Scientific Reports in Life Sciences 6 (4): 101-108

DOI: https://doi.org/10.5281/zenodo.17702009

Scientific reports in life sciences

http://www.scientific-reports.com

From silence to recall: cognitive persistence and adaptation during hibernation in small mammals

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Received: 22 September 2025 / Revised: 05 November 2025/ Accepted: 09 November 2025/ Published online: 06 December 2025.
How to cite: Naderi, M. (2025). From silence to recall: cognitive persistence and adaptation during hibernation in small mammals, Scientific Reports in Life Sciences 6(4), 101-108. **DOI:** https://doi.org/10.5281/zenodo.17702009

Abstract

Small mammals, particularly those living in complex arboreal and terrestrial environments, rely on advanced spatial and social memory, yet they face extreme cognitive challenges during hibernation and torpor. This review synthesizes breakthrough studies from recent years on how memory persists, degrades, or is restructured in hibernators. Topics include spatial mapping, olfactory and social recognition, molecular neuroprotection, ecological drivers, and comparative perspectives across rodents, bats, and other taxa. I identify high-impact gaps, highlight the transformative potential of integrative field-genomic approaches, and advocate for comparative, cross-taxa studies to resolve outstanding paradoxes in neuroecology.

Keywords: Olfactory Memory, Rodents, Cognition, Hibernation, Neuroecology

Introduction

Hibernation is a profound physiological state characterized by prolonged periods of metabolic depression, reduced body temperature, and suppressed neural activity. These seasonal bouts of torpor allow many small mammals—particularly rodents and bats—to survive extreme fluctuations in resource availability and climatic conditions. Although hibernation is typically viewed as an energy-conservation strategy, it also affects neural stability, synaptic architecture, and cognitive processes, raising important questions about how animals preserve memory across extended dormant periods. Animal cognition research has made great strides in recent decades, demonstrating that even small mammals possess sophisticated memory systems matching their ecological and social complexity. In particular, the ability to encode, consolidate, and recall spatial and social information is pivotal for survival, resource management, and reproduction in fluctuating environments (Adolphs, 2009). Among small mammals, forest rodents—such as dormice (*Glis glis*), tree squirrels (*Sciurus* spp.), and chipmunks (*Tamias* spp.)—have emerged as model systems for studying spatial memory, owing to their reliance on three-dimensional navigation in arboreal habitats (Sharma et al., 2010). Yet, other species like ground squirrels (*Spermophilus citellus*) and marmots (*Marmota* spp.), along with fossorial species and even bats, also exhibit remarkable memory skills adapted to their niches (Mateo & Johnston, 2000; Millesi et al., 2001). We know that hibernation significantly increases survival and alters life history trajectories across mammals, with hibernators showing markedly slower life histories than non-hibernators (Turbill et al., 2011). However, a unique and unresolved paradox in cognitive physiology centers on memory persistence during hibernation and prolonged torpor. Many small mammals enter states of near-complete metabolic suppression for months, leading to drastic reductions in brain activity, synaptic signaling, and cerebral perfusion (Sonntag & Arendt, 2019; Drew et al., 2023). Classic neurobiology suggests such conditions should severely disrupt or erase memory traces, particularly those underpinning critical ecological behaviours. However, empirical research in the last decade has revealed a startling diversity of outcomes: some species maintain strong spatial recall and social recognition after torpor, while others show marked deficits, especially in laboratory learning paradigms (Millesi et al., 2001; Henke-von der Malsburg et al., 2023; Weltzin et al., 2006). Notably, some classic studies—such as those on Alpine marmots—showed no detectable memory loss, even in tasks learned months before hibernation (Clemens et al., 2009). Spatial memory is especially challenged in environments with complex vertical structures, ephemeral resources, and shifting predation risks. For example, dormice and tree squirrels must accurately recall the location of food caches and nests throughout active and dormant seasons (Wilkinson et al., 2017; Millesi et al., 2001). The ability to recover cached food, which may be hidden months earlier, requires long-term memory encoding and retrieval, robust to seasonal disturbances and inactivity. Field studies using