Hibernation ecology of brown bears in Sweden

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Keywords: Scandinavia, brown bear, Ursus arctos, *den type, hibernation, physiology*

Abstract: Hibernation is an adaptive strategy to cope with unfavourable environmental conditions. Bears are the only large mammal that use this strategy during winter. They reduce their body temperature by several degrees and their metabolism by 20–50 % during hibernation. However, bears have an exceptional position among hibernators, because they are the only mammal with delayed implantation, gestation, parturition, and lactation during hibernation. Bears do not consume food but must rely on fat reserves during winter and give birth to one to three cubs during hibernation. In general, the length of hibernation is shorter at more southern latitudes and increases towards the north, and bears lose 20–45 % of their body weight during this time. Three types of winter dens are used by brown bears in Scandinavia: excavated anthill and soil dens (74 % of all dens), natural cavity dens (11 %), and open nest dens (15 %). Reproductive success in female brown bears is affected by the choice of den type, and females hibernating in better insulated dens have a higher probability of producing offspring. Brown bears prefer to den in forested areas that provide shelter from wind and cold temperatures, as well as at higher altitudes and areas with steeper slopes. Bears are especially sensitive to human disturbances during hibernation and prefer to den far from human infrastructure and settlements.

Introduction

Hibernation in mammals, i.e. the time period that an animal spends in a dormant or "sleeping" state, is an adaptive strategy to cope with unfavourable environmental conditions, such as winter (Nelson 1973; Nelson et al. 1973). It most commonly occurs in small mammals, such as ground squirrels, marmots, or bats, and can last from several days up to several months, depending on the species, ambient temperature, time of year, and an individual's body condition (Nelson 1973; Geiser 1998; Humphries et al. 2003). The physiology of a hibernating mammal in winter is profoundly different from its active state during the other times of the year. Hibernation is in generally characterised by physical inactivity, a reduction of physiological functions, low metabolic rate, and a reduction of the body temperature to as low as 0 °C (Barnes 1989; Geiser 2004; Friebe 2015).

Hibernating mammals do not necessarily remain torpid, i.e. inactive, throughout the entire hibernation season. Rather, hibernation usually is characterised by bouts of torpor that last several days or weeks, but are interrupted by periodic bouts with higher activity, i.e. short-term arousals. During those active bouts, the biochemical and physiological parameters return to an almost normal level, probably to recover from the physiological costs caused by metabolic depression (Prendergast et al. 2002; Humphries et al. 2003; Astaeva/Klichkhanov 2009). These time periods generally also

Bear and Human: Facets of a Multi-Layered Relationship from Past to Recent Times, with Emphasis on Northern Europe, ed. by Oliver Grimm (Turnhout: Brepols, 2023), pp. 109–120 BREPOLS PUBLISHERS 10.1484.M.TANE-EB.5.134328

are used to consume food and water, as well as to urinate and defecate (Pinter 1984; Wang 1989; Pulawa/Florant 2000; Boyles et al. 2020).

Bears formerly were not considered "true hibernators", because their body temperature does not decrease as dramatically during winter as it does in other hibernating mammals, such as ground squirrels (*Sciuridae*) (Geiser 1998; Heldmaier 2011; Tøien et al. 2011). Also, hibernating bears can "wake up" very quickly from hibernation and even leave the den when disturbed, in comparison to small hibernating mammals, that need up to several days to wake up from deep hibernation. Based on advances in our understanding of physiology and biochemistry, hibernation is now more accurately defined as comprehensive metabolic suppression rather than only based on a decline in body temperature (Carey et al. 2003; Geiser 2004). Ursids reduce their metabolism by 20–50 % during winter, and therefore are considered as true hibernators (Heldmaier et al. 2004; Heldmaier 2011). However, bears have an exceptional position among hibernating mammals, because they are the only north-temperate species with delayed implantation, gestation, parturition, and lactation during hibernation (Ramsay/Dunbrack 1986; Spady et al. 2007; Robbins et al. 2012). The physiological and biochemical processes that regulate hibernation in bears are of great interest in human medicine and thus have become an emerging field in ecological biomimicry studies (e.g. Stenvinkel et al. 2012; Berg von Linde et al. 2015; Fröbert et al. 2020).

