Hibernation in Black Bears: Independence of Metabolic Suppression from Body Temperature

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Black bears hibernate for 5 to 7 months a year and, during this time, do not eat, drink, urinate, or defecate. We measured metabolic rate and body temperature in hibernating black bears and found that they suppress metabolism to 25% of basal rates while regulating body temperature from 30° to 36°C, in multiday cycles. Heart rates were reduced from 55 to as few as 9 beats per minute, with profound sinus arrhythmia. After returning to normal body temperature and emerging from dens, bears maintained a reduced metabolic rate for up to 3 weeks. The pronounced reduction and delayed recovery of metabolic rate in hibernating bears suggest that the majority of metabolic suppression during hibernation is independent of lowered body temperature.

Man
amalian hibernation is well characterized in species such as marmots, ground squirrels, bats, and dasyurid marsupials (1). These small (~5 kg) hibernators undergo regulated decreases in core body temperature (Tb) to near or below freezing during torpor bouts that last days to weeks (2–5). Torpor is periodically interrupted by arousals to normothermia (35° to 38°C) that usually last for less than one day (6, 7). During torpor, metabolic rates of small hibernators decrease to 2 to 5% of basal metabolic rate (BMR) (8–10). However, the relative contributions of temperature-dependent (described by Qt, a rate coefficient for a 10°C change in Tb) and temperature-independent mechanisms of metabolic suppression depend on the size of animals and stage of entry into torpor (11). In contrast, the relations between Tb and metabolism in the large hibernators of the bear family Ursidae have remained unknown because technical limitations have prevented continuous, long-term monitoring in these 30 to 200 kg or larger animals. We used telemetry and respirometry to record Tb, metabolic rates, and heartbeat patterns of black bears, Ursus americanus, through their hibernation and post-hibernation recovery.

Black bears were nuisance animals captured in south-central or interior Alaska in late autumn 3 different years and transported to facilities at the Institute of Arctic Biology, University of Alaska Fairbanks. Radio transmitters for Tb and electromyogram (EMG)/electrocardiogram (ECG) were surgically implanted (12), and animals were transferred to outdoor enclosures in an isolated wooded area. Bears hibernated inside 0.8 m3 wooden nest boxes with straw for bedding and equipped with infrared cameras, activity detectors, and telemetry-receiving antennas. Food and water were not provided. Air was continuously collected from the closed hibernacula to record O2 consumption (a measure of metabolic rate). After
the spontaneous emergence of bears from their dens in spring, Tb recordings were continued, and minimum metabolism after 24 hours of fasting was determined every four nights for 1 month.

Hibernating black bears kept a curled posture (Fig. 1), similar to that previously described (13), that facilitates heat preservation and water economy. Animals changed position twice a day to once every 2 days, when they stood, occasionally groomed, and rearranged bedding material. Tb, which is normally 37° to 38°C, decreased to average levels of 33.0°C (31.7° to 34.0°C, n = 4 bears) in mid hibernation (defined as 21 January to 20 February). Minimum Tb was 30.4°C (29.4° to 32.5°C, n = 4 bears). Before emergence in mid-April, Tb gradually increased over 2 to 4 weeks to 36° to 37°C (Fig. 2). Hibernating bears did not show spontaneous, periodical arousals to normothermic levels of Tb, as do small hibernators. This may be because Tb did not decrease below 30°C, a level that may reflect a threshold below which neural deficits, such as loss of neuronal structure (14), begin to occur that require regular returns to high Tb. Hibernating fat-tailed dwarf lemurs that are regularly warmed by the sun to above 30°C also do not show spontaneous arousals (15). Diurnal rhythms in Tb also were not evident in mid-winter; instead, there were unexpected 1.6- to 7.3-day cycles of Tb with 2° to 6°C amplitude. Cycles were shortest during coldest conditions and most regular in the smallest bears (Fig. 2B, top). Tb was higher and more stable in free-ranging black bears studied in Wyoming and Colorado, which could be due to milder ambient temperatures (16). In spring when conditions were warmer in our study, multi-day Tb cycles were also less evident (Fig. 2). High-amplitude multi-day cycles of Tb may be a feature of thermoregulation, when gradients between Tb and environmental temperatures are large. Early studies on hibernating black bears in Alaska or arctic Canada reported Tb of 32° to 35°C (17, 18) and could not reveal any multi-day patterns because of intermittent measurements.

