor body condition status (*n* = 24) and bears with normal body condition status (*n* = 52) with the categorization of ‘normal’ and ‘poor’ as described above. We then overlapped the distributions of HCC values for the two groups and selected a threshold HCC value that would provide high sensitivity (≥ 90%) that the observed HCC ≥ the threshold HCC if a bear is in poor body condition. We gave less attention to specificity as a test performance measure on the assumption that, from a conservation recovery standpoint, it would be more important to correctly identify bears in poor body condition than to correctly identify bears in normal body condition. Following this, we used the threshold HCC to estimate the proportion of bears sampled by barbwire snag that were in normal versus poor body condition within each of the five bear management units. Finally, we performed a nonparametric multiple comparison of proportions to see if we could detect population-level differences in body condition.

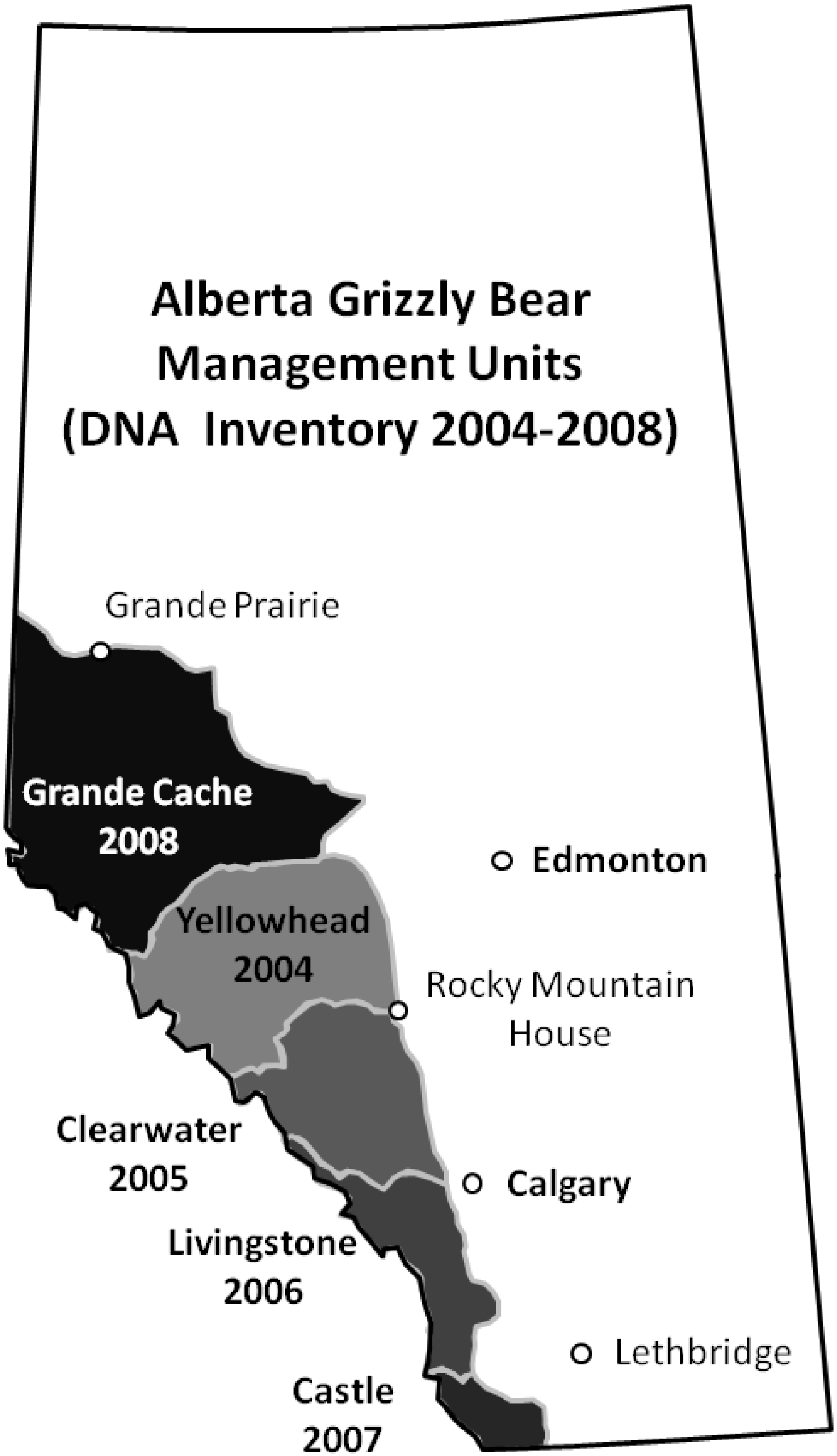

Figure 1. Alberta grizzly bear management areas sampled by barbwire hair snag from 2004-2008 for DNA inventories to estimate population size and density.

RESULTS

We found significant differences (univariate ANOVA – $F = 140.9$, $p \leq 0.001$) in mean hair cortisol concentrations (HCC) between sources (Fig. 2a). However, for some pair-wise comparisons, it appears that these differences may have been attributable to differences in the situation of hair collection rather than the source of hair. For example, the mean HCC for Alberta bears sampled during live-capture (mean ± SE: 4.74 ± 0.248 pg/mg) was almost four-fold greater than that for Alberta bears sampled by barbwire hair snag (1.25 ± 0.199 pg/mg). For other comparisons, the situation of hair collection was similar suggesting that differences in mean HCC related more to the source of hair. For example, the mean HCC for Nunavut bears (3.71 ± 0.375 pg/mg) sampled by barbwire snag was three-fold greater than that for Alberta bears sampled in the same manner. The mean HCC for Sweden bears (2.16 ± 0.116 pg/mg) was intermediate to other sources, but the situation of hair collection also was unique for this source. The mean HCC for Mongolia was the lowest (0.93±0.20 pg/mg) among sources, but the sample size for this source was quite small (*n*= 10).

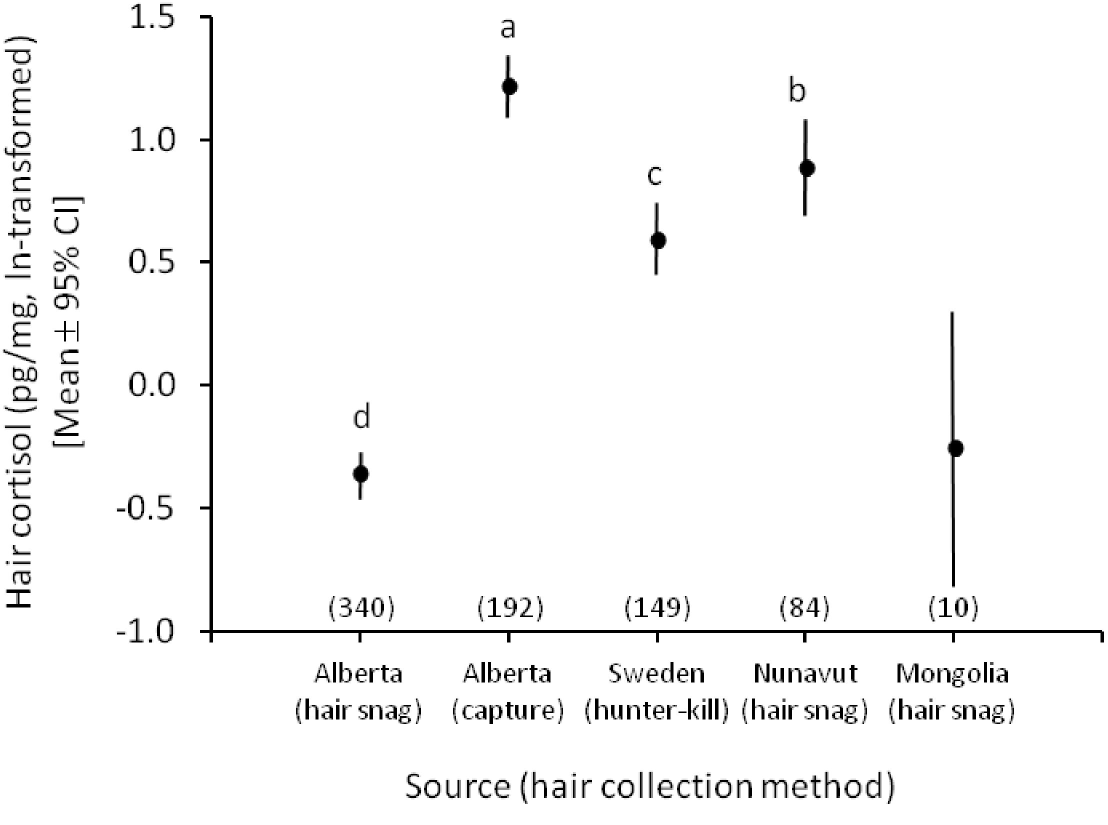

Figure 2a. Comparison of mean hair cortisol concentration between different sources of brown bear hair and different methods of hair collection. Sample sizes are provided in parentheses

along the abscissa. Letters 'a'-'d' are used to indicate significant differences ($p \leq 0.05$) between means where a > b > c > d based on Tukey's b-test for a *post-hoc* comparison of means.

Although the median HCC was less than the mean for each source (Alberta-hair snag: 0.86 pg/mg, Alberta-live capture: 2.90 pg/mg, Sweden: 1.97 pg/mg, Nunavut: 2.23 pg/mg, Mongolia: 0.77 pg/mg), the pattern of differences between sources and/or situations of hair collection was essentially the same (Fig. 2b; independent samples median test – $\chi^2 = 124.1$, $p \leq 0.001$). Mean and median HCC were similar between female and male brown bears within each source except Nunavut (Tables 2a and b) where values for males were approximately 50% greater than values for females.

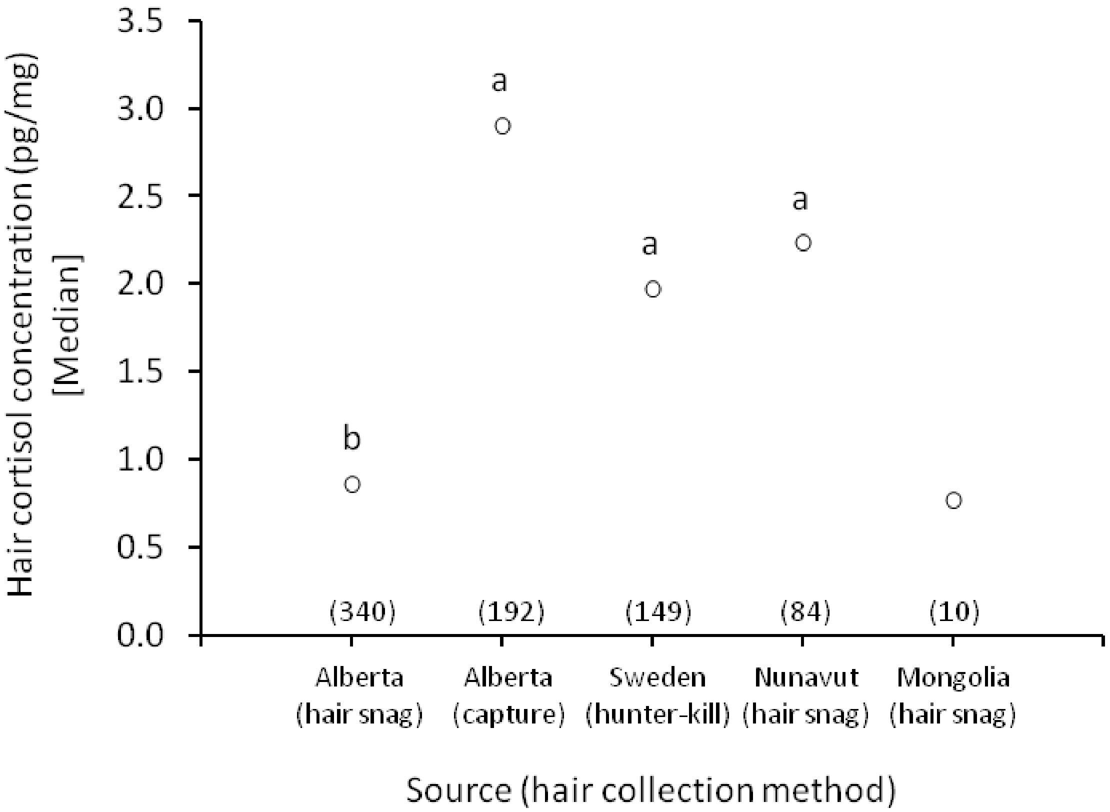

Figure 2b. Comparison of median hair cortisol concentration between different sources of brown bear hair and different methods of hair collection. Sample sizes are provided in parentheses along the abscissa. Letters 'a' and 'b' are used to indicate significant differences ($p \leq 0.05$) between medians where a > b based on all pair-wise comparisons.

Table 2a. Comparison of mean hair cortisol concentrations between female and male brown bears from several sources.

Source	Hair cortisol concentration (pg/mg) Females [mean ± SE, *N*]	 Males [mean ± SE, *N*]	Statistical significance[A]
Alberta (hair snag)	1.27±0.133 184	1.18±0.138 156	0.430
Alberta (live-capture)	5.10±0.668 91	4.42±0.437 101	0.845
Sweden	2.20±0.158 60	2.13±0.163 89	0.629
Nunavut	2.90±0.430 48	4.78±0.969 36	0.020
Mongolia	0.73 1	0.96±0.217 9	na

[A] Statistical significance ($p \leq 0.05$) based on *t*-test for comparison of means using ln-transformed data. 'na' indicates not applicable due to small sample size.

Table 2b. Comparison of median hair cortisol concentrations between female and male brown bears from several sources.

Source	Hair cortisol concentration (pg/mg) Females [median, *N*]	 Males [median, *N*]	Statistical significance[A]
Alberta (hair snag)	0.87 184	0.81 156	0.650
Alberta (live-capture)	2.89 91	3.00 101	0.885
Sweden	2.07 60	1.96 89	0.462
Nunavut	1.97 48	2.94 36	0.008
Mongolia	0.73 1	0.81 9	na

[A] Statistical significance ($p \leq 0.05$) based on independent samples median test. 'na' indicates not applicable due to small sample size.

The availability of supplementary data from live-captured bears in Alberta and hunter-killed bears in Sweden (Table 1), and the fact that the same types of measurements were recorded at both sources, allowed us to begin exploring what factors influence HCC and if these factors are similar between sources. Using the same combination of biological and physical attributes, we identified some differences between sources in explanatory variables (Table 3). For example, HCC increased with age in Sweden bears but showed no association with age in Alberta bears. HCC did increase with body (contour) length in Alberta bears, but the overall model for Alberta lacked in explanatory power accounting for only 4% of the variation in HCC. In contrast, the Sweden model which was composed of the same explanatory variables accounted for approximately 28% of the variation in HCC. Also notable with the Sweden model was that a weak but statistically significant difference between female and male bears was uncovered when controlling for age and physical attributes.

