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Quick guide

Ground squirrels

Rafael Dai Pra[1,2,3], Sviatoslav N. Bagriantsev[1,*], and Elena O. Gracheva[1,2,3,*]

What are ground squirrels? Ground squirrels are mammals that belong to the rodent family Sciuridae, which also includes chipmunks, marmots, and prairie dogs (Figure 1). Ground squirrels are close relatives of the grey tree squirrels commonly found in the streets and parks of many cities across the US. As the term 'ground squirrel' suggests, they live in underground burrows, where they build complex tunnel structures that can be one to two meters deep. Ground squirrels are thought to have originated in Siberia, from where they radiated to Europe, North America, and Asia (Figure 1).

What is so special about biological economy in ground squirrels? Animal life history determines how body energy is redistributed between growth, survival, maintenance, and reproduction. Ground squirrels are one of the most resilient animals to environmental challenges. Every year they survive up to 7 months in the cold without food and water (Figure 2). To endure prolonged periods of resource shortage and cold temperature, ground squirrels undergo hibernation. During hibernation, animals cycle between two major physiological states, torpor and interbout arousal. Torpor is a state of immobility and reduced metabolism when ground squirrels have decreased body temperature (2–4°C), heart rate (2–3 beats per minute), and breathing rate (2–3 breaths per minute). During interbout arousal, ground squirrels temporarily return to an active-like state, partially restoring bodily functions for 24–48 hours. Although the physiological significance of interbout arousal remains unknown, it appears to be an essential physiological state of hibernation. The remarkable flexibility of ground squirrels suggests the presence of molecular and cellular adaptations in all major organs and systems. Whereas the mechanisms that underlie this phenomenon are poorly understood, recent advances have begun to shed light on some of the key features of the biological economy of hibernation.

How do ground squirrels survive hypothermia and cold during hibernation? Prolonged cold exposure and hypothermia are the major challenges presented to animals during cold winter (Figure 2). It poses the danger of tremendous energy expenditure, pain, and damage to cells and tissues. Ground squirrels enter torpor to avoid these difficulties. During torpor, all cells and organs experience a massive functional shut-down to conserve energy. However, ground squirrels can restore all bodily functions within just a few hours upon arousal from hibernation. This fact suggests that during torpor cells exist in a semi-functional state, often referred to as 'suspended animation'. Ground squirrels also use several different cellular and molecular adaptations to tolerate hypothermia and adapt to cold. These adaptations include decreased cold sensitivity of the TRPM8 receptor in the peripheral somatosensory system and of the CNGA3 ion channel in the brain, decreased activity of voltage-gated sodium channels that allow neurons to communicate with each other, and reduced sensitivity to highly reactive oxygen species to prevent cellular damage. All these physiological changes are part of the mechanism that keeps hibernating cells in a semi-active state, supports hypothermia, promotes long-term survival in cold environments, and enables fast restoration of cellular functions upon emergence from hibernation.

How do ground squirrels survive without water and food for up to 8 months? Most mammals cannot withstand water deprivation for more than several days. In contrast, hibernating ground squirrels do not drink for up to 8 months of the year (Figure 2). Despite extreme water deprivation, ground squirrels do not develop chronic kidney pathologies or experience physiological signs of dehydration. Water deprivation normally increases serum osmolality and leads to thirst. Remarkably, despite not having access to water, torpid ground squirrels have decreased serum osmolality. Whether this occurs due to general changes in metabolism, or via

