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Scandinavian Brown Bear Research Project

- A 40 year research summary

Aimee Tallian, Jon Arnemo, Alina Evans, Andrea Friebe, Ole Fröbert, Jenny Hansen, Rick Heeres, Anne Hertel, Alexander Kopatz, Jenny Mattisson, Andrés Ordiz, Ole-Gunnar Støen, Alexandra Thiel, Andreas Zedrosser, and Jonas Kindberg

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40 Skandinaviska
Björnprojektet

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Brown bear in Scandinavia © Alexander Kopatz

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Abstract

Tallian, A., Arnemo, J., Evans, A., Friebe, A., Fröbert, O., Hansen, J., Heeres, R., Hertel, A., Kopatz, A., Mattisson, J., Ordiz. A., Støen, O.G., Thiel, A., Zedrosser, A., and Kindberg. J. 2025. Scandinavian Brown Bear Research Project - A 40 year research summary. NINA Report 2589. Norwegian Institute for Nature Research.

The Scandinavian Brown Bear Research Project (SBBRP) is one of the world's longest running research projects on brown bears. In the following report, we describe the current state of knowledge about brown bears in Scandinavia, summarize key findings, methodologies, and implications of the research conducted under the SBBRP over the last four decades, and outline future directions. This report is divided into 8 sections; each section also includes 'Key Points' in the beginning, which summarizes important information found in each section.

Section 1 provides background information, including a short history of the SBBRP and how its research and mission have evolved through time, as well as descriptions of our core study areas in Sweden, and an overview of both current and historical methodologies. Section 2 gives an overview of the brown bear population in Scandinavia. This includes details about their current and historical ranges and how those have been influenced by management, gives an overview of their population ecology including population size and demography, describes the general characteristics of brown bears, discusses health and disease, and summarizes what we know about brown bear genetics and connectivity. Section 3 discusses brown bear behavior and ecology including their diet and foraging patterns, their habitat, movement, dispersal, home range characteristics, and space use, the fundamentals of their mating system, reproduction, and overall fitness, and their social and individual behavior putting those into the context of intraspecific interactions, and describes their denning ecology. Section 4 describes the Scandinavian brown bear in the context of interactions with other species in the landscape. This includes prey species such as moose, reindeer, and livestock, as well as sympatric predators such as wolves, wolverine, and lynx. Section 5 discusses human-brown bear interactions from multiple angles. This includes how human disturbance can affect bear behavior, the effects of hunting on the bear population as well as on their behavior and evolution, and also looks at what we know about direct human-bear encounters in Scandinavia. Section 6 gives an overview of general brown bear physiology, describes what is known about ecotoxicology in bears such exposure to lead (Pb), and summarizes how bears have been used as translational models in human medical research. Section 7 is focused on research tools and ethics, highlighting how the SBBRP has been at the forefront of brown bear capture-anesthesia methodology over the last 40 years, as well as describing our research on how capture can affect bear physiology and behavior.

Finally, Section 8 discusses the future and long-term goals of the SBBRP and highlights core areas of future research and development. Our long-term goal is to continue to monitor the Scandinavian brown bear population and facilitate local management decisions, contribute to the understanding of brown bear biology and ecology in the context of our changing world, and provide nature-based solutions based on brown bear physiology to the field of human medicine.

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Foreword

The Scandinavian Bear Project is one of the longest running brown bear research projects in the world. Over the past 40 years, the project has tagged and tracked over 940 bear individuals to learn more about their biology, physiology, behavior and ecology. The project has continuously collected data on bear biology and these long time series are becoming more valuable with each passing year. Together with our partners, we have published over 350 scientific papers, contributed more than 150 management-related reports, and produced a wide range of content aimed at management and the public such as talks, interviews, and our website www.brownbearproject.com.

In this report, we summarize key findings, methods, and results of the research conducted over the past four decades, as well as discuss research needs for the future. Our long-term goal is to continue to monitor the Scandinavian bear population and provide knowledge for management, and to contribute to the understanding of bear biology and ecology in a changing world. We will also be working on nature-based solutions in human medicine, which comes from our work on understanding bear physiology, especially linked to the amazing adaptation that bears have for hibernating 6-7 months a year.

We would especially like to thank all the researchers, field staff, volunteers, PhD students, Masters students, and undergraduates who have put in so many hours of data collection and analysis over the years. Without their dedication, it would not have been possible for the project to generate all the data and knowledge gained over the past four decades. We would also like to thank our long-term partners and funders, the Swedish Environmental Protection Agency and the Norwegian Environment Agency, whose continuous support has provided the foundation for this unique and long-term research project. Special thanks to the Norwegian Institute for Nature Research, the Swedish Hunters' Association, and the Swedish University of Agricultural Sciences for their administration and support of the project, and all the staff in the administration at both national and regional levels who have supported the project throughout these years.

March 12, 2025 – Aimee Tallian, Jon Arnemo, Alina Evans, Andrea Friebe, Ole Frö-bert, Jenny Hansen, Rick Heeres, Anne Hertel, Alexander Kopatz, Jenny Mattisson, Andrés Ordiz, Ole-Gunnar Støen, Alexandra Thiel, and Andreas Zedrosser, and Jonas Kindberg

1 Background

1.1 The Scandinavian Brown Bear Research Project (SBBRP)

The Scandinavian Brown Bear Research Project (SBBRP) is one of the world's longest running research projects on brown bears. Since its inception in 1984, the project has marked and followed over 940 individual bears to learn more about their biology, physiology, behavior, and ecology. An early core goal of the project was to focus on following individual bears from birth to death (Swenson & Brunberg 2023), a method that continues to this day and had resulted in a valuable individual-based dataset that can be used to answer a wide variety of questions about brown bear biology and ecology. Together with our collaborators, the SBBRP has published over 350 scientific peer-reviewed articles, contributed more than 150 management-related reports, and produced a wide array of content geared towards the general public. The project has educated multiple new generations of science professionals by mentoring numerous post-doctoral researchers, doctoral students, master's students, bachelor's students, and volunteers from around the world (Swenson & Brunberg 2023).

However, it is important to understand that our knowledge about the brown bear in Scandinavia has grown significantly over the last 40 years, alongside the growth of our project and the novel scientific and methodological developments. For example, early on in the project in the late 1980's and 1990's, research efforts focused primarily on the fundamentals of bear biology. In other words, how many bears are there, where are they, and what are their general physical characteristics and behavior patterns (e.g., diet, denning, mating and reproduction, and home range behavior). On a worldwide scale, research on brown bears had really only just begun, starting with the Craighead brothers in North America in the late 1960's and early 1970's. In general, we knew very little about brown bear biology, ecology, and behavior at this point in time and our understanding of the bear population in Scandinavia was minimal at best. Thus, this early information was crucial for understanding and conserving Scandinavia's recovering brown bear population and resulted in a variety of management-related research papers and recommendations.

The SBBRP was still relatively small at this stage but began to grow starting in the late 1990's and early 2000's, incorporating additional field staff, students, and outside collaborators into the program (Swenson & Brunberg 2023). The growth in project personnel and output coincided with the growth of the Scandinavian bear population itself, which increased from 950-1200 in 1994 to about 3300 in 2008 (Swenson et al. 2017). In parallel with the growth of the project, our understanding of the Scandinavian brown bear population increased rapidly starting in the early 2000's. For example, updated bear population estimates were made using a combination of new genetic methodologies and citizen science (hunters) data collection programs which helped track the rapid expansion and growth of the population. Early DNA analysis techniques began to shed light on the genetic structure of the population, and we began to monitor bear health and disease prevalence, a process that continues today. Our understanding of bear behavior also grew quickly, with research being conducted on bear habitat and space use, movement and dispersal, and mating systems and subsequent reproduction and mortality including sexually selected infanticide. We also continued to identify important bear foods and evaluate how access to them affected their behavior and fitness. This included exploring the role of brown bears as predators of ungulates such as moose and reindeer and setting those findings in context for managers.

While the SBBRP continued to focus on monitoring the Scandinavian brown bear population and describing fundamental bear biology, other research topics began to evolve and increase starting in the 2010's. During this time period, the SBBRP began to put the bear in the context of the human-dominated landscape in which it lives, and our understanding of how humans affect bears started to coalesce. We began to explore the effects of human infrastructure and disturbance on bear behaviors, such circadian rhythm, foraging patterns, movement, and their functional role as apex predators. This also included exploring the relationship between bear hunting and bear behavior, demonstrating that bear hunting has important effects on Scandinavia's bears beyond just limiting their population size, e.g., hunting also effects their general behavior, life history traits, and interspecific interactions. DNA monitoring techniques continued to develop, which allowed us to explore more complex issues such as the potential and consequences of genetic bottlenecks in the population and gene flow and connectivity within the Scandinavian population itself and with other populations in Finland and Russia. These new genetic techniques also helped pave the way for the more sophisticated and accurate assessments of brown bear population size that we see today. Medical researchers also began to use the brown bear as a translational model in human medicine which helped shed light on brown bear physiology in general while advancing our understanding of human metabolic and cardiovascular disorders. This research, which remains ongoing, has the potential to transform both the prevention and treatment of a wide array of human diseases. Alongside advancing human medical research, the SBBRP began to explore the effects of capture and immobilization on bear physiology and behavior, leading the way in developing safe and ethical handling protocols for brown bears and other bear species.

All the research conducted throughout these different periods contributed to the conservation and management of the brown bear population in Scandinavia and continues to do so today. We are now in the mid 2020's and a new era of bear research is currently at our fingertips. While the project has conducted extensive research on brown bear biology over the last 40 years, only more recently have we begun to put bears into the context of the complex, multispecies ecosystem they live in. Indeed, shifting from single species to multispecies research is an important current trend across the world of biology. The SBBRP has already begun to move this way by exploring the nature of interactions between bears, wolves, and moose. We plan to continue to lead the way by establishing a long-term multispecies research area in Sweden in collaboration with other projects, such as the Scandinavian Wolf Research Project and the SLU Moose Research Project.

We have also recently begun to explore individual variation in bear behavior. Understanding this is important because wide individual variation in behavior is what gives a species the flexibility needed to adapt to shifting environments, which is key in the context of global climate change. We also plan to continue to monitor the size and distribution of the brown bear population in Scandinavia and further explore fundamental bear biology, ecology, and their relationships with humans. For example, an ongoing study is currently looking at the effect of lead (Pb) exposure in bears, its effect on their long-term health, and the potential for downstream exposure in humans. We will also continue the important work of using bears as a translational model in human medical research, helping to transform the prevention and treatment of human diseases.

Over the last 40 years, the SBBRP has made important scientific contributions to our understanding of a range of subjects including brown bear biology and ecology, animal welfare, and human health, all of which are covered in this report. The project has both contributed to the conservation and management of the Scandinavian brown bear population as well as to the world's overall understanding of brown bear biology and ecology. The project has also contributed a host of new methods to the world of science, ranging from new genetics and genotyping techniques to the development of safe and ethical capture and immobilization of large carnivores, as well as methods for analyzing diets, monitoring population size and trends, and archiving scientific data. Over time, we also developed ties with bear researchers in other nations, contributing to increased understanding of bear biology and subsequent management of brown bears in Pakistan, Spain, Slovenia, Albania, Macedonia, Serbia, North America, Mongolia, and regions of the Himalayas, as well as to spectacled bears (*Tremarctos ornatus*) in Ecuador, and sun bears (*Helarctos malayanus*) in Borneo.

The SBBRP provides unique, long-term, continuous data on bear biology that becomes more valuable with each passing year. Our long-term goal is to continue to monitor the Scandinavian brown bear population and facilitate local management decisions, contribute to the understanding of brown bear biology and ecology in the context of our changing world, and provide nature-based solutions to the field of human medicine based on brown bear physiology. For more information on the future vision of the SBBRP, see Section 8.1 The future of the SBBRP. We offer many thanks to Naturvårdsverket and Miljødirektoratet for their continued funding and support.

1.2 Core study areas

The Southern Study Area

The Southern Study Area is the core study area where the SBBRP has conducted most of its research since 1985. Located in Dalarna, Gävleborg, and Jämtland Counties in south-central Sweden (61°N, 15°E), the study area encompasses approximately 20,000 km^2. The study area has not been static through time, but rather contracted and expanded to adapt to logistic and research requirements. For example, at one point, the Southern Study Area included areas in and around Fulufjället National Park and the Älvdalens skjutfält or Älvdalens Military Range. The SBBRP stopped focused research efforts in Fulufjället National Park in 2022 due to distance-related logistical constraints. More recently, increased military activity has created access issues for the region within the Älvdalens Military Range. Thus, we will likely decrease our presence in the western portion of the study area and instead expand northward to encompass up-and-coming multispecies research efforts in the area around Kårböle. Furthermore, the study area temporarily expanded to encompass the Idre Sámi Siida, or herding community, along its western border to collaboratively evaluate bear-reindeer interactions (2019-2024).

<u>The landscape:</u> The region is mostly composed of bogs, lakes, streams, and boreal forest which is dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), but deciduous trees such as mountain birch (*Betula pubsecens*), silver birch (*Betula pendula*), European aspen (*Populus tremula*), and gray alder (*Alnus incana*) are also relatively common. The boreal forest is intensively managed (about 80% of the forested area is managed) which results in a landscape that is comprised of clear cuts and forest at various stages of successional growth, most of which is less than 35 years old (Swenson et al. 1999b). Ground cover includes a shrub layer dominated by common juniper (*Juniperus communis*), willows (*Salix* spp.), and rowan (*Sorbus aucuparia*) and a ground layer that includes a variety of mosses, lichens, grasses, heather, and berries including blueberries (*Vaccinium myrtillus*), crowberries (*Empetrum hermaphoditum*), and lingonberries (*Vaccinium vitis-idaea*). The topography can generally be described as a rolling landscape, with elevations ranging between 200 and 1000 m. The elevation is greater in the western portion of the study area, near the border with Norway, where a small portion of the study area is above tree line (750 m). The mean temperature varies between summer and winter, averaging about -7° C in mid-winter (January) and 15° C in mid-summer (July) with annual precipitation ranging between 600 and 1,000 mm. The growing season generally lasts between 150 and 180 days, while snow covers the ground between late October until early May.

<u>The bear population:</u> This study area is centered in the southern part of the core brown bear distribution in Scandinavia. The majority of the bear population lives in this area, and it therefore also hosts the highest densities of brown bears in Scandinavia, averaging approximately 30 bears per 1000 km^2 (Bischof et al. 2020, Kindberg et al. 2011). Brown bears are intensively hunted across the entire area, except for in Fulufjället National Park, with the annual bear hunt starting from August 21 and ending by October 15, or earlier if quotas are filled. Up to this point (2023), almost 677 bears have been captured, collared, and followed in the study area using both VHF and GPS technology.

<u>Human footprint:</u> The Southern Study Area is generally sparsely populated, with about 4 to 7 inhabitants per km^2 (Ordiz et al. 2013b). However, the network of forestry roads used for logging in the region is quite dense, with about 0.7 km of forestry roads per square km and some high-traffic roads (0.14 km of high-traffic roads per square km). Logging and forestry are the main industries in the area, although semi-domestic reindeer herding does occur in the western portion of the study area in the Idre Sámi Siida.

The Northern Study Area

The Northern Study Area was active between 1984 and 2013 and was located in Norrbotten County in northern Sweden just 100 km north of the arctic circle in an area that encompassed approximately 8,000 km^2 (67°N, 18°E). Other more focused research efforts have taken place in and around this study area, including collaborations that involved the two Sámi Siida of Udtja and Gällivare.

The landscape: The northern study area covered more rugged terrain characterized by deep valleys, mountains, and high plateaus and glaciers. The valleys were dominated by Scots pine and Norway spruce, with mountain birch growing near the tree line, or below 600 m, with an understory of lichen (*Cladina* sp.) and ericaceous heather (*Ericaceae* sp.). The mountains and higher elevation plateaus reached up to 2000 m and were above tree line. The mean temperature varied between summer and winter, averaging about -13° C in mid-winter (January) and 13° C in mid-summer (July) with annual precipitation ranging between 500 and 1,000 mm. The growing season generally lasted between 110 and 130 days, while snow covered the ground between late October through late May. Unlike the southern study area, this study area included a large amount of protected national park land.

The bear population: The bear population here was much smaller than the population in the Southern Study Area, with bear densities only reaching 7 bears per 1000 km^2. The bear population in this area was subject to legal hunting, but such hunting was restricted to a smaller proportion of the study area outside of protected areas. Between 1984 and 2013, about 254 individual brown bears, both male and female, were radiomarked and followed, mostly using VHF telemetry but using some GPS technology during the end of the study period.

Human footprint: The Northern Study Area is even more sparsely populated than the Southern Study Area, with about 0.3 to 1.2 inhabitants per km^2. Logging is equally intensive in the coniferous forest in the Northern Study Area. Semi-domestic reindeer herding took place within the majority of the study area, which spanned several Sámi Siida.

1.3 Current and historical methodologies

Marking and tracking

Target animals: A primary goal of the SBBRP is to follow individual bears through their life cycle from birth to death. The project has largely focused on following females and their cubs, often marking cubs early in life and recapturing them later-on to maintain their presence in the study, although we have collared many males over the years as well. Bears are generally captured in early spring after they have emerged from their dens, although more recent efforts have also included summer and in-den winter captures to collect data for human medicine research.

Capture, immobilization, and marking: The SBBRP has been capturing and marking brown bears since 1984. Methods have evolved over the years but have always used the most recent and available protocols (Arnemo et al. 2012, Kreeger & Arnemo 2007) approved by the Swedish Ethical Committee on Animal Research; current permit Dnr 5.8.18-03376/2020. Current methods include darting bears via helicopter using a remote drug delivery system (DANiNJECT®). All precautions are taken to decrease the stress from the capture event and maintain safety for both the animal and crew. Once immobilized, each individual is clinically examined and their vital signs (e.g., body temperature, heart rate, breathing rate) monitored throughout. GPS collars are fitted according to the size, age, and sex of the bear. The weight of the radio collar and other equipment do not exceed 2% of the animal's body mass. Bears are also marked with a microchip and an inner-lip tattoo so they can be identified in future captures. Surgically implanted VHF abdominal transmitters were also used in the past to facilitate recapturing specific individuals; however, this is only performed sparingly now. Biological samples from all marked individuals are also taken. This includes blood, hair, skin, feces, and urine samples, as well as the upper 1st premolar tooth to determine the age of animals not followed from birth.

Physiological monitoring: Starting in 2010, a subsample of bears has been fit with temperature loggers and heart rate monitors, respectively. Temperature loggers are surgically placed into the abdominal cavity, while heart rate monitors are placed under the skin (subcutaneous) in the chest just above the heart. Temperature loggers monitor fluctuations in body temperature that are recorded every temperature every 2-4 or 30 minutes. Heart rate monitors record average heart rate daily, one at night and one during the day, although some newer models record heart rate every 2 minutes.

Tracking: Bears are currently fit with GPS collars from Vectronic Aerospace. Multiple models of collars have been placed on bears, which offer a variety of functions. The current baseline function of collars includes GPS-satellite tracking with locations uploaded remotely to the WRAM database at SLU (www.wram.slu.se) at regular intervals. In general, bear collars are set to take positions every 30 minutes or 1 hour, however, this baseline setting is changed to a more fine-scale fix rate for more intensive studies. All collars are also equipped with a VHF beacon which can be used to locate the animal during capture or the collar when the GPS battery is depleted. All current GPS collars are also equipped with accelerometers which measure ‘animal’ activity. Many GPS collars also offer a ‘proximity function’ which emits a weak UHF signal and detects UHF signals from other collars; once detected, the collar will temporarily switch to predefined fix rates. The collars also have a ‘virtual fence’ function whereby collars will switch to predefined fix rates when they come into a predefined area. The functions that automatically change into predefined fix rates give an opportunity to save battery or get finer scale data when needed. GPS locational data are core part of our data collection efforts and have been used to explore a wide variety of questions related to brown bear biology, ecology, and behavior. Early in the project we also tracked bears using collars equipped only with a VHF beacon (1984-2010), which provided key early information on brown bear biology. However, this technology is now outdated and is no longer used.

Population Monitoring

Current DNA-based population monitoring: Genetic tagging, or the identification of single individuals using their unique DNA-profile, e.g., noninvasively from feces, hair, or tissue or other biological material from recovered dead animals, has been used to monitor bear populations in Sweden and Norway since 2001 and 2005, respectively. In short, each piece of genetic material collected points to a unique individual at a unique time and location on the landscape, providing a minimum number of individuals detected each year. Determining the number of identified individuals using the DNA, i.e., the minimum number of individuals as well as the estimated number of individuals, is crucial to the wildlife management (Bellemain et al. 2005, Bischof et al. 2020, Kindberg et al. 2011) to evaluate whether national population management goals are met (Bischof et al. 2016, Kopatz et al. 2021).

Data collection for Norway started in 2005 and from 2009, this data collection has been annually conducted nationwide. Efforts involve both managers and the public, mainly hunters. This data is used in a model to estimate the number of annual reproductions in Norway (Bischof et al. 2012). Rovdata (www.rovdata.no) is responsible for the monitoring of bears in Norway. In Sweden, the first regional survey was conducted in 2001. At first these were performed at irregular intervals in different regions but later a rotating schedule was introduced so that every region would have a population survey every 5th year. The survey, starting the 21st of August and continuing until the end of October, is mainly conducted by hunters via opportunistic sampling of scats. These are sent to a genetic lab for registration and analysis (currently The Swedish Museum of Natural History). The individual detection data are then fed into a closed capture-mark-recapture model in Program MARK to estimate population size (Bischof et al. 2020). The most commonly used models include mixture models to account for individual heterogeneity. These models are robust estimators of wildlife populations as they can account for variation in individual detection, time, and imperfect detection (not all animals are detected). Data for both countries are maintained in RovBase, a joint database for monitoring large carnivores in Scandinavia. An updated method, Open Population Spatial Capture Recapture Model developed by the RovQuant research group in collaboration with the SBBRP, uses individual-based DNA detections to estimate brown bear population size, density, survival, and reproduction (Bischof et al. 2020).