radio-tracking, GPS telemetry, and RFID have demonstrated astonishing accuracy in cache recovery, even after hibernation (Bieber et al., 2021). Social memory is equally vital. Recognition of kin and conspecifics, mate choice, territorial defense, and avoidance of inbreeding rely heavily on olfactory and acoustic cues in many small mammals (Mateo & Johnston, 2000; Bullmann et al., 2019; Sharma et al., 2010). Chemical communication via pheromones and scent marks is particularly important in arboreal rodents and ground squirrels, acting as a “memory substrate” for social interactions even during dormancy (Hurst & Beynon, 2008). Despite this, few studies have rigorously tested the stability of individual-specific scent profiles or the persistence of vocal signatures over hibernation and deep torpor. Neuroscientific investigations have revealed that hibernation induces profound changes in cellular and synaptic architecture. In many species, brain activity drops to fractions of baseline rates, and neurons undergo protective modifications to preserve function and minimize injury from repeated cooling and rewarming cycles (Sonntag & Arendt, 2019; Rial et al., 2010). The hippocampus, which governs spatial and contextual memory, exhibits cyclic restructuring and sometimes "rejuvenation" after arousal, which can paradoxically enhance specific learning abilities post-hibernation (Weltzin et al., 2006). Molecular studies highlight the upregulation of heat-shock proteins, oxidative stress buffers, and neuroprotective gene networks, such as those involving circadian rhythm and synaptic plasticity loci (Drew et al., 2023; Power et al., 2023). There is significant interspecies and inter-individual variation in memory retention after hibernation. Studies on ground squirrels (*Spermophilus citellus*) show retention of social recognition but variable success in maze learning and spatial tasks (Millesi et al., 2001; Mateo & Johnston, 2000). Mouse lemurs, a hibernating primate group, display sex-dependent memory resilience and persistent object recognition abilities, even as some types of recall falter (Henke-von der Malsburg et al., 2023). Bats, perhaps the most extreme hibernators, show nearly complete preservation of memory for learned foraging locations and conspecifics, likely reflecting lineage-specific adaptations (Ruczynski et al., 2011). Environmental drivers such as food abundance, mast seed cycles, climate variability, and predation risk play essential roles in shaping both the need for and outcomes of cognitive resilience. For instance, years of mast failure in European forests correlate with delayed or altered hibernation onset in edible dormice, which must adjust memory strategies for fluctuating food economies (Ruf & Bieber, 2023; Bieber et al., 2021). Microhabitat structure, soil and ambient temperature, body mass, and arousal frequency all interact to influence post-hibernation cognitive outcomes. Modern biologging and ecological monitoring now allow the integration of daily activity patterns, torpor depths, and behavioral performance metrics—providing real-world context to laboratory and genomic findings (Bullmann et al., 2019; Bieber et al., 2021). Despite rapid advances, important questions remain. Most studies have focused on a few model species in controlled settings, neglecting phylogenetic diversity and ecological realism. The persistence of olfactory and acoustic identity cues, and their roles in post-hibernation social networks, are unresolved. Mechanistic links between molecular changes, neural circuits, and complex behavior are only beginning to be elucidated. This review synthesizes the latest understanding of memory retention in small hibernating mammals, integrating spatial, social, and sensory perspectives. We draw from comparative experiments, field ecology, neurogenomics, and evolutionary theory to highlight transformative findings and outstanding gaps. By proposing integrative future research—combining behavioral assays, advanced field tracking, and genomic profiling—I aim to catalyze a new era in cognitive ecology: elucidating how memory persists under the most extreme ecological and physiological constraints. Despite progress, the cognitive consequences of hibernation remain poorly understood. Studies differ widely in design, memory type assessed, and species examined, leading to inconsistent interpretations. Some research demonstrates remarkable retention of spatial and social memory after months of torpor, whereas other studies indicate partial or domain-specific deficits. Moreover, most investigations focus on a limited group of model species, providing only a fragmented view of how memory is encoded, stabilized, and recalled across diverse hibernating taxa.