Hibernation ecology

Depending on the climatic zone and environmental conditions, brown bears (*Ursus arctos*) can spend more than half of their life in winter dens and may hibernate between five to seven months in a given year (Friebe et al. 2001; Manchi/Swenson 2005; Bojarska/Selva 2011). In general, the length of hibernation is shorter at more southern latitudes and increases towards the north. For example, some individual bears in southern European areas, such as Croatia or Spain, may not hibernate at all (Huber/Roth 1997; Nores et al. 2010), whereas all bears hibernate in northern Europe, for example in Sweden (Friebe et al. 2001; Manchi/Swenson 2005).

Brown bears do not consume food during hibernation and therefore must build up fat reserves for the long period of caloric deprivation during winter (Hellgren 1998; López-Alfaro et al. 2013). In late summer and autumn, bears enter a physiological state called hyperphagia, which is defined as period of highly increased caloric intake and highly increased search for food. Hyperphagia can result in a caloric intake up to 20,000 kcal/day (Nelson 1987), and brown bears may add up to 40 % of their body mass in fat before hibernation (Fig. 1; Nelson 1980; Nelson et al. 1983). Activity, heart rate and body temperature start to drop slowly several weeks before den entry, and bears usually enter the den upon arrival of the first snow and when ambient temperature reaches 0 °C (Evans et al. 2016). The first demographic group of bears to start hibernating is pregnant females, followed by females with older dependent offspring and subadult bears (Friebe et al. 2001; Manchi/Swenson 2005). The demographic group that starts hibernating latest and leaves the den earliest in the spring is adult males, followed by subadult individuals and females with older dependent offspring. Females that have given birth during hibernation are the demographic group that leave the den latest (Friebe et al. 2001; Manchi/Swenson 2005). For example, pregnant females start hibernating as early as late September in Sweden and leave their den with their young as late as early May the following spring (Friebe et al. 2001; Manchi/Swenson 2005).

Bears lose 20–45 % of their body weight while in the den during hibernation. However, the amount of weight loss during winter depends on several factors, such as the duration of denning, the bear's sex and age, and the reproductive status, whether a female is solitary, pregnant, or accompanied by cubs (Nelson et al. 1973; Kingsley et al. 1983; López-Alfaro et al. 2013).

In the hibernation state, a bear's oxygen demand is reduced to approximately 25–50 % of the active state, and the respiration rate is decreased to 1–2 times per minute (Hellgren 1998; Tøien et al. 2011). The low respiratory quotient of bears during hibernation indicates a pure fat combustion, i.e. they mainly use body fat for maintaining physiological functions, while conserving lean body mass like carbohydrates and proteins (Nelson et al. 1973; Nelson 1980; Boyer/Barnes 1999). Fat serves as an efficient caloric storage medium, as it features high energy density. To regain the stored energy, fat needs to be metabolised. Burning body fat produces water and carbon dioxide; the carbon dioxide is exhaled, and the water stays in the blood to keep the animal hydrated (Nelson et al. 1973). In contrast to all other hibernating mammals, bears do not urinate during hibernation. However, azotemia (increased blood levels of nitrogen that can induce kidney failure) does not develop in hibernating bears (Stenvinkel et al. 2012). Instead, the urea production is decreased, and any urea produced is recycled and resynthesised into skeletal muscles and other body proteins, to preserve lean body mass (Nelson 1989; Harlow et al. 2001; Stenvinkel et al. 2018).

