

Energetics of hibernation and reproductive trade-offs in brown bears

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ABSTRACT

Brown bears give birth and nurture their young for the first 3–5 months while fasting in hibernation. During this period, bears use body reserves to support the energy and protein costs of reproduction. Limited reserves may restrict reproductive investment. We developed a model to assess the energetic costs of reproduction during hibernation and to determine how maternal condition, length of lactation, litter size, and length of hibernation affect brown bear reproductive success. Increasing litter size by one cub was more costly than increasing the lactation period by 14 days. For hibernating females, ~73% of their mass loss during lactation was lean mass. Minimum levels of fat reserves necessary to support reproduction varied from 19% to 33% depending on number of cubs and length of lactation while denning. Reproduction was not possible if body fat content was below 19% and length of hibernation was over 120 days. While the importance of fat or energy reserves at the beginning of hibernation has been long recognized, the importance of consuming high-protein foods after hibernation may be equally important. Therefore, more attention should be given to understanding pre- and post-hibernation nutritional factors affecting reproduction and the trade-offs between available food resources, maternal condition, and reproductive investment and success in wild bear populations.

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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 (Barbosa 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 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, 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,

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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; Ramsay and Dunbrack, 1986; 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 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 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 determining 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; Mazaris et al., 2006; Starfield and Bleloch, 1986), and exploring new scenarios including survival thresholds (Faring, 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

Table 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)	$7.2 \times \text{BM}^{1.09}$ (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) and Farley and Robbins (1995)
Neonatal body composition	12% protein, 1% fat	Oftedal et al. (1993)
Gestation period	60 days	Robbins (pers. commun.)
Neonatal mass	0.650 kg	Robbins et al. (2012a)
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), and Robbins (1993)

kg, kilograms; BM, body mass (kg).

^a This equation is presented on p. 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.

(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 (Barbosa 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; Kooijman, 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 and Table 1). The model was developed in Stella 10 (Isee System 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; Robbins, 1993). 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.

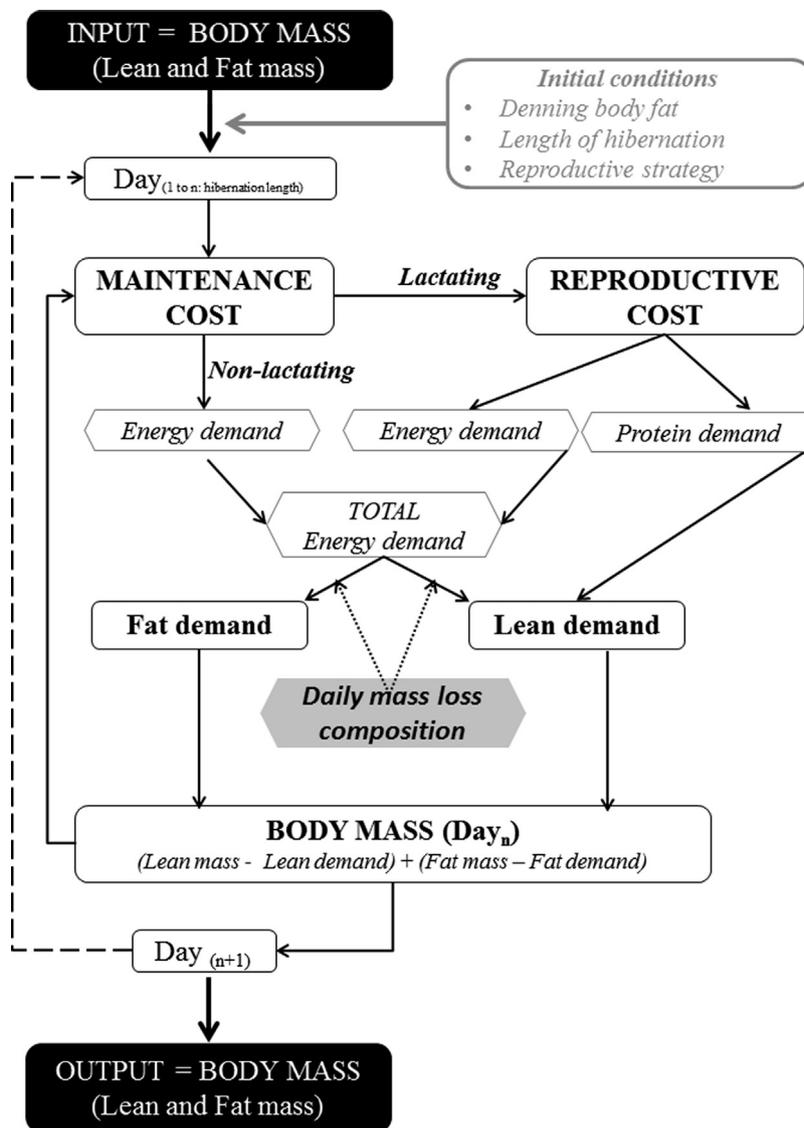


Fig. 1. Model diagram and schedule. Equations and parameters are in Table 1. The model starts with the inputs of the initial conditions on day 1 of denning and ends at den emergence. Each day the model accounts for daily energy and protein demands based on body mass and reproductive cost. Reproductive 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.

