# University of Alberta

LINKING ENERGETICS OF INDIVIDUALS TO BEAR POPULATIONS

by

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A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

in

Wildlife Ecology and Management

Department of Renewable Resources


Spring 2014
Edmonton, Alberta

## DEDICATION

*"A man can achieve everything he wants,*

*if he stops worrying about who obtains the credit"*

I dedicate this work to Robert Hudson, who inspired this research and motivated me to move across all obstacles.

I am thankful to have had the opportunity to learn about generosity and human kindness from him.

**ABSTRACT**

Dynamics in wildlife populations emerge from the interactions between individuals and their environment. Constraints between individual nutrition and food availability are therefore fundamental to understanding how species adapt to environmental variability and to identify mechanisms controlling population-level processes. Brown bears (*Ursus arctos*) exhibit a wide variety of life history traits across its distribution that may be a consequence of differences in their diet. Amount and quality of nutritional resources influence individual energy storage and this plays a central role in female reproductive success. Using energetic simulations models I integrated existing knowledge of energetics and nutrition to explore how the interactions among the ecology and physiology of brown bears, and the nutritional quality of the bear's habitat influence body mass and thus reproductive success. The model simulates the transfer of energy and protein from the environment to the individual, accounting for allocation in maintenance, growth and reproduction. Results reveal that: lean tissue and high protein foods play a fundamental role in reproductive success of bears. The relationship between protein available early in the season and energy available late in the season determine the allocation of nutrients in growth and reproduction and thus influence life history traits such as body size. Minimum levels of fat reserves necessary to support reproduction during hibernation varied from 19% to 33% of the total body mass depending on the number of cubs and length of lactation. However, when nutritional environments are poor (resource limiting) lactating bears require higher levels of denning body fat to support lactation after den emergence. Interactions between the digestive tract capacity of bears and food resource quality limit mass gain in bears and thus female reproductive success.

Results reveal that brown bear populations in Alberta are restricted by the nutritional quality of its environment. This has two management consequences for Alberta's threatened population: (1) it limits the carrying capacity of bears resulting in small population sizes; and (2) rate of population recovery will be slower than what has been observed in other populations such as the Greater Yellowstone Ecosystem. This study provides insight into how nutritional factors control reproductive success in brown bears how this ultimately affects population processes.

# ACKNOWLEDGEMENT

I would like to thank to my supervisor Dr. Scott Nielsen. His support and guidance have been fundamental to continue and finishing this project.

I would like to thank Dr. Charlie Robbins, his help has been essential to develop this research. Also for the remarkable experience at the Washington State University Bear Center and the opportunity to work with such a welcoming group of people; Joy, Jennifer, Jasmin, Laura, Danielle, Justin.

Special gratitude I feel for Dr. Xianli Wang and MSc. Sean Coogan who have helped me with revisions, thoughtful suggestions and great friendship. Also to Dr. Jennifer Fortin and Dr. Andreas Zedrosser for their collaboration and friendship.

All my gratitude to the staff at the Department of Renewable Resources; Amanda, Nicole, Mike, Christie, Annette, Ian, Nash and Tammy.

To all my friends that have made all these years a wonderful and fructiferous experience; Trish, Diana, Simon, Karen, Stacy, Claudia, Allison, Mizohu, Lori, Virginia, Anayansi and Gabriela.

To my sweet husband Bjarne; for his enthusiasm and support accepting many hours alone at home and taking care of our little one. To my little son Tor, who has taught me the true meaning of a "reproductive trade-off".

To the Scandinavian Brown Bear Research Project (SBBRP) for providing the information to validate the hibernation model.

This project was partially funded by the Natural Sciences and Engineering Council (NSERC) and Alberta Innovates Biosolutions

**TABLE OF CONTENT**


**CHAPTER 1: INTRODUCTORY CHAPTER**

| | | |
|---|---|---|
| **1.** | **INTRODUCTION** | 1 |
| **1.1** | **Brown bears** | 2 |
| **1.2** | **Brown bears in Alberta** | 5 |
| **1.3** | **Dissertation Outline** | 6 |
| **2.** | **REFERENCES** | 8 |

**CHAPTER 2: ENERGETICS OF HIBERNATION AND REPRODUCTIVE TRADE-OFFS IN BROWN BEARS**

| | | |
|---|---|---|
| **1.** | **INTRODUCTION** | 15 |
| **2.** | **METHODS** | 17 |
| **2.1** | **Model design and purpose** | 17 |
| **2.2** | **Reproduction sub-model** | 18 |
| **2.3** | **Initial model conditions** | 20 |
| **2.4** | **"Daily mass loss composition" algorithm, model calibration and validation** | 20 |
| **2.5** | **Sensitivity analysis** | 22 |
| **2.6** | **Model simulation experiments** | 23 |
| **3.** | **RESULTS** | 23 |
| **3.1** | **Model parameterization and sensitivity** | 23 |
| *3.1.1* | *Daily mass loss composition" parameterization, model calibration and validation* | 23 |
| *3.1.2* | *Model sensitivity* | 24 |
| **3.2** | **Energetics of hibernating bears** | 25 |
| *3.2.1* | *Energetic reproductive costs of brown bears* | 25 |
| *3.2.1.* | *Bioenergetic trade-offs* | 25 |
| *3.2.3* | *Relationship between body condition and survival* | 26 |
| **4.** | **DISCUSSION** | 27 |
| **4.1** | **Conclusions** | 30 |
| **5.** | **REFERENCES** | 31 |

**CHAPTER 3: ASSESSING THE NUTRITIONAL QUALITY OF BROWN BEAR DIETS AMONG INTERIOR ECOSYSTEMS IN NORTH AMERICA**


| | | |
|---|---|---|
| **1.** | **INTRODUCTION** | 47 |
| **2.** | **METHODS** | 50 |
| **2.1** | **Brown bear food habits** | 50 |
| *2.1.1* | *West-central Alberta food habits* | 50 |
| *2.1.2* | *Flathead food habits* | 50 |
| *2.1.3* | *Greater Yellowstone Ecosystem food habits* | 51 |
| **2.2** | **Food items and nutritional values** | 52 |
| **2.3** | **Model structure** | 53 |
| *2.3.1* | *Model calculations* | 54 |
| **3.** | **RESULTS** | 55 |
| **3.1** | **Digestible energy and protein per food item (fresh food base)** | 55 |
| **3.2** | **Digestible energy in bear diets** | 55 |
| **3.3** | **Digestible protein in bear diets** | 56 |
| **3.4** | **Key food items** | 56 |
| *3.4.1* | *Energy contribution per food item* | 56 |
| *3.4.2* | *Protein contribution per food item* | 57 |
| **4.** | **DISCUSSION** | 58 |
| **4.1** | **Conclusions** | 61 |
| **5.** | **REFERENCES** | 63 |


**CHAPTER 4: LINKING INDIVIDUAL NUTRITION TO BROWN BEAR POPULATIONS**


| | | |
|---|---|---|
| **1.** | **INTRODUCTION** | 76 |
| **2.** | **METHODS** | 79 |
| **2.1** | **Model structure** | 79 |
| **2.2** | **Sub-models** | 79 |
| *2.2.1* | *Target mass gain* | 79 |
| *2.2.2* | *Food intake* | 81 |
| *2.2.2.1* | *Stomach capacity* | 81 |
| *2.2.2.2* | *Daily energy target* | 82 |
| *2.2.3* | *Reproductive cost* | 83 |
| *2.2.4* | *Energy balance* | 83 |
| *2.2.5* | *Protein balance* | 85 |
| *2.2.6* | *Mass gain* | 86 |
| *2.2.7* | *Hibernation* | 86 |
| **2.3** | **Model initialization** | 87 |
| **2.4** | **Model calibration** | 87 |
| **2.5** | **Sensitivity analysis** | 88 |

**2.6** **Model simulation experiments** 88
*2.6.1* *Bear diets* 89
*2.6.1.1* *Hypothetical diets* 89
*2.6.1.2* *Observed brown bear diets* 89
*2.6.2* *Reproductive conditions and target body mass* 90

**3.** **RESULTS** 90
**3.1** **Calibration and sensitivity** 90
**3.2** **Energetic reproductive cost** 91
**3.3** **Hypothetical diets** 91
**3.4** **Bear diets among ecosystems** 92

**4.** **DISCUSSION** 92
**4.1** **Conclusions** 96

**5.** **REFERENCES** 97

**CHAPTER 5: GENERAL DISCUSSION AND CONCLUSIONS**

**1.** **FINDINGS AND FUTURE STEPS** 109
**1.1** **Energetic components of hibernation** 110
**1.2** **Nutritional quality of brown bear diets** 111
**1.3** **Brown bears' energetic balance** 112
**2.** **MANAGEMENT IMPLICATIONS FOR BROWN BEAR POPULATIONS IN ALBERTA** 113
**3.** **FINAL CONCLUSIONS** 114
**4.** **REFERENCES** 115

**APPENDICES**
**3-A** TABLE 3-A 120
**4-A** DIET INFORMATION 131
**4-B** PROPORTION OF LEAN AND MASS GAIN 133
**4-C** STOMACH CAPACITY ALGORITHM 135
**4-D** ADJUST OF LACTATION COST 137
**4-E** MODEL CALIBRATION AND PARAMETERIZATION 140

# LIST OF TABLES


| | | |
|---|---|---|
| **Table 2-1** | Parameters and equations used in the hibernation model. Parameters were held constant during all model simulation experiments. | 44 |
| **Table 2-2** | Sensitivity analysis represents the variation in the "average daily mass loss" during lactation due to changes in model parameter. | 43 |
| **Table 2-3** | Energy and protein demand for different reproductive strategies. | 44 |
| **Table 3-1** | Nutritional information used to obtain the digestible energy and protein in one kilogram of fresh diet. | 73 |
| **Table 4-1** | Model calibration results | 104 |
| **Table 4-2** | Table 4-2 Sensitivity analysis results. | 104 |

## LIST OF FIGURES


| | | |
|---|---|---|
| **Figure 2-1** | Model diagram and schedule. The model simulates the body mass loss during hibernation. | 39 |
| **Figure 2-2** | Calibration and validation model results. | 40 |
| **Figure 2-3** | Effect of female body condition (% of denning body fat content) on total body mass loss (kg) and energy cost (kcal) and with increasing hibernation length. | 41 |
| **Figure 2-4** | Percent of lean mass loss for different reproductive strategies and initial fall body fat contents (%). | 42 |
| **Figure 2-5** | Estimated survival time for bears having different denning body fat contents and experiencing different reproductive strategies | 43 |
| **Figure 3-1** | Digestible energy (kcal/kg fresh food) and (b) protein (g/kg fresh food) per brown bear food item (grouped category of food items). | 69 |
| **Figure 3-2** | Digestible energy (kcal) and protein (g) in one kilogram fresh brown bear diet across different ecosystems. | 70 |
| **Figure 3-3** | Percent digestible energy contribution per food item category (fresh diet base) across ecosystems. | 71 |
| **Figure 3-4** | Percentage of digestible protein contributed per food item category (fresh diet base) across ecosystems. | 72 |
| **Figure 4-1** | Model diagram and schedule | 105 |
| **Figure 4-2a** | Energy and protein requirements for lactation. | 106 |
| **Figure 4-2b** | Amount of food (kg) necessary to supply maximum milk requirements per cub. | 106 |
| **Figure 4-3** | Energy requirements and denning body mass for Non-lactating, Pregnant and Lactating bears under different neutral diets. | 107 |
| **Figure 4-4** | Energy requirements for Non-lactating, Pregnant and Lactating bears under different diets. Diets resemble the food habits in the Foothill and Mountain ecosystems of Alberta (Canada, Munro et al., 2006), Flathead of southeast British Columbia (McLellan and Hovey, 1995) and the Greater Yellowstone Ecosystems (USA, Mattson et al., 1991; Fortin et al., 2013). | 108 |

# CHAPTER 1

# INTRODUCTORY CHAPTER

## 1. INTRODUCTION

Why do species occupy particular ecosystems?

Why do con-specifics differ in life history traits among populations?

What are the factors driving population dynamics?

How will species respond to landscape change?

These are core questions in the disciplines of ecology and wildlife management. To better understand these questions, a deeper knowledge is needed of how animals interact with their environment (Robbins, 1993; Schwartz and Hobbs, 1995; Barbosa et al., 2009).

A basic element of these interactions is that all living organisms must transfer energy and matter from their environment to themselves in order to live and reproduce (Robbins, 1993; Lovegrove, 2006). Energy is the fuel used in all chemical reactions that support life (Stevenson, 2006; Barbosa et al. 2009), and proteins are the main component of the structural body mass and enzymatic activity in animals (Robbins, 1993; Caolin, 2004). Environmental factors (e.g. food availability and quality) and organism's physiological characteristics (e.g. metabolic demands, digestive capacity) constrain these energetic flows, thereby affecting the supply of energy and protein necessaries for maintenance, growth and reproduction. Because these constraints directly influence survival and reproduction they have potential to shape life history traits and differentiate populations (Garland and Carter, 1994; Barboza et al., 2009).

Studies of wildlife nutrition and energetics can provide a mechanistic perspective of how wildlife and habitat interact and its effect on individual fitness. Wildlife nutrition links the nutrients demands of the organism with the nutrients supplies from their habitat (Barbosa et al., 2009; Raubenheimer et al., 2009), establishing the physiological elements

that are critical to life (Robbins, 1993). Energetic studies often assess the rate and at which individuals assimilate energy from the environment to support maintenance, growth and reproduction, accounting for the constraints in energy acquisition and allocation (Kooijman, 2000; Stevenson, 2006).

Together, these approaches have revealed that individual nutrition and energetic constraints influence reproduction, behaviour and survival through different mechanisms. In mammals, reproduction is influenced by the nutrients (fat, protein and mineral) content of the mother's body which passes to her offspring during pregnancy and lactation. Energy and nutrient requirements, in combination with the spatial-temporal distribution of food resources, influence food habits and foraging behaviour (Robbins, 1993; Nielsen et al., 2010; Coogan et al., 2012). Individual survival is affected by the body reserves (lipid and protein) that can be used in fasting periods (Caolin, 2004; Dunn et al., 1982; McCue, 2010), and low nutritional conditions increase vulnerability to disease and predation (Robbins, 1993; Barbosa et al 2009).

In my dissertation I have used brown bears (*Ursus arctos*) as a focal species to explore how constraints in energy and nutrient acquisition and allocation influence reproductive success and I link this to population processes, such as population density, carrying capacity and growth rates. In this introductory chapter, I first present background information necessary to understand the ecology and physiology of brown bears and how this influences individual nutrition and energetics. I follow this by presenting the main questions and objectives of my research and how they are organized in this document.

## 1.1 Brown bears

Brown bears are one of most extensively distributed large carnivore in the world, occupying a wide range of habitats from tundra, desert and montane environments to temperate forest (McLellan et al., 2008; McCarthy et al., 2009; Bojarska and Selva, 2011). Bear populations exhibit a variety of life history traits, such as body size, litter size, age of first litter primiparity (age of first litter) and inter-litter interval (Hilderbrand

et al., 1999b; Ferguson and McLoughlin, 2000; Zedrosser et al., 2009; 2011). Differences in life history traits might be highly influenced by the spatial and temporal variability in food resources, which ultimately constraint the energy and protein intake and storage necessary to support reproduction (Farley and Robbins, 1995; Bojarska and Selva, 2011; López-Alfaro et al., 2013; Nielsen et al., 2013).

A critical energetic bottleneck faced by all reproductive female brown bears is the hibernation or denning phase. The denning period generally extends between 120 to 210 days depending on food availability (Farley and Robbins, 1995; Friebe et al., 2001; Schwartz et al., 2003; Hilderbrand et al., 2000). During this phase, bears stop eating, reduce their activity and minimize their protein catabolism to decrease energetic costs (Watts and Jonkel, 1988; Barboza et al., 1997; Tøien et al., 2011; Robbins et al., 2012a). Throughout this phase, lactating females give birth and start nourishment. Litter size varies between 1 and 3 cubs, and depending on maternal denning body fat content, nourishment of cubs through lactation can last for 60 to 74 days during hibernation (Robbins et al., 2012b). To support maintenance and reproduction costs during hibernation, bears use the fat and lean mass accumulated during the active period (Farley and Robbins, 1995; Robbins et al., 2012b).

Brown bears accumulate lean mass during the spring and early summer, while fat reserve is accumulated during late summer and early fall (Hilderbrand et al., 1999a; Felicetti et al., 2003). Fat mass gained before to hibernation has been recognized as a key factor in the reproductive success of bears (Atkinson and Ramsay, 1995; Atkinson et al., 1996; Farley and Robbins, 1995; Hilderbrand et al., 2000; Robbins et al., 2012b). Energy storage as fat provides approximately seven times more energy than energy storage as lean mass (Blaxter, 1989). However, lean tissue provides the protein necessary for fetus develop and milk production (Blaxter, 1989; Robbins, 1993; Farley and Robbins, 1995; Molnár et al., 2009). Consequently, lean mass gained before to hibernation also has an important role in reproductive success (López-Alfaro et al., 2013). Despite the importance of body reserves on female reproductive success, little is known about minimum thresholds of fat and lean mass necessary to support reproduction and how these vary among environments typical of current brown bear range.

The nutritional quality of food resources available affects the energy and protein intake and therefore affects the reproductive success of bears. Brown bears have an omnivorous foraging strategy (Robbins et al., 2004; 2006), and depending on food availability, bear diets can go from largely carnivorous to largely herbivorous (Hilderbrand et al., 1999b; Bojarska and Selva, 2011). A number of studies have shown how food resources influence life history traits in bears. Hilderbrand et al. (1999b) found that the proportion of meat, especially salmon (*Oncorhynchus spp.*), has a direct impact in female body size, litter size and population density. But in a similar analysis, McLellan (2011) found that when populations having access to salmon are excluded from this analysis, amount of dietary meat is negatively correlated to population density. In addition, primary productivity and seasonality influence reproductive traits such as age of primiparity and inter-birth interval (Ferguson and McLoughlin, 2000).

Food habits and nutritional studies have been among the first steps taken to understand bear-habitat relationships (Mattson et al., 1991; Hovey and McLellan, 1995; Munro et al., 2006; Fortin et al., 2013). Studies of food habits often describe changes in diet composition (food items) through the active period, while nutritional studies measure the energy and protein contents for different bear food items such as: ungulates, salmon, berries, ants, green vegetation, mushrooms, roots and nuts (Hamer and Herrero, 1987; Pritchard and Robbins, 1990; Noyce et al., 1997; Welch et al., 1997; Swenson et al. 1999; Rode et al., 2001; Mattson et al., 2004; Coogan et al., 2012). These studies, however, do not provide a nutritional evaluation for the complete diet, which has limited our capacity to compare among ecosystems and understand the nutritional mechanisms affecting the reproductive success of bears and thus differences in life history traits.

Nutritional quality of the bear diet, together with bear physiological factors, constrains the total energy and protein assimilated and therefore influences fitness in bears. Necessary food intake is based on energy and protein requirements, which increase with reproduction (Robbins, 1993). Energy maintenance cost depends on the individual body mass (McNab, 2008) and for brown bears this cost increases from 1 – 3 times depending on the diet protein content (Pritchard and Robbins 1989; Rode et al., 2000; Felicetti et al.,

2003; Robbins et al., 2007; Erlenbach et al., 2014). Protein maintenance cost depends on the metabolic body mass (EUN, Robbins, 1993) and dry matter intake (MFN, Pritchard and Robbins, 1989). Digestive tract capacity in relation to food digestibility, limits the rate of nutrient intake (Robbins, 1993; Barbosa et al., 2009). Finally, the spatial distribution of food resources determines foraging efficiency (Welch et al., 1997; Rode et al., 2001; Robbins et al., 2007).

Physiological and nutritional elements influencing bear body mass dynamics influence reproductive success in bears and therefore affect population dynamics. Several studies have highlighted the importance of food resources on brown bear reproductive success and population dynamic (Hilderbrand et al., 1999b; Ferguson and McLoughlin, 2000; McLellan, 2011; Nielsen et al., 2010; 2013). Little has been done, however, to integrate different aspects of brown bear physiology and their nutritional landscape in understanding the mechanisms influencing bear body mass dynamics under different environmental conditions.

### 1.2 Brown bears in Alberta

In 2010 the brown bear population in Alberta was listed as a threatened species due to their small population size (~700 bears), life history attributes and the potential negative impacts of human interventions in bear habitat (ASRD and ACA, 2010). Bear populations are limited to the western part of the province associated with the foothills, mountains and western boreal forest (Munro et al., 2006). Alberta populations differ dramatically in individual density (4.8 to 18.1 bear/1000 $km^2$) and body condition (ASRD and ACA, 2010). Differences in population density are also observed in areas outside Alberta. In southwest British Columbia, bear density is 25-55 individuals/1000 $km^2$ (McLellan 2011; Zedrosser et al., 2011) and in the Yellowstone ecosystem (USA) it is 13-16 individuals /1000$km^2$ (Zedrosser et al., 2011).

Lower population densities in Alberta may be a consequence of two processes. First, the limited concentration of nutritious food resources (e.g., lack of salmon or low berry

production), and a short growing season (Munro et al., 2006) limit the store of lean and fat mass before to denning, affecting maternal reproductive success. Second, the increase in mortality rates due to habitat disturbances (e.g., forest harvesting, energy developments, road building; Nielsen et al. 2004b; Nielsen et al. 2008).

Over the past decade numerous habitat studies have increased our knowledge of brown bear-habitat interactions in Alberta (Munro et al. 2006; Nielsen et al. 2003, 2004a, b, c, 2006, 2010). Recent emphasis has focussed on assessing nutritional landscapes (Nielsen et al. 2010) and relating this to individual body condition, reproductive success and population dynamics (Nielsen et al., 2013). However, studies that link individual energetic requirements and nutritional landscape to population level phenomena have not been fully explored. This knowledge is necessary to define population recovery targets in Alberta, together with improving land management plans.

### 1.3 Dissertation Outline

In this dissertation I have explored how key elements in the physiology of brown bears and their nutritional landscape interact to affect reproductive success. To reach this goal I built two mechanistic simulation models. First, is a Nutritional Landscape model (NL model) that simulates the temporal changes in the digestible protein (kg) and energy (kcal) available in one kilogram of fresh diet. These diets represent the combination of different food items (e.g., berries, vegetation, ungulates) among ecosystems by approximating the average food habits of bears in Alberta (Munro et al., 2006), Flathead (McLellan and Hovey, 1995) and Yellowstone (Mattson et al., 1991; Fortin et al., 2013). Second, is an energetic model that integrates brown bear physiology and ecology with nutritional landscape information to simulate the daily body mass dynamics (fat and lean mass gain/loss) of brown bears. During hibernation, body mass dynamics depends on maintenance and reproduction costs. Throughout the active period, the model incorporates daily nutritional intake using the diet information from the NL model. The model operates on a set of scenarios reflecting reproductive strategies (non-

lactating/lactating, litter size, lactation period) and environmental conditions (hibernation length, bear diets) using a set initial body condition.

I used these models to explore three questions. In Chapter 2 ("Energetic of hibernation and reproductive trade-offs in brown bears") I identified the energetic constraints and reproductive energetic costs for lactating bears during hibernation. For this purpose I used the energetics model in the hibernation phase to address three specific questions: 1) what are the energetic trade-offs for hibernating female brown bears, 2) how does environmental variability affect reproductive success based on maternal condition, lactation period, litter size and hibernation length and 3) what are the minimum body fat requirements necessary to support reproduction under different hibernation lengths.

In Chapter 3 ("Assessing the nutritional quality of brown bears diets among interior ecosystems in North America") I evaluate the nutritional quality of brown bear diets. I used the NL model to ask two specific questions: 1) what are the differences in nutritional quality (e.g., amount of digestible protein and energy) of bear diets in west-central Alberta, the Flathead, and both the historical (1977 - 1987) and recent (2007 – 2009) diet in the Great Yellowstone ecosystem; and 2) what food resources are most critical for providing energy and protein to bears in each ecosystem.

In Chapter 4 ("Linking individual nutrition to brown bear populations: an energetic perspective") I used the energetics model (from hibernation to the end of the active period) to explore three specific questions: 1) what are the energy and protein requirements of bears during the active period; 2) what are the trade-offs and key elements of bear physiology and nutritional quality of foods available that influence body mass dynamics; and 3) what is the impact of Alberta's food resources on reproductive success of bears and population recovery.

Finally, Chapter 5 represents the conclusions chapter where I summarize the results and management implications of my research. I also discuss their implications in a broader framework suggesting future research topics. This dissertation is structured as "Paper Format". Chapters 2, 3 and 4 have been formatted for Journal of Ecological Modelling.

## 2. REFERENCES

ASRD & ACA (2010) Status of the Grizzly Bear (*Ursus arctos*) in Alberta: Update 2010. Alberta Sustainable Resources Development. Wildlife Status Report No. 37 (Update 2010). Edmonton, AB. 44 pp.

Atkinson SN, Ramsay MA. The effects of prolonged fasting of the body composition and reproductive success of female clack bears (*Ursus maritimus*). Funct Ecol 1995;9:559-667.

Atkinson SN, Nelson RA, Ramsay MA. Changes in body composition of fasting polar bears the effect of relative fatness on protein conservation. Physiol Zool 1996;69:304-316.

Barbosa PS, Parker KL, Hume ID. Integrative wildlife nutrition. 1st ed. Berlin: Springer-Verlag; 2009.

Barbosa PS, Farley SD, Robbins CT. Whole-body urea cycling and protein turnover during hyperphagia and dormancy in growing bears (*Ursus americanus and U. arctos*). Can J Zool 1997;75:2129-2136.

Bojarska K, Selva N. Spatial patterns in brown bear *Ursus arctos* diet: the role of geographical and environmental factors. Mammal Review. 2011:42;120-143.

Blaxter KL. Energy metabolism in animals and man. 1st ed. United Kingdom: Cambridge University press; 1989.

Caolin M. Modeling of lipid and protein depletion during total starvation. Am J Physiol-Endoc M 2004;287:790-798.

Coogan SCP, Nielsen SE, Stenhouse GB. Spatial and temporal heterogeneity creates a "brown tide" in root phenology and nutrition. ISRN Ecology 2012;2012:1-10.

Dunn MA, Houts SK, Hartsook EW. Effects of fasting on muscle protein turnover, the composition of weight loss, and energy balance of obese and nonobese zucker rats. J Nutr 1982;112:1862-1875.

Erlenbach JA, Rode KD, Raubenheimer D, Robbins CT. Nutrition wisdom of bears: Macronutrient selection and metabolism. J Mammal 2014:in press.

Farley SD, Robbins CT. Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. Can J Zool 1995;73:2216-2222.

Felicetti LA, Robbins CT, Shipley LA. Dietary protein content alters energy expenditure and composition of the gain in grizzly bears (*Ursus arctos horribilis*). Physiol Biochem Zool 2003;76:256-261.

Ferguson SH, McLoughlin PD. Effect of energy availability, seasonality and geographic range on brown bear life history. Ecography 2000;23:193-200.

Fortin JK, Schwartz CC, Gunther KA, Tiesberg JE, Haroldson MA, Evans MA, Robbins CT. 2013. Dietary adjustability of grizzly bears and American blanck bears in Yellowstone National Park. J Wildl Manage 77:270-281.

Friebe A, Swenson JE, Sandegren F. Denning chronology of female brown bears (*Ursus arctos*) in central Sweden. Ursus 2001;12:37-46.

Garland T, Carter PA. Evolutionary physiology. Annu Rev Physiol 1994;56:579-621.

Hamer D, Herrero S. Grizzly bear food and habitat in the front ranges of Banff National Park, Alberta. International Conference of Bear Research and Management 1987;7:199-213.

Hilderbrand GV, Jenkins SG, Schwartz CC, Hanley TA, Robbins CT. Effect of seasonal differences in dietary meat intake on changes in body mass and composition in wild and captive brown bears. Can J Zool 1999a;77:1623-1630.

Hilderbrand GV, Schwartz CC, Robbins CT, Jacoby ME, Hanley TA, Arthur SM, Servheen C. Importance of meet, particular salmon, to body size, population productivity and conservation of North American Brown Bears. Can J Zool 1999b; 77:132-138.

Hilderbrand GV, Schwartz CC, Robbins CT, Hanley TA. Effect of hibernation and reproductive status on body mass and condition of coastal brown bears. J Wildl Manage 2000;64:178-183.

Kooijman SALM. Dynamic energy and mass budgets in biological systems. 2nd ed. Cambridge: Cambridge University Press; 2000.

López-Alfaro C, Robbins CT, Zedrosser A, Nielsen SE. Energetic of hibernation and reproductive trade-offs in Brown Bears. Ecol. Modell 2013;270:1-10.

Lovegrove BG. The power of fitness in mammals: perception from the African slipstream. Physiol Biochem Zool 2006;79: 224-236.

Mattson DJ, Blanchard BM, Knight RR. Food habits of Yellowstone grizzly bears, 1977-1987. Can J Zool 1991;69:1619-1629.

Mattson DJ, Barber K, Maw R, Renkin R. Coefficients of productivity for Yellowstone's grizzly bear habitat: U.S. Geological Survey, Biological Resources Discipline, Biological Science Report USGS/BRD/BSR–2002-0007. 2004

McCarthy TM, Waits LP, Mijiddorj B. Status of the Gobi bear in Mongolia as determined by noninvasive genetic methods. Ursus 2009;20:30-38.

McLellan B. 2011. Implications of high-energy and low-protein diet on the body composition, fitness, and competitive abilities of black (*Ursus americanus*) and grizzly (*Ursus arctos*) bears. Can J Zool 89:546-558.

McLellan BN, Hovey FW. The diet of grizzly bears in the Flathead River drainage of southeastern British Columbia. Can J Zool 1995;73:704-712.

McLellan BN, Servheen C, Huber D, (IUCN SSC Bear Specialist Group). *Ursus arctos*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1. <www.iucnredlist.org>. Downloaded on 19 October 2013; 2008.

McCue M. Starvation physiology: Reviewing the different strategies animals use to survive a common challenge. Comp Biochem Phys A 2010;156:1-18.

McNab BK. An analysis of the factors that influence the level and scaling of mammalian BMR. Comp Biochem Phys A Mol Integr Physiol 2008;151:5-28.

Molnár PK, Klanjscek T, Derocher AE, Obbard ME, Lewis MA. A body composition model to estimate mammalian energy stores and metabolic rates from a body mass and body length, with application to polar bears. J Exp Biol 2009;212:2313-2323.

Molnár PK, Derocher AE, Thiemann GW, Lewis MA. Predicting survival, reproduction and abundance of polar bears under climate change. Biol Conserv 2010;143:1612-1622.

Munro RHM, Nielsen SE, Stenhouse GB, Boyce MS. Seasonal and diet patterns of grizzly bear diet and activity in west-central Alberta. J Mamm 2006;87:1112-1121.

Nielsen SE, Boyce MS, Stenhouse GB. Grizzly bears and forestry: I. Selection of clearcuts by grizzly bears in west-central Alberta, Canada. For Ecol Manage 2004a:199;51-65

Nielsen SE, Herrero S, Boyce MS, Benn B, Mace RD, Gibeau ML, Jevons S. Modelling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies Ecosystem of Canada. Biol Conserv 2004b;120:101-113.

Nielsen SE, Munro RHM, Bainbridge EL, Stenhouse GB, Boyce MS. Grizzly bears and forestry II. Distribution of grizzly bear foods in clearcuts of west-central Alberta, Canada. For Ecol Manage 2004c:199;67-82

Nielsen SE, Stenhouse GB, Beyer HL, Huettmann F, Boyce MS. Can natural disturbance-based forestry rescue a declining population of grizzly bears? Biol Conserv 2008:141;2193-2207

Nielsen S, Cattet MRL, Boulanger J, Cranston J, McDermid GJ, Shafer ABA, Stenhouse GB. Environmental, biological and anthropogenic effects on grizzly bear body size: temporal and spatial considerations. BMC Ecol 2013;13-31

Nielsen SE, Boyce MS, Stenhouse GB, Munro RHM. Development and testing of phenologically driven grizzly bear habitat models. Ecoscience 2003; 10:1-10.

Nielsen SE, McDermid G, Stenhouse, GB, Boyce, MS. Dynamic wildlife habitat models: Seasonal foods and mortality risk predict occupancy-abundance and habitat selection in grizzly bears. Biol Conserv 2010;143:1623-1634.

Noyce KV, Kannowski PB, Riggs MR. Black bears as ant-eaters: seasonal associations between bear myrmecophagy and ant ecology in north-central Minnesota. Can J Zool 1997;75:1671-1686.

Pritchard GT, Robbins CT. Digestive and metabolic efficiencies of grizzly and black bears. Can J Zool 1990;68:1645-1651.

Raubenheimer D, Simpson SJ, Mayntz D. Nutrition, ecology and nutritional ecology: toward and integrated framework. Funct Ecol 2009;23:4-16

Robbins CT, Lopez-Alfaro C, Rode KD, Tøien Ø, Nelson LO. Hibernation and seasonal fasting in bears: the energetic cost and consequences for polar bears. J Mammal 2012a; 93:1493-1503.

Robbins CT, Meray B-D, Fortin J, Lynne Nelson O. Maternal condition determines birth and growth of newborn cubs. J Mammal 2012b;93:540-546

Robbins CT, Fortin JK, Rode KD, Farley SD, Shipley LA, Felicetti LA. Optimizing protein intake as a foraging strategy to maximize mass gain in an omnivore. Oikos 2007;116:1675-1682.

Robbins CT, Schwartz CC, Gunther KA, Servheen. Grizzly bear nutrition and ecology studies in Yellowstone National Park. Yellowstone Science 2006;14:19-26.

Robbins CT, Schwartz CC, Felicetti LA. Nutritional ecology of ursids: A review of newer methods and management implications. Ursus 2004;15:161-171.

Robbins CT. Wildlife feeding and nutrition. 2nd ed. San Diego, USA: Academic Press; 1993.

Rode KD, Robbins CT, Shipley LA. Constraints on herbivory by grizzly bears. Oecologia 2001;128:62-71.

Rode KD, Robbins CT. Why bears consume mixed diets during fruit abundance. Can J Zool 2000;78:1640-1645.

Stevenson RD. Ecophysiology and conservation: The contribution of energetics: Introduction to the symposium. Integrative and comparative biology 2006;46:1088-1092.

Schwartz CC, Hobbs NT. Forage and Range Evaluation. In Bioenergetic of wild herbivores. Editors: Hudson RJ, White RG. 1995. CRC Press Inc. Boca Raton, Florida, USA; 1995

Schwartz CC, Miller SD, Haroldson MA. Grizzly bear. In: G. A. Feldhamer, B. C. Thompson, and J. A. Chapman (eds), Wild mammals of North America: biology, management, and conservation, pp. 556-586. Johns Hopkins University Press, Baltimore, Maryland, USA; 2003

Swenson JE, Jansson A, Rilg R, Sandegren F. Bears and ants: myrmecophagy by brown bears in central Scandinavia. Can J Zool 1999;77:551-561.

Tøien Ø, Blake J, Edgar DM, Grahn DA, Heller HC, Barnes BM. Hibernation in black bears: Independence of metabolic suppression from body temperature. Science 2011;331:906–909.

Watts PD, Jonkel C. Energetic cost of winter dormancy in grizzly bear. J Wildl Manage 1988;52:654–656.

Welch CA, Keay J, Kendall KC, Robbins CT. Constraints on frugivory by bears. Ecol 1997;78:1105-1119.

Zedrosser A, Dahle B, Stoen OG, Swenson JE. The effect of primiparity on reproductive performance in brown bears. Oecologia 2009;160:847-854.

Zedrosser A, Steyaert SMJG, Gossow H, Swenson JE. Brown bear conservation and the ghost of persecution past. Biol Conserv 2011;144:2163-2170.

# CHAPTER 2[1]

# ENERGETICS OF HIBERNATION AND REPRODUCTIVE TRADE-OFFS IN BROWN BEARS

## 1. INTRODUCTION

Maternal fitness is partly a function of a mothers' ability to transfer energy and protein from the environment to her offspring (Brown et al., 1993; Lovegrove, 2006). Environmental factors (e.g. food availability) and an organism's physiology (e.g. metabolic demands) constrain this energy flux (Lovegrove, 2006). Reproduction constitutes one of the most expensive energetic demands in mammals, and lactation is more costly than gestation (Robbins, 1993; Stearns 1992). Thus, strategies used to allocate reproductive energy in different environments should be under strong selection and have the potential to differentiate populations (Barboza et al., 2009; Garland and Carter, 1994).