Table 3. Model coefficients describing variation in the hair cortisol concentrations of brown bears sampled in Sweden and Alberta based on analyses using the same potential explanatory variables.

	Alberta (N = 93, adjusted R^2 = 0.04)			Sweden (N = 101, adjusted R^2 = 0.28)		
Variable	*b*	SE	*p*	*b*	SE	*p*
Sex:						
female	-0.095	0.183	0.604	-0.237	0.115	0.039
male	0	(reference category)		0	(reference category)	
Age	-0.040	0.062	0.518	0.139	0.041	<0.001
Age^2	0.003	0.002	0.269	-0.004	0.002	0.023
Mass	-0.965	0.452	0.033	0.269	0.337	0.424
Chest girth	0.337	0.627	0.591	-1.557	0.609	0.010
Contour length	4.328	1.298	<0.001	-1.754	0.978	0.073
Constant	-17.978	5.658	<0.001	14.907	3.448	<0.001

To further evaluate the HCC of live-captured bears from Alberta, we expanded the suite of potential explanatory variables to include body condition, season of capture, and several capture-related variables (Table 4). Bears in normal body condition tended to have a lower HCC (adjusted mean ± SE: 4.56 ± 1.160 pg/mg, n = 72) than bears in poor body condition (6.42 ± 0.883 pg/mg, n = 21; Wald χ^2 = 5.11, p = 0.024). This difference also remained consistent over the three capture seasons (Fig. 3a) although HCC tended to be lower during late hyperphagia than during the preceding seasons (Wald $\chi^2 = 6.26$, $p = 0.044$). Bears captured by culvert trap had markedly higher HCC (7.77 ± 1.196 pg/mg, $n = 23$) than measured in bears captured by leg-hold snare or by remote drug delivery from a helicopter (3.21 ± 0.619 pg/mg, $n = 70$; Wald $\chi^2 = 41.52$, $p \leq 0.001$; Fig. 3b). Bears that were captured while wearing a radio-telemetry device (radio-collar and/or radio-ear tag) from a previous capture had higher HCC (6.38 ± 0.730 pg/mg, $n = 32$) than bears without these devices (4.60 ± 1.085 pg/mg, $n = 61$; Wald $\chi^2 = 9.06$, $p = 0.003$; Fig. 3c). The frequency of physical injuries also was higher in bears wearing radio-telemetry devices (43 of 145 [30%] vs. 17 of 159 [11%]) (Pearson $\chi^2 = 17.22$, $p \leq 0.001$). Although injuries were not recorded in any standardized manner, a review of our field records indicated that injuries to bears wearing radio-telemetry devices were associated with ear-tags (both radio and non-radio types) in 19 cases, radio-collars in 14 cases, previous snare-induced injuries in 5 cases, and injuries of unknown cause in 5 cases. Injuries to bears not wearing radio-telemetry devices were associated with ear-tags in 5 cases and unknown cause in 12 cases. The number of times that a bear was captured was inversely associated with the HCC (Wald $\chi^2 = 13.39$, $p \leq 0.001$). This expanded model for Alberta bears accounted for approximately 34% of the variation in HCC, a marked improvement over the model presented in Table 3.

We were able to consider the question of whether or not sudden death can cause an immediate, significant increase in HCC (acute effect) by comparing HCC between twenty “normal-health” Alberta live-capture bears and twelve Alberta bears that died suddenly. We found no significant differences in mean HCC between the two groups (normal-health: 4.38 ± 0.901 pg/mg, sudden death: 3.49 ± 0.863 pg/mg; $t = 0.429$, $p = 0.671$]. A comparison between median HCC yielded similar results (normal-health: 2.62 pg/mg, sudden-death: 2.53 pg/mg; independent samples median test – $p = 1.000$). These findings do not give credence to the possibility that the higher HCC in Sweden bears relative to Alberta hair-snag bears and Mongolia bears could be explained by the fact that hair samples were collected from hunter-killed bears in Sweden.

To determine if long-term capture effects on HCC were significant enough to account for the difference in HCC between Alberta bears sampled during live-capture and Alberta bears sampled by hair snag, we compared HCC between three sub-groups of Alberta bears sampled by hair snag. Bears that were sampled twice within the same hair growth cycle, first by live-capture and then by hair snag, had higher mean HCC (3.78 ± 2.229 pg/mg, $n = 10$) than did Alberta bears sampled first by live-capture and then by hair snag, but in different hair growth cycles (1.05 ± 0.293 pg/mg, $n = 41$), and Alberta bears sampled by hair snag only (1.25 ± 0.101 pg/mg, $n = 299$) (univariate ANOVA – $F = 4.59$, $p = 0.010$, observed power = 0.775). Although the power of this analysis was < 0.80, the outcome was similar when comparing median HCC (same hair cycle: 2.02 pg/mg, $n = 10$; different hair cycle: 0.51 pg/mg, $n = 41$; hair snag only: 0.90 pg/mg, $n = 299$; independent samples Kruskal-Wallis test, $p = 0.010$).

Table 4. Model coefficients describing variation in the hair cortisol concentrations of brown bears sampled in Alberta based on analysis using the full suite of potential explanatory variables.

	Alberta (N = 93, adjusted R^2 = 0.34)		
Variable	*b*	SE	*p*
Sex:			
female	-0.010	0.157	0.950
male	0	(reference category)	
Age	-0.042	0.055	0.444
Age^2	0.003	0.002	0.124
Mass	-0.838	0.368	0.023
Chest girth	0.728	0.360	0.043
Contour length	3.081	1.259	0.014
Body condition status:			
normal	-0.379	0.168	0.024
poor	0	(reference category)	
Season of capture:			
hypophagia (den emergence – Jun 14)	0.562	0.227	0.013
early hyperphagia (Jun 15 – Aug 7)	0.450	0.257	0.080
late hyperphagia (Aug 8 – den entry)	0	(reference category)	
Capture method:			
culvert trap	0.877	0.136	<0.001
leg-hold snare or helicopter capture	0	(reference category)	
Radio-telemetry:			
no radio-collar and/or radio-ear tag	-0.401	0.133	0.003
wearing radio-collar and/or radio-ear tag	0	(reference category)	
Capture number	-0.198	0.054	<0.001
Constant	-17.978	5.658	<0.001

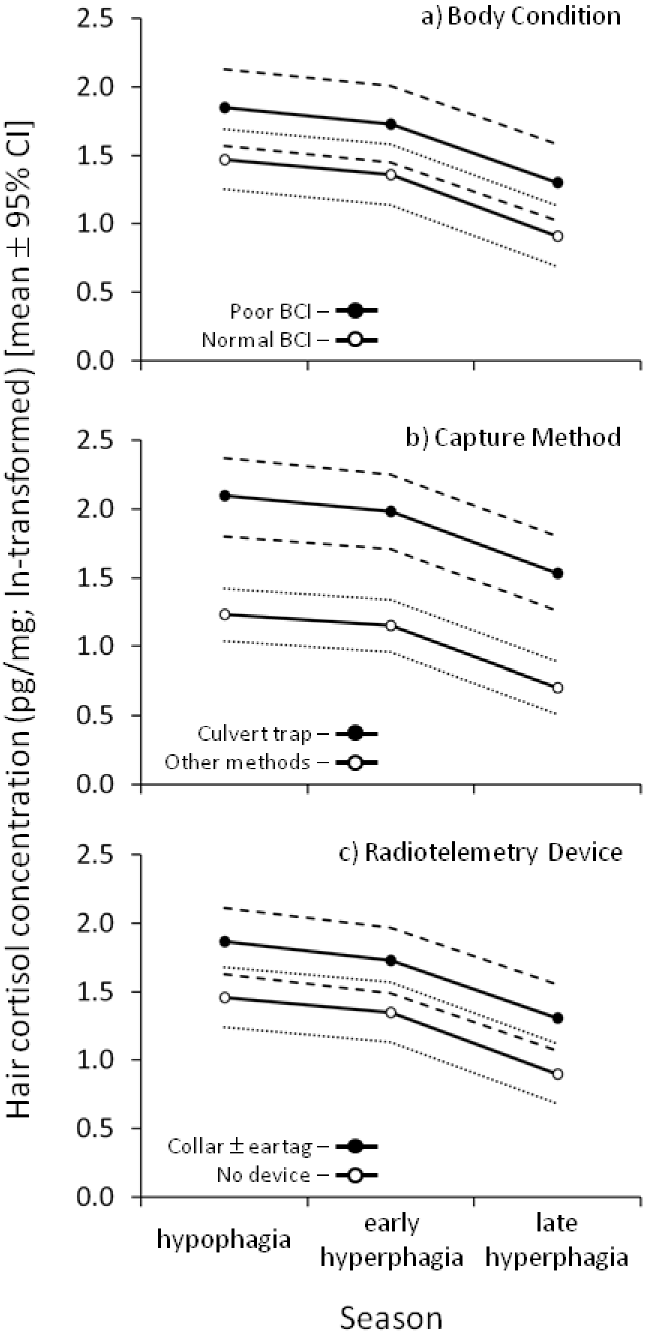

Figure 3. The effects of a) body condition, b) capture method, and c) radiotelemetry device on the predicted hair cortisol concentration for an adult brown bear during different capture seasons. Predicted mean values and 95% confidence intervals (hatched lines) were estimated from the model presented in Table 4 and adjusted for an 8-year old bear.

When applying HCC as a direct measure of long-term stress across five bear management units (BMU) in Alberta (Fig. 1), the highest median HCC occurred in the Livingstone, Castle, and Grande Cache BMUs (Table 5). The lowest median HCC occurred in the Yellowhead BMU, while the median HCC for the Clearwater BMU was intermediate in value (Independent samples median test – $\chi^2 = 23.02$, $p \leq 0.001$; homogeneous subsets 'a', 'ab', and 'b' based on all pair-wise comparisons where a ≥ ab ≥ b and a > b). Although not shown in Table 5, we found similar results when comparing mean HCC between BMUs ([Livingstone – 1.60 ± 0.266 pg/mg, $n = 75$; Castle – 2.04 ± 0.770 pg/mg, $n = 26$; Grande Cache – 1.05 ± 0.067 pg/mg, $n = 144$] ≥ [Clearwater – 1.25 ± 0.227 pg/mg, $n = 43$] ≥ [Yellowhead – 0.75 ± 0.132 pg/mg, $n = 52$]; univariate ANOVA – $F = 4.22$, $p = 0.002$; Tukey's b-test for *post hoc* comparison of means – $p \leq 0.05$).

Table 5. Median hair cortisol concentration (HCC) and predicted body condition status of Alberta grizzly bear management units (BMU) based on the HCC of hair samples collected from 340 grizzly bears during hair-snag genetic inventories conducted in the province from 2004-2008.

BMU (Year)	Median HCC^A (pg/mg) [minimum - maximum]	Predicted Body Condition Status^B (count, percent) Normal (HCC < 2.05 pg/mg)	Poor (HCC ≥ 2.05 pg/mg)
Grande Cache (2008)	0.89^a [0.16 - 4.31]	127 (88.2%)	17 (11.8%)
Yellowhead (2004)	0.35^b [0.16 - 4.85]	47 (90.4%)	5 (9.6%)
Clearwater (2005)	0.86^{ab} [0.16 - 6.57]	34 (79.1%)	9 (20.9%)
Livingstone (2006)	1.07^a [0.16 - 14.94]	60 (80.0%)	15 (20.0%)
Castle (2007)	1.01^a [0.16 - 15.62]	22 (84.6%)	4 (15.4%)

[A] Independent samples median test – $\chi^2 = 23.02$, $p \leq 0.001$; homogeneous subsets 'a', 'ab', and 'b' based on all pair-wise comparisons.

[B] Multiple comparison of proportions by BMU – Pearson $\chi^2 = 5.05$, $p = 0.282$.

To apply HCC as an indirect measure of body condition we calculated sensitivity and specificity values as test performance measures across a range of HCC values from 1.63-10.00 pg/mg (Fig. 4). We obtained a sensitivity of 91.7% (0.917) and a specificity of 44.2% (0.442) when selecting HCC ≥2.05 pg/mg as the threshold value. At this level of performance, 22 of 24 bears in poor body condition were correctly “diagnosed” as poor body condition (i.e., high sensitivity), whereas 29 of 52 bears in normal body condition were incorrectly diagnosed as poor body condition (i.e., low specificity). When we used the threshold HCC to divide Alberta bears sampled by hair snag (*n* = 340) based on estimated body condition status, we did not detect significant differences between BMUs in their proportions of bears in poor body condition (Table 5; multiple comparison of proportions by BMU – Pearson $\chi^2 = 5.05$, $p = 0.282$).

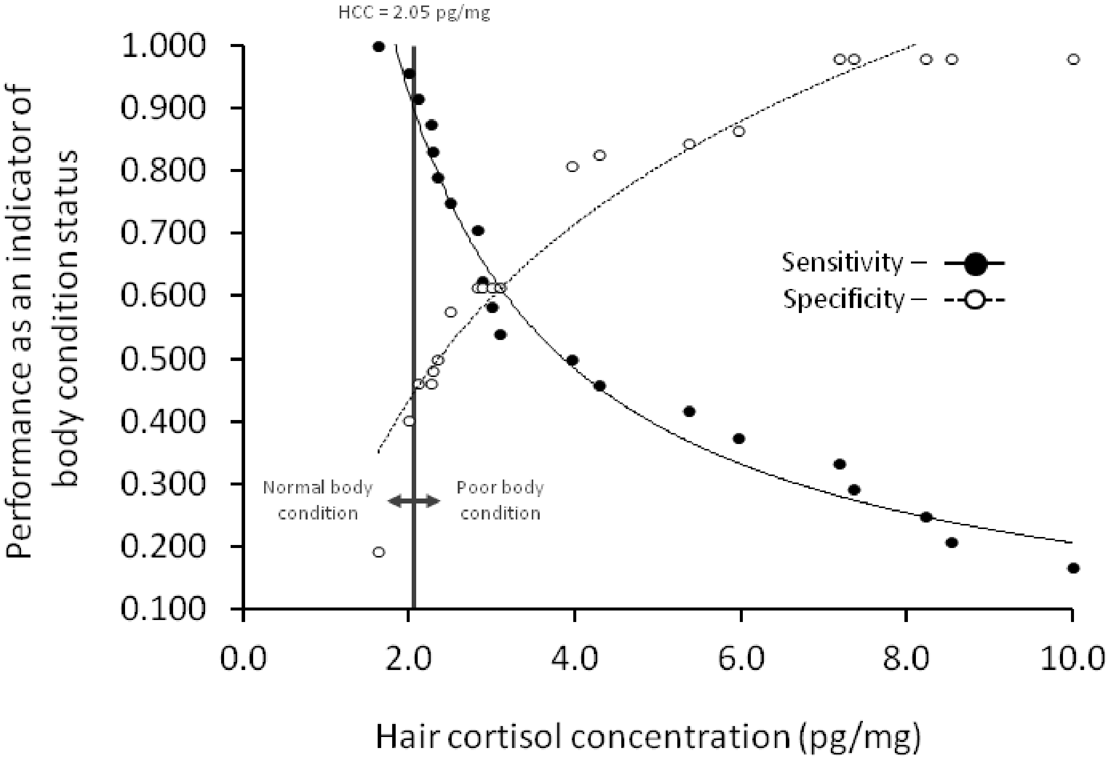

Figure 4. Performance curves for the application of hair cortisol concentration (HCC) as an indicator of body condition status in Alberta brown bears. The selection of an HCC threshold value of 2.05 pg/mg provides high sensitivity (91.7%) to detect bears in poor body condition, but low specificity (44.2%) to detect bears in normal body condition.