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, 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 to 400 g for European brown bears (Hissa, 1997) and up to 650 g 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 in order 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 during hibernation 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 (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 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% to 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; 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% and 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 and 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 and 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 not known, we assumed a random value between 20% and 30% body fat.

2.5. Sensitivity analysis

We used a Sensitivity Index (S_x) 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 Eq. (1):

$$S_x = \frac{(RV_1 - RV_0)/RV_0}{(P_1 - P_0)/P_0} \quad (1)$$

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, lactating two cubs during 60 days and with denning fat content varying randomly between 22% and 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 30–50% (Caolin, 2004; Chérel 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%

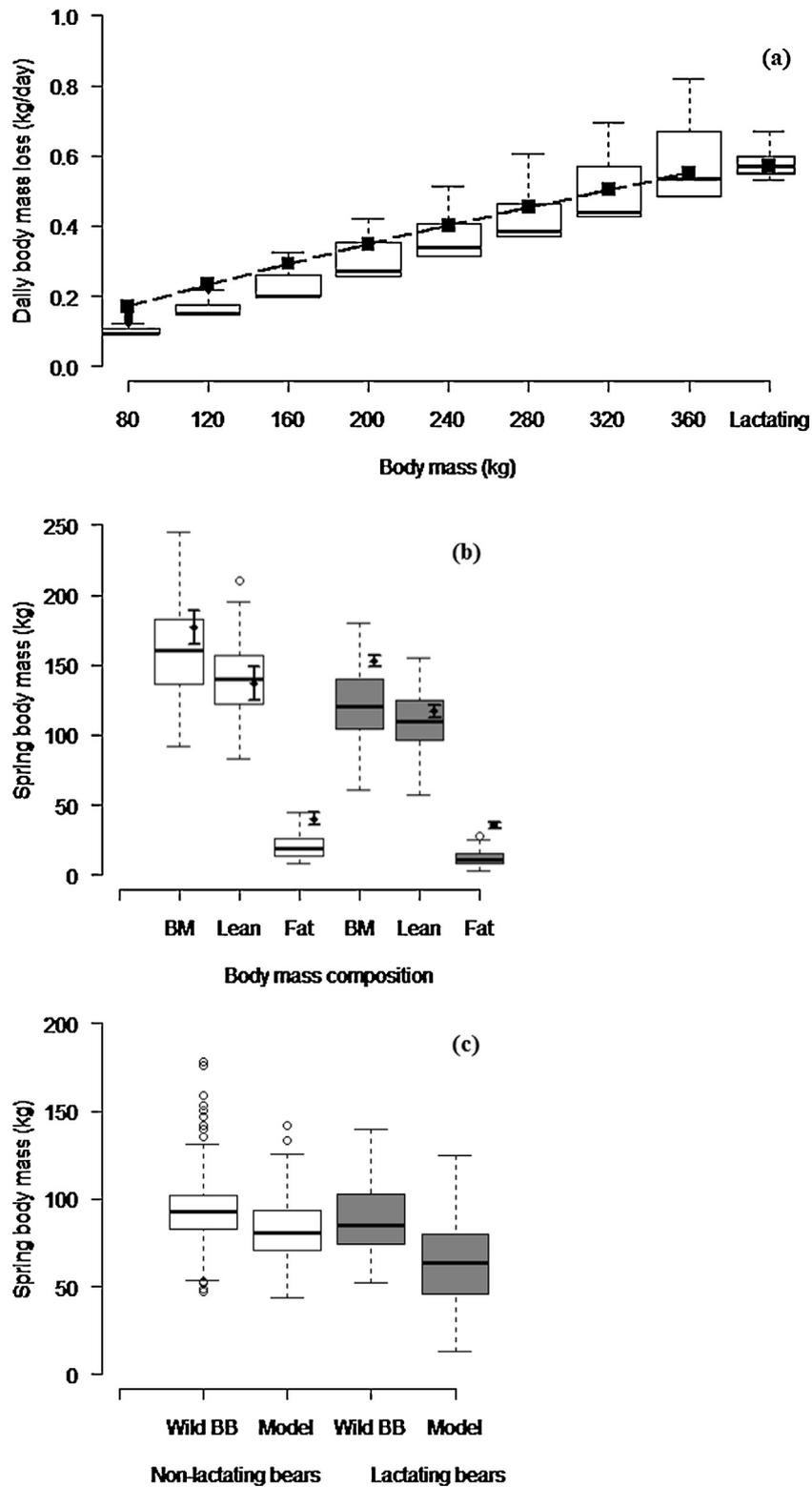


Fig. 2. Calibration and validation model results. Two independent, North American brown bear studies (Farley and Robbins, 1990; Hilderbrand et al., 2000) were used to adjust the parameters and evaluate model performance. For model validation we used information from the Scandinavian Brown Bear Research Project. In all simulations, one hundred repetitions were run for each scenario. White boxplots are for non-lactating bears, and gray 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. (a) 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 (a) with black diamonds and a dashed line. (b) 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. (c) Compares spring body mass between model results from this study and free-ranging female brown bears in Sweden.

Table 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	Change in the parameter						
	Parameter value	–50%	–25%	–10%	+10%	+25%	+50%
Milk efficiency	0.85	–0.37	–0.23	–0.17	–0.34	–0.14	–
Milk energy content	^a	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	0.00	0.00
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

^a Farley and Robbins (1995).

beyond which all energy necessary for maintenance and reproduction was supplied by fat. When the body fat content was $\leq 17\%$, 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. 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. 2b). Model validation (Fig. 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 and length of hibernation). Second, the results of Farley and 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 denning was less costly than an increase in litter size from 1 to 2 cubs (Table 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 ~3–10 kg of fat, and protein requirements can be met by ~9–28 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 3). Gestation costs were minimal (between 1% and 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. 3a–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.

Table 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 (kcal)	Protein (kg)	Fat mass		Lean mass		BM (kg)
			(kg)	(%)	(kg)	(%)	
Lact. 60 days, 1 cub	30,918 (1949)	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 (2650)	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 (3559)	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 (4835)	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.