Numerous studies and tests of new methods have been conducted in or on the Scandinavian brown bear population since these methods were developed and are used and constantly improved for more effective monitoring and management. Such methods are also routinely updated to implement the latest technological advancements based on next-generation sequencing (Norman & Spong 2015, Norman et al. 2013), and to compare data from Scandinavian population monitoring to neighboring populations (Kopatz et al. 2024). The SBBRP has also utilized and evaluated a variety of other population monitoring methods. Other methods for monitoring population parameters and trends include:

Large Carnivore Observation Index (LCOI): The Swedish Association for Hunting and Wildlife Management has been collecting data on observations of bears made by Swedish moose hunters since 1998 (Ericsson & Wallin 1999, Kindberg et al. 2009, Kindberg et al. 2011). Observations are collected during the first 7 days (within the first 30 days) of each year's moose hunt. Hunters also report the time they spent in the field, which can then be used to correct for effort. The LCOI observational data are closely correlated with relative bear density (Kindberg et al. 2009), and these data have been previously used to estimate population size and growth at the national and county level (Kindberg et al. 2011).

Hunting data: Hunters in Sweden are required by law to report all shot bears and submit them for a compulsory inspection on the day the kill is made (Bischof et al. 2008). Although such hunting data can sometimes be a reliable proxy for population parameters and trends, our research suggests bear hunting data in Sweden represent a biased sample of the population and should thus be used cautiously within a management context (Leclerc et al. 2016a). All hunting data is stored in Rovbase.

Diet Analysis

Scat analysis: The SBBRP has been systematically collecting bear scats since 2015 in order to understand and track bear diet, a process which continues today. Field crews track and collect scats from all GPS collared bears each year, collecting a scat from each animal once every one or two weeks throughout their active period (April/May until late October) (De Cuyper et al. 2023). Scats are carefully collected to ensure that they have come from the focal individual. Each scat is then weighed, washed, and visually examined to identify dietary items, which are identified in as much taxonomic detail as possible (De Cuyper et al. 2023).

Predation studies: The SBBRP has conducted a variety of predation studies over the years to assess brown bear predation on ungulates. Predation studies vary slightly in methodology, but all generally use a combination of GPS cluster-analysis and field site-visits to identify prey remains and quantify kill rates. GPS 'cluster analysis' is used to pinpoint areas of localized bear activity and select locations for field visits. Locations of interest, or 'clusters' are defined by applying several parameters to GPS locational data (e.g., distance between GPS locations, number of locations within a defined area, time interval between GPS fixes). After identifying the clusters, field crews visit the site and search for prey remains, generally within a 30 m radius of the clustered GPS points, and record cause of death, species, age, and sex. We also often collect biological samples such as scat and hair for DNA analysis and record other pertinent information such as site characteristics like habitat type and cover. Following bears in this way over multiple seasons has allowed us to estimate kill rates on both moose (Rauset et al. 2012) and reindeer (Støen et al. 2022b).

Den monitoring

We began monitoring bear dens in our Southern Study Area starting in 1987, and this process continues today. Data collected includes den location, den type (e.g., in an anthill, tree, or in the soil or rocky outcropping), the dens dimensions, a description of the surrounding habitat, and any track and sign in the area. Scat samples are also collected. Thus, the SBBRP has collected a time series of data representing bear den-site selection over almost 40 years.

2 The Scandinavian Brown Bear Population

2.1 History of the Scandinavian brown bear population

KEY POINTS

- The brown bear historically ranged across the Scandinavian Peninsula but began to decline in the mid-1800's due to human persecution.
- The brown bear population began to increase again during the early 1900's when government-funded hunting bounties were terminated in Sweden.
- Management programs diverged between Sweden and Norway in the early 1900's and management goals and styles remain different today.
- The brown bear population in Scandinavia has rebounded and stabilized over the last several decades.

The brown bear once ranged across most of the European continent. This includes Scandinavia, where bears were spread across the Scandinavian Peninsula up to at least the mid-1600's, including many of the area's larger islands with the exception of Gotland in Sweden (Swenson et al. 2000). Evidence from mitochondrial DNA (mtDNA) suggests that brown bears in Europe come from two different genetic lines originating in the east (Russia) and west (continental Europe) (Bray et al. 2013, Ersmark et al. 2019, Taberlet et al. 1995). The western line can be further subdivided into those originating from the Iberian Peninsula and from the Balkan Region. Bears first arrived in Scandinavia at least 6200 years ago during a post-glacial expansion after the Holocene glacial retreat (Bray et al. 2013). A second wave of immigration came from continental Europe at least 5300 years ago. Today, these populations remain genetically distinct, with founder mtDNA from the eastern wave (Russia), remaining in Scandinavia's northern population (Jämtland/Trøndelag and further north), and mtDNA from the western wave (both the Iberian and Balkan regions) found in the more southern population (Hedmark/Härjedalen and further south) (Bray et al. 2013). Nevertheless, mtDNA initially part of the eastern wave, now found in Scandinavia's northern population, were identified in samples during the last glacial maximum in the region of today's France and Belgium. This indicates that the lineages may not have been that distinctly distributed, and that the history or recolonization may be more complex than previously assumed based on earlier studies (Ersmark et al. 2019). Further, previously conducted studies showed that genetic diversity must have been higher among historic brown bear samples from before the bottleneck (Schregel et al. 2015, Xenikoudakis et al. 2015).

Sometime starting in the mid-1800's and possibly even earlier, the Scandinavian bear population began to decline and the distribution shrink. This was in large part due to predator removal programs that were heavily subsidized in Norway and Sweden starting in the mid-1800's; brown bear eradication was considered a priority by both nations (Swenson et al. 1995). High premiums were paid for hunting bears, and hunters were further incentivized by the money they could earn selling bear skins and meat (Swenson et al. 1995). The Scandinavian bear population was estimated at ~4700 individuals in the mid 1800's (Swenson et al. 1995). At that point, the majority (3100 or ~65%) of the bear population was found in Norway with the remainder of the population (1600-1700 or ~35%) found in southcentral or northern Sweden; bears were functionally extirpated in southern Sweden by the mid 1800's (Swenson et al. 1995). Heavy hunting continued during this time and the population continued to decrease, with the decline happening more quickly in Sweden, likely simply because there were fewer bears there already. Bears disappeared from south to north and from lowland to mountainous areas, i.e., they disappear first in the southern and low elevation areas in Sweden. This finally resulted in a major population bottleneck and remnant populations of about 130 bears distributed between a few discrete inaccessible mountain areas by the 1920's (Swenson et al. 1995).

Near the turn of the century, the Swedish Hunters' Association and the Swedish Academy drafted plans to save the Scandinavian brown bear from extinction. This represents the beginning of divergent management goals and actions between Sweden and Norway. Sweden abolished bounties in 1893 and introduced several measures that helped reverse the population decline by around 1930 (Swenson et al. 1995). In 1942, the Swedish population was estimated at 294 bears, and it was decided their population was large enough to withstand hunting; license hunting was reintroduced in Sweden in 1943. Norway abolished national bounties in 1930, but local bounties were allowed until 1972. The bear population increased about 1.5% per year from 1942 to 1991 (Swenson et al. 1994). In 1994, the Scandinavian population was estimated to be about 650-700 individuals in Sweden and 22-35 in Norway. Since then, the brown bear population has rebounded and functionally stabilized; as of 2022, there were an estimated 2587-3080 bears in Sweden (www.naturvardsverket.se) while the Norwegian population remained small, estimated at about 111-142 individuals (Bischof et al. 2020). Hunting remains legal in both countries although management strategies for Sweden and Norway remain divided.

2.2 Population ecology and current status

KEY POINTS

- As of 2022, there are an estimated 2824 (range = 2587-3080) bears in Sweden and about 126 (range = 111-142) bears in Norway. The population growth rate was high between ~1985 and ~1995 but has since decreased and stabilized.
- The population is biased towards females and is relatively young (i.e., there are more females than males and there are few older individuals).
- On average, female brown bears in Scandinavia reproduce every 2.5 years, have an average litter size of 2.4 cubs (range = 1-4), and keep their cubs for between 1.5 to 2.5 years.
- Cubs of the year have the highest natural mortality of any age class, the majority of which occurs during mating season and is caused by infanticide.
- Regulated hunting is the highest cause of brown bear mortality in Scandinavia.

Current distribution and population size

The Scandinavian brown bear is currently distributed across three core areas on the Scandinavian Peninsula (Bischof et al. 2020, Kindberg et al. 2011). The majority of the bear population resides in Sweden with a small portion living in Norway. In Sweden, the core population is found in Dalarna, Jämtland, and Gävleborg Counties, with the rest of the population found in the counties to the north including Norrbotten and Västerbotten (Kindberg & Swenson 2018). In Norway, small pockets of bears persist in the counties Innlandet, Trøndelag, Nordland, Troms, and Finnmark, primarily adjacent to the border of Sweden, Finland and Russia (Bischof et al. 2020). Although the aforementioned regions represent core areas, male bears move across large ranges, particularly during mating season, and can potentially be found anywhere outside the main distribution (Dahle & Swenson 2003b).

The two most recent estimates of the Scandinavian bear population were made for Sweden by the SBBRP in 2017 and then for Sweden and Norway by RovQuant in 2018, with the different methods providing relatively similar estimates (Bischof et al. 2020, Kindberg & Swenson 2018). Kindberg and Swenson (2018) used the observations from the national DNA monitoring program to calculate the population trend and estimated 2877 (range = 2771-2980) bears resided in Sweden as of 2017 (Kindberg & Swenson 2018). RovQuant used a spatial capture-mark-recapture model to estimate the population of multiple large carnivores in Scandinavia, and reports an estimated 2615 (range = 2499-2732) bears in Sweden and about 140 (range = 124-162) bears in Norway as of 2018 (Bischof et al. 2020). Previous to that, the last population estimates from Sweden were from 2008 (3298 bears) and 2013 (2800 bears) and were also based on the national monitoring scheme (Kindberg & Swenson 2014, Kindberg et al. 2011). Since 2018 the Museum of Natural History (NRM) has been responsible for DNA analyses and population estimates in Sweden Their latest report estimates the number of bears in Sweden to be 2587-3080 in 2022. A study by RovQuant estimated the Norwegian part of the population in 2022 to be between 111-142 (Dupont et al. 2023).

Population demography

Population demography refers to the study of a population's composition, growth, and structure, including factors such as population size and density, birth and death rates (fecundity and mortality), emigration and immigration rates, age structure, and sex ratio. Understanding the demography of the Scandinavian brown bear population is crucial for management and conservation efforts as it can be used to predict future population trends, assess the impact of management measures, and develop conservation strategies. In Scandinavia, demographic data are collected through national genetic sampling and monitoring efforts, statistics recorded from license bear hunts, and long-term individual monitoring conducted by the SBBRP. Here, we describe what we currently know about the demography of the Scandinavian brown bear population and put it into context.

Population trends and growth rate: During the period of recovery between 1942 and 1991, the bear population increased at a relatively stable rate of about 1.5% per year, meaning the population doubled every 46 years (Swenson et al. 1994). This trend appears to have stabilized and leveled out. The most recent report in 2018 used hunter-collected bear observation data to estimate the bear population trend in Sweden between 1999 and 2017 and suggests that the bear population size in Sweden began to stabilize in the early 2000's (Kindberg & Swenson 2018). As of now, 2023, high hunting quotas aimed at population reduction will likely decrease population growth rate and the overall size of the population in the coming years. Further research should be dedicated toward monitoring this emergent situation.

The growth rate of any population is influenced by birth and death rates within the population as well as immigration and emigration into and out of the population. A positive growth rate indicates that the population is increasing, while a negative rate suggests a declining population. Bear population growth is regulated by both intrinsic factors (i.e., the behavior of the species and characteristics of the population) and extrinsic factors (i.e., processes external to the population such as habitat and food availability and mortality from outside sources such as hunting) (Odden et al. 2014). In general, changes in reproductive rates (e.g., the number of females, mean litter size, reproductive intervals, cub survival, and the probability a female will reproduce) have the greatest potential to affect bear population growth rate (Van de Walle et al. 2021a).

However, in Scandinavia, processes external to the population such as hunting play a key role in bear population size and growth, i.e., population growth rates decline sharply when hunting quotas are increased (Van de Walle et al. 2021b) (see the Survival and Mortality section below and Section 5.1 Human disturbance and brown bear behavior for more details on the effects of regulated hunting on the Scandinavian bear population). However, there are several bear behavioral characteristics that are likely density dependent (the behaviors shift when bear density increases or decreases) which interlink to have regulatory (intrinsic) effects on bear population growth (Odden et al. 2014). This includes bear movement and home range size, sex-specific dispersal, social inhibition of breeding, and infanticide (Odden et al. 2014). Immigration and emigration likely have minimal effect on bear population growth in Scandinavia. The population is generally isolated from the rest of Europe (Kopatz et al. 2014), although there is evidence for a higher rate of gene flow from Scandinavia to Karelia (i.e., more emigration) than from Karelia to Scandinavia (i.e., less immigration) at the transborder area where the two populations meet (Kopatz et al. 2021). However, considering the level of gene flow, the actual migration rates are estimated to be low (Kopatz et al. 2021).

Population density: Population density refers to the number of bears per unit area. The most recent estimates in Scandinavia from 2018 indicated that bear density ranged between 0 and ~7.5 bears per 100 km^2 throughout the bear distribution area in Scandinavia, with the highest densities occurring in the southernmost and central core areas (Bischof et al. 2020).
Understanding bear population density in Scandinavia is important as it can affect both population characteristics (e.g., underlying behavior and physiology) and population vital rates (i.e., reproduction and survival) of both the bear population as well as their primary prey populations (e.g., moose and reindeer). Bear density is generally influenced by a mixture of habitat and resource availability combined with human tolerance. As with other species, bear density also affects other aspects of the bear population. For example, variation in the body size of female brown bears is negatively related to bear density, meaning bear body size decreases as bear density increases (Zedrosser et al. 2006). This is likely due to competition; an increase in population density increases competition for food resources which can result in an overall decrease in body size and weight within the population (Zedrosser et al. 2006). Such results are to be

expected, as density dependent effects on wild animal populations are found throughout the animal kingdom.

Age structure: The ages of hunter-killed bears can be used as a proxy for population age structure which can be broken down into different age classes: cubs-of-the-year (0-1 year old), yearlings (1-2 years old), two-year-olds (2-3 years old), subadults (3-5 years old), and adults (>5 years). In Scandinavia, the mean age of hunter-killed bears (between 1990-2015) was about 5 years old (Frank et al. 2017). The age structure of the brown bear population in Scandinavia is likely heavily influenced by hunting (Frank et al. 2017), with harvest eventually resulting in a younger population, or an age structure biased toward young animals. There are no observable differences in vulnerability to hunting across different ages in Scandinavia (Bischof et al. 2009). Therefore, in a population that starts off with the majority of individuals in lower age classes, if harvest rates are spread evenly across all age classes, a relatively greater proportion of older aged animals will be harvested, eventually resulting in a population that has many more young than old animals. We expect this to be occurring in Scandinavia now, although little is truly known about the age structure of the bear population. This is important because a reduction in the population-wide age of females would have knock on effects on cub reproduction and survival (Frank et al. 2017, Gosselin et al. 2015, Zedrosser et al. 2009). We therefore suggest further research into the age structure of the bear population and its effect on bear behavior and population viability is relevant in the coming years.

Sex ratio: The population estimates suggests that the bear population in Scandinavia is biased towards females; 59% (range = 56%-61%) of the population is female (Bischof et al. 2020). This is likely the result of regulated hunting that protects females with cubs, resulting in female survival being subsequently higher than male survival (Frank et al. 2017). Monitoring the sex ratio of the population is essential for understanding reproductive dynamics and genetic diversity.

Reproductive rates: Mean litter size, mean litter interval, and reproductive rates for the Scandinavian bear population were first estimated in 1998; on average, female brown bears in Scandinavia reproduce every 2.4-2.6 years and have an average litter size of 2.3-2.4 cubs (range = 1-4) resulting in a mean reproduction rate (litter size / litter interval) of 0.92-0.96 (Sæther et al. 1998). Litter size was also reported again in 2005, 2012, and 2018 and were generally consistent with previous results; mean litter size was estimated at 2.27-2.37 cubs (Bischof et al. 2018, Gonzalez et al. 2012, Zedrosser & Swenson 2005). One of those studies also noted that public estimates of bear litter sizes (i.e., reports of cub sightings made by the public) were low and need to be corrected for bias (Zedrosser & Swenson 2005), thus the best method for estimating litter size is via continued population monitoring.

Reproductive rates, including the number of cubs born per female, the interval between litters, and cub survival, are critical for assessing the population's growth potential. Importantly, these estimates must be regularly updated as the reproductive rates of a population can change over time based on individual and environmental conditions. Litter size, for example, is related to a variety of factors. A bears first litter tends to be smaller than their subsequent litters (i.e., after the individual has already given birth once before (Zedrosser et al. 2009), which means a younger population may have overall smaller litter sizes. Litter size is also likely correlated with female body size, meaning larger females tend to have more cubs per litter (Swenson et al. 2007a).

Interval between litters is also affected by a number of factors. For example, the probability that one year olds stay with their mother for a second year is greater when the yearlings are small (i.e. have a low body mass) and is more likely to happen when there are two cubs in the litter compared to 3 or 4 (Dahle & Swenson 2003a). The protection of females with cubs during fall hunts results in females keeping their cubs for longer (for 2.5 compared to 1.5 years) which makes the interval between litters longer and can potentially decrease growth rates (Van de Walle et al. 2021b). Infanticide, however, can decrease reproduction intervals; males kill cubs which results in females coming into estrous sooner than they otherwise would have (Bellemain et al. 2006a, Steyaert et al. 2014). Factors affecting cub survival are discussed in the next subsection Survival and Mortality.

Survival and mortality: Brown bear survival and mortality rates are influenced by a range of factors in Scandinavia including age, sex, and bear density, but are primarily driven by humans via regulated hunting. Understanding survival and mortality rates is crucial for assessing the health and viability of the bear population.

Age-dependent survival and infanticide: As with most other animals, mortality is highest for bears during their first year of life, i.e., for cubs of the year (Swenson et al. 2001b). The majority of mortality occurs during the mating season, most likely resulting from infanticide by male bears (Zedrosser et al. 2009). In Scandinavia, cub survival varies between regions. For example, a study conducted in 2001 suggests that cub loss is low (~4%) in the northern part of Sweden, but comparatively much higher in the southern population (~34%) (Swenson et al. 2001b). This is likely explained by increased infanticide in the south because the male population there has higher turnover rates (i.e., more males die in the south and are then replaced by new males that are more likely to kill local unrelated cubs) (Swenson et al. 2001b, Swenson et al. 1997b). One-year olds, or yearlings, have a higher survival rate than cubs of the year, and cubs that stay with their mother longer (i.e., until they are 2 years old) have higher survival rates than those that that leave as yearlings (Gosselin et al. 2015). Interestingly, females that settle closer to their mothers home range have a higher lifetime survival (Hansen et al. 2023). For detailed information on infanticide in the Scandinavian bear population see Section 3.3 Mating, reproduction, and fitness. Adult females have higher survival rates than adult males as females with cubs are protected during regulated hunts (Bischof et al. 2008).

Natural causes: Like all wild animals, brown bears can die from natural causes including old age, disease, starvation, and injuries from fights with other bears. From 1983 to 2022, only 92 of 560 deaths (16%) of adult marked bears were due to natural causes; 40 were from bears killing other bears and 4 from starvation, and the others were unknown natural deaths (Thienel et al. 2023). The SBBRP has documented only a few cases of adult bears being killed by other bears, and all of these were adult female bears with yearlings; these were possibly the result of females being killed by males during attempted infanticide. Bears in Scandinavia generally do not live long enough to die from old age, and diseases are not prevalent in the population.

Human-related mortality: Humans are the number one cause of death for marked bears in Scandinavia. From 1983 to 2022, 468 of 560 deaths (84%) of marked bears were due to human impact (Thienel et al. 2023). Of the 560, 369 were due to license hunting, 93 due to protection hunts, and 6 due to vehicle and other types of collisions (Thienel et al. 2023). Regulated license hunting in Scandinavia constitutes an additive source of mortality for the bear population, i.e., mortality due to hunting is not compensated by a decrease in mortality from other causes (i.e., compensatory mortality). Bears involved in conflicts with humans, such as semi-domestic or domestic livestock depredation, are also removed via specially permitted protection hunts (Swenson et al. 2017). As one might expect, increased hunting quotas result in a corresponding increase in mortality in the population (Van de Walle et al. 2021). Hunting quotas and offtake has changed through time in Scandinavia. Illegal poaching also likely occurs within the population with an unknown effect on overall survival and mortality. Finally, vehicle and train collisions can result in bear fatalities, which is more common in the core bear area in southern Sweden that is characterized by extensive road networks and higher bear densities.

2.3 General bear characteristics and behavior

KEY POINTS

Brown bears…

- Are generally solitary in nature, except for females rearing cubs.
- Have overlapping home ranges (males tend to have the largest home ranges and females with cubs of the year the smallest).
- Are generally crepuscular animals, meaning they are most active during dawn and dusk, although they can be active during other parts of the day and night.
- Are opportunistic omnivores and predators with a highly varied diet that changes seasonally. The main foods in Scandinavia include berries, meat from newborn moose, and insects (ants).
- Are hibernators, meaning they den during winter where they remain dormant for several months relying on stored fat for energy.
- Mate between May and June and give birth in the den between December and March to 1-4 cubs (mean is 2.4).
- Are generally tolerant towards humans in Scandinavia.

Characteristics

Scandinavian brown bears are robust, sturdy animals with a strong neck and jaws, round, prominent ears, and a noticeable hump over their shoulders; the hump is composed of powerful muscles that assist them with activities such as digging. The color of their fur varies, ranging from light to dark brown, while individual bears can have different shades of fur, and some may appear almost black or exhibit a lighter, almost blonde coloration. Bear cubs often have a distinctly bright collar that is lost as they age.

Brown bears have a distinctive facial profile with a prominent snout. Their eyes are relatively small compared to the size of their head. Brown bears eyesight is not as acute as their sense of smell, which they use to detect food and navigate their environment. Bears have strong, long, non-retractable claws that aid in foraging. Their hindfoot makes a track similar to that of a human foot, while the front paw leaves a track that is wider and shorter. Foot size, and therefore track size, vary in relation to body size, while track size can also vary based on the substrate. In general, it is only possible to differentiate between large males (mean front pad = 14 cm; mean back pad = 22.3 cm) and small subadult females (2-3 years old; mean front pad = 10.3 cm; mean back pad = 17.3 cm); track sizes from all other age classes and sexes overlap (Mattisson et al. 2019). Bears have teeth that are well-suited for their omnivorous diet, possessing sharp canines for tearing meat and molars for grinding plant material. Over time, the teeth of older bears often show signs of wear due to years of use.