DISCUSSION

In this study, we explored what factors influenced hair cortisol concentration (HCC) at the level of individual bears with the intent of ascertaining if HCC is a reliable indicator of long-term stress with potential application as a wildlife conservation tool. HCC differed significantly between brown bears from different areas of their distributional range that included several populations in Canada, Sweden, and Mongolia. By examining HCC in conjunction with supplementary data collected from the same animals, we were able to identify a range of biological, physical, and capture-related attributes that appear to influence HCC over the long-term, i.e., weeks to months. We also were unable to identify any measurable difference in HCC between normal-health bears sampled during live capture and bears that were sampled following sudden death which suggests that death does not cause an immediate (acute) increase in HCC. Taken together, these findings support the measure of HCC as an indicator of long-term stress that is unlikely to be influenced by acute stressors that occur on an infrequent basis. At a population-level, we demonstrated how HCC could be used remotely (e.g., sampling by barbwire hair snag) as a direct measure of long-term stress to compare between populations or monitor populations over time. We also demonstrated how HCC could be used in much the same manner as a medical diagnostic test to remotely detect bears in poor body condition with high sensitivity, but low specificity. These final steps point toward ways in which the HCC could be applied as a wildlife conservation tool.

Life history effects on HCC

The most plausible explanation for the finding that HCC was influenced by gender in Nunavut and to a lesser extent Sweden, and by age in Sweden is that hypothalamus-pituitary-adrenal (HPA-) axis activity can vary by life-history stage in brown bears. The recognition that life-history stages and the activity of the HPA-axis are intimately linked is well established across a wide variety of mammals (reviews in Boonstra 2005, Reeder and Kramer 2005). Typically, females have higher baseline glucocorticoids (with cortisol being the major glucocorticoid in most mammals) and a more robust stress response than males; an observation that has been attributed to the differential effects of sex steroids on females and males (Handa et al. 1994, McCormick *et al*. 2002). However, relative to males and non-pregnant females, stress-induced glucocorticoids are markedly decreased during pregnancy, as well as during lactation, as a consequence of increased protein-binding (mostly corticosteroid-binding globulin) of glucocorticoids (Chow *et al*. 2011, Lightman *et al*. 2001, Stern *et al*. 1973). This likely has the effect of buffering females from elevated glucocorticoids or large fluctuations in glucorticoid levels, both of which can adversely affect developmental processes and the subsequent health and survival of offspring (Wadhwa *et al*. 2001, Weinstock 2005). Because the cortisol extracted from hair is in an active form (free, not protein-bound), the higher HCC detected in male bears from Nunavut and Sweden suggests a few possibilities. One is that males may face more stressful environmental conditions that females. Sexual segregation is known to occur in some brown bear populations (Dahle and Swenson 2003, Rode *et al*. 2006) and, under this condition, so presumably would exposure to environmental stressors. Another possibility is that the proportions of pregnant and/or lactating bears represented in the hair samples received from Nunavut and Sweden were greater than in those received from sources in Alberta. In this case, female bears would be predicted to have lower

HCC on average than males due to increased protein-binding of glucocorticoids. Confirmation of either or both explanations would require additional data lacking from this study.

Superimposed on sex differences in HPA activity, aging is believed to be associated with reduced control of the HPA axis with the nature of this change varying between and within species (Reeder and Kramer 2005). For example, baseline glucocorticoid levels increase with age in rats (Dellu *et al*. 1996), but remain unchanged in aging non-human primates (Goncharova and Lapin 2002). However, one age-related change that appears to be consistent for many mammals is a gradual impairment of the negative feedback system for the HPA axis which results in a slower return to baseline glucocorticoid levels following exposure to a stressor (Sapolsky *et al*. 1983). This may explain the greater HCC that we observed in older brown bears from Sweden. The reason why we didn't also detect an age effect in live-captured bears from Alberta is not certain. The age statistics and ranges were quite similar between sources (mean ± SE, minimum-maximum: Sweden – 6.3 ± 0.54 yrs, 1-25 yrs, $n = 101$; Alberta – 7.5 ± 0.50 yrs, 2-22 yrs, $n = 93$), so it is unlikely that differences in age distribution could provide an explanation. Perhaps any similar age-related increase in the HCC of live-captured bears from Alberta was simply obscured by the apparent greater influence of body length (see Tables 3 and 4). Although the results are not presented in this report, we did find a weakly significant (partial correlation analysis – $p = 0.049$), positive association between age and HCC when controlling for contour length.

Body condition effects on HCC

The finding that HCC was lower in Alberta bears with normal body condition than those with poor body condition is consistent with findings in other studies where associations between body condition and glucocorticoid levels in other biological media, including blood (Romero and Wikelski 2001, Wingfield and Kitaysky 2002) and feces (Cabezas *et al*. 2007, Gladbach *et al*. 2011), have been examined. In some cases, energy deficiency resulting from insufficient food availability and limited physiological energy stores is the primary stressor causing a prolonged stress response and loss of body condition (du Dot *et al*. 2009, Ortiz *et al*. 2001). The association between increasing stress and diminishing body condition is typically tight in this situation. In other cases, adverse environmental conditions aside limited food availability initiate a prolonged stress response which in turn may draw on physiological energy stores to meet the requirements of essential metabolic processes (McNamara and Buchanan 2005). In this situation, the association between stress and body condition may be weak or absent. The association between HCC and body condition (as reflected by the body condition index [BCI]) in Alberta bears was weak (Pearson $r = -0.21$, $p = 0.014$, $n = 137$) which suggests that for many bears it was not primary energy deficiency but other stressors affecting HCC levels.

Although we selected the 25th percentile BCI value by sex and capture season as the threshold between normal and poor body condition status, this decision was somewhat arbitrary in the sense that we do not know at what BCI level is health likely to be compromised. Nonetheless, when we estimate percent body fat (BF) from BCI values using a prediction curve developed by Baldwin and Bender (2010; see Fig. 2 on p. 49), the equivalent BF values for females are 3% during hypophagia (den emergence to June 14), 7% during early hyperphagia (June 15 to August 7), and 21% during late hyperphagia (August 8 to den entry). Recently, Robbins et al. (2012) determined in a study of six captive female brown bears that no female with a BF ≤20% immediately prior to den entry produced cubs even though breeding occurred. This suggests that our selection of the 25th percentile BCI is at least close to the body condition level, especially prior to den entry, where reproduction may be compromised for females. The equivalent BF values for males are 8% during hypophagia, 5% during early hyperphagia, and 17% during late hyperphagia, but we do not know if adverse health consequences are likely to occur at these levels.

Seasonal variation in baseline and stress-induced HPA-axis activity appears to be the norm for many animals (Romero 2002, Vera *et al*. 2011). The pattern that we observed in Alberta brown bears does fit that described for some mammals, as well as reptiles, amphibians, and birds, in which glucocorticoid levels are highest during the breeding season and lower at other times of the year (Romero 2002). The highest HCC were measured during hypophagia and early hyperphagia which also is concurrent with the breeding season for brown bears in Alberta (Stenhouse *et al*. 2005). However, seasonal differences in HCC for Alberta bears also could be explained seasonal differences in body condition. The season of late hyperphagia is when bears are attaining their greatest amount of body fat in preparation for entering winter dens. Given the inverse association between HCC and body condition, HCC should be lowest at this time. Regardless of cause, controlling for seasonal variation should be an important consideration when monitoring HCC in a population over time or comparing HCC among populations.

Capture effects on HCC

The combined effects of capture-related factors accounted for most of the variation in HCC (28 of 34%) explained by the model shown in Table 4, and was enough to explain the difference in mean HCC between Alberta bears sampled following live-capture (4.74 ± 0.248 pg/mg) and Alberta bears sampled by barbwire snag (1.25 ± 0.199 pg/mg). Capture method had the most influence with bears captured by culvert trap having on average an HCC over two-fold higher than HCC values measured in bears captured by leg-hold snare or by remote drug delivery from helicopter. Macbeth *et al*. (2010) previously reported this culvert trap-effect and demonstrated that contamination of hair with urine and feces while a bear is held in a trap can alter the permeability of the hair and through inward diffusion increase the concentration of cortisol within the hair shaft. This, however, may not provide the full explanation because not all bears are exposed to urine and feces in culvert traps and because, in cases where bears have been contaminated, field personnel preferentially seek non-soiled hair to sample (Macbeth *et al*. 2010). Further to this, we have recently found that serum corticosteroid binding globulin (CBG) levels in many of the bears for which HCC was measured were lower in those captured by culvert trap (4.13 ± 0.403 μg/ml) than those captured by other methods (5.85 ± 0.185 μg/ml) (Brian Chow, unpublished results). This finding also could explain a higher HCC in culvert trapped-bears because with lower CBG presumably there would be more circulating free cortisol to diffuse into growing hair. However, CBG levels are believed to be relatively insensitive to short-term stressors associated with capture and handling (Chow et al. 2010, Tinnikov 1999), thus the basis for the association between high HCC and capture by culvert trap remains uncertain.

The presence of a radio-telemetry device, whether it is a radio-collar and/or a radio-ear tag, deployed at a previous capture was associated with a significantly higher HCC (6.38 ± 0.730 pg/mg, *n* = 32) than measured in bears without these devices (4.60 ± 1.085 pg/mg, *n* = 61). While some of this difference may have been attributable to physical injury as a direct result of wearing these devices, e.g., neck lacerations and chronic-active inflammation and infection around the ear tag insertion hole, injuries were not observed in the majority of bears (70%) wearing radio-telemetry devices which suggests that the presence of these devices alone was a significant stressor for some animals. A critical assumption of radio-telemetry studies has long been that the radio-transmitters themselves do not influence an animal's behavior, physiology, or survival (Coté *et al*. 1998, Pollock *et al*. 1989, Barron *et al*. 2010). However, several recent studies have challenged this assumption by documenting negative effects of radio-telemetry or attachment devices in a variety of animals, including reptiles (Knapp and Abarca 2009, Lentini *et al*. 2011), fishes (Jepsen *et al*. 2008, Stakėnas *et al*. 2009), birds (Barron *et al*. 2010, Saraux *et al*. 2011), and both terrestrial and marine mammals (Swenson et al. 1999, Léchenne *et al*. 2011, Walker *et al*. 2011). Although we are not aware of previous reports on the potential for negative effects of radio-telemetry devices on the behavior and physiology of brown bears, or other species of *Ursidae* for that matter, the results from this study show that the increase in HCC associated with wearing these devices was similar to the increase in HCC associated with being in poor body condition. The implications of this finding are potentially far-reaching and suggest the possibility that, in the worse case, research findings and management or policy decisions derived from telemetry-based studies could be unsuspectingly biased. We strongly recommend further study to address several key questions that should include: (1) Do telemetry devices have an overall effect on the fitness (reproduction and survival) of bears? (2) Which features of bear behavior, physiology, and ecology are affected? (3) What characteristics of bears influence radio-transmitter effects? (4) What characteristics of telemetry devices influence their effects? The long-term goal in addressing these questions is to be able to knowledgeably balance the benefits of using radio-telemetry against the potential costs to bears and the reliability of the data obtained (Barron *et al*. 2010).

The number of captures that a bear experienced also influenced the HCC, but in a manner that was contrary to what might be predicted. In general, bears that were captured several times had lower HCC than bears that had not been captured previously. However, the statistical significance of this apparent capture effect appears to have been highly influenced by a single bear that had been captured eight times and had a low HCC (2.10 pg/mg) relative to other live-captured bears in Alberta. When we excluded the data for this individual from the analysis, the association between HCC and number of captures was no longer significant (Pearson $r = 0.03$, $p = 0.736$, $n = 92$). Further, comparing mean HCC between bears captured once (4.23 ± 0.514 pg/mg, $n = 59$) and bears captured 2-5 times (4.56 ± 0.598 pg/mg, $n = 33$) did not yield a significant difference (*t*-test for independent samples – $p = 0.360$). Thus, with this correction, we found no evidence to suggest number of captures influenced HCC.

We found no evidence to indicate the sudden death of a bear could cause an immediate increase in HCC. Although current opinion holds widely that the HCC should not increase measurably following an acute stress response, Sharpley *et al*. reported both diurnal variation in HCC (Sharpley *et al*. 2010) and transient localized changes in HCC in response to local pain (Sharpley *et al*. 2009). They attributed these transitory fluctuations to cortisol production by skin and hair follicles via their own neuroendocrine system known as the “peripheral HPA axis”, a distinct entity from the central HPA axis which involves cortisol production and secretion from the adrenal glands (Arck *et al*. 2006, Ito *et al*. 2005, Paus *et al*. 2006). Cortisol levels in blood often increase rapidly to very high levels during stressful agonal periods immediately prior to death (Erkut *et al*. 2004), but cortisol levels in blood collected following death may be similar to normal values obtained during life (Finlayson 1965, Palmiere and Mangin 2012). However, despite the possibility of agonal changes in blood cortisol or peripheral HPA axis activity in brown bears, we were unable to detect any differences in HCC between twenty “normal-health” Alberta live-capture bears and twelve Alberta bears that died suddenly. Therefore, we have no reason to conclude that the HCC values measured in hunter-killed bears from Sweden were confounded by a fatal gunshot or the preceding hunt.