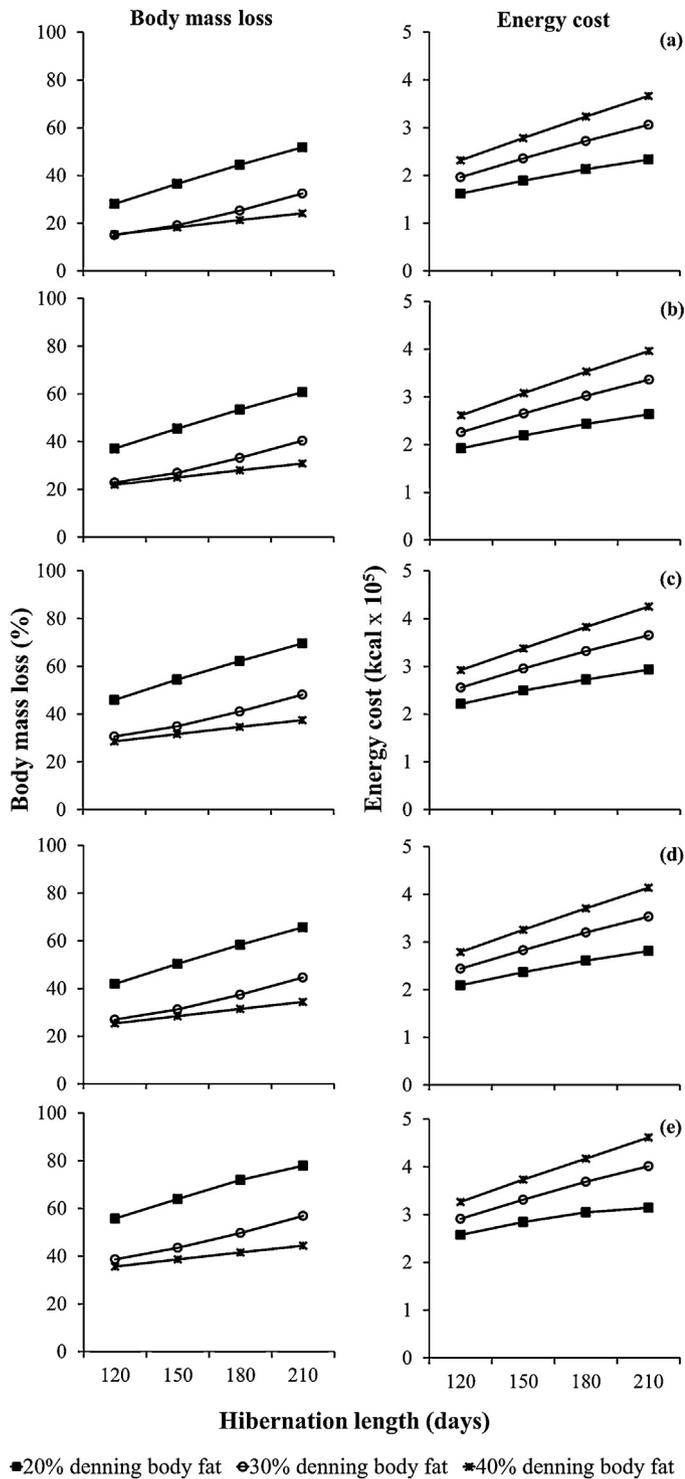


Fig. 3. Effect of female body condition (% of denning body fat content) on total body mass loss (kg) and energy cost (kcal) and with increasing hibernation length. The right column of figures is the percentage of body mass loss during hibernation relative to the initial fall body mass. The left column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

As expected, the threshold for mortality (i.e., 30% loss of lean mass) was reached faster when denning body fat was lower (Fig. 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 $\geq 40\%$, 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. 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 11 days. For the same length of hibernation, lactating bears needed $\sim 3\%$ 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 (%).

Non-lactating bear $Y = 11.4X - 68$ (2)

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

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

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

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

4. Discussion

Several empirical studies have measured loss of body mass and metabolic rates of hibernating bears (Atkinson and Ramsay, 1995; Atkinson et al., 1996; Farley and Robbins, 1995; Hilderbrand 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 et al., 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% and 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 et al., 1992; Dunn et al., 1982), seals (Vierrier et al., 2011; Worthly 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