Another measure to conserve energy and adapt to the reduced respiratory rate is decreased heart rate during hibernation. The bear's heart rate can be as low as 10 beats per minute (bpm) during hibernation, compared to the heart rate of approximately 50 bpm of sleeping bears in summer (Nelson et al. 2003; Folk et al. 2008; Laske et al. 2018). Simultaneously with the lowered heart and respiratory rate, the bear's body temperature drops, but only 2–6 °C below the summer core temperature of 37–38 °C. Bears maintain this body temperature by undergoing periodic muscular shivering (French 1986; Hissa et al. 1994; Tøien et al. 2011).

Thus, compared to other hibernators, the body temperature remains above the critical values for brain and muscle activity. Continuous electroencephalogram EEG recordings of American black bears (*Ursus americanus*) during the hibernation season revealed that they are predominantly asleep but are cycling between rapid-eye-movement and non-rapid-eye-movement sleep with very few phases of wakefulness (Folk et al. 2008; Rogers et al. 2020). Nevertheless, periodical short-term bouts of activity with frequent, small movements have been reported during hibernation (Friebe et al. 2013; 2014). The relatively high body temperature enables bears to wake up spontaneously from hibernation, and they are then capable of rapid responses with high mobility and endurance (Evans et al. 2012).

Although bears continue to produce some feces during hibernation, they do not defecate, which again is in contrast with all other hibernating mammals. Therefore, the feces accumulate in the intestine. The intestinal walls absorb water from the feces and, thus, a dry and hard fecal plug develops. Bears also groom during active hibernation periods, and some of these materials are swallowed during the self-grooming process, such as plant materials, hair, and skin. These indigestible materials pass through the digestive tract and become part of the fecal plug (Rogers 1981). Additionally, hair and claws from cubs can sometimes be found in fecal plugs, which indicates that female bears consume the body of cubs that died in the den (A. Friebe, personal observation). This fecal plug is the first scat produced after hibernation and is commonly found close to den sites (A. Friebe, personal observation).

Pregnancy and birth during hibernation

Brown bears in Scandinavia mate during spring and early summer, with the peak of the mating season around the 1st of June (Steyaert et al. 2012). Brown bears exhibit delayed implantation, i.e. the embryo (blastocyst) does not implant immediately, but is maintained free-floating in the uterus in a state of suspended dormancy for four to five months until implantation occurs in November/December, after the onset of hibernation (Spady et al. 2007; Friebe et al. 2014).

For successful implantation and reproduction, females require a minimum amount of body mass and fat (~19 %) prior to hibernation. This determines whether the implantation of blastocysts happens or not (Elowe/Dodge 1989; Atkinson/Ramsay 1995; López-Alfaro et al. 2013). Gestation in bears lasts approximately 56 days (Friebe et al. 2013). This short period limits the energetic costs of reproduction by truncating embryonic development, which in turn reduces the size of offspring and thus the initial costs of lactation. Brown bears commonly give birth to one to three cubs, which are born in the den in January/February (Zedrosser et al. 2011; Friebe et al. 2014). Bear cubs are naked at birth and weigh about 300–500 g (Robbins et al. 2012). The milk of bears is very rich in protein and fat (Derocher et al. 1993; McDonald/Fuller 2005; López-Alfaro et al. 2013), and brown bear cubs in Sweden weigh approximately 5 kg when leaving the den for the first time in late April to early May (A. Friebe, personal observation).

Den types

Dens are an essential part of brown bear ecology and reproduction, because pregnant females give birth to cubs while hibernating in their dens during winter. Brown bears normally hibernate alone in their dens, except for females that give birth or that are still accompanied by older dependent offspring. In general, most brown bears hibernate in a new den every winter and there is little or no reuse of the same den over successive years (Ciarniello et al. 2005; Elfström/Swenson 2009).