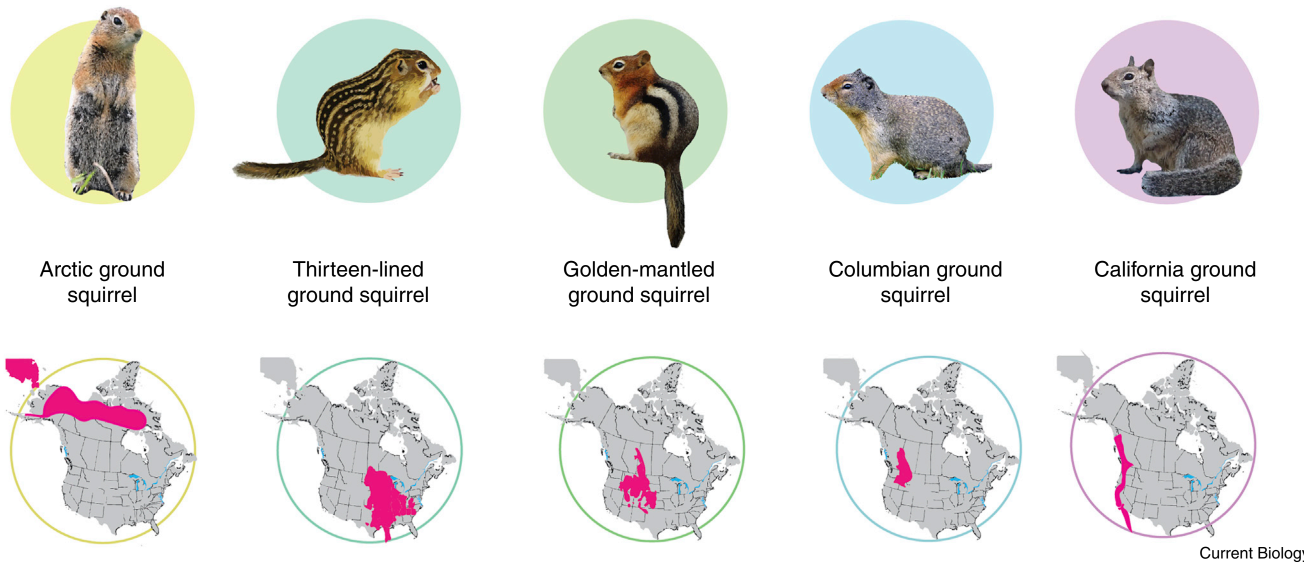

Figure 1. Hibernating ground squirrels and species ranges in USA and Canada.
Ground squirrels have a wide geographical distribution. They are thought to have radiated from Siberia to Europe, North America, and Asia. In USA and Canada, ground squirrels can be found in most states, covering a wide range of geographical and climatic habitats. Arctic ground squirrel image from Alan Schmierer/Flickr (CC BY 1.0). Thirteen-lined ground squirrel image courtesy of the Gracheva laboratory. Golden-mantled ground squirrel image from Smatric/wikicommons (CC BY-SA 4.0). Columbian ground squirrel image from David Hill (CC BY 2.0). California ground squirrel image from S. Rae/Flickr (CC BY 2.0).

reversible sequestration of solutes from the extracellular fluid, remains to be determined. During interbout arousal, when squirrels return to an active-like state, serum osmolarity returns to normal, yet squirrels exhibit negligible thirst drive. Such a remarkable resistance to dehydration persists throughout the entire hibernation period. Although the physiological mechanism of this process is unknown, the suppression of water-seeking behavior is essential for survival, because it allows animals to remain in the safety of the underground burrow.

In most mammals, cold exposure robustly increases feeding. Despite the prolonged cold exposure during winter, ground squirrels ingest little to no food during hibernation. To survive several months without eating, ground squirrels double or triple their body weight by increasing their food intake and fat accumulation during summer months. The accumulated fat constitutes the main energy resource for the hibernation season. The mechanisms by which ground squirrels slow down metabolism and rapidly gain weight are not fully elucidated.

When is the reproduction season of ground squirrels? Ground squirrels are seasonal breeders and typically reproduce once a year. They reproduce almost immediately after leaving their underground burrows after hibernation is over. That mating happens after hibernation suggests that the reproductive axis undergoes activation during hibernation. This strategy provides the benefit of ‘first male advantage’ and may help increase the survival of both the offspring and parents during spring, when temperatures are favorable and food is plentiful. Depending on the species, gestation in ground squirrels is ~30 days, and lactation ~27–30 days. Therefore, timing is critical for the offspring and parents to thrive and start building up fat to prepare for the next hibernation season. After offspring are born, ground squirrels undergo testicular regression and follicular development arrest. The shutdown of the reproductive axis is thought to facilitate the accumulation of fat and set up an optimal economic strategy that allocates resources to body maintenance and survival, away from reproduction. Furthermore, as maintenance of the reproductive system is an energy-demanding process, gonadal regression may help to conserve resources during hibernation.

What can we learn from hibernating ground squirrels? Studies of the unique physiology of hibernating ground squirrels began in the 18th century and led to important discoveries. Brown adipose tissue, originally named the ‘hibernating gland’, was described and characterized in hibernators. Fundamental comparative studies on the function of thyroid and adrenal glands, as well as the reproductive system, were conducted in ground squirrels at the beginning of the 19th century. More recently, ground squirrels have been used to study other organs and systems. For example, because these animals spend most of the year in the dark without experiencing deterioration of the visual system, they are also studied to understand cone photoreceptor-driven vision.