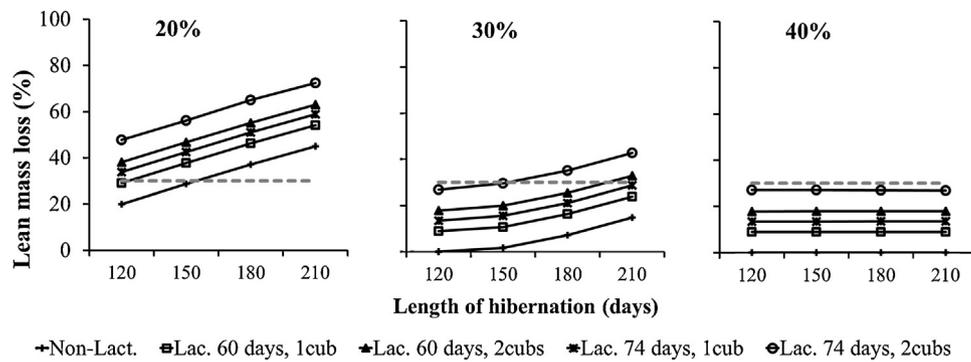


Fig. 4. Percent of lean mass loss for different reproductive strategies and initial fall body fat contents (%). Fall lean mass was assumed to be 100 kg for all bears. 20%, 30%, 40% of denning body fat content. Gray dash line represents the survival threshold of 30% lean mass loss.

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 overestimates 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 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 25–30% 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 very 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).

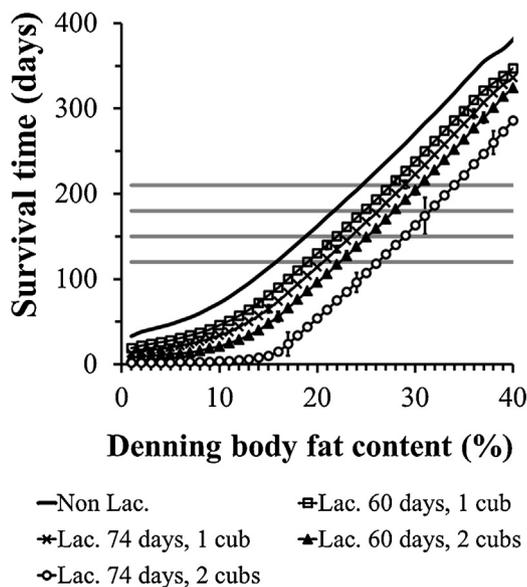


Fig. 5. Estimated survival time for bears having different denning body fat contents and experiencing different reproductive strategies. The lines represent the number of days before 30% of lean mass loss is reached (survival threshold). Initial body lean mass was 100 kg. Bars are three times SD. Horizontal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

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 et al., 1993) and the reduced growth rate of triplets relative to twins while nursing in the den in brown bears (Robbins et al., 2012a) 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, 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).

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