HCC as a conservation tool

Thus far, we’ve considered factors that influence HCC levels in an individual bear. This knowledge is essential to determining if and how HCC can be applied as a marker of long-term stress in brown bears, or more broadly in wild mammals. Our findings support using HCC in this manner, but also give insight into what other factors must be considered in its application. The next step in widening the application of HCC as a marker of long-term stress is to ascertain its effectiveness at the population level because it is only at this level that its utility as a wildlife conservation tool can be made certain. We suggest two approaches, one that requires more knowledge to be fully effective, and the other that can be used now but has clear limitations.

In order for HCC to serve as a useful tool for conservationists, it should fluctuate with environmental variables and correlate with fitness parameters (Breuner et al. 2008, Busch and Hayward 2009). From concurrent research investigating linkages between HCC and environmental attributes in Alberta brown bears, we do know that the combination of inter-annual variability in local weather and regional climate, and local anthropogenic features, explain approximately 30% of the variation in HCC (Stenhouse *et al*., manuscript in preparation). Presumably, most of this explanatory power is additive to the 34% already explained by the model in Table 4. What we are lacking, however, is information on the association between HCC and the two measures most relevant to fitness, survival and reproductive success. With this information, which is the focus of our current studies, we will be able to use the HCC as a direct measure of long-term stress at the population level. More specifically, we should be able to identify threshold HCC values above which survival is likely to be reduced or reproductive success is likely to be compromised. At this point, however, we're limited to making comparisons among groups of bears (as in Figures 2a and 2b or Table 5), but unable to fully explain the ramifications of significant differences. Although survival and reproductive rates are not available for all bear management units (BMU) in Alberta, it is noteworthy that the median HCC values by BMU shown in Table 5 parallels the density of bears within each BMU adjusted for the area of lands protected from land-use activity. The Yellowhead BMU had the lowest median HCC at 0.35 pg/mg and lowest density at 6 bears per 1000 km^2 of protected land. Conversely, the Livingtone and Castle BMUs had the highest median HCC at 1.07 pg/mg and 1.01 pg.mg, and the highest densities at 32 and 100 bears per 1000 km^2, respectively. For some species, high population densities have been correlated with increased stress levels with this association attributed to increase antagonistic interactions and competition (Raouff *et al*. 2006, Sheriff *et al*. 2012).

Hair cortisol concentration may also be applied at the population level as an indirect marker of poor body condition in much the same way that diagnostic tests are used in the health professions to detect disease, e.g., serum high density lipoprotein (HDL) cholesterol as a marker for coronary heart disease. However, as an indirect marker of body condition, the usefulness of HCC will be determined by its strength of association with body condition. In this study, the association in Alberta grizzly bears was weak. So, we took a conservative approach in selecting a threshold HCC value (≥ 2.05 pg/mg) by ensuring it was highly sensitive (i.e., correctly identify 91.7% of the bears in poor body condition in a population), but not very specific (i.e., correctly identify 44.2% of the bears in normal body condition in a population). In a situation where energy deficiency is a primary stressor, for example in food-limited populations such as the Nunavut brown bears sampled in this study (Gau *et al*. 2002), the association between HCC and body condition should be considerably stronger offering the possibility of establishing a threshold HCC that is both highly sensitive and highly specific.

Conclusions

With this study, we extended the work of Macbeth *et al*. (2010) to determine what factors influence HCC at the level of the individual bear. We found significant differences in HCC levels between brown bears representing different geographic areas across the species' distributional range, as well as between different bear management units within one geographic area. Through a series of analyses using available supplementary data, we determined that HCC can be influenced by sex and age, as well as physical attributes (body mass and body length), but not necessarily in a consistent manner across populations. Through a detailed analysis of brown bears in Alberta, we also identified body condition, season of hair collection, and several capture-related factors that influence HCC. Most troubling in this regard was the finding that the presence of radio-telemetry devices on bears was associated with significantly higher HCC than measured in bears without these devices. Because of the potentially far-reaching implications of this finding, further study is urgently needed to better understand the overall effects of telemetry devices on bears and other wildlife, and to knowledgeably balance the benefits of using radio-telemetry against potential wildlife health and welfare costs and the reliability of the data obtained.

Overall, we found no evidence to discount HCC as a reliable indicator of long-term stress. Thus, we suggest that the differences in HCC levels between brown bears representing different geographic areas as shown in Figures 2a and 2b truly represents differences in long-term stress levels. The differences in mean HCC between Alberta bears sampled following live-capture and Alberta bears sampled by barbwire snag were largely explained by long-term effects of capture and handling. We propose that the high HCC levels in Nunavut bears may reflect long-term nutritional stress in a food-limited environment. Although we lack plausible explanations for the relatively high HCC in Sweden bears and low HCC in Mongolia bears, these findings could certainly serve as a basis for future research hypotheses.

We also believe that the differences in HCC levels between Alberta BMUs reflect real differences in long-term stress, but again a full appreciation of causative factors is lacking. Although differences in population density may play a role, survival and reproductive rates by BMU are what is required to confirm the effectiveness of HCC as a wildlife conservation tool. If associations between HCC and fitness parameters are strong, then HCC should have considerable value for monitoring of long-term stress in populations, particularly in conjunction with genetic sampling using DNA from bear hair collected with barbed wire hair traps. There also may be some value in using HCC to monitor body condition trends, especially in food-limited environments, but further research is required to substantiate this application.

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Chapter 3.

Habitat selection for regenerating clear-cut forests by brown bears: A comparative analysis between Alberta and Sweden

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1. Executive Summary

Brown bears are generalist omnivores that frequently use disturbed habitats – including young regenerating clear-cut forests – to meet their resource (food) demands. Little is known, however, about how specific forest management practices, including silvicultural treatments and harvest design (e.g., size and shape of clear-cuts), effect bear habitat, how this varies among sex and offspring status classes and populations, and how availability of these or alternate habitats affects their habitat use (i.e., functional responses in habitat selection). To address these knowledge gaps, we examined seasonal habitat selection of regenerating clear-cut forests ≤ 60 years of age by brown bears for two long-term studies occurring in different hemispheres (Alberta and Sweden), but within a shared Holarctic boreal forest ecosystem. Using ~1.9 million GPS telemetry locations for 157 individuals across 12 different years (1999-2010 in Alberta; 2005-2010 in Sweden), we developed seasonal (monthly) habitat selection models between May and October for each individual bear and evaluated secondly how selection (response variable) varied among bears (sex-offspring classes), seasons, habitat availability, and study areas using generalized linear models. We found that brown bears selected regenerating clear-cut patches relative to all other habitats available (mostly mature forests) with peak selection occurring most often between 10 to 25 years post-harvest in Alberta and 20 to 40 years post-harvest in Sweden. Bears in Sweden selected clear-cut consistently across all seasons, while bears in Alberta reduced their selection for clear-cuts in late summer and fall when younger-aged clear-cuts were selected. This seasonal reduction in habitat selection for clear-cuts in Alberta may be due to negative effects associated with mechanical site preparation (scarification) that reduce populations of long-lived fruiting shrubs, while providing a short-term pulse in short-lived fruiting resources, such as raspberry, in younger clear-cuts. In both study areas, dominant bears selected larger clear-cut patches over that of smaller clearcuts suggesting that security (hiding cover) was less important than the size of the resource patch which presumably would increase foraging efficiency. Recent trends in Alberta towards harvesting larger clear-cuts may therefore benefit dominant individuals assuming human access is managed. Females with cubs of the year, however, selected for smaller clear-cuts presumably for greater security and avoidance of dominant males. We found evidence for functional responses in habitat selection where availability of habitats being selected affected selection for those habitats. Future work should consider the effects of silvicultural treatments, including silvicultural thinning which is common in Sweden, but rare in Alberta, on food resource abundance and habitat use by brown bears.

2. Introduction

Brown bears are generalist omnivores that frequently use or even depend on disturbed habitats to meet their resource (food) demands. Dominant disturbance regimes common to brown bear habitat include both natural sources, such as fire (Zager et al., 1983), avalanches (McLellan and Hovey, 2001) and insect epidemics (McLellan, 1989), to anthropogenic sources, such as roadside verges (Roever et al., 2008a) and forest clear-cut harvesting (Nielsen et al., 2004a). In some cases the dependence upon these disturbances may lead to attractive sink dynamics (Nielsen et al., 2006; 2008) whereby anthropogenically-derived disturbances, such as roadsides or clear-cuts, attract bears to these areas due to the presence and concentration of food resources (Nielsen et al., 2004b; Roever et al., 2008b), although use of these areas also increase mortality risk (Nielsen et al., 2004c). How best to manage anthropogenic disturbances in order to minimize their negative effect (i.e., reduced survival associated with human-bear conflict), while also potentially enhancing their positive effect (i.e., habitat carrying capacity) is a major management challenge (Nielsen et al., 2008). Since many brown bear populations occur in human-managed forested environments, modifications to forest management likely offers the greatest opportunity for managing brown bear habitat and populations.

Although some studies have found that brown bears avoid clear-cut harvests (Zager et al., 1983; McLellan and Hovey, 2001), many others have found habitat use of clear-cuts to be either equal to availability (neutral) or selected (Mace et al., 1996; Wielgus and Vernier, 2003; Nielsen et al., 2004a; Stewart et al., 2012). Nielsen et al. (2004a) suggested that differences observed among studies may simply be due to landscape effects as it relates to availability of natural disturbances (e.g., fires, avalanches) and natural openings. Where openings are limited, such as in fire-suppressed forested ecosystems, bears readily use clear-cut harvests as an alternate habitat. This suggests the presence of a functional response in habitat selection (i.e., Mystrud and Ims, 1998) where selection for clear-cuts should be inversely related to the amount of natural disturbances or openings.

As well as understanding landscape-level compositional effects on use of clear-cuts by grizzly bears, more information is needed on how specific forest management practices, including silvicultural treatments and harvest design (e.g., size and shape of clear-cuts), affect bear habitat. Although numerous studies have examined general habitat selection for clear-cuts relative to other habitats, few have examined the details regarding how the characteristics (age, size, site history, etc.) of individual clear-cuts themselves affect their use by bears (see however, Nielsen et al., 2004a; Stewart et al., 2012). If clear-cut size and shape affect the use of those habitats by brown bears, then simple recommendations can be made to change forest harvest designs to benefit bears. Likewise, understanding the specific ages or conditions when brown bears select clear-cuts would help to better design harvest rotations, silvicultural treatments to extend or limit its attractiveness to bears, and timing for managing human access.

Given these knowledge gaps and management needs, we tested 3 primary hypotheses: (1) regenerating forest hypothesis; (2) landscape structure hypothesis; and (3) functional response (landscape composition) hypothesis. The *regenerating forest hypothesis* (H_1) predicted that brown bears would select regenerating clear-cuts over mature forests due to dietary advantages associated with disturbed habitats. The *landscape structure hypothesis* (H_2) predicted that irregular-shaped and smaller-sized clear-cuts would be selected (on a per unit area basis) over more regular-shaped and larger clear-cuts when clear-cuts were young since there would be little hiding (security) cover. Conversely, larger clear-cut patches should be selected over smaller clear-cuts for older clear-cuts since food resource abundance should be more concentrated due to the larger size of the resource patch and hiding cover sufficient for security purposes. And finally the *functional response (landscape composition) hypothesis* (H_3) predicted that the strength of selection for clear-cuts would be locally dependent on the availability of clear-cuts or other open-vegetated (alternate) habitats. We assessed these hypotheses using a comparative analytical approach between two study areas – Alberta and Sweden – where brown bears have been studied within an actively managed forest landscape. This comparative approach emphasizes natural differences in forest management practices between regions, while also evaluating whether consistent patterns of habitat selection emerge despite study area differences. If so, this would suggest common behavioral mechanisms of habitat selection in brown bears for recent disturbances in forested landscape, while also helping identify the habitat value of actively managed forests and different harvest designs (e.g., clear-cut size, shape, etc.) for brown bears.

3. Material and methods

3.1. Study areas

3.1.1. Alberta

The Alberta study area covered 52,537 km^2 and was located in the eastern foothills of the Canadian Rocky Mountains in west-central Alberta (~53.5°N, -117.5°W; Figure 1). Elevations vary from 574 and 3490 m in rolling low mountainous terrain (just east of the Rocky Mountain ranges). Summer and winter temperatures average 11.5 and -6.0 ºC, respectively, with a normal annual precipitation of 538 mm (Beckingham et al., 1996). Snow cover lasts from late October until early May with the growing season averaging 160 to 185 days. The area is managed intensively with a number of resource extraction activities occurring including forestry, oil and gas, and open-pit coal mining (White et al., 2011). The forest harvest footprint covers 11.9% of the study area (Table 1) with road densities averaging 0.54 km/km^2. Linear exploration disturbances (seismic lines) are also common throughout the area and are frequently kept open due to human recreational activity. Closed conifer forests are dominated by lodgepole pine (*Pinus contorta*), and to a lesser extent by spruce (*Picea glauca, P. mariana, P. engelmannii*). Deciduous stands of trembling aspen (*Populus tremuloides*) and/or balsam poplar (*P. balsamifera*) are more uncommon in the southern (Yellowhead) part of the study area (Nielsen et al., 2004a), but more common or even dominant in parts of the northern (Grande Cache) study area.

Prior to 1950, periodic stand-replacing fires were the primary disturbance, averaging 20% of the landscape burned per 20-year period yielding a 100-year fire cycle (Andison, 1998). Since the 1950s, however, there has been a reduction in fires which is associated with the initiation of industrial forestry and fire suppression (Andison, 1998; Nielsen et al., 2008). Although some stands in remote regions are in advanced stages of succession due to fire suppression, large areas have or continue to be harvested providing the only major mechanism of forest disturbance. The majority of the study area occurs on crown land (federally owned), but is managed by the province of Alberta for timber under long-term (40-year) forest management agreements with forest companies. Traditional forest management in the area centers on a two-pass harvest design with small clear-cuts (<40 ha) designed in a checkerboard pattern within a larger management block (Nielsen et al., 2008). Adjacent stands are subsequently harvested after at least 15 years (reforestation green-up period) has passed (Smith et al., 2003). Mean cutblock size in the study area in Alberta was 25.4 ha. Timber extraction in the Alberta study area is still within its first rotation.

3.1.2. Sweden

The study area in Sweden covered 15,933 km^2 and was located in rolling low mountainous terrain in the Dalarna and Gävleborg counties of south-central Sweden (~61N, 14E; Figure 1). Elevations range from 200 m in the east to 1000 m in the west with timberline at 750 m. Very little of the landscape is above timberline. Summer and winter temperatures averaged 15 and -7.0 ºC, respectively, and precipitation averaged 500–1,000 mm annually. Snow cover lasts from late October until April with a growing season of approximately 180 days. The area is covered by an intensively managed boreal forest interspersed with natural bogs and lakes. Roads are common within the Sweden study area with an average density 0.99 km/km^2. Forests are dominated by Scotch pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), although deciduous trees such as mountain birch (*Betula pubsecens*), silver birch (*Betula pendula*), European aspen (*Populus tremula*), and gray alder (*Alnus incana*) are also common (Zedrosser et al., 2006).