In Scandinavia, adult males typically weigh between 150 to 350 kg or more (mean = ~250 kg), while adult females are generally smaller, ranging from 80 to 200 kg (mean = ~150 kg) (Swenson et al. 2007a). They reach peak body mass at around 7 to 8 years old (Swenson et al. 2007a). The large variation in size makes it functionally impossible to distinguish between solitary male and female bears in the field. Interestingly, bears in Scandinavia appear to gain mass during spring compared to bears in southern Europe (Dinara Mountains) which lose mass post hibernation (Swenson et al. 2007a). This is perhaps due to the greater availability and use of protein-rich food in Scandinavia during spring (Swenson et al. 2007a).

General behavior

Solitary nature: Scandinavian brown bears are typically considered solitary animals (i.e., nonsocial), especially males. Females seem to be slightly more social than males; adult females have been observed moving together for short periods of time (SBBRP observation). Otherwise, males and females associate during the breeding season, and of course females associate with their cubs during the rearing process. For more details on social and individual behavior see Section 3.1 Diet and foraging.

Communication: Bears use a mixture of vocalizations, body language, and scent marking to communicate with each other. Huffing or low growling sounds are used to assert dominance or warn of aggression when stressed. Stressed bears will also pop their jaws which makes a unique popping sound. Body language also plays a key role in communication. For example, when aggravated or threatened, bears may charge forward and/or stomp on the ground with their front legs and paws. Standing up, however, is generally done to increase their viewshed, rather than used as a warning. Marking behavior, including biting, scratching, stripping bark, and rubbing trees/other objects with their back, shoulders, and head, and scent-marking by urinating at the base of rub trees, is a key form of communication between bears as it can transfer information to others without direct interaction (González-Bernardo et al. 2021, Jojola et al. 2012, Penteriani et al. 2021). Visual signaling (signs that bears can see) can provide information about whether another bear was present (Penteriani et al. 2021), while information conveyed by scent marking (signs that bears can smell) includes individual identification including sex as well as information about reproductive status (González-Bernardo et al. 2021).

Home ranges: Brown bears are not territorial (i.e., they do not actively defend an area), but rather have overlapping home ranges (Dahle & Swenson 2003b). Males have larger home ranges than females, while female home range size is dependent upon their reproductive status. In other words, females with cubs of the year have smaller home ranges (small cubs are less mobile and more vulnerable), while females with larger cubs and solitary females have comparatively larger home ranges (Dahle & Swenson 2003b). Both females and males will disperse from their natal home range (i.e., their mothers home range), but males disperse more often (Zedrosser et al. 2007b). For more details on what affects home range size see Section 3.2 Habitat, movement, dispersal, home range, and space use.

Movement and activity: Brown bears are generally crepuscular animals, meaning they are most active during dawn and dusk. However, their activity patterns are flexible and vary between individuals, which means they can be active during other parts of the day and night (Ordiz et al. 2017a). Bears may also be more active at different times of the day depending on the availability of prey or the level of human disturbance (Ordiz et al. 2014, Ordiz et al. 2017a). For example, bears move more during the night and twilight hours and less during the daytime in areas with more human disturbance (e.g., higher road density; Ordiz et al. 2014). Regardless of the time of day they chose to be active, brown bears are efficient travelers and can move quickly over long distances. Bears are also proficient swimmers and can easily cross bodies of water, including lakes and rivers. For more details on bear movement and activity patterns see Section 3.2 Habitat, movement, dispersal, home range, and space use.

Mating, reproduction, and cub rearing: Brown bears have a polygamous mating system, meaning males mate with several females and females with several males. In Scandinavia, brown bear mating season typically occurs between May and June. Mean age at primiparity for females (i.e., the age that females reproduce for the first time) was estimated at 4.7 (south) and 5.3 (north) years old and ranged between age 4 and 7 (Zedrosser et al. 2007a, Zedrosser et al. 2009). Female brown bears have delayed implantation, meaning fertilized eggs remain dormant in the uterus for about five months, prior to implantation in November–December (Steyaert et al. 2012). The gestation period is around 6 to 8 months and females give birth to cubs in the den typically between January and March, with an average litter size of about 2.4 (range = 1 to 4) cubs (Bischof et al. 2018, Steyaert et al. 2012). In Scandinavia, female bears care for their cubs for between one and half to two and half years, after which the cubs move away from the female and the female may reproduce again (Dahle & Swenson 2003a, Steyaert et al. 2012). Infanticide is relatively common in the bear population, with males killing young cubs likely to induce the female into estrous sooner (Bellemain et al. 2006a, Steyaert et al. 2014). For more details on mating, reproduction, and fitness see Section 3.3 Mating, reproduction, and fitness.

Diet: Brown bears are opportunistic omnivores with a highly varied diet that changes seasonally (Stenset et al. 2016). In general, they feed on vegetation, including berries, grasses, roots, fungi, and protein in the form of insects, small mammals, ungulates, and other carrion. Bears are efficient predators of newborn ungulates (e.g., moose and reindeer calves; Rauset et al. 2012, Støen et al. 2022b, Swenson et al. 2007b) and are also effective scavengers (Tallian et al. 2017), but only rarely kill adult ungulates (Dahle et al. 2013). During spring and summer, bear diet in Scandinavia is predominantly made up of moose (i.e., newborn calves) and ants (*Formica* spp. and *Camponotus herculeanus*) (Stenset et al. 2016, Swenson et al. 1999a). During autumn, berries dominate the diet; the most important are bilberry (*Vaccinium myrtillus*), followed by crowberry (*Empetrum hermaphoditum*), and then lingonberry (*Vaccinium vitis-idaea*). Research suggests the proportion of berries in fall diet is stable between years, but the relative importance of the species varies (i.e., bears switched to crowberries when bilberries were less abundant; Stenset et al. 2016). For more details on the diet of the Scandinavian brown bear population see Section 3.4 Social and individual behavior and intraspecific interactions.

Denning and hibernation: Scandinavian brown bears hibernate during winter when they remain dormant for several months relying on stored fat for energy. During fall, bears enter into what is known as hyperphagia which is characterized by increased appetite and behavioral changes that help them gain fat reserves before entering hibernation (Fuchs et al. 2019). During hibernation, bear's metabolic rate significantly decreases, leading to a lowered body temperature, heart rate, and respiration rate, and they remain inactive, ingesting no food or water (Stenvinkel et al. 2013). Bears hibernate in dens, of which the most common type in Scandinavia's southern bear population are made from excavated abandoned anthills (Manchi & Swenson 2005). Bears also use dens in rock crevices or caves, and between or under boulders and, in rare cases, they use open dens that are made from branches, plants, and moss piled to form something resembling a large nest (Manchi & Swenson 2005). In Scandinavia, the mean date of den entry is 27 October (5 October-18 November) for males (Manchi & Swenson 2005) and 28 October (24 September-20 November) for females (Friebe et al. 2001), while mean date of den emergence is 4 April (6 March–25 April) for males (Manchi & Swenson 2005) and 20 April (6 March–14 June) for females (Friebe et al. 2001). Hibernation can last up to 6 to 7 months in Scandinavia, with females remaining in the den longer than males, and pregnant females staying in the longest (Manchi & Swenson 2005). For more details on denning and hibernation see Section 6.

Tolerance towards humans: Brown bears can exhibit varying levels of tolerance and aggression towards humans depending on the ecosystem. In Scandinavia, however, bears tend to be unaggressive and avoid people (Moen et al. 2019, Moen et al. 2012, Ordiz et al. 2019, Ordiz et al. 2013b). When bears were approached by humans in a series of approach studies performed by the SBBRP, the animals either moved away immediately or stayed in place and hid; no bears ever exhibited aggressive behavior towards humans when approached (Moen et al. 2019, Moen et al. 2012, Ordiz et al. 2019, Ordiz et al. 2013b). That being said, bears can act aggressively towards humans and injuries and even fatalities can occur, particularly when hunting bears (Støen et al. 2018). For more details on human-bear interactions see Section 5.2 The effects of hunting on the population, behavior, and evolution.

2.4 Bear health, parasites, and disease

KEY POINTS

- The brown bear population in Scandinavia is generally healthy (i.e., they have relatively low prevalence of disease, parasites, and infections).
- Bears are hosts for ticks that carry diseases, such as Lyme disease, that can affect human health; the prevalence of ticks and tick-borne diseases will likely increase as the climate changes.
- Congenital deformities have been detected in the Scandinavian brown bear population, but instances appear to be rare.
- Bears are known to have high levels of lead (Pb) in their blood, which may affect their health and behavior as well as affect human health when bear meat is consumed.

The population of brown bears in Scandinavia is generally a healthy one, meaning they are currently only minimally affected by pathological conditions such as parasites, disease, infections, and malformities (Swenson et al. 2020). However, individual bear health can be influenced by multiple factors including interactions with other organisms and human activities. Understanding their health, including parasite loads and disease dynamics, is essential for effective conservation and management efforts, particularly in the context of climate change. For example, it helps us understand fundamental aspects of bear behavior as well as assess current and future risks to the population.

Parasites

Like many wild animals, bears can host a variety of internal and external parasites. Examples of internal parasites include gastrointestinal worms such as helminths and nematodes, while external parasites include ticks and fleas (Swenson et al. 2020). Such parasites can affect bear health, particularly when infestations are severe. We know little about the internal parasite load of brown bears in Scandinavia, although external parasites have been observed. For example, chewing lice (*Trichodectes* spp.) were detected on two adult bears captured in 2014/2015, which caused extensive localized hair loss and skin discoloration (Esteruelas et al. 2016). There is also evidence that ticks (*Ixodes Ricinus*) are prevalent in the bear population, especially in the more southern bear population where the climate is warmer and more suitable for ticks (Paillard et al. 2015). This is important because ticks carry diseases, such as Lyme borreliosis and tick-borne encephalitis, which can affect both bear health but also spill over into human populations. Indeed, the prevalence of ticks and tick-borne diseases in wildlife populations is expected to increase at higher latitudes and elevations as the climate changes (Lindgren et al. 2000), which coincides with the incidence of tick-borne diseases in humans (Jore et al. 2011). Paillard et al. (2015) suggests that the long-term monitoring of large mammals, including bears, can provide insight into the shifting patterns of ticks and tick-borne diseases through time.

Disease

While brown bears can be susceptible to various diseases, in general, infectious disease is not a common cause of mortality for Scandinavian brown bears (Mörner et al. 2005). This has been substantiated by various research accounts. For example, Ursids in general seem to have low susceptibility to prion diseases (Stewart et al. 2012). Although rabies (a viral disease that can lead to aggressive or abnormal behavior and subsequent death in both infected animals and humans) has been observed in brown bears (Swenson et al. 2020), there is no evidence that it is currently present in the Scandinavian population. However, research does suggest that Scandinavian bears have high levels of antibodies for to the causative agent of Lyme disease (*Borrelia burgdorferi*) but not tick-borne encephalitis (Paillard et al. 2015), although it is unclear to what extent Lyme disease actually affects bear health. Examples of genetic defects have been observed in the population, although they are likely rare. For example, congenital hydrocephalus was detected in a cub who had the same father as his mother (Kübber-Heiss et al. 2009), a congenital heart defect was observed in an adult female (Ågren et al. 2005), and an adult female was observed with 6 toes on the hind foot.

Exposure to pollutants

Like many wildlife species around the world, brown bears in Scandinavia may be exposed to pollutants and contaminants in their environment. These pollutants can originate from various sources including industrial activities, agriculture, and human settlements. One such pollutant is lead (Pb), which is a global health problem for both humans and wildlife. Lead is a highly toxic heavy metal that can disrupt a wide variety of biological functions in living organisms and is dangerous for both wildlife and humans (Bellinger et al. 2013). Recent research found high lead concentrations in the blood of Scandinavian brown bears, and suggests that the bear population is subject to life-long lead exposure which may negatively affect both individual and population health (Fuchs et al. 2023, Fuchs et al. 2021). Importantly, lead exposure in brown bears may have direct consequences for human health when consumed (Fuchs et al. 2021, Hampton et al. 2023). For detailed information about lead exposure in the Scandinavian brown bear population, see Section 6.2 Ecotoxicology: Lead (Pb) exposure in Scandinavian brown bears.

2.5 Genetics and connectivity

KEY POINTS

- Brown bears expanded into Scandinavia from the south, originating from central Europe, via a northern route from eastern Europe and northwestern Eurasia after the last glacial retreat.
- Scandinavian brown bears can be clustered into three genetic subgroups; these genetic differences align to a high degree with the different phylogeographic expansion routes, and the grouping is still maintained today due to various reasons, e.g., habitat preferences, isolation by distance etc.
- Although not at a critically low level, genetic diversity is lower in the Scandinavian bear population compared to neighboring Finnish and Russian populations.
- Finland and Russia represent the nearest bear populations that entertain low to moderate levels of connectivity to the Scandinavian population and thus may contribute with new genetic material.
- Evidence suggests the population of Finland and Scandinavia have met at their respective expansion fronts.

Population genetics

The characteristics of individual and groups of brown bears are influenced by the environment they live in and thus they can differ across a range of scales, e.g., both within and between populations due to varied background conditions and population history. Studying these differences between or among groups or populations of organisms at the DNA-level constitutes the field of population genetics. Various molecular methods assess the genetic characteristics and variation between individuals (i.e., genetic diversity) to identify similarities and differences among groups. Every bear has a unique DNA-profile, except for identical twins, which means individuals can be identified, counted, and their sex established, and populations can be grouped based on how genetically similar they are. Comparing the genetic profiles of bears, both at the individual and population level, provides us with knowledge about their history, status, health, and relatedness, as well as the long-term effect of management actions. This is important because high genetic diversity increases the ability of bear populations to cope with their current environment and any subsequent future changes.

Population history and phylogeography: Initial genetic studies on the Scandinavian brown bear assessed the timing and recolonization routes of brown bears after the last glacial maximum. Studies using maternally inherited mitochondrial DNA (mtDNA) showed that bears recolonized from central Europe to southern Scandinavia, and eastern Europe and northwestern Eurasia into northern Scandinavia (Ersmark et al. 2019, Taberlet & Bouvet 1994, Taberlet et al. 1995, Xenikoudakis et al. 2015). So far, Ersmark et al. (2019) is the most comprehensive study on the phylogeography of the Scandinavian brown bear population and their results provided new evidence that recolonization after the LGM may had it source in central Europe (today’s Belgium and France) rather than the Iberian Peninsula, as previously assumed (Taberlet & Bouvet 1994, Taberlet et al. 1995). The most recent study suggested that the current genetic substructure of the bear population in Scandinavia is similar to the subgrouping found in historic samples Xenikoudakis et al. (2015), indicating that the current subpopulation structure is likely the product of historical ecological processes. Xenikoudakis et al. (2015) further identified numerous mtDNA-haplotypes among historic brown bear samples from Sweden, that are not present anymore, illustrating that once lost haplotypes but also alleles, will be lost forever. Like these maternal patterns, the y-chromosomal haplotypes are inherited from the father to the male offspring. Here, the Scandinavian brown bear population can be characterized with substantially low Y-haplotype diversity, compared to the neighboring Finnish-Russian population. Assessments found six different y-haplotypes in Scandinavia while in individuals from the Karelian population (northern Norway, Finland, and north-western Russia) 44 haplotypes could be identified leading to the assumption that the y-haplotype diversity in north-eastern Europe might be even higher; highlighting again the consequences of the past bottleneck of the Scandinavian brown bear population.

Current genetic structure of the Scandinavian brown bear: Genetic assessments showed that the Scandinavian brown bear population is structured into three genetic units, or clusters (Manel et al. 2004, Schregel et al. 2017, Tallmon et al. 2004, Waits et al. 2000), partly shaped due to isolation-by-distance, especially in the northern parts (Schregel et al. 2018). However, reasons for the persisting, historic substructure are also linked to current conditions and characteristics of the Scandinavian population. A similar genetic structure as today was identified also using historical samples, suggesting that the distinct subdivision, although overlapping, cannot be explained by the genetic bottleneck or by overhunting and anthropogenic fragmentation in recent times (Xenikoudakis et al. 2015). Areas with high brown bear densities inversely affect natal dispersal as males do not have to disperse far to find mating partners unrelated to them (Støen et al. 2006a). A combination of availability of suitable habitat, individual bear density, and differences in relatedness among bears in multiple areas can affect dispersal as well as influence successful reproduction of individuals outside the area they were born. It seems that current anthropogenic pressures are helping to further this population subdivision (Frank et al. 2021). On a more local scale, brown bears in Scandinavia can display fine-scale population structure and make these individuals more prone to spatial and temporal changes in the environment and landscape; especially caused by human settlements and infrastructure inbreeding (Frank et al. 2021, Norman et al. 2017). Such individuals can show higher levels of relatedness among each other that further increases the risk of inbreeding (Frank et al. 2021, Nellemann et al. 2007, Norman et al. 2017).

Current genetic diversity: Genetic diversity appears to be lower in brown bears from the Scandinavian population compared to the neighboring Karelian brown bear population in Finland and Russia. However, it is not at a critically low level. The populations in Finland and Russia likely consist of a much larger and more diverse gene pool and thus have greater genetic variation than the bear population on the Scandinavian Peninsula (Kopatz et al. 2014, Kopatz et al. 2021, Schregel et al. 2015). The genetic characteristics, including genetic diversity, contain important knowledge as this information is usually strongly linked to previous, current, and perhaps ongoing processes of population structure, that again, can have large effects on a population, especially when (sub) populations are fragmented and the focal population is isolated. Genetic drift, the random shuffling of genes within a population, can further lead to homogenization and, in the worst case, inbreeding. Anthropogenic pressure can amplify these effects and thus be detectable in the genetic make-up. For instance, genetic analyses combined with data on hunting pressure showed that different levels of harvest intensity can influence the genetic variation and subsequent structure of the Scandinavian bear population (Frank et al. 2021). Genetic diversity should be carefully monitored because a substantial reduction in genetic diversity, nuclear as well as sex-specific DNA and as partly reported for the Scandinavian brown bear population, can have severe consequences to the viability of a population (Ersmark et al. 2019, Kopatz et al. 2014, Schregel et al. 2015, Xenikoudakis et al. 2015). Low levels of genetic diversity can lead to severe inbreeding effects and extinction on the long-term, especially when a population is isolated and subject to drastic environmental changes (Heuertz et al. 2023, Pearman et al. 2024). Conservation and management should therefore aim to not only conserve the number of individuals, but also their adaptive potential.

Population connectivity

The number of brown bears in Scandinavia has increased over the last few decades and bears have re-expanded their presence into areas in which they were wiped-out decades ago (Chapron et al. 2014, Swenson et al. 1998). Simultaneously, brown bears also recovered in the neighboring country of Finland, helped by a strong influx of migrating brown bears from Russia (Kopatz et al. 2014). A recent assessment comparing genetics among male brown bears in Norway, Sweden, and Finland, revealed asymmetric, or unequal, gene flow between bears from Scandinavia and Finland. In brown bears, males are usually the sex that shows the highest rates of long-distance dispersal and thus is representative for inter-population connectivity. In other words, bears seem to move more often from Scandinavia to Finland, and less often from Finland to Scandinavia, i.e., more bears with genetic characteristics from Scandinavia have been detected in Finland than vice versa (Kopatz et al. 2021). That assessment indicates that both expansion fronts appear to have met, and connectivity may increase in the future. However, DNA-based monitoring data from all three countries should be harmonized and analyzed together to monitor this process (Kopatz et al. 2024). Any halt of migration and gene flow may affect the newly gained connectivity and may increase isolation of the Scandinavian brown bear population.

3 Brown Bear Behavior and Ecology

3.1 Diet and foraging

KEY POINTS

- Bears are omnivores, predators, and scavengers that rely on a wide variety of food resources. The use of food resources varies between seasons, individuals, and across years.
- Ants are a particularly important food resources after the denning period, making up an estimated 7% of their diet and 10-20% of their annual energy intake.
- Bears in Scandinavia predominantly prey on newborn moose and semi-domestic reindeer calves where their populations overlap. In general, moose calves make up an estimated 14-30% of their annual energy, but there is large variation in predatory behavior among bears.
- Berries, including blueberries, crowberries, and lingonberries are the most important summer-fall food source for bears in Scandinavia. In total, berries make up an estimated 45% of their annual energy intake.
- In general, bear diet has been examined in one of Scandinavia's core bear population in central Sweden. Diet may be a bit different in Norway and northern Sweden.

The brown bear is both an omnivore and a predator. In Scandinavia, bears get most of their energy intake from berries, ants, and ungulates (particularly moose calves), but they also eat many other types of grasses, forbs, and fungi. Their diet varies between seasons and years coinciding with the different pulses of food resources on the landscape and their nutritional needs (Stenset et al. 2016). For example, during spring, bears need food that can help them grow and build muscle mass, while in the summer and fall they must renew their fat reserves for the coming winter. Therefore, protein-rich foods tend to dominate the diet during spring and early summer while bears seek foods rich in carbohydrates, which are more easily converted to fat, during later summer and fall (De Cuyper et al. 2023). Bears also generally have a high-fiber diet throughout the year (De Cuyper et al. 2023). Interestingly, bears seem to have similar nutrient intakes regardless of their foraging strategy and their sex/reproductive status, which is attuned for preparing for the hibernation period (De Cuyper et al. 2023). However, bears in Scandinavia appear to eat less meat than might be expected, or observed in other systems (Mikkelsen et al. 2023).

Here, we cover the wide variety of foods they generally use and describe how diet can vary between seasons and years when different food sources are more or less available. For this section, we define the seasons as: spring = April-May, summer = June-July, fall = August-October.