Material and Methods

A structured literature search was conducted between January and October 2024 to identify studies investigating memory, learning, or cognitive processes before and after hibernation in mammals. The search included Web of Science, Scopus, PubMed, and Google Scholar. Boolean operators (AND/OR) were applied to refine searches, and reference lists of key papers were manually screened for additional relevant publications. The following keyword combinations were used: initial terms such as "memory retention" and "hibernation" were expanded with "spatial memory," "social memory," "torpor," "ecological drivers," "olfactory memory," and "brain plasticity," each tailored to probe different facets of cognitive biology across mammals. The initial search yielded 147 publications. After screening titles and abstracts, 56 articles remained for full-text evaluation. Of these, 21 studies met the inclusion criteria and were retained for detailed synthesis. For each study, the following information was extracted: species, memory type (spatial, social, olfactory, associative, or object memory), experimental design, duration and depth of hibernation, main findings regarding memory retention or loss, and ecological context. Studies were then grouped by species and memory type to facilitate comparative interpretation across taxa. Because empirical studies are relatively few and heterogeneous in design, a narrative synthesis was used rather than a meta-analysis. Patterns were evaluated across species, memory domains, and hibernation strategies (obligate vs. facultative hibernators). The synthesis also considered ecological relevance, methodological limitations, and consistency of findings to identify overarching themes and knowledge gaps.

Results and Discussion

Diversity of Memory Outcomes in Hibernating Mammals

The literature reveals a striking variability in how hibernation affects memory performance across small mammals. Field and laboratory studies on forest rodents such as dormice and tree squirrels repeatedly demonstrate that animals are often capable of relocating caches, nest sites, or foraging routes upon arousal, suggesting remarkable persistence of spatial memory despite torpor-induced neural inactivity (Millesi et al., 2001; Bieber et al., 2021). Complementing these patterns, Alpine marmots demonstrate one of the strongest cases of complete memory preservation: individuals retained operant conditioning skills and habituation responses after ~6 months of hibernation, with post-hibernation performance indistinguishable from pre-hibernation levels (Clemens et al., 2009). Experimental paradigms—using maze tasks or object recognition—further confirm that retrieval accuracy following hibernation is typically above chance and, in some cases, indistinguishable from pre-hibernation performance. Similar results were found in Alpine marmots, where operant conditioning tasks and habituation responses remained fully intact after six months of hibernation (Clemens et al., 2009). However, this resilience is not universal. Other studies, particularly those focusing on less ecologically relevant or artificial learning tasks, have documented measurable deficits in recall after hibernation (Henke-von der Malsburg et al., 2023).In ground-dwelling mammals such as European ground squirrels, the outcomes appear context-dependent: while social recognition and kin discrimination are robust, more abstract spatial tasks see a decline post-hibernation, possibly due to task novelty or stress-related factors (Mateo & Johnston, 2000; Millesi et al., 2001). These results highlight that the ecological relevance of memory—whether the task reflects natural behaviour—may be crucial in determining its persistence. Comparative evidence from bats (Ruczynski et al., 2011) and certain amphibians or invertebrates suggests taxon-specific adaptations for neural protection. Bats, for instance, recall both learned locations and social partners across months of torpor, supporting the hypothesis that natural selection has favored not only the maintenance of core cognitive abilities but also lineage-specific neuroprotective mechanisms.