Commercial exploitation of timber in the Swedish study area started in the late 1800s (Linder and Östlund, 1998). Prior to exploitation the forest was dominated by old forest stands >200 years of age. Forest commons and the State Forests were established in the late 1800s, when delineation (separation of private and public land) and enclosure (division of land among the different landowners in the villages) were carried out. Most of the unclaimed forest land was allotted as forest commons to landowners in existing villages, but some parts were designated State Forests under the administration of the National Forest Service (Linder and Östlund, 1998). This resulted in an owner structure that was characterized by the possession of several spatially disconnected and irregular-shaped and often small stands. Subsequent intensive forest management and fire protection have resulted in a forest landscape dominated by relatively young and dense stands (Linder and Östlund 1998). Since the late 1800s, both the number of large trees and the volume of snags have been reduced by about 90%, and the area of old stands has diminished to < 1% (Linder and Östlund, 1998). Until the 1940s, natural regeneration without any soil treatment was the most common regeneration technique, and commercial and pre-commercial thinning of stands, with the intention of creating evenly-aged stands was introduced. From the 1950s, large-scale clearcutting was the dominant felling system, which in most cases was followed by planting of tree-seedlings. In the 1990s, silvicultural practices have been directed towards the promotion of more natural conditions so the size of clearcuts has decreased, and natural regeneration has again increased (Linder and Östlund, 1998). Due to the historic development of landownership and exploitation, cutblocks in Sweden are usually irregular shaped and unevenly distributed along forestry roads. Dead-end roads are commonly built to gain access to new cutblocks. The mean cutblock size in the Swedish study area was 40.7 ha (~60% larger than those in Alberta) with timber extraction in its second and third rotation.

3.2. Study area population characteristics

Based on >25 years of research in Sweden and >16 years of research in Alberta, brown bears between the two areas have comparable life-history characteristics (Table 2) (Zedrosser et al., 2012). Both are arctic-interior populations, with similar ecological conditions, life-history traits (Ferguson and McLoughlin, 2000) (Zedrosser et al., 2012), and diets (Dahle et al., 1998; Munro et al., 2006). Protein consumption is highest in spring and early summer for both populations, consisting mainly of ungulate neonates and insects (mainly ants (*Formica* spp., *Camponotus* spp.) in Sweden (Dahle et al., 1998) and Canada (Munro et al., 2006). Insect consumption is highest in both study areas in July prior to fruit ripening. Late summer and fall diets are dominated by graminoids, herbs, and berries. The primary source of berries in Canada is from russet buffaloberry/soopolallie (*Shepherdia canadensis*), mountain huckleberry (*Vaccinium membranaceum*) and to a lesser extent dry hillside blueberry (*V. myrtilloides*) and lingonberry (*V. vitis-idaea*) (Munro et al., 2006). In Sweden berries are mainly from dwarf Ericaceae shrubs, especially blueberry (*V. myrtillus*), crowberry (*Epetrum* spp.), and lingonberry (Dahle et al., 1998). Neither study population has access to spawning salmon (*Oncorhynchus* spp., *Salmo* spp.).

In both areas, brown bears face resource extraction, agriculture, urbanization, and recreation (Nielsen et al., 2004; Nellemann et al., 2007). In Sweden, however, brown bears have increased from ~130 animals in the 1930s to >3,200 animals in 2008 (Kindberg et al., 2009), and have been hunted since the 1940s (Swenson et al., 1994). In contrast, they are designated as threatened in Alberta, with about 691 bears in the province (Alberta Sustainable Resource Development and Alberta Conservation Association, 2010), within an area ~50% larger than that of Sweden (661,848 km^2 vs. 449,964 km^2). Regulated hunting occurred until 2002, became increasingly restricted and was stopped in 2006 (Alberta Sustainable Resource Development and Alberta Conservation Association, 2010).

3.3. Selection of bears for analysis

We considered three sex and offspring dependent classes of bears for this study: males, females, and females with dependent cubs of the year. We did not distinguish solitary females from females with yearlings or 2-year-olds since previous research has demonstrated that habitat selection in adult females differs only when having cubs of the year (Steyaert et al., 2012). Because cub loss is common in Sweden and occurs mostly during the months May and June (i.e. the mating season; Swenson et al., 1997; Zedrosser et al., 2009), females that lost their cubs were assigned to the 'female' sex-offspring class for the month following cub loss.

3.4. Animal location (habitat use) and home range definitions

All bears were captured as a part of long-term research projects. GPS-location data were collected from bears captured from 2005-2010 in Sweden, and from 1999-2010 in Alberta using GPS radiocollars. Capture and handling are described in Cattet et al. (2003) for Alberta and Arnemo et al. (2011) for Sweden. In Sweden bears were fitted with GPS Plus, Vectronic Aerospace GmbH radiocollars with an a relocation frequency scheduled at 30 minutes, although for some studies bears were programmed with relocation frequencies at 1 or 10 minutes. In Alberta, bears from the Yellowhead and Grande Cache populations units were fitted with either a Televilt GPS-Simplex or an ATS (Advanced Telemetry Systems) GPS radiocollars with a relocation frequency of every 1 or 4 hours. Daily behaviour patterns of bears between the study areas were similar with diurnal patterns typical having the highest activity during dusk and dawn hours and a resting behaviour during midday and midnight hours (Munro et al., 2006; Moe et al., 2007). In this study we did not distinguish between diurnal behaviours in analyses of habitat selection, but rather evaluated general seasonal changes in habitat selection at a monthly temporal resolution during the active period (i.e., May through October).

Across both studies, we gathered animal use information from GPS telemetry on 157 unique bears totaling 1,916,188 relocation events (Alberta: 152,514 relocations from 72 bears; Sweden: 1,763,674 relocations from 85 bears). Because we were interested in testing whether sex-offspring status affected habitat selection of clear-cuts, animal locations were labeled as either male, female with cubs of the year, or females without cubs of the year (i.e., solitary or with yearlings). Based on these sex-offspring classes, sample sizes for each study area consisted of 38 male and 34 female bears in Alberta with 8 female bears monitored while having cubs of the year. In Sweden sample sizes for sex-offspring classes consisted of 35 male and 50 female bears with 26 female bears monitored while having cubs of the year. In many instances, females with cubs of the year were also categorized as females in different years (or months if cubs were lost in their first year).

Home ranges were defined for each bear using Minimum Convex Polygons (MCPs) using the ArcView 3.2 extension Animal Movement (Hooge and Eichenlaub, 1997). For some peripheral study bears we clipped MCP home ranges to jurisdictional boundaries, such as the border with British Columbia for the Alberta population. Home ranges were used to define availability of habitats for each animal using random sampling. A sample intensity of 5 locations per square kilometer with a minimum distance between random locations of 50 m was used for each animal based on MCP polygons.

3.5. Characterizing habitat classes for 3rd order habitat selection

We defined our study area into 6 broad habitat categories including 4 seral forest stages and 2 non-forested habitat types. These 6 categories were: (1) young regeneration (seedling to sapling stages defined as 0–9 years of age), (2) advanced regeneration (poles, defined as 10–25 years age), (3) young maturing forest (26–60 years of age), (4) mature forest (>60 years of age), (5) non-treed vegetated habitats (e.g., meadows, wetlands, shrubland), and (6) non-habitat (e.g., barren, snow, ice, or water). Young regenerating forests (seedling to sampling stage) were characterized by having an open canopy structure resulting in the dominance of an herbaceous and shrub groundcover. Advanced regenerating forests (regenerating pole stage) were transitional habitats where tree canopy cover begins to develop, as well as maturation of dwarf fruiting shrubs. Young maturing forests (26-60 years post-disturbance) were characterized by vertical rather than horizontal stand growth with dominance by trees being established thus resulting in reductions in food resource availability and habitat selection by bears (Nielsen et al., 2004a; 2004b). And finally, mature forests are considered fully-developed forests. To match animal location data among years, annual habitat maps were defined for each study area (1999 to 2010 in Alberta; 2005 to 2010 for Sweden) using base maps (1998 for Alberta and 2000 for Sweden), Alberta Vegetation Inventory (AVI) data, and remote sensing imagery (e.g., Landsat and SPOT5).

3.6. Characterizing age, size, and shape of clear-cut patches for 4th order selection

For each clear-cut, we collected information on year of harvest to calculate age of harvest at time of animal use, the size of harvest in hectares, and the shape of clear-cuts. Age was based on the year of harvest from GIS databases. In contrast, size and shape of clear-cuts were based on landscape definitions of 'patches' defined as forest stands having similar aged and distinct habitat boundaries (edges), not necessarily individual clear-cut boundaries (Figure 2a). For instance, two young stands harvested in the same cutblock and year, but separated only by a road or two young maturing forest stands adjacent to one another that were harvested a few years apart were considered a single 'patch' since no real difference in forest structure existed between harvest polygons. To define boundaries (edges) of these patches, we considered stand boundaries with significantly different stages of growth (age) or forested and non-forested boundaries. Because the structure and habitat characteristics of a regenerating forest change more rapidly in early stages of succession than in later stages, the importance of age differences between stands was itself a function of stand age. Specifically, a boundary between stands was considered to form an 'edge' (E_1) if the difference in ages between the two stands was equal to or greater than half the sum of the two ages or,

$$E_1 \text{ if } (age_2 - age_1) \geq 0.5 \times (age_2 + age_1). \qquad \text{(eq. 1)}$$

Otherwise it was considered part of the same patch (E_0). This emphasized differences in adjacent early seral stands harvested in different years (e.g., 2 versus 5 year old stands), but not adjacent mature stands harvested in different years having relatively similar stand structure (Figure 2a). Like that of the first analysis for 3rd order habitat selection, annual landscapes defining clear-cut patches were produced for each study area and year. Once patches were defined, patch size (hectares) was calculated.

Using defined patches, a shape index was calculated for each patch to indicate how similar in shape the harvest patch was to a circle. More specifically, we used the shape index from Hunter (1990), which is defined as,

$$Shape\ index = \frac{Perimeter\ length}{2(\sqrt{Area} \times \pi)} \qquad \text{(eq. 2).}$$

Based on this index, a circle would have a value of 1, while increasingly complex polygons would be increasingly larger than one. Figure 2b illustrates shape indices for defined clear-cut patches for a cutblock in west-central Alberta.

3.7. Statistical methods

3.7.1. 3rd order habitat selection (habitat types)

We estimated general habitat selection for clear-cuts ≤60 years of age using habitat selection ratios (w_i, Manly et al. 2002) for each bear and month combination. Selection ratios were summarized with a one-sample *t*-test against a null value of 1.0 (proportion use = proportion available) to identify general selection patterns by season and study area. Only those selection ratios for a bear-month combination having at least 50 monthly telemetry observations were considered. As well, only bears having a reasonable amount of clear-cut habitats available from which to select from were considered. Here we set that threshold at 5% of their home range.

To more fully understand sex-offspring, study area, and seasonal effects, we also estimated monthly habitat selection coefficients across the active period (May through October) for 6 defined 'habitat' types, including 3 clear-cut age classes, using resource selection functions (RSFs) with logistic regression models used to estimate selection coefficients (Manly et al., 2002; Johnson et al., 2006). Given that our predictors of habitat selection were based on categorical variables (habitat types), we used binary (0 or 1) 'dummy' coding to identify each habitat type with mature forests (>60 year old stands) used as the reference category (control). Selection of different clear-cut seral stages were therefore compared (and reported) against selection with mature forests.

To account for potential differences among animals (sex, reproductive class, etc.), a two-stage RSF analysis (Manly et al., 2002; Nielsen et al., 2002; 2009) was used where a RSF model was fit for each individual bear and month combination (minimum sample size of use locations equal to 50) and subsequently combined into sex-offspring groups by month classes (second-stage) using summary statistics (mean and standard errors) with sample weights (analytical weights) of habitat selection coefficients. We used the two-stage analytical approach to acknowledge the final unit of replication was the animal, not the telemetry location, while also allowing a random intercept and multiple random slopes to be fit for each factor for each bear (Nielsen et al., 2009). Although the two-stage model is seemingly similar to a mixed effect RSF model (e.g., Gillies et al., 2006), mixed effect models cannot easily estimate numerous random slopes and are further limited in their ability to evaluate secondary hypotheses related to animal-level differences in selection, such as differences between sex-offspring groups, study area effects, and functional responses in habitat selection due to changes in habitat availability. Sample weights for each observation (selection coefficient by bear-month) were estimated as inverse variance weights (Hedges, 1983) using the estimates of standard errors from the selection coefficient (Nielsen et al., 2009), as in meta-analyses (Ellis, 2010). This accounted for differences in precision of selection coefficients among bears. All analyses were performed in STATA 12.1 (StataCorp 2011).

Final group-level estimates of selection for the three regenerating forest classes were graphed by month to illustrate general similarities and differences among seasons, sex-offspring classes, and study site combinations. The regenerating forest hypothesis (H_1) and the functional response hypothesis (H_3) were evaluated for 3rd order habitat selection. Methods for evaluating these hypotheses are discussed in more detail below ('*Evaluating support for major hypotheses*').

3.7.2. 4th order habitat selection (within clear-cut patches)

Fourth order (within clear-cut patch) habitat selection was evaluated for each bear and month combination using only the GPS telemetry (30,588 observations in Alberta and 860,371 observations in Sweden) and random locations occurring within clear-cuts ≤ 60 years of age. For each location, the age of the regenerating forest, the size in hectares (log [area + 1]) of the patch, and the shape of clear-cut patch were identified using GIS. As in 3rd order habitat selection methods, RSF models were estimated for each bear and month combination. However, due to high collinearity between clear-cut patch shape and patch area (size), patch shape was removed from all models. We fit a quadratic term for stand age since previous work has shown that bears typically select for intermediate-aged regenerating forests (see Nielsen et al., 2004a). And finally, we fit an interaction term between age and size (log[area + 1]) of clear-cut patch to test for 'security' or hiding cover effects. By evaluating these factors, we could test two competing hypotheses that have forest management and planning applications; specifically, the 'habitat security' hypothesis versus a 'food resource concentration' (optimal foraging) hypothesis. In the former hypothesis, we expected that the size of the clear-cut patch would be less important as the clear-cut aged since forest cover would reduce visibility of animals proving security (cover). The alternate hypothesis, on the other hand, would suggest that food resource concentration would be the most important factor and thus if a certain age of clear-cut resulted in the greatest concentration of resources then it would be most 'profitable' to forage in larger patches.