The main functions of a den are reduction of energy loss during winter, as well as protection against disturbance from conspecifics or other species, including humans (Petram et al. 2004; Sahlén et al. 2011; Shiratsuru et al. 2020). The construction of the winter den seems to be an innate behaviour. Cubs of the year that had lost their mother and thus never had the possibility to learn how to construct a den, have built dens and successfully hibernated there on their own (Swenson et al. 1998). However, bears certainly gain experience in building dens and the construction improves over the years (Petram et al. 2004; González-Bernardo et al. 2020). Several studies have shown that den construction and the habitat where a den is located affect individual fitness. The insulation properties of snow contribute to constant temperature and additionally decrease energy costs for the bear (Nelson et al. 1983; Servheen/Klaver 1983; Elfström et al. 2008).

Bear dens are normally small in relation to the size of the bear. They often have an inner radius less than 1 m and a small entrance (A. Friebe, unpublished data), which can be completely covered with snow during winter. The snow seals the inner part of the den effectively from the weather conditions on the outside, contributing to increased thermal insulation (Craighead/Craighead 1972). To improve insulation properties, bears normally gather vegetation as insulating bedding materials, which helps to minimise energy loss (Reynolds et al. 1976; Tietje/Ruff 1980).

Generally, three types of dens are used by brown bears in Scandinavia: excavated anthill and soil dens (comprising 74 % of all dens; A. Friebe, unpublished data), natural cavity dens (11 %), and open nest dens (15 %; see Fig. 2). Excavated dens are preferred in many landscapes, including Scandinavia (Linnell et al. 2000). The space around an animal's body is kept tight to increase energy efficiency in excavated dens, which likely decreases the energetic costs of hibernation (Tietje/Ruff 1980; Shiratsuru et al. 2020). In comparison, natural cavity dens cannot be adjusted, and a suitable cavity may be difficult to find. In Scandinavia, the excavated anthill den is the most widely used den type, followed by dens dug in soil (Manchi/Swenson 2005). An anthill den is excavated in an abandoned ant mound that is overgrown with vegetation. The main difference between an anthill den and the other den types is the composition of the walls. The walls of anthill dens are composed by loose organic material interspersed with roots that provide stability and create an additional air layer for insulation. In comparison, soil dens usually miss this insulating air layer and may also contain more moisture (Schoen et al. 1987). Anthill dens are significantly more often used by females than by males, likely due to the higher degree of insulation compared to other den types, which is especially important for pregnant females (Elfström/Swenson 2009). Reproductive success in female brown bears is affected by the choice of den type, and female brown bears hibernating in better insulated dens have a higher probability of producing offspring (Klenzendorf et al. 2002). Nowack (2015) observed in Sweden that females hibernating and giving birth in anthill dens on average produced larger litters and had more male offspring, compared to females that hibernated and gave birth in other den types.

Hibernation in natural cavity dens is comparatively rare in Scandinavia, but more common in southern European populations, such as in Slovenia and Croatia (Huber/Roth 1997; Petram et al. 2004). Natural cavities are less insulated than excavated dens, however, they do not require as much energetic investment prior to use.

The least insulated den type is open dens, often also referred to as nest dens or basket dens. These dens usually contain only a thick layer of bedding material and are commonly placed close to the base of a tree or rocks. The construction lacks walls or a roof, and the only insulation is provided by the bedding material and the snow that covers the hibernating bear during winter (Martorello/Pelton 2003; Seryodkin et al. 2003; Elfström et al. 2008). These types of dens primarily are used by large adult males in Scandinavia, which also makes them more vulnerable to disturbance during hibernation (Elfström/Swenson 2009; Sahlén et al. 2015). Males have a larger body and more fat reserves than females and smaller bears and are therefore probably better suited to bear the energetic costs of a den without protective walls or roof. However, bears using open dens hibernate for a shorter period compared to bears using other den types, which indicates that the open structure probably is less efficient when it comes to thermal insulation and energy loss, especially in periods where there is little or no snow (Elfström/Swenson 2009). In southern European countries with less severe winters, also female bears use open dens more frequently (González-Bernardo et al. 2020).

