# 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 denned. 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) | $7.2 \times BM^{1.09}$ (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.