As in the above two-stage RSF methods for 3rd order analyses, summary statistics were estimated for each sex-offspring group and month combination using sample weights to estimate the 'second-stage' of the RSF models. Final coefficients were tabulated by group (study site and sex-offspring class) and month and tested for significance (from 0) based on a simple intercept model using a generalized linear model (Gaussian family and identity link) with sample weights. Specific hypotheses related to landscape structure (H_2) and functional responses (H_3) were evaluated for 4th order habitat selection. Methods for evaluating these hypotheses are discussed in more detail in the following section.

3.8. Evaluating support for major hypotheses

We tested for support of our competing hypotheses and for general functional responses, sex-offspring and study area (Alberta versus Sweden) effects in habitat selection coefficients for each month and scale of analysis (i.e., 3rd or 4th order habitat selection) using generalized linear models (Gaussian family and identity link) with sample weights (inverse variance) with Akaike Information Criteria (AIC_c) used to rank support of models (Burnham and Anderson, 2002). In total, 10 *a priori* models (hypotheses) were tested, including a null (intercept) model and different combinations of sex, sex-offspring, study site, and functional response variables (Table 3).

Functional responses for 3rd order habitat selection were based on availability of seral forest classes (0-9 years, 10-25 years, and 26-60 years) and amount (%) of natural openings, while 4th order functional responses in habitat selection were based on average age of clear-cut within each animals home range since we assumed that responses to age should be dependent on the range of ages available, particularly for brown bears in Alberta where many home ranges of bears only encompassed recent or young clear-cuts.

4. Results

4.1. 3rd order habitat selection (habitat types)

Amount of clear-cut habitats (≤60 years old) within brown bear home ranges was noticeably different between study areas. Alberta's bears ranged from having a minimum of 1.6% of their home range in clear-cuts to a maximum of 42.8% of their home range, while Sweden ranged from a minimum of 19.8% to 61.5%. Habitat selection ratios were estimated for 851 unique bear and month combinations whose home ranges contained at least 5% clear-cut habitat and a minimum of 50 use locations per month per bear. Regardless of study area, sex-offspring class, season (month), or age of regenerating clear-cuts (≤60 years old), brown bears selected (i.e., selection ratios, w_{0-60}) clear-cut habitats ($w_{0-60} = 1.29$, SE = 0.03, $t = 11.25$, $df = 850$, $p < 0.001$) relative to the remaining matrix of habitats thus supporting our regenerating forest hypothesis (H_1). Evaluations of selection ratios by study area, however, revealed that overall selection ratios were noticeably higher for bears in Sweden ($w_{0-60} = 1.36$, SE = 0.020, $t = 17.89$, $df = 528$, $p < 0.001$) than in Alberta ($w_{0-60} = 1.18$, SE = 0.06, $t = 3.08$, $df = 321$, $p = 0.001$).

Habitat selection of clear-cuts by habitat types, including the 3 regenerating forest habitats, demonstrated that selection varied by age of regenerating clear-cut, month, sex-offspring class, and study area (Figure 3A). As a general rule, recent clear-cuts (0–9 years) were selected more by brown bears in Alberta than in Sweden. Peak selection for recent clear-cuts in Alberta occurred in August with the lowest period of selection in May. In contrast, bears in Sweden generally used recent clear-cuts according to their availability (use=available), although increases in selection were notable during September and October for all sex-offspring classes and earlier in the year (June-July) for male bears. Model comparisons of our 10 *a priori* hypotheses demonstrated that differences in habitat selection among animals for recent (0–9 years) clear-cuts were explained most (AIC$_c$ weights) between July and September by sex and study area effects (1b), by functional responses and sex-offspring classes in June and October (4a), and by a null (0 or constant model) during May (Figure 4A).

Selection of young regenerating clear-cuts (10–25 years) was consistent for all sex-offspring classes and study sites, especially during June, July and August when bears were about two times more likely to use young regenerating clear-cuts than mature forests (Figure 3B). Selection for young regenerating clear-cuts diminished noticeably, however, for bears in Alberta during September and October, especially for females with cubs of the year, while bears in Sweden continued to select young regenerating clear-cuts throughout the late summer and fall period. Model comparisons of our 10 *a priori* hypotheses demonstrated that differences in habitat selection among animals for young regenerating (10–25 years) clear-cuts were explained most (AIC$_c$ weights) by models containing study area effects. During the second half of the active season (August – October), a functional response in habitat availability and study area interaction (3b) explained habitat selection of young regenerating clear-cuts best, while a sex and study area interaction (1b) described habitat selection best during May and July, and finally a functional response-study area interaction and sex-offspring class and study area interaction (4c) was most supported during June (Figure 4B). Study area differences were generally due to lower levels of selection for young regenerating clear-cuts in Alberta relative to Sweden (especially late in the active season), while the sex-offspring study area interaction was most notable for the differences in selection of young regenerating clear-cuts during September-October by female bears with cubs of the year relative to female bears without cubs of the year (Figure 3B).

Patterns of selection for old regenerating clear-cuts (26–60 years) by brown bears in Alberta and Sweden were the most dissimilar of the age-classes tested. In Sweden bears consistently selected older clear-cuts regardless of month, while selection in Alberta was evident only during the first half of the active season (May–July) with a major decline in selection of older clear-cuts for bears in Alberta during August, September, and October (Figure 3C). These changes were reflected in the candidate models tested for individual-level differences in habitat selection. During May, September, and October, differences in habitat selection were explained best by the global model (4c) defining functional responses by study area and sex-offspring study area interactions, while habitat selection of old clear-cuts in June and August were explained best by a functional response study area interaction (Figure 4C). And finally, in July habitat selection of old clear-cuts were explained best by sex-study area interactions.

4.2. 4th order habitat selection (within clear-cut patches)

Overall, brown bears selected clear-cut patches that were intermediate in age (10-30 years) and depending on sex-offspring class and study area either large or small in size (Table 4; Figure 5). Specifically, male bears in both study areas selected large clear-cuts over that of small clear-cuts on a per unit area basis with peak habitat selection for clear-cut ages of 10 and 25 years in Alberta (Figure 5A) and 20 to 30 years in Sweden (Figure 5D). Female bears (without COY) in

Sweden selected habitats similar to male bears in Sweden (i.e., large clear-cuts 20 to 30 years old; Figure 5E). In contrast, females without COY in Alberta selected for smaller clear-cut patches, but at similar ages (10-25 years) to that of male bears (Figure 5B). And finally, female bears with COY displayed segregation of habitats with the other sex-offspring classes. In Alberta, females with COY selected for very young clear-cuts (< 5 years old) regardless of size (Figure 5C), although sample sizes were very small and influenced strongly by selection for young clear-cuts in May (Table 4). Females with COY in Sweden on the other hand, selected for small clear-cut patches opposite to that of males and females without COY, although age (20 to 30 years) of clear-cut selected was still similar to the other sex-offspring classes (Figure 5F).

Differences in habitat selection among animals within clear-cuts of different ages were explained most (AIC_c weights averaged for Age + Age^2) by functional responses (average clear-cut age) during May and September (i.e., model 3a), by a functional response by study area interaction in August and October (3b), and by study site differences with a functional response, sex-offspring interactions (4b) during June and July (Figure 6A). Differences in habitat selection among animals based on size of clear-cuts were supported most by a null model (0) during October, by a sex difference (1a) in May and September, by a functional response and study site interaction (3b) during August, and by study site differences with a functional response, sex-offspring interactions (4b) during June and July (Figure 6B). And finally, age and size of clear-cut interactions were supported most for sex-offspring study area interactions (model 2b) during May, by functional response and study area interactions (3b) during June, by study site differences with a functional response, sex-offspring interactions (4b) during June and July, and by a null model (0) during September and October (Figure 6C).

5. Discussion

5.1. Regenerating forest hypothesis

In both Alberta and Sweden, brown bears selected for clear-cut patches over the surrounding matrix habitats. This supports our regenerating forest hypothesis (H_1) where generalist omnivores, such as brown bears, respond positively to forest disturbances, particularly where forests dominate the landscape like that of the Holarctic boreal forests and where natural fire regimes are suppressed. Our results further support previous studies showing neutral (used according to availability) to positive associations in selection of clear-cuts including, Mace et al. (1996) in the Swan Mountains of Montana, Wielgus and Vernier (2003) in the Selkirk Mountains of British Columbia, Nielsen et al. (2004a) in the Alberta foothills, and Swenson et al. (1999) in central Sweden. In contrast to these supporting studies, Zager et al. (1983) and McLellan and Hovey (2001) showed negative associations with clear-cuts, although in both of these cases human traffic on roads associated with clear-cuts may have negatively affected habitat use of clear-cuts as well as the presence of alternate, productive regenerating forest habitats that were associated with major historic fires. Research on food resource availability and abundance in clear-cuts supports a pulse in food resources exceeding that of mature forests prior to canopy closure (Martin, 1980; Swenson et al., 1999; Nielsen et al., 2004b), although silvicultural site preparation techniques that damage the roots of long-lived fruiting shrubs negatively affects late season food resources (Martin, 1980; Nielsen et al., 2004b). The presence of alternate resource patches, such as large historic fires, suggests that a functional response in habitat selection (Mysterud and Ims, 1998) for clear-cuts (i.e., the functional response hypothesis, H_3) is an important consideration in understanding why some populations appear to favor clear-cut forests more than others.

5.2. Landscape characteristics hypothesis

Although numerous studies have examined general 3rd order habitat selection for clear-cuts, few have examined the details of the characteristics (e.g., age, size, site history) of individual clear-cuts being selected (see however, Nielsen et al., 2004a). When examining habitat selection among general structural classes or ages of clear-cuts, recent clear-cuts (0-9 years) were selected more by brown bears in Alberta than in Sweden with peak selection of recent clear-cuts in Alberta occurring in August when grizzly bears typically forage on fruit (Munro et al., 2006). In Sweden, use of recent clear-cuts was largely based on availability (neutral) except late in the year (September-October) when selection for recent clear-cuts increases. Lower use of clear-cut patches in Sweden may reflect the openness of clear-cuts where hiding cover (security) may be more important. Young regenerating clear-cuts (10-25 years) were strongly selected by both brown bear populations, although selection was attenuated late in the year for brown bears in Alberta, particularly for females with cubs of the year. This age class corresponds to the period of maximum fruit and ant resource abundance just prior to canopy closure (Swenson et al., 1999; Nielsen et al., 2004b). Older (26-60 years) clear-cuts were neutral to moderately selected, although an even stronger decline in selection was notable for the late season period in Alberta.

The age of the clear-cut selected may, however, depend on the size of the clear-cut patch which we refer to as our *landscape structure hypothesis* (H_2). Specifically, trade-offs may occur between hiding cover (security) needs in recent clear-cuts, especially for vulnerable sex-offspring classes, and for foraging efficiencies gained by larger resource patches (i.e., larger clear-cut patches). Our results support this hypothesis. When brown bears selected more for younger clear-cut patches, those patches tended to be smaller in size, while selection for older clear-cut patches was associated with larger patch sizes. Interactions with sex-offspring classes were noticeable, however, with male brown bears in both study areas consistently selecting for the larger, intermediate-aged clear-cut patches, while female bears in Alberta and females with cubs of the year in Sweden both selected for smaller clear-cut sizes. In the case of females with cubs of the year in Alberta, patch size and age were both inversely related to habitat selection. These patterns could be due to sexually-segregated habitat selection associated with intra-specific competition (Nielsen, 2005), sexually-selected infanticide mechanisms promoting sexually-segregated habitat selection (Swenson et al., 1997), or both, although sample sizes of females with cubs of the year in Alberta were small. The fact, however, that females with cubs of the year in Sweden still selected small clear-cuts over large clear-cut even after a period of years when hiding/security cover would be present suggests that these animals were segregating themselves from other bears (and not humans) by using smaller resource patches.

In contrast to patterns of selection for size of clear-cut patch, selection for age of clear-cut patch appeared to be more consistent across sex-offspring classes and study areas, although seasonal differences were evident. This suggests that bears were selecting clear-cuts at maximum or peak availability in food resources, which in this study averaged between 10 to 25 years post-harvest in Alberta and 20 to 40 years post-harvest in Sweden. This is consistent with prior research on food resource availability and habitat selection of brown bears (Martin, 1980; Nielsen et al., 2004a; 2004b). This is also the time period when regenerating trees begin to dominate the site reducing light availability. Seasonal differences, however, were present with the strongest effects evident during July when both populations were actively using clear-cut patches, especially for myrmecophagy activities (Swenson et al., 1999; Munro et al., 2006).

5.3. Functional response hypothesis

Our functional response in habitat selection (Mysterud and Ims, 1998) hypothesis was supported for most variables and seasons (months) by second-stage analyses of habitat selection among individual bears and comparisons with other *a priori* candidate models explaining differences in habitat selection. This suggests that the landscape context in which an animal is exposed is critical to understanding observed selection patterns. Further work is needed to explore these relationships in full detail and to make specific predictions for management purposes. Regardless, it is apparent from prior research that when alternate natural disturbances, such as regenerating forests from wildfire, are present, brown bears will generally select for those habitats over that of similar-aged clear-cuts (Zager et al., 1983; McLellan and Hovey, 2001). The benefits of forest harvesting are therefore greatest in fire-suppressed landscapes dominated by mature forests.

6. Conclusions

Although increases in human activity associated with expanding forest management in Alberta is a major conservation concern (Nielsen et al., 2006; 2008), it is evident that forest harvesting provide an important mechanism for regenerating young seral forests in Holarctic boreal landscapes where natural upland openings are rare and major natural disturbances, such as fire, are suppressed (Johnson et al., 2001). Intermediate-aged (10 to 40 years post-harvest) clear-cuts were selected for most by brown bears with a positive relationship between selection and patch size evident for the dominant sex-offspring classes. This suggests that patch size of the resource is more important than security, although regenerating trees likely provide sufficient cover by that age of stand. When younger regenerating stands were selected, such as by females with cubs of the year in Alberta, size of clear-cut was inversely related to habitat selection suggesting that security (hiding cover) was more important at that age of stand when tree cover is low and for that sex-offspring class. Although past trends in Alberta have been towards smaller clear-cut sizes (Stewart et al., 2012), natural disturbance-based harvest designs (Hunter 1990) with larger clear-cuts are now being implemented. Our results suggest that this would positively affect brown bear habitat selection for dominant bears, but potentially negatively affect female bears with cubs of the year as they tended to select for smaller clear-cuts. Future work should address whether in-block retention of trees as patches or diffuse standing trees would mitigate the negative responses to clear-cut size observed by females with cubs of the year. Future work should also consider the effects of silvicultural treatments on food resource abundance and habitat use by brown bears, particularly for long-lived fruiting shrubs. Prior work by Nielsen et al. (2004a; 2004b) suggests that certain mechanical site preparation techniques can negatively affect food resource abundance and habitat selection by brown bears, although use of prescribed fire appears to increase abundance of long-lived fruiting shrubs (Martin, 1980; Nielsen, personal obs.) More studies are needed to evaluate whether these responses are consistent among populations and what practices beside prescribed fire can mitigate these effects. Finally, silvicultural thinning which is commonly used in Scandinavia, but rare in Alberta, should be experimented with in Alberta for wildlife enhancement purposes shortly after stand closure.