Denning habitat

Numerous studies have described the denning habitats of brown bears worldwide (e.g. Linnell et al. 2000; Ciarniello et al. 2005; Elfström/Swenson 2009; Sahlén et al. 2011; Smereka et al. 2017; Mangipane et al. 2018; González-Bernardo et al. 2020). In general, the habitat surrounding a den site is highly variable and its selection depends on the available habitat types within a bear's home range. The specific ecological factors affecting a bear's den site selection are local climatic and habitat characteristics, as well as ground cover and terrain characteristics. Bears seem to select denning locations carefully in good time before actual hibernation. For example, female bears in Sweden visit the area where they finally build their dens more than once a month during the active season, probably because a suitable and safe den site is important for the survival of the cubs (Friebe et al. 2001; Sahlén et al. 2011). A study of denning behaviour in Sweden has shown that bears that had not visited their denning area prior to hibernation were more likely to abandon their den due to disturbances (Sahlén et al. 2015).

Brown bears generally prefer to den in forested areas that provide shelter from wind and cold temperatures, as well as at higher altitudes and in areas with steeper slopes (Ciarniello et al. 2005; Elfström et al. 2008; Libal et al. 2011). Dens are better insulated at higher altitudes due to higher snow cover, which has a positive impact on the energetic efficiency during hibernation (Libal et al. 2011). Den construction also seems to be easier on a slope compared to flat ground, and the den is likely better protected from flooding due to rain or melting snow. Additionally, a den on a steep slope probably provides better protection against disturbance, as it is more difficult to access (Haroldson et al. 2002).

Brown bears are sensitive to disturbances in the denning area and during hibernation, especially to human activities during the time of the initiation of hibernation. This is likely also an important reason why bears in general choose den sites far from infrastructure and human settlements (Swenson et al. 1997; Sahlen et al. 2015). In addition, a thick vegetation cover that favours the concealment of the den entrance seems to be an important factor to avoid human-caused disturbance (Elfström et al. 2008; Ordiz et al. 2012; Eriksen et al. 2018). Bears may abandon their winter dens if disturbed. Den abandonment rates are high in Sweden, on average 22 % of dens are abandoned on an annual basis, and most abandonments occur during the start of hibernation (Sahlen et al. 2015). Approaching dens on foot has been documented to cause den abandonment (Goodrich/Berger 1994; Linnell et al. 2000; Evans et al. 2012); other causes seem especially related to forestry activities carried out with heavy harvester vehicles during winter or proximity to roads that are cleared from snow on a regular basis (Elfström et al. 2008; Elfström/Swenson 2009). Den abandonment carries a high metabolic cost. Body temperature and heart rate increase when bears are forced to change their den sites, and they require about two to three weeks to return to the physiological hibernation level after disturbance (Evans et al. 2016). A study on American black bears (*U. americanus*) showed that bears that changed dens during winter had a greater weight loss than undisturbed bears (Tietje/Ruff 1980). In addition, several studies have demonstrated that disturbance of pregnant female brown bears during winter can lower their reproductive success, especially if disturbance occurs during the middle or end of the hibernations season (Smith 1986; Elowe/Dodge 1989; Goodrich/Berger 1994; Swenson et al. 1997). Mid-winter or late winter den abandonments probably cause an increased energy cost, as the bear is deeper in hibernation and the snow cover makes locating new suitable dens difficult (Evans et al. 2012).

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Fig. 1. Researchers measure the body fat composition of a sedated five-year-old male brown bear after hibernation. Bioelectrical Impedance Analysis is used, i.e. a very weak electric current measures the body fat content of an individual (photo A. Friebe).


A


B

Fig. 2. Den types used by brown bears in Scandinavia. a: Excavated ant hill den; b: Entrance to a natural rock cavity den; c: Open nest den (photos A. Friebe).