Mechanisms Underpinning Memory Preservation

Several converging lines of evidence illuminate the physiological and molecular strategies supporting memory in hibernators. Modern neuroanatomical work shows that the hippocampus, long associated with spatial memory, undergoes cyclical remodeling: synaptic pruning during torpor is followed by accelerated regrowth upon arousal (Weltzin et al., 2006). This process, far from resulting in “blank-slate” brains, seems to preserve circuit architecture vital for ecological memory, while protecting neurons from damage induced by metabolic stress. Behavioural evidence supports the idea that these neural changes do not erase stored information. Alpine marmots, despite marked synaptic restructuring during deep torpor, showed fully intact long-term memory across diverse learning tasks (Clemens et al., 2009). At the molecular level, hibernators express elevated levels of heat-shock proteins, antioxidants, and factors regulating synaptic plasticity. Recent genomic and transcriptomic studies have identified key alleles associated with resilience to neuronal inactivity and rapid recovery—supporting the view that hibernators represent a powerful case study for adaptive brain evolution (Drew et al., 2023; Power et al., 2023).

Sensory Modalities, Social Memory, and Communication

The role of olfactory and acoustic cues in memory retention has begun to receive critical scientific attention. While olfactory discrimination can be impaired after long torpor—as shown, for example, in laboratory rodents (Bullmann et al., 2019)—field-based observations increasingly suggest that social bonds, territorial boundaries, and hierarchical relationships persist across seasons in many species. Nonetheless, definitive longitudinal studies linking individual-specific odor signatures to memory outcomes after hibernation remain limited. Similarly, acoustic communication, critical in various ground squirrels and some arboreal species, may provide a robust substrate for social memory, but studies investigating the stability of vocal signatures across torpor are still rare. This remains a gap ripe for innovative, technology-enabled research.

The Influence of Ecological and Environmental Drivers

There is a growing consensus that the “memory resilience” of a given species or population is profoundly shaped by ecological context. Fluctuations in resource availability—such as mast seeding years in beech forests or drought events in arid shrublands—have immediate effects on arousal frequency, hibernation duration, and post-dormancy behaviour. In some populations, individuals emerging from longer-than-average hibernation periods have been observed to update spatial maps rapidly, possibly indicating a trade-off between brain maintenance costs and the evolutionary value of memory stability (Ruf & Bieber, 2023). The energetic limitations imposed by hibernation strongly support the 'expensive brain hypothesis,' which suggests that brain size evolution is constrained by periods of reduced energy intake (Heldstab et al., 2018). Climate variability and habitat alteration, now accelerating in many temperate regions, may thus test the limits of cognitive adaptation in hibernating mammals. Climate-driven changes in temperature regimes can alter the physiological processes of hibernating mammals. For example, Doublet et al. (2023) demonstrated that warmer winters influence telomere dynamics in hibernating greater horseshoe bats, suggesting potential long-term fitness consequences. Advances in field telemetry and data-logging offer unprecedented opportunities to correlate environmental data with fine-scale behavioral tracking, promising new insights into adaptive strategies.

Methodological Breakthroughs and Future Research Frontiers

Recent years have seen a methodological revolution in this field. Miniaturized GPS, RFID, and automated maze systems now allow longitudinal, high-resolution measurement of cognition in wild, free-ranging animals. High-throughput genomics and single-cell transcriptomics are beginning to clarify the gene networks and pathways responsive to dormancy and arousal. These integrative, multi-level approaches mark a transformative step—moving from isolated behavioural assays to richly contextualized, mechanistic models. Yet, outstanding gaps persist. Most comparative analyses are restricted to single habitats or species, and few studies have systematically integrated olfactory, acoustic, spatial, and genetic markers across the hibernation cycle. The role of sexual dimorphism, ontogeny, and inter-individual variation remains under-explored.

Synthesis and implications

The synthesis of these findings suggests that memory retention in hibernating mammals is neither absolute nor universally compromised. Instead, its persistence reflects deep evolutionary roots, fine ecological tuning, and powerful physiological solutions to the challenge of neural inactivity. The most successful systems appear to be those where memory is adaptive—necessary for survival or reproduction upon arousal—and tightly linked to behaviours under direct natural selection. This interdisciplinary field now stands poised for a breakthrough: by combining experimental and observational data from diverse species, integrating behavioural, sensory, and molecular evidence, and situating these findings within a robust evolutionary framework, the coming decade promises to close some of biology's most fascinating gaps regarding the resilience of animal memory under extreme conditions.

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