The Tb of a female bear remained at normothermic levels through the end of January (Fig. 2C, bottom), when she gave birth to a 243-g cub that died because of a congenital diaphragmatic hernia (12). Afterwards, her Tb became more variable and decreased toward levels of other hibernating bears. High and stable Tb patterns occurred during pregnancy in a European brown bear (19). Bears have delayed implantation, and pregnancy starts in late November after denning (20). We suggest that low and fluctuating Tb may not be favorable for embryonic development, and, thus, hibernating bears maintain normothermia while pregnant.

O2 consumption in hibernating bears varied from minimum levels of 0.06 ml g⁻¹ h⁻¹ sustained for as much as one day to brief peaks of >0.35 ml g⁻¹ h⁻¹ accompanied by movement (Fig. 3A). Tb declined when metabolism and shivering were minimal and increased during intense shivering and heightened metabolism. This varying pattern of endothermic thermoregulation can explain the wide range in metabolic rates found in the only previous metabolic study of hibernating bears (18). Predicted BMR for carnivores (21, 22) averages 0.228 ml g⁻¹ h⁻¹. Here, we show BMR (defined as overnight resting and fasting metabolic rate measured 1 month after emergence from hibernation) was 0.276 ml g⁻¹ h⁻¹ (range from 0.267 to 0.285 ml g⁻¹ h⁻¹, n = 3 bears); the mean Tb was 37.8°C. A comparison of the changes in metabolism and corresponding Tb in three nonpregnant bears (Fig. 3B) revealed that during mid-hibernation, when Tb was 32.2°C (30.9° to 33.6°C), minimum metabolic rate (12) was 0.069 (0.056 to 0.086) ml g⁻¹ h⁻¹, or 24.9% of BMR. A reduction to only 0.179 ml g⁻¹ h⁻¹ (64.9% of BMR) would be expected because of

![Fig. 1. Black bear hibernating in its artificial den.](image-url)
direct effects of the 5.5°C decrease in \( T_b \), when a \( Q_{10} \) of 2.2 is assumed (1). When bears emerged from dens in mid-April with \( T_b \) of 36.6°C (36.1° to 37.4°C), metabolic rate averaged 0.149 (0.127 to 0.170) ml g\(^{-1}\) h\(^{-1}\) or 52.9% of BMR and stabilized at BMR levels after 2 to 3 weeks (Fig. 3B). Bears began feeding over this period, and their return to BMR may in part involve resumption of a full capacity of the digestive system. In alpine marmots, hibernation is accompanied by a 70% decrease in mass of stomach and intestines, which was reversed in spring (23). Hypothyroidism of hypothalamic origin reported in hibernating black bears (24) may also contribute to metabolic suppression.

Decreased metabolism in hibernating bears reduces the need for transport of blood gases and nutrients. Heart rate (HR) of three non-pregnant bears in mid-hibernation decreased from summer resting levels (Fig. 4A) of 55 (44.5 to 63.7) beats per min to 14.4 (8.9 to 20.1) beats per min, which is similar to minima of 8 to 12 beats per min in a captive hibernating black bear reported by Folk (25). Hibernating bears showed a marked variation in inter-beat intervals through the breathing cycle, encompassing a profound sinus arrhythmia (Fig. 4, B and C). Typically, a group of rapid heartbeats occurred as inspiration ended followed by interbeat intervals of 8 to 20 s after expiration. Bursts of shivering were synchronous with rapid heartbeats and breathing (Fig. 4C). At emergence, sinus arrhythmia was less pronounced, and average resting HR was 23.7 (16.1 to 31.1) beats per min. HR during hibernation was reduced to 26.2% and at emergence was 43.0% of summer levels. Similar reductions in HR during hibernation with a transition at emergence have been observed in grizzly bears (26).