Insects

Ants: During spring, ants are an important food source for bears in Scandinavia. Ants are a relatively abundant and available food source on the landscape, which makes them particularly important during the spring post-denning period (Swenson et al. 1999a). Red forest ants (specifically *Formica aquilonia* and *Formica polyctena*) and carpenter ants (*Camponotus herculeanus*) are consumed the most by bears in Scandinavia (Swenson et al. 1999a). Although red forest ants represent the majority of ant biomass consumed during spring, carpenter ants are more preferred, meaning relative to their availability, they are selected the most often (Swenson et al. 1999a). Furthermore, bears continue to eat carpenter ants during summer and fall, while their intake of forest ants drops off. Red forest ants (high in protein) are mound-builders and live in large above-ground colonies while carpenter ants (easily digestible and high in fat) live in dead wood, form smaller colonies, are less abundant, and therefore more difficult to get. In general, the carpenter ants preferred by bears tend to be high in energy content, low in formic acid, and behave relatively passively when their nests are disturbed (Swenson et al. 1999a).

Altogether, ants make up about 10-20% of the total annual energy intake of the Scandinavian brown bear and about ~7% of their major diet when compared with berries and moose meat (Johansen 1997, Mikkelsen et al. 2023). However, it is possible that shifting habitat conditions based on landscape practices and climate change have changed ant predation patterns over the last 25 years and may continue to do so. For example, carpenter ant availability is likely linked to forestry practices, with intensive clear-cutting resulting in more dead wood on the landscape in which the carpenter ants thrive (Frank et al. 2015, Swenson et al. 1999a). Scandinavian brown bears feed more on ants than bears in North America, perhaps because red forest ants are more widely available; the amount of available ant biomass was 3 times greater than moose biomass (including both calves and adults) in the Southern Study Area (Swenson et al. 1999a). Thus, this protein-rich food source is very important to bears in this region during spring and summer which is reflected in the diet. For example ants appear to contribute twice as much to their diet compared to moose (Mikkelsen et al. 2023).

Other: Other insects that have been found in small amounts in their diet include other ants (*Formica exsecta* and *Formica lugubris*), moth lacewings (*Oliarces clara*), maggots (*Diptera* spp.), bees, bumblebees and wasps (*Hymenoptera* spp.), and beetles (*Coleoptera* spp.) (Dahle et al. 1998, Elfstrom et al. 2014, Stenset et al. 2016, Swenson et al. 1999a).

Ungulates and other sources of meat

Ungulates, or hooved animals, play an important role in the diet of the Scandinavian brown bear. The nature of this relationship has far-reaching consequences for both the ungulate prey of bears as well as the general management of the bear population. For more information on the nature and consequences of bear predation on ungulates in Scandinavia, see Section 4.1 Bears as predators. Below, we summarize the extent to which these different ungulates contribute to bear diet.

Moose: Moose calves are the most heavily utilized ungulate by bears in Scandinavia and are a key part of their energy intake during the moose birthing period (mid-May to early June). Bears are generally best at hunting newborn moose within the first 4 weeks of the newborn's life (Swenson et al. 2007b), which means there is a short window during which bears incorporate moose into their diet (from mid-May through the end of June). Research suggests that, on average, bears take between 6.5 and 7.6 moose calves per year, which equals about 14-30% of their annual energy intake (Rauset et al. 2012, Swenson et al. 2007b). Nevertheless, there is large variation in bear predatory behavior; some bears do not kill a single moose calf, while others take 10 or more per spring (Ordiz et al. 2020a). Thus, moose meat may be a very important part of the diet of some bears, but relatively unimportant for others.

Bears are also capable of killing adult moose, which happens more often during April and May when moose are in generally weaker condition from winter and during the birthing period when females are more vulnerable (Dahle et al. 2013). Although predation on adult moose seems to happen more rarely in Scandinavia than for example in North America (Dahle et al. 2013), the protein provided from an adult moose kill during spring is a rich resource for the successful hunter. Bears are also adept scavengers and protein can be acquired from both bear-killed and wolf-killed remains, where bears and wolves overlap, as well as from moose slaughter remains left by hunters (Tallian et al. 2017, Tallian et al. 2022). However, scavenging behavior may vary between individuals. For example, females with cubs of the year seem to scavenge less often on slaughter remains than other bears, likely to avoid interactions with other bears (Elfstrom et al. 2014).

Reindeer: In semi-domestic reindeer herding areas, reindeer calves are also an important contributor to bear diet, and a continual source of conflict for reindeer herders. In our Northern Study Area, we estimated each adult bear takes about 10.2 reindeer calves per year (range 8.6 – 11.5) (Støen et al. 2022b). Similar to moose, bears also hunt newborn reindeer during their first 4 weeks of life. Reindeer calves are therefore also available in a pulse from early to late May, after which bears likely switch to moose calves (Støen et al. 2022b). Bears also kill adult reindeer, the majority of which also occurs during the birthing period (Støen et al. 2022b). Thus, where the two overlap, reindeer provide a pulse of protein-rich food during the post denning period.

Sheep: In contrast to Sweden, Norway has 1.9 million free-ranging domestic sheep (ssb.no), which means that sheep play an important role in the diet of bears in Norway, but not Sweden. For example, an early study conducted in the late 1980's and early 1990's suggests that bears in Nord-Trøndelag received as much as 65-87% of their annual energy intake from ungulates, which was mostly made up of sheep (Dahle et al. 1998). How much sheep currently contribute to bear diet in Norway remains unknown. However, a 2022 pilot study in Trøndelag explored the potential for using molecular methods to monitor sheep consumption via scat collection (Kopatz et al. 2023). They found sheep DNA in only 5% of the sampled scats, most of which was detected in August (Kopatz et al. 2023).

Other: Bears are opportunistic feeders and have a wide diet breadth. Other sources of meat have been found in their diet including a variety of bird and rodent species (Dahle et al. 1998) and domestic livestock such as pig and cattle (Elfstrom et al. 2014).

Plants

Berries: Berries are one of the most important food sources for bears in Scandinavia and constitute the majority (89%) of their diet (Mikkelsen et al. 2023). Berries have matured by the late summer to early fall, during which time the bear switches diet yet again. As previously mentioned, berries contain high-calorie carbohydrates that can be easily converted to the fat bears need to endure the hibernation period. Bears preferentially eat blueberries (*Vaccinium myrtillus*), crowberries (*Empetrum* spp.), and lingonberries (*Vaccinium vitis-idaea*) with their preference changing between seasons (Hertel et al. 2016a, Stenset et al. 2016). For example, crowberries and lingonberries are selected more during spring, likely because there are berries remaining from the previous year, while blueberries are preferred during fall when they have come into season. An adult bear can eat up to a third of its own body weight in berries in one day, which equals about 20,000 calories. Altogether, berries make up about 45% of a bear's annual energy intake in Sweden. Although berry production can fluctuate from year to year in Scandinavia, the general occurrence of berries in bear diet appears to remain relatively stable (Stenset et al. 2016). This is because bears compensate for decreased availability of one berry species by switching to another. For example, when blueberry production is low, bears eat more crowberries (Stenset et al. 2016). However, berries are not an equally important food source for all bears across Scandinavia. In Norway, for example, only 6%-17% of a bears annual energy intake comes from berries; the majority comes from sheep (Dahle et al. 1998). They also appear to be less important in the far north of Scandinavia where bears eat more meat (Persson et al. 2001). This variation illustrates that food availability is a very important driver of the seasonal and geographical changes in bear diet. For example, in southern Europe bears rely on so-called hard mast (oak and beech nuts) in the fall, and less so on soft mast (berries), reflecting the availability of different food items at different latitudes, e.g., in Slovakia (Štofik et al. 2013).

Grasses, forbs, and other plants and fungi: Scandinavian bears also use a wide range of grasses (graminoids) and herbaceous flowering plants (forbs) to supplement their diet throughout the year (Dahle et al. 1998, Elfstrom et al. 2014). They appear to eat grasses rather steadily through spring and summer but slightly less in fall while their use of forbs peaks during the summer months when flowers are in bloom (Dahle et al. 1998, Stenset et al. 2016). Bears also eat spore producing plants (cryptograms) such as ferns, horsetail reeds, and thistles (Dahle et al. 1998, Stenset et al. 2016). Mushrooms (fungi) appear more in their diet during fall (Dahle et al. 1998, Stenset et al. 2016).

Brown bear diet in context

The majority of the studies on bear diet in Scandinavia have been conducted in our Southern Study Area, apart from the reindeer predation studies that were conducted in the Northern Study Area. This is important as bears in Scandinavia have access to different food resources as well as varied amounts of those resources depending on where they live. That means different foods may be more or less important for local bear populations across Scandinavia. For example, an early diet study based on scat collect between 1978 and 1982 in the Pasvik Valley in northeastern Norway suggests that bears are more carnivorous in the far north (Persson et al. 2001). Unlike southern Scandinavia, meat from ungulates, particularly adult moose, were the most important foods during spring and summer, with meat from ungulates contributing 85% of their energy content (Bojarska & Selva 2012, Persson et al. 2001). Furthermore, berries were also important during fall, but ungulates remained an important source of energy for northern bears as well, and the contribution of insects and vegetation was minimal (Persson et al. 2001). Thus, the diet of Scandinavian brown bears as described above should be understood with the caveat that it in general describes the diet of bears in the southern population, unless otherwise noted.

3.2 Habitat, movement, dispersal, home range, and space use

KEY POINTS

- Bears in Scandinavia primarily dwell in the boreal forest, favoring rugged forested terrain compared to flatter forested terrain and bogs, but habitat use is affected by a variety of factors.
- Bears in Scandinavia are generally crepuscular, meaning they are the most active during the early morning and the evening/night.
- Bear home range size (from largest to smallest) is as follows: adult males – subadult males – solitary adult females – females with yearlings / subadult females – females with cubs of the year, yet there is seasonal variation.
- The home ranges of female bears overlap, especially those of related females. The larger home ranges of male bears typically overlap several female home ranges.
- Male bears are more likely to disperse (move away from their mother's home range) and resettle further away than females.

Brown bear home ranges

Brown bears occupy home ranges, or an area where the bear lives and obtains its resources. Unlike territories of group-living species, these areas are not defended and commonly overlap with the home ranges of other individual bears (Dahle & Swenson 2003b). Nevertheless, it is interesting to note that there are areas that seem to be occupied quite exclusively by closely related individuals (Støen et al. 2005). Adult home range size across the entire bear 'active period' (approximately May through September) was preliminarily evaluated in 2003 using VHF technology (Dahle & Swenson 2003b). These results suggest that, in general, average home range size was greater in the north compared to the south (Dahle & Swenson 2003b). Adult male home ranges were larger than adult females', while solitary female home ranges were larger than those of females with yearlings or females with cubs of the year (see Table) (Dahle & Swenson 2003b). Similarly, subadult males also have larger home ranges than subadult females (Dahle et al. 2006). These home ranges are generally larger than those reported from central and southern Europe, for example Romania (Pop et al. 2018), Bulgaria (Gavrilov et al. 2015), Croatia and Bosnia and Herzegovina (De Angelis et al. 2021), and Spain (Ordiz et al. 2007), but are similar to home range sizes reported for bears in boreal forests in North America (Dahle & Swenson 2003b). Variation in home range size during summer only (May-August) was more recently explored using GPS data in 2019 and the findings are put into context below (Mattisson et al. 2019). While the estimates provided below are a general guideline for bear home range size in Scandinavia, it is important to understand that the home range size of individual bears can vary widely depending on their reproductive status and environment, e.g., habitat quality, food availability, bear population density, season, and human disturbance.

Factors affecting bear home range size

Female reproductive status: Female with cubs of the year generally have smaller home ranges than solitary females or females with yearlings (see Table) (Dahle & Swenson 2003b, c). Newborn cubs are small and have limited mobility which likely restricts the mothers' movements directly after den emergence. The home range size of females with cubs of the year slowly increases throughout the rest of the season after the risky mating period ends and as the cubs become more mobile (Dahle & Swenson 2003c, Mattisson et al. 2019). Females with larger cubs and solitary females have comparatively larger home ranges (Dahle & Swenson 2003b).

Mating season: Adult males increase their range during mating season (May-June), when they roam broader areas in search of females (Mattisson et al. 2019). For example, a recent report shows that mean adult male home range size was 865 and 1022 km^2 in May and June, which then decreased to 725 and 547 km^2 in July and August (Mattisson et al. 2019). Like males, solitary females increase their range size during the mating season while in search of mates, although their range size is still small compared to males (190 and 266 km^2 in May and June and 167 and 151 km^2 in July and August) (Mattisson et al. 2019). On the other hand, females with cubs of the year restrict their ranges during mating season to avoid contact with infanticidal males (Steyaert et al. 2013a), which is an important cause of cub mortality (Dahle & Swenson 2003c).

Food availability: Food availability is often a primary driver of brown bear home range size with the general rule being that a high amount of food decreases home range size, while less food increases home range size. Although this is likely true to some extent in Scandinavia, we find little evidence for this. For example, bear home range size does not increase during years with low berry production, their primary fall food source, as might be expected (Hertel et al. 2019b). This is likely because there is a relatively continuous distribution of berries across the Scandinavian landscape. This indicates that bears are not very food limited during the hyperphagia season in Scandinavia (Hertel et al. 2019b). An earlier study from 2006 also found that subadult home range size was not linked to variation in local food condition, which is intuitive as dispersing bears would likely not be limited by food availability (Dahle et al. 2006). However, this should be interpreted with caution as climate change may create greater swings in berry and other food availability which may affect bear home ranges in the future.

Population density: In general, a high bear population density can lead to smaller home ranges as bears compete for limited resources. This is true in Scandinavia, where we observed that home range size estimates for both sexes and age classes (male/female and adult/subadult) of bears in the south decreased as local bear density increased (Dahle et al. 2006, Dahle & Swenson 2003b).

Habitat quality and human disturbance: The type and quality of available habitat can also play a significant role in bear home range size. As described below, bears in Scandinavia generally prefer rugged forested terrain and avoid human-related infrastructure (Martin et al. 2010). Human activities, such as logging, road construction, and recreational activities may degrade habitat and lead to larger home ranges as bears move to avoid these disturbances, but this remains unknown.

Habitat selection and space use

The majority of what we know about bear habitat selection in Scandinavia comes from the Southern Study Area. At a broad scale, bears in Scandinavia primarily dwell in the boreal forest, largely preferring rugged forested terrain compared to flatter forested terrain and bogs. However, it is important to understand that the types of habitats bears use is driven by both human activities as well as the time of day and seasonal pulses of different foods.

Factors affecting bear habitat selection and space use

Time of day: Habitat selection naturally varies between resting periods (when bears seek cover) and active periods (when bears are foraging for food). In general, bears choose habitats with relatively dense vegetation and limited visibility when they rest, especially during daytime and in summer, when there is more human activity in the forest (Ordiz et al. 2011). For example, when resting during the day, bears are more likely to use dense patches of forest or forested bogs and avoid open areas such as clearcuts (Moe et al. 2007). When they are active during the morning and dusk, however, they use habitats that provide access to food resources.

Seasonal food availability: Bears use habitats differently at different times of year and in a way that coincides with the availability of seasonal food sources. For example, during the spring ungulate birthing period when bears prey on both newborn moose and/or reindeer, bears use habitats where they are more likely to find newborn calves. Bears in Scandinavia primarily prey on newborn moose and, during the birthing season, they use areas closer to old clear cuts and deciduous forests; moose commonly use deciduous forests during the birthing period (Twynham et al. 2021). With bears that overlap reindeer areas in Scandinavia, they generally use more rugged terrain, closer to wetlands and coniferous forests during this period where they are more likely to find reindeer with newborns (Twynham et al. 2021). During the prime berry season, on the other hand, bears move to areas with either high probability of blueberry occurrence and high abundance, or a high probability of lingonberry abundance, which generally included mature or missed forests or clear cuts (Hertel et al. 2016a, Moe et al. 2007).

Reproductive status and individual variation: The choice of resting area also differs between females according to their reproductive status. For example, compared to solitary females, females with cubs of the year rest in habitats that have more open vegetation, i.e., tall dense forest with more tall pine trees and fewer spruce and broadleaved trees (Swenson 2003). These tall trees are excellent for cubs to climb to avoid danger, thus this choice of habitat is likely a strategy to avoid infanticide from male bears during the mating period (Swenson 2003). We also see consistent individual variation in habitat selection among brown bears. For example, when controlling for availability of the habitat, some bears are more likely to use boggy areas and clear cuts than others (Leclerc et al. 2016b).

Human disturbance: Like other large carnivores in Scandinavia, bears generally avoid areas with a lot of human activity and human-related infrastructure including cities, towns and cabin fields, houses, and roads (especially large roads) (Leclerc et al. 2016b, Milleret et al. 2018, Moe et al. 2007) although there are exceptions to this. They also alter their fundamental behavior when they are in closer proximity to humans (Martin et al. 2010, Nellemann et al. 2007, Ordiz et al. 2011, 2017b) For more details on the effects of human disturbance on habitat selection and space use see Section 5.1 Human disturbance and brown bear behavior.

Movement and Dispersal

Movement and circadian rhythm: Bears in Scandinavia are generally the most active during two different time periods over the course of a day – early in the morning (~400-800) and during the evening/night (~1800-2200) (Martin et al. 2013). However, how far they move and how much they move can vary depending on their age, sex, and the season. For example, males tend to move greater distances than females (Dahle & Swenson 2003b), a pattern that is even more pronounced during the mating season (Mattisson et al. 2019). Females also change their movement patterns based on season. For example, they tend to be relatively inactive right after they emerge from their den, with short active periods during morning and evening (Martin et al. 2013). Activity picks up after that and remains high during the mating, post-mating, and hyperphagia periods (Martin et al. 2013). Females with cubs of the year tend to move more during the daylight hours right after den emergence and during the mating season, compared to other females, likely in an attempt to avoid infanticide (Martin et al. 2013). During the mating season, however, solitary females in estrous will travel farther than at other times of the year, likely in search of mates. This period also coincides with the spring predation period, however, and it is possible that females travel further during this time to increase the chances of running into newborn moose, not just to maximize the chances of finding mates. Bear movement patterns can also be affected by humans and in general, bear movements generally peak in the hours without outdoor human activity (Ordiz et al. 2017a). For example, bears move most in the nocturnal and twilight hours and less during daytime in areas with higher road density compared to more roadless areas (Ordiz et al. 2014).

Dispersal and resettlement: Dispersal is defined as an animal leaving the home range of their mother (i.e., their natal home range), traveling a certain distance, and settling their own home range. In general, male bears are more likely to disperse than females. Data from the Northern and Southern Study Areas in Scandinavia showed that 32% (N) and 46% (S) of females and

81% (N) and 92% (S) of males dispersed before reaching the age of 5 (Støen et al. 2006a). Furthermore, males have a 94% probability of leaving their natal home range, while females only have a 41% probability (Zedrosser et al. 2007b). The majority of males disperse when they are two years old, while the majority of females disperse when they are three (Støen et al. 2006a). Male dispersal often occurs within a single year whereas female dispersal may occur over multiple years (Støen et al. 2006a). Males also tend to move further away from their natal home ranges than females (see graph). For example, the longest dispersal distance recorded was 90 km for females and 467 km for males (Støen et al. 2006a).

The likelihood that a bear disperses, and how far they eventually go, can be affected by a number of factors other than sex. For example, high local bear density increases the likelihood that a bear will disperse as well as the eventual distance they travel. This implies that bears in northern Scandinavia, where bear density is lower, are less likely to disperse. Bears in the southern Scandinavia population, on the other hand, are more likely to disperse and also tend to move further away (Støen et al. 2006a). At the family-unit level, competition between parents and siblings can also drive dispersal patterns. For example, daughters settled twice as far away from their natal range when their mother was alive compared to when she was dead (Hansen et al. 2023). A type of ‘dominance hierarchy’ among female siblings from the same litter, which is based on body size, may cause the subordinate sisters to disperse (Zedrosser et al. 2007b). The presence of human-related disturbance has also been shown to affect dispersal movement patterns in male bears (Thorsen et al. 2022).

The dispersal and resettlement patterns of bears is important to understand because these patterns affect population range expansion and internal and external connectivity, i.e., connectivity within Scandinavia’s three subpopulations and connectivity with other populations such as those in Finland and Russia. Internal and external population connectivity affects gene flow, and therefore the genetic health of the population (Kopatz et al. 2012, Schregel et al. 2017). Bear dispersal patterns should be continuously monitored due to their important effect on the population’s expansion front, connectivity, and genetic health.

3.3 Mating, reproduction, and fitness

KEY POINTS

- Brown bears are promiscuous, i.e., they mate with multiple partners. Mating season is between mid-May and early July; however, the development of the embryo is delayed until after they enter the den when it finally becomes implanted in the uterine wall.
- Sexually selected infanticide, the killing of unrelated cubs by adult males to gain access mating opportunities with the mother, occurs in Scandinavian brown bears and may be an adaptive mating strategy for males. Females exhibit multiple behaviors as a counter strategy to avoid losing their cubs.
- Females generally start reproducing between 4 and 5 years old and stop reproducing around 28 or 29.
- Females give birth to between 1 and 4 cubs in their dens and keep their cubs for between 1 ½ to 2 ½ years.
- Female reproductive success is positively linked to body size and condition, berry abundance, competition from other females, and infanticide by males.
- In the Northern Study Area, bears have a later parturition date and a later den exit, maintaining a similar amount of time before den exit, except for younger mothers in years following lower food availability who often exit the den earlier likely because they have lower fat reserves.
- Decreased berry abundance in the fall could impact the reproductive and hibernation phenology of Scandinavian brown bear females and lead to a lower cub survival with potential consequences on the population dynamics.

Mating system

Brown bears have a polygamous mating system, meaning males may mate with several females and females may mate with several males (Bellemain et al. 2006a, Schwartz et al. 2003, Steyaert et al. 2012). However, females are the sole care givers once cubs are born, and males show no paternal investment and do not help to raise their young. Brown bears are a long-lived species that reproduce relatively slowly, i.e., they have a slow life history. They take several years to reach sexual maturity (Zedrosser et al. 2007a, Zedrosser et al. 2009), and their cubs require between 1 and 2 years of maternal care during which time the female does not reproduce (Dahle & Swenson 2003a). Their reproductive cycle is flexible; some females remain with their cubs for 1 ½ years while others remain with them for 2 ½ years (Dahle & Swenson 2003a, Van de Walle et al. 2021b). Females have the ability to reproduce again if they lose their newborn cubs before or during mating season (Bellemain et al. 2006a, Steyaert et al. 2014). Because females can come into reproductive readiness (estrous) when they lose their cubs during the mating season, infanticide (the killing of cubs by adult males) can be influential in their mating system and reproductive behavior (Bellemain et al. 2006a, Gosselin et al. 2017, Steyaert et al. 2012).