7. Acknowledgements

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Table 1. Area (km^2) and percent composition of land cover classes for the Alberta, Canada and Sweden study areas.

Land cover class	*Alberta*		*Sweden(2005)*	
	Area (km^2)	Percent	Area (km^2)	Percent
Clear-cut (0-60 yrs.)				
Recent[a]	1,398	3.7	701	4.8
Young regenerating[b]	1,970	5.2	1,176	8.0
Old regenerating[c]	1,242	3.3	3,591	24.6
Sub-total	4,610	12.2	5,468	37.4
Mature forest[d]	25,877	68.1	6,651	45.5
Vegetated non-forest land	3,943	10.4	1,853	12.7
Barren land	3,591	9.4	642	4.4

[a] 0 to 9 years post-harvest; [b] 10 to 25 years post-harvest; [c] 26 to 60 years post-harvest; [d] >60 years since post-harvest

Table 2. Brown bear life-history parameters in Canada (Alberta) and Sweden (see also Zedrosser et al., 2012). The number of individuals a parameter estimate is based on is given in parentheses.

Life history parameter	**Alberta**	**Sweden**
Age (years) at primiparity	5.8 (13)	5.0 (59)
Inter-litter interval (years between successful litters)	2.5 (10)	2.3 (124)
Mean date of den entry:		
Adult male	November 22 (15)	October 27 (33)
Adult female without dependent offspring	November 9 (41)	October 25 (43)
Mean date of den exit:		
Adult male	April 4 (13)	April 4 (33)
Adult female without dependent offspring	April 11 (24)	April 13 (13)
Adult female with cubs of the year	April 17 (11)	May 7 (21)
Timing of breeding season	~May 15 – July 31	~May 15 – July 7
Median home range size (km^2): Adult male	899 (22)	833–1,055 (36)
Adult female (without dependent offspring)	273 (39)	217–280 (52)
Mean population density (per 1000 km^2)	~14	~29

Table 3. Description of secondary hypotheses tested for 3rd and 4th order habitat selection of clear-cut patches in Alberta and Sweden by brown bears.

Model ID	Model structure	Habitat selection hypothesis
0	Null (intercept)	Constant
1a	Sex	Sexually-segregated
1b	Sex × Site	Sexually-segregated and site interaction
2a	Sex-offspring	Sex-offspring segregated
2b	Sex-offspring × Site	Sex-offspring segregated and site interaction
3a	Functional responses	Varies as a function of habitat availability
3b	Functional responses (FR) × Site	Varies as a function of habitat availability and site interaction
4a	FR + Sex-offspring	Varies as a function of habitat availability and sex-offspring status
4b	FR + Sex-offspring + Site	Varies as a function of habitat availability, sex-offspring status and site
4c	FR × Site + Sex-offspring × Site	Varies as a function of habitat availability and site interaction, as well as sex-offspring status and site interaction

Table 4. Average (sample size of bears in parentheses) seasonal (May – October) 4th order habitat selection of clear-cut patch characteristics (e.g., age and size of patch) used by brown bears in Alberta and Sweden. Average coefficients reported by sex-offspring class and study site (Ab = Alberta; Sw = Sweden) with significant ($p<0.05$) differences from zero indicated by a superscript § symbol.

Variable and group	May	June	July	August	Sept.	Oct.	May-Oct
β Age							
Ab-Male	0.165§ (8)	0.060 (10)	0.058 (13)	-0.167 (8)	0.252 (7)	-0.087 (5)	0.047
Sw-Male	0.036§ (34)	0.081§ (34)	0.081§ (31)	0.055§ (27)	0.058§ (21)	0.061§ (17)	0.062§
Ab-Female	0.097 (12)	0.021 (11)	0.152§ (15)	-0.003 (14)	0.132 (5)	0.080 (6)	0.080§
Sw-Female	0.038§ (46)	0.073§ (48)	0.108§ (46)	0.061§ (45)	0.048§ (40)	0.059§ (37)	0.065§
Ab-Female$_{COY}$	-0.256 (2)	-0.129 (3)	-0.020 (3)	-0.183 (3)	-0.037 (2)	-0.008 (2)	-0.106
Sw-Female$_{COY}$	0.008 (19)	0.056§ (19)	0.067 (15)	0.071§ (8)	0.035 (8)	0.058 (6)	0.049§
[1]β Age^{2}							
Ab-Male	-0.035§ (8)	-0.006 (10)	-0.044§ (13)	-0.028 (8)	-0.029 (7)	0.005 (5)	-0.023§
Sw-Male	-0.004§ (34)	-0.010§ (34)	-0.011§ (31)	-0.008§ (27)	-0.010§ (21)	-0.011§ (17)	-0.009§
Ab-Female	-0.012 (12)	-0.001 (11)	-0.040§ (15)	-0.036§ (14)	-0.054§ (5)	0.000 (6)	-0.024§
Sw-Female	-0.005§ (46)	-0.010§ (48)	-0.015§ (46)	-0.008§ (45)	-0.007§ (40)	-0.009§ (37)	-0.009§
Ab-Female$_{COY}$	-0.013 (2)	-0.015 (3)	-0.040 (3)	0.025 (3)	-0.011 (2)	-0.017 (2)	-0.012
Sw-Female$_{COY}$	-0.002 (19)	-0.006 (19)	-0.008§ (15)	-0.011§ (8)	-0.006 (8)	-0.009 (6)	-0.007§
β Size							
Ab-Male	-0.368§ (8)	0.124 (10)	-0.099 (13)	-0.077 (8)	0.613 (7)	0.058 (5)	0.042
Sw-Male	0.078§ (34)	0.195§ (34)	0.254§ (31)	0.173§ (27)	0.186§ (21)	0.101 (17)	0.165§
Ab-Female	0.177 (12)	0.033 (11)	-0.130 (15)	-0.404§ (14)	-0.375§ (5)	-0.812§ (6)	-0.252
Sw-Female	0.001 (46)	0.174§ (48)	0.157§ (46)	0.168§ (45)	0.093§ (40)	0.083 (37)	0.112§
Ab-Female$_{COY}$	-2.060§ (2)	-0.263 (3)	-0.838§ (3)	-0.022 (3)	-0.025 (2)	0.332 (2)	-0.479
Sw-Female$_{COY}$	-0.079 (19)	0.066 (19)	0.070 (15)	0.102 (8)	0.110 (8)	-0.069 (6)	0.033
β Age x Size							
Ab-Male	0.004 (8)	-0.001 (10)	0.018§ (13)	0.036§ (8)	-0.017 (7)	0.018 (5)	0.010
Sw-Male	-0.002§ (34)	-0.004§ (34)	-0.004§ (31)	-0.005§ (27)	-0.003§ (21)	-0.003 (17)	-0.003§
Ab-Female	-0.009 (12)	0.001 (11)	0.003 (15)	0.024§ (14)	0.011 (5)	-0.004 (6)	0.004
Sw-Female	-0.001 (46)	-0.003§ (48)	-0.002§ (46)	-0.003§ (45)	-0.002§ (40)	-0.003§ (37)	-0.002§
Ab-Female$_{COY}$	0.081 (2)	0.032 (3)	0.044§ (3)	0.016 (3)	-0.002 (2)	-0.020 (2)	0.025
Sw-Female$_{COY}$	0.001 (19)	-0.004§ (19)	-0.002 (15)	0.000 (8)	-0.001 (8)	-0.006 (6)	-0.002

[1] Age^{2} is reported as coefficients to the power of 1x10^{1}

Figures

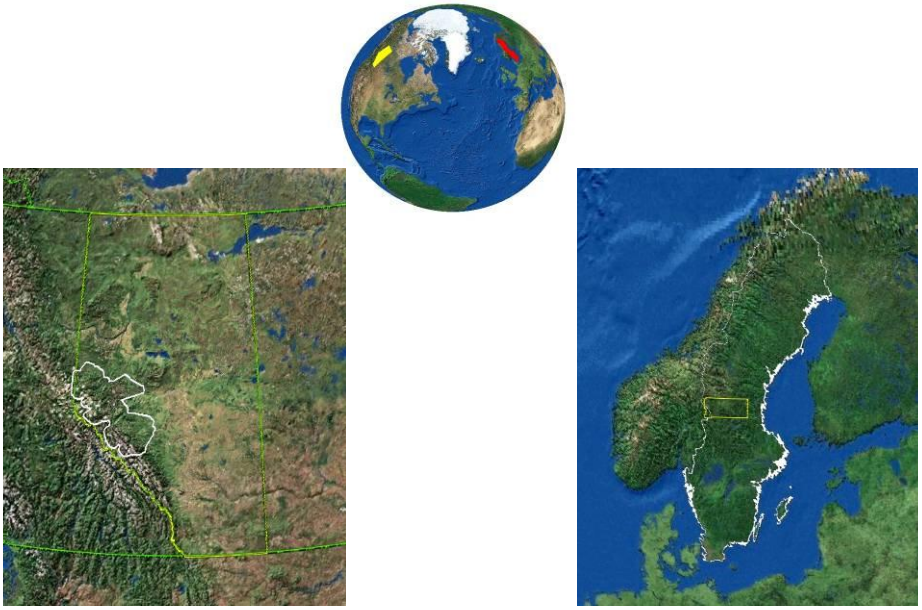

Figure 1. Locations of two brown bear study areas in west-central Alberta, Canada and central Sweden.

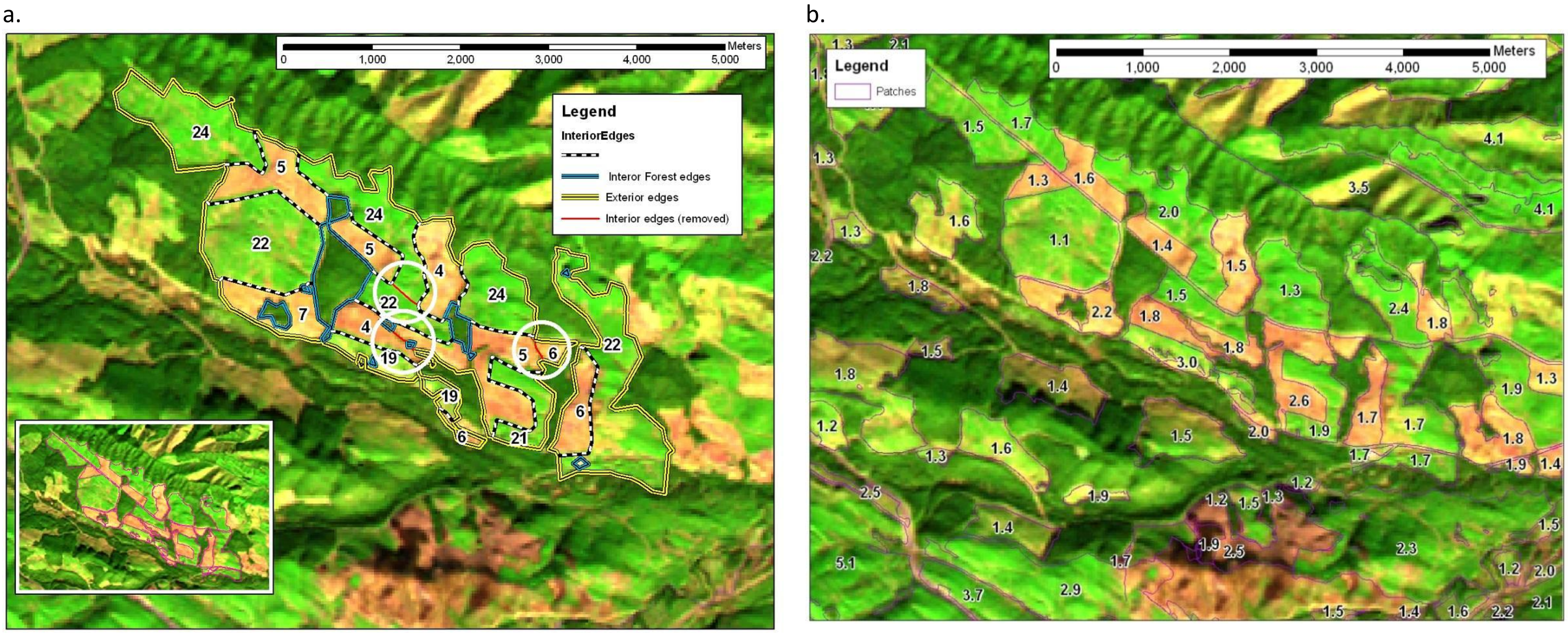

Figure 2. Example of patch edge delineation (a.) and shape index (b.) for clear-cuts in west-central Alberta, Canada.