Black bears share attributes of hibernation with small hibernators, including a decrease in metabolic rate, lack of diurnal \( T_b \) patterns, reduced HR, and surviving without feeding or drinking for approximately half a year. However, \( T_b \) in hibernating bears is far higher than in small hibernators, which is in part due to the estimated lower levels of thermal conductance in bears (approximately 20%) as compared with ground squirrels [supporting online material (SOM) text and table S1] (10). Whereas smaller hibernators
show long torpor bouts interrupted by regular arousal episodes, black bears in Alaska exhibit distinct cyclic non-diurnal $T_h$ patterns. Bear metabolism is reduced by 53% from BMR, even when $T_h$ has returned to normothermal levels. These observations expand the phenotype of mammalian hibernation that occurs in diverse animals over body mass ranges from 0.005 to 200 kg. Insights into how hibernating bears achieve and cope with these reductions in energy need and $T_h$, as well as conservation of muscle (27, 28) and bone mass (29) despite prolonged seasonal inactivity and disuse, could lead to the development of novel clinical therapies. Current molecular and genetic approaches (28, 30) in combination with better physiological knowledge can increase our understanding of the regulation of hibernation in small and large hibernators and their evolution.

References and Notes
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LysM-Type Mycorrhizal Receptor Recruited for Rhizobium Symbiosis in Nonlegume Parasponia

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Rhizobium–root nodule symbiosis is generally considered to be unique for legumes. However, there is one exception, and that is Parasponia. In this nonlegume, the rhizobial nodule symbiosis evolved independently and is, as in legumes, induced by rhizobium Nod factors. We used Parasponia andersoni to identify genetic constraints underlying evolution of Nod factor signaling. Part of the signaling cascade, downstream of Nod factor perception, has been recruited from the more-ancient arbuscular endomycorrhizal symbiosis. However, legume Nod factor receptors that activate this common signaling pathway are not essential for arbuscular endomycorrhizae. Here, we show that in Parasponia a single Nod factor–like receptor is indispensable for both symbiotic interactions. Therefore, we conclude that the Nod factor perception mechanism also is recruited from the widespread endomycorrhizal symbiosis.

The rhizobial nodule symbiosis is widespread in the legume family (Fabaceae). Although this nitrogen-fixing symbiosis provides the plant with a major advantage, it is in principle restricted to a single family, and it is a major challenge for future agriculture to transplant this symbiosis to nonlegumes (1). The genus Parasponia could provide a key to this, because it encompasses the only nonlegume species that acquired also the rhizobium symbiosis (2, 3), where “rhizobium” refers to all species and genera that form nodules on legumes. Parasponia comprises several tropical tree species and belongs to Celtidaceae (4). Celtidaceae (order Rosales) and Fabaceae (order Fabales) are only remotely related. Further, not a single species phylogenetically positioned between Parasponia and Fabaceae is able to establish such rhizobium symbiosis. Hence, in all probability the common ancestor of present Parasponia species gained the rhizobium-nodule symbiosis independent from legumes. Therefore, a legume-Parasponia comparison provides a key to identifying genetic constraints underlying this symbiosis. In this study, we focused on parallel evolution of the recognition of the rhizobial signal that starts the symbiotic interaction, the Nod factor.

Parasponia makes lateral rootlike nodules that are associated with cell divisions in the root cortex (5). Rhizobium enters the Parasponia root intercellularly and becomes imbedded in a dense matrix. Rhizobium obtains an intracellular lifestyle when it reaches a nodule primordium. There, cortical cells are infected via threadlike structures that remain connected to the plasma membrane. These so-called fixation threads branch, fill up the cells, and provide a niche to rhizobia to fix nitrogen (5). This is illustrated by the expression, in these threads, of the rhizobium nifH gene that encodes one of the subunits of nitrogenase (fig. S1). In contrast, rhizobia enter most legume roots via root hair–based intracellular infection threads, and the bacteria are released in nodule cells as membrane-surrounded nitrogen-fixing organelle-like structures (symbiosomes) that harbor a single or only a few bacteria. Legume nodules are considered to be genuine organs with a unique ontogeny (6). The fact that the Rhizobium symbiosis is very common in 65-million-year-old Fabaceae led to the conclusion that the symbiotic

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