Ground squirrels employ a collection of flexible adaptations that allow them to thrive in inhospitable environments. By studying these reversible adaptive changes, we can reveal general principles of cellular maintenance under extreme conditions and understand how life in mammals can persist under prolonged periods of hypothermia, cold exposure, starvation, and dehydration. Additionally, elucidation of the mechanisms these animals use to cope with adverse conditions will pave the way to develop new therapeutic venues

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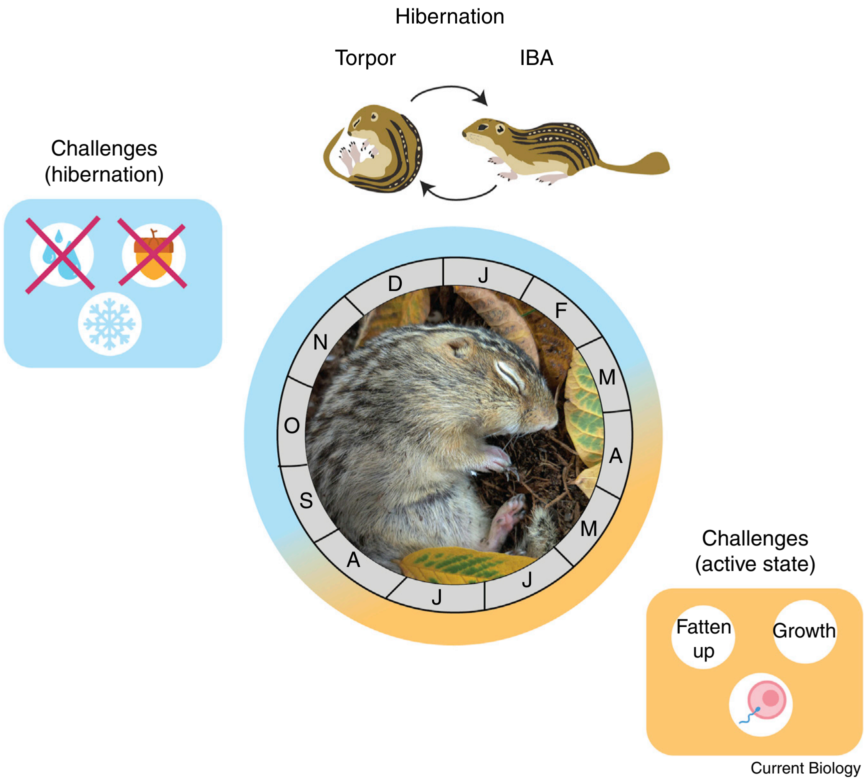

Figure 2. Challenges to the biological economy of hibernating ground squirrels.
During hibernation (September to April), ground squirrels cycle between torpid and interbout arousal (IBA) states, facing the challenge of adapting their physiology to prolonged hypothermia and the lack of food and water. Upon exiting hibernation, ground squirrels reproduce, grow and accumulate fat from May to August in preparation for the next hibernation season.

for treatment and prevention of obesity, nerve injury, muscle atrophy, and other conditions. In addition, it may improve the use of therapeutic hypothermia in emergency medicine and aid in the development of approaches to induce hibernation in humans, such as to endure prolonged space flights.

Where can I find out more?

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Quick guide

Storage roots

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What are storage roots? Some plants bear belowground storage organs. However, not all of these are storage roots. The swollen hypocotyls of beet, corms of ensete and taro, and potato tubers are actually stems, while other crops such as carrot, sweet potato and cassava develop true storage roots. A storage root is a specialized underground organ that undergoes modifications during its development to store nutrients. Many storage roots are used as food, and several that accumulate high levels of carbohydrates, such as sweet potato and cassava, are staple crops important for food security. Although the evolutionary origin of storage roots is not clearly defined, the trait appears to have evolved multiple times in angiosperms. For example, phylogenetic analyses suggest that storage roots could have been gained and lost at least 10 times in the morning glories (Convolvulaceae) and many more times in the Passifloraceae.

How do storage roots develop? Storage roots develop through secondary growth, the process by which stems, roots and hypocotyls expand in girth. Secondary growth is the consequence of the accumulation of vascular tissues (xylem/wood and phloem/bark) and is mediated by the cambium, a pool of stem cells that resemble empty cylinders and appear as empty circles when seen in 2D transversal sections. Cambium cells are programmed to give rise, exclusively, to the xylem and phloem. The xylem develops towards the inside of the vasculature system and the phloem towards the outer part of the vasculature system (Figure 1A).

In general, both xylem and phloem are composed of many thick and rigid transporting cells as well as a few parenchyma cells, which are soft and swollen and act as carbohydrate stores (Figure 1B). However, a clear trait that differentiates storage roots