Sexually selected infanticide: Research in Scandinavia suggest that brown bears exhibit sexually selected infanticide, in which adult males kill unrelated cubs in order to increase their chances of fathering more cubs during their lifetime (Bellemain et al. 2006a). Although it is possible males kill young for reasons other than facilitating reproduction, e.g., to decrease competition, our research has shown that the main requirements for cub killing as mating strategy are met: First, killing all cubs results in the mother coming into estrous sooner than she would have otherwise, 2) the males killing the cubs are not the cubs father, 3) the infanticidal male is likely to be the father of the next litter, and 4) infanticide only occurs during mating season (Bellemain et al. 2006a, Steyaert et al. 2014). Sexually selected infanticide is relatively common in the bear population in Scandinavia, with males killing young cubs to induce the female into estrous sooner, and both resident and immigrant males commit infanticide with cubs they have not fathered (Bellemain et al. 2006a, Steyaert et al. 2014).

Because of this, females have several counter strategies to protect their cubs of the year from male infanticide. First, mating with multiple partners, especially with partners who have more overlapping home ranges, may help hide the fathers identity (Bellemain et al. 2006a). Although it remains uncertain, delayed implantation (described below) may also further help hide paternity (Friebe et al. 2014). Finally, they move through and use the habitat in their home range during the mating season in a way that avoids males (Steyaert et al. 2013a). For example, females with cubs of the year restrict their movement, and use areas that are closer to humans, and in less rugged and more open areas, which is opposite of what males select for during this time (Steyaert et al. 2013a). This creates a type of ‘human-shield’ effect whereby females with cubs of the year trade off risks associated with close proximity to humans, presumably to decrease the chances of losing their cubs (Steyaert et al. 2016a). Indeed, females appear to change movement strategies after the loss of their cubs; females who lose all of the cubs prior to or during mating season start the roaming behavior typical of mating females within 1 or 2 days of cub loss (Steyaert et al. 2014). However, protecting their young comes at a cost for female bears (Steyaert et al. 2013b). Females who have cubs of the year have a lower quality diet during the mating season than other females, but not during other times of year (Steyaert et al. 2013b), further reinforcing that females trade-off foraging for the safety of their cubs (Steyaert et al. 2013b). Bear hunting has huge implications for patterns of infanticide in Scandinavia’s bear population, for more on this subject please see Section 5.2 The effects of hunting on the population, behavior, and evolution.

Mate choice: The mating season begins in late May and lasts through early July (Dahle & Swenson 2003c). During this time, both males and females will roam more (i.e., increase their travel distance and area used) to find mates (Dahle & Swenson 2003c). Males tend to mate with multiple partners to increase their chances of fathering more cubs, while females have multiple partners to decrease the chances of male-induced infanticide (Bellemain et al. 2006b). For example, females tend to mate with males that are larger and whose home ranges overlap more with theirs (Bellemain et al. 2006b). Interestingly, between 14% to 28% of litters with ≤3 cubs had cubs with different fathers (Bellemain et al. 2006a), which likely further reduces the chances of cub loss to infanticidal males (Bellemain et al. 2006a). Only about 2% of the cubs are the result of incestuous mating in Scandinavia.

Sexual maturity and age of last reproduction: The average age that females reproduce for the first time (i.e., age at primiparity) was estimated at 4.7 years old in the Southern Study Area and 5.3 years old in the Northern Study Area, with a range between age 4 and 7 (Zedrosser et al. 2007a, Zedrosser et al. 2009). Interestingly, females that disperse farther away from their mothers home range reach sexual maturity almost a year earlier than females that remain nearby; at 4.3 compared to 5.2 years old (Støen et al. 2006b). This reproductive suppression is likely due to increased competition between females, i.e., older dominant females have better access to resources than younger subordinate females, but young females who move to newer areas with a lower bear density may have better access to food (Støen et al. 2006b). The probability of having cubs declines sharply after the age of 28 or 29 (Schwartz et al. 2003).

Reproduction

Estrous: Female bears are sexually receptive, or in estrous, between mid-May and early July each year. However, only solitary females or females who will wean their cubs that year are sexually receptive, although as previously mentioned, females with cubs of the year may enter estrous if they lose their cubs before or during the mating season (Steyaert et al. 2012). The majority (91%) of females that lose all of their cubs before or during mating season re-enter estrous and produce cubs the following year (Steyaert et al. 2014).

Implantation: Bears are the only mammals for which delayed implantation, active gestation, parturition, and lactation have been reported during hibernation, a period when they do not eat, drink, urinate or defecate for several months. After mating, the female experiences an obligatory ‘embryonic diapause’, which is when the embryos halt development very early on (at the blastocyst stage) and remain free-floating in the uterus rather than attaching to the uterine wall (Kordek & Lindzey 1980, Wimsatt 1963). The termination of embryonic diapause is marked by the reactivation of the corpus luteum (a mass of cells that forms in the ovaries during estrous which is responsible for progesterone production early in pregnancy), leading to a surge in progesterone (Tsubota & Kanagawa 1993, Tsubota et al. 1987). Following this, embryo implantation typically occurs in November-December, after the female has entered her den (Friebe et al. 2014, Lemière et al. 2022). In carnivores exhibiting delayed implantation, a period known as the ‘secretory phase’, lasting several days, intervenes between corpus luteum reactivation and blastocyst implantation, during which the uterus prepares to receive the fertilized eggs. The duration of the secretory phase in bears remains unknown, hindering precise determination of active gestation length. In our Southern Study Area, the mean date of implantation was 1 December, and the mean date of birth for mature females was 12 January (Lemière et al. 2022).

Excluding the secretory phase, the active gestation in brown bears is estimated to last between 56 and 60 days based on body temperature and progesterone levels (Friebe et al. 2014, Lemière et al. 2022, Tsubota et al. 1987). The active gestation phase is characterized by heightened metabolism due to sustained high progesterone levels and the presence of fetuses (Shimozuru et al. 2013). During gestation, body temperature is elevated and stable, ranging between 37–38°C compared to the typical 34–36°C, and drops to near hibernation levels around parturition (Friebe et al. 2014, Lemière et al. 2022). Gestation onset is presumed to occur in November-December when progesterone levels and body temperature (Friebe et al. 2014) begin to rise. Implantation is improbable before body temperature stabilizes at near-active levels, as various studies indicate the necessity of a high and stable body temperature for embryo development during the active gestation phase in both hibernating and non-hibernating mammals (Laburn et al. 2002, McAllan & Geiser 2014, Schmidt et al. 2020). Thus, a recalculated gestation length in the Scandinavian brown bear is 49-53 days (Lemière et al. 2022).

Birthing in the den: Parturition typically occurs around January-February in the den with the cubs weighing between 350 to 500 g, depending on the size of the mother and the number of cubs (Friebe et al. 2014). Bears demonstrate a sharp drop in body temperature and activity levels coinciding with parturition (Friebe et al. 2014, Lemière et al. 2022). These activity and thermal patterns provide distinctive markers facilitating parturition determination in free-ranging populations. The females lactate and provide food for their young in the den for 3-4 months before emerging in spring (Steyaert et al. 2012). Unlike the mother, the newborn cubs are awake, physically active, have normal physiological functions, and have sleep cycles similar to other mammalian young (Friebe et al. 2014).

Litter size: In Scandinavia, females reproduce every 2-3 years, (depending on how long females keep their cubs) (Dahle & Swenson 2003a, Van de Walle et al. 2018), giving birth to an average of 2.4 - 2.7 cubs (range = 1 to 4) (Bischof et al. 2018, Gonzalez et al. 2012, Steyaert et al. 2012). Litter size (i.e., the number of cubs) is related to the age of the mother; older mothers tend to have larger litters (Gonzalez et al. 2012). On average, females that give birth for the first time tend to have slightly smaller litters; 1.9 cubs compared to 2.4 cubs for females that had already reproduced once (Zedrosser et al. 2009). In general, prime aged-females, or females between the ages of 9 and 20 years old, produce the most offspring (Schwartz et al. 2003). There are two documented occurrences of mixed-age litters in Scandinavia, which appear to have occurred when the mother thought her cubs died, subsequently mated, and then were subsequently reunited with their cubs (Swenson & Haroldson 2008).

Reproductive success: Reproductive success in female brown bears is tied to body weight and condition, which is linked to food availability, especially the availability of important fall food such as berries (Hertel et al. 2018, Lemière et al. 2022). Bear body weight increases when blueberries are more abundant, and female body weight plays an important role in cub production (Hertel et al. 2018). For example, lighter females have lower reproductive success compared to heavier females in poor blueberry years, but reproductive success is stable for all bears when blueberry abundance is high (Hertel et al. 2018). Interestingly, this seems to be more important for younger females (< 8 years old), which unlike older adult females, delayed giving birth, spent less time in the den with their cubs, and subsequently had lower reproductive success in years with low blueberry abundance (Lemière et al. 2022). In other words, “some bears are more vulnerable to food shortages than others” (Hertel et al. 2018). This is important in the context of climate change, as decreased fall berry production could negatively affect their hibernation patterns and subsequently, their reproductive success in general (Lemière et al. 2022).

There is a trade-off between litter size and cub body mass that likely affects overall cub survival (Gonzalez et al. 2012, Van de Walle et al. 2020). Evidence suggests that mothers invest more in their heavier cubs, while smaller cubs suffer the consequences of having more siblings (Van de Walle et al. 2020). Cub survival increases when adult male mortality is higher in the previous years, probably because of decreased chances of sexually selected infanticide (Swenson et al. 2001b). First-time mothers have a greater chance of losing their cubs compared with females who have been a mother before, although this is slightly tempered if the first time mother is older when she reproduces for the first time (Zedrosser et al. 2009). First time mothers are most likely to lose their cubs either directly after den emergence, especially when food is less available, or during mating season due to infanticidal males (Zedrosser et al. 2009). We have also observed female-female reproductive suppression in females living near one another (Hansen et al. 2023, Ordiz et al. 2008). Females who settle closer to their mother’s home range appear to have lower reproductive success, possibly due to delayed primiparity or reproductive suppression by their mothers (Hansen et al. 2023). Interestingly, a female’s probability of having cubs is influenced by whether or not the female closest to them had cubs; when the neighboring female also had cubs, the females chances of having cubs that year decreased (Ordiz et al. 2008). Finally, cub survival was greater when yearlings (1 ½) stayed with their mother an extra year, i.e., they were weaned at 2 ½ (Zedrosser et al. 2013). This is likely in part because hunters are prohibited from harvesting family groups (Zedrosser et al. 2013). For more on cub survival within the population see Section 2.2 Population ecology and current status.

In Scandinavia, male reproductive success has been shown to increase with population density, likely because there is greater access to more females as female densities are lower near the population expansion front (Zedrosser et al. 2007a). In general, older and larger males generally seem to sire more cubs, or have greater reproductive success, then younger smaller males, possibly because they are better competitors (Zedrosser et al. 2007a). Inbred males appear to have lower reproductive success than males with a more diverse genetic makeup (Zedrosser et al. 2007a). Interestingly, individual male reproductive success was higher in the Northern Study Area than in the Southern Study Area (Zedrosser et al. 2007a). In the North, age was more important while body size was more important in the South. This is likely because one older male dominated reproduction in the North at the time, while in the South where there are more bears, body size related to competition likely was key for access to females (Zedrosser et al. 2007a).

Cub rearing

In Scandinavia, female bears care for their cubs for between 1 ½ to 2 ½ years, after which the cubs are ‘weaned’ and gain independence from their mother who may then reproduce again (Dahle & Swenson 2003a, Steyaert et al. 2012). Mothers usually separate from their cubs early in the mating season when her estrous begins, and family breakup is often associated with the presence of an adult male (Dahle & Swenson 2003d). Our research has previously shown that 95% of cubs are weaned as yearlings (i.e., at 1 ½ years) in our Southern Study Area (Dahle & Swenson 2003d). In the Northern Study Area, however, only 47% are weaned as yearlings while the remaining 53% move away from their mother as two year olds (i.e., 2 ½ years) (Dahle & Swenson 2003a). Why some females keep their cubs an extra year is an important question because the length of maternal care directly affects the timing of reproduction and subsequently population growth rate and size. In the Northern Study Area, where the environment is harsher and more limiting, it appears that yearling body mass, and factors that affect yearling body mass such as litter size and the mother's body mass, directly affected how long the cubs stayed with the mother. In this area, smaller cubs stayed with their mother an extra year (Van de Walle et al. 2021b). However, how long cubs stayed with their mother in the Southern Study Area is not affected by yearling growth, but may be more correlated with other activities such as hunting pressure (Van de Walle et al. 2021b). Indeed, hunting pressure may be driving longer maternal care, as family groups are protected from hunting, and keeping cubs an extra year provides a buffer from hunting pressure (Van de Walle et al. 2018). For more information on the effects of hunting see Section 5.2 The effects of hunting on the population, behavior, and evolution.

3.4 Social and individual behavior and intraspecific interactions

KEY POINTS

- Brown bears are a solitary species, but they communicate and interact throughout their active period and sociality peaks during the mating season. Additionally, family groups including dependent offspring and their mother are highly social during the natal period.
- Females also provide 1.5 – 2.5 years of intense maternal care during which offspring learn from their mother.
- The social organization of female brown bears is based on multiple generations of related females with highly overlapping home ranges, known as matrilines.
- Outside of mating and the natal period, bears have highly reduced number of social encounters.
- Bears use scent communication in gathering information (e.g., rubbing trees) about the identities of their neighbors.

Scandinavian brown bears are solitary animals that live individually, rather than in groups. However, that does not mean that the Scandinavian bear population does not have an underlying social organization or that bears never interact. Indeed, bears in Scandinavia interact with other bears in various ways during their active period and have a complex matrilineal social structure, i.e., a structure based on the multiple generations of related females (Støen et al. 2005). They also display a wide array of behaviors that can vary between individuals, at least some of which is driven by social learning (Hertel et al. 2023). Individuality is important as the variation in individual behaviors is ultimately what underlies the ‘average’ patterns we see in nature. Furthermore, species that show a lot of variation in behavior between individuals are thought to be more robust in terms of adapting to anthropogenic disturbances or changes in the food base, for example incurred by future climate shifts.

Social organization

Female brown bears in Scandinavia have a complex matrilineal social organization, i.e., their social organization is based on multiple generations of related females with overlapping home ranges. Two types of female group formations have been reported in the Scandinavian system: 1) some females form multigenerational groups where related females occupy exclusive areas and 2) other matrilines are more dispersed and females establish among nonrelated females or between other matrilinear groups (Støen et al. 2005). In general, females settle home ranges that overlap or are close to their mother’s home range, while males often disperse and move farther away from their mother’s home range in order to seek out unrelated potential mates (Støen et al. 2006a, Støen et al. 2006b, Zedrosser et al. 2007b). This ‘sex-biased’ dispersal pattern means that females are generally geographically located closer to their relatives, while males are more randomly distributed across the landscape (Støen et al. 2005). The short dispersal distance of females means the home range a newly independent female is more likely to overlap with that of her mother and with other female relatives, e.g., sisters and aunts. (Støen et al. 2005).

Female bears have also shown a preference for establishing a home range where they overlap ‘familiar’ but unrelated individuals, where familiarity with the individual was gained during the natal period (Hansen et al. 2022). Within matrilines, competition for space occurs in areas with higher density. Newly independent females appear to be in competition with both their mother and female siblings for space use following family breakup (Hansen et al. 2023). Dispersal behavior may be related to bear density, the ongoing expansion of the bear population, and habitat limitations. For example, areas with high bear density and less turn over may host the more established matrilineal groups, while female bears may disperse to lower bear density areas or within the expansion front where there is less competition, and they can establish more easily among other females (Støen et al. 2005). High harvest rates increase male turnover and relatedness in matrilineal groups decreases (Frank et al. 2021). It can be advantageous for a young female to establish near her mother and there appears to be competition between sisters to do so; the larger sister is more likely to establish close to home (Hansen 2023, Zedrosser et al. 2007b). However, this does also come with some cost in the form of reproductive suppression; on average, females that establish near their mother wait an extra year before they begin having cubs (Støen et al. 2006a).

Bear individuality

Understanding variation in the behavior of individual animals is an up-and-coming topic within ecology. Recognizing and appreciating this variation in individual behavior is essential for understanding the underlying mechanisms behind the broadscale patterns we see in nature. Furthermore, behavioral diversity among individual brown bears contributes to their overall adaptability, genetic resilience, and ecological roles within their ecosystem.

Bears in Scandinavia exhibit a wide range of different behaviors including how far they travel, what routes they use, the times of day they are active, and their diet preferences (Hertel et al. 2023, Hertel et al. 2021, Ordiz et al. 2017a). For example, bear diet varies quite a lot between individuals, and dietary specialization is shown to be primarily driven by maternal effects, social and experiential learning, and habitat characteristics rather than genetic relatedness (Hertel et al. 2023). Meaning, bears learn and because they learn, they behave in different ways, including utilizing different food sources (Hertel et al. 2023). Individuals also use their habitat differently from one another. For example, on average, younger bears and those living in areas with higher density of bears and roads tend to be more nocturnal, mostly moving at night. However, older bears and bears who have good foraging habitat in their home ranges tend to move more during the day (Hertel et al. 2017). Likewise, the movement patterns and habitat preferences of older, resident male bears and younger, dispersing males show that older males show clear preference and avoidance patterns while younger males do not. Even within groups, there is a great deal of individual variability in for example risky movement behavior or proximity to human settlements (Thorsen et al. 2022).

Yet, even within these broader patterns we see variation in behaviors between individuals. Some bears are seemingly more bold and explorative and willing to take greater risks than others (Hertel et al. 2019a) and some are more consistent in their behavior while others are less consistent (Hertel et al. 2021). For example, bears that are more active, especially during the daytime, tend to be less consistent in their behavior (or behave in a more random way) while bears that are less active are more stable in their behavior, especially when they are active at nighttime (Hertel et al. 2021). How stable or random bears behave, is important, as bears that are more random in their behavior may be better adapted to random events, and it may be an adaptive response to reduce risk (either with humans or risk from interspecific interactions) (Hertel et al. 2021).

Interactions with other bears

As summarized in Section 2.3 General bear characteristics and behavior, brown bears both communicate indirectly via visual and scent marking as well as interact directly with one another. Brown bears interact most often during mating season, when males and females in estrous actively search for one another (Dahle & Swenson 2003c). Furthermore, brown bears appear to tolerate related individuals more than non-kin (Støen et al. 2005). Bears may also interact when scavenging for meat, either when a bear approaches another bears kill, or when they are both scavenging carrion, e.g., either from hunter harvest remains or wolf-killed prey. It is possible that bears may interact more at scavenge sites where they overlap with wolves, as wolves provide more sources of carrion on the landscape (Wilmers et al. 2003), although whether this increases bear-bear interactions in Scandinavia remains unknown. Bears do also kill one another

(Swenson et al. 2001a, Swenson et al. 2001b). This most commonly occurs when males kill cubs of the year to induce a female to mate and reproduce sooner than she otherwise would, or sexually selected infanticide, which is discussed in detail in Section 3.3 Mating, reproduction, and fitness. However, adult bears do occasionally kill other adult bears (Swenson et al. 2001a).

3.5 Denning ecology

KEY POINTS

- Mean date of den entry: 27 October (range= 5 October-18 November) for males and 18 October (2 October-5 November) for females.
- Mean date of den emergence: 4 April (range= 6 March–25 April) for males and 20 April (6 March–14 June) for females.
- Mean duration of hibernation (5-7 months): 161 days for males, 181 days for all females, with 196 days for pregnant females, and 168 days for solitary females and females with cubs.
- About 22% of bears abandon their first den for a second; 95% of these events occur before mid-December and are likely driven by human activities or other disturbance.

Brown bears hibernate in dens during winter, the time of year when their food supply is almost nonexistent. In preparation for the denning period, bears enter a phase called ‘hyperphagia’ where the animals are heavily focused on eating and maximizing weight gain. In Scandinavia, bears have been reported to increase their body mass by over 40% during this phase (Evans et al. 2012, Swenson et al. 2007a). This is important because during the denning period, they remain inactive for between 5 to 7 months relying on stored fat for energy (López-Alfaro et al. 2013, Sahlén et al. 2011). Although bears are born with the instinct to den, there still appears to be a learning curve when it comes to den choice and preparation (Shiratsuru et al. 2020).

Den selection and preparation

In Scandinavia, bears hibernate in dens within their home range, making a new den each year rather than using an old one (Manchi & Swenson 2005). New dens are often made near previous years’ den sites with the exception of subadult bears, especially males, who select dens further away from previous dens than adults (Manchi & Swenson 2005). For example, recently independent subadult males den near their mother during their first winter, then move long distances before denning again the next winter (Manchi & Swenson 2005). This pattern is connected to dispersal, as these young bears are in the dispersing phase, with males dispersing the furthest (Manchi & Swenson 2005). Most bears visit and explore their denning area several times during summer, suggesting they may actively seek out and assess denning areas and choose their dens in advance (Friebe et al. 2001, Manchi & Swenson 2005). Indeed, females have been observed visiting their next denning area almost once a month throughout the summer and fall (Friebe et al. 2001). Bears must choose their den wisely, as a poor den type and location may have fitness consequences for them the following spring (e.g., via potential for disturbance and den abandonment).

Abandoned anthills that are excavated to suit the bears needs are the most common type of den used in the Southern Study Area (Manchi & Swenson 2005). Other den types include cavities dug into the soil (often built at or into slopes) or below uprooted trees, built in stone/rocky caves or outcroppings, or open air ‘basket dens’ which are shallow depressions in the ground that are covered with branches and twigs and the only insulation from above is the snowfall that encases them in a type of igloo. Abandoned anthills are used more often by females than males, possibly because the thick, stable, overgrown walls provide good insulation from the cold and protection from disturbance (Elfström & Swenson 2009, Elfström et al. 2008). On the other hand, the more open basket dens are almost exclusively used by large adult males who stay in those den types almost a month less compared to bears using other dens (Elfström & Swenson 2009). Regardless of the den type chosen, all bears make a bed consisting of tree branches, twigs, moss, and underbrush.