Brown bear (*Ursus arctos*) reproductive costs are especially high because, unlike most mammals, fetal and early neonatal growth occurs after the female has entered the winter den and begun fasting (Atkinson and Ramsay, 1995; Farley and Robbins, 1995; Oftedal et al., 1993; Ramsay and Dunbrack, 1986). To support these energetic costs, bears rely on fat and lean reserves accumulated during their active, non-hibernating period (Atkinson and Ramsay, 1995; Farley and Robbins, 1995). Limitations to the accumulation of fat mass and lean mass (muscle tissue) during the active period may therefore restrict reproductive investments resulting in variations in litter size and length of lactation during hibernation (Robbins et al., 2012b). By identifying the major energetic trade-offs

[1] A version of this chapter has been published as: López-Alfaro C, Robbins CT, Zedrosser A, Nielsen SE. Energetic of hibernation and reproductive trade-offs in Brown Bears. Ecological Modelling 2013;270:1-10

in reproduction, we can better understand how bears have adapted to different ecosystems and thus predict their responses to environmental change.

Food resources vary both spatially and temporally (Coogan et al., 2012; Nielsen et al., 2003; Nielsen et al., 2010). Brown bears have developed several adaptive strategies for dealing with environmental uncertainties in resource supply, which ultimately affects maternal body condition and reproductive effort. For example, females that are too lean (< 20% body fat) at the start of hibernation will not implant developing embryos, whereas fat mothers will implant embryos, give birth earlier, and produce better or more milk than lean mothers (Hissa, 1997; Robbins et al., 2012b). Depending on maternal condition, the date of implantation and thus birth can vary by 39 or more days (Bridges et al., 2011; Robbins et al., 2012b). Thus, fatter mothers are able to nurse their cubs longer in the den and thereby produce larger cubs with a better chance of survival following den emergence (Robbins et al., 2012b). Brown bear litter size commonly varies from 1 to 3 cubs, which may be a consequence of maternal condition, body size, age, and human persecution history (Zedrosser et al., 2011). Cubs born in larger litters are often smaller at den emergence than those born in smaller litters (Derocher and Stirling, 1998; Farley and Robbins, 1995; Robbins et al., 2012b). Total lactation cost may not, however, increase in proportion to litter size, as the total new-born mass of litters of triplets was 17% less than that of twins (Robbins et al. 2012b). Consequently, the amount of milk produced by a lactating female brown bear is likely determined by the amount of available reserves that exceed her own survival needs, and not by cub demand.

In bears, the proportion of lean tissue versus fat reserves used to supply energy is largely influenced by the body fat content at the time of denning (Atkinson and Ramsay, 1995; Robbins, 1993). When body fat reserves are high, the main source of energy is fat, but when fat reserves are low, due either to inadequate active season food resources or prolonged hibernation, lean mass is increasingly used as an energy source (Caolin 2004; Dunn et al., 1982; McCue, 2010). Because of this, most hibernation studies have focused on the role of fat in determining reproductive success (Atkinson and Ramsay, 1995; Atkinson et al., 1996; Farley and Robbins, 1995; Hilderbrand et al., 2000). Little effort

has been made to understand the role of protein reserves in affecting bear reproductive success and the temporal processes of lean tissue and fat depletion during hibernation.

Energetic costs of hibernating female brown bears depends on several factors including: (1) reproductive investment related to the number of cubs born, length of lactation in the den and the amount and quality of milk produced, (2) maternal condition when entering the den determine fat and lean reserves available for self-survival and reproduction, and (3) length of hibernation. Although each of these factors is well-known, little is known about the trade-offs between them. Due to the multitude of factors that affect the energetic budget of bears, empirical approaches to assessing these trade-offs is impractical or difficult to implement. Model simulations have become an important tool for understanding complex processes in ecology (Starfield, 1997; Owen-Smith, 2007), determining key parameters in population dynamics (López-Alfaro et al., 2012; Mazari et al., 2006; Starfield and Bleloch, 1991), and exploring new scenarios including survival thresholds (Fahrig, 1998; Hildenbrandt et al., 2006; Molnár et al., 2010; Wiegand et al., 1998). In this study we developed a simulation model of hibernating female brown bears using published equations and parameters for individual energetic components. Our objectives were to evaluate the energy and protein costs of reproduction for hibernating female brown bears, to identify energetic trade-offs between reproductive investment and self-survival, and evaluate how these trade-offs might vary under different environmental conditions. Variables assessed include maternal condition (denning body fat content), length of lactation, litter size, and length of hibernation.

## 2. METHODS

### 2.1 Model design and purpose

Energetic demands of hibernating females can be divided into maintenance and reproductive costs. Energy maintenance cost (MtbHib) is a function of body mass (Table 1; Blaxter, 1989; Robbins et al., 2012a; Tøien et al., 2011). During hibernation bears are able to recycle the nitrogen from their urea and thus conserve protein (Barbosa et al.,

1997; Tøien et al., 2011). In our model we therefore assumed no protein requirements for physiological maintenance. For lactating bears, the energy and protein costs of fetal growth and milk production were added to the expected maintenance cost for non-lactating bears (see reproduction sub-model). Tissue reserves that can be used to support these costs were partitioned into lean and fat mass. As long as abundant fat is available to meet energy requirements, bears conserve protein during hibernation (Barboza et al., 1997; Ramsay and Dunbrack, 1986). Energy stored as fat has nearly seven times more energy than lean mass (energy content of fat: 9.1 kcal/g; lean mass: 1.2 kcal/g; Blaxter, 1989, Farley and Robbins, 1995). However, lean mass provides the protein used for growth of the fetus and neonate (Caolin, 2004; Koijman, 2000; Molnar et al., 2009).

Our model simulates the energetic balance of hibernating bears by integrating the main metabolic mechanisms that determine the use of lean and fat reserves during hibernation for non-lactating and lactating bears (Fig. 1, Table 1). The model was developed in Stella 10 (Isee Systems, Inc., 2006) using a daily time step. Day one corresponds to den entry and the final model simulation day corresponds to den emergence. Each day the model accounts for the use of lean and fat reserves to supply the energy and protein costs of hibernation using two separate pathways (i.e., one for lean and the other for fat). We used an algorithm called "Daily mass loss composition" to estimate the daily proportion of each body component that is lost depending on the animal's body fat content. Daily mass loss composition was parameterized based on the fit with other studies (see section 2.4). Protein content of the lean mass was assumed to be 21.1% (Blaxter, 1989; Farley and Robbins, 1995). Because metabolic rate increases at the beginning and the end of hibernation (Friebe et al., 2013; Robbins et al., 2012b; Tøien et al., 2011,), we increase MtbHib during the initial and final two weeks of hibernation to a maximum of 50% above baseline rates.

### 2.2 Reproduction sub-model

The reproduction sub-model simulates the energetic cost of gestation and lactation, which vary with litter size and length of lactation. Gestation cost was assumed to be the cost of

the growth of the fetus and gravid uterus. The cost of fetal growth was set at 80% of the total gestation cost, while gravid uterus was the remaining 20% (Robbins, 1993). Costs for fetal growth includes the energy used to maintain fetal tissues as well as the protein and fat accumulated in growth. Because there was no available information on the body composition of neonatal brown bears, we used data from the closely related American black bear (*Ursus americanus*; Oftedal et al., 1993).

Brown bears are delayed implanters that breed in May and June with the developing embryos implanting for sufficiently fat bears by early November (Spady et al., 2007). Small, altricial cubs are born in early January after a gestation period of 60 days (Ramsay and Dunbrack, 1986; Robbins et al., 2012b). Neonatal mass varies from 250 – 400 g for European brown bears (Hissa, 1997) and up to 0.650 kg for North American brown bears (Robbins et al., 2012b). In our simulations, we assumed the newborn body mass to be constant at 0.650 kg (Robbins et al., 2012b). Because fetal growth across a wide range of mammals follows a curvilinear function that sharply increases during the final third of pregnancy (Robbins, 1993), we distributed the energy and protein accumulated by cubs during gestation to be proportional to this curve with an assumed gestation period of 60 days (Ramsay and Dunbrack, 1986; Robbins et al., 2012b). We varied birth dates over a 14 day interval to explore the energetic costs of early and late births. Length of lactation therefore varied from 60 to 74 days pre-emergence and is defined by the initial model condition.

Energy and protein demands for lactation were based on those reported in Farley and Robbins (1995). Daily milk production per cub was multiplied by the number of cubs, which was defined as the original litter size. We used this approach to explore why lactating females do not seem to increase milk production in proportion to the number of cubs (Robbins et al., 2012b). We included a "milk production efficiency" parameter, to represent the conversion efficiency of the mother's tissue energy to milk energy and we set the value to 85% (Blaxter, 1989).

## 2.3 Initial model conditions

Initial inputs included maternal body mass (kg), initial body fat content (%), length of hibernation (days), length of lactation (days), and number of cubs. Each condition is described below.

*Body mass and initial body fat content*: Body masses of the females were based on those of Farley and Robbins (1995). Because we wanted to explore the energetic trade-offs faced by hibernating bears of different body condition, we set lean mass at 100 kg and varied initial body fat content from 20%, 30% and 40%. Consequently, initial body masses were 125, 143 and 167 kg, respectively.

*Length of Hibernation*: In general, hibernation length increases with latitude (Johnson and Pelton, 1980) with the number of days ranging from 120 to 210 days (Schwartz et al., 2003). We used the following four hibernation lengths to reflect this range: 120, 150, 180 and 210 days.

*Length of lactation and number of cubs:* To evaluate reproductive costs, we simulated lactating bears with a litter size of either 1 or 2 cubs and birth at either 60 or 74 days before den emergence. This resulted in the following five reproductive strategies: (1) Non-lactating (Non-Lac.), (2) Lactating for 60 days and one cub (Lac. 60 days, 1 cub), (3) Lactating for 60 days and two cubs (Lac. 60 days, 2 cubs), (4) Lactating for 74 days and one cub (Lac. 74 days, 1 cub) and (5) Lactating for 74 days and two cubs (Lac. 74 days, 2 cubs). We did not simulate litters of three cubs because lactation costs are similar to that of twins (Robbins et al., 2012b).

## 2.4 "Daily mass loss composition" algorithm, model calibration and validation

Most studies of hibernating bears have measured the average mass lost across the entire hibernation period and have related this to body fat content at den entry (Atkinson et al., 1996; Farley and Robbins, 1995; Robbins et al., 2012a). Because we were interested in

exploring the dynamics of body mass loss and the role of protein reserves on a daily time step, we parameterized an algorithm to estimate the daily proportion of fat and lean mass used to supply energy demands depending on the body fat content (%) on that day. The composition of mass loss in other species depends on the time-specific body composition, and protein is used as an energy source only when certain thresholds of fat depletion have been reached (Dunn et al., 1982; McCue, 2010). Below this threshold, the proportion of lean reserves used as energy sources increases linearly.

We parameterized the threshold under which lean mass is used as an energy source and calibrated the model using two empirical studies for hibernating brown bears (Farley and Robbins, 1995; Hilderbrand et al., 2000). For parameterization, we ran the model using threshold values from 5% - 20% in increments of 1%. We chose the parameter value that gave us the most similar result in comparison to the empirical data (Farley and Robbins, 1995 and Hilderbrand et al., 2000). In addition we also validated the model with independent data from a long-term study of free-ranging brown bears in Sweden (Swenson et al., 1995; Zedrosser et al., 2009, 2013). We replicated the conditions described in these studies and compared the model outcome with their results.

For the study of Farley and Robbins (1995), we simulated the body mass loss for bears with an initial mass of 80, 100, 150, 200, 250, 300 and 350 kg during 120 days of hibernation. Because denning body fat content was not reported in their study, we assumed a random value between 22% to 30% body fat. For lactating bears, we simulated gestation and lactation for 2 cubs born 60 days before den emergence and a maternal fall body mass of between 150 to 170 kg.

For the Hilderbrand et al. (2000) study (Fig. 2b), we simulated the hibernation of non-lactating and lactating bears with 2 cubs across 189, 208, and 227 days of hibernation. For non-lactating bears, fall body mass varied randomly between 218 and 278 kg and body fat content varied randomly between 26 and 40%. For lactating bears, fall body mass varied randomly between 200 and 260 kg and body fat content varied randomly between 22 and 43%.

We subsequently used data of free-ranging Scandinavian brown bears (Swenson et al., 1995; Zedrosser et al., 2009, 2013) collected between 1984-2012 to validate that the adjusted model could accurately predict the characteristics of mass loss and reproduction for hibernating bears (Fig. 2c). All females were ≥ 5 years. Fall body masses were based on bears killed during the regular hunting season in August and September. Spring body masses were from bears captured in late April and early May (Arnemo et al., 2011). We simulated the hibernation of non-lactating and lactating bears with 2 cubs during 181 days of hibernation (Friebe et al., 2001). Body mass was estimated randomly from a normal distribution curve with an average of 130.9 ± 29.1 kg. Because denning body fat content was unknown, we assumed a random value between 20% to 30% body fat.

### 2.5 Sensitivity analysis

We used a Sensitivity Index (Sx) to estimate the effects of parameters on model predictions (Bendoricchio and Jorgensen, 2001). The Index relates changes in a variable's response with changes in the parameter using Equation 1:

Eq. 1 $$Sx = \frac{(RV_{1-} RV_0)/RV_0}{(P_{1-} P_0)/P_0},$$

where $RV_0$ is the response variable in the base condition, $RV_1$ is the response variable after changing the parameter, $P_0$ is the parameter in the base condition and $P_1$ is the parameter change with all other parameters kept constant. Sensitivity was assessed for five model parameters (Table 2) with an increase and decrease in parameters of 5%, 25% and 50%. We used the "average daily mass loss (kg) during lactation" as the response variable and ran the model for 120 days; initial body mass of 160 kilograms, nursing two cubs over 60 days and with denning fat content varying randomly between 22-30%.

### 2.6 Model simulation experiments

We ran simulations for all three initial body fat contents, four lengths of hibernation and five reproductive strategies. Because "lactation strategies" have a source of estimated variability (e.g., milk energy and protein content), we ran 100 repetitions for each combination. To measure the reproductive energetic cost, we accounted for the energy (kcal) and protein (kg) needed to support reproduction and converted these to fat and lean mass, respectively.

We explored survival time for hibernating bears with different reproductive strategies based on their denning body fat content. For this purpose we ran the model and recorded fasting mortality when 30% of lean mass was depleted independently of the remaining body fat reserves or when 95% of fat mass was depleted. Fasting studies in other mammals have shown that animals die from protein depletion, which can range as high as 30 to 50% (Caolin 2004; Cherel et al., 1992; Le Maho et al., 1988).

## 3. RESULTS

### 3.1 Model parameterization and sensitivity

#### *3.1.1 "Daily mass loss composition" parameterization, model calibration and validation*

Parameterization of "daily mass loss composition" for both lactating and non-lactating bears suggested a body fat threshold of 17% beyond which all energy necessary for maintenance and reproduction was supplied by fat. When the body fat content was ≤ 17%, the contribution of fat to energy needed decreased linearly to zero with the difference provided by lean mass. Simulations for bears less than 250 kg (Fig. 2-2a) resulted in marginal underestimates of average daily mass loss compared to measures from Farley and Robbins (1995), while slightly overestimating body mass and fat loss and underestimating lean mass loss when compared to Hilderbrand et al. (2000) (Fig. 2-2b). Model validation (Fig. 2-2c) with data from free-ranging bears produced slight

underestimates of spring body mass for non-lactating and lactating female bears. However, the range of values produced by the simulations was within the range of observations. Thus, the general results of the calibration and validation suggested that the model realistically estimated body mass loss by bears across different length of hibernation.

Differences observed in body mass loss between simulations and empirical studies (Farley and Robbins 1995; Hilderbrand et al 2000) could be explained by several factors. First, we had to assume certain ranges of values because some required information that was not measured (i.e. denning body fat content, length of hibernation). Second, the results of Farley & Robbins (1995) showed a non-linear relationship between daily mass loss and body mass which is not represented in the equation used to estimate the MtbHib. Third, the model may overestimate energetic demands for fatter bears because it is based on overall body mass and does not consider the ratio of fat to lean mass, which probably has a higher metabolic rate than fat. Fourth, cost of lactation was calculated based on a single study where female lean mass was approximately 100 kg (Farley and Robbins 1995), and milk production in the model did not vary with maternal body size and condition.

### *3.1.2 Model sensitivity*

Sensitivity analysis showed that the model was sensitive to the milk energy content, "milk production efficiency", and the "daily mass loss composition" parameters (Table 2). An increase of 10% in "milk energy content" increased the average daily mass loss by 25%. An increase of 10% in "daily mass loss composition parameter" increased "average daily mass loss" by 26%. Neonatal mass and length of gestation period had a low impact on model outputs. Changes of up to 50% in these parameters resulted in < 2% change in average daily mass loss.

## 3.2 Energetics of hibernating bears

### *3.2.1 Energetic reproductive costs of brown bears*

Reproductive costs increased as either more cubs were produced or length of lactation increased, although the cost of a 14 day increase in length of lactation while denned was less costly than an increase in litter size from 1 to 2 cubs (Table 2-3). Total reproductive costs across the range of litter size and lactation length ranged from ~30,000 to 93,000 kcal and from ~2 to 6 kg of protein. This amount of energy could be met by the female mobilizing ~3 to 10 kg of fat, and protein requirements can be met by ~9 to 28 kg of lean mass. Lean mass necessary to supply protein demands for reproduction averaged ~73% of the total body mass loss necessary to support reproduction (Table 2-3). Gestation costs were minimal (between 1 – 4 % of the total reproductive cost) when compared to the cost of lactation.

### *3.2.2 Bioenergetic trade-offs*

As expected, an increase in length of hibernation increased energy demands and therefore total body mass loss for all reproductive classes (Fig. 2-3 a, b, c, d, e). The increase in body mass loss for bears of different initial body fat content was not, however, consistent with an increase in energy demands. Energy demands were higher for fatter bears, although the percentage of body mass loss was lower. The rate of increase in energy requirements through the hibernation period was constant, but the increase in the rate of body mass loss varied with initial body fat content. Because leaner bears must use lean mass earlier than fat bears, lean bears lost a greater proportion of body mass than fat bears.

As expected, the threshold for mortality (i.e., 30% loss of lean mass) was reached faster when denning body fat was lower (Fig. 2-4). The combination of long hibernation and low fat reserves limited reproduction. Minimum levels of fat reserves necessary to support reproduction varied from 19% to 33%. Reproduction was not possible if body fat content was below 19% and length of hibernation was over 120 days. When initial body

fat content was ≥ 40%, lean mass loss was constant for all reproductive strategies because lean mass loss was solely used for meeting the protein needs of milk production (Fig. 2-4).

*3.2.3 Relationship between body condition and survival*

There was a slight curvilinear increase in survival time as the initial body fat content increased (Fig. 5). When denning body fat content was over 15%, each one unit increase in the percent body fat content at the start of hibernation increased the survival time by 12 days. For the same length of hibernation, lactating bears needed ~3% more body fat than non-lactating bears to sustain the 'cheapest' reproductive strategy (i.e. lactation of 60 days and 1 cub). As the number of cubs increased from one to two or the length of lactation increased from 60 to 74 days, an additional 2% body fat content was required to meet those needs.

The additional survival time ($Y$ in days) above that occurring for bears having a minimum of 15% body fat can be predicted by the following equations, where $X$ = denning body fat content (%).

Eq. 2 Non-lactating bear $Y = 11.4X - 68$

Eq.3 Lact.60 days, 1 cub $Y = 10.5X - 78$

Eq.4 Lact.74 days, 1 cub $Y = 10.7X - 98$

Eq.5 Lact.60 days, 2 cubs $Y = 10.7X - 115$

Eq.6 Lact.74 days, 2 cubs $Y = 10.5X - 153$

## 4. DISCUSSION

Several empirical studies have measured loss of body mass and metabolic rates of hibernating bears (Atkinson 1996; Atkinson and Ramsay 1995, Farley and Robbins 1995; Hildebrand et al. 2000; Robbins et al. 2012b; Tøien et al., 2011; Watts 1990). Recent simulation studies have explored how physiological and environmental conditions influence energetic trade-offs, reproductive success, and survival in polar bears (*Ursus maritimus*; Molnar et al., 2009; Robbins et al., 2012a). Our study is the first to integrate different sources of information on body mass loss, metabolic rates, and reproduction during hibernation in brown bears. We also evaluate energy and protein costs in separate pathways for reproduction and the dynamics of lean and fat depletion for different reproductive strategies as affected by length of hibernation and female condition.

The cost to produce cubs during hibernation accounted for 15% - 53% of the body mass lost for lactating bears relative to non-lactating bears. Fetal development accounted for a small proportion of the total cost of reproduction (i.e., $\leq$ 1%), which is consistent with previous observations that bears produce very altricial offspring with the vast majority of the growth in the den occurring after birth (Hissa, 1997; Oftedal, 1993; Ramsay and Dunbrack, 1986).

Protein transferred from the mother to the cub(s) for their growth accounted for more than 73% of the loss of body mass that occurred above the maternal maintenance cost, and between 12% - 45% of the total body mass lost during hibernation. Variation in body mass loss was due to the number of cubs, the length of hibernation, and maternal body fat content at the start of hibernation. The importance of lean mass to survival and reproduction has also been observed in other species, such as rodents (Cherel, 1992; Dunn et al., 1982), seals (Vierrier et al., 2011; Worthy and Lavigne, 1983), penguins (Robin et al. 1988), and ungulates (Barbosa and Parker, 2008; Parker et al., 2009). In caribou (*Rangifer tarandus*), survival and reproductive success during winter was best explained by protein and fat reserves rather than just fat (Parker et al., 2009). Despite evidence for the importance of protein in caribou and bears, the role of protein in

starvation and reproduction in wild mammals is still not well understood (Parker et al., 2009).

Our assessment of the lactation costs included the range of lactation periods (60-74 days) observed in denned, captive bears (Robbins et al. 2012b). We recognize that this length of lactation probably underestimates the length of lactation for many wild bears in either more northern latitudes or in deeper snow conditions. For example, Friebe et al. (2013) observed a probable birth date at the end of January and den emergence in late April, i.e. a lactation period > 90 days in a bear population in south-central Sweden. Thus, we expect that our estimates of energy and protein requirements for reproduction are minimums and could dramatically increase as larger cubs are nursed past 74 days. However, a thorough assessment of the effects of longer lactation periods on body mass loss requires additional studies and data.

Adult brown bears accumulate lean mass reserves mostly during the spring and early summer (Hilderbrand et al. 1999; McLellan 2011), and rich protein diets during spring enhance body mass gain (Swenson et al. 2007). However, nutritional studies of bears have most often focused on the importance of body fat accumulation during the late summer and fall (Atkinson and Ramsay 1995; Derocher and Stirling 1998; McLellan 2011; Schwartz et al., 2006). Based on the evidence of other species in combination with our results, reproductive success among brown bear populations may also be explained by available protein early in the spring which is used to replenish that lost during early lactation during denning and to provide the doubling of milk protein content once the mother exits the den (Farley and Robbins, 1995). We therefore recommend more attention be placed on understanding the role of protein in bear reproductive success, as well as relating the protein content of bear diets with the spatial variability in reproductive success.

Our results illustrated that minimum fat reserves necessary for maintenance and reproduction differ among environments. Non-lactating bears needed ~ 19% of body fat to survive 150 days of hibernation, ~ 22% to survive 180 days, and ~ 24% to survive 210 days. Reproductively active females need to increase their denning body fat content by ~

5.7% units above these levels to successfully give birth to 2 cubs 60 days before den emergence. Consequently, such females would need a minimum of 25% to 30% body fat at the start of hibernation to successfully reproduce, depending on the length of the fast. This result is consistent with prior bear studies. For example, no polar bear with an initial body fat content < 20% was observed with cubs the following spring (Atkinson and Ramsay, 1995), only 14% of American black bears were observed with spring cubs when their body fat content averaged 19% prior to denning (Belant et al. 2006), and brown bears with ≤ 20% body fat at denning did not produce cubs (Robbins et al., 2012b).

The difference of ~5.7% of fat necessary to support reproduction during the shorter lactations simulated in this study may be difficult to detect in field studies because it is likely within the error of bioelectrical impedance analysis (BIA, Farley and Robbins 1994), which is commonly used to determine body fat content in wild bears. However, BIA measurements may be useful to understand the links between body fat content and reproductive success in wild bears with longer lactation periods in the den that would increase the required maternal body fat content.

Our results suggest that an increase in litter size of one cub was more costly than a two week increase in the length of lactation. Therefore, inter-population differences in litter size may be adaptive and reflect long-term differences in food resources, whereas variation in the timing of birth might be the primary mechanism used to adapt to inter-annual food variability within a population. For example, the number of cubs produced by American black bears did not vary with female body mass (e.g., as a surrogate of body condition, Noyce et al., 2002), and the same captive brown bears always produced either twins or triplets irrespective of their body fat content, assuming body fat content was above the minimum threshold for reproduction (Robbins, pers. observation.).

In our model we assumed that the energetic cost to produce twins was the same as that for triplets. We based this assumption on the negligible cost of fetal development (Hissa, 1997; Oftedal, 1993) and the reduced growth rate of triplets relative to twins while nursing in the den in brown bears (Robbins et al. 2012) and polar bears (Derocher and Stirling 1998). The reduced size of triplets relative to twins may reduce cub survival once

out of the den and be independent of the mother's denning condition (Derocher and Stirling 1996). Thus, the production of larger cubs at den emergence (i.e., twins rather than triplets) may be the preferred strategy in environments where food resources are either marginal or highly variable, whereas the production of more cubs (i.e., triplets rather than twins) may be the preferred strategy in environments with abundant, high quality, relatively stable food resources (Ferguson and McLoughlin 2000; McGinley et al. 1987). Other factors, such as body size, age, and human persecution history, may also influence reproductive strategies and thereby explain some of the differences observed between bear populations (Derocher and Stirling 1998; Zedrosser et al. 2009; Zedrosser et al. 2011).

### 4.1 Conclusions

Evaluating reproductive trade-offs based on energetic requirements is essential to understanding how species adapt to different environmental conditions. Although these processes are difficult to study in a controlled setting for a large mammal, model simulation provides a tool for developing 'experiments' and testing hypotheses that will improve our knowledge and understanding (Owen-Smith, 2007). We built a model that simulated the body mass loss for hibernating brown bears to assess reproductive cost and explore limits on energetic trade-offs in reproduction. Our model provided significant insight into nutritional factors controlling reproduction in bears that might be applicable to other ursids. The similarities between predictions of our model with field observations suggest that we can exploit the synergism between these two approaches to understand nutritional factors that control bear reproduction. This will become particularly important as global warming reduces sea ice and, therefore, seal availability for polar bears and potentially alters terrestrial food resources for many other species of bears (Robbins et al. 2012b).

## 5. REFERENCES

Arnemo JM, Evans A, Fahlman Å, Ahlqvist P, Andrén H, Brunberg S, Liberg O, Linnell JDC, Odden J, Persson J, Sand H, Segerström P, Sköld K, Strømseth TH, Støen O-G, Swenson JE, Wabakken P. 2011. Biomedical protocols for free-ranging brown bears, wolves, wolverines and lynx. Hedmark University College, Evenstad, Norway.

Atkinson SN, Ramsay MA. The effects of prolonged fasting of the body composition and reproductive success of female clack bears (*Ursus maritimus*). Funct Ecol 1995;9:559-667.

Atkinson SN, Nelson RA, Ramsay MA. Changes in body composition of fasting polar bears the effect of relative fatness on protein conservation. Physiol Zool 1996;69:304-316.

Barbosa PS, Parker KL. Allocating protein to reproduction in arctic reindeer and caribou. Physiol Biochem Zool 2008;81:835-855.

Barbosa PS, Parker KL, Hume ID. Integrative wildlife nutrition. 1st ed. Berlin: Springer-Verlag; 2009.

Barbosa PS, Farley SD, Robbins CT. Whole-body urea cycling and protein turnover during hyperphagia and dormancy in growing bears (*Ursus americanus* and *U. arctos*). Can J Zool 1997;75:2129-2136.

Bendoricchio G, Jorgensen SE. Fundamentals of ecological modelling. 3rd ed. Oxford, UK Elsevier Science; 2001.

Blaxter KL. Energy metabolism in animals and man. 1st ed. United Kingdom: Cambridge University press; 1989.

Brides AS, Vaughan MR, Fox JA. American black bear estrus and parturition in the Alleghany Mountains of Virginia. Ursus 2011;22:1-8.

Brown JH, Marquet PA, Taper ML. Evolution of body size: consequences of an energetic definition of fitness. Am Nat 1993;142:573-584

Caolin M. Modeling of lipid and protein depletion during total starvation. Am J Physiol-Endoc M 2004;287:790-798.

Cherel Y, Robin JP, Heitz A, Cargari Ch, Le Maho Y. Relationship between lipid availability and protein utilization during prolonged fasting. J Comp Physiol B 1992;162:305-313.

Coogan SCP, Nielsen SE, Stenhouse GB. Spatial and temporal heterogeneity creates a "brown tide" in root phenology and nutrition. ISRN Ecology 2012; Article ID 618257:1-10.

Derocher AE, Stirling I. Aspect of survival in juvenile polar bear. Can J Zool 1996;74:1246-1252.

Derocher AE, Stirling I. Maternal investment and factors affecting offspring size in polar bears (*Ursus maritimus*). J Zool 1998;245:253-260.

Dunn MA, Houts SK, Hartsook EW. Effects of fasting on muscle protein turnover, the composition of weight loss, and energy balance of obese and nonobese zucker rats. J Nutr 1982;112:1862-1875.

Faring L. When does fragmentation of breeding habitat affect population survival? Ecol Modell 1998;150:273-292

Farley SD, Robbins CT. Development of two methods to estimate body composition of bears. Can J Zool 1994;72: 220-226.

Farley SD, Robbins CT. Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. Can J Zool 1995;73:2216-2222.

Ferguson SH, McLoughlin PD. Effect of energy availability, seasonality and geographic range on brown bear life history. Ecography 2000;23:193-200.

Friebe A, Swenson JE, Sandegren F. Denning chronology of female brown bears (*Ursus arctos*) in central Sweden. Ursus 2001;12:37-46.

Friebe A, Zedrosser A, Swenson JE. Detection of pregnancy in a hibernator based on activity data. Eur J Wildl Res 2013;59:731-741.

Garland T, Carter PA. Evolutionary physiology. Annu Rev Physiol 1994;56:579-621.

Hilderbrand GV, Jenkins SG, Schwartz CC, Hanley TA, Robbins CT. Effect of seasonal differences in dietary meat intake on changes in body mass and composition in wild and captive brown bears. Can J Zool 1999;77:1623-1630.

Hilderbrand GV, Schwartz CC, Robbins CT, Hanley TA. Effect of hibernation and reproductive status on body mass and condition of coastal brown bears. J Wildl Manage 2000;64:178-183.

Hildenbrandt, H., Müller, M.S., Grimm, V. How to detect and visualize extinction thresholds for structured PVA models. Ecol Modell 2006;191:545-550

Hissa R. Physiology of the European brown bear (*Ursus arctos arctos*). Ann Zool Fennici 1997;34:267-287.

Isee System, Inc. An introduction to system thinking. Hanover: New Hampshire; 2006.

Johnson KG, Pelton MR. Environmental relationships and denning period of black bears in Tennessee. J Mammal 1980;61:653-660.

Kooijman SALM. Dynamic energy and mass budgets in biological systems. 2nd ed. Cambridge: Cambridge University Press; 2000.

Le Maho Y, Robin JP, Cherel Y. Starvation as treatment for obesity - the need to conserve protein. News Physiol Sci 1988;3:21-24.

López-Alfaro C, Estades C, Aldridge D, Saucedo C, Gill R. 2012. Individual-based modeling as decision tool for the conservation of the huemul (*Hippocamelus bisulcus*) in southern Chile. Ecol Modell 2012;244:104-116.

Lovegrove BG. The power of fitness in mammals: perception from the African slipstream. Physiol Biochem Zool 2006;79: 224-236.

McCue M. Starvation physiology: Reviewing the different strategies animals use to survive a common challenge. Comp Biochem Phys A 2010;156:1-18.

McGinley MA, Temme DH, Geber MA. Parental investment in offspring in variable environments: Theoretical and empirical considerations. Am Nat 1987;130:370-398.

Mazaris AD, Broder B, Matsinos YG. An individual based model of a sea turtle population to analyze effects of age dependent mortality. Ecol Modell 2006;198:174-182.

McLellan B. Implications of high-energy and low-protein diet on the body composition, fitness, and competitive abilities of black (*Ursus americanus*) and grizzly (*Ursus arctos*) bears. Can J Zool 2011;89:546-558.

Molnár PK, Klanjscek T, Derocher AE, Obbard ME, Lewis MA. A body composition model to estimate mammalian energy stores and metabolic rates from a body mass and body length, with application to polar bears. J Exp Biol 2009;212:2313-2323.

Molnár PK, Derocher AE, Thiemann GW, Lewis MA. Predicting survival, reproduction and abundance of polar bears under climate change. Biol Conserv 2010;143:1612-1622.

Noyce KV, Coy PL, Garshelis DL. Bone prominence and skin-fold thickness as predictors of body fat and reproduction in American black bears. Ursus 2002;13:275-284.

Nielsen SE, Boyce MS, Stenhouse GB, Munro RHM. Development and testing of phenologically driven grizzly bear habitat models. Ecoscience 2003; 10:1-10.

Nielsen SE, McDermid G, Stenhouse GB, Boyce MS. Dynamic wildlife habitat models: Seasonal foods and mortality risk predict occupancy-abundance and habitat selection in grizzly bears. Biol Conserv 2010;143:1623-1634.

Oftedal TO, Alt LG, Widdowson ME, Jakubasz RM. Nutrition and growth of suckling black bears (*Ursus americanus*) during their mothers' winter fast. Brit J Nutr 1993;70:59-79.

Owen-Smith N. Introduction to modeling in wildlife and resources conservation. 1st ed. Oxford, UK; Blackwell Publishing; 2007.

Parker KL, Barboza PS, Gillingham MP. Nutrition integrates environmental responses of ungulates. Funct Ecol 2009;23:57-69

Ramsay MA, Dunbrack RL. Physiological constraints on life history phenomena, the example of small bear cubs at birth. Am Nat 1986;127: 735-743.

Robbins CT, Lopez-Alfaro C, Rode KD, Tøien Ø, Nelson LO. Hibernation and seasonal fasting in bears: the energetic cost and consequences for polar bears. J Mammal 2012a; 93:1493-1503.

Robbins CT, Meray B-D, Fortin J, Lynne Nelson O. Maternal condition determines birth and growth of newborn cubs. J Mammal 2012b;93:540-546

Robbins CT. Wildlife feeding and nutrition. 2nd ed. San Diego, USA: Academic Press; 1993.

Robin JP, Frain M, Sardet C, Groscolas R, and Le Maho Y. Protein and lipid utilization during long-term fasting in emperor penguins. Am J Physiol Regul Integr Comp Physiol 1988;61-68.

Schwartz CC, Miller SD, Haroldson MA. Grizzly bear. in Feldhamer GA, Thompson BC, Chapman JA, editors. Wild Mammals of North America: Biology, Management, and Conservation. 2nd ed. Baltimore, Maryland, USA; Johns Hopkins University press; 2003. P. 556-586.

Schwartz CC, Haroldson MA, White GC, Cherry S, Keating KK, Moody D, Servheen C. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. Wildl Monogr 2006; 113:1–68.

Spady TJ, Lindburg SG, Durrant BS. Evolution of reproductive seasonality in bears. Mammal Rev 2007; 37:21-53.

Starfield AM. A pragmatic approach to modeling for wildlife management. J Wildl Manage 1997; 61:261-270.

Starfield A, Bleloch AL. Building Models for Conservation and Wildlife Management, 2nd ed. Burgess International Group Inc.; New York, NY, 253pp. 1991.

Stearns SC. The evolution of life histories. Oxford University Press, New York, USA. 1992.

Swenson JE, Wabakkel P; Sandegren F; Bjarvall A; Franzen R; Soderberg A. The near extinction and recovery of brown bears in Scandinavia in relation to the bear management policies of Norway and Sweden. Wildl Biol 1995;1:11-25.

Swenson JE, Adamic M, Huber D, Stokke S. Brown bear body mass growth in northern and southern Europe. Oecologia 2007;153:37-47.

Tøien Ø, Blake J, Edgar DM, Grahn DA, Heller HC, Barnes BM. Hibernation in black bears: Independence of metabolic suppression from body temperature. Science 2011;331:906–909.

Vierrier D, Groscolas R, Guinet Ch, Arnould JPY. Development of fasting abilities in subantartic fur seal pups: balancing the demands of growth under extreme nutritional restrictions. Funct Ecol 2011;25:704-717.