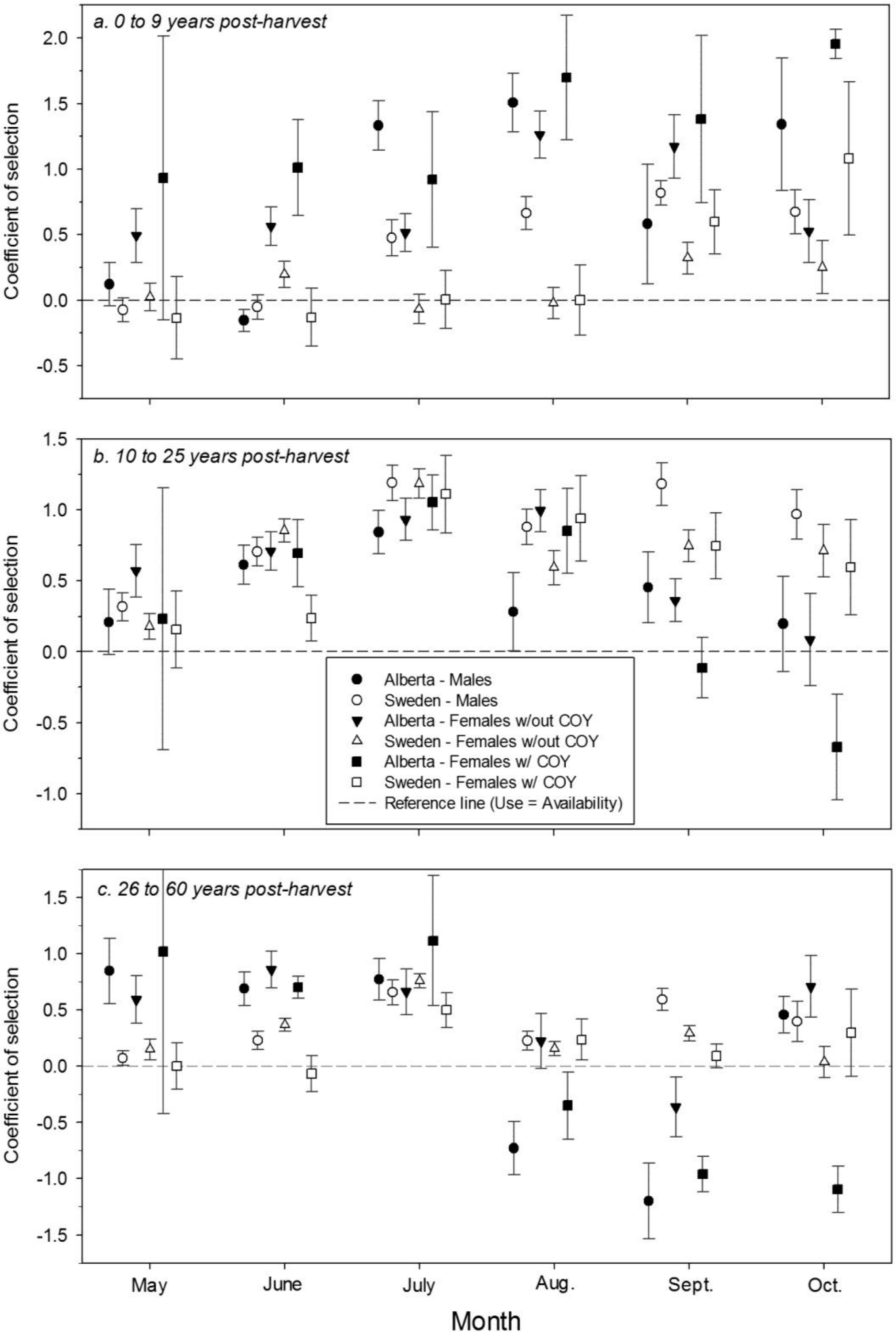

Figure 3. Patterns of habitat selection by sex-offspring class and study area for 3 different post-harvest age classes (a. 0-9 years; b. 10-25 years; c. 26-60 years). Selection coefficients (±SE) are based on averaged (inverse variance weights) animal-specific RSFs.

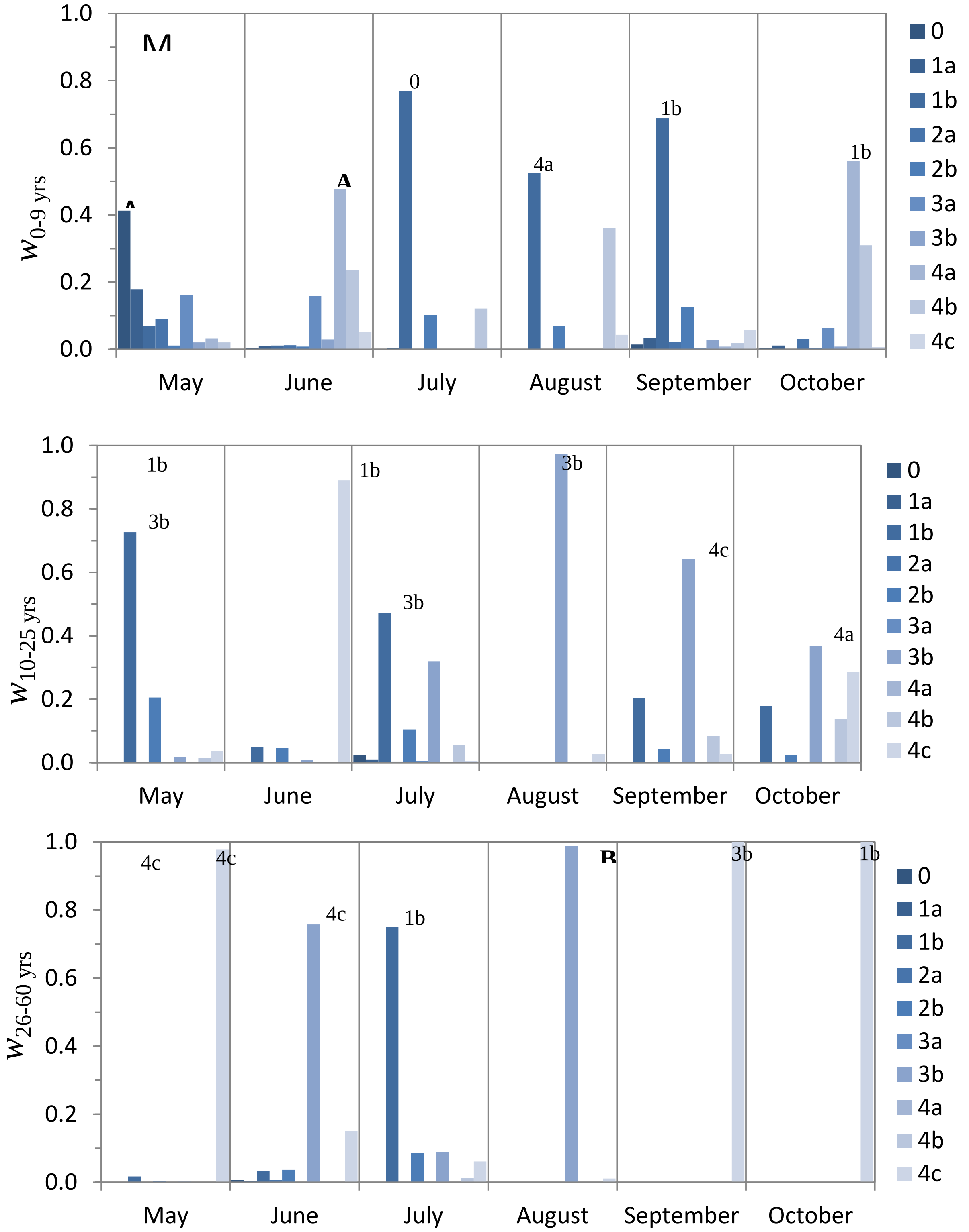

Figure 4. Akaike weights (w_i) from AIC$_c$ scores ranking support among 10 *a priori* models describing 3rd order habitat selection for clear-cuts by brown bears in Alberta and Sweden based on general age classes (**A**. 0–9 years; **B**. 10–25 years; **C**. 26–60 years). See Table 3 for description of hypotheses.

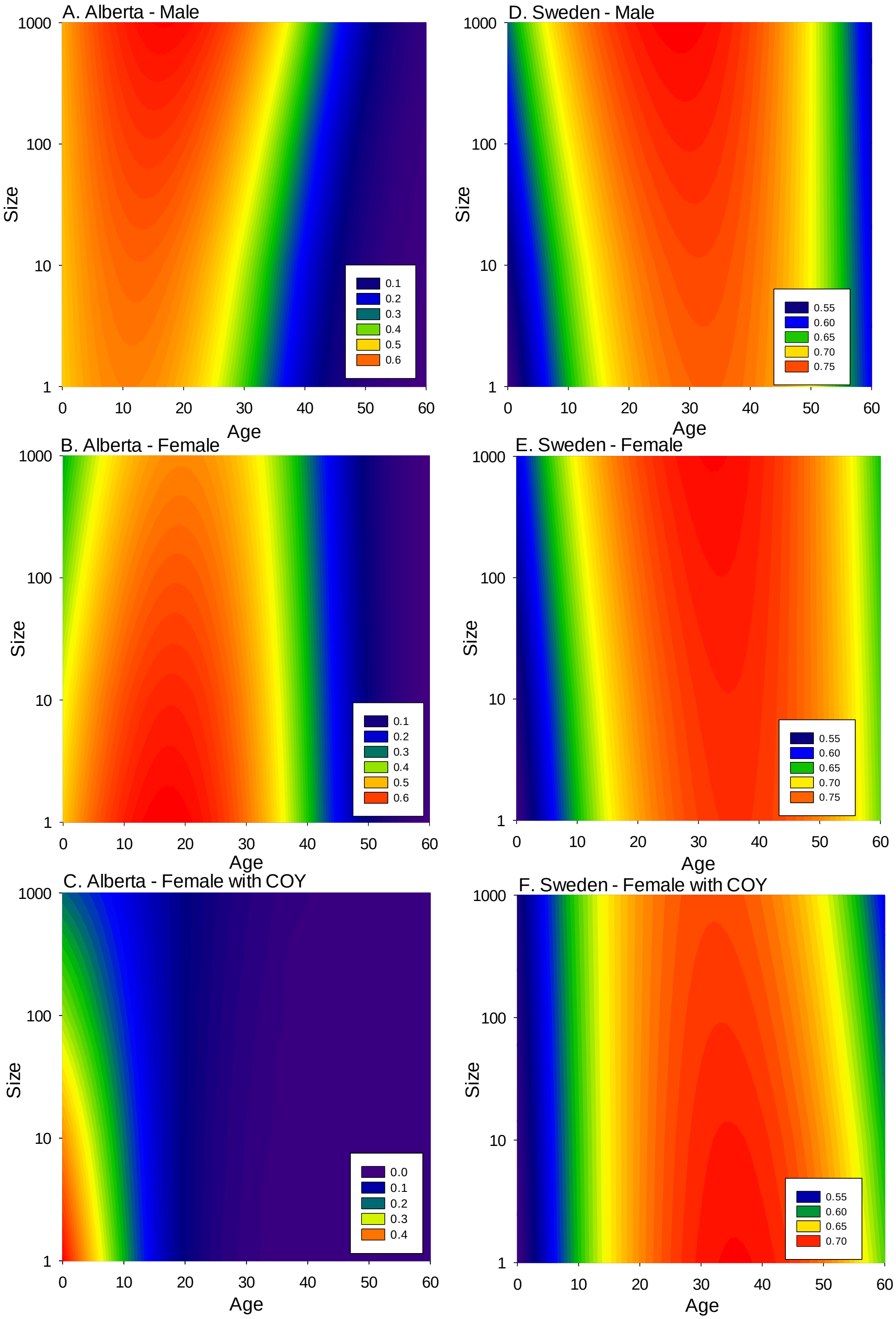

Figure 5. Multi-seasonal (average) predicted habitat selection responses to age and size of clear-cuts by study area (Alberta vs. Sweden) and sex-offspring class.

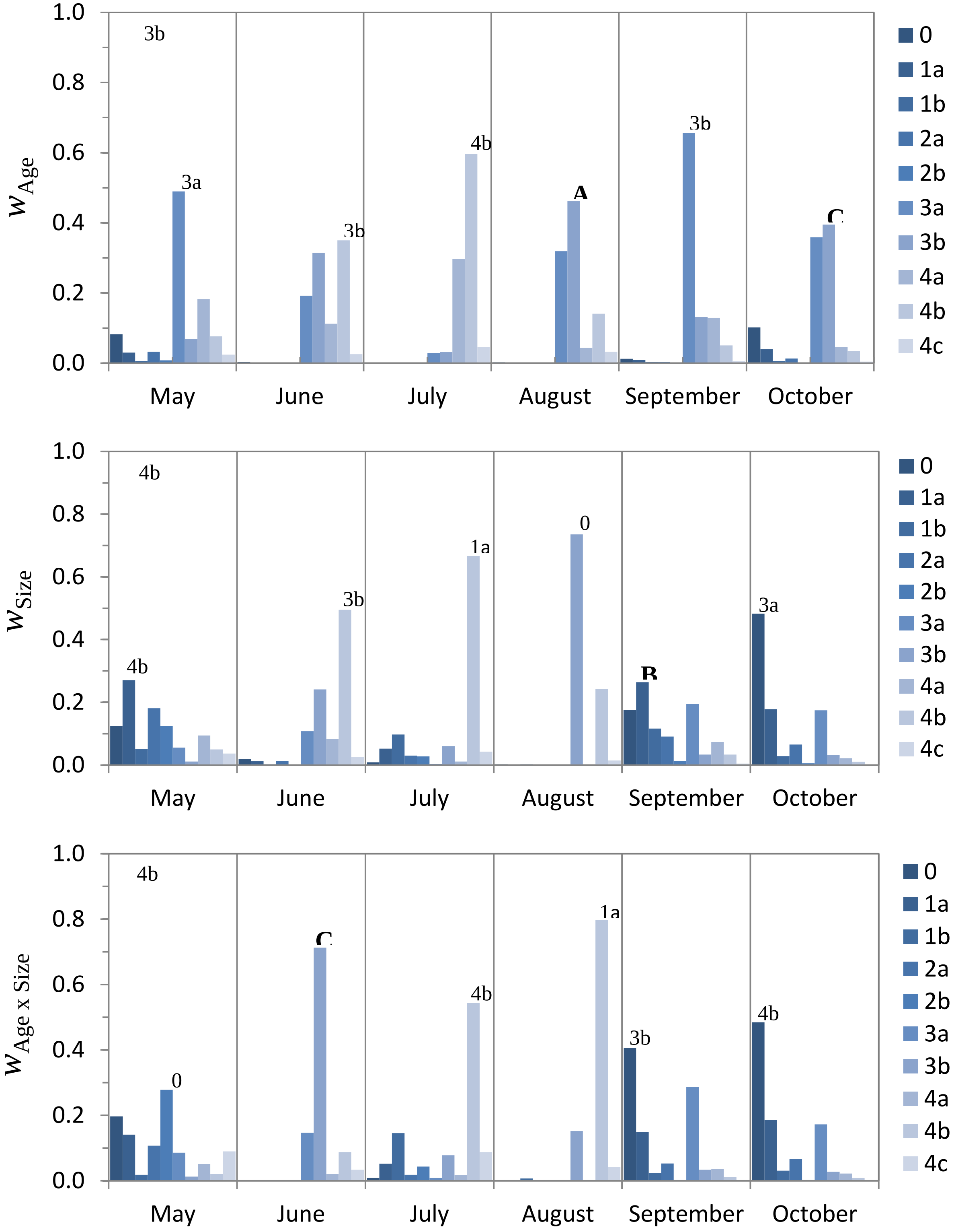

Figure 6. Akaike weights (w_i) from AIC$_c$ scores ranking support among 10 *a priori* models describing 4th order habitat selection within clear-cuts by brown bears in Alberta and Sweden

based on age (A.), size (B.), and age x size interactions (C.). See Table 3 for descriptions of hypotheses.