Insulation is key and den attributes associated with insulative properties, such as wall and roof thickness and cavity size, can affect body condition post-hibernation (Shiratsuru et al. 2020). As one might expect, the better insulated dens are correlated with better spring body condition which is not necessarily a function of den type per se, but rather the 'quality' of the chosen site (Shiratsuru et al. 2020). Intuitively, we have found that bears excavate dens in relation to their size, meaning larger bears create larger cavities (Shiratsuru et al. 2020). However, there appears to be somewhat of a learning curve to den preparation. For example, older bears seem to prepare dens better-fit to their size compared to more inexperienced subadults (Shiratsuru et al. 2020). Regardless, we have found no effect of den cavity size on bear body condition after they emerge from their den (Shiratsuru et al. 2020).

Bears of all sex and age classes tend to select for dens with similar surrounding habitats (Elfström et al. 2008), although adult male den site selection does differ from females and younger bears (Elfström & Swenson 2009). In general, bears in Scandinavia tend to den most often in open canopy forests (e.g., Scots pine) and areas with thicker vegetation, and less often in more closed canopy forests (e.g., older Norway spruce and Scots pine), younger or mountain coniferous forests, clear cuts, and bogs (Elfström et al. 2008). Bears avoid denning in alpine mountain-birch or deciduous forests and areas with peat or exposed bedrock (Elfström et al. 2008). They also select for steeper slopes and easterly aspects. Bears also tend to avoid humans. In general, brown bears select den sites at least 2 km from infrastructure with regular human activity, e.g., main roads and buildings (Linnell et al. 2000). Bears in Scandinavia also tend to select dens that are more concealed and in more difficult to access terrain when the potential for human disturbance is higher, e.g., when they are closer to roads and human settlements (Sahlén et al. 2011). Furthermore, adult males tend to den further away from main roads and houses than other bears, suggesting they are less tolerant of human activities (Elfström & Swenson 2009). Altogether, this suggests that bear den site selection and behavior are likely heavily influenced by human activities. See Section 5.1 Human disturbance and brown bear behavior.

Den entry

Activity, heart rate, and body temperature start to drop slowly several weeks before den entry (Evans et al. 2016a), with a marked reduction in activity prior to entering the den, sometimes called 'pre-denning activity' (Sahlén et al. 2015a). This marked reduction in activity generally begins about a week or so before bears enter the den (Sahlén et al. 2015a).Many bears exhibit this marked reduction in activity before reaching their den area (58%), while others do so after they arrive (42%) (Sahlén et al. 2015a). Either way, bears tend to stay in the denning area for about 4-5 days before they enter the den (Sahlén et al. 2015a). Interestingly, younger bears appear to spend more time near the den prior to den entry, possibly because they are inexperienced at building dens (Sahlén et al. 2015a).

The mean date of den entry for bears in Scandinavia is 27 October (range= 5 October-18 November) for males (Manchi & Swenson 2005) and 18 October (2 October-5 November) for females (Friebe et al. 2014). Most bears go into their dens at around the same time with the exception of solitary and pregnant females who may enter their dens about 10 days earlier than females with cubs of the year or yearlings (Friebe et al. 2001). Den entry seems to be generally initiated by environmental cues, mainly first snow fall and when cold temperatures (≤ 0°C) arrive (Evans et al. 2016a), however, bears will begin hibernation before first snow fall if the snow arrives late and the temperatures dip down (Friebe et al. 2014, Manchi & Swenson 2005). Interestingly, pregnant bears also tend to den earlier when there was more food available in their environment throughout the active part of that year, possibly because they reached their peak fat storing capacity (Friebe et al. 2014).

The hibernation period

Duration: Brown bears in Scandinavia spend between 5 to 7 months in their winter dens. In general, the length of time they stay in their winter dens decreases as they get older and as their body size increases, i.e., older, younger bears den for longer, while larger bears den for shorter periods (Evans et al. 2023, Manchi & Swenson 2005). Females stay in their dens longer than males, with pregnant females having the longest denning period (Friebe et al. 2001, Manchi & Swenson 2005). Male bears spend an average of 161 days in their den, while female bears spend on average 181 days, with pregnant females spending an average of 196 days, solitary females and females with cubs 168 days (Friebe et al. 2001, Manchi & Swenson 2005). For more on the physiology of hibernating bears and the implications of their physiology during hibernation for human health see Section 6.1 Ecophysiology of Scandinavian brown bears and Chapter 19: Bear physiology and human health.

Den abandonment: Bears do occasionally abandon their dens and move to new locations for the remainder of the winter, moving up to 30 km before denning again (mean of 5.1 km) (Swenson et al. 1997a). In Scandinavia, around 22% of bears abandoned their dens, of which 95% of these den changes occurred before December 15, early in the hibernation period (Sahlén et al. 2015a). Although bears will switch dens later in winter, i.e., after December 15, if the disturbance is great enough, bears that abandon their den later in spring often do not attempt to den again (Sahlén et al. 2015a, Swenson et al. 2007a). In general, females are generally less likely to abandon their dens than males (Sahlén et al. 2015a). Interestingly, prior visitation to the denning area also appears to decrease the chances that a bear will abandon its den (Sahlén et al. 2015a).

Bears might change their dens for a variety of reasons, however, it has been suggested that human disturbance might the driving cause of den abandonment in Scandinavia (Swenson et al. 1997a), and there multiple lines of evidence to support this. For example, abandoned dens are more likely to be located closer to plowed roads, which might increase the potential for human disturbance (Elfström & Swenson 2009). Bear often abandon dens when people visit the area, especially if they visit early in the denning period or approach within 200 m of the den site (Linnell et al. 1996, Linnell et al. 2000). It is not ideal for bears to have to abandon the den and select a new one. The energy used to wake up and find and prepare a new den can decrease their body condition after den emergence as well as have fitness consequences. For example, of pregnant females that changed dens, 60% lost cubs compared to only 6% of pregnant females that stayed in the same den (Swenson et al. 1997a). See Section 7.2 Effects of capture on Scandinavian brown bears for information on disturbance effects of capture during hibernation.

Den emergence

The mean date of den emergence for bears in Scandinavia is 4 April (range= 6 March–25 April) for males (Manchi & Swenson 2005) and 20 April (6 March–14 June) for females (Friebe et al. 2001). The end of hibernation and subsequent den emergence are closely linked to internal physiological cues linked with thermoregulation, rather than environmental cues such as daylength or the timing of snow melt (Evans et al. 2016a). Likely, when the temperature in their dens became too warm, they moved outside to better maintain their body temperature (Evans et al. 2016a). Females with newborn cubs emerge from their dens almost 1 month later than the other bears, and generally stay close to their den site in the days following, likely because the small cubs are not able to travel far, but also to decrease the risk of infanticide (Friebe et al. 2001).

Differences with latitude

With a few exceptions, most research on bear denning behavior in Scandinavia has been conducted in the Southern Study Area. What we do know is that bears in northern Scandinavia hibernate longer than they do in the south; they enter their dens earlier and leave their dens later (Manchi & Swenson 2005). On average, northern males and females spent an extra 45 and 37 days in their dens, respectively, than their southern counterparts (Manchi & Swenson 2005).

Snowfall and freezing temperatures arrive earlier and last longer in the north which both limits the growing and foraging season as well as triggers denning activity.

4 Multispecies Interactions

4.1 Bears as predators

KEY POINTS

- Bears are omnivores and opportunistic, rather than obligatory, predators but still readily prey on newborn ungulates. They are also scavengers.
- Neonate moose are the primary prey for most bears in Scandinavia but bears also prey on newborn reindeer where their range overlaps.
- Moose: The most recent estimates suggest that bears kill, on average, between 4.25 and 7.2 moose calves per year. However, kill rates likely vary based on bear and moose densities.
- Reindeer: Bears in forested reindeer calving areas kill, on average, 10.2 reindeer calves per year. Current studies are assessing kill rates in mountainous reindeer areas.
- There is a lot of individual variation in predatory behavior among bears, with some killing many newborn ungulates each spring and others none.
- In Scandinavia, bears appear to generate only very minor fluctuations in moose population dynamics, while hunter harvest has an overwhelming effect on moose demography.

Brown bears are omnivores and opportunistic, rather than obligatory, predators. They are powerful and can deliver a swift, lethal blow to smaller prey such as newborn calves but capturing and killing larger animals such as adult ungulates is not an easy task even for an adult bear. Thus, when bears hunt larger prey, they generally target weaker or more vulnerable individuals, for example, moose or other ungulates that are in poor condition following a long winter or females that are giving birth (Swenson et al. 2010). Even still, our research suggests that bears only have a 9% success rate when hunting adult moose, meaning only 9% of attempted hunts end successfully for the bear (Swenson et al. 2010). Interestingly, hunting success appears to be greater on the fringe of the core bear distribution as compared to the middle (Swenson et al. 2010). Yet, we still know relatively little about how bears actually hunt in Scandinavia and/or what their relative success is with their primary ungulate prey, neonate moose and reindeer. Even with small, vulnerable prey, successful hunts are not guaranteed. Understanding bear predatory behavior is important because those behaviors are the underlying mechanisms that drive bear predation patterns and their subsequent effect on prey population dynamics.

Predation on moose

Bears in Scandinavia primarily prey on newborn moose and only occasionally kill adults; in general, yearling moose are more vulnerable to bear predation than older moose, and cows are more vulnerable than bulls (Dahle et al. 2013, Rauset et al. 2012, Swenson et al. 2007b). Three studies have been conducted to assess bear predation on moose in Scandinavia.

An initial study was conducted between 1994 and 1998 in our Southern Study Area which followed radio-collared moose to assess cause-specific mortality for both calves and adults. At that time, brown bear density was estimated to be between 10 and 30 individuals per 1,000 km^2 and moose density was estimated at between 400 and 1,340 per 1,000 km^2. This study estimated that each individual bear (all older than 2 years old) takes about 6.5 moose calves per year, or approximately 26% of all moose calves born in the area (Swenson et al. 2007b). Females that lost their calves in spring produced more calves the following year (1.54 calves/female) than females that kept their calves (1.11 calves/female), which reduced the net loss of calves due to predation to about 22% (Swenson et al. 2007b). Of the moose calves killed, 93% were taken during their first four weeks of life. Bears killed 0.8% of radio-collared adult female moose per year, and no adult male moose, which represented 0.5-1.5% of the moose population (Dahle et al. 2013).

A second study was conducted between 2004 and 2006 in our Southern Study Area which followed radio-collared adult female bears (> 4 years old) to assess bear-moose kill rates. Bear densities were likely relatively similar to the previous study, while local winter moose densities were estimated at 500 individuals per 1000 km^2, which is up to half of what was reported in the 1994-1998 study (Rauset et al. 2012). This study estimated an average individual kill rate of 7.6 moose calves per bear per year, with a range between 6.1 to 9.4 calves per bear (Rauset et al. 2012), which was more or less comparable to the first study. However, it is important to note that the 2004-2006 study only estimated the kill rate of adult female bears, and 67% of them (12 of 18) were solitary and had no cubs during the study year, the remaining 4 had yearlings. Thus, the estimate likely does not represent kill rates across the bear population as a whole.

The most recent study was conducted in our Southern Study Area between 2014 and 2015 and followed a wider range of bear demographic classes, i.e., single adult females and males and both sexes of subadults, but still no females with cubs (Ordiz et al. 2020b). Bear density in the area was likely similar or higher than the previous studies, while moose density was likely lower and at this point a couple of wolf packs had moved into the area. This study estimated that bears killed 4.25 moose calves per season but found quite a bit of variation in kill rates between individuals. For example, at the extremes, some bears killed up to 10 calves during the parturition period while others killed none (Ordiz et al. 2020b). While adult single female and male bears were equally predatory, adults of both sexes killed more calves than younger, subadult bears. The lower average kill rate observed here could reflect shifting animal densities (i.e., more bears and fewer moose would decrease average kill rates). However, caution should be used as the lower average kill rate could also possibly be caused by the coarse methodologies used in the study, i.e., cluster searches were defined as ≥ 2 hourly GPS positions within 30 m of one another (Ordiz et al. 2020b). Current research suggests that this GPS collar fix rate would likely result in missed predation events and underestimate bear kill rates (Tallian et al. 2023a).

It should be noted that the estimates and results outlined should be extrapolated to present times with caution. Two of the above studies are over 20 years old, and the system and dynamics have changed (moose and bear densities have fluctuated and wolves have since recolonized in some of the bear range). The most recent estimates of kill rates were estimated using coarse metrics. A new study that began in 2023 in the Ljusdal and Härjedalen Municipalities (Gävleborg and Jämtland Counties, respectively) is attempting to quantify bear kill rates, and assess the combined impact of wolves and bears, in the context of the current multipredator system.

Predation on reindeer

Our first study assessing bear predation on reindeer was conducted between 2010 and 2012 in our Northern Study Area in close collaboration with the two Sámi Siida of Udtja and Gällivare (Støen et al. 2022b). These Sámi Siida are situated in the boreal forest, a habitat where Sámi reindeer herders reported high calf losses. This study placed GPS proximity collars on bears and UHF transmitters on reindeer to assess predation. The results suggest that, on average, bears visiting calving grounds killed 0.4 calves per day and 10.2 (with a range between 8.6 and 11.5) calves per bear, which accounted for between 39-62% of all reindeer calf mortality in these Siidas (Støen et al. 2022b). The kill rates varied considerably among individual bears, primarily due to the duration of their presence on the calving grounds. The number of days spent in these areas emerged as the key factor influencing predation outcomes. Bears also killed some adult reindeer, although kill rates were low. Although females with cubs of the year do prey on moose calves, collared females with cubs of the year were not observed killing reindeer calves in this study.

Sámi reindeer herders in mountain habitats have also reported high calf loss to bears, which resulted in a subsequent request to assess bear-reindeer predation in Sámi Siida that are situated in the mountains. Our group is currently conducting a study in collaboration with the Idre Sámi Siida in central Sweden (a temporary extension of our Southern Study Area) to assess bear-reindeer predation patterns including hunting behavior, kill rates, and predation rates. This project began in 2019, and the final field season was in 2024. Bear predation on semi-domestic reindeer is a key source of human-wildlife conflict in northern Sweden (Støen et al. 2022b, Tallian et al. 2023b), but less so in Norway where fewer bears inhabit reindeer herding areas (Tveraa et al. 2014).

Predation on sheep

Studies conducted in the late 1980s and early 1990's suggests that bears in Norway prey heavily on free-ranging domestic sheep where they overlap (Knarrum et al. 2006, Mysterud & Warren 1997) and rely on them for a large proportion of their annual energy intake (Dahle et al. 1998). It is well understood that sheep and lamb losses and compensations are both positively associated with bear density (Mabille et al. 2015, 2016). However, bear-sheep predation dynamics such as kill rates between bears and sheep in Norway have not been more recently assessed.

Bears as scavengers

It should be noted that bears are also opportunistic scavengers who find meat from a wide range of sources including hunter-killed ungulate remains, carcasses from ungulates who died during winter, road-killed ungulates, and by stealing kills from other carnivores, including other bears. There is some evidence that bears in Scandinavia may have a dominance hierarchy at carcasses, similar to other systems. For example, females with cubs of the year are much less likely to scavenge on hunter-killed carrion, likely to avoid negative interactions with other bears (Elfstrom et al. 2014). Bears used >50% of wolf kills in our studies in central Sweden, whereas we did not record any wolf visit at bear kills (Ordiz et al. 2020a).
Bears and prey population dynamics

Compensatory versus additive predation explained: To understand prey population dynamics, it is first important to understand the difference between compensatory and additive predation. In compensatory predation, predation on one species tends to offset, or compensate, for other mortality factors affecting the prey population. Essentially, when predation is compensatory, it helps regulate the prey population by removing individuals that might have died from other causes like disease, starvation, or old age. This means that the total mortality rate of the prey population remains relatively stable, and predation serves to maintain the prey population at a sustainable level. On the other hand, additive predation occurs when the predation on a prey population is in addition to other sources of mortality. In this case, predation does not offset or compensate for other factors, rather it adds to the overall mortality of the prey population. This can result in a more significant reduction in the prey population, potentially leading to population declines or local extinctions if predation rates are high and not balanced by factors like prey reproduction.

The effect of bears on moose population dynamics: Bears appear to generate only very minor fluctuations in moose population dynamics, while hunter harvest has an overwhelming effect on moose demography (Gervasi et al. 2012). Although bear predation is known to be additive to other sources of predation with ungulates (Griffin et al. 2011), humans likely usurp this effect, taking over as the primary driver of moose population dynamics in Scandinavia (Gervasi et al. 2012). Our research corroborates that while bears likely affect some moose population vital rates, like newborn survival, they are likely not the primary driver of long-term moose population dynamics in Scandinavia (Tallian et al. 2021).

First, bears do not typically kill adult moose and are therefore not an important source of adult mortality within the moose population (Dahle et al. 2013). However, bears can affect calf survival and recruitment, which is an important driver of population growth (Rauset et al. 2012, Swenson et al. 2007b). For example, one recent study which used data from 2000 to 2017 suggests that moose calf/cow ratios, which are a loose index of calf recruitment, are negatively correlated with bear densities; calf/cow ratios decreased by 7% in northern Sweden where bears are their only main predator and by 18% in central Sweden where both bears and wolves prey on moose calves (Tallian et al. 2021). Yet, long-term trends suggest that both calf/cow ratios and moose densities broadly declined over the last ~20 years across Sweden, including areas where wolves and bears were absent, and that these declines may have been driven by a variety of human-related factors (Tallian et al. 2021). Furthermore, moose have an indirect compensatory mechanism to bear predation; moose that lose calves have a higher likelihood of having twins the following year, likely because of the energy conserved by not lactating the previous year (Swenson et al. 2007b).

However, these results should be interpreted with caution as we do not truly have accurate estimates of the combined effect of predation (bears and wolves) and hunting on moose population dynamics. A new study that began in 2023 in the Ljusdal and Härjedalen Municipalities (Gävleborg and Jämtland Counties, respectively), where locals report high wolf and bear densities and low moose calf survival, attempts to estimate the kill rates of brown bears on moose calves across all sex and reproductive classes of bears. Importantly, local wolf kill rates and hunter harvest rates will also be assessed which will help provide a clearer picture of the role bears play in moose population dynamics. This study is further detailed in Section 8.1 Future research for the SBBRP.

4.2 Bears and other carnivores

KEY POINTS

- Brown bears and wolves are both apex predators that compete directly and indirectly for food.
- Bears decrease wolf kill rates where they overlap in Scandinavia due to a combination of interference and exploitation competition. Which type of competition is dependent on the season.
- Wolves and bears seem to spatially separate on the landscape more than would be expected by chance.
- Lynx and brown bear have little diet overlap in Scandinavia and they don’t appear to interact often. Bears do not seem to scavenge lynx kills very often.
- Although little is known about how bears and wolverine interaction, both species are efficient scavengers, have more diet overlap (in the form of carrion) than lynx, and thus there is more potential for competition.

There has been a large-scale shift in ecology from single-species studies to a focus on holistically understanding multispecies interactions. Bears move through landscapes that are heavily dominated by humans and interact with other large carnivores in the ecosystem, all of which can affect their behavior, including predation patterns and subsequent prey population trends (Ordiz et al. 2017a, Tallian et al. 2021). Bears are generally not very effective predators of adult ungulates, such as moose, although they do occasionally prey on them. However, bears are incredible efficient scavengers. For example, they will eat the remains of animals that died during winter, remains of hunter-killed ungulates, and will also steal kills from subordinate carnivores (Tallian et al. 2017). Thus, bears may compete with other predators in two main ways: directly (e.g., by stealing kills or excluding them from a resource, also known as interference competition) and indirectly (by competing for shared food sources, also known as exploitation competition) (Tallian et al. 2022). Most research on interactions between bears and other predators has largely focused on wolves. However, we also put into context interactions with the other large carnivores on the Scandinavian Peninsula: lynx and wolverine.

Wolves

Brown bears and wolves are both apex predators in Scandinavia that compete directly and indirectly for food (Tallian et al. 2022). Moose are the primary prey for both bears and wolves in Scandinavia (Rauset et al. 2012, Sand et al. 2008, Sand et al. 2005). Bears primarily prey on newborn moose during the weeks surrounding calving season and rarely kill adults (Dahle et al. 2013, Rauset et al. 2012), while wolves prey on both adults and young, but select for young of the majority of the year (Sand et al. 2008, Sand et al. 2005). For example, newborn moose comprise the great majority (~90%) of wolf diet during the moose calving season and wolves continue to select for young of the year as they age through the season, right up until calving season when the pattern begins anew (Sand et al. 2008, Sand et al. 2005).

In Scandinavia, it appears that two types of competition occur between wolves and bears. Interference competition occurs when bears first emerge from their dens and wolves are hunting larger calves from the previous year (Tallian et al. 2022). During this time, bears can scavenge from wolf kills and potentially limit wolf access to kills, although to what degree this occurs remains unknown (Tallian et al. 2022). Exploitation competition occurs during the calving season when wolves and bears share the same prey (Tallian et al. 2022). During this time, bears and wolves prey on newborn calves, successively depleting the supply of shared food (Tallian et al. 2022). The ultimate result of this is that competition from bears decreases wolf kill rates, which might result in fitness consequences for the wolf population (Tallian et al. 2017). On the other hand, bears may benefit from wolves as they provide them with food subsidies (Wilmers et al. 2003). Theft of wolf-killed prey often happens during spring when wolves are preying on larger bodied prey (e.g., last year's calves and adults). Bears visit at least 50% of the wolf kills in central Sweden, yet the visitation rate is lower during spring-early summer when both bears and wolves are preying on neonate moose that provide little left for scavenging (Ordiz et al. 2020a).

Competition might be such that it slowed down the expansion of wolves into core bear habitat between 1990 and 2012 in Scandinavia (Ordiz et al. 2015), i.e., the probability of wolf pack establishment was negatively related to bear density (Ordiz et al. 2015, Sanz-Perez et al. 2018). Where bear and wolf populations overlap, the two species tend to segregate at a fine spatial scale more than would be expected by chance, suggesting that they actively avoid each other (Milleret et al. 2018). Compared to bears, wolves selected more for young forest, rugged terrain, and moose occurrence, although both wolves and bears avoid humans, especially during daytime (Milleret et al. 2018).