Watts PD. Weight loss in three species of ursids under simulated denning conditions. Ursus 1990;8:139-141.

Welch CA, Keay J, Kendall KC, Robbins CT. Constraints on frugivory by bears. Ecology 1997;78:1105-1119.

Wiegand, T., Naves, J., Stephan, T., Fernandez, A. Assessing the risk of extinction for the brown bear (*Ursus arctos*) in the Cordillera Cantabrica, Spain. Ecol Monogr 1998;68:539-570.

Worthy GAJ, Lavigne DM. Energetics of fasting and subsequent growth in weaned seal pups, *Phoca groenlandica*. Can J Zool. 1983;61:447-456.

Zedrosser A, Dahle B, Stoen OG, Swenson JE. The effect of primiparity on reproductive performance in brown bears. Oecologia 2009; 160:847-854.

Zedrosser A, Steyaert SMJG, Gossow H, Swenson JE. Brown bear conservation and the ghost of persecution past. Biol Conserv 2011;144:2163-2170.

Zedrosser A., Pelletier F, Bishof R, Festa-Bianchet M, Swenson JE. Determinants of lifetime reproduction in female brown bears: early body mass, longevity, and hunting regulations. Ecology 2013;93:231-240.

**Figure 2-1.** Model diagram and schedule. Equations and parameters are in Table 1. The model starts with the inputs of the initial conditions on day 1 of denning and ends at den emergence. Each day the model accounts for daily energy and protein demands based on body mass and reproductive cost. Reproductive cost varies with litter size (one or two cubs) and length of lactation (60 or 74 days). The amount of lean and fat mass loss each day is estimated using the composition of the daily mass loss algorithm. Daily mass loss algorithm is a function of the day's body fat content. The model estimates daily energy and protein costs in separate pathways.

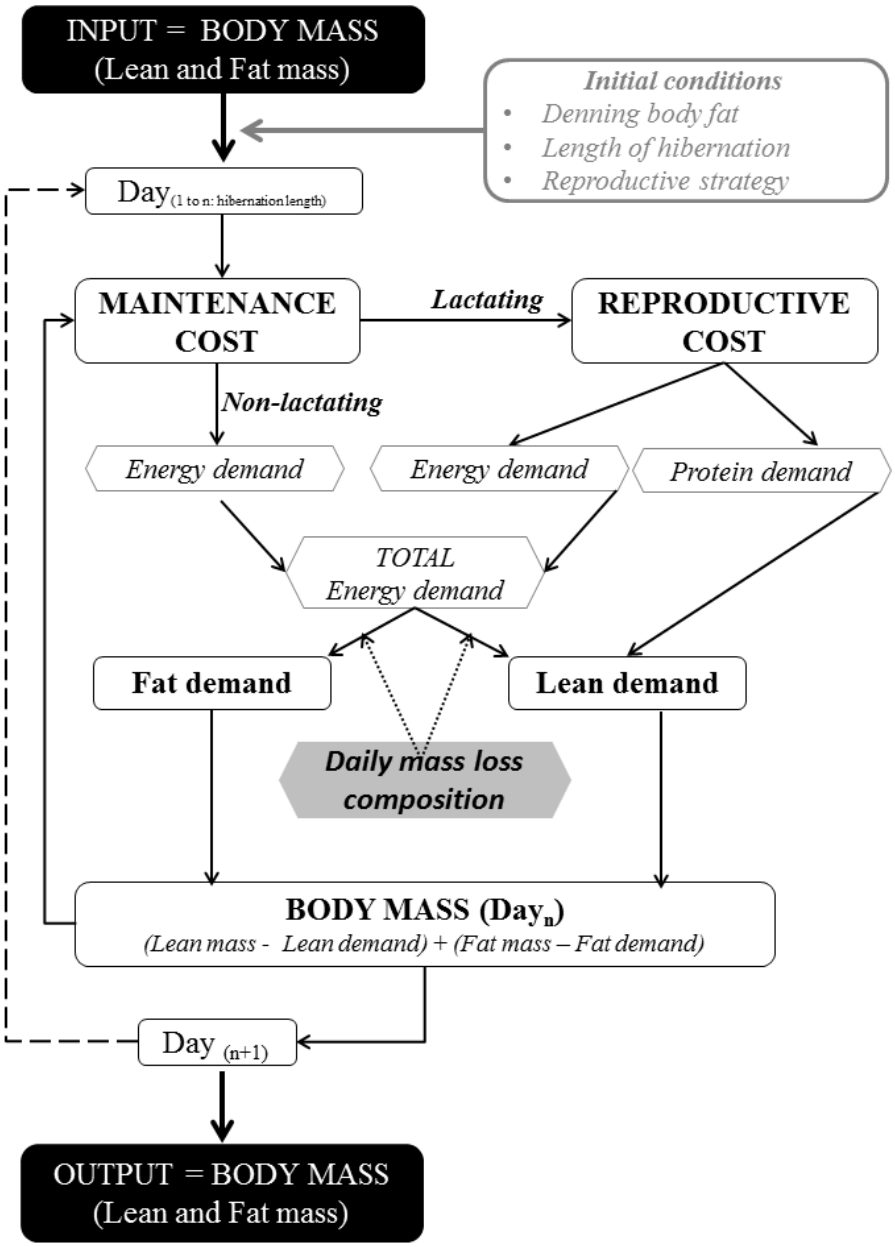


**Figure 2-2**. Calibration and validation model results. Two independent, North American brown bear studies (Farley and Robbins 1990, Hilderbrand et al. 2000) were used to adjust the parameters and evaluate model performance. For model validation we used information from the Scandinavian Brown Bear Research Project. In all simulations, one hundred repetitions were run for each scenario. White boxplots are for non-lactating bears, and grey boxplots are for lactating bears. The box represents first and third quartiles with the inside line being the median. Whiskers off boxes represent (vertical dash lines) the range of observations. Fig. 2-2a Comparison of the daily body mass loss among the results from this study and data published in Farley and Robbins (1995). Estimates of Farley and Robbins (1995) were based on the regression line in their Fig. 5 for non-lactating bears, and are here presented in Fig. 2-2a) with black squares and a dashed line. Fig. 2-2b) compares spring body mass (total body mass, fat mass, and lean mass) between results from this study and Hilderbrand et al. (1999). Results by Hilderbrand et al. (1999) are presented with black diamonds, with 95% confidence interval obtained from their Table 1. Fig. 2-2c) compares spring body mass between model results from this study and free-ranging female brown bears in Sweden.

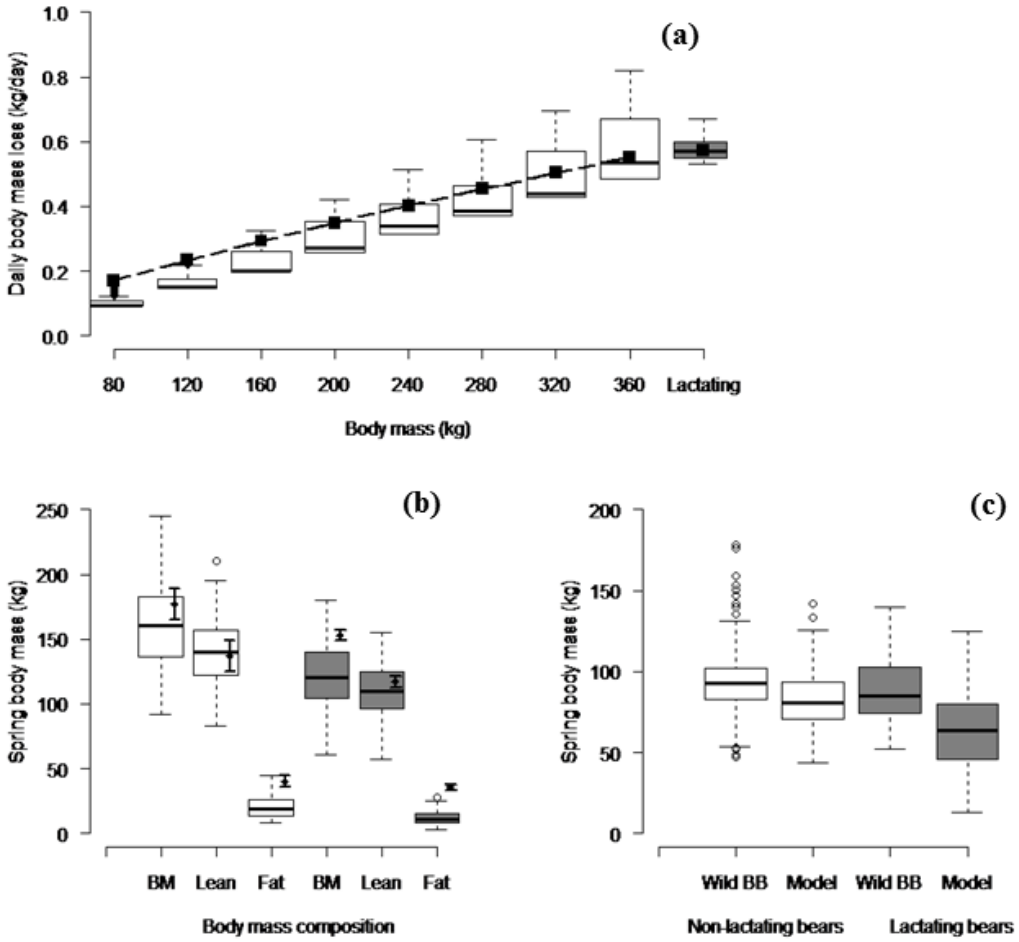


**Figure 2-3.** Effect of female body condition (% of denning body fat content) on total body mass loss (kg) and energy cost (kcal) and with increasing hibernation length. The right column of figures is the percentage of body mass loss during hibernation relative to the initial fall body mass. The left column is the energy costs of hibernation estimated from the loss of lean and fat. (a) is Non lactating, (b) is Lactating 60 days 1 cub, (c) Lactating 74 days 1 cub, (d) Lactating 60 days 2 cubs. (e) Lactating 74 days 2 cubs.

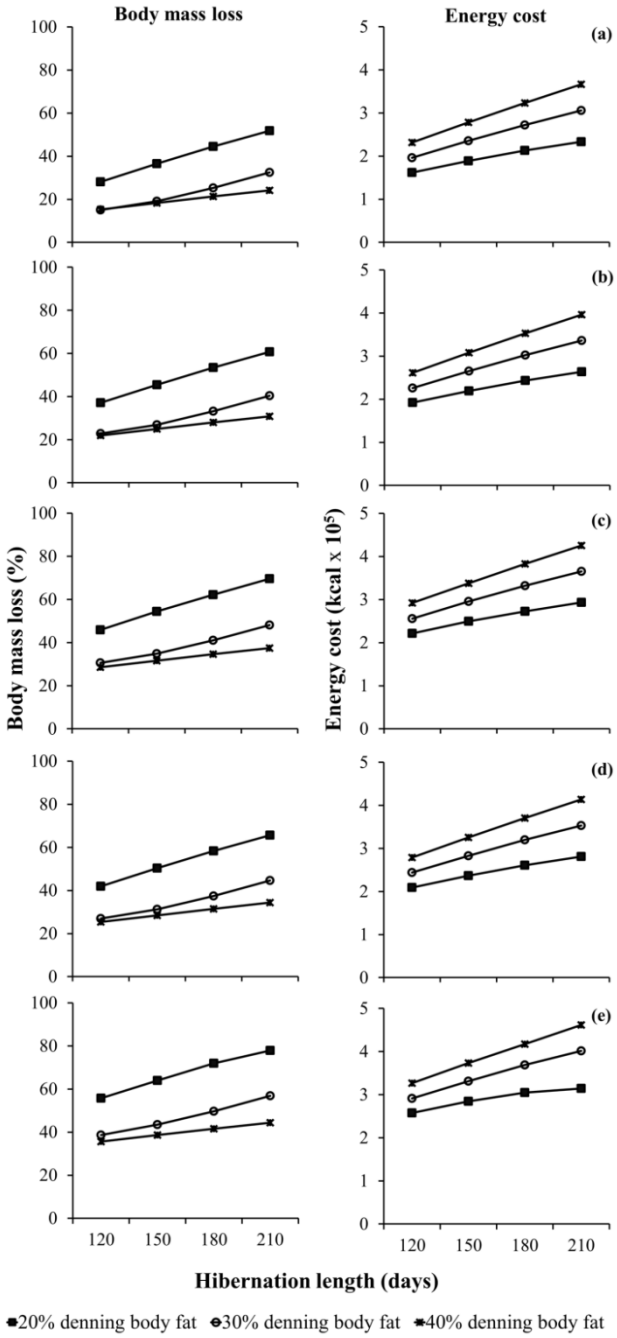


**Figure 2-4.** Percent of lean mass loss for different reproductive strategies and initial fall body fat contents (%). Fall lean mass was assumed to be 100 kg for all bears. 20%, 30%, 40% of denning body fat content. Grey dash line represents the survival threshold of 30% lean mass loss.

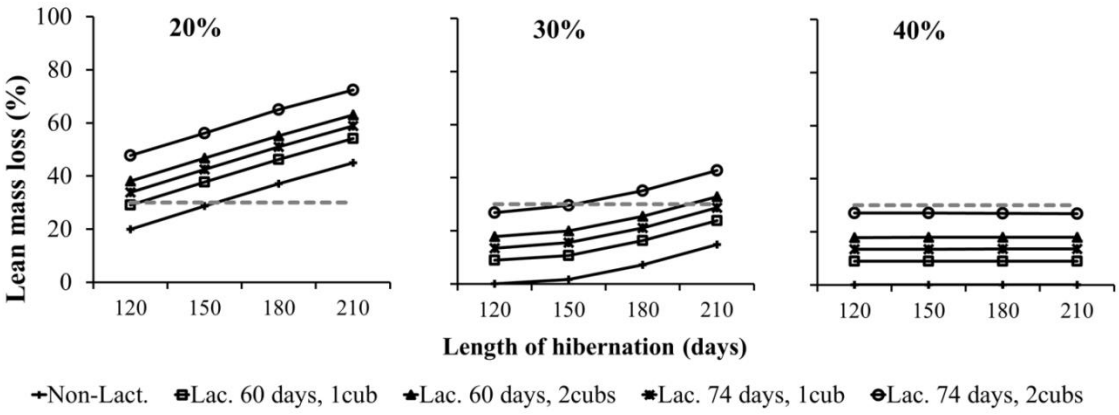


**Figure 2-5.** Estimated survival time for bears having different denning body fat contents and experiencing different reproductive strategies. The lines represent the number of days before 30% of lean mass loss is reached (survival threshold). Initial body lean mass was 100 kg. Bars are three times SD. Horizontal grey lines represent a different length of hibernation (120, 150, 180 and 210 days).

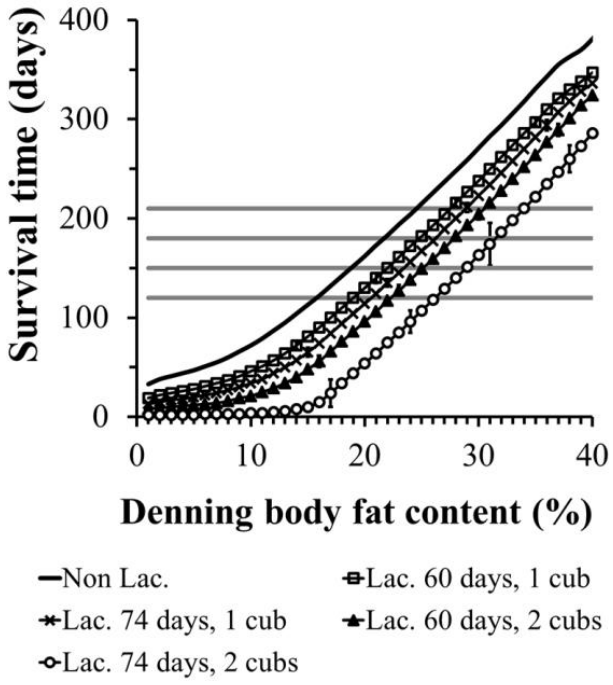


**Table 2-1.** Parameters and equations used in the hibernation model. Parameters were held constant during all model simulation experiments.

| *Model parameter* | Values/equations | References |
|---|---|---|
| Metabolism in hibernation (MtbHib) | $7.2*BM^{1.09}$ (kcal/day) | Robbins et al. (2012a)[a] |
| Lean energy content | 1200 kcal/kg lean mass | Blaxter (1989), Farley and Robbins (1995) |
| Lean protein content | 0.211 kg/kg lean mass | Farley and Robbins (1995) |
| Fat energy content | 9100 kcal/kg fat mass | Blaxter (1989), Farley and Robbins (1995) |
| Neonatal body composition | 12% protein, 1% fat | Oftedal et al. (1993) |
| Gestation period | 60 days | Robbins (pers. comm.) |
| Neonatal mass | 0.650 kg | Robbins et al. (2012) |
| Milk production efficiency | 0.85 | Blaxter (1989) |
| Daily mass loss composition | See calibration results | Atkinson et al. (1996); Caolin (2004); Dunn et al. (1982); McCue (2010); Robbins (1993). |

kg = kilograms; BM = Body mass (kg); [a], This equation is presented on page 1497 in Robbins et al. (2012a). The equation represents the average energetic costs over longer period of hibernation, and is ~50% higher than the minimal metabolic rates observed in brown, black, and polar bears.

**Table 2-2.** Sensitivity analysis represents the variation in the "average daily mass loss" during lactation due to changes in model parameter (e.g. an increase of 10 % on the milk efficiency parameter reduces in 34% the average daily mass loss). "Parameter value" represents the original value of the parameter as used in the model experiments.

| Parameters | Parameter value | Change in the parameter | | | | | |
|---|---|---|---|---|---|---|---|
| | | -50% | -25% | -10% | +10% | +25% | +50% |
| *Milk efficiency* | 0.85 | -0.37 | -0.23 | -0.17 | -0.34 | -0.14 | - |
| *Milk energy content* | *(b) | 0.17 | 0.17 | 0.23 | 0.25 | 0.18 | 0.19 |
| *Neonatal mass* | 0.650 kg | 0.01 | 0.02 | 0.03 | -0.01 | 0 | 0 |
| *Gestation period* | 60 days | -0.02 | 0.01 | -0.01 | -0.02 | -0.01 | -0.01 |
| *Daily mass loss - composition parameter* | 17 % body fat. | 0.05 | 0.10 | 0.20 | 0.26 | 0.35 | 0.44 |

*(b): Farley SD, Robbins CT. Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. Can J Zool 1995;73:2216-2222.

**Table 2-3.** Energy and protein demand for different reproductive strategies. Body mass reserves required to supply energetic demands for reproduction were estimates based on the fat, lean energy, and lean protein content. Reproductive demands do not include maintenance cost (MtbHib) for the mother.

| Reproductive strategy | Reproductive demands | | Body mass required for reproduction | | | | |
|---|---|---|---|---|---|---|---|
| | Energy | Protein | Fat mass | | Lean mass | | BM |
| | (kcal) | (kg) | (kg) | (%) | (kg) | (%) | (kg) |
| *Lact. 60 days, 1 cub* | 30,918 *(1,949)* | 2.00 *(0.08)* | 3.40 *(0.21)* | 26.4 | 9.47 *(0.37)* | 73.6 | 12.87 |
| *Lact. 74 days, 1 cub* | 46,960 *(2,650)* | 2.93 *(0.10)* | 5.16 *(0.29)* | 27.1 | 13.91 *(0.46)* | 72.9 | 19.07 |
| *Lact. 60 days, 2 cubs* | 62,216 *(3,559)* | 4.00 *(0.14)* | 6.84 *(0.39)* | 26.5 | 18.94 *(0.65)* | 73.5 | 25.77 |
| *Lact. 74 days, 2 cubs* | 93,532 *(4,835)* | 5.86 *(0.17)* | 10.28*(0.53)* | 27.0 | 27.77 *(0.85)* | 73.0 | 38.05 |

SD in parenthesis. "BM" = Body mass. (%) related to the BM. "Lac. 60 days, 1 cub" = Lactating for 60 days and one cub; "Lac. 60 days, 2 cubs" = Lactating for 60 days and two cubs, "Lac. 74 days, 1 cub" = Lactating for 74 days and one cub"; "Lac. 74 days, 2 cubs" = Lactating for 74 days and two cubs.

# CHAPTER 3

# ASSESSING THE NUTRITIONAL QUALITY OF BROWN BEAR DIETS AMONG INT50ERIOR ECOSYSTEMS IN NORTH AMERICA

## 1. INTRODUCTION

Among wide ranging species, conspecific animals occupying different habitats often differ in body size, reproductive traits and density between populations (Ferguson and McLoughlin, 2000; Herfindal et al., 2006; Zedrosser et al. 2011). Differences in life history traits between populations are frequently associated with food availability (Hilderbrand et al., 1999b; Ferguson and McLoughlin, 2000). Variations in diets influence the supply of energy and protein necessary for maintenance, growth and reproduction (Barbosa et al., 2009). Food habits and nutritional studies are among the first steps taken to understand wildlife-habitat relationships. Generally, these studies describe the seasonal diet composition of a species within a population, and often include information regarding the energy and protein content of foods. Such studies often lack an explicit nutritional evaluation for the complete diet, including a measure of the key nutritional elements influencing fitness. This absence of an explicit nutritional evaluation limits our capacity to compare between ecosystems and comprehend nutritional mechanisms affecting individual fitness (Homyack, 2010; Bojarska and Selva, 2011).

Brown bears (*Ursus arctos*) are widely distributed and can be found in a variety of habitats (McLellan et al., 2008; Bojarska and Selva, 2011). Nutritional differences in those habitats often lead to variation in body and litter size, inter-litter interval, and population densities (Hilderbrand et al., 1999b; Zedrosser et al., 2011). Brown bears are flexible omnivores (Robbins et al., 2004), and depending on food availability, bear diets can range from largely carnivorous to largely herbivorous (Hilderbrand et al., 1999b;

Bojarska and Selva, 2011). There have been several efforts to understand how food resources influence life history traits in bears. These studies have integrated information on food habits in different ecosystems to illustrate; 1) the influence of dietary meat intake on body size and population density (Hilderbrand et al., 1999b; Ferguson and McLoughlin, 2000; McLellan, 2011); 2) the importance of primary productivity and seasonality on bear reproductive traits, such as age of primiparity and inter-birth interval (Ferguson and McLoughlin, 2000); and 3) the significance of digestible energy and other nutrients on the dietary patterns of brown bears (Bojarska and Selva, 2011). However, quantitative methods to evaluate and compare between the nutritional quality of ecosystem-specific bear diets have not been explored.

In general, interior brown bear populations in North America are composed of smaller, more herbivorous bears than coastal populations with access to salmon (*Oncorhynchus* sp.; Hilderbrand et al., 1999b). Population densities and reproductive success also vary between inland and coastal populations with inland (interior) densities and reproductive success being lower (Mowat et al., 2005; Ferguson and McLoughlin, 2000; Zedrosser et al., 2011). Alberta's bear populations occur along the eastern slopes of the Canadian Rocky Mountains and adjacent Foothills to the east. Alberta brown bear subpopulations differ in individual densities (5 to 18 bears/1000km$^2$) and body condition (ASRD & ACA, 2010) with spring body mass for females averaging 108 kg (SE=8; Zedrosser et al., in revision). Brown bears have been designated as a provincially threatened species in Alberta, in part due to their low reproductive rate which limits their recovery (ASRD and ACA, 2010). In contrast, the Flathead ecosystem (west slopes of the Canadian Rockies) is located in the southeast part of British Columbia adjacent to south-western Alberta and sustains a productive brown bear population. Bear densities there are among the highest recorded for interior populations with densities ranging from 25 to 55 bears/1000km$^2$, but spring body mass for females are similar to Alberta at 97-114 kg (McLellan 1989, 2011).

Further south along the Rocky Mountains, the Greater Yellowstone Ecosystem (GYE) supports a productive population with spring and summer female body masses of 112 kg (SE=5; Schwartz et al., 2013). The GYE population has increased from 135 individuals in 1983 (Schwartz et al., 2006a) to 593 individuals in 2010 (Cain, 2012). Despite this recovery during the past three decades, the current GYE bear population now faces some

nutritional challenges. Cutthroat trout (*Oncorhynchus clarki*) populations in Yellowstone Lake, which once made up an important part of diets of bears (Mattson et al., 1991), have markedly declined due to the introduction of non-native trout (*Salvelinus namaycush*) and "whirling disease" (*Myxoblus cerebralis*) (Koel et al., 2005;2006*;* Fortin et al., 2013; Tiersberg et al., in revision). Whitebark pine (*Pinus albicaulis*) nuts, a key food that affects reproductive success (Mattson et al., 1992; Schwartz et al., 2006b), has also declined due to whitebark pine blister rust (*Cronoartium ribicola*) and mountain pine beetle (*Dendroctonus ponderosae*; Greater Yellowstone Whitebark Pine Monitoring Working Group 2006; Haroldson and Podruzny 2010; Fortin et al., 2013). While the proportion of meat in the diets of brown bears in the GYE has remained either constant (female bears) or declined (male bears) (Fortin et al., 2013), a reduction in the elk population that began in approximately 1995 (Eberhardt et al., 2007; Barber-Meyer et al., 2008; Middleton et al. 2013; Ripple et al., 2013) may ultimately reduce the dietary proportion of meat and thereby decrease the nutritional quality of bear diets with subsequent effects on population productivity.

Reproductive success of bears depends on both maternal fat (Farley and Robbins, 1995; Robbins et al., 2012a) and lean mass reserves (López-Alfaro et al., 2013) before denning. For brown bears, lean mass growth occurs primarily during spring and early summer, while fat mass accumulation occurs mostly during summer and early fall before hibernation (Hilderbrand et al., 1999a; Felicetti et al., 2003; McLellan, 2011; Schwartz et al., 2013). In my study, ecosystem-specific brown bear food habits and nutritional information are integrated into a dynamic model to estimate the amount of digestible energy and protein in one kilogram of fresh bear diet. We used this model to ask two questions: 1) what are the differences in nutritional quality (i.e., amount of digestible protein and energy) of bear diets in west-central Alberta, the Flathead, and both the historical (1977 - 1987) and recent (2007 – 2009) GYE; and 2) what food resources are most critical for providing energy and protein to bears in each ecosystem.

We hypothesized that because fat and lean mass accumulation are positively related to reproductive success in bears, digestible protein in spring and early summer and digestible energy in late summer and fall should be higher in the Flathead and GYE than in west-central Alberta. Based on differences in individual body size, we expect protein

to be lower in the Flathead than in the GYE. Due to the recent decrease in trout and pine nuts in the diets of GYE bears, differences in the nutritional quality should be apparent between historical and recent diets.

## 2. METHODS

### 2.1 Brown bear food habits

Four published brown bear food habits studies were used to quantify ecosystem specific nutritional quality (Mattson et al., 1991; McLellan and Hovey, 1995; Munro et al., 2006; Fortin et al., 2013).

#### *2.1.1. West-central Alberta brown bear food habits*

In west-central Alberta, noticeable differences in diet were exhibited between bears living in the Mountain versus Foothills and were therefore separated as in Munro et al. (2006). Bear food habits presented in Munro et al. (2006) were based on 665 scats of 18 brown bears collected between April and October 2001–2003. The diet of Foothills bears in Munro et al. (2006) was examined from late April to early October in bi-monthly periods, while the diet of mountain bears was examined from late April to late September, hence we extended to early October.

#### *2.1.2 Flathead food habits*

Information on food habits for the Flathead region of southeastern British Columbia, Canada was obtained from McLellan and Hovey (1995). This study was based on 1100 scats collected between April and November 1978 – 1991 from 77 radio-collared brown bears. Diet descriptions extended from early April to early November, which we divided into bi-monthly periods, but we only use the period between late April and early October to compare with the other bear diets. McLellan and Hovey's (1995) study was conducted

before correction factors for different food item digestibility were developed (Hewitt and Robbins; 1996). Thus, we correct dry matter intake using the corresponding correction factors (CF) from Hewitt and Robbins (1996) as applied in Fortin et al. (2013): ungulates CF=3, insects CF=1.1, horsetail (*Equisetum* spp.) CF=0.16, graminoids CF= 0.24, forbs CF=0.26, roots CF=1, and fruits CF=1.2 (Hewitt and Robbins, 1996).

### *2.1.3 Greater Yellowstone Ecosystem food habits*

Two diet studies were used to characterize the historical (1977 – 1987) and recent diets of brown bears in GYE. The first study by Mattson et al. (1991) included Yellowstone National Park and surrounding National Forest and was based on 3,423 scats from 96 radio-collared bears. Diet descriptions extended from April to October by month, which we divided into bi-monthly periods for dynamic modelling. As in the Flathead study, dry matter intake was corrected using the above correction factors plus ones for rodents (CF=4), insects and false-truffles (CF= 1.1), and seeds (CF=1.5) (Hewitt and Robbins, 1996).

The recent GYE food habit study (Fortin et al., 2013) included the area immediately surrounding Yellowstone Lake. The diets estimated for Yellowstone bears was divided into male and female, each containing both adults and subadults. Scats were collected between 2007 and 2009 (n=778). Diet descriptions extend from May to September for males and to October for females and in monthly periods (Fortin et al., 2013; Fortin, unpublished). Therefore we extended the periods to cover from late April to early October.

When comparing the “recent” and “historical” diets of GYE bears, it must be remembered that Fortin et al., (2013) study occurred in the immediate area surrounding Yellowstone Lake whereas the Mattson et al., (1991) study occurred across the much larger Greater Yellowstone Ecosystem.

**2.2 Food items and nutritional values**

Bear foods identified in the Alberta, Flathead, and GYE studies were grouped into eight categories: green vegetation, berries, roots, ants, terrestrial meat, nuts, cutthroat trout, and false-truffles (mushrooms) (Table 3-1). Nutritional information for each category was estimated using published data (see Table A1 supplementary material). Nutritional information included six components: dry matter (%, DM); dry matter digestibility (%, DMDig); gross energy (kcal/kg, GrossE); energy digestibility (%, EDig); crude protein content (%, PC); and protein digestibility (%, PDig). All components, except DM, are expressed on a dry matter basis. Some nutritional values, the number of samples was small and precluded an estimate of variation. In those cases we assumed a standard deviation equal to 10% or 20 % of the average nutritional value.

The green vegetation category included seven species of grasses, forbs, and horsetails (*Equsetum* spp.). Nutritional values for green vegetation were estimated for three phenological stages: spring - early summer (from 15 April to 31 May); summer and late summer (from 1 June to 31 July); and early fall (1 August to 15 October). To match with the plant phenology in the Mountain ecosystems in Alberta, spring - early summer stage was extended until June 15.

The root category included thirteen species (Table 3-3, Appendix 3-A). For the Alberta ecosystem, we used nutritional estimates for one root species: alpine sweetvetch (*Hedysaraum alpinum*) (Coogan, 2012). For the Flathead and GYE we used all root species to estimate the average and SD of nutritional parameters (Pritchard and Robbins, 1990; Mattson et al., 1997; 2004; Hammer and Herrero, 1987; Coogan et al., 2012; Fortin, unpublished). To estimate the DM content, we used values of human-diet roots obtained from USDA National Nutrient Database (http://ndb.nal.usda.gov/) because other estimates were unavailable.

The nuts category included white bark pine and other conifer seeds (*Pinus edulis*). In the Alberta and Flathead ecosystem, we used the average and SD nutritional information of all nuts. In the GYE, we used nutritional information only for whitebark pine nuts (Fortin, unpublished). Nutritional information for the berry category was obtained from six

common species in Alberta, Flathead and GYE (Welch et al., 1997; Pritchard and Robbins 1990; Coogan et al., 2012; Fortin, unpublished). For ants, nutritional information included values for workers and pupae (Noyce et al., 1997; Swenson et al., 1999; Mattson et al., 2001; Coogan et al., 2012).

In the terrestrial meat category, we included ungulates and rodents (Mattson et al., 1991; McLellan et al., 1995; Fortin et al., 2013), but the nutritional information included deer (*Odocoileus* spp.), elk (*Cervus elaphus*), bison (*Bison bison*) and moose (*Alces alces*) (Pritchard and Robbins, 1990; Mattson et al., 2004; Fortin, unpublished).

Nutritional information for false-truffles (mushrooms) corresponds to *Rhizopogon* spp (Mattson et al., 2002; Fortin, unpublished; Appendix 3-A, Table 3-A1). Miscellaneous food categories reported in Munro et al., (2006), and garbage and debris, reported in Mattson et al., (1991), were not considered in our analysis.

### 2.3 Model structure

Stella 10.2 (isee Systems Inc. 2012) was used to build a model that estimated the digestible energy and protein in one kilogram of fresh bear diet using the food habits and nutritional information described above (Table 3-1). The model estimated results in a daily time step, where day one corresponds to April 15, and the final day corresponds to October 15, for a total of 180 days. The model input was digestible dry matter intake per food item obtained from food habits information. Because this data comes in bi-weekly periods, the model interpolates between these values to obtain the digestible dry matter per food item per day. Nutritional values per food item were randomly estimated in each repetition using a normal distribution curve built with the average and SD values in Table 1. One hundred repetitions were run per simulated scenario. Model outputs included daily digestible energy and protein (fresh diet base). Digestible energy and protein contributions per food group were also estimated to identify key food resources. Results were reported on a “kilogram of fresh diet” rather than “dry matter” base because it simplifies future estimations of foods requirements (kg) and potential daily food intake.

### *2.3.1 Model calculations*

The model runs in two consecutives calculations. First, the model estimates the grams (g) of each food item (fi) in one kilogram of fresh diet (gr.FFdiet(fi)). To transform the digestible dry matter per food item (gr.DigestableDM(fi)) to grams of fresh food (gr.FF(fi)), the gr.DigestableDM(fi) is divided by their corresponding dry matter digestibility (%.DMDig(fi)) and dry matter content (%.DM(fi)).

Eq.1 $$\text{gr. FFood (fi)} = \frac{\text{gr.DigestableDM(fi)}}{\text{\%.DMDig(fi)} * \text{\%.DM(fi)}}$$

The grams of each food item in the fresh diet base is obtained by dividing the gr.FFood(fi) by the sum of all food items and multiplying by 1000 (g).

Eq.2 $$\text{gr. FFdiet(fi)} = \frac{\text{gr.FFood(fi)}}{\sum_{\text{fi}=1}^{\text{n}} \text{gr.FFintake(fi)}} * 1000$$

In the second phase, the model uses the gr.FFdiet (fi) and the nutritional values (Table 3-1) to estimate the contribution of digestible energy and protein per food item and later adds these contributions to obtain the total digestible energy and protein in one kilogram of fresh diet.

Digestible energy per food item (kcal.DigestibleE(fi)) is the product of gr.FFdiet(fi), dry matter content (%.DM(fi)), gross energy (kcal.GrossE(fi)) and energy digestibility per food item (%.EDig(fi)). DM, GrossE and EDig are obtained from data in Table 3-1.

Eq.3 $$\text{kcal. DigestibleE(fi)} = \text{gr. FFdiet(fi)} \times \text{\%. DM(fi)} \times \text{kcal. GrossE(fi)} \times \text{\%. EDig(fi)}$$

Digestible energy for the total diet (kcal.DigestibleE (diet)) is the sum of the digestible energy per food items.

Eq.4 $$\text{kcal.DigestibleE(diet)} = \sum_{\text{fi}}^{\text{n}} [\text{kcal. DigestibleE(fi)}]$$

Digestible protein per food item is the product of the gr.FFdiet(fi), dry matter content (%.DM(fi)), protein content (%.PC(fi)), and protein digestibility (%.PDig(fi)) per food item. PC, PDig were obtained from data in Table 1. Digestible protein for the total diet (gr.DigestibleP (diet)) is the sum of the digestible protein per food items.

Eq.5 $\text{gr.DigestibleP(fi)} = \text{gr. FFdiet(fi)} \times \%.\text{DM(fi)} \times \%.\text{PC(fi)} \times \%\text{PDig(fi)}$

Eq.6 gr. DigestibleP (diet) = $\sum_{fi=1}^{n}[\text{gr. DigestibleP(fi)}]$

To obtain the digestible energy and protein per food item we used equations 3 and 4, using 1000 g of fresh food with 100 repetitions run.

## 3. RESULTS

### 3.1 Digestible energy and protein per food item (fresh food base)

Digestible energy and protein (gr/kg fresh food) was noticeably different between food items (Fig. 3-1). Plant matter had lower levels of digestible energy and protein than animal matter, seeds and false-truffles. Seeds have the highest level of digestible energy because of their very low water content, followed by false-truffles, terrestrial meat and trout (Fig. 3-1a). Digestible energy in one kilogram of green vegetation, berries or roots are ~1/7 than in nuts and ~1/5 than in terrestrial meat (Fig. 3-1a). Digestible protein was higher in trout, ungulates, false-truffles and ants. Digestible protein contribution of terrestrial meat is ~3 to 5 times higher than green vegetation and roots (Fig. 3-1b).

### 3.2 Digestible energy in bear diets

Estimated digestible energy varied through the season in all ecosystems (Fig 3-2a). Bear diets in the GYE had the highest levels of digestible energy. The recent GYE and Flathead diets displayed two distinct peaks: one in spring (until the 15$^{th}$ of May), and

other in late summer (from the 15th August). The historical GYE diet had the highest digestible energy content during spring and summer which subsequently decreased in late summer; however, it maintains one of the highest levels of digestible energy throughout the three seasons. Bear diets in western Alberta had the lowest levels of digestible energy in all three seasons. These diets showed one peak of digestible energy during early summer (15th of May to 30th June). During late summer and early autumn, recent diets in Yellowstone provide ~2 times more digested energy than in the Flathead and ~3 to 4 times more digestible energy than the Foothills and Mountains in western Alberta.

## 3.2 Digestible protein in bear diets

Digestible protein varied through the seasons for all ecosystems (Fig. 3-2b). Digestible protein was highest in the spring and early summer in all ecosystems, but the GYE and Flathead showed a second peak in the fall. The Flathead diet had protein levels higher than the recent male diet in GYE during early spring, but in summer protein levels decreased to less than ~50% of the recent male diet in GYE. Diets in Alberta have the lowest levels of digestible protein through the entire season. Digestible protein in Alberta Mountain diet was ~1/5 than in the recent GYE female diet during spring and early summer. The Flathead had digestible protein levels ~2-3 times higher than those in the Foothills and Mountains of Alberta during spring.

## 3.4 Key food items

### *3.4.1 Energy contribution per food item*

In the Alberta Foothills, ungulates, roots and green vegetation were the main energy sources in spring, while in summer, green vegetation contributed over 60% of digestible energy available in bear diets (Figure 3-3a). In late summer, berries supplied 25% to 40% of the digestible energy in the Foothills of Alberta; while in early fall roots supplied over 75% of the digestible energy. In the Alberta Mountain diet, roots provided over 70% of the digestible energy during spring and early summer, while green vegetation and berries

were the main sources during summer and early fall (Fig. 3-3b). In the Flathead, ungulates provided 50% to 70% of the digestible energy during spring, while in early summer green vegetation contributed ~50%. In late summer and early fall, berries contributed over 90% of the digestible energy in the Flathead diets. In early fall, terrestrial meat contributed ~40% of digestible energy in Flathead diets (Fig. 3-3c).

In the recent GYE female diets, terrestrial meat, i.e., primarily ungulates, contributed ~80% of the digestible energy during the spring and early summer (Fig. 3-3f). The contribution of terrestrial meat decreased to 20 to 30% during the rest of the year. In summer, green vegetation contributed ~25% of the digested energy in the recent-female diet, while in late summer and early fall, whitebark pine nuts contributed ~30% and false-truffles ~15%. During early fall, roots contributed ~ 20% to recent-female digestible energy. For recent-male diets in the GYE, terrestrial meat was the main source of digestible energy throughout all seasons, contributing ~50% (Fig. 3-3e). Green vegetation contributed ~40% for the energy in spring and summer. In late summer and early fall, whitebark pine nuts contributed ~30% of the digestible energy. In the historical diet, trout provided over 65% of the digestible energy during early summer to fall. During late summer and before denning, whitebark nuts contributed over 50% and terrestrial meat ~20% of the digestible energy for GYE bears (Fig. 3-3f).

### *3.4.2 Protein contribution per food item*

In the Foothills, green vegetation, roots and ungulates were the main source of digestible protein in spring, while during the rest of the season green vegetation provided over 60% of the dietary protein (Fig. 3-4a). Terrestrial meat provided ~25% of the protein through all seasons in the foothills, while in late summer and early fall roots contributed ~40%. In the Mountains of Alberta, roots contributed ~90% of the digestible protein in the spring, but declined to ~20% by early summer. In the Mountains, green vegetation provided more than 50% of the digestible protein in summer and more than 90% in early fall (Fig. 3-4b). In the Flathead, terrestrial meat provided most of the digestible protein (~70%) in spring and fall. In summer (June to July 15$^{th}$), green vegetation was the main source of

protein in the Flathead bear diet (>50%) but declined during fall. Ants contributed ~20% of the digestible protein in Flathead bear diets during the summer (Fig. 3-4c).

For recent diets in the GYE, terrestrial meat was the main source of digestible protein, ranging between 40 and 80% through the seasons (Fig. 3-4d, e). Whitebark pine nuts contributed 10% to 20% of the digestible protein during summer and early fall. Green vegetation contributed ~30% of the digestible protein during the summer in the recent-female diet in Yellowstone and ~30% of the recent-male diet during spring and summer. In the historical GYE diet, terrestrial meat was the main source of digestible protein (~95%) in spring after which cutthroat trout contributed ~75% to digestible protein through the late summer. In late summer and early fall, whitebark pine nuts contributed ~30% to the digestible protein (Fig. 3-4f).

## 4. DISCUSSION

Bear diets differ in their patterns of digestible protein and energy across ecosystems and seasons. These patterns can be associated with differences in population density and body size. The nutritional quality of bear diets were higher in the GYE, followed by Flathead and Alberta ecosystems. Ecosystems in Alberta, particularly the mountains, had the lowest levels of digestible energy and protein through all seasons, and this result is consistent with the low reproductive rates observed in Banff National Park (Garshelis et al., 2005) and low individual densities in the Mountain and Foothill ecosystems (ASRD and ACA, 2010). There are other nutritional aspects of Alberta ecosystems that might also contribute towards low densities. For example, these ecosystems have a shorter growing season and, therefore, the amount of time during the year that bears have for foraging (Munro et al., 2006). Also, habitat disturbances (e.g. logging, energy development, and road building) may increase the production of berries, green vegetation and roots in new open areas, but increase human-bear conflicts and therefore increase bear mortalities (Nielsen et al., 2004a,b; Nielsen et al. 2006; Nielsen et al. 2008).

Diets in the Flathead ecosystem had protein levels similar to the recent-average diet in the GYE during spring, but energy levels were not as high as in the GYE diets during late summer and fall. A rich protein diet in spring may improve lean mass accumulation and milk production for lactating females, which would likely enhance reproductive success (Farley and Robbins, 1995; Hilderbrand et al., 1999; López-Alfaro et al., 2013). McLellan (2011) observed that black bears (*Ursus americanus*) in the Flathead can gain weight during the spring. A similar pattern was observed in northern brown bear populations in Sweden, which either maintained or gained mass in spring when compared with southern populations (Swenson et al., 2007). The authors suggest that the increase in body mass during spring may be due to more abundant sources of protein in northern ecosystems (Swenson et al., 2007). Meat-rich diets have also been correlated with bear body size and population density (Hilderbrand et al., 1999b), but when populations without access to salmon are excluded; meat diets have a negative relationship with population density (McLellan, 2011). Bears in the Flathead have one of the smallest body sizes among North America brown bear populations but one of the highest population densities among interior bear populations (Zedrosser et al., 2011). McLellan (2011) suggested that female brown bears in the Flathead might have adapted to a less nutritious plant diet that included abundant, low protein berries in the fall by being smaller. The smaller size would reduce their energy needs while the abundant, fall berries would provide energy for fattening before hibernation.

While we agree with McLellan's hypothesis, we highlight the importance of meat in the nutritional quality of bear diets in this ecosystem. Terrestrial meat was an important source of digestible protein and energy in this ecosystem in all seasons, which may help explain the high population density observed in the Flathead ecosystem.

Major differences in nutritional quality of bear diets across ecosystems were largely due to the presence or absence of a few highly nutritious food items, such as terrestrial meat (mainly ungulates), pine nuts or trout. For example, the digestible protein in one kilogram of ungulates is ten times higher than in one kilogram of roots, and the digestible energy in one kilogram of nuts is seven times higher than in one kilogram of green vegetation. As a consequence, small changes in consumption of nutritious foods have large impacts on the nutritional quality of bear diets. However, individual capacity to switch between food

items is constrained by factors that were not measured in this study, such as food abundance and distribution and bear physiology (e.g. digestion rate, stomach capacity). In Alberta ecosystems, roots and green vegetation are the main source of protein and energy at the beginning and end of the active period, respectively; however their low nutritional value constrains the total energy and protein intake and therefore reduce reproductive success. For example, in the Flathead and recent diets in the GYE, most of the protein comes from terrestrial meat, and the majority of energy is obtained from ungulates, berries and nuts. Bears in Alberta ecosystems, need to consume 10 kg of roots to obtain the same amount of protein as one kilogram of ungulates. Also bears in Alberta need to consume ~4.3, or 6.7 kg of roots, to obtain the same amount of energy as from one kilogram of ungulate, or nuts respectively.

There are two other environmental factors that might also influence individual nutrition and thus differences in population productivity. First, there are differences in the length of the growing season among ecosystems. For example, in the Flathead ecosystem bear food was available for seven months (beginning of April to the end of October; McLellan and Hovey, 1995) while in the Alberta ecosystem and GYE food was reported for six months (Munro et al., 2006; Fortin et al., 2013). Also severe winter conditions in the Mountain ecosystems might delay food availability in spring while early winter conditions may reduce food availability in the fall. Longer growing seasons benefit bear nutrition by increasing the time they can gather energy and protein reserves, and by reducing the length of hibernation and thus the requirements of lean and fat mass reserves necessary to support the denning phase (López-Alfaro et al., 2013). Second, environmental conditions influence food abundance in the ecosystems. Food abundance will limit nutrient intake depending the functional response and the nutritional quality of the food (Barboza et al., 2009). Functional response defines the rate of intake and nutritional quality influences the amount of food necessary to support energy and protein requirements.

Recent diets in the GYE have the highest levels of energy and protein due to the largely carnivorous diet across all three seasons. High protein levels is consistent with their larger individual body size, when compared with other interior North American brown bears, and with their rapid rate of population recovery during the last three decades

(Schwartz et al., 2006a**;** Cain, 2012). Comparisons between historical (Mattson et al., 1991) and recent (Fortin et al., 2013) diets do reveal, however, a change in the nutritional quality due to the loss of key foods which may affect fitness and population density in the future. The absence of trout and lower consumption of nuts has reduced the total digestible energy during spring and summer. Trout was the main source of energy from May to mid–August in the historical diet, while the contribution of nuts was important from mid-August to September. Digestible energy in the recent GYE diets was dominated by terrestrial meat and green vegetation during summer, but bears need to eat ~4 kg of green vegetation to supply the same amount of digestible energy as one kilogram of trout. During late summer and early fall, nut consumption was lower with bears needing to eat ~7 kg of berries, or ~2 kg of terrestrial meat, or ~7 kg of roots, or ~5 kg of green vegetation to supply the same amount of digestible energy as one kilogram of nuts. Protein levels also decreased due to the shift in food items. Recent average diet (female and males) were ~50% lower in digestible protein during early- summer than the historic diet. Bears need to eat ~5 kilograms of green vegetation to supply the same amount of digestible protein as one kilogram of terrestrial meat or nuts. Thus, while bears will readily switch to the next most nutritious food as more nutritious foods disappear (e.g., ungulates or pine nuts), the loss of high quality foods may have a disproportionate effect on bear productivity when increased intake cannot fully replace the reduction in dietary quality.

## 4.1 Conclusion

Important differences in the nutritional quality of grizzly bear diets were observed among several interior ecosystems. Patterns observed suggest that individual body size and reproductive fitness are influenced by the seasonal availability of protein and energy. Small changes in the availability of highly nutritious foods can have disproportionate effects on the nutritional quality of bear diets. These changes in nutritional quality will have an even greater impact when food availability and foraging efficiency due not permit increase consumption to balance the reduction in nutritional quality.

Previous studies have illustrated the differences in brown bear diets and their correlation with life history traits (Hilderbrand et al., 1999b**;** Ferguson and McLoughlin, 2000; Bojarska and Selva, 2011; McLellan, 2011). However, these differences have not been previously quantified or assessed for the entire active period. This study is one of the first to comparatively evaluate the ecosystem-specific brown bear diets for interior populations of grizzly bears and develop this assessment for the entire active season. This approach can also be used to evaluate the impact of environmental changes and management decisions on bear nutrition and ultimately population productivity. Additional studies on the limitations to intake will be important in understanding the impact of changes in dietary quality.

## 5. REFERENCES

ASRD & ACA (2010) Status of the Grizzly Bear (*Ursus arctos*) in Alberta: Update 2010. Alberta Sustainable Resources Development. Wildlife Status Report No. 37 (Update 2010). Edmonton, AB. 44 pp.

Barber-Meyer SM, Mech LD, White PJ. Elk calf survival and mortality following wolf restoration to Yellowstone National Park. Wildl Monog 2008;169:1–30

Barbosa PS, Parker KL, Hume ID. Integrative wildlife nutrition. 1st ed. Berlin: Springer-Verlag; 2009.

Bojarska K, Selva N. Spatial patterns in brown bear *Ursus arctos* diet: the role of geographical and environmental factors. Mammal Review. 2011:42;120-143.

Cain S. 2012. Grand Teton National Park recreational use. Page 45 *in* FT van Manen, MA Haroldson and K West, editors. Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 2011. U.S. Geological Survey, Bozeman, Montana, USA.

Coogan SCP. Getting to the root of the matter: grizzly bears and alpine sweetevtch in west-central Alberta, Canada. MSc thesis University of Alberta 2012.

Coogan SCP, Nielsen SE, Stenhouse GB. Spatial and temporal heterogeneity creates a "Brown Tide" in root phenology and nutrition. ISRN Ecology 2012;2012:1-10.

Eberhardt LL, White PJ, Garrott RA, Houston DB. A seventy-year history of trends in Yellowstone's Northern elk herd. J Wildl Manage 2007;71:594–602.

Farley SD, Robbins CT. Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. Can J Zool 1995;73:2216-2222.

Felicetti LA, Robbins CT, Shipley LA. Dietary protein content alters energy expenditure and composition of the gain in grizzly bears (*Ursus arctos horribilis*). Physiol Biochem Zool 2003;76:256-261.

Ferguson SH, McLoughlin PD. Effect of energy availability, seasonality and geographic range on brown bear life history. Ecography 2000;23:193-200.

Fortin JK, Schwartz CC, Gunther KA, Tiesberg JE, Haroldson MA, Evans MA, Robbins CT. 2013. Dietary adjustability of grizzly bears and American blanck bears in Yellowstone National Park. J Wildl Manage 77:270-281.

Garshelis DL, Gibeau ML, Herrero S. Grizzly bear demographics in and around Banff National Park and Kananaskis country, Alberta. J Wildl Manage 2005;69:277-297.

Herfindal I, Solberg EJ, Sæther BE, Hogda KA, Andersen R. Environmental phenology and geographical gradients in moose body mass. Oecologia 2006:150, 213-224.

Hewitt DG, Robbins CT. 1996. Estimating grizzly bear food habits from fecal analysis. Wildlife Society Bulleting 24:547-550.

Hilderbrand GV, Jenkins SG, Schwartz CC, Hanley TA, Robbins CT. Effect of seasonal differences in dietary meat intake on changes in body mass and composition in wild and captive brown bears. Can J Zool 1999a;77:1623-1630.

Hilderbrand GV, Schwartz CC, Robbins CT, Jacoby ME, Hanley TA, Arthur SM, Servheen C. Importance of meet, particular salmon, to body size, population productivity and conservation of North American Brown Bears. Can J Zool 1999b; 77:132-138.

Homyack JA. Evaluating habitat quality of vertebrates using conservation physiology tools. Wildl Res 2010;37:332-342.

Isee System, Inc. An introduction to system thinking. Hanover: New Hampshire; 2006.

Koel TM, Arnold JL, Bigelow PE, Ertel BD, Mahony DL. Yellowstone Fisheries & Aquatic Sciences: annual Report, 2002. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming, USA. 2003.

Koel TM, Bigelow PE, Doepke PD, Ertel BD, Mahony DL. Nonnative lake trout results in Yellowstone cutthroat trout decline and impacts to bears and anglers. Fisheries 2005;30:10–19.

López-Alfaro C, Robbins CT, Zedrosser A, Nielsen SE. Energetic of hibernation and reproductive trade-offs in Brown Bears. Ecol. Modell 2013;270:1-10.

Mattson DJ, Blanchard BM, Knight RR. Food habits of Yellowstone grizzly bears, 1977-1987. Can J Zool 1991;69:1619-1629.

Mattson DJ, BM Blanchard, Knight RR. Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. J Wildl Manag 1992;56:432-442.

Mattson DJ, Barber K, Maw R, Renkin R. Coefficients of productivity for Yellowstone's grizzly bear habitat: U.S. Geological Survey, Biological Resources Discipline, Biological Science Report USGS/BRD/BSR–2002-0007. 2004

Mattson DJ, Podruzny SR, Haroldson MA. Consumption of fungal sporocarps by Yellowstone grizzly bears. Ursus 2002;13:159-168.

Mattson DJ. Selection of microsites by grizzly bears to excavate biscuitroots. J Mammal 1997;78:228-238.

Mattson DJ, Reinhart DP. Bear use of white-bark pine seeds in North America, in Schmidt, W.C., and Holtmeier, F.-K., compilers, Proceedings — international workshop on subalpine stone pines and their environment: the status of our knowledge: U.S. Forest Service General Technical Report INT-GTR-309, p. 212-220. 1994.

Mattson DJ. Myrmecophagy by Yellowstone grizzly bears. Can J Zool 2001;79:779-793.

McLellan BN. Dynamics of a grizzly bear population during a period of industrial resource extraction. I. Density and age-sex composition. Can J Zool 1989;67:1856-1860.

McLellan BN, Hovey FW. The diet of grizzly bears in the Flathead River drainage of southeastern British Columbia. Can J Zool 1995;73:704-712.

McLellan BN, Servheen C, Huber D, (IUCN SSC Bear Specialist Group). *Ursus arctos*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1. <www.iucnredlist.org>. Downloaded on 19 October 2013; 2008.

McLellan BN. Implications of high-energy and low-protein diet on the body composition, fitness, and competitive abilities of black (*Ursus americanus*) and grizzly (*Ursus arctos*) bears. Can J Zool 2011;89:546-558.

Middleton AD, Morrison TA, Fortin JK, Robbins CT, Proffitt KM, White PJ, McWhirter DE, Koel TM, Brimeyer DG, Fairbanks WS, Kauffman MJ. Grizzly bear predation links the loss of native trout to the demography of migratory elk in Yellowstone. Proc Royal Soc B 2013; 280:20130870

Mowat G, Heard DC, Seip DR, Poole KG, Stenhouse G, Paetkau DW. Grizzly *Ursus arctos* and black bear *U. americanus* densities in the interior mountains of North America. Wildlife Biol 2005;11:31-48.

Munro RHM, Nielsen SE, Stenhouse GB, Boyce MS. Seasonal and diet patterns of grizzly bear diet and activity in west-central Alberta. J Mamm 2006;87:1112-1121.

Nielsen SE, Boyce MS, Stenhouse GB. Grizzly bears and forestry: I. Selection of clearcuts by grizzly bears in west-central Alberta, Canada. For Ecol Manage 2004;199:51-65

Nielsen SE, Herrero S, Boyce MS, Benn B, Mace RD, Gibeau ML, Jevons S. Modelling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies ecosystem of Canada. Biol Conserv 2004;120:101-113.

Nielsen SE, Boyce MS, Stenhouse GB. A habitat-based framework for grizzly bear conservation in Alberta. Biol Conserv 2006;130:217-229.

Nielsen SE, Stenhouse GB, Beyer HL, Huettmann F, Boyce MS. Can natural disturbance-based forestry rescue a declining population of grizzly bears? Biol Conserv 2008:141;2193-2207

Noyce KV, Kannowski PB, Riggs MR. Black bears as ant-eaters: seasonal associations between bear myrmecophagy and ant ecology in north-central Minnesota. Can J Zool 1997;75:1671-1686.

Pritchard GT, Robbins CT. Digestive and metabolic efficiencies of grizzly and black Bears. Can J Zool 1999;68:1645-1651.

Ripple WJ, Beschta RL, Fortin JK, Robbins CT. Trophic cascades from wolves to grizzly bears in Yellowstone. J Anim Ecol 2013;83:223-233.

Robbins CT. Wildlife feeding and nutrition. 2nd ed. Tony J. Cunha Editor. Academic Press, San Diego; 1993.

Robbins CT, Schwartz CC, Felicetti LA. Nutritional ecology of ursids: A review of newer methods and management implications. Ursus 2004;15:161-171.

Rode KD, Robbins CT, Shipley LA. Constraints on herbivory by grizzly bears. Oecologia, 2001;128:62-71.

Schwartz CC, Haroldson MA, White GC. Study area and methods for collecting and analyzing demographic data on grizzly bears in the Greater Yellowstone Ecosystem.

Pages 9-16 in C.C. Schwartz, MA. Haroldson GC, White RB, Harris S, Cherry KA, Keating D, Moody, Servheen C editors. 2006a.

Schwartz CC, MA Haroldson, GC White, RB Harris, S Cherry, KA Keating, D Moody & C Servheen. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. Wildlife Monog 2006b;161:1-68.

Schwartz CC, Fortin JK, Tiesberg JE, Harold MA, Servheen C, Robbins CT, Van Manen FT. Body and diet composition of sympatric black and grizzly bears in the Greater Yellowstone Ecosystem. J Wildlife Manage 2013;78:68-78.

Swenson JE, Jansson A, Rilg R, Sandegren F. Bears and ants: myrmecophagy by brown bears in central Scandinavia. Can J Zool 1999;77:551-561.

Tiersberg JE, Haroldson MA, Schwartz CC, Gunther KA, Fortin JK, Robbins CT. Contrasting Past and Current Numbers of Bears Visiting Yellowstone Cutthroat Trout Streams 2014: in revision.

Welch CA, Keay J, Kendall KC, Robbins CT. Constraints on frugivory by bears. Ecol 1997;78:1105-1119.

Zedrosser A, Steyaert SMJG, Gossow H, Swenson JE. 2011. Brown bear conservation and the ghost of persecution past. Biol Conservation 144:2163-2170.

Zedrosser A, Cattet M, Swenson JE, Stenhouse G. One species, two populations, three patterns of growth; brown bears in Canada and Sweden. 2014: in revision.

**Figure 3-1:** (a) Digestible energy (kcal/kg fresh food) and (b) digestible protein (g/kg fresh food) per brown bear food item category. Error bars are SE (n=100 repetitions). Digestible energy and protein were estimated based on the average nutritional values of each food category (Table A1, supplementary material). Nutritional values include dry matter, energy and protein content and digestibility.

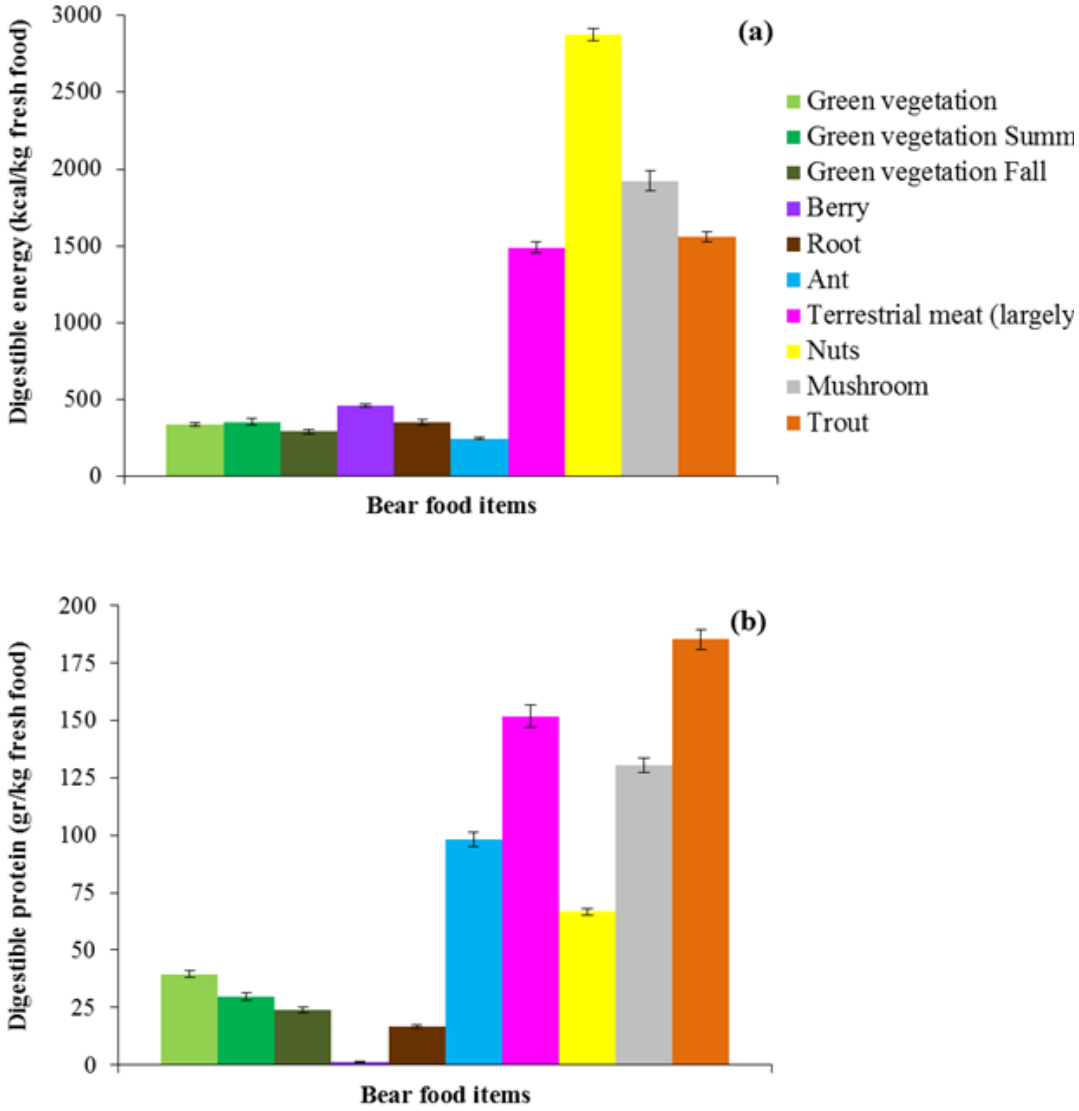


**Figure 3-2:** (a) Digestible energy (kcal) and (b) digestible protein (g) in one kilogram fresh brown bear diet across different ecosystems. Error bars indicate the 95% confidence interval. Ecosystem diets include the "Foothills" and "Mountains" of west-central Alberta (Canada), "Flathead" river drainage in southeast British Columbia (Canada) and the Greater Yellowstone Ecosystem (GYE, USA). For the GYE, we present the recent diets for both male ("GYE-Male, recent") and female + sub-adults ("GYE-Female, recent"), the average recent diet ("GYE-Average, recent"), and the historical diet "GYE-Historical" diets. Digestible energy and protein were estimated based on the proportion of digestible dry matter intake obtained from food habit studies in these ecosystems (McLellan and Hover 1995; Mattson et al. 1991; Munro et al. 2006; Fortin et al. 2013) and the nutritional information presented in Table 1.

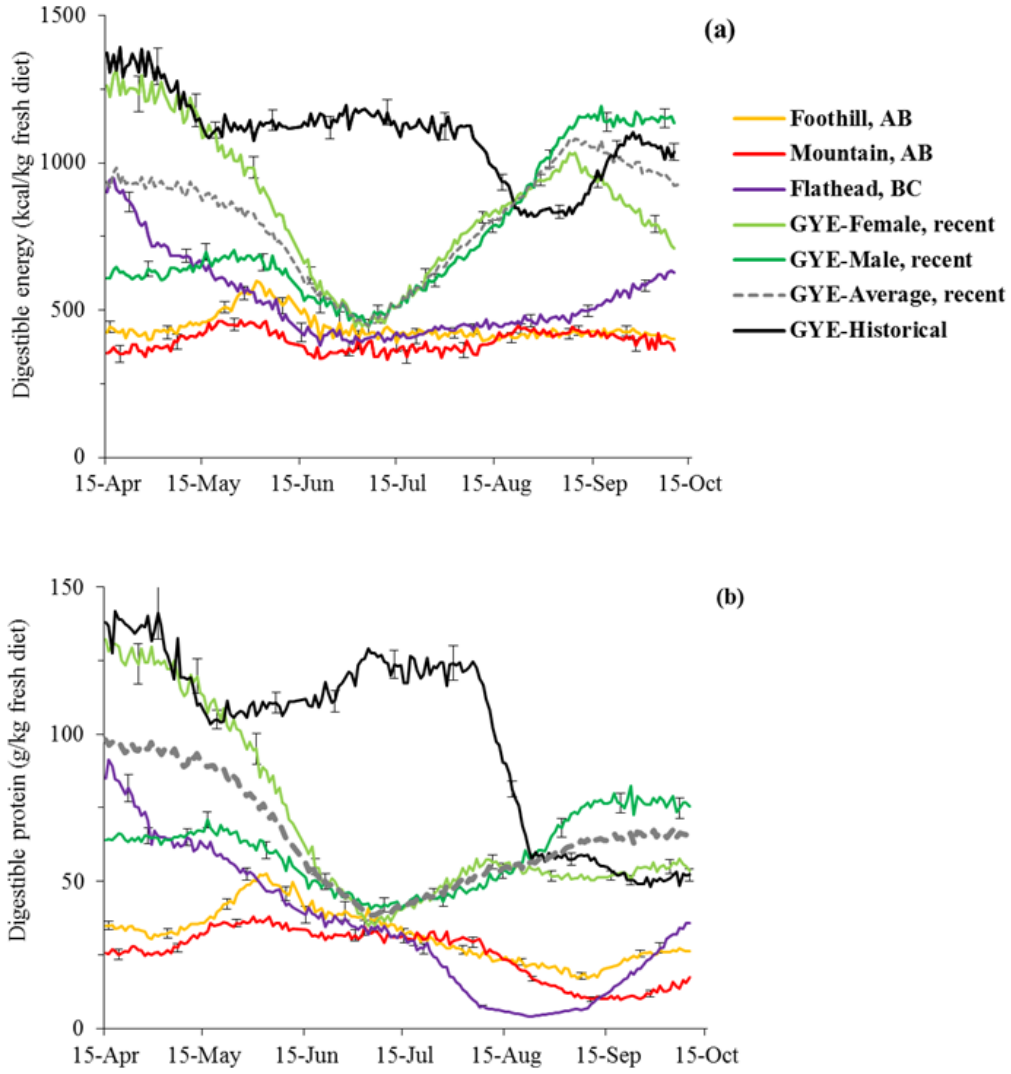


**Figure 3-3:** Percent digestible energy contribution per food item category (fresh diet base) across ecosystems. Contribution was estimated based on the total digestible energy in the diet. Ecosystem diets include: Foothills and Mountains of west-central Alberta (Canada), Flathead River drainage in British Columbia (Canada) and the Greater Yellowstone Ecosystem (GYE, USA). For the GYE, we present the recent diets for both male ("GYE-Male, recent") and female + sub-adults ("GYE-Female, recent"), the average recent diet ("GYE-Average, recent"), and the historical diet "GYE-Historical" diets.

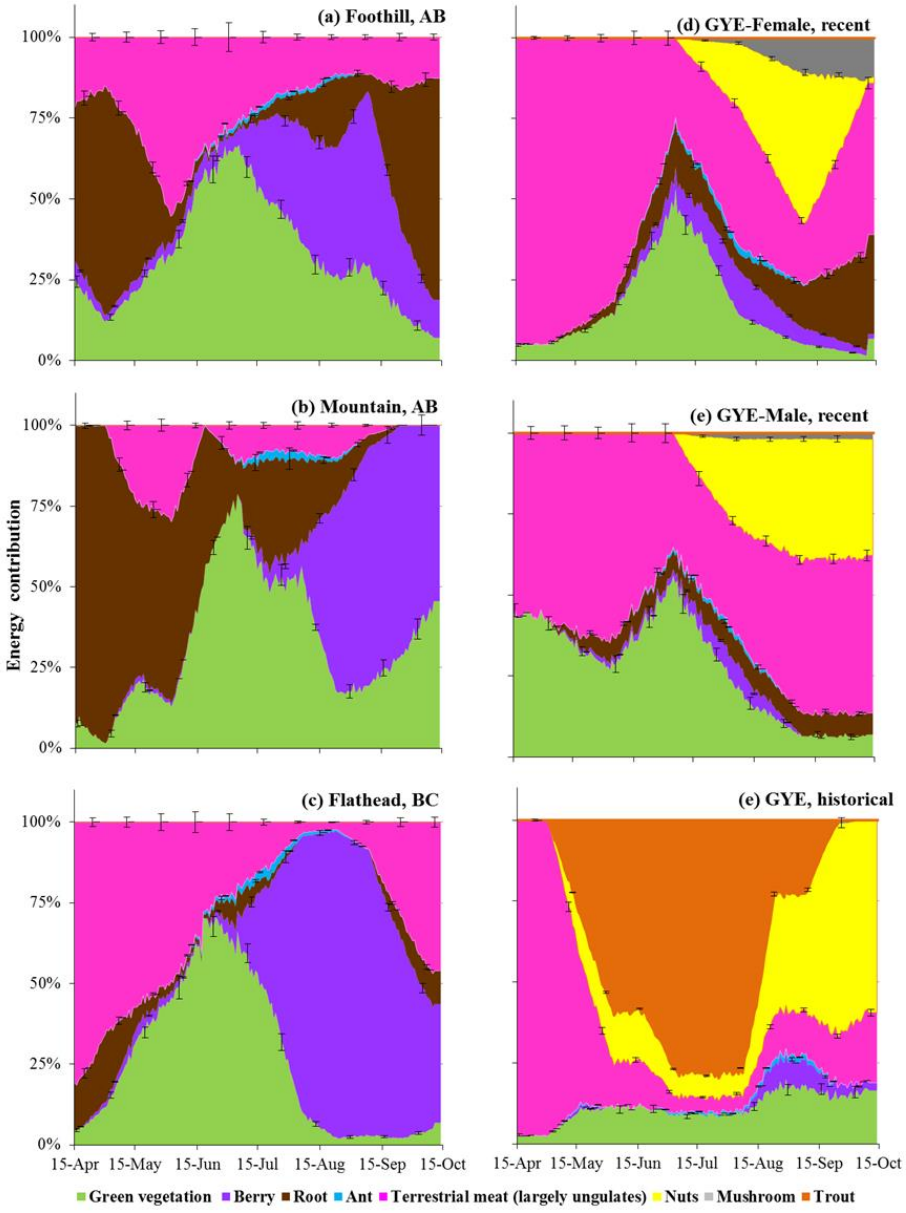


**Figure 3-4:** Percentage of digestible protein contributed per food item category (fresh diet base) across ecosystems. Contribution was estimated based on the total digestible protein in the diet. Ecosystem diets include: Foothills and Mountains of west-central Alberta (Canada), Flathead River drainage in British Columbia (Canada) and the Greater Yellowstone Ecosystem (GYE, USA). For the GYE, we present the recent diets for both male ("GYE-Male, recent") and female + sub-adults ("GYE-Female, recent"), the average recent diet ("GYE-Average, recent"), and the historical diet "GYE-Historical" diets.

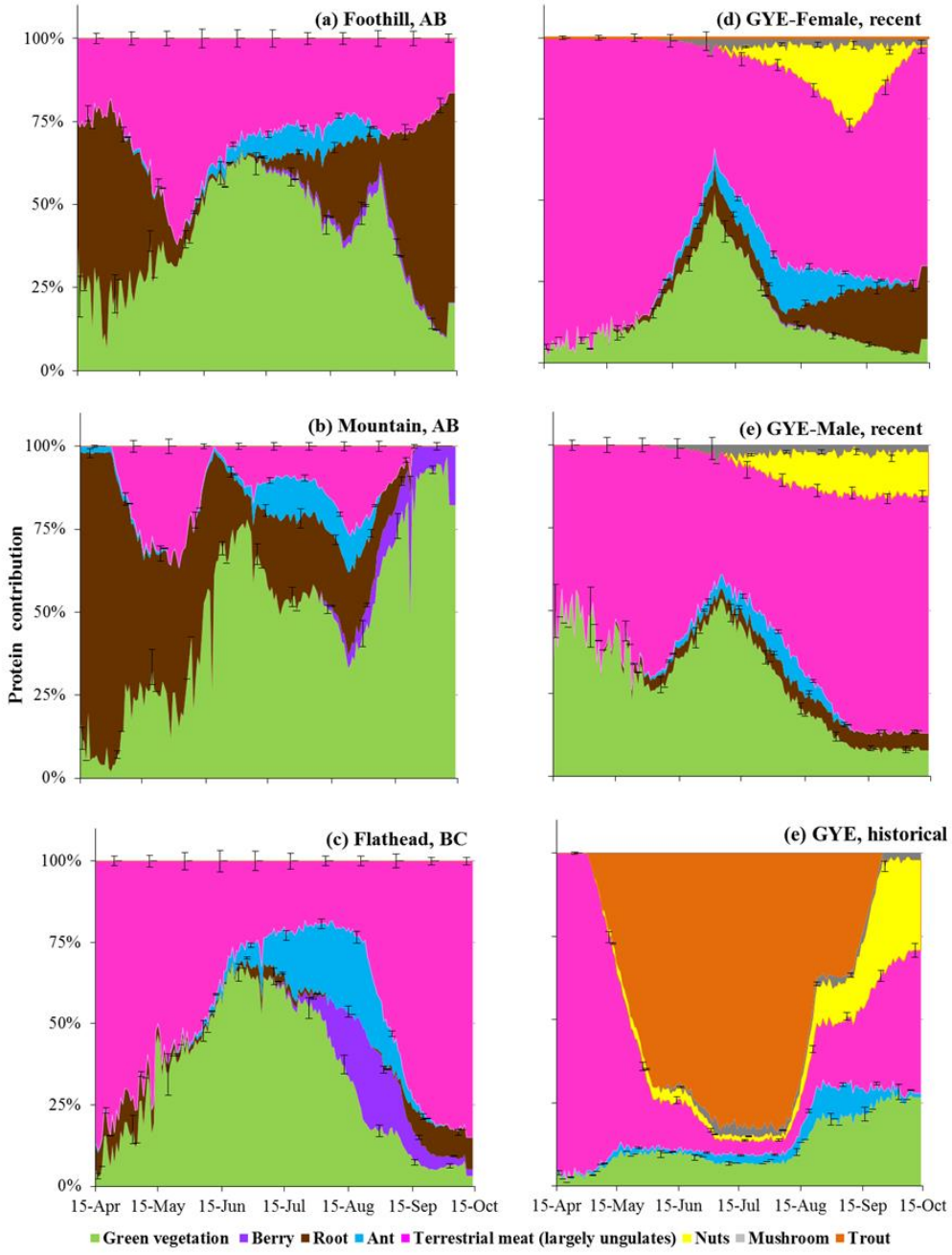


**Table 3-1.** Nutritional information used to obtain the digestible energy and protein in one kilogram of fresh diet. Estimations are based on Table 3-A1 in Appendix 3-A.

| | DM | DMDig | GrossE | EDig | PC | PDig | References |
|---|---|---|---|---|---|---|---|
| Vegetation early Springe - early Summer | 20.1 (5.1[1]) | 36.6 (8.8) | 4,505 (450[2]) | 41.3 (8.2) | 25.9 (3.7) | 74.5 (0.6-15.6) | DM from Rode et al., (2001), DMDig from Mattson et al., (2004) and Rode et al., (2001). EDig from Mattson et al., (2004) and Coogan (unpublished). PC from Rode et al. (2001), Mattson et al., (2004) and Coogan (unpublished). |
| Vegetation early Summer - late Summer | 21.5 (8.9) | 27.8 (12.2) | 4,505 (450[2]) | 35.3 (12.4) | 19.9 (5.3) | 68.0 (8.3) | DM from Fortin (unpublished). DMDig from Coogan (unpublished) and Fortin (unpublished). GrossE from Fortin (unpublished). EDig from Mattson et al., (2004) and Coogan (unpublished). PC, PDig and TDF from Mattson et al. (2004), Coogan (unpublished) and Fortin (unpublished). |
| Vegetation late Summer - early Fall | 28.3 (9.6) | 18.4 (7,7) | 4,522 (450[2]) | 24.3 (11.7) | 14.7 (5.8) | 61.2 (9.0) | DM from Rode et al., (2001) and Fortin (unpublished). DMDig from Rode et al. (2001), Coogan (unpublished) and Fortin (unpublished). GrossE from Fortin (unpublished). EDig from Mattson et al., (2004), and Coogan (unpublished). PC, PDig and TDF from Rode et al., (2001), Mattson et al. (2004), Coogan (unpublished) and Fortin (unpublished). |
| Berries | 18.3 (2.8) | 63.9 (11.0) | 4,280 (215) | 60.0 (10.1) | 4.6 (0.8) | 14.8 (4.1) | DM from Welch et al., (1997), Pritchard and Robbins (1990). DMDig from Welch et al (1997, Table 1), Pritchard and Robbins (1990) and Coogan et al. (2012). GrossE, EDig and ProtC from Pritchard and Robbins (1990) and Coogan et al. (2012). PDig from Coogan et al. (2012). |

**Table 3-1.** Nutritional information used to obtain the digestible energy and protein in one kilogram of fresh diet. Estimations are based on Table 3-A1 in Appendix 3-A. (continuation)

| | DM | DMDig | GrossE | EDig | PC | PDig | References |
|---|---|---|---|---|---|---|---|
| Roots (*1, Alberta ecosystem) | 23.3 (8.2) | 38.2 (*3.8*[2]) | 3,957 (396) | 39.9 (4,0[2]) | Coogan et al., 2012. | | DM from Pritchard and Robbins (1990), USDA (2012) and Fortin (unpublished). DMDig from Pritchard and Robbins (1990) and Coogan et al. (2012). GrossE from Pritchard and Robbins (1990), USDA (2012) and Fortin (unpublished). EDig from Pritchard and Robbins (1990), Coogan et al., (2012) and Mattson et al., (2004). PC and PDig from Coogan et al., 2012. |
| Roots (*2, Flathead and GYE) | 23.3 (8.2) | 38.2 (*3.8*[2]) | 3,380 (1,193) | 45.8 (8.6) | 9.0 (3.3) | 44.3 (15.5) | DM from Pritchard and Robbins (1990), USDA (2012) and Fortin (unpublished). DMDig from Pritchard and Robbins (1990) and Coogan et al. (2012). GrossE from Pritchard and Robbins (1990), USDA (2012) and Fortin (unpublished). EDig from Pritchard and Robbins (1990), Coogan et al., (2012) and Mattson et al., (2004). PC and PDig from Pritchard and Robbins (1990), Mattson et al., (2004), Hammer and Herrero (1987), Coogan et al., (2012) and Fortin (unpublished). |
| Ants | 27.4 (2.8) | 76.6 (9.8) | 4,716 (1,598) | 18.7 (1.3) | 46.3 (14.2) | 77.6 (7.2) | DM, DigDM, EDig, from Swenson et al., (1999). GrossE, PC, PDig from Noyce et al., (1997), Swenson et al., (1999) and Coogan (2012). PDig from Pritchard and Robbins (1989). |
| Ungulate | 25.0 (5.2[1]) | 93.0 (9.3[2]) | 6,221 (774) | 93.1 (9.3[2]) | 67.4 (16.0) | 86.7 (3.5) | DM, GrossE from Pritchard and Robbins (1990) and Fortin (unpublished). DigDM from Pritchard and Robbins (1990). EDig from Pritchard and Robbins (1990), and Mattson et al., (2004). PC and PDig from Pritchard and Robbins (1990), Mattson et al., (2004) and Fortin (unpublished). |

**Table 3-1.** Nutritional information used to obtain the digestible energy and protein in one kilogram of fresh diet. Estimations are based on Table 3-A1 in Appendix 3-A. (continuation)

| | DM | DMDig | GrossE | EDig | PC | PDig | References |
|---|---|---|---|---|---|---|---|
| Nuts | 90.6 (4.5) | 41.2 (*4,1*[2]) | 6,340 (364) | 49.8 (5.0[1]) | 12.0 (2.2) | 61.0 (3.8) | DM from Pritchard and Robbins (1990) and Fortin (unpublished). DMDig from Pritchard and Robbins (1990). GrossE from Pritchard and Robbins (1990), Fogel and Trapped (1978), Coogan (2012) and Fortin (unpublished). EDig from Pritchard and Robbins (1990) and Mattson et al., (2004). PC from Pritchard and Robbins (1990), Mattson et al., (2004), Coogan (2012) and Fortin (unpublished). PDig from from Coogan (2012) |
| Cutthroat trout | 27.3 (5.2[2]) | 89.8 (9.0[2]) | 5,987 *599*[2] | 94.5 (9,5[2]) | 67.5 (6.8[2]) | 95.2 (9.5[2]) | DM, Grosse, PC, PDig from Pritchard and Robbins (1990) and Fortin (unpublished). DMDig, EDig from Pritchard and Robbins (1990) |
| Mushroom | 84.0 (16.8[1]) | 83.5 (3.9) | 4,500 (1,200) | 51.1 (4.5) | 21.9 (2.7) | 72.3 (7.2[2]) | DM, DMDig, GrossE, EDig, PC and PDig from Fortin (unpublished). |

DM = Dry matter (% of fresh matter); DMDig (%) = Digestible dry matter; GrossE = Gross energy (kcal); EDig = Energy digestibility; PC (%) = Protein content; PDig (%) = Protein digestibility. DMDig, GrossE, EDig, PC and PDig in a dry matter base.
1: Standard deviation estimated as the 20% of average value.
2: Standard deviation estimated as the 10% of average value.

# CHAPTER 4

# LINKING INDIVIDUAL NUTRITION TO BROWN BEAR POPULATIONS: AN ENERGETIC PERSPECTIVE

## 1. INTRODUCTION

Wildlife populations are regulated by both bottom-up (food resources) and top-down (survival) factors (Testa, 2004; Nielsen et al., 2010; Zedrosser et al., 2013). These factors operate at the individual level by affecting reproductive success and mortality (Robbins, 1993; Barboza et al., 2009; Parker et al., 2009). Top-down controls are associated with predation and human induced mortalities such as harvest and road accidents (Benn and Herrero, 2002; Zedrosser et al., 2011; 2013). Bottom-up controls are associated with food availability. Vulnerability to starvation, disease and predation are influenced by the individual's nutritional status (Worthy et al., 1983; Robbins, 1993; Barbosa et al., 2009; Robbins et al. 2012b; López-Alfaro et al., 2013). Nutritional requirements in relation to food resource distribution influence food habits, foraging behavior, nutrient intake, and ultimately reproductive success (Robbins, 1993; Bojarska and Selva, 2011; López-Alfaro et al., 2013). Despite the importance of nutritional factors on individual fitness and population demography (Testa, 2004; Zedrosser et al., 2006; Parker et al., 2009; Nielsen et al., 2010, 2013;), the mechanisms that link individual nutrition and nutritional landscapes have not been widely explored (Homyack, 2010).

Brown bears (*Ursus arctos*) occur across North America, Europe and northern Asia, but many of their populations have declined precipitously and are threatened or endangered (McLellan et al., 2008; McCarthy et al., 2009; ASRD and ACA, 2010). Brown bears are omnivores (Robbins et al., 2004), which allowed them to occupy a diversity of habitats including prairie and shrub steppe to temperate forests, tundra and alpine (Hilderbrand et al., 1999b; McLellan et al., 2008; Bojarska and Selva, 2011). The requisite dietary flexibility to occupy such diverse communities resulted in different life histories. For example, adult female body size ranges from 100 to 250 kg, birth interval ranges from 2.3 to 4.4 yrs, age at first reproduction ranges from 4 to 8 yrs. Population densities range

from 2 to 65 bears/1000 $km^2$ for interior populations and over 500 bears/1000 $km^2$ for populations with access to salmon (Hilderbrand et al., 1999b; Swenson et al., 2001; Støen et al., 2006; Miller et al., 1997; 2003; Garshelis et al., 2005; Zedrosser et al., 2011; Mowat et al., 2013).

Brown bears are born during hibernation and stay with their mother for 1 to 2 yrs (Farley and Robbins, 1995; Schwartz et al., 2003; Robbins et al., 2012b). The first four to five months of lactation occur while the mother is fasting in the den, but lactation continues for many months after the mother resumes eating. Thus, the mother must use energy and nutrients accumulated during the previous active period to support early cub growth (Farley and Robbins, 1995; Robbins et al. 2012b; López-Alfaro et al., 2013), but milk production and cub growth increase rapidly after den emergence as the mother uses both reserves and current dietary energy and nutrients to meet the increased cub demand (Farley and Robbins, 1995). Depending on the balance between meeting cub demand from maternal reserves or the immediate diet, minimum thresholds of body reserves necessary to support early reproductive costs may exceed that determined for hibernation alone (López-Alfaro et al., 2013).

Bear physiology and food nutritional quality interact to constrain nutrient assimilation, and, therefore, affects the maternal capacity to transfer necessary nutrients to her offspring. Energy and protein requirements determine necessary food intake (Robbins, 1993). Energy maintenance cost depends on body mass (basic metabolic rate, McNab, 2008). In brown bears, maintenance cost increases from 1 – 3 times depending on dietary protein intake (Felicetti et al., 2003; Robbins et al., 2007; Erlenbach et al., 2014). Protein maintenance depends on metabolic body mass and dry matter intake (Pritchard and Robbins, 1989; Robbins, 1993). Energy and protein requirements of reproduction are dominated by milk production, which is low during hibernation and increases quickly after den emergence reaching a maximum in summer (Farley and Robbins, 1995). Digestive tract capacity limits the rate of energy and protein intake and in relation with food quality. Finally, food availability (spatial distribution) influences foraging efficiency and therefore the rate of nutrient intake (Rode et al., 2001; Welch et al., 1997; Robbins et al., 2007)

The mechanisms that link individual energy and nutrient requirements to brown bear population dynamics include metabolic demands, digestive physiology, foraging efficiency, and the nutritional quality of available food resources (Rode et al., 2001; Welch et al., 1997; Robbins et al., 2007). The relationship and trade-offs among these factors affect the individual's capacity to acquire and store the energy and matter necessary for reproduction and therefore has the potential to regulate bear populations.

Brown bears in Alberta were listed as a threatened species in 2010 (ASRD and ACA, 2010). The low population (691 individuals) and low reproductive rate in Alberta may be a consequence of three processes: first, bear habitats in Alberta have limited high-quality food resources (i.e., lack of salmon and limited fruit production) which results in a low diet quality (Chapter 3); second, bears occur in areas where a short growing season limits the time available for foraging and growth and increases hibernation length and cost (Munro et al. 2006); third, habitat disturbances such as forest harvesting, energy developments, and road building have increased human-bear conflicts and therefore mortality rates (Nielsen et al. 2004c; Nielsen et al. 2008).

Several research studies in Alberta have increased our understanding of brown bear habitat relationships (Munro et al. 2006; Nielsen et al., 2002; 2003; 2004a, b; 2006; 2008; 2010; 2013)**.** However, there is still a lack of understanding of how individual physiology and foraging interact with the nutritional landscape to influence bear reproductive success and thus population processes. In this study I built an energy and protein model to understand the nutritional interactions that influence individual body mass dynamics during a year. I used that model to explore three specific questions: 1) what are the energy and protein requirements of bears during the active period; 2) what are the trade-offs and key elements of bear physiology and nutritional quality of foods available that influence body mass dynamics; and 3) what is the impact of Alberta's food resources on reproductive success of bears and population recovery.

## 2. METHODS

### 2.1 Model structure

I developed a dynamic system model in Stella 10 (Isee Systems, Inc., 2006) to simulate body mass dynamics for bears consuming different diets. Model inputs are individual the body mass at the start and the bear diet, model outputs are individual body mass over time and body mass gain/loss per day. The model operates in a daily time step for 365 days with day 1 being den entry at the start of hibernation. Body mass (kg) is separated into lean and fat mass, and those two components are modeled in separate compartments. The model works in two phases: hibernation and active. A detailed introduction of the hibernation phase can be founded in López-Alfaro et al. (2013). For the active phase, the physiological components are represented as six sub-models that operate in consecutives steps: target gain, food intake, reproductive cost, energy balance, protein balance, and mass gain dynamics (Fig.4-1). Each is presented in more detail below in the Sub-models section. During the active phase, the model simulates lean and fat mass dynamics (i.e., gain or loss) based on energy and protein costs of maintenance, growth, and reproduction relative to the gains from foraging. Diets are characterized by energy and protein content, dry matter and digestibility, and energy and protein digestibility and are based on Chapter 3 and details are presented in Appendix 4-A.

### 2.2 Sub-models

#### *2.2.1. Target mass gain*

This sub-model estimates the amount of energy that the individual must consume to reach mass gain requirements. The mass gain requirements is based on the idea that the individual has to reach a lean mass and fat mass at the end of the active period to either survive or reproduce during hibernation (see 2.3.1; López-Alfaro et al., 2013).

The relative proportions of the lean and fat mass gained during the active period are based on the observed composition of body mass gain in captive and wild brown bears (Hilderbrand et al., 1999a; Felicetti et al., 2003), and they follow a sigmoidal function.

The highest rate of lean mass gain occurs during spring and early summer (Appendix 4-B, Fig. 4-B1), and the highest rate of fat mass gain occurs during late summer and early fall (Appendix B, Fig. 4-B2). These two curves are set at the initial conditions according to the length of the active period (details are presented in Appendix B).

Target lean mass (TgLean (kg)) and target fat mass (TgFat (kg)) are defined with the initial conditions (see 2.3.1). Later, at the end of hibernation or day one of the active period, the model defines the kilograms of lean and fat mass that the individual must gain in order to reach the target lean mass and the target fat mass. Thus, target lean mass gain (TgLeanGain (kg)) and target fat mass gain (TgFatGain (kg)) are estimated as the difference between the TgLean or TgFat, and the emergence lean mass ($ActulaLean_{emergence\ day}$ (kg)) or emergence fat mass ($ActualFat_{emergence\ day}$(kg)) respectively (equations 1 and 2).

Eq.1 $TgLeanGain\ (kg) = TgLean - (ActualLean_{(emergence\ day)})$

Eq.2 $TgFatGain\ (kg) = TgFat - (ActualFat_{(emergence\ day)})$

TgLeanGain and TgFatGain are distributed proportional to the curves of lean mass gain and fat mass gain; consequently "daily lean mass gain target" ($DayTgLeanGain_{(day=n)}$) and "daily fat mass gain target" ($DayTgFatGain_{(day=n)}$) are estimated each day as the difference between TgLeanGain and TgFatGain, and actual lean ($ActualLean_{day=n}$) and fat mass ($ActualFat_{day=n}$) respectively (equations 3 and 4). If actual lean or fat mass are greater than the target lean and fat mass (equations 3 and 4 are negative), the model assumes zero mass gain.

Eq.3 $DayTgLeanGain_{(day=n)} = TgLeanGain_{(day=n)} - ActualLean_{(day=n)}$

Eq.4 $DayTgFatGain_{(day=n)} = TgFatGain_{(day=n)} - ActualFat_{(day=n)}$

Finally, the sub-model determines the "Daily energy mass target" (DEMassTg (kcal)) based on $DayTgLeanGain_{(day=n)}$ and $DayTgFatGain_{(day=n)}$, and the energy content of lean and fat mass (1200 kcal/kg lean; 9100 kcal/kg fat mass; Blaxter, 1989; Farley and Robbins, 1993) as shown in equation 5.

Eq.5 $DEMassTg\ (kcal) = TgLeanGain_{(day=n)} \times 1200\ kcal + TgFatGain_{(day=n)} \times 9100\ kcal$

*2.2.2. Food intake*

Intake regulation is a complex process guided by internal and external processes. Physical and physiological factors, such as stomach capacity, passage rate, bite size, and bite rate influence maximum daily intake (Welch et al., 2001, Rode et al., 2001), whereas energy requirements and subsequently energy balance have strong feedback mechanisms that drive foraging decisions (Robbins 1993; Barbosa et al., 2009). External factors, such as food abundance and quality, restrict foraging efficiency and total nutrient intake (Barbosa et al., 2009). The model uses a simplified structure to estimate the "daily fresh food intake" based on two physiological factors: stomach capacity and daily energy target.

*2.2.2.1 Stomach capacity*

Brown bears can eat a mass of fresh food equal to from 10% (high energy diets) to 35% (low energy density) of their body mass (kg) per day (Hilderbrand et al., 1999a; Welch et al., 2001, Rode et al., 2001; Erlenbach et al., 2014). Also, this maximum digestive capacity (MaxDigCap) as a percentage of the body mass increases during the season and reaches a maximum during summer and early fall, referred to as the hyperphagia period. The model uses an algorithm that estimates the MaxDigCap (%) depending on the day of the active period (equation 6). This algorithm was built and calibrated with empirical studies and details are presented in Appendix 4-C.

Eq.6 $MaxDigCap\ (\%) = 30 / \{1 + [(185 - actual\ day) / (185 - 50)]^{1.5}\}$

Mean retention times ranged from 7 to 14 hrs depending on the type of food (Pritchard and Robbins, 1989). Because the model operates in a daily time step, the model assumes that all food consumed during a day is digested during that day. Thus, the maximum amount of food that can be consumed and digested during a day equals stomach capacity

(StmCap, kg) as defined by both physical capacity **(**Hilderbrand et al., 1999a; Welch et al., 2001, Rode et al., 2001; Erlenbach et al., 2014) and retention time (Pritchard and Robbins, 1989) and it is estimated as a percent of body mass (equation 7).

Eq.7 StmCap (kg) = BM × MaxDigCap

*2.2.2.2 Daily energetic target (DayETg).*

The "Daily energy target" (DayETg (kg) is the amount of food an individual must eat to meet the predicted energy requirement. Total energy requirement (kcal, TotEnergeticReq) is the sum of the daily energy mass target (DEMassTg; see target mass gain sub-model), maintenance cost (TotMtn; see energy balance sub-model), and reproductive cost (EMilk; see reproduction sub-model) (equation 8).

Eq.8 TotEnergeticReq (kcal) = DayEMassTg + TotMnt + EMilk

Daily energy target" (DayET (kg)) is estimated based on TotEnergyCost (kcal) divided by the energy content of the food (kcal/kg, EC) and its digestibility (%, EDig) (equation 9).

Eq.9 DayETg (kg) = TotEnergyCost / (EC(diet (kcal/kg fresh food)) × EDig (diet (%))

Finally, the daily food intake (DayFFintk (kg)) is the minimum of either StmCap or DayETg (equation 10). The model assumes that there are no external restrictions on the amount of food or foraging efficiency. This means that the individual eats until the stomach capacity constrains food intake or until the individual reaches the amount of energy necessary to support maintenance, reproduction, and daily growth goal.

Eq. 10 DayFFintk (kg) = Min(StmCap, DayETg)

The model also estimates the dry matter intake (DMintk (kg)) using the DayFFintk and diet dry matter content of the diet (equation 11).

Eq.11 DMintk = DayFFintk / DM (diet)

*2.2.3 Reproductive cost*

This sub-model operates when initial conditions define “lactating bear” and it starts in hibernation when females give birth (López-Alfaro et al., 2013). During the active period the sub-model estimates the daily energy (kcal/day, EMilk) and protein demands (kg/day, PMilk) for lactation based on the results of Farley and Robbins (1995) and the "milk production efficiency”, which is the efficiency of converting the mother’s tissue to milk energy and protein and is set at 85% Blaxter (1989).

In Farley and Robbins (1995) study the lactation period was 300 days in total; 60 days during hibernation and 240 days during the active period. I adjusted these results to the simulation conditions; 256 days of lactation in total, 74 days during the hibernation and 184 days during the active period. To do this we estimate the total energy (kcal) and protein cost of lactation (kg) from Farley and Robbins (1995) using the integral of the regression curve to distribute this cost over 256 days (details are presented in Appendix 4-D).

*2.2.4. Energy balance*

This sub-model determines the available energy for mass gain (EGain) based on the energy intake and energy costs. First, the sub-model estimates the digestible energy intake (DigEintk, kcal) based on the daily fresh food intake (DayFFintk) and its energy content (kcal/kg diet, EC) and digestibility (%, EDig) (equation 12).

Eq.12 $\text{DigEintk (kcal)} = \text{DayFFintk} \times \text{EC} \times \text{Edig}$

Second, the sub-model estimates the total energy requirements (TotMntR) as the sum of 1) the maintenance cost, 2) the increase in the maintenance cost due to excessive or inadequate dietary protein, and 3) the urinary energy losses.

Studies on captive bears showed that low or high dietary protein content increases maintenance cost and decrease the rate of mass gain (Rode and Robbins, 2000; Felicetti

et al., 2003; Robbins et al., 2007; Erlenbach et al., 2014). Similar observations have been seen in humans where both low and high protein diets induced thermogenesis (Westerterp et al., 1999; Mikkelsen et al., 2000; Halton and Hu, 2004). However, there are differences in the physiological processes behind the increase in maintenance cost. Under low protein diets individuals increase food intake to supply minimum protein requirements for maintenance, generally overeating energy which is dissipated as heat. While under high protein diets, individuals are forced to process proteins and eliminate the excess of nitrogen in the urea, which increase energy utilization (Mikkelsen et al., 2000).

Erlenbach et al. (2014) presented a regression curve of the maintenance cost (kcal/$kg^{0.75}$/day) as a function of the dietary protein content (PC, dry matter base). In order to distinguish between basic maintenance cost and the effect of dietary protein content, we assumed the lowest value of the curve as the basic maintenance cost, 106 kcal of digestible energy/$kg^{0.75}$/day. We discount this value from the curve to estimate the effect of dietary protein content (Diet-PC) on the maintenance cost (equation 13).

Eq.13 Diet-PC (kcal/$kg^{0.75}$/day) = $-0.0008 \times PC^3 + 0.1903 \times PC^2 - 10.083 \times PC + 153.93$

Urinary losses correspond to the cost of nitrogen excretion and vary from 6.9 ± 2.3% of digestible energy for meat-based diets to 3.9 ± 1.7% for plant-based diets (Pritchard and Robbins, 1990). I set this value at 8% to capture the higher end of loss (equation 14). Below are the equations to estimate energy costs:

Eq.14 Uloss (kcal) = DigEintk × 0.08

Total maintenance requirement is estimated using equation 15.

Eq.15 TotMntR (kcal) = Mnt + Diet-PCs + Uloss

Finally, the energy available for mass gain (EGain (kcal), equation 16) is the difference between the digestible energy intake (DigEintk) and the total maintenance and lactation requirements. Energy lactation cost (kcal, EMilk) is obtained from reproductive sub-model (see 2.2.3):

Eq.16 EGain (kcal) = DigEintk - TotMntR - EMilk

*2.2.5 Protein balance*

The protein balance sub-model determines the available protein for mass gain as the difference between the digestible protein intake and protein cost for maintenance and reproduction. Digestible protein (DigPintk (kg), equation 17) corresponds to the amount of protein in the DayFFintk and is estimated from the dietary protein content (PC, %) times its digestibility (PDig, %).

Eq.17 DigPintk (kg) = DayFFintk × PDig × PC

Protein maintenance requirements are the sum of the metabolic fecal nitrogen (MFN) and endogenous urinary nitrogen (EUN) losses. MFN represents the minimal constant losses in feces and depends on the amount of feces and thus digestibility of foods. Because this factor also occurs in the protein digestibility coefficient, it is not included in the protein balance sub-model. Consequently the only protein maintenance cost assessed in the model is the EUN, and it is a function of metabolic body mass ($BM^{0.75}$, Robbins, 1993). To estimate EUN, we used a normal distribution ($\mu$ = - 0.160, $\sigma$ =0.0022) to estimate the nitrogen loss (mg), and set the nitrogen content in protein as 16% (equation 18).

Eq.18 EUN = BMR ($BM^{0.75}$ × (*normal*(0.160, 0.022)) × 6.25 / 1000

Finally, the protein available for mass gain (PGain (kg), equation 16) is the difference between the digestible protein intake (DigPintk) and the EUA and lactation requirements (equation 19). Protein lactation cost (kg, PMilk) is obtained from reproductive sub-model (see 2.2.3):

Eq.19 PGain = DigPintk - EUN - PMilk

*2.2.6. Mass gain*

This sub-model determines the dynamics of lean and fat mass (loss/gain) per day depending on the energy (EGain) and protein (PGain) available for mass gain and DEMassTg. If the energy and protein available for mass gain is positive and DEMassTg is positive, then the bear gains mass. In contrast, if energy and protein available for mass gain are negative, the bear loses body mass. If DEMassTg is negative, then the bear maintains its body mass.

This sub-model uses several hierarchical rules based on the following assumptions:

a) Gain in lean and fat mass is estimated as the lesser of either ingested energy and protein available for mass gain or the DEMassTg. Thus, if either energy or protein is ingested above the intake target, excess energy and protein become gain as long as it does not exceed the mass gain target.
b) One kilogram of gain in lean mass requires 0.211 kg of protein and 1200 kcal/kg; one kilogram of gain in fat mass requires 9100 kcal (Blaxter, 1989; Robbins, 1993).
c) When protein is available, the model prioritizes gain in lean mass over fat mass; consequently, the energy available for gain in fat mass is obtained after discounting the energy used for gain in lean mass.
d) When the individual is fasting and, therefore, loses mass, lean and fat are used as an energy source.

*2.2.7 Hibernation*

This sub-model estimates the body mass loss during hibernation. Energy maintenance cost (MtbHib) is a function of body mass (Robbins et al., 2012). Because bears are able to recycle nitrogen from protein catabolism (Barbosa et al., 1997; Tøien et al., 2011), the model assumes no protein requirements for physiological maintenance. Thus, the reproductive cost includes fetus develop and lactation. Energy and protein demands for lactation were based on Farley and Robbins (1995). Reproductive cost is multiplied by the number of cubs and includes the "milk production efficiency” parameter (see reproductive cost sub-model). The model uses an algorithm, namely the daily mass loss

composition, to estimate the use of fat or lean tissue as an energy source. This algorithm depends on the individual body fat content: when body fat content is > 17%, all energy comes from fat reserves; when body fat content was ≤ 17%, the contribution of fat to energy decreases linearly to zero with the increase of difference provided by lean mass (López-Alfaro et al., 2013).

### 2.3 Model initialization

Model inputs include 1) Length of hibernation that was set at 180 days and, therefore, length of active period was 186 days. 2) Reproductive status (i.e., non-lactating, pregnant, or lactating). Non-lactating bears are barren through hibernation and the following active period. Pregnant bears are barren through hibernation and during the active period will mate and try to achieve the target body mass to give birth during the following season. Lactating give birth 106 days into hibernation and then lactate with two cubs for the rest of the year.

We assumed an individual with 100 kg of lean body mass from which only 30% can be lost to supply energy and protein. Therefore initial lean mass and target lean mass was 100 kg in all simulated experiments. Target body fat going into hibernation was estimated based on the energetic cost of hibernation, which depends on length of hibernation and reproductive status (López-Alfaro et al., 2013). For non-lactating and non-pregnant bears, initial body fat and target body fat was 22%. For pregnant bears, initial body fat was 22% and target body fat at 35%. For lactating bears, initial body fat was 35% and target body fat was 22%

### 2.4 Model calibration

The model was calibrated and adjusted using two empirical studies of brown bears (Hilderbrand et al., 1999a; Robbins et al., 2007). Details are presented in Appendix 4-E. In these studies, captive bears were used in feeding trials for ~14 days to assess the effects of different diets on gains in body mass.

We replicated the conditions described in these studies (e.g. diet information; period of year; initial bear body mass) and compared the model outcome with their results. Four diets were used in the simulated experiments: white-tailed deer diet from Hilderbrand et al. (1999a), and berry-diet, salmon-diet, salmon and fruit diet from Robbins et al. (2007).

### 2.5 Sensitivity analysis

We used a Sensitivity Index (Sx) to estimate the impact of parameters on model outputs (Bendoricchio and Jorgensen, 2001). This Index relates changes in a variable's response with changes in the parameter (equation 22).

Eq.20 $Sx = [(RV_1 - RV_0)/RV_0] / [(P_1-P_0)/P_0]$

where $RV_0$ is the response variable in the base condition, $RV_1$ is the response variable after changing the parameter, $P_0$ is the parameter in the base condition and $P_1$ is the parameter change with all other parameters kept constant. Sensitivity was assessed for four model parameters (Table 4-2) with an increase and decrease in parameters of 10%, 25% and 50%. A neutral diet scenario with medium level of digestible energy and digestible protein was used with the response variable being "total food intake".

### 2.6 Model simulation experiments

Two factors are considered in the simulation experiment: thirteen different bear diets (nine hypothetical and four brown bear diets) and three different target body masses (3 levels). In each experimental scenario 100 repetitions were run. Sources of variability are in diet information (Appendix 4-A), energy and protein cost of lactation (Appendix 4-D) and EUN (equation 18).

### *2.6.1 Bear diets*

Two set of diets were used to explore the relationship between bear diet and physiology, as well as its effects on the dynamics of body mass. First, we used a simple representation of bear diets in order to control for nutritional variables (Hypothetical diets). Second, we used the observed bear diets in the Foothill and Mountains of Alberta (Munro et al., 2006), the Flathead of southeast British Columbia (McLellan and Hovey, 1995), and the Greater Yellowstone Ecosystem female diet (USA, Fortin et al., 2013). Inputs for bear diets were based on information from Chapter 3 and are presented in Appendix 4-A.

#### *2.6.1.1 Hypothetical diets*

Nine diets were created based on the combination of three levels of energy (E) and three levels of protein content (P). Levels were denominated as: high (H), medium (M) and low (L).

Energy levels were: Low E = 600, Medium E = 1200, and High E = 2400 kcal/kg fresh diet. Protein levels were defined in a fresh food base (%/kgFF) and dry matter base (%/kgDM); Low P = 5% (kgFF) and 10% (DM); Medium P = 10% (kgFF) and 35% (DM), High P = 15% (kgFF) and 60% (DM).

Other nutritional values were set at: DM = 20%; DMDig = 70%; ProtDig = 80%; EDig = 80%. All nutritional values were kept constant through the active period. Values represent the range of variation among the bear diets in Alberta, Flathead, and Greater Yellowstone Ecosystems (Chapter 3)

#### *2.6.1.2 Observed brown bear diets*

Four known bear diets were also simulated. These diets resemble the bear food habits in the Foothill and Mountain in Alberta (Canada, Munro et al. 2006), Flathead in southeast British Columbia (Canada, McLellan and Hovey, 1995), and female bears in the Greater Yellowstone Ecosystem (Fortin et al., 2013). Nutritional information is based on a fresh

diet base and dietary protein content in a dry matter base was also used to estimate the Diet-PC.

*2.6.2 Reproductive conditions and target body mass.*

Three reproductive conditions were simulated, Non-lactating, Pregnant and Lactating. When the simulation experiment was run for a 'Lactating' bear with the diets of Alberta (Foothill and Mountain) and the Flathead, results indicated that individuals were not able to reach the body target mass (100 kg of lean mass and 22% of denning body fat). Therefore we increased the denning body fat content (initial conditions) until bears were able to reach this target body mass resulting in 45% of initial denning body fat necessary. Therefore, the initial conditions for the simulation experiments are:

- Initial lean mass and target body lean mass was 100 kg under all scenarios.
- Non-Lactating: initial fat content and target body fat was 22%.
- Pregnant: initial fat content was 22% and target body fat was 35% for the GYE diet and 45% for the Alberta and Flathead diets.
- Lactating: initial fat content was 22%. Target body fat was 35% for GYE diets and 45% for the Alberta and Flathead diets.

## 3. RESULTS

### 3.1 Calibration and sensitivity

Regressions obtained in the simulation feeding trial experiments were able to estimate the efficiency of gain (slope of the regression) but they overestimate the maintenance cost ($g/kg^{0.75}/day$) for the salmon-berry diet and salmon diet and underestimate the maintenance cost for the deer-diet (Table 4-1).

The model was sensitive to the energy digestibility and dry matter content (Table 4-2).

### 3.2 Energetic reproductive cost

Under simulation conditions which assumes a bear body size ~120-170kg, the total lactation cost per cub (hibernation + active period) was 687,898 (SD = 14,464) kcal and 33.9 (SD = 0.9) kg of protein. Maximum lactation cost was ~4,000 kcal/per cub/day and ~300 gr of protein/per cub/day (Fig.4-2a). These results consider the efficiency of milk production (0.85). During the active period the lactation cost for two cubs born 74 days before emergence as 1,274,792 (SD = 31,871) kcal and 60.7 (SD = 1.7) kg of protein.

Intake of food items necessary to supply maximum energy (~4,000 kcal/per cub/day) and protein demand per day (200gr of protein/ per cub/day) was estimated using the digestible energy and digestible protein per food item (Chapter 3). As expected, higher levels of digestible energy and protein in food items decreased the amount of food necessary to supply lactation cost. Ungulates, pine nuts, and trout required lower levels of food intake to supply energy and protein (Fig. 4-2b).

### 3.3 Hypothetical diets

Energy demand varies between 0.8 - 3.4 kcal x $10^6$ for Non-lactating and between 1.1 - 3.6 kcal x $10^6$ for Pregnant bears. Differences in the energy requirements were mainly due to the impact of the dietary protein content, which ranges between 0.14 – 2.5 kcal x $10^6$ for both reproductive strategies (Fig 4-3a, b).

In a protein balanced diet (PC = 20%), the increase in energy demand from non-lactating to pregnant conditions was ~ 12%. Increase in energy demand from non-lactating to lactating bear was between 180% and 225%.

Target body mass was not reached in diets with low energy levels and high or low protein levels (HP-LE and LP-LE; Fig. 4-2a, b, c). Target body mass was also not reached at medium energy level and when energy requirement increases due to an increase in the body mass target or lactation, (Fig. 4-2b, c). These results emerge as a consequence of the stomach capacity constraint. Total protein requirements were 12.9 kg (SD=0.19) for Non-lactating and Pregnant bears. From this, total growth requirements were ~6.7 kg and

maintenance requirements were ~6.2 kg (SD=0.19). For lactating bears, protein requirements were 72.2 kg (SD=1.08). Protein requirement increased five-fold between non-lactating to lactating bears.

### 3.4 Bear diets among ecosystems

Non-lactating and Pregnant bears were able to reach target body mass using the four bear diets. Lactating bears using the GYE and Flathead diet were able to reach the target body mass starting with 35% of denning body fat.

Lactating bears using Alberta diets had to increase their denning body fat to 45% to reach target body mass. Under these diets, individual body mass gain was constrained by the combination of available nutritional conditions, high energy requirements for lactation and the bears' physiology. Lactating bears must use body tissue to support lactation after den emergence.

For the Non-lactating scenario, total energy demand varied between 0.9 - 1.4 kcal x $10^6$. Major differences were due to the impact of dietary protein content which contributed from 20% in the Greater Yellowstone Ecosystem to 44% in the Mountain ecosystems (Fig. 4-4a). The increase in energy requirements for a non-lactating to pregnant bears was 55% for the AB-Foothill, 43% for the AB-Mountain, 27% for the Flathead, and 33% for GYE ecosystems. In the Foothill and Mountain ecosystems, the higher increase in energy demands were due to the increase in the fat mass target from 35% to 45% of denning fat (Fig. 4-4a, b). The increase in energy requirements from a non-lactating to a lactating bears was 109% for the AB-Foothill, 97% for the AB-Mountain, 106% for the Flathead, and 155% for GYE ecosystems (Fig. 4-4a, c).

## 4. DISCUSSION

The interaction between brown bear physiology and nutritional quality of food available affect bear mass gain dynamics and thus have important consequences to female reproductive success. Dietary energy and protein content, together with stomach capacity

were key factors constraining fat and lean mass gain. These factors are important on maintenance cost and mass gain (Rode and Robbins, 2000; Robbins et al., 2007; Erlenbach et al., 2014), but their impacts in bear reproductive success independently or interactively have not been studied.

Under low quality diets (lower nutrient content) individuals are forced to increase their food intake to support energetic demands (Barboza et al., 2009). Food intake is affected by the organism's life history traits including mouth volume, bite rate size, digestive tract capacity, and time for digestion (Rode and Robbins 2001; Barboza et al., 2009). The model developed here simplified these factors into the "stomach capacity" parameter, which defines the maximum amount of food that an individual can eat in a day (kg/day). Under simulated conditions, when digestible energy is low (<=600 kcal/kg of fresh diet), nutrient intake is limited by the stomach capacity restricting the ability to reach minimum levels of body reserves to support hibernation. This constraint also emerges when digestible energy is moderate (1200 kcal/kg of fresh diet), but energy requirements increase due to an increase in target body mass or lactation. Because energy requirements are proportional to the individual body mass, it is expected that minimum threshold in digestible energy increases in accordance to the increase of body size.

Energy content has a positive effect on the nutritional quality of a bear's diet, but protein content has a contradictory role. High protein levels help support the elevated protein demands for lactation, although high or low levels of protein increase the energy requirements for maintenance in a quantity that restricts body mass gain. In our simulations, lactating bears were most affected by high protein diets being unable to reach minimum body mass reserves necessary to support maintenance cost during hibernation.

Lactation is the most expensive energetic cost during mammal reproduction (Robbins, 1993; Laurenson, 1995). Increase in energy expenditure for lactating individuals can go from 2 to 5 times above BMR (Hanwell and Peaker 1977; Oftedal, 1985; Laurenson, 1995). In our assessment, energy requirements for lactating brown bears were 1 to 2 times higher than that for non-lactating bears. Protein requirements for lactating bears were 5 times higher than for non-lactating bears. The importance of protein in reproductive success has been illustrated for other large mammals such as ungulates (Barboza and

Parker, 2008; Parker et al., 2009), seals (Oftedal, 1999; Verrier et al., 2011), and giant panda (*Ailuropoda melanoleuca*; Pan et al., 1988). For lactating brown bears, protein requirements during hibernation represent 12-45% of total body mass loss (López-Alfaro et al., 2013). Bears give birth to very altricial cubs (Ramsay and Dunbrack, 1986), thus protein resources are critical for neonate's growth and survival (Derocher and Stirling, 1996) after den emergence. Despite evidence for the role of proteins in mammals' reproductive success, there is a lack of attention in nutritional studies (Parker et al., 2009). This also extends to bears. For example, most of the food and nutritional studies of brown bears focus their analysis on the food energy content and fat accumulation during summer and early fall, overlooking the relevance of food protein content and lean mass accumulation early in the season (Ferguson and McLoughlin, 2000; Bojarska and Selva, 2011; McLellan, 2011).

To meet lactation requirements, females must increase their food intake, mobilize body reserves or a combination of both. An increase in food intake during lactation has been observed in other species (Oftedal, 1999), e.g. cheetahs (*Acinonyx jubatus*) double their food intake during lactation (Laurenson, 1995), koalas (*Phascolarctos cinereus*) during the peak of lactation increase food intake by ~40% (Krockenberger, 2003), and humans increase their energy intake by ~23% (Prentice and Prentice, 1988). In our simulations, bears increase their food intake from 60% to 150% depending on the nutritional quality of their diet.

Model results shows that in poor nutritional ecosystems the increase in food intake was insufficient to cover lactation cost. This can be illustrated in the Mountain ecosystems of Alberta where lactating females need to eat 20 kg of roots a day only to supply the milk protein requirements for one cub. As a consequence, in poor nutritional ecosystems, lactating bears need to accumulate higher levels of denning body fat to be able to use as a reserve to support lactation after den emergence. The use of body tissue to support milk production is common not only among fasting species, but also among species with high energy requirements. For example, among fasting species, seals (*Arctocephalus gazelle; Cystophora cirstata; Halichoerus grypus; Mirounga angustirostris*) and black bears (*Ursus americanus*) transfer between ~20-35% of body fat and between ~5-25% of lean tissue to support lactation (Oftedal, 1999). Dairy cows also benefit from mass gain

before lactation because food intake is insufficient to support high levels of milk production (Remppis et al., 2011)

There are three adaptive reproductive strategies that brown bears can use in poor nutritional environment. First, increase birth-interval in order to have more seasons to accumulate body reserves. Longer birth-interval has been observed in brown bear populations under low nutritional quality or seasonality (Ferguson and McLoughlin, 2000; Garshelis et al., 2005). For example, a brown population in Banff National Park (Canada) that is located in Mountain ecosystems of Alberta that lack nutritious foods and overall have a low nutritional quality (Munro et al., 2006; Chapter 3). Birth-interval in this population is ~5 years (Garshelis et al., 2005), which is one of the longest observed in North America (Ferguson and McLoughlin, 2000). Second, bears in poor nutritional environments can reduce investment in lactation. Cubs of lean mothers grow slower than cubs of fat mothers during hibernation, which might be consequence of later birth and/or low quantity/quality of the milk (Robbins et al., 2012). Thus, it is expected that after den emergence, milk production can be adjusted according to the nutritional resources available for the mother. Third, bears in poor nutritional environments can decrease litter size. Hilderbrand et al. (1999b) found an inverse relation among dietary meat (e.g. as a surrogate of high levels of digestible energy and protein, Chapter 3) and litter size. These three adaptive strategies have effect individual reproductive success, which influences the population growth rate and therefore population dynamics.

Our results suggest that brown bear populations in Alberta are highly limited by bottom-up controls. The low nutritional condition in Alberta has two consequences for management. First, is a limitation in the number of individuals than can be sustained in these ecosystems (carrying capacity), especially when compared to better nutritional environments such as the Flathead or GYE. Second, is an expected low rate of population growth and thus slower recovery rates for persecuted populations than observed elsewhere like the GYE. Human-induced mortalities in Alberta might therefore have a greater effect on population recovery than elsewhere (Garshelis et al., 2005).

## 4.1 Conclusions

Understanding how landscapes and individual physiology interact to affect individual nutrition allows us to better understand population-level processes. For brown bears, interactions between their digestive tract capacity and food resources constraints that affect their ability to acquire the energy and protein influence reproductive success.

Due to the importance of protein in lactation and in energy requirements, we suggest that bear food habits and nutritional studies should consider this component, especially during spring and summer when individuals accumulate lean mass and lactation peaks.

Brown bear population recovery in Alberta must consider the nutritional limitations faced by these populations and how they might vary among ecosystems or management areas. When estimating the carrying capacity of brown bears it is necessary to integrate other aspects of the landscape and species traits such as: food productivity, spatial and temporal distribution of food resources, foraging efficiencies and competition.

## 5. REFERENCES

ASRD, ACA. Status of the Grizzly Bear (*Ursus arctos*) in Alberta: Update 2010. Alberta Sustainable Resources Development. Wildlife Status Report No. 37 (Update 2010). Edmonton, AB. 44 pp; 2010.

Barbosa PS, Parker KL. Allocating protein to reproduction in arctic reindeer and caribou. Physiol Biochem Zool 2008;81:835-855.

Barbosa PS, Parker KL, Hume ID. Integrative wildlife nutrition. 1st ed. Berlin: Springer-Verlag; 2009.

Barbosa PS, Farley SD, Robbins CT. Whole-body urea cycling and protein turnover during hyperphagia and dormancy in growing bears (*Ursus americanus* and *U. arctos*). Can J Zool 1997;75:2129-2136.

Bendoricchio G, Jorgensen SE. Fundamentals of ecological modelling. 3rd ed. Oxford, UK Elsevier Science; 2001.

Benn B, Herrero S. Grizzly bear mortality and human access in Banff and Yoho National Parks, 1971–1998. Ursus 2001;13:213-221.

Blaxter KL. Energy metabolism in animals and man. 1st ed. United Kingdom: Cambridge University press; 1989.

Bojarska K, Selva N. Spatial patterns in brown bear *Ursus arctos* diet: the role of geographical and environmental factors. Mammal Review. 2011:42;120-143.

Derocher AE, Stirling I. Aspect of survival in juvenile polar bear. Can J Zool 1996;74:1246-1252.

Erlenbach JA, Rode KD, Raubenheimer D, Robbins CT. Nutrition wisdom of bears: Macronutrient selection and metabolism. J Mammal 2014:in press.

Farley SD, Robbins CT. Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. Can J Zool 1995;73:2216-2222.

Felicetti LA, Robbins CT, Shipley LA. Dietary protein content alters energy expenditure and composition of the gain in grizzly bears (*Ursus arctos horribilis*). Physiol Biochem Zool 2003;76:256-261.

Ferguson SH, McLoughlin PD. Effect of energy availability, seasonality and geographic range on brown bear life history. Ecography 2000;23:193-200.

Fortin JK, Schwartz CC, Gunther KA, Tiesberg JE, Haroldson MA, Evans MA, Robbins CT. 2013. Dietary adjustability of grizzly bears and American blanck bears in Yellowstone National Park. J Wildl Manage 77:270-281.

Garshelis DL, Gibeau ML, Herrero S. Grizzly bear demographics in and around Banff National Park and Kananaskis country, Alberta. J Wildl Manage 2005;69:277-297.

Halton TL, Hu FB. The effect of high protein diets on thermogenesis, satiety and wwight loss: A critical review. J Am Coll Nutr 2004:23;373-385.

Hanwell A, Peaker M. Physiological effects of lactation on the mother. Symp. Zool. Soc. London 1977:41; 297-312.

Hilderbrand GV, Jenkins SG, Schwartz CC, Hanley TA, Robbins CT. Effect of seasonal differences in dietary meat intake on changes in body mass and composition in wild and captive brown bears. Can J Zool 1999a;77:1623-1630.

Hilderbrand GV, Schwartz CC, Robbins CT, Jacoby ME, Hanley TA, Arthur SM, Servheen C. Importance of meet, particular salmon, to body size, population productivity and conservation of North American Brown Bears. Can J Zool 1999b; 77:132-138.

Homyack J. Evaluating habitat quality of vertebrates using conservation physiology tools. Wildlife Research 2010:37;332-342

Isee System, Inc. An introduction to system thinking. Hanover: New Hampshire; 2006.

Krockenberger A. Meetng the energy demands of reproduction in female koalas, Phascolarctos cinerus: evidence for energetic compensation. J Com Physiol B 2003:173;531-540.

Laurenson MK. Behavioural cost and constraints of lactation in free-living cheetahs. Animal behavior 1995:50;815-826

López-Alfaro C, Robbins CT, Zedrosser A, Nielsen SE. Energetic of hibernation and reproductive trade-offs in Brown Bears. Ecol. Modell 2013;270:1-10.

McCarthy TM, Waits LP, Mijiddorj B. Status of the Gobi bear in Mongolia as determined by noninvasive genetic methods. Ursus 2009;20:30-38.

McLellan B. 2011. Implications of high-energy and low-protein diet on the body composition, fitness, and competitive abilities of black (*Ursus americanus*) and grizzly (*Ursus arctos*) bears. Can J Zool 89:546-558.

McLellan BN, Hovey FW. The diet of grizzly bears in the Flathead River drainage of southeastern British Columbia. Can J Zool 1995;73:704-712.

McLellan BN, Servheen C, Huber D, (IUCN SSC Bear Specialist Group). *Ursus arctos*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1. <www.iucnredlist.org>. Downloaded on 19 October 2013; 2008.

McNab BK. An analysis of the factors that influence the level and scaling of mammalian BMR. Comp Biochem Phys A Mol Integr Physiol 2008;151:5-28.

Mikkelsen PB, Toubro S, Astrup A. Effect of fat-reduced diets on 24-h energy expenditure: comparisons between animal protein, vegetable protein, and carbohydrate. Am J Clin Nutr 2000;72:1135–41.

Miller SD, White GC, Sellers RA, Reynolds HV, Schoen JW, Titus K, Barnes VG, Smith RB, Nelson RR, Ballard WB, Schwartz CC. Brown and black bear density estimation in Alaska using radiotelemetry and replicated mark-resight techniques. Wildlife Monogr 1997:133;5–55.

Miller SD, Sellers RA, Keay JA. Effects of hunting on brown bear cub survival and litter size in Alaska. Ursus 2003;14:130–152.

Mowat G, Heard DC, Schwarz CJ. Predicting grizzly bear density in western North America. PLoS ONE 2013:8;e82757.

Nielsen SE, Boyce MS, Gordon B. Stenhouse, Munro RHM. Modeling grizzly bear habitats in the Yellowhead ecosystem of Alberta: Taking autocorrelation seriously. Ursus 2002:13;45-56.

Nielsen SE, Boyce MS, Stenhouse GB. Grizzly bears and forestry: I. Selection of clearcuts by grizzly bears in west-central Alberta, Canada. For Ecol Manage 2004:199;51-65.

Nielsen SE, Munro RHM, Bainbridge EL, Stenhouse GB, Boyce MS. Grizzly bears and forestry II. Distribution of grizzly bear foods in clearcuts of west-central Alberta, Canada. For Ecol Manag 2004:199;67-82.

Nielsen SE, Stenhouse GB, Boyce MS. A habitat-based framework for grizzly bear conservation in Alberta. Biological Conservation 2006:130;217-229.

Nielsen SE, Stenhouse GB, Beyer HL, Huettmann F, Boyce MS. Can natural disturbance-based forestry rescue a declining population of grizzly bears? Biol Conserv 2008:141;2193-2207.

Nielsen SE, Boyce MS, Stenhouse GB, Munro RHM. Development and testing of phenologically driven grizzly bear habitat models. Ecoscience 2003; 10:1-10.

Nielsen SE, McDermid G, Stenhouse, GB, & Boyce, MS. Dynamic wildlife habitat models: Seasonal foods and mortality risk predict occupancy-abundance and habitat selection in grizzly bears. Biol Conserv 2010; 143:1623-1634.

Nielsen S, Cattet MRL, Boulanger J, Cranston J, McDermid GJ, Shafer ABA, Stenhouse GB. Environmental, biological and anthropogenic effects on grizzly bear body size: temporal and spatial considerations. BMC Ecology 2013:13-31

Oftedal OT. Pregnancy and lactation. In: The Bioenergetics of Wild Herbivores. Ed. Hudson RJ, White RG. DD. 215-238. Boca Raton, Florida, CRC Press. 1985: 215-238

Oftedal OT. Use of maternal reserves as a lactation strategy in large mammals. Proc Nut Soc 1999:59;99-106.

Pan W, Oftedal OT, Zhu X, Childs S, Wang D, Kleiman DG. Milkc omposition and nursing in a giant panda (*Ailuropoda melanoleuca*). Acta Scientarium Naturalium Universitatis Pekinensis 1988:34;350–351

Parker KL, Barboza PS, Gillingham MP. Nutrition integrates environmental responses of ungulates. Funct Ecol 2009;23:57-69

Pritchard GT, Robbins CT. Digestive and metabolic efficiencies of grizzly and black bears. Can J Zool 1990;68:1645-1651.

Ramsay MA, Dunbrack RL. Physiological constraints on life history phenomena, the example of small bear cubs at birth. Am Nat 1986;127:735-743.

Remppis S, Steingass H, Gruber L, Schenkel H. Effects of energy intake on performance mobilization and retention of body tissue, and metabolic parameters in dairy cows in special regard to effect of pre-partum nutrition and lactation – A Review. Asian-Australasian J Anim Sc 2011:24;540-572.

Robbins CT, Meray B-D, Fortin J, Lynne Nelson O. Maternal condition determines birth and growth of newborn cubs. J Mammal 2012;93:540-546

Robbins CT, Fortin JK, Rode KD, Farley SD, Shipley LA, Felicetti LA. Optimizing protein intake as a foraging strategy to maximize mass gain in an omnivore. Oikos 2007;116:1675-1682.

Robbins CT. Wildlife feeding and nutrition. 2nd ed. San Diego, USA: Academic Press; 1993.

Rode KD, Robbins CT, Shipley LA. Constraints on herbivory by grizzly bears. Oecologia 2001;128:62-71.

Rode KD, Robbins CT. Why bears consume mixed diets during fruit abundance. Can J Zool 2000;78:1640-1645.

Schwartz CC, Miller SD, Haroldson MA. Grizzly bear. in Feldhamer GA, Thompson BC, Chapman JA, editors. Wild Mammals of North America: Biology, Management, and Conservation. 2nd ed. Baltimore, Maryland, USA; Johns Hopkins University press; 2003.

Støen OG, Zedrosser A, Sæbø S, Swenson JE. Inversely density-dependent natal dispersal in brown bears *Ursus arctos*. Oecologia 2006;148:356–364.

Swenson JE, Sandegren F, Brunberg S, Segerstrom P. Factors associated with loss of brown bear cubs in Sweden. Ursus 2001;12:69–80.

Testa JW. Interaction of top-down and bottom-up life history trade-offs in moose (*Alces alces*). Ecology 2004;85:1453-1549

Tøien Ø, Blake J, Edgar DM, Grahn DA, Heller HC, Barnes BM. Hibernation in black bears: Independence of metabolic suppression from body temperature. Science 2011;331:906–909.

Verrier D, Groscolas R, Guinet C, Arnould JPY. Development of fasting abilities in subantartic fur seal pups: balancing the demands of growth under extreme nutritional restructions. Funct Ecol 2011;25:704-717.

Welch CA, Keay J, Kendall KC, Robbins CT. Constraints on frugivory by bears. Ecology 1997;78:1105-1119.

Westerterp KR, Wilson SA, Rolland V. Diet induced thermogenesis measured over 24 h in a respiration chamber: effect of diet composition. Int J Obes Relat Metab Disord 1999;23:287–92.

Worthy GAJ, Lavigne DM. Energetic of fasting and subsequent growth in weaned harp seal pups, *Phoca groenlandica*. Can J Zool 1983;61:447-456.

Zedrosser A, Dahle B, Swenson J. Population density and food conditions determine adult female body size in brown bears. J Mammal 2006;87:510-518.

Zedrosser A, Steyaert SMJG, Gossow H, Swenson JE. Brown bear conservation and the ghost of persecution past. Biol Conserv 2011;144:2163-2170.

Zedrosser A, Pelletier F, Bischof R, Festa-Bianchet M, Swenson J. Determinants of life time reproduction in female brown bears: early body mass, longevity, and hunting regulations. Ecology 2013:94;231-240.

**Table 4-1**: Model calibration results. Model simulations were obtained by replicating the conditions of empirical studies. Regressions were obtained with 20 days of measurement replicating empirical studies conditions.

| Empirical study | Diet | Empirical study results | Model simulation results |
|---|---|---|---|
| Robbins et al., 2007 | Salmon-Berry | ΔBM = 0.106 x DigEintk – 10.8 | ΔBM = 0.103 x DigEintk – 13.4 |
| Robbins et al., 2007 | Salmon | ΔBM = 0.093 x DigEintk – 21.5 | ΔBM = 0.095 x DigEintk – 21.5 |
| Robbins et al., 2007 | Berry | ΔBM = 0.053 x DigEintk – 14.4 | ΔBM = 0.073 x DigEintk – 20.2 |
| Hilderbrand et al., 1999a | Deer | ΔBM = 0.93 x DigDMintk – 32.5 | ΔBM = 0.88 x DigDMintk – 21.8 |

ΔBM = change in body mass ($g/kg^{0.75}$/day); DigDMintk = Digestible dry matter intake ($g/kg^{0.75}$/day); DigEintk = Digestible energy intake ($kcal/kg^{0.75}$/day)

**Table 4-2:** Sensitivity analysis results. Sensitivity analysis represents the variation in the "fresh food intake" due to changes in model parameter. "Parameter value" represents the original value of the parameter as used in the model experiments.

| | Change in the parameter | | | | | | |
|---|---|---|---|---|---|---|---|
| **Parameters** | *Parameter value* | *-50%* | *-25%* | *-10%* | *+10%* | *+25%* | *+50%* |
| MaxDigCap | *Eq.8* | 0.04 | 0.01 | 0.00 | 0.01 | 0.01 | 0.01 |
| DM | *0.25* | -0.15 | -0.10 | -1.15 | -0.07 | -0.06 | -0.05 |
| DMDig | *0.50* | 0.07 | 0.07 | 0.01 | 0.07 | 0.07 | 0.07 |
| EDig | *0.55* | -0.90 | -1.40 | -0.13 | -0.96 | -0.84 | -0.69 |

**Figure 4-1:** Model diagram and schedule. The model starts with the inputs and initial conditions on day 1 (see 2.3.1; target gain sub-model). Day one hibernation starts and follows the schedule described in López-Alfaro et al. (2013). During the active period, each day the model starts estimating the daily food intake (food intake sub-model). Energy and protein costs for maintenance are estimated based on the actual body mass and diet characteristic. Energy and protein costs for reproduction are estimated based on the lactation day. The model balances the total energy and protein intake with the energetic requirements to estimate the total energy and protein available for growth (energy balance, protein balance and reproduction sub-models). Lean and fat mass gain are estimated based on the available resources and target gains. Finally lean and fat mass gain or losses are incorporated in the body mass. Then a new day starts. (Fig. 4-1)

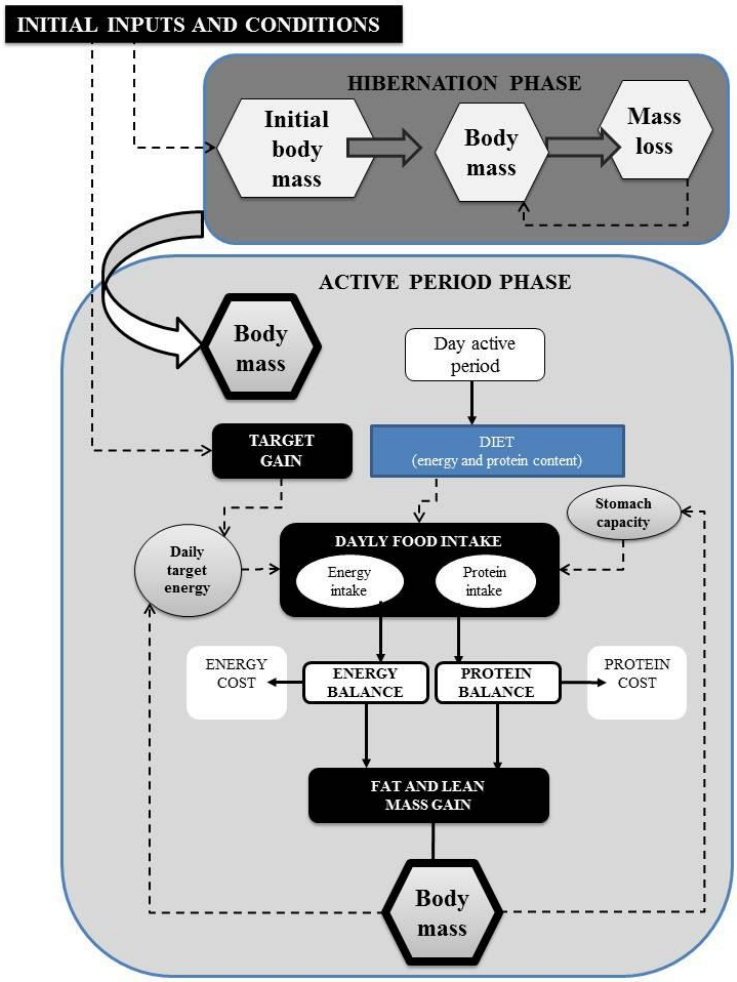


**Figure 4-2a**: Energy and protein requirements for lactation. Lactation energetic costs were based Farley and Robbins (1995) and values were adjusted to the length of the active period (185 days). Estimation includes "milk conversion parameter (0.85; Blaxter, 1989)"

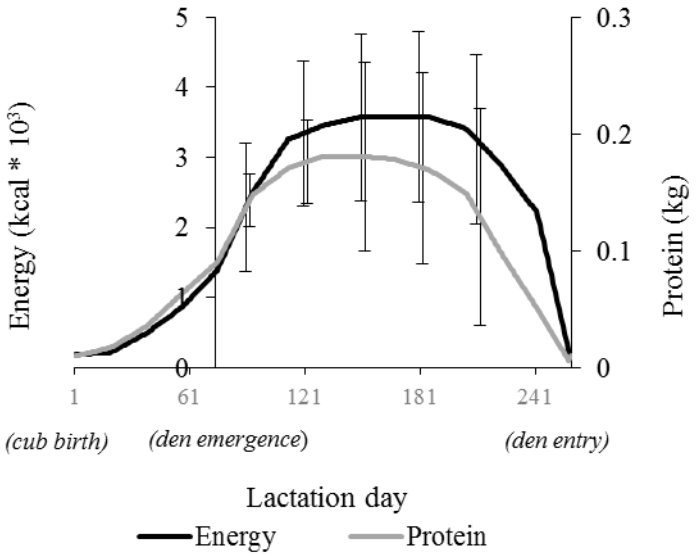
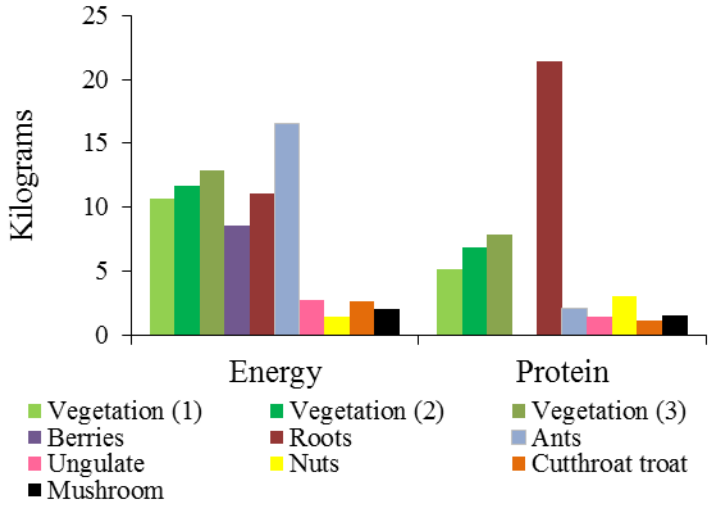
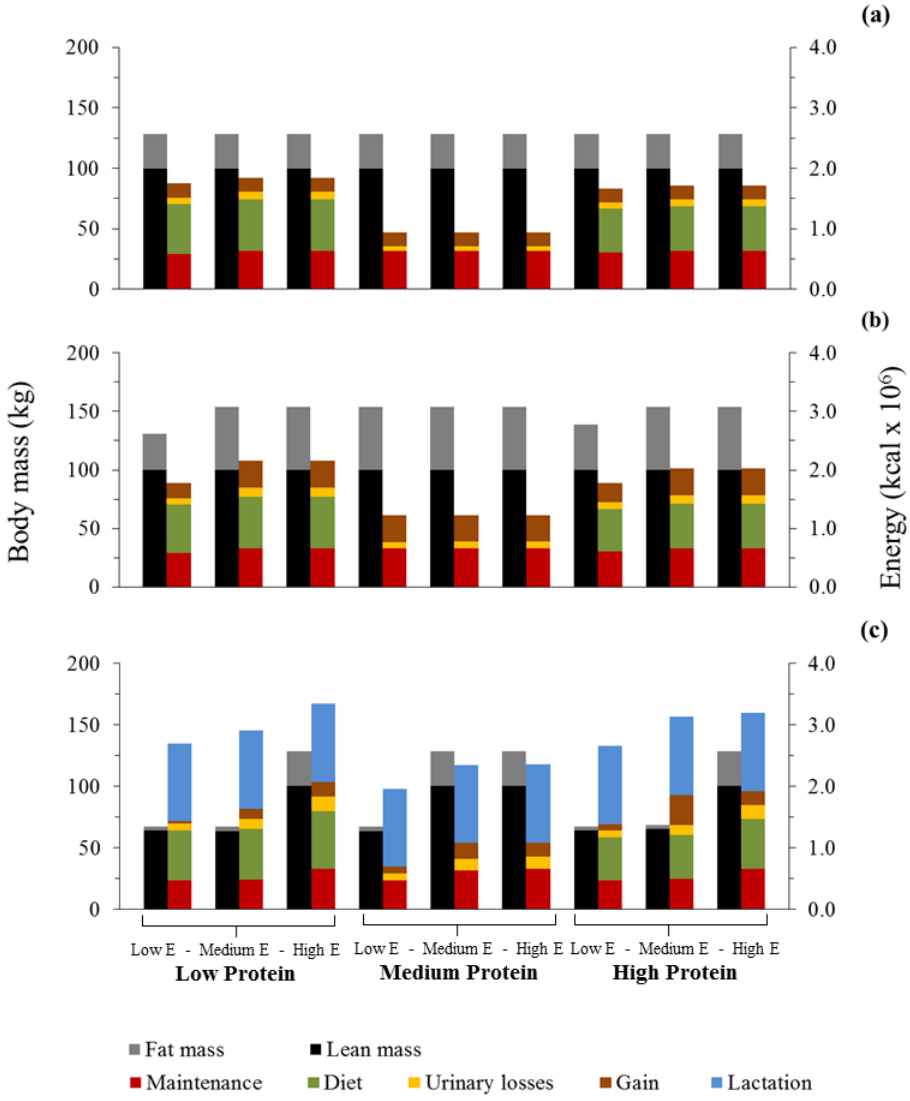



**Figure 4-2b:** Amount of food (kg) necessary to supply maximum milk requirements per cub. Maximum energy requirement is 4000 kcal/day and maximum protein requirement is 0.2 kg/day. Digestible energy and digestible protein per food item was obtained from Chapter 3. Berries were not considered for protein assessment due to their low protein content.



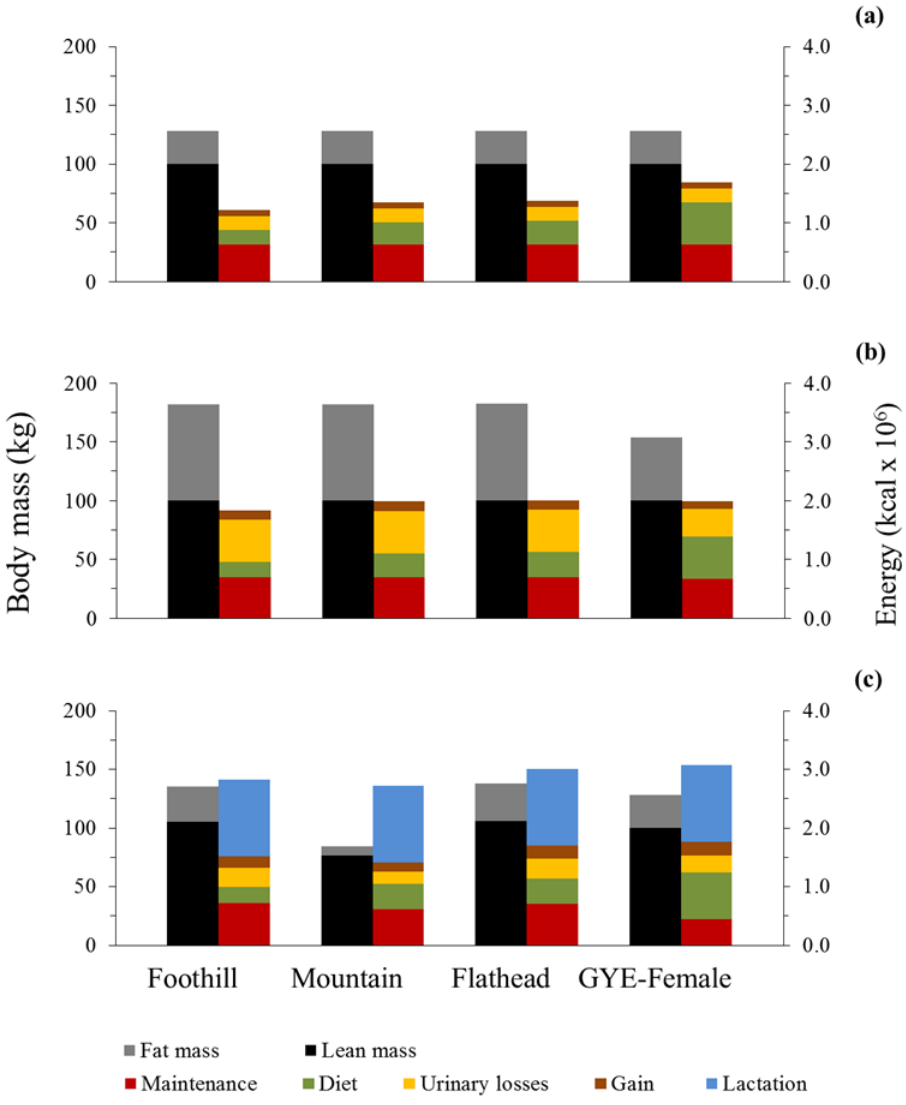

Vegetation (1) = green vegetation in spring and early summer. Vegetation (2) = green vegetation in summer and late summer. Vegetation (3) = green vegetation in late summer and early fall.

**Figure 4-3:** Denning body mass (primary axis Y) and energy requirements (secondary axis Y) for Non-lactating (a), Pregnant (b), and Lactating (c) bears under different neutral diets. Energetic requirements are measure during the active period and varied with the diet and target body mass. Lean and fat represent the body mass reached at the active period (before the next hibernation). "Maintenance" includes basic metabolic rate and activity cost in captivity. "Diet" represents the increase in maintenance cost due to the dietary protein content. "Urinary losses" is based on the energy intake. "Gain" represents energy content of the lean and mass gain during the active period. Lactation represents the energy cost of milk production (Appendix 4-D). Diets represent the combination of three levels (low, medium, and high) of energy (E) and protein (P) content.




nitial denning body mass and target lean mass was 100 kg. For Non-lactating (a) initial fat mass and target body fat was 22%. For Pregnant (b) initial body fat was 22% and target body fat was 35%. For Lactating (c) initial body fat was 35% and target body fat was 22%.

**Figure 4-4:** Denning body mass (primary axis Y) and energy requirements (secondary axis Y) for Non-lactating (a), Pregnant (b), and Lactating (c) bears under different diets. Energetic requirements are measure during the active period and varied with the diet and target body mass. Lean and fat represent the body mass reached during the active period (before the next hibernation). Maintenance" includes basic metabolic rate and activity cost in captivity. "Diet" represents the increase in maintenance cost due to the dietary protein content. "Urinary losses" is based on the energy intake. "Gain" represents energy content of the lean and mass gain during the active period. Lactation represents the energy cost of milk production. Diets resemble the food habits in the Foothill and Mountain ecosystems of Alberta (Canada, Munro et al., 2006), Flathead of southeast British Columbia (McLellan and Hovey, 1995), and GYE (female diet, Fortin et al., 2013).




Initial denning body mass and target lean mass was 100 kg. For Non-lactating (a) initial fat mass and target body fat was 22%. For Pregnant (b) initial body fat was 22% and target body fat was 45% for the Foothill, Mountain and Flathead and 35% for GYE-Female scenarios. For Lactating initial body fat was 45% for the Foothill, Mountain and Flathead and 35% for GYE-Female scenario and target body fat was 22%.

# CHAPTER 5

# GENERAL DISCUSSION AND CONCLUSIONS

In this thesis I explored how the interaction between the physiology of the brown bears and the nutritional quality of the bear's habitat influence body mass of bears and thus reproductive success. This work allows us to understand how population properties emerge from the interactions between individuals and their environment (Grimm and Railsback, 2005). This work also helps reveal how brown bears adapt to environmental variability and how they might respond to landscape changes.

To address the objectives of my dissertation, I used system dynamics modelling to integrate nutritional, physiological and ecological characteristics of brown bears, together with their landscape. The model simulates the transfer of energy and protein from the environment to the individual, accounting for allocation in maintenance, growth and reproduction. Because the model assesses energy, it uses the same principles commonly used in energetic and dynamic energy budget (DEB) studies (Kooijman, 2000). For example, it divides the animal's body mass into structural and storage components, and it assumes that the composition of both components remains constant (Kooijman, 2000). The model developed in this dissertation differs, however, from other studies in simultaneously assessing the transfer and allocation of protein. To my knowledge, the incorporation of nutritional components other than energy has not been widely applied in energetic studies. This characteristic of the model allowed me to detect key factors that traditional energetic studies would not have captured. For example, it revealed the importance of protein in reproductive success.

## 1. FINDINGS AND FUTURE STEPS

In this section I will discuss my findings in a broader perspective, and I will consider some of the future steps that can be taken to enhance our understanding of bear-habitat relationships and its influence on the reproductive success of bears.

### 1.1 Energetic components of hibernation

I started my research by assessing the energetic-reproductive trade-off that occurs during hibernation. Several of the energetic components of hibernation among bears have been studied. These include measurements of the metabolic rate and body mass loss (Watts and Cuvler 1988; Watts and Jonkel 1988; Watts, 1990; Atkinson et al., 1996; Hilderbrand et al., 2000; Tøien et al., 2011) and reproductive components such as energy and protein content in fetus growth and milk production (Oftedal, 1993; Farley and Robbins 1995). The relationship between maternal condition and cub growth has been previously illustrated elsewhere (Derocher and Stirling 1996; 1988; Robbins et al., 2012b), demonstrating the importance of maternal body condition on reproductive success.

Despite knowledge of these key relationships, no previous effort has been made to integrate, in a comprehensive way, these relationships or to explore the energetic trade-offs that occur during hibernation among brown bears. The use of a mechanistic dynamics model allowed me to examine constraints between reproductive investment (litter size and length of lactation) and environmental conditions (length of hibernation). Energy and protein costs of reproduction, and the minimum denning body fat content required for reproduction, were assessed using the mechanistic dynamics model. To my knowledge these calculations have not been made for this species before. Assessment of model performance revealed that the model produced realistic results and since the principles applied were general, it can be easily adapted to other bear species.

Regardless of the effectiveness of model predictions, there are two aspects that require further study: lean tissue depletion and lactation cost. Both the threshold under which lean tissue is used as an energy source and the threshold of lean mass loss that determines individual survival have a high impact on model outputs, and therefore on the bears' energetic balance. Knowledge of body composition of bears will be helpful in defining the "structural" body mass and survival threshold of body mass loss (Molnár, 2010).

Lactation cost was assessed for a maximum of 74 days, but it is expected that bear populations with longer hibernation periods (e.g. in northern latitudes) also have an extended lactation period in the den and thus have higher energetic costs for lactation. Another aspect that requires further study is how maternal condition influences the

amount and quality of the milk (Robbins et al., 2012b) given that this largely influences cub growth.

### 1.2 Nutritional quality of bear diets

In the second step of my dissertation, I explored the nutritional differences of bear diets in different ecosystems where interior populations of brown bears have been well-studied and related this to differences in life history traits and population density. Previous studies have examined differences in brown bear diets and revealed their correlation with reproductive success and population parameters such as density (Hilderbrand et al., 1999b**;** Ferguson and McLoughlin, 2000; Bojarska and Selva, 2011; McLellan, 2011). However, these differences have not been previously quantified or assessed for the entire active period.

The use of bear food habits and food nutritional information was insufficient to quantify and compare the nutritional quality of bear diets. To resolve this, I integrated nutritional information using a dynamic model that assesses the digestible energy and protein per kilogram of fresh diet. I applied this method to three well-studied interior bear ecosystems in western North America, the Alberta foothill and mountain ecosystem, the Flathead ecosystem of southeastern British Columbia and the Greater Yellowstone Ecosystem.

Model results revealed that differences in digestible energy between the Yellowstone and Alberta Mountain diet were 3-fold, while there was a 6-fold difference in digestible protein. The model also identified key food resources and predicted the nutritional consequences of reductions in consumption of nutritious foods, such as the loss of trout and whitebark nuts in the Great Yellowstone Ecosystem.

Previous comparative studies have focused on one or two food items. This study integrates the whole diet and it extends throughout the entire active season. This allows us to gain a wider perspective about the nutritional patterns of brown bear diets. Future research should be directed at obtaining information on bear food habits over the entire active period, and at increasing the nutritional information for bear food items.

### 1.3 Brown bears' energetic balance

In the final step of my research, I explored how the interactions between bear physiology and ecology, and nutritional landscape, influence individual body mass gain and therefore reproductive success. Previous studies have shown the impact of nutritional quality on bear body mass gain, and have examined physiological limitations on nutrient intake (Welch et al., 1997; Hilderbrand et al., 1999a; Rode et al., 2001; Felicetti et al., 2003; Robbins et al., 2007; Erlenbach et al., 2014). No studies have, however, integrated this information into a comprehensive framework to explore individual constraints on energy and protein acquisition and allocation.

I used a mechanistic model that simulates the lean and fat mass dynamics over a one year period extending from hibernation to the next hibernation period. Results show an interaction between the nutritional quality of the diet, the bear's digestive capacity and the individual requirements that constrain body mass gain. Results also reveal the mechanisms influencing low reproductive success by bears in poor nutritional ecosystems (low digestible energy and protein). This is an important first step toward a deeper understanding of how processes at the population level emerge from interactions between physiology of bears and their nutritional landscape.

The model has also been helpful in pointing to further knowledge gaps, including:

a) *Energy expenditure:* The model estimates the basic metabolic rate (BMR) using a general carnivorous equation (McNab, 2008). Obtaining the specific measurements of BMR for *ursid* species will be beneficial to improving predictions and estimates of energetic studies (e.g. Mólnar et al., 2009; 2010; Robbins et al., 2012a; present study)

b) *Reproductive costs:* Only one previous study has measured milk composition among brown bears (Farley and Robbins, 1995), while another one has related maternal conditions to milk production (Robbins et al., 2012b). This lack of information on milk composition and maternal condition also extends to other *ursid* species (e.g. few studies have measured milk composition in polar bears (Baker et al., 1963; Derocher et al., 1993; Arnould and Ramsay, 1994). Future research should focus on the cost of

lactation under different environmental conditions and explore how investments in lactation vary depending on maternal condition, body size and length of hibernation.

c) *Lean and fat dynamics:* Results demonstrate that lean tissue and fat reserves are equally important for reproductive success among bears. Composition of the mass gain (lean vs. fat) also has important effects on the energetic balance (Chapter 4). Studies have illustrated seasonal differences in the dynamics of lean and fat accumulation (Hilderbrand et al., 1999a; Felicetti et al., 2003; McLellan, 2011). However, there are still knowledge gaps in our understanding of how this process operates across the entire active period, as well as the influence of the diet on mass gain composition.

## 2. MANAGEMENT IMPLICATIONS FOR BROWN BEAR POPULATIONS IN ALBERTA

In 2008 a recovery plan for grizzly bears in Alberta was published (ASRD, 2008). Among the strategies suggested were development of land planning tools and the reduction in human-bear conflict. Priority areas for conservation were defined using parameters related to human-induced mortalities and the presence of food resources (Nielsen et al., 2009; 2010). The models that I have developed can be used to improve these tools. For example, using the information on the presence of food (Nielsen et al., 2010) and the landscape model developed in Chapter 3, it is possible to estimate the spatial and temporal distribution of the digestible energy and digestible protein in the landscape.

Human-induced mortalities have been recognized as the main threat to bear populations in Alberta. However, previous studies have pointed to the nutritional limitation of these ecosystems (Munro et al., 2006; Nielsen et al., 2010). My results suggest that the nutritional conditions in Alberta's ecosystems limit the reproductive rates of brown bears. From a management perspective there are two consequences: reduced carrying capacity and slower rates of population recovery.

Nutritional carrying capacity can be understood as the relationship between the individual nutrient requirement and the supply of nutrients from its environment (Schwartz and Hobbs, 1995). Low levels of digestible energy and protein in Alberta's ecosystems limit the numbers of bears that can be sustained within the province. Estimates of the nutritional carrying capacity can be done using the individual energetic requirements estimated in Chapter 4, and the spatial and temporal variations on digestible energy and digestible protein as nutrient supply.

Slow reproductive rates directly influence the rates of population recovery. Because brown bear population in Alberta are also affected by human-induced mortalities, further studies are necessary to explore the relative importance of nutritional (bottom-up) and mortality-related (top-down) factors on population recovery.

## 3. FINAL CONCLUSIONS

Wildlife ecology and management generally work at the level of populations focussing on aspects such as population viability and distribution (Grimm and Railsback, 2005). However, population properties emerge as a consequence of the interactions among individuals and their environment (Robbins, 1993; Barbosa et al., 2009). Understanding the mechanisms and the constraints of this interaction allows us to fully comprehend the dynamics of, and evolutionary processes affecting, populations.

Using simulation models, I integrated existing knowledge of the ecology and physiology of brown bears to explore mechanisms influencing the dynamics of body mass under different environmental conditions. The results have contributed to our understanding of how the environment influences population patterns observed in this species.

Energetic, nutritional and physiological studies are increasingly used to predict how populations will respond to landscape disturbances (Homyack, 2010). Model simulations, together with empirical data, help provide some of these answers (Molnár, 2010). As my dissertation demonstrates, interactions and collaborations among different research areas can enhance our capacity to understand and provide solutions for a living and changing planet.

## 4. REFERENCES

ASRD . Alberta Grizzly Bear Recovery Plan 2008-2013. 2008. Alberta Sustainable Resource Development, Fish and Wildlife Division, Alberta Species at Risk Recovery Plan No. 15. Edmonton, AB. 68 pp.

*Arnould JPY, Ramsay MA. Milk produc*tion and milk consumption in polar bears during the ice-free period in western Hudson Bay. Can J Zool 1994;72:1365-1370.

Atkinson SN, Nelson RA, Ramsay MA. Changes in body composition of fasting polar bears the effect of relative fatness on protein conservation. Physiol Zool 1996;69:304-316.

Baker BE, Harngton CR, Symes AL. Polar bear milk. Can J Zool 1963:41;1035-1039.

Barbosa PS, Parker KL, Hume ID. Integrative wildlife nutrition. 1st ed. Berlin: Springer-Verlag; 2009.

Bojarska K, Selva N. Spatial patterns in brown bear Ursus arctos diet: the role of geographical and environmental factors. Mammal Review. 2011:42;120-143.

Derocher AE, Andriashek D, Arnould JPY. Aspects of milk composition and lactation in polar bears. Can J Zool 1993:71;561-567.

Derocher AE, Stirling I. Aspect of survival in juvenile polar bear. Can J Zool 1996;74:1246-1252.

Derocher AE, Stirling I. Maternal investment and factors affecting offspring size in polar bears (*Ursus maritimus*). J Zool 1998;245:253-260.

Erlenbach JA, Rode KD, Raubenheimer D, Robbins CT. Nutrition wisdom of bears: Macronutrient selection and metabolism. J Mammal 2013: in press.

Farley SD, Robbins CT. Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. Can J Zool 1995;73:2216-2222.

Felicetti LA, Robbins CT, Shipley LA. Dietary protein content alters energy expenditure and composition of the gain in grizzly bears (*Ursus arctos horribilis*). Physiol Biochem Zool 2003;76:256-261.

Ferguson SH, McLoughlin PD. Effect of energy availability, seasonality and geographic range on brown bear life history. Ecography 2000;23:193-200.

Fortin JK, Schwartz CC, Gunther KA, Tiesberg JE, Haroldson MA, Evans MA, Robbins CT. 2013. Dietary adjustability of grizzly bears and American blanck bears in Yellowstone National Park. J Wildl Manage 77:270-281.

Grimm V, Railsback SF. Individual-based Modeling and Ecology. Princeton University Press; 2005.

Hilderbrand GV, Jenkins SG, Schwartz CC, Hanley TA, Robbins CT. Effect of seasonal differences in dietary meat intake on changes in body mass and composition in wild and captive brown bears. Can J Zool 1999;77:1623-1630.

Hilderbrand GV, Schwartz CC, Robbins CT, Jacoby ME, Hanley TA, Arthur SM, Servheen C. Importance of meet, particular salmon, to body size, population productivity and conservation of North American Brown Bears. Can J Zool 1999b; 77:132-138.

Hilderbrand GV, Schwartz CC, Robbins CT, Hanley TA. Effect of hibernation and reproductive status on body mass and condition of coastal brown bears. J Wildl Manage 2000;64:178-183.

Homyack JA. Evaluating habitat quality of vertebrates using conservation physiology tools. Wildl Res 2010;37:332-342.

Kooijman SALM. 2000. Dynamic Energy and Mass Budgets in Biological Systems (2nd edn). Cambridge University Press, Cambridge, United Kingdom.

McLellan B. 2011. Implications of high-energy and low-protein diet on the body composition, fitness, and competitive abilities of black (*Ursus americanus*) and grizzly (*Ursus arctos*) bears. Can J Zool 89:546-558.

McLellan BN, Hovey FW. The diet of grizzly bears in the Flathead River drainage of southeastern British Columbia. Can J Zool 1995;73:704-712.

McLellan BN, Servheen C, Huber D, (IUCN SSC Bear Specialist Group). *Ursus arctos*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1. <www.iucnredlist.org>. Downloaded on 19 October 2013; 2008

McNab BK. An analysis of the factors that influence the level and scaling of mammalian BMR. Comparative Biochemistry and Physiology A. Comparative Physiology 2008;151:5–28.

Molnár PK. Modelling future impacts of climate change and harvest on the reproductive success of female polar bears (*Ursus maritimus*). PhD Thesis, University of Alberta 2009.

Molnár PK, Klanjscek T, Derocher AE, Obbard ME, Lewis MA. A body composition model to estimate mammalian energy stores and metabolic rates from a body mass and body length, with application to polar bears. J Exp Biol 2009;212:2313-2323.

Molnár PK, Derocher AE, Thiemann GW, Lewis MA. Predicting survival, reproduction and abundance of polar bears under climate change. Biol Conserv 2010;143:1612-1622.

Munro RHM, Nielsen SE, Stenhouse GB, Boyce MS. Seasonal and diet patterns of grizzly bear diet and activity in west-central Alberta. J Mamm 2006;87:1112-1121.

Nielsen SE, Cranston J, Stenhouse GB. Identification of priority areas for grizzly bear conservation and recovery in Alberta, Canada. J Conserv Planning 2009;5:38-60.

Nielsen SE, McDermid G, Stenhouse, GB, & Boyce, MS. Dynamic wildlife habitat models: Seasonal foods and mortality risk predict occupancy-abundance and habitat selection in grizzly bears. Biol Conserv 2010; 143:1623-1634.

Oftedal TO, Alt LG, Widdowson ME, Jakubasz RM. Nutrition and growth of suckling black bears (Ursus americanus) during their mothers' winter fast. Brit J Nutr 1993;70:59-79.

Prentice AM, Prentice A. Energy cost of lactation. Ann Rev Nutr 1988:88;63-79.

Robbins CT, Lopez-Alfaro C, Rode KD, Tøien Ø, Nelson LO. Hibernation and seasonal fasting in bears: the energetic cost and consequences for polar bears. J Mammal 2012a; 93:1493-1503.

Robbins CT, Meray B-D, Fortin J, Lynne Nelson O. Maternal condition determines birth and growth of newborn cubs. J Mammal 2012b;93:540-546

Robbins CT, Fortin JK, Rode KD, Farley SD, Shipley LA, Felicetti LA. Optimizing protein intake as a foraging strategy to maximize mass gain in an omnivore. Oikos 2007;116:1675-1682.

Robbins CT. Wildlife feeding and nutrition. 2nd ed. San Diego, USA: Academic Press; 1993.

Rode KD, Robbins CT, Shipley LA. Constraints on herbivory by grizzly bears. Oecologia 2001;128:62-71.

Schwartz CC, Hobbs NT. Forage and Range Evaluation. In Bioenergetic of wild herbivores. Editors: Hudson RJ, White RG. CRC Press Inc. Boca Raton, Florida, USA; 1995.

Tøien Ø, Blake J, Edgar DM, Grahn DA, Heller HC, Barnes BM. Hibernation in black bears: Independence of metabolic suppression from body temperature. Science 2011;331:906–909.

Watts PD. Comparative weight loss in three species of ursids under simulated denning conditions. International Conference on Bear Research and Management 1990;8:139–141.

Watts PD, Cuyler C. Metabolism of the black bear under simulated denning conditions. Acta Physiologica Scandinavica 1988;134:149–152.

Watts PD, Jonkel C. Energetic cost of winter dormancy in grizzly bear. J Wildl Manage 1988;52:654–656.

Welch CA, Keay J, Kendall KC, Robbins CT. Constraints on frugivory by bears. Ecol 1997;78:1105-1119.

**Table 3-A1:** Nutritional information of bear food items. Information includes: DM = Dry matter (%); DMDig (%) = Digestible dry matter; GrossE = Gross energy (kcal); EDig = Energy digestibility; PC (%) = Protein content; PDig (%) = Protein digestibility; DigP(g)=Digested protein; TDF (%) = Total dietary fiber. DM in a fresh matter base. DMDig, GrossE, EDig, PC, PDig and TDF in a dry matter base.

| | DM | DMDig | GrossE | Edig | PC | PDig | DigP | TDF | Reference |
|---|---|---|---|---|---|---|---|---|---|
| **GREEN VEGETATION ANNUAL** | | | | | | | | | |
| Alfalfa - Leaves&Stem (Medicago sativa) | | 18.5 (1) | 4412 | 24.7 | 22.1 (2.8) | 16 (2.5) | 72.0 | 59.6 (0.7) | Coogan (2012, Table 1&2) -(Annual average values) |
| Clover - Leaves&Stem (Trifolium spp) | | 20 (3.6) | 4382 (270) | 40.4 | 19.4 (1.3) | 13.6 (1.8) | 70.0 | 58.5 (2.6) | Coogan (2012, Table 1&2) -(Annual average values) |
| Clover Flower (Trifolium spp) | | 38.9 | | | 27.1 | 20.4 (0.4) | 75.0 | 44.9 | Coogan (2012, Table 1&2) -(Annual average values) |
| Clover White | 14.1 | 46.1 (0.4) | 5311 | 51.1 (0.4) | 30.2 | 23.2 | 77.0 | 42 | Pritchard & Robbins (1990, Table 1&2) |
| Cow parsnip - Leaves and Stem (Heracleum lanatum) | | 11.3 (3.8) | 3640 (570) | 17.4 (3.1) | 13.9 (2.2) | 8.7 (1.9) | 63.0 | 64.8 (2.7) | Coogan (2012, Table 1&2) -(Annual average values) |
| Dandelion | | | | 45.6 (5.8) | 19.2 (6.7) | 13.5 | 70.0 | 17.4 (7.2) | Mattson et al., 2004. PDig estimated using Pritchard and Robbins (1990) |
| Dandelion -Flower (Taraxacum officinale) | | 46.8 (1.4) | | 46.9 (1.2) | 17 (0.3) | 11.5 (0.4) | 68.0 | 39.2 (2.1) | Coogan (2012, Table 1&2) -(Annual average values) |
| Dandelion -Leabes & Stems (Taraxacum officinale) | | 48 (2.9) | 3828 (70) | 47.9 (2.4) | 17 (2) | 11.5 (1.8) | 68.0 | 38.4 (2.1) | Coogan (2012, Table 1&2) -(Annual average values) |
| Elk thistle | | | | 18.8 (11.1) | 4.1 (1.6) | 0.2 | 4.0 | 15.2 (3.2) | Mattson et al., (2004) |
| Horsetail | | | | 32 (8.6) | 13.3 (5.6) | 8.3 | 62.0 | 21.7 (4.7) | Mattson et al., (2004) |

**Table 3-A1:** Nutritional information of bear food items. Information includes: DM = Dry matter (%); DMDig (%) = Digestible dry matter; GrossE = Gross energy (kcal); EDig = Energy digestibility; PC (%) = Protein content; PDig (%) = Protein digestibility; DigP(g)=Digested protein; TDF (%) = Total dietary fiber. DM in a fresh matter base. DMDig, GrossE, EDig, PC, PDig and TDF in a dry matter base. (continuation)

| | DM | DMDig | GrossE | Edig | PC | PDig | DigP | TDF | Reference |
|---|---|---|---|---|---|---|---|---|---|
| **GREEN VEGETATION ANNUAL** (continuation) | | | | | | | | | |
| Horsetails (Equisetum arvense) | | 31.8 (3.3) | 3890 (130) | 34.4 (2.7) | 20.4 (2.2) | 14.5 (1.9) | 71.0 | 50 (2.4) | Coogan (2012, Table 1&2) -(Annual average values) |
| Horsetails (Equisetum sylvaticum) | | 46.3 (5.4) | 4172 | 46.3 (4.5) | 20 (4.6) | 14.16 (4.1) | 71.0 | 39.7 (3.9) | Coogan (2012, Table 1&2) -(Annual average values) |
| Spring beauty | | | | 48.7 (7.4) | 25.4 (5.8) | 18.9 | 74.0 | 14.2 (2.2) | Mattson et al., (2004) |
| **VEGETATION SPRING TO EARLY SUMMER** | | | | | | | | | |
| Clover (May) | | | | | 30.5 | 23.4 | 77.0 | | Coogan (**) |
| Clover (Spring) | | | | 52.8 (3.5) | 25.7 (2) | 19.2 | 75.0 | 12.6 (1.3) | Mattson et al., 2004. |
| Clover White (spring-early summer) | 15 (1.4) | 45.4 (2.9) | | | 27.6 (1.5) | 20.9 | 76.0 | 40.1 (4.2) | Rode et al., (2001, Table 2) (Trifolium ripens giganteum) |
| Dandelion (May) | | | | | 29.8 | 22.8 | 77.0 | | Coogan (**) |
| Graminoids (Spring, Emergence - May15) | | | | 33.9 (8.1) | 20.7 (3.9) | 14.8 | 71.0 | 21.2 (3.9) | Mattson et al. 2004 |
| Grasses (spring-early summer) | 25.2 (1.2) | 27.8 (4.6) | | | 20.5 (2.4) | 14.6 | 71.0 | 52.4 (4.1) | Rode et al. (2001,Table 2) - (Poa pratensis, Phleumpratense, and Bromus gracilis) |
| Horsetails (May) | | | | 37.2 | 26.8 | 20.2 | 75.0 | 47.6 | Coogan (**) |

**Table 3-A1:** Nutritional information of bear food items. Information includes: DM = Dry matter (%); DMDig (%) = Digestible dry matter; GrossE = Gross energy (kcal); EDig = Energy digestibility; PC (%) = Protein content; PDig (%) = Protein digestibility; DigP(g)=Digested protein; TDF (%) = Total dietary fiber. DM in a fresh matter base. DMDig, GrossE, EDig, PC, PDig and TDF in a dry matter base. (continuation)

| | DM | DMDig | GrossE | Edig | PC | PDig | DigP | TDF | Reference |
|---|---|---|---|---|---|---|---|---|---|
| **VEGETATION SUMMER AND LATE SUMMER** | | | | | | | | | |
| Clover (Early hyperphagia) | | | | 38.6 (8.4) | 20.3 (3.3) | 14.4 | 71.0 | 19.2 (4.2) | Mattson et al., (2004) |
| Clover (Estrus) | | | | 42.7 (12) | 21.5 (2.7) | 15.5 | 72.0 | 16.7 (6.1) | Mattson et al., (2004) |
| Clover (July) | | 23.3 (14.1) | | 27.4 (11.7) | 19.5 (3.5) | 13.7 (3.1) | 70.0 | 56.1 (10.1) | Coogan (**) |
| Clover (June) | | | | | 32.7 (5.6) | 25.4 (4.9) | 78.0 | | Coogan (**) |
| Cow Parsnip (July) | | 7.5 (3.6) | | 14.3 (3) | 15.1 (1.9) | 9.8 (2.1) | 65.0 | 67.5 (2.6) | Coogan (**) |
| Cow Parsnip (June) | | 21.9 | | 26.2 | 26.8 | 20.2 | 75.0 | 57.1 | Coogan (**) |
| Dandelion (June) | | 52.8 (2.7) | | 51.9 (2.2) | 19.9 (2.2) | 14.1 (2) | 71.0 | 34.9 (1.9) | Coogan (**) |
| Dandelion(July) | | 40.7 (3.8) | | 41.8 (3.2) | 16.1 (5.4) | 10.7 (4.7) | 66.0 | 43.6 (2.7) | Coogan (**) |
| Fireweed (Early hyperphagia) | | | | 56.9 (4.6) | 23 (4.5) | 16.8 | 73.0 | 9.2 (1) | Mattson et al., (2004) |
| Fireweed (Estrus) | | | | 43.6 | 15.8 | 10.5 | 66.0 | 8.4 | Mattson et al., (2004) |
| Graminoids (Early hyperphagia, july16 - Aug30) | | | | 17.5 (12.4) | 15 (5.9) | 9.8 | 65.0 | 29.4 (5.9) | Mattson et al., (2004) |
| Graminoids (Estrus, may15 - July 15) | | | | 31.4 (9.1) | 20.1 (4.6) | 14.2 | 71.0 | 23 (4.6) | Mattson et al., (2004) |

**Table 3-A1:** Nutritional information of bear food items. Information includes: DM = Dry matter (%); DMDig (%) = Digestible dry matter; GrossE = Gross energy (kcal); EDig = Energy digestibility; PC (%) = Protein content; PDig (%) = Protein digestibility; DigP(g)=Digested protein; TDF (%) = Total dietary fiber. DM in a fresh matter base. DMDig, GrossE, EDig, PC, PDig and TDF in a dry matter base. (continuation)

| | DM | DMDig | GrossE | Edig | PC | PDig | DigP | TDF | Reference |
|---|---|---|---|---|---|---|---|---|---|
| **VEGETATION SUMMER AND LATE SUMMER** (continuation) | | | | | | | | | |
| Horsetails (July ) | | 28.5 | | 31.7 | 21.9 (2.2) | 15.8 (2) | 72.0 | 51.4 | Coogan (**) |
| Horsetails (June) | | | | | 29. | 22.7 | 77.0 | | Coogan (**) |
| Angelica | 17.7 (0.9) | 26.2 | 4878 (325) | | 15 (6.1) | 9.8 | 65.0 | 54 (11.8) | Fortin (**). DMDig and PDig from Pritchard and Robbins (1989) |
| Elk thistle | 8.6 (1.2) | 36.4 | 3804 (23.4) | | 7,1 (2.6) | 2.8 | 39.0 | 46.7 (2.7) | Fortin (**). DMDig and PDig from Pritchard and Robbins (1989) |
| Elymus | 42 (2.7) | 6.0 | 4434 (147) | | 8.8 (5.1) | 4.3 | 49.0 | 68.5 (0.4) | Fortin (**). DMDig and PDig from Pritchard and Robbins (1989) |
| Fireweed | 20.1 (4.3) | 26.8 | 4482 (94.5) | | 19.2 (7.4) | 13.5 | 70.0 | 53.6 (2.9) | Fortin (**). DMDig and PDig from Pritchard and Robbins (1989) |
| Cow parsnip | 17.2 (6.3) | 33.7 | 4471 (549) | | 19.2 (13.8) | 13.5 | 70.0 | 48.6 (4.4) | Fortin (**). DMDig and PDig from Pritchard and Robbins (1989) |
| Fern-leaved lovage | 17.8 (2.9) | 28.6 | 4457 (241) | | 19.7 (3.9) | 13.9 | 71.0 | 52.3 (0.5) | Fortin (**). DMDig and PDig from Pritchard and Robbins (1989) |
| Timothy | 28.4 (3.5) | 12.8 | 4828 (82) | | 17.4 (12.1) | 11.9 | 68.0 | 63.7 (9.4) | Fortin (**). DMDig and PDig from Pritchard and Robbins (1989) |
| Dandelion | 16.8 (1.6) | 40.7 | 4442 (609) | | 15.1 (3.1) | 9.8 | 65.0 | 43.6 (5.5) | Fortin (**). DMDig and PDig from Pritchard and Robbins (1989) |
| Clover | 25.2 (4.6) | 30.7 | 4746 (35) | | 25.3 (4.6) | 18.8 | 74.0 | 50.8 (1.5) | Fortin (**). DMDig and PDig from Pritchard and Robbins (1989) |

**Table 3-A1:** Nutritional information of bear food items. Information includes: DM = Dry matter (%); DMDig (%) = Digestible dry matter; GrossE = Gross energy (kcal); EDig = Energy digestibility; PC (%) = Protein content; PDig (%) = Protein digestibility; DigP(g)=Digested protein; TDF (%) = Total dietary fiber. DM in a fresh matter base. DMDig, GrossE, EDig, PC, PDig and TDF in a dry matter base. (continuation)

| | DM | DMDig | GrossE | Edig | PC | PDig | DigP | TDF | Reference |
|---|---|---|---|---|---|---|---|---|---|
| **VEGETATION LATE SUMMER TO EARLY FALL** | | | | | | | | | |
| Clover (August) | | 16.6 (9.4) | | 21.9 (7.8) | 16.1 (1.5) | 10.7 (1.4) | 66.0. | 60.9 (6.8) | Coogan (**) |
| Clover (Late hyperphagia) | | | | 46.8 (8.9) | | | | | Mattson et al., 2004 |
| Clover (September) | | 17.3 | | 22.4 | 15.3 (0.9) | 10 (0.8) | 65.0 | 60.4 | Coogan (**) |
| Clover White (late summer - fall) | 15.9 (4.2) | 34.2 (3.7) | | | 29.1 (0.8) | 22.2 | 76.0 | 48.3 (4.2) | Rode et al. (2001, Table 2) |
| Cow Parsnip (August) | | 11.4 (14.4) | | 17.5 (11.9) | 9.7 (6.9) | 5.1 (1.7) | 53.0 | 64.7 (10.3) | Coogan (**) |
| Dandelion (August) | | | | | 9.7 (0.7) | 5.1 (0.6) | 53.0 | | Coogan (**) |
| Graminoids (Late hyperphagia, Sep1 - den) | | | | 13 (8) | 9 (4) | 4.469 | 50.0 | 31.2 (4) | Mattson et al., 2004 |
| Grasses (late summer - fall) | 26.9 (3.1) | 21.9 (2.1) | | | 19.3 (1.4) | 13.5 | 70.0 | 57.1 (3.7) | Rode et al. (2001, Table 2) - (Poa pratensis, Phleumpratense, and Bromus gracilis) |
| Horsetails (August) | | | | | 17.1 (4.3) | 11.6 (3.8) | 68.0 | | Coogan (**) |
| Fireweed | 30.92 (2.95) | 15.3 | 4420 (39.5) | | 9.05 (3.25) | 4.5 | 50.0 | 61.9 | Fortin (**). DMDig and PDig from Pritchard and Robbins (1989) |
| Fern-leaved lovage | 23.1 (1.2) | 23.3 | 4705 (244) | | 17.08 (1.16) | 11.6 | 68.0 | 56.1 (5.74) | Fortin (**). DMDig and PDig from Pritchard and Robbins (1989) |
| Bluegrass | 44.6 (5.2) | 7.4 | 4441 (12.7) | | 10.47 (3.43) | 5.8 | 55 | 67.5 (5.7) | Fortin (**). DMDig and PDig from Pritchard and Robbins (1989) |

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| | DM | DMDig | GrossE | Edig | PC | PDig | DigP | TDF | Reference |
|---|---|---|---|---|---|---|---|---|---|
| **BERRIES** | | | | | | | | | |
| Huckleberry (V. membranaceum) | 14.6 | 72.5 | | | 3.7 | | | 20.7 | Welch et al., (1997, Table 1). |
| Soapberry | 18.0 | 70.3 | | | | | | 22.3 | Welch et al., (1997, Table 1) |
| Blueberries | 17.9 | 63.8 (0.1) | 4472 | 67.2 (0.5) | 5.6 | 1.1 | 18.9 (9.6) | 24.3 | Pritchard & Robbins (1990, Table 1&2) |
| Crowberry (Empetrum nigrum) | | 35.7 (3.5) | 4197 (400) | 37.7 (2.9) | 3.5 (0.1) | | | 47.2 (2.5) | Coogan (**) |
| Vaccinum myrtilloides | | 65.5 (3.1) | 4077 (300) | 62.4 (2.6) | 4.7 (0.2) | 0.6 (0.2) | 13 | 25.7 (2.2) | Coogan (**) |
| Vaccinum scoparium | | 68.8 | 4145 | 65.2 () | 4.9 | 0.9 | 18 | 23.4 | Coogan (**) |
| Vaccinum vitis-idaea | | 68.1 (4) | 4101 (160) | 64.5 (3.3) | 4.4 (0.7) | 0.4 | 9 | 23.9 | Coogan (**) |
| Buffaloberry (Shepherdia canadensis) | | 66.4 (1.25) | 4257 (295) | 63.15 (1.05) | 3.8 | | | | Coogan et al. 2012., DMDig, GrossE, EDig, PDig, TDF are average value from Table 1&2. PC from Table 3.PDig estimated using Pritchard and Robbins (1990) |
| Berries (bearberry, strawberry,red twinberry, gooseberry, dwarf huckleberry, globe huckleberry, grouse whortleberry) | 22.5 (7.1) | | 4712 (88.1) | | 6 (0.9) | | | 18.8 (2.2) | Fortin (**). |

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| | DM | DMDig | GrossE | Edig | PC | PDig | DigP | TDF | Reference |
|---|---|---|---|---|---|---|---|---|---|
| **ROOTS** | | | | | | | | | |
| Tubers (carrots-yams) | 16.8 | 57.8 (1.8) | 4123 () | 57.6 (2.6) | 8.3 | 4.4 | 52.7 (6.1) | 18.1 | Pritchard and Robbins (1990, Table 1 & 2). Digestibility estimation correspond to black bears (Ursus americanus). |
| Hedysarum alpinum | | 41.1 (1.5) | 3711 (330) | 42.4 (1.5) | 12.6 (0.5) | 7.6 (1.9) | 60.0 | 43.1 (1.3) | Coogan (2012; Table 1 & 2), (Annual average values) Independent laboratory. PDig from Pritchard and Robbins (1989) |
| Hedysarum alpinum | | 35.2 (1.5) | 4203 (260) | 37.3 (1.5) | 15.7 (0.2) | 10.3 (1.8) | 66.0 | 47.5 (1.3) | Coogan (2012; Table 1 & 2), (Annual average values). PDig from Pritchard and Robbins (1989) |
| Hedysarum alpinum (Pink Hedysarum) | | | | | 12.5 | 7.6 | 60.4 | | Hamer and Herrero (1987). We estimated a general average value from Figure 3. PDig from Pritchard and Robbins (1989) |
| Yellow Hedysarum | | | | | 10.8 | 6.0 | 56.0 | | Hamer and Herrero (1987). We estimated a general average value from Figure 4. PDig from Pritchard and Robbins (1989) |
| Pocket gopher cache | | | | 47.9 (18.6) | 8.6 | 4.1 | 48.0 | | Mattson et al., 2004 (Table 8 and 9). |
| Vole cache | | | | 71.5 | 5.1 | 1.0 | 20.0 | | Mattson et al., 2004 (Table 8&9). PDig from Pritchard and Robbins (1989) |
| Pondweed root | | | | 68.4 (8.6) | 8.7 (0.6) | 4.2 | 48.0 | | Mattson et al., 2004 (Table 8&9). PDig from Pritchard and Robbins (1989) |

**Table 3-A1:** Nutritional information of bear food items. Information includes: DM = Dry matter (%); DMDig (%) = Digestible dry matter; GrossE = Gross energy (kcal); EDig = Energy digestibility; PC (%) = Protein content; PDig (%) = Protein digestibility; DigP(g)=Digested protein; TDF (%) = Total dietary fiber. DM in a fresh matter base. DMDig, GrossE, EDig, PC, PDig and TDF in a dry matter base. (continuation)

| | DM | DMDig | GrossE | Edig | PC | PDig | DigP | TDF | Reference |
|---|---|---|---|---|---|---|---|---|---|
| **ROOTS** (continuation) | | | | | | | | | |
| Yampa root | | | | 71.8 (8) | 5.9 (1.7) | 1.7 | 29.0 | | Mattson et al., 2004 (Table 8&9). PDig from Pritchard and Robbins (1989) |
| Sweet-cicely root | | | | 63.6 (14.2) | 7.8 (1.5) | 3.4 | 44.0 | | Mattson et al., 2004 (Table 8&9). PDig from Pritchard and Robbins (1989) |
| Biscuitroot | | | | 63.3 (8.7) | 5.2 (1.4) | 1.2 | 22.0 | | Mattson et al., 2004 (Table 8&9). PDig from Pritchard and Robbins (1989) |
| Carrot | 22.0 | | 4100 | | | | | | USDA, 2012 |
| Yam (Dioscorea spp.) | 30.4 | | 1180 | | | | | | USDA, 2012 |
| Sweet potato (Ipomoea batatas) | 22.72 | | 860 | | | | | | USDA, 2012 |
| Elk thisle | 13.8 (1.6) | | 3942 (76) | | 13.5 (2.5) | 8.4 | 62.0 | 48 (9) | Fortin (**). PDig from Pritchard and Robbins (1989) |
| Glacier Lily | 13.8 (2.7) | | 4124 (81) | | 8.5 (1.6) | 4.0 | 47.0 | 22.9 (8) | Fortin (**). PDig from Pritchard and Robbins (1989) |
| Licorice root | 28 (3.8) | | 3827 (470) | | 6.6 (0.6) | 2.4 | 36.0 | 36.3 (6.7) | Fortin (**). PDig from Pritchard and Robbins (1989) |
| Yampa root | 38.7 (10.4) | | 3729 (132) | | 5.2 (1.9) | 1.1 | 22.0 | 28.7 (8.3) | Fortin (**). PDig from Pritchard and Robbins (1989) |

**Table 3-A1:** Nutritional information of bear food items. Information includes: DM = Dry matter (%); DMDig (%) = Digestible dry matter; GrossE = Gross energy (kcal); EDig = Energy digestibility; PC (%) = Protein content; PDig (%) = Protein digestibility; DigP(g)=Digested protein; TDF (%) = Total dietary fiber. DM in a fresh matter base. DMDig, GrossE, EDig, PC, PDig and TDF in a dry matter base. (continuation)

| | DM | DMDig | GrossE | Edig | PC | PDig | DigP | TDF | Reference |
|---|---|---|---|---|---|---|---|---|---|
| **ANTS** (continuation) | | | | | | | | | |
| Camponotus herculeanus | 31.2 | 88.4 | 2190 | 20.6 | 43.8 | 34.7 | 79.0 | 9.3 | Swenson et al., (1999, Table 5). PDig from Pritchard and Robbins (1989). |
| Formica spp | 26.7 | 77.1 | 2080 | 17.7 | 55.9 | 46.7 | 84.0 | 17.4 | Swenson et al., (1999, Table 5). PDig from Pritchard and Robbins (1989). |
| Formica spp pupae | 24.4 | 64.3 | 2370 | 17.8 | 54.9 | 45.7 | 83.0 | 11.3 | Swenson et al., (1999, Table 5). PDig from Pritchard and Robbins (1989). |
| Acanthomyops spp (worker) | | | 5300 | | 30.9 (5.8) | 21.5 | 69.0 | | Noyce et al., (1997, Table 7). PDig from Pritchard and Robbins (1989). Study in black bear. |
| Acanthomyops spp (pupae) | | | 6000 | | 40.1 (3.8) | 30.7 | 77.0 | | Noyce et al., (1997, Table 7). PDig from Pritchard and Robbins (1989). Study in black bear. |
| Camponotus spp (workers) | | | 4800 | | 34.5 | 25.1 | 73.0 | | Noyce et al., (1997, Table 7). PDig from Pritchard and Robbins (1989). Study in black bear. |
| Camponotus spp (aletes) | | | 6500 | | 26.4 | 16.9 | 64.0 | | Noyce et al., (1997, Table 7). PDig from Pritchard and Robbins (1989). Study in black bear. |
| Formica spp. (workers) | | | 4400 | | 27.0 | 17.5 | 65.0 | | Noyce et al., (1997, Table 7). PDig from Pritchard and Robbins (1989). Study in black bear. |
| Formica aserva (Larvae) | | | 5260 | | 55.9 | 46.7 | 84.0 | | Coogan (2012; Table 1&2) |
| Formica aserva (ants) | | | 4730 | | 50.7 | 41.4 | 82.0 | | Coogan (**) |
| Formica ulkei (larvae) | | | 6360 | | 66.8 | 57.7 | 86.0 | | Coogan (2012; Table 1&2) |
| Formical ulkei (ants) | | | 6600 | | 69.1 | 60.0 | 87.0 | | Coogan (**) |

**Table 3-A1:** Nutritional information of bear food items. Information includes: DM = Dry matter (%); DMDig (%) = Digestible dry matter; GrossE = Gross energy (kcal); EDig = Energy digestibility; PC (%) = Protein content; PDig (%) = Protein digestibility; DigP(g)=Digested protein; TDF (%) = Total dietary fiber. DM in a fresh matter base. DMDig, GrossE, EDig, PC, PDig and TDF in a dry matter base. (continuation)

| | DM | DMDig | GrossE | Edig | PC | PDig | DigP | TDF | Reference |
|---|---|---|---|---|---|---|---|---|---|
| **UNGULATES** | | | | | | | | | |
| Deer | 26.1 | 93 (1.3) | 7316 | 94.6 (0.7) | 45.1 | 40.4 | 89.5 (1.5) | 6.3 | Pritchard & Robbins (1990, Table 1 & 2). Digestibility was measure on Black Bear |
| Wapiti (spring and estrus) | | | | 90.0 | 80.0 | 71.0 | 89.0 | | Mattson et al., (2004, Table 8 & 9). PDig from Pritchard and Robbins (1989) |
| Wapiti (early hyperphagia) | | | | 92.0 | 62.0 | 52.6 | 85.0 | | Mattson et al., (2004, Table 8 & 9). PDig from Pritchard and Robbins (1989) |
| Wapity (late hyperphagia) | | | | 93.0 | 45.0 | 35.7 | 79.0 | | Mattson et al., (2004, Table 8 & 9). PDig from Pritchard and Robbins (1989) |
| Bison and moose (spring and estrus) | | | | 92.0 | 81.0 | 72.0 | 89.0 | | Mattson et al., (2004, Table 8 & 9). PDig from Pritchard and Robbins (1989) |
| Bison and moose (early hyperphagia) | | | | 94.0 | 67.0 | 57.9 | 86.0 | | Mattson et al., (2004, Table 8 & 9). PDig from Pritchard and Robbins (1989) |
| Bison and moose (late hyperphagia) | | | | 96.0 | 53.0 | 43.8 | 83.0 | | Mattson et al., (2004, Table 8 & 9). PDig from Pritchard and Robbins (1989) |
| Bison | 23.1 | | 5691 | | 86.5 | 77.6 | 90 | | Fortin (**). PDig from Pritchard and Robbins (1989) |
| Mule deer | 25.7 | | 5656 | | 86.6 | 77.7 | 90 | | Fortin (**). PDig from Pritchard and Robbins (1989) |

**Table 3-A1:** Nutritional information of bear food items. Information includes: DM = Dry matter (%); DMDig (%) = Digestible dry matter; GrossE = Gross energy (kcal); EDig = Energy digestibility; PC (%) = Protein content; PDig (%) = Protein digestibility; DigP(g)=Digested protein; TDF (%) = Total dietary fiber. DM in a fresh matter base. DMDig, GrossE, EDig, PC, PDig and TDF in a dry matter base. (continuation)

| | DM | DMDig | GrossE | Edig | PC | PDig | DigP | TDF | Reference |
|---|---|---|---|---|---|---|---|---|---|
| **NUTS** | | | | | | | | | |
| Pinus edulis | 95.0 | 41.2 (0.9) | 6484 | 50.1 (3.1) | 8.8 () | 5.0 | 57.2 (3.1) | 40.3 | Pritchard and Robbins (1990, Table 1&2). DMDig, EDig and PDig measure for black bears |
| Confier seeds | | | 7000 | | | | | | Fogel and Trapped (1978, Table 4) |
| Whitebark pine nut | | | | 49.2 | 12.8 | | | 34.8 | Mattson et al., (2004, Table 8&9) |
| Whitebark pine nut | | | | 49.4 | 12.8 | | | | Mattson and Reinhart (1994, Table 1) |
| Whitebark pine nut | | | 6111 | | 14.8 | 9.6 | 65 | | Coogan et al., (2012, Table 1&2) |
| Whitebark pine nut | 86.1 | | 5764 | | 11.6 | | | 80.2 | Fortin (**) |
| **CUTTHROAT TROUT** | | | | | | | | | |
| | 25.0 | 89.8 (1.1) | 5715 | 94.5 (1.1) | 69.6 | 66.6 | 95.2 (0.6) | 11.1 | Pritchard & Robbins (1990, Table 1 & 2). DMDig, EDig and PDig measure for black bears |
| | 29.5 (4.6) | | 6258 (299) | | 65.4 (8.1) | 62.2 | 95 | | Fortin (**). Pdig estimation from Pritchard and Robbins (1980) |
| **MUSHROOM** | | | | | | | | | |
| Rhizopogon spp | 34.5 (11.5) | | 4884 (141) | | 11 (2.4) | | | 52.1 (11.2) | Fortin (**) |

# APPENDIX 4-A

## DIET INFORMATION

**Figure 4-A1:** Nutritional characteristic of bear diets in different ecosystems, in a fresh matter base. Diets resemble the food habits in the Foothill (a) and Mountain (b) ecosystems of Alberta (Canada, Munro et al., 2006), Flathead (c) of southeast British Columbia (McLellan and Hovey, 1995), and GYE (d) (female diet, Fortin et al., 2013). Dry matter (DM, %), dry matter digestibility (DMDig, %), energy content (GrossE, kcal/kg), energy digestibility (EDig, %), protein content (PC, %), protein digestibility (PDig, %)

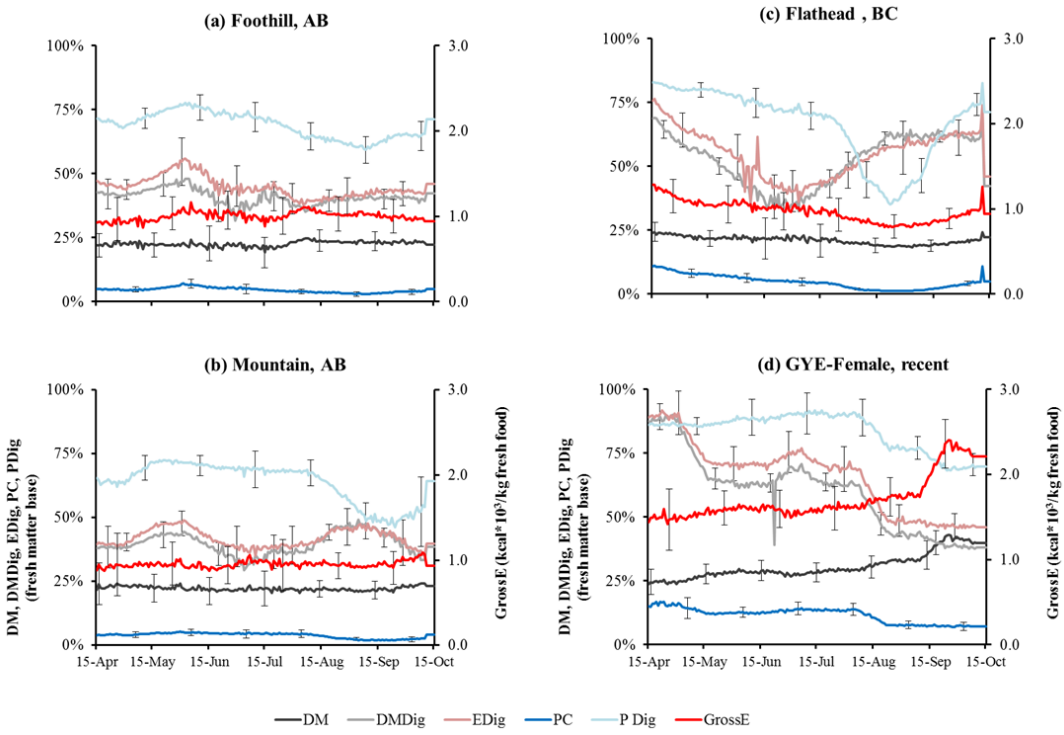
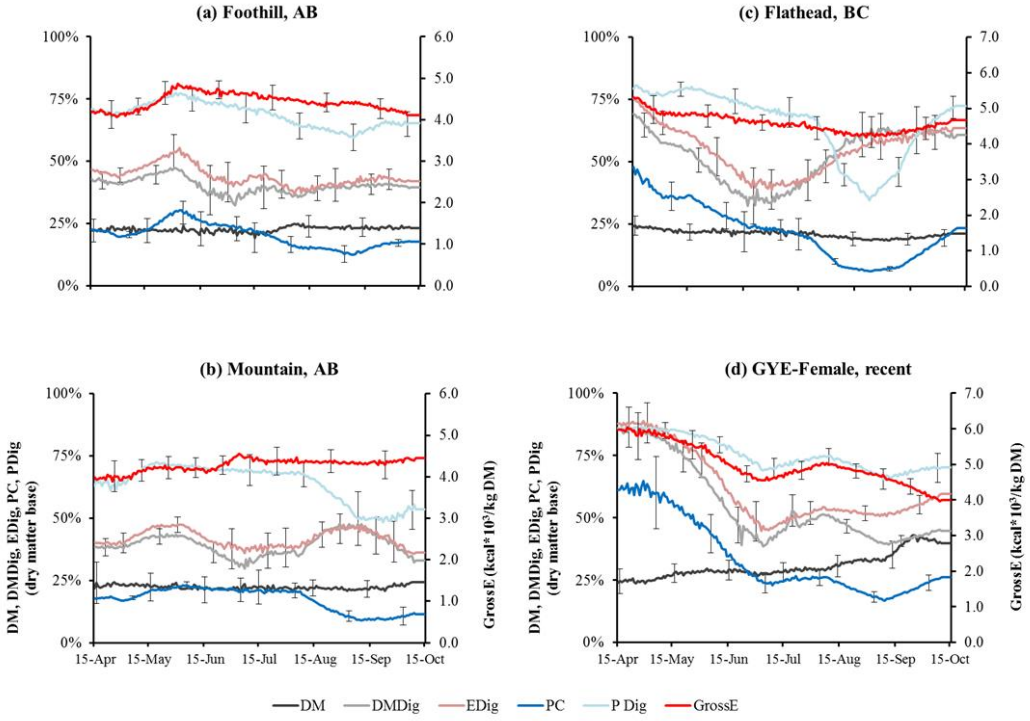


**Figure 4-A2:** Nutritional characteristic of bear diets in different ecosystems, in a dry matter base. Diets resemble the food habits in the Foothill (a) and Mountain (b) ecosystems of Alberta (Canada, Munro et al., 2006), Flathead (c) of southeast British Columbia (McLellan and Hovey, 1995), and GYE (d) (female diet, Fortin et al., 2013). Dry matter (DM, %), dry matter digestibility (DMDig, %), energy content (GrossE, kcal/kg), energy digestibility (EDig, %), protein content (PC, %), protein digestibility (PDig, %)



# APPENDIX 4-B
# PROPORTION OF LEAN AND MASS GAIN

The proportion of the lean and fat mass gain (%) during the active period follows a sigmoidal function. For lean mass gain, the highest rate of gain occurs during spring and early summer and for fat mass gain, the highest rate of gain occurs during late summer and early fall or hyperphagia period (Hilderbrand et al., 1999a; Felicetti et al., 2003).

The shape of the sigmoidal curve is dominated by two parameters: inflexion point and slope. The inflexion point represents the highest rate of mass gain and slope represents the average rate of gain. Days of active period was set at 185. Equation 4-A1 is the generic function for a sigmoidal curve. Equation 4-A2 is the curve used to estimate the proportion of lean mass gain, inflexion point was 80 and slope was 4 (equation) and equation 4-A2 (Figure 4-A1).
Equation 4-A3 is the curve used to estimate the e proportion of fat mass gain, inflexion point was 120 and slope was 5 (Figure 4-A2).

Eq. 4-B1 = $100 / \{1 + [(\text{active period} - \text{actual day}) / (\text{active period} - \text{inflexion})]^{\text{slope}}\}$
Eq. 4-B2 = $100 / \{1 + [(185 - \text{actual day}) / (185 - 80]^4\}$
Eq. 4-B3 = $100 / \{1 + [(185 - \text{actual day}) / (185 - 120)]^4\}$

**Figure 4-B1:** Proportion of lean mass gain.

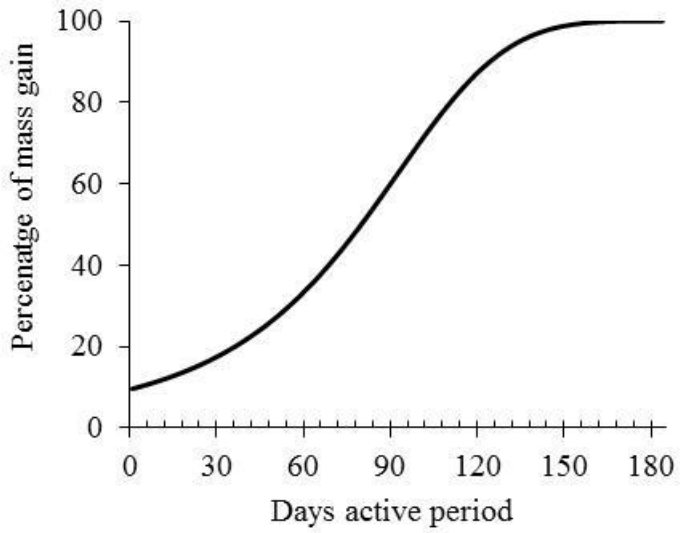
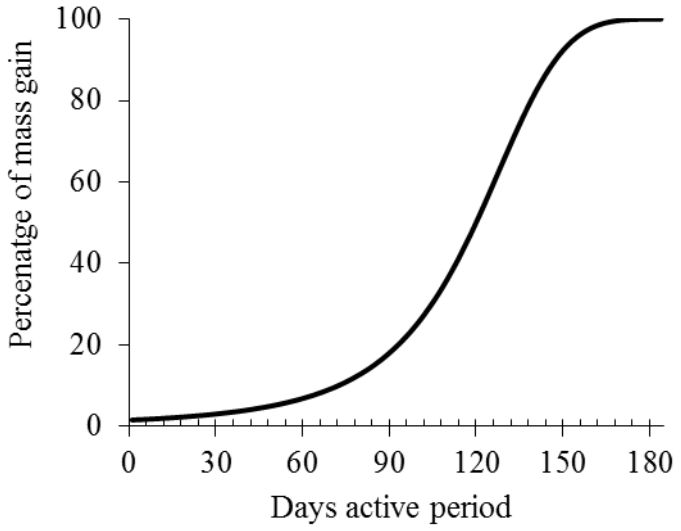



**Figure 4-B2:** Proportion of fat mass gain



# APPENDIX 4-C
# STOMACH CAPACITY ALGORITHM

The model used a simplified structure to estimate the maximum food intake per day that is based on the stomach capacity (StmCap). Previous studies have shown that the maximum daily food intake (kg fresh food/day) varies between 10 to 35% of the body mass depending on the type of diet and the period of the active phase (Hilderbrand et al., 1999a; Welch et al., 2001, Rode et al., 2001; Erlenbach et al., 2014). During summer and early fall brown bears increase their food intake, period known as the hyperphagia phase.

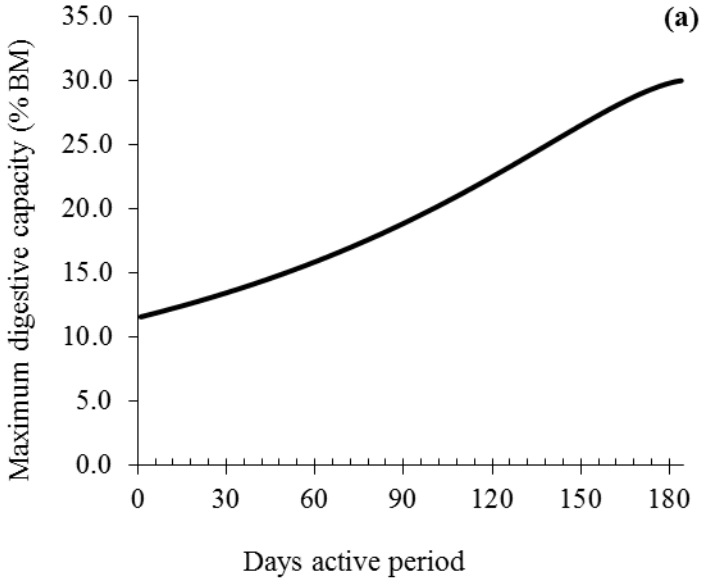
To cover both aspects I used an algorithm that determines the maximum digestive capacity (MaxDigCap) depending on the day. This algorithm was adjusted in the calibration and parameterization process, details are presented in Appendix 4-E.

**Result:**

MaxDigCap follows a sigmoidal curve (Figure 4-B1) and the shape of the curve is dominated by two parameters: inflexion point and slope. The inflexion point represents the highest rate of food intake and slope represents the rate of food intake. Days of active period was set at 185. Figure 4-B1 represents the MaxDigCap parameter depending on the day of the active period, inflexion point was 50 and slope was 1.5 (equation 4-B2).

Eq. 4-C2 = $30 / \{1 + [(185 - \text{actual day}) / (185 - 50)]^{1.5}\}$

**Figure 4-C:** Maximum digestive capacity parameter (MaxDigCap).



# APPENDIX 4-D

## ADJUST OF LACTATION COST

Farley and Robbins (1995) measured the energy and the protein intake per cub in mother's milk during 300 days; 60 days during the hibernation and 240 days during the active period. Because the model uses a different length of hibernation and active period it was necessary to adjust the curves of energy and protein intake to the model conditions.

Simulation conditions were: 256 days of lactation in total; 74 days during the hibernation and 184 days during the active period. To adjust the curves I assumed that the total energy and protein intake are the same as Farley and Robbins (1995), but the costs distribute different. Also I kept the energy and protein lactation costs low during the hibernation phase.

The first step was to estimate the total energy (kcal) and protein intake (kg) using the information presented in Farley and Robbins (1995). For this purpose I obtained the regression curve for the energy and protein intake depending on the day (Fig. 4-C1a,b). Second, I obtained the integral of these regressions to estimate the energy intake (kcal/day/cub) and the protein intake (gr/day/cub) in 300 days. Equation 1 is the regression curve of the energy intake (kcal/day/cub), and equation 2 is the integral of this regression. Equation 3 is the regression curve of the protein intake (gr/day/cub) and equation 4 is the integral of this regression. X in day of lactation or cub age. Energy intake in 300 days is ~584,576 (resolving equation 4-C2) and protein demand ~28.6 (resolving equation 4-C4).

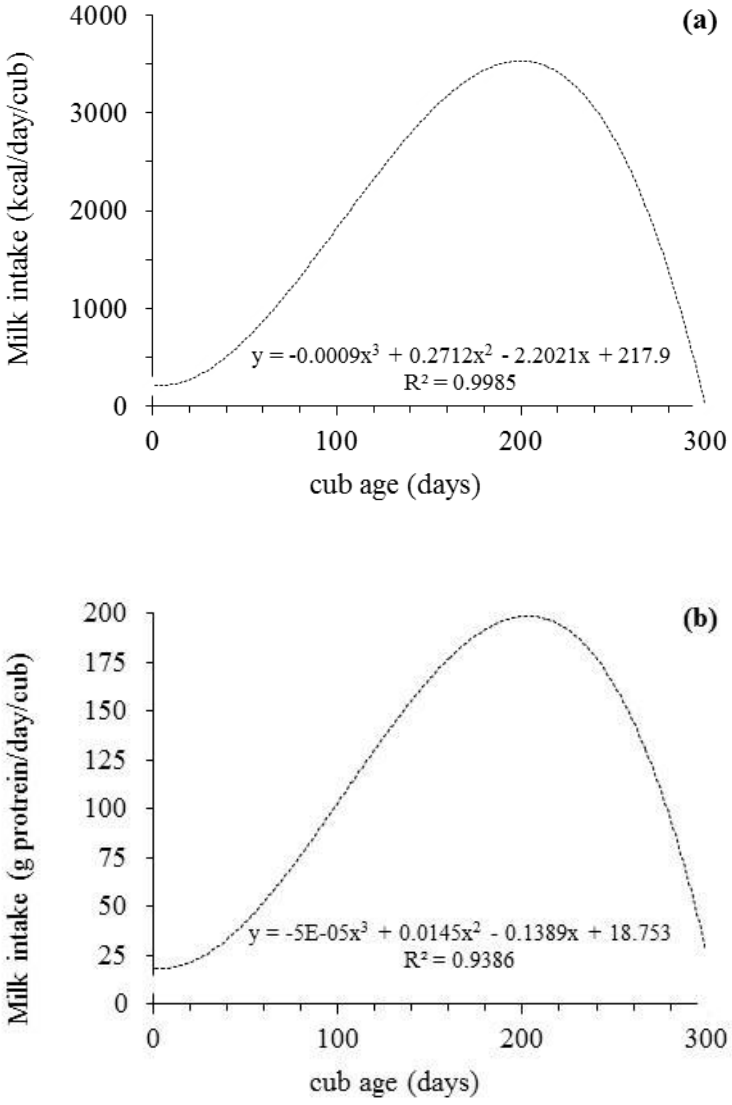
Eq. 4-D1 $\quad \text{Energy} = -0.0009 \times X^3 + 0.2712 \times X^2 - 2.2021 \times X + 217.9$

Eq. 4-D2 $\quad \int(\text{energy}) = -0.0009 \times X^4/4 + 0.2712 \times X^3/3 - 2.2021 \times X^2/2 + 217.9 \times X$

Eq. 4-D3 $\quad \text{Protein} = -0.00005 \times X^3 + 0.0145 \times X^2 - 0.1389 \times X + 18.753$

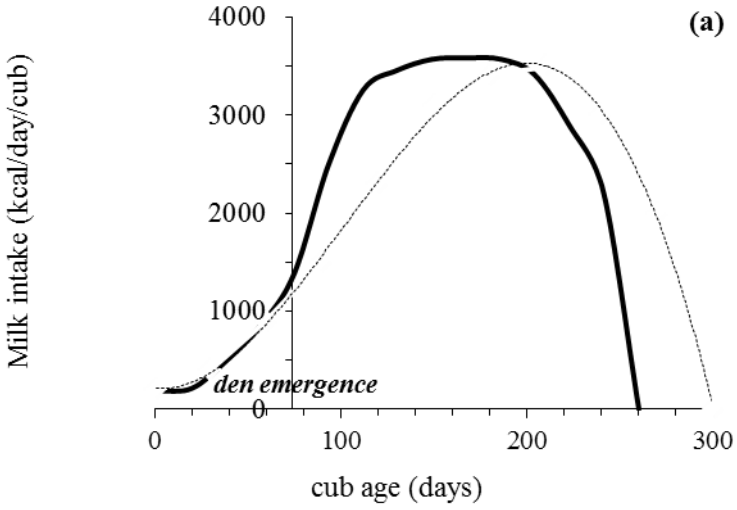
Eq. 4-D4 $\quad \int(\text{protein}) = -0.00005 \times X^4/4 + 0.0145 \times X^3/3 - 0.1389 \times X^2/2 + 18.753 \times X$

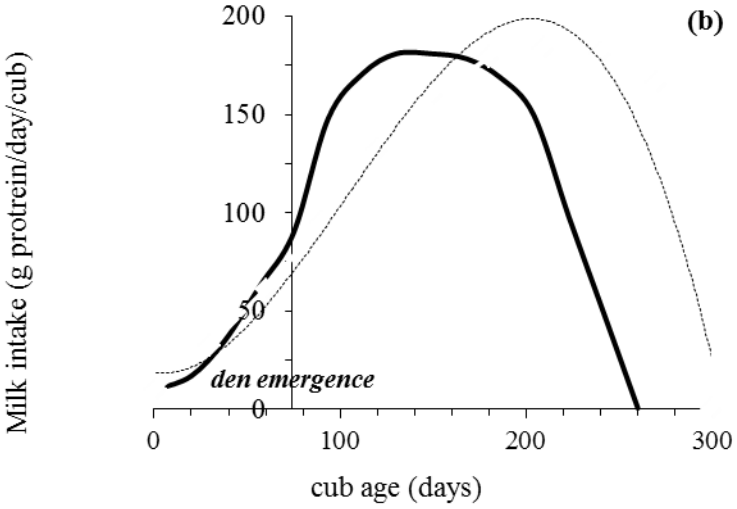
**Figure 4-D1:** Daily energy (a) and protein (b) intake per cub from maternal milk. Regressions curves were draw from Fraley and Robbins (1995).




Third, I distributed the total energy and protein intake in 74 days during the hibernation and 184 days during the active period (Fig. 4-D2 a,b). I used the same level of variation showed in Farley and Robbins (1995). I ran 100 repetitions. To estimate the lactation cost the model uses and efficiency parameter of 0.85 (Blaxter, 1989), that represent the efficiency of converting maternal tissue into milk.

**Figure 4-D2:** Daily energy (a) and protein (b) intake per cub used in the model simulation (continues line). Curves are based on Fraley and Robbins (1995; segmented lines) and they were adjusted to the length of the lactation period in the simulated conditions.



# APPENDIX 4-E
# MODEL CALIBRATION AND PARAMETERIZATION

This appendix details the method and results for the model calibration and parameterization. Parameterization was developed for curves that describe the proportion of fat and lean mass gain, stomach capacity and standing cost. General results for the curves of fat and lean mass gain, are presented on Appendix 4-B, and results for the stomach capacity is presented on Appendix 4-C.

To calibrate and parameterize the model I used two previous empirical studies of brown bears: Hilderbrand et al. (1999a), and Robbins et al. (2007). These studies used captive bears in feeding trials for ~10 to 14 days. The goal was to assess the effects diets on gains in body mass. I replicated the conditions described in these feeding trials studies (e.g. diet information; period of year; initial bear body mass) and compared the model outcome with their results. I chose the parameter value that gave the most similar result in comparison to the empirical data.

Information such as initial body mass and body fat content per bear was not reported in these studies; I assumed therefore these conditions. In all simulated experiments the model was run for six bears with different body size. Initial body mass were 56, 111, 167, 222, 278 and 333 kg of body mass. Spring body fat content was 10%. Target body mass was defined as an increase in body lean mass of 20% and reach a fat mass of 40% (Table 4-F1).

I defined the day at which the model starts to simulate each feeding trial experiments based on the information reported in these studies. This parameter determines the proportion of lean and fat mass gain (see Fig. 4-E1).

Simulated experiments ran for 20 days for each bear, similar to the experimental trials of captive bears. Because model simulations have to be adjusted during initial days, the model was run for 40 days with the first 20 days (initial conditions) eliminated. Empirical studies reported the body mass gain depending on the digestible dry matter intake or digestible energy thus I obtained the same regressions to compare results.

**Details of the feeding trials simulation experiments:**

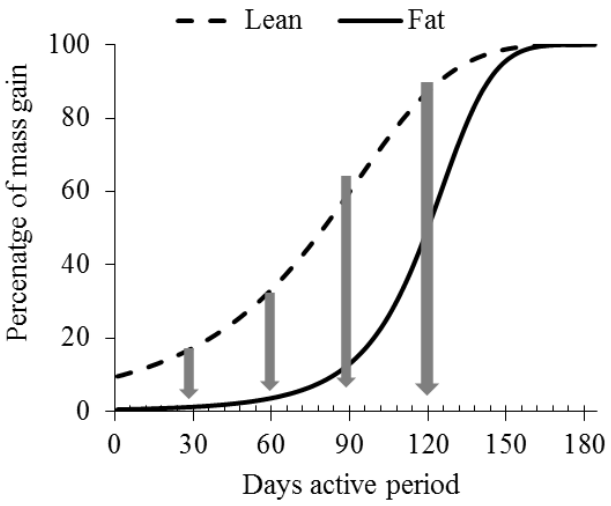
Hilderbrand et al. (1999a) studied the diet of white-tailed deer (deer-diet) and chinook-salmon (salmon-diet). Nutritional information is presented on Pritchard and Robbins (1989). The deer-diet trial was developed early in the season; consequently the model simulation experiment started on day 30. The salmon-diet trial was developed late in the season; consequently, model simulation experiment started on day 120.

The Robbins et al. (2007) study compared three diets. The two previous diets representing the berry-diet from Rode and Robbins (2000) and the salmon-diet from Hilderbrand et al. (1999a) and a new diet of both salmon and fruit. The trials were developed in summer and therefore the model simulation started on day 120.

**Table 4-E1:** Represent initial model conditions used in the simulation of feeding trials experiments.

| Bear number | Initial conditions (kg) | | | Target body mass (kg) | | |
|---|---|---|---|---|---|---|
| | Spring lean | Spring fat | Spring BM | Fall lean | Fall fat | Fall BM |
| 1 | 50 | 6 | 56 | 60 | 40 | 100 |
| 2 | 100 | 11 | 111 | 120 | 80 | 200 |
| 3 | 150 | 17 | 167 | 180 | 120 | 300 |
| 4 | 200 | 22 | 222 | 240 | 160 | 400 |
| 5 | 250 | 28 | 278 | 300 | 200 | 500 |
| 6 | 300 | 33 | 333 | 360 | 240 | 600 |

**Figure 4-E1:** Grey arrows represent the start of the feeding trial experiments. Curves represent the proportion of the lean and fat mass gain (Appendix 4-A).




**Calibration and parameterization results:**

Model calibration showed that the best set of parameters was: stomach capacity shown in Appendix 4-C and the proportion of the lean and fat mass gain are shown in Appendix 4-B.

Efficiencies of gain for the salmon-berry-diet and salmon-diet were similar between simulated and empirical studies. The model overestimates the efficiency of gain for the berry-diet in 0.02 g (kg0.75/day) and for the deer-diet the model underestimates the efficiency of gain in 0.05 g (kg0.75/day).

The model overestimates the maintenance cost for the salmon-berry diet in ~28.2 kcal of digestible energy ($kg^{0.75}$/day) and for the berry diet in ~5 kcal of digestible energy ($kg^{0.75}$/day). The model underestimates the maintenance cost for the salmon-diet in ~29.1 kcal of digestible energy ($kg^{0.75}$/day) and for the deer-diet in 10 g of dry matter intake ($kg^{0.75}$/day)

Differences observed in the maintenance cost between simulation and empirical studies can be explained by several factors. First, empirical studies do not report or measure

information that is necessary to include in the model, for example the initial body lean and fat mass of each bear. Because of this in the simulated experiments initial conditions were assumed. Second, the model is sensitive to the composition of gain, lean v/s fat mass, which affect the efficiency of gain.

**Figure 4-E2:** Model calibration and parameterization results. Feeding trial simulation experiments are in black circle and regression equation in bold characters. Empirical studies are in segmented line and italic character. Salmon-Berry, Salmon and Berry diet from Robbins et al. (2007), Deer diet from Hilderbrand et al. (1999a).