Lynx

Lynx in southern and central Scandinavia primarily prey on roe deer (Andren & Liberg 2015, Gervasi et al. 2014, Odden et al. 2006), and have little diet overlap with bears, thus little potential for exploitation competition. However, lynx in other areas depend mainly on reindeer, and partly sheep, as a prey (Mattisson et al. 2011b, Odden et al. 2013). Thus the probability of bears and lynx interacting is greater in areas where they share habitat (May et al. 2008) as well as prey. Lynx are not avid scavengers; thus, they likely do not show up at bear killed prey very often. However, bears may scavenge lynx kills, as documented elsewhere. Research in other systems has shown that brown bears can steal up to 50% of lynx kills in areas where bear densities are high (Krofel et al. 2012). Although it likely occurs to some extent, this does not appear to be a common phenomenon in Scandinavia. For example, a lynx study conducted in Northern Sweden, in and around Sarek, found that only 5% (5 of 95) lynx-killed reindeer were visited by brown bears, even though bears were relatively common in the area (Mattisson et al. 2011a).

Wolverine

There is not much known about direct interactions between wolverines and bears, but they are both efficient scavengers and attracted to similar resources. Wolverines have been observed feeding at bear kills in Scandinavia, albeit rarely, which means there is potential for exploitation competition between the two in the form of depleted carrion (Mattisson et al. 2016). It is also possible that bears might scavenge from wolverine kills, although this remains unknown. Black bears have been observed killing wolverines in North America, suggesting the potential for direct interference competition between bears species and wolverine (Inman et al. 2007). A study from south-eastern Norway, showed that wolverine tend to use more high-elevation open rugged terrain than bears, who more commonly use rugged forested terrain at lower elevations (May et al. 2008). This suggested that bears and wolverine occupied slightly different niches and had less chance for direct and indirect interactions (May et al. 2008). However, as the wolverines have increased in areas of lowland forest habitat since then (Aronsson & Persson 2017), there is an increasing potential for competition between wolverines and bears in accessing carcasses to scavenge in areas where they co-occur.

4.3 Bears and their influence on the environment

KEY POINTS

- Brown bears are apex predators that can affect ungulate population dynamics through their predation on newborn calves.
- In Scandinavia, the effect of brown bears on moose population dynamics is likely dampened or absent because of human activities. In other words, moose population dynamics are likely more affected by hunter harvest and forestry practices than from bear predation.
- Bears also eat ants in Scandinavia, which may have cascading effects within the landscape in ways we still do not understand.
- Bears also affect their landscape by eating, defecating, and spreading viable berry seeds across the landscape.

Bears as apex predators

An apex predator is a species at the top of a food chain that has no natural predators, preying on other species without being preyed upon itself. Large carnivores, including brown bears, can therefore play an important role in ecosystem function through the direct and indirect effects of predation; direct effects include directly decreasing the number of prey on the landscape through predation, while indirect effects include shifting prey behavior. Also known as ‘top-down control’, these shifts in prey behavior and population size can have trickle down effects within the ecosystem, generally via the altered or decreased foraging of plants by the prey species, which can subsequently affect a wide range of other plant and animal species.

The baseline ecosystem that bears live in in Scandinavia is primarily driven by human activities, ranging from large-scale forestry, agriculture and farming, villages, roads, and other infrastructure. Forestry is a prime example of this, with forestry practices in Scandinavia indirectly increasing the moose population by providing more forage than would otherwise be on the landscape. On the other hand, the annual moose hunt in Scandinavia has the opposite effect and helps to control or decrease the moose population. Bears are also hunted, which can affect both the population size as well as their fundamental behavior. Hunted carnivores also behave differently (see Section 5.2 The effects of hunting on the population, behavior, and evolution for more details) which may alter predation patterns and indirectly affect moose population dynamics (Ordiz et al. 2013a). In Scandinavia our research suggests that the brown bears functional role as an apex predator is likely dampened by anthropogenic effects in a variety of ways (Ordiz et al. 2021, Ordiz et al. 2013a). For example, the combination of human-driven alterations to the forest landscape, moose management and harvest practices, and the altered behavior of the hunted bear population means humans likely usurp top-down control from the bear population, and that bears are only one small portion of what drives moose population dynamics and the subsequent effects those have on the ecosystem in Scandinavia.

Predation on ants

Red wood ants (*Formica rufa*) are an anthill building keystone species in the Scandinavian forests, meaning they have a large impact on their ecosystem through nutrient cycling, seed dispersal and removal, and their predation on other invertebrates (Stockan & Robinson 2016). Ants are an important part of brown bear diet in Scandinavia, and they consume them the most during spring and summer period (Stenset et al. 2016, Swenson et al. 1999a). Interestingly, bear predation on ants may have a cascading effect on ecosystem function in ways we still do not yet understand. For example, anthill size is an indicator of ant numbers, and we know that anthills are smaller in areas with a high density of bears compared low bear density (Moen 2018).

However, the effect of bears is yet again tampered down by humans; even in areas with high bear density, anthill sizes are larger near human settlements that bears avoid (Moen 2018).

Bears and plants

There is some evidence that bears may affect plant dynamics in the Scandinavian forests by eating, passing, and spreading berry seeds in their feces. For example, a recent study in 2019 found that berry seeds suffered no damage when passing through a bear's gut (Steyaert et al. 2019). Furthermore, seeds that were still encased in the berry (i.e., did not pass through the bear) germinated almost one month later than seeds that were releases from the fruit (e.g., seeds that had passed through the bear) (Steyaert et al. 2019). Thus, alongside the other forest animals that rely on berries, bears in Scandinavia may facilitate blueberry seed dispersal and germination (Steyaert et al. 2019).

5 Bears and Humans

5.1 Human disturbance and brown bear behavior

KEY POINTS

- Scandinavia's human-dominated landscape affects brown bear behavior including movement and foraging patterns.
- Bears, especially males, generally avoid human infrastructure such as roads, villages, and other developed areas. Females with cubs, however, select areas closer to human settlements, likely to avoid infanticidal males.
- Bears generally avoid encounters and become more physiologically stressed when they are near human settlements.
- Bears are more active when people are not, meaning they become more nocturnal when they are disturbed.
- Bears select den sites that have less potential to be disturbed by humans. However, when disturbed, bears may abandon or switch dens after human disturbance which can cause lower reproductive success.

Like most large carnivores, brown bears require a lot of space to fulfill their biological needs. Although the number of people living in rural Scandinavia has been declining, the number of roads and amount of infrastructure has remained steady or increased. This includes a wide network of forestry roads and activities and the construction of new recreational cabins, cabin fields, and recreational areas, especially around national parks. The brown bear population has functionally recovered in Scandinavia (Chapron et al. 2014) after a period of steady growth and exists alongside human development and activities. Although bears could benefit from human activities in some ways, e.g., via scavenging on hunter-killed remains, any close proximity to humans or the use of human-derived resources may create problems for both bears and people. Brown bear behavioral responses to human disturbance and other anthropogenic pressures might lead to indirect habitat loss, decreased ability to forage, and lower reproductive success (Brown et al. 2023b). These effects could ultimately have population-level consequences (Brown et al. 2023b). Thus, it is important to understand how the presence of people and the associated infrastructure affects bear behavior and thereby potentially affect population dynamics.

Activity patterns, movement, and habitat use

Brown bears generally avoid encounters with people (Ordiz et al. 2011) and exhibit a physiological stress response to humans; i.e. they are more stressed when they are near human settlements (Støen et al. 2015). Like other large carnivores in Scandinavia, bears typically avoid areas with high human activity and human-related infrastructure including cities, towns and cabin developments, houses, recreational areas, and roads (Leclerc et al. 2016b, Milleret et al. 2018, Moe et al. 2007, Nellemann et al. 2007). Bears also become more nocturnal in response to human disturbance, avoiding human presence during daylight hours (Ordiz et al. 2017a). Although some bears may use smaller roads to facilitate movement, for example during mating season (Thorsen et al. 2022), roads are usually an impediment to bear movement in Scandinavia which may ultimately affect bear behavior, dispersal, and gene flow and (Bischof et al. 2017). In areas where there are many roads, bears also tend to be more nocturnal and move more often during the dark and twilight hours compared to more roadless areas (Ordiz et al. 2014). In general, bears also tend to select daytime bed sites in denser vegetation that offers concealment when they are close to human settlements (Ordiz et al. 2011).

The summer/fall seasons are particularly busy in the forests of Scandinavia when people are out hunting and collecting berries. Bears are hunted in Scandinavia (see Section 5.2 The effects of hunting on the population, behavior, and evolution), but bear hunting is not the only type of hunting activity that bears respond to. Moose hunting occurs during fall and evidence suggests that this creates a ‘landscape of fear’ that bears respond to by avoiding areas with high moose hunting activity (Brown et al. 2023b). Mortality risk was greater for bears that selected higher-risk areas than those that selected low-risk areas when foraging for bilberries during the hunting season (Lodberg-Holm et al. 2019). During summer and fall bears are more likely to select places on the landscape that offer more concealment, such as young regenerating coniferous forests, as well as areas further away from roads and human access (Brown et al. 2023b, Ordiz et al. 2011). Day beds tend to be the most concealed during this time of year (Ordiz et al. 2011).

Female bears tend to use areas within their home range that offer high-quality food while also avoiding the risk of human disturbance (Martin et al. 2010). For example, female bears generally avoid disturbed areas and select for more rugged terrain (or steeper slopes) during times when human activity in the forest is high, such as summer and fall (Martin et al. 2010). However, not all female bears avoid human areas. During the spring mating season, females with cubs of the year use areas that are less rugged and more open as well as closer to humans (Steyaert et al. 2013a). This creates a type of ‘human-shield’ effect whereby females with cubs of the year trade off potential disturbance from people in order to avoid infanticidal males and decrease their chances of losing their cubs (Steyaert et al. 2016a). Females who lose their cubs prior to or during mating season move away from human areas, apparently no longer needing to make that trade-off (Steyaert et al. 2014).

Male bears also seem to respond to human activity in different ways depending on their life stage, for example whether they are a resident with a home range or in the dispersal phase (Thorsen et al. 2022). Resident males avoid areas that are near buildings or large public roads, but they used smaller forestry roads to facilitate their movements, i.e., they moved through the landscape faster when they were near smaller roads (Thorsen et al. 2022). Dispersers, on the other hand, only avoid human infrastructure moving through the landscape, likely because they were unfamiliar with the terrain in front of them and unable to avoid it on a broad scale (Thorsen et al. 2022).

When directly approached by people, bears tend to either flee or hide (Moen et al. 2012, Ordiz et al. 2013b, Sahlén et al. 2015b). Well hid bears may stay in their hideout if the people pass more than approximately 100 m away; if people come closer bears move away silently and often unnoticed by the people to avoid encounters. However, both these types of encounters affect the bears’ behavior in the days following the event. For example, following encounters with people, bears that flee move on average 1 km away, and then reduce their movements after reaching a different location (Moen et al. 2012, Ordiz et al. 2019). Bears also alter their foraging and resting routines from about 2 days and up to a week after the encounter occurred, moving more during the nighttime and less during the daytime than normally, presumably to avoid encountering humans again (Ordiz et al. 2019, Ordiz et al. 2013b).

Foraging behavior

Human alteration of habitat, especially through forestry practices, can change the availability of food and brown bear foraging patterns. For example, ants are more prevalent in clear cuts, which bears select for in order to utilize that resource (Frank et al. 2015). Forestry practices also have a large effect on berry occurrence and abundance, resulting in brown bears foraging more in mature forests and clearcuts where berries occur more often and in greater abundance (Hertel et al. 2016a). Unlike in North America, bears in Scandinavia do not generally approach human settlements to obtain anthropogenic food sources; bear diets are generally the same whether they are near settlements or in more remote areas (Elfström et al. 2014).

Mating and reproduction

It is possible that human disturbance could disrupt normal mating behaviors and interactions between bears. For example, females with dependent young select areas near humans, presumably to avoid potentially infanticidal males; this is commonly called the ‘human shield effect’ (Steyaert et al. 2016a). Consequently, female bears that select for more human-related areas increase the probability that their cubs survive (Steyaert et al. 2016a). Additionally, females who remain with their offspring an additional year (until they are 2 ½) tend to use areas closer to buildings and towns while males tend to avoid these areas (Van de Walle et al. 2019). Again, this is possibly due to a human shield effect, meaning females may use these areas to avoid interactions with males during mating season that might result in them weaning their cubs (Van de Walle et al. 2019).

Denning behavior

Bears also tend to select their dens in a way that avoids potential human disturbance. In general, brown bears select den sites at least 2 km from infrastructure with regular human activity, e.g., main roads and buildings (Linnell et al. 2000). Bears in Scandinavia also tend to select dens that are more concealed and in more difficult to access terrain when the potential for human disturbance is higher, e.g., when they are closer to roads and villages (Sahlén et al. 2011). Furthermore, adult males tend to den further away from main roads and houses than other bears, suggesting they are less tolerant of human activities (Elfström & Swenson 2009). It has been suggested that human activity around the den site is the main reason bears will abandon, or switch, dens in Scandinavia (Swenson et al. 1997a). Several studies have since demonstrated that bears select their den sites to reduce such risks of disturbance (Elfström & Swenson 2009, Elfström et al. 2008). For example, abandoned dens are more likely to be located closer to plowed roads, which might increase the potential for human disturbance (Elfström & Swenson 2009). Bear often abandon dens when people visit the area, especially if they visit early in the denning period or approach within 200 m of the den site (Linnell et al. 1996, Linnell et al. 2000). It is not ideal, but not uncommon for bears to have to abandon the den and select a new one. The energy used to wake up and find and prepare a new den can decrease their body condition after den emergence as well as have fitness consequences. For example, of pregnant females that abandoned their dens, 60% lost cubs compared to only 6% of pregnant females that lost cubs and did not abandon their den (Swenson et al. 1997a).

5.2 The effects of hunting on the population, behavior, and evolution

KEY POINTS

- Bears are hunted in both Sweden and Norway; Sweden has established license hunts and both Sweden and Norway allow for ‘protection’ hunts.
- Most bears in Sweden are hunted by licensed bear hunters who use dogs; still hunting, stalking, and baiting are also used.
- Hunting is the primary driver of brown bear population dynamics in Scandinavia; hunting directly decreases bear numbers but also indirectly alters population dynamics by 1) shifting age and sex structure, 2) altering social structure, 3) shifting individual bear behavior, and 4) selecting for certain life history or genetic traits.
- Bears in Scandinavia alter their behavior in response to hunting pressure; they move more during non-daylight hours, avoid risky areas, and show increased signs of stress and move further after encounters with hunters.
- Bears trade-off food for safety (they forage in areas that are safer but less productive) during the fall hunting season, a critical time of year for gaining fat before denning. This could affect their spring body condition and reproductive success.
- Bear hunting likely affects bears underlying social structure and dynamics; it increases sexually selected infanticide and may break down the matrilineal home range structure of the population.
- The indirect effects of hunting on the bear population can influence population growth rates in unexpected ways and thus deserve more attention by researchers and managers in Scandinavia.

An overview of hunting in Scandinavia

Bears in Scandinavia are subject to hunting. Sweden and Norway have established legal license hunts and allow for ‘protection’ hunts where people may target specific problem bears or bears in specific areas outside of the normal hunting season. In Sweden, the number of bears harvested is set by the county authorities for each county after delegation from the Swedish Environmental Protection Agency. The quotas are thus set on county level, and often further divided into hunting zones within the counties, in accordance with the management goals and plans decided in the respective county's "wildlife delegation" (Swenson et al. 2017). These delegations are generally comprised of stakeholders, including local politicians, landowners, and other interested parties such as reindeer herding representatives in those counties where reindeer herding occurs. The wildlife delegation therefore has an indirect way of affecting the hunting quotas as these are set to reach the overall management goals within the county. In Sweden, bear hunting is allowed between 21 August and 15 October (30 September in parts of Norrbotten), with a few exceptions when the hunting period may end earlier if the quota is filled. The hunt is open to all hunters that have the pre-requisite license, paid the hunting permit fee, and has appropriate firearm, and hunters may harvest as many bears as they wish within the quota limits. However, hunters must report harvested bears to the appropriate authorities within 1 hour; unrecovered shot bears must also be reported and are similarly deducted from the quota if not considered unharmed. Hunting with dogs is permitted, and baiting for hunting purposes is allowed; baiting was banned in 2001 then reinstated again in 2013 (Swenson et al. 2017). Hunters are only allowed to harvest solitary bears; females with any aged cubs, or family groups, are protected during the hunt. Nation-wide quotas have shifted through time, depending on management goals and strategies. There is little evidence for illegal harvest of bears in Sweden, or poaching, especially in northern Sweden. However, this is difficult to monitor and has thus never been quantified (Swenson et al. 2010). Harvest quotas have increased drastically in recent years. In 2018 the harvest was 288 bears while for 2023 the harvest was 648 bears with a distribution of 55% females and 45% males (Ågren & Höök 2023). In addition to these license hunts there are bears removed in protective hunts during spring.

Bear hunting in Norway is different than in Sweden. Norway has eight large predator management regions, each with its own large predator management plan. The plans are reflective of the overarching goals set for the region, and designate areas prioritized for large predators as well as areas prioritized for free-range grazing livestock. There is a national goal of 13 yearly reproductions as well as regional goals, that differs between regions. When the population goal is reached in a region, the setting of quotas is moved from the Norwegian Environmental Agency to the regional management authority. Regions without a population goal can also decide on license hunts. In Norway, protected hunts are allowed between 1 June and 15 October, and license hunting is allowed between 21 August and 15 October. Females with accompanying cubs are protected in the license hunt. Hunting with dogs is permitted, but hunting with bait is strictly prohibited. Hunters need to register as bear hunters in the national hunter registry. Norway's bear population is much smaller than Sweden, and thus there are fewer hunts here.

What bears are harvested and how

Bears are harvested by both bear hunters, or those who are in the forest with the specific aim of hunting bears, and opportunistically by moose hunters as well. Between 1981 and 2004, bears were primarily hunted using dogs (37%), by still hunting (30%), by stalking (16%), or by baiting (18%) (Bischof et al. 2008). During the years baiting was banned (2001-2012), hunting methods included dogs (71%), still hunting (21.5%), and stalking (7.5%) (Swenson et al. 2010). The ban on bear baiting had no overall effect on general harvest patterns; the age and sex of killed bears remained the same (Bischof et al. 2008). In general, there is relatively little difference in the age and sex of harvest bears with regards to the hunting method used (Bischof et al. 2008). Bear hunters in Scandinavia are likely not selective when it comes to age and sex; the opportunity to encounter a bear comes so infrequently that hunters will likely attempt to harvest what they encounter (Bischof et al. 2008). Young male bears are more likely to be harvest by hunters who use the sit and wait method, likely because those young males are the most mobile and therefore the most likely to be encountered (Bischof et al. 2008).

Hunting and population dynamics

Hunting is the primary driver of brown bear population dynamics in Scandinavia. Hunting bears directly decreases bear numbers in Scandinavia and is additive to natural sources of mortality (Bischof et al. 2009). However, hunting also indirectly alters population dynamics by 1) shifting the age and sex structure of the population, 2) altering the social structure, 3) shifting individual bear behavior, and 4) selecting for certain life history or genetic traits (Bischof et al. 2018, Frank et al. 2017, Gosselin et al. 2015). These indirect effects are important because changes in bear behavior and population structure can alter the survival and reproductive patterns of the population, creating a feedback loop from hunting that continues after offtake has occurred (Bischof et al. 2018, Frank et al. 2017, Gosselin et al. 2015).

Population growth rate: Bear population growth rate is primarily driven by the presence and success of reproductive females, i.e., population growth is highest when there are many females who produce multiple cubs that survive to adulthood (Gosselin et al. 2015, Van de Walle et al. 2021a). Thus, protecting females with cubs is a key way to increase population growth (Van de Walle et al. 2021a). For example, the protection of family groups may lead to an increased protection of those females that keep their cubs an extra year (to 2 ½) compared to other females, which may ultimately lengthen litter interval, lower individual reproductive potential, and decrease population growth rate (Van de Walle et al. 2018). Furthermore, protecting family groups also decreases the population of bears that can potentially be hunted, which increases hunting pressure on solitary bears (Van de Walle et al. 2021a). This may contribute to a decrease in population growth rate if the number of male bears on the landscape becomes too few, or the male population is kept at a young age (Van de Walle et al. 2021a). Functionally all population demographic rates (i.e., the survival of females and cubs and the reproductive output of all age classes of females) are affected by hunting which ultimately contributes to decreased population growth (Gosselin et al. 2015).

Age and sex structure: Hunter harvest also likely affects the age structure of the population, although this remains unquantified. A younger age structure in general may result in decreased reproductive success; first time mothers are less successful while prime-aged females are the most successful (Zedrosser et al. 2009).

Hunting and bear behavior

Hunting activity peaks in the early hours of the day during the hunting season, which means risk from hunting is highest during that time, and lower during the other hours of the day (Hertel et al. 2016b). License hunted bears are more at risk when they are in close proximity to human infrastructure and activities such as roads and villages (Steyaert et al. 2016b). Mortality risk from management removals is highest for bears when they are near human infrastructure such as settlements, buildings, roads, and on agricultural land (Steyaert et al. 2016b). Management bears were killed in closer proximity to human infrastructure (Steyaert et al. 2016b).

Activity patterns and movement: Bears in Scandinavia alter their movement and activity patterns in response to hunting pressure (Hertel et al. 2017, Ordiz et al. 2012). For example, bears that experience hunting pressure, i.e., solitary males and females, begin to move more during non-daylight hours once the hunting season starts (Hertel et al. 2017, Ordiz et al. 2012). Family groups that are not hunted also shift their movement patterns in a similar way, but to a much lesser extent (Ordiz et al. 2012). Bears also respond directly to hunting itself. A recent study that explored the effect of simulated hunts (with dogs) on bear behavior and stress found that bears traveled longer distances at higher speeds after an encounter with a hunting team (Le Grand et al. 2019). Furthermore, hunted bears also appeared to go through more acute stress, showing increased heart rates and body temperatures directly after a hunting encounter (Le Grand et al. 2019).

Foraging behavior: Altered movement patterns often translate into altered foraging behavior during the fall hunting season. Bears respond to temporal risk (i.e., risk is greater during the daytime) by foraging less during the morning hours in the hunting season (i.e., they move less in general during this time), and they forage less effectively and on poorer quality berries during that time (Hertel et al. 2016b). They decreased their foraging activity, their food intake, and they ate poorer quality foods during this time (Hertel et al. 2016b). Furthermore, their chosen foraging strategy may expose them to more or less risk during this time period, i.e., bears that forage in risky places are more likely to be shot (Lodberg-Holm et al. 2019). In general, bears select for areas where blueberries are more likely to occur, but will avoid these areas during the hunting season if they are high risk, meaning they are more likely to be shot there (Lodberg-Holm et al. 2019). This results in a food for safety trade-off where bears limit their chances of being shot by foraging in areas that are safer but less productive (Lodberg-Holm et al. 2019). This is important because fall is a critical time of the year for bears, when they enter into hyperphagia and eat profusely to prepare for the denning season. Altered movement and foraging patterns during fall may affect their ability to gain fat before denning, which can affect their body condition in spring as well as their reproductive success (Hertel et al. 2016b, Ordiz et al. 2012).

Mating and reproduction: Increased sexually selected infanticide is another indirect effect of bear hunting in Scandinavia (Gosselin et al. 2017, Swenson et al. 1997b). Males only kill cubs that aren’t their own. Removing males from an area increases the chance that new males will move, which increases the potential for cubs to be killed. For example, females with home ranges in proximity to male bear harvest locations within the previous 1.5 years have an increased risk of cub loss (Gosselin et al. 2017). The subsequent effects of infanticide in the population mean that harvesting one adult male is the equivalent of removing between ½ to 1 female bear from the population (Swenson et al. 1997b).

Social behavior: The underlying social structure of the bear population in Scandinavia is likely altered via hunter harvest. For example, female survival is lower when harvest rates are high, which can result in a breakdown of the matrilineal partially territorial structure of the bear population in Scandinavia (Frank et al. 2021). When bears are shot it creates ‘home range vacancies’ in the landscape that may then be filled in by other dispersing bears (Frank et al. 2018). Thus, hunter harvest changes the competitive landscape that would otherwise exist, releasing bears from competition with one another. Bears of the same sex as those that were harvested use the harvested home range of the bear more after they have been shot (Frank et al. 2018). Interestingly, surviving males who were less related to the harvested bear were more likely to use his previous home range (Frank et al. 2018). Females still stay close to home and use home ranges of related females, regardless of whether they have been shot or not (Frank et al. 2018).

Human-induced selection of traits

Hunters also tend to select for certain behaviors in bears, which might alter the trend of behaviors within the population (Leclerc et al. 2019). For example, research suggests that hunters tend to shoot males that move less in general and are less active during legal hunting hours, and shot both males and females that were closer to roads, which may select for boldness traits (Leclerc et al. 2019). A study on reproduction effort in relation to the body weight of brown bears under intense harvest pressure in 1) areas with long-term (>500 years) harvest with 2) areas with a shorter period (<50 years) of harvest found that there is greater reproductive effort in populations with long-term intense harvest pressure (Swenson et al. 2010). Thus, hunting the bear population in Scandinavia could result in a life history shift within the population whereby bears will begin to reproduce at a younger age and at a lower body weight, i.e., prioritizing reproduction over body growth.

What it all means

Hunting pressure clearly plays a key role in the Scandinavian bear population, affecting everything from their behavioral patterns to their population demography (Frank et al. 2017). This occurs both directly through hunter harvest but also indirectly by altering the age and sex structure of the population as well as their social interactions and behavior. Furthermore, hunting bears likely diminishes their ecological role as predators within the ecosystem, indirectly affecting other species (Ordiz et al. 2013a). It is our view that the indirect effects of hunting on the bear population in Scandinavia deserve more attention by researchers and managers as they can influence population growth rates in unexpected ways (Frank et al. 2017).

5.3 Human-bear encounters

KEY POINTS

- The probability of being attacked and injured/killed by a bear in Scandinavia is extremely low.
    - Between 1970 and 2016 (~40 years), 44 encounters between bears and people resulted in attacks that caused injury (42) or death (2).
    - Between 1750 and 1962 (>200 years), 75 encounters between bears and people resulted in attacks that caused injury (48) or death (27).
- Most injuries in Scandinavia are associated with hunting activities, especially bear-hunting activities.
- Bears tend to be the most dangerous when they are threatened or wounded, or when they have young cubs.
- When approached, bears either flee (80%-90% of the time) or hid (10%-20% of the time). No approach by researchers ever resulted in aggressive behavior from a bear.
- People in Scandinavia are often fearful of encountering brown bears; targeted strategies may help reduce this fear.

The brown bear is a large carnivore, and its size, strength, speed, and explosive power mean it can potentially be very dangerous to humans. Thus, brown bears conjure awe, respect, and often fear across their range in the northern hemisphere, including in Scandinavia. People in Scandinavia have been both injured and killed by bears (Støen et al. 2018, Swenson et al. 1999b), and many people in Norway and Sweden are reportedly afraid of encountering bears and potential bear attacks (Ericsson et al. 2010, Røskaft et al. 2003). The SBBRP has explored how many people are injured or killed annually by bears in Scandinavia and the context surrounding those attacks. We have also studied how brown bears react in close encounters with humans and how this knowledge can reduce human injuries and help reduce fear among people so that humans and bears might coexist better in the landscape.

Bear attacks in Scandinavia

Brown bears in Scandinavia are usually very shy, avoid people and are generally not aggressive when encountered in the wild. The actual risk of being attacked by a bear is quite low in Scandinavia, for example, people are much more likely to be injured or killed by domestic animals, such as dogs, horses, and cattle, than by bears (Støen et al. 2018, Swenson et al. 1999b). For example, between 1977 and 2016, only 44 encounters between bears and people resulted in attacks that caused injury (42) or death (2). The vast majority of these incidents included adult men (42). One incident included a woman doing forestry inventory and one incident a young boy falling into a den while skiing off-piste (Støen et al. 2018). The majority of cases surrounded hunting activities, including bears, moose, or small game hunting (33) and 62% of all attacks (26) were associated with a hunter shooting at or shooting the bear at relatively close range, about 8-9 m (Støen et al. 2018).This is relevant because bears are especially dangerous when they are threatened or wounded (Bombieri et al. 2019, Støen et al. 2018, Swenson et al. 1999b).

Outside of hunting activities, only 16 attacks on individuals occurred over nearly 40 years. Among 11 non-hunters that were attacked by bears, eight of the incidents involved females with young cubs. This is a pattern observed worldwide, where most attacks are defensive and are the result of a female defending her cubs, especially cubs of the year (Bombieri et al. 2019). Historical records from the period between 1750 and 1962 when the bear population was higher but diminishing due to bounty hunting, a total of 75 attacks were reported that caused injury (48) or death

(27) (Swenson et al. 1999b). Again, the majority (52%) of these instances were associated with bear hunting or hazing (39), with the second-most common being livestock herding (13) (Swenson et al. 1999b).

The likelihood of encountering a bear in the wild within Scandinavia, and such an encounter leading to an attack or injury, appears to be extremely low, despite the potential for such encounters having increased due to the bear population tripling over the last fifty years in Scandinavia (Bombieri et al. 2019, Støen et al. 2018, Swenson et al. 1999b). Nonetheless, the incidence of bear encounters resulting in attacks has risen in parallel with the growing bear population. The primary factor contributing to the increase in encounters leading to injuries is the rise in bear hunting, which has increased in tandem with the bear population size (Støen et al. 2018, Swenson et al. 1999b). Conversely, the rate of non-hunters sustaining injuries, despite increases in both human and bear populations, does not exhibit a similarly strong correlation (Støen et al. 2018).

Bear behaviour when encountering humans

In 2006, the SBBRP began several studies exploring how bears would behave when they encountered people in the forest. During these studies, one or two researchers would approach GPS collared bears on foot (exhibiting normal hiking behavior) to within ~50 m and assess the bears' reactions using fine-scale GPS positioning and visual cues if seen. Over the course of six years, researchers approached bears almost 300 times, including females with cubs (Ordiz et al. 2013b). Bears were only seen or heard by the researchers in 14-26% of all approaches (Moen et al. 2012, Ordiz et al. 2013b, Sahlén et al. 2015b). In other words, in the large majority is instances, the approaching people would have never known a bear was nearby without the benefit of GPS technology. Throughout the studies, no bear ever acted aggressively towards the approaching researchers, i.e., threatened, bluff charged, or attacked (Moen et al. 2012, Ordiz et al. 2013b, Sahlén et al. 2015b). Altogether, this confirms that the Scandinavian brown bear is both shy and non-aggressive.

In the most cases, the bears left the area immediately upon being approached (single bears left 80%-89% of the time, females with cubs 95%) while the remaining bears stayed in place and hid (Moen et al. 2012, Sahlén et al. 2015b). The average flight distance i.e., the distance to the approaching humans when the bears flee, was between 69 and 115 m, depending on whether the bear was up and active or not (Moen et al. 2012). Active bears (e.g., bears that were traveling or foraging) were more likely to flee when people were farther away than resting bears, meaning active bears fled more quickly upon approach then resting bears (Moen et al. 2012). Young bears were more likely to flee than older bears and bears were more likely to hide if they were located in more dense vegetation (Moen et al. 2012). Bears in Scandinavia generally either flee or hide from humans when they approach, and the encounter can influence the bears behavior for several days (see Section 5.1 Human disturbance and brown bear behavior for more details).

Managing fear of bears

Many individuals in Scandinavia experience fear of brown bears, which may cause them to reduce their outdoor activities in areas with bear populations. A crucial question for management is how to assist these individuals in managing their fear, enabling them to continue engaging with regular outdoor activities despite the presence of bears. The main reason people are afraid of bears seems to be the perception that bears are dangerous, uncontrollable, and unpredictable (Johansson et al. 2012). Potential intervention methods include information and education, exposure to bears and their habitat, collaboration and participation, and financial incentives (Johansson et al. 2016a). In collaborations with psychologists, we have explored the effectiveness of several of these proposed interventions.

Individual exposure to bear habitat with a guide informing them about bear biology, the danger of bears, and how bears normally behave when encountering humans seems to be a viable method for decreasing fear (Johansson et al. 2019, Johansson et al. 2016b). Here, the guide serves as a role model for the participants about how to think about bears and behave when meeting a bear. Some of the exposure studies also included either a bear approach, i.e., joining researchers in the field who then approached a radio-collared bear within 50 m (Johansson et al. 2019, Johansson et al. 2016b) or a guided walk in a park with captive bears. All three exposure methods reduced peoples fear (Johansson et al. 2019). The bear approach had the strongest effect, however a guided walk in bear habitat is the most practical method as an intervention and does not involve captured or radio-collared animals.

We also evaluated whether informational meetings, for example after a bear has approached a village, might reduce fear and increase social trust (Johansson et al. 2017). This study found that the people who found the information credible reported a decrease in fear towards bears and increase in social trust, suggesting informal community meetings may prove a useful intervention tool as well (Johansson et al. 2017).

Management recommendations

Although the probability of being attacked and injured or killed by a brown bear in Scandinavia is extremely low, there are several strategies managers might implement to further mitigate this risk. The most efficient mitigation to reduce injuries by bears is to educate hunters about how to avoid dangerous encounters with bears. This includes both bear hunters and how they might hunt bears in a safe manner as well as other game hunters on how to behave if they encounter bears. In terms of mitigating fear of bears, we have made a handbook for how to address concern or fear of bears including practical advice and the scientific knowledge base for the recommendations that might be practical for managers to use when people express fear of bears that impede their daily life (Støen et al. 2022a).

6 Bear Physiology and Human Health

6.1 Ecophysiology of Scandinavian brown bears

KEY POINTS

- During the active period, brown bears have a mean body temperature of 37-38 °C and heart rate of 65±20 beats per minute (bpm).
- Both body temperature and heart rate are dramatically reduced during hibernation; mean body temperature is 33.6 °C and mean heart rate is 16 bpm.
- Bown bears adjust their biological rhythms to the seasonal environment they inhabit. Rhythms in physiology and activity show simultaneity during the active state but are partly disconnected from each other during hibernation, when bears are most sheltered from the environment.
- Body temperature is likely the main driver of immune function regulation during hibernation.
- Higher oxygen affinity in winter likely maintains a relatively constant tissue oxygen tension during hibernation.

Understanding the fundamental baseline physiology of brown bears allows us to assess how physiological parameters can vary between seasons, life stages and events, and potential stressors such hunting. Over the last 14 years, we have applied heart rate loggers developed for humans and we adapted them for bears (Laske et al. 2018) and used internal temperature loggers for body temperature. We then explored variation in these physiological measures with respect to season, hibernation periods, and stressors. In general, bear physiology changes at seasonal and daily scales and can also depend on a variety of environmental factors (Thiel et al. 2022). The use of biologgers has allowed us to fill in important knowledge gaps in the basic ecology and physiology of free-ranging brown bears while also providing a solid foundation for exploring further details on conservation, management, and implicates of climate variability on bear biology.

Physiology during the active phase

Body temperature: During the active period, the body temperature of bears generally ranges between about 37-38 °C, depending on their body size. For example, we have also observed consistently higher body temperature with sequentially smaller bears during summer n(Evans et al. 2023). Body temperatures follow a diel rhythm and are higher from sunset to late morning compared to midday, which corresponds to the time when they are the most active (Thiel et al. 2022).

Heart rate: During the active period, the baseline heart rate of bears generally ranges between about 65±20 beats per minute (bpm), but can overall be quite variable, depending on the time of day and year as well as body size of the bear (Blanchet et al. 2019, Evans et al. 2023). Similar to body temperatures, heart rates are the highest when they are the most active, commonly during and between sunset and sunrise (Thiel et al. 2022) and during the late summer (August) compared to early spring (May) (Blanchet et al. 2019). Body size also affects heart rates, but only during summer; smaller bears have higher daytime heart rates than larger bears (Evans et al. 2023). Bear heart rates also increase when they travel long distances relatively quickly, i.e., >50 m in 1 hour (Blanchet et al. 2019). Furthermore, bears that had cubs generally had a lower heart rate than those that had no cubs, especially during May, likely because of the decreased movement and activity associated with caring for young cubs (Blanchet et al. 2019). However, after August, bears with cubs generally have higher rates than solitary bears (Blanchet et al.

2019). In general, bear heart rates increased with metabolic rates, which are both highest during the hyperphagia period before denning (Blanchet et al. 2019). The hyperphagic shift in brown bears does not increase to the same extent as seen in Asiatic black bears (Fuchs et al. 2019).

Heart rate variability and stress: Heart rate variability (HRV) can be considered as an indicator of stress. Stress produces changes in HRV rates and although heart rates are highly affected by movement while HRV is less so (Støen et al. 2015). In this context, low HRV indicates high stress, or a “fight or flight” response, while high HRV indicates low stress and a “rest and digest” response (Støen et al. 2015). Our research suggests that bears are more stressed (lower HRV) when they are near human settlements, especially during the fall berry season when more people tend to be in the forests harvesting berries and hunting (Støen et al. 2015).

The physiology of hibernation

Northern mammals show a host of behavioral, ecological, and physiological strategies for survival in harsh climates. Bears are unique in that they hibernate six months of the year without eating, drinking, urinating, or defecating, and the females give birth in their dens. For more information on denning patterns see Section 3.5 Denning ecology. Although there are numerous previous studies on the physiology and ecology of hibernation in bears, many gaps in our knowledge remain. Also, most physiological studies have been conducted in laboratory conditions, independently from the bear’s natural ecology. Captures during the winter hibernation period and the deployment of biologging devices have allowed for addressing fundamental questions about the basic biology of the bear’s annual cycle, including hibernation. For information on how capture procedures, including the implantation of biologgers, affects brown bears see Section 7.2 Effects of capture on Scandinavian brown bears.

Activity, heart rate and body temperatures begin to drop slowly several weeks before bears entre their den (Thiel et al. 2022). Denning appears to be tightly coupled with metabolic suppression and slowing down in biological rhythms (Thiel et al. 2022). During arousal, body temperature begins to rise almost two months before den exit (Thiel et al. 2022). An initial spike in body temperature is driven by ambient temperature, independently of autonomic nervous system activity which only became active three weeks before den exit (Evans et al. 2016a). The difference between body temperature and ambient temperature decreased gradually. Although the sympathetic nervous system began to restore euthermic metabolism three weeks before den exit, it was not until ambient temperature reached the bear’s lower critical temperature that bears exited the den (Evans et al. 2016a).

Body temperature: During the core hibernation period, bear body temperatures remain low, averaging 33.6 °C (ranging between 30.2-37.3 °C) (Evans et al. 2023). Furthermore, the body temperature of hibernating bears is consistently lower with sequentially smaller bears (Evans et al. 2023). Interestingly, observed lowered levels of leukocytes during hibernation were, when compared across species, explained by the decline in body temperature during hibernation, suggesting that body temperature is the main driver of immune function regulation during hibernation (Evans et al. 2023). Furthermore, pregnant females have higher body temperatures during pregnancy, which then drops back down after they have given birth in the den (Friebe et al. 2014).

Heart rate: Heart rates also remain lower during the main hibernation period, averaging 16 bpm (ranging between 7-70 bmp (Evans et al. 2023)). Unlike their active period, however, heart rates during hibernation are not associated with bear body mass (Evans et al. 2023).

Hematological and biochemical parameters: In blood samples taken during winter, analyzed together with similar sized bears in spring and summer, we found significant shifts in hematological and biochemical measurement in winter (February-March) compared to in spring and summer (April-July) (Græsli et al. 2015). This reflects the lowered metabolic, kidney, and liver activity and a shift to a lipid-based (fat-based) metabolism during hibernation (Græsli et al. 2015). As a previous study has shown that metabolic rate and oxygen consumption are independent from lowered body temperature, we investigated changes in oxygen binding affinity of red blood cells from hibernating bears, which consistently showed higher oxygen affinity than their summer counterparts. This likely maintains a relatively constant tissue oxygen tension during hibernation.

6.2 Ecotoxicology: Lead (Pb) exposure in Scandinavian brown bears

KEY POINTS

- Scandinavian brown bears are highly exposed to environmental lead (Pb).
- Sources of Pb are anthropogenic; mainly lead-based ammunition, leaded gasoline, and industrial activity.
- No level of exposure to Pb is known to be without harmful effects.
- The mean Pb lead level in Scandinavian brown bears was 8 times higher than the established threshold for developmental neurotoxicity in humans.
- The mean Pb concentration in bears during hibernation was significantly higher than when they were active.
- **Caution when consuming**: Most bear edible tissues exceeded the maximum allowable Pb concentrations in meat and offal from domestic livestock. Additionally, 98% of hunted bears were shot with lead-based ammunition, further increasing contamination of bear meat products with Pb.

Bears as sentinels for ecosystem health

A recent study has begun attempting to use bears as sentinels for ecosystem health, from the One Health perspective. The most recent research has focused on assessing the amount of lead (Pb) and lead isotopes in the blood, milk, muscle, and tissues of bears and identify sources and pathway of lead exposure. However, all collected samples have also been analyzed for 72 different elements, which will be included in future studies to assess ecosystem health in a wider context. In the Scandinavian brown bear, so-called reference ranges for blood or serum element concentrations have been established (Græsli et al. 2014). Such reference values can be used for health assessment of individual animals or to compare different populations of the same bear species. Typically, only essential elements are included in such studies and often the number of elements are limited. Blood concentrations of nonessential (toxic) trace elements are often reported separately from individual elements (Fuchs et al. 2021) or as a group containing the classical heavy metals, As, Cd, Hg and Pb (Fuchs et al. 2023). The same approach is also seen in extensive monitoring programs, such as the Arctic (Arctic Monitoring and Assessment Programme 2021).

Background and context

Trace elements: The term ‘trace elements’ is used to indicate elements that are present in living tissues in very small amounts. Some trace elements are known to be nutritionally essential, others are potentially essential (inconclusive evidence) and the remainder are considered to be nonessential (US National Research Council 1989). Fourteen elements, listed alphabetically (with the chemical symbol in parentheses), are commonly referred to as trace elements: aluminum (Al), arsenic (As), copper (Cu), cadmium (Cd), chromium (Cr), fluorine (F), iodine (I), iron (Fe), lead (Pb), manganese (Mn), mercury (Hg), molybdenum (Mo), selenium (Se), and zinc (Zn).

Essential trace elements: Essential trace elements include copper (Cu), chromium (Cr), fluorine (F), iodine (I), iron (Fe), manganese (Mn), molybdenum (Mo), selenium (Se), and zinc (Zn). These nine elements have different roles in mammalian physiology, e.g., they may function as catalysts in enzyme systems, they participate in oxidation-reduction reactions in energy metabolism, or they are ingredients in vital molecules such as hemoglobin, myoglobin, and thyroxine. Meeting the body’s physiological needs requires an optimal, balanced intake of essential trace elements, and the concentrations of these elements in the blood and tissue are naturally regulated within certain levels to sustain a healthy organism. All essential trace elements are toxic if consumed at sufficiently high doses and/or for long enough periods. On the other hand, if the intake and blood or tissue concentrations are below critical levels, diseases due to deficiencies may develop.

Nonessential (toxic) trace elements: By definition, the nonessential trace elements, aluminum (Al), arsenic (As), cadmium (Cd), mercury (Hg), and lead (Pb), have no known biological function in mammals and birds. They are, however, frequently ingested as contaminants in food or water and may be highly toxic even at very low levels of intake. The World Health Organization has stated that there is no level of exposure to lead that is known to be without harmful effects (World Health Organization 2023). Several of these nonessential elements accumulate in the body (bioaccumulate) due to long half-lives in the body (e.g. 10-30 years for lead in humans) and may reach toxic tissue levels during the lifetime of an individual. This is especially true for species, such as the brown bear, with a long lifespan, i.e., bears can live for 20-30 years. Mercury is known to ‘biomagnify’, which means that its concentration increases from one trophic level to the next within the food web. Interactions between various nonessential elements are an important aspect. This is known as the ‘cocktail effect’, a term used for the harmful effects from the combination of several toxic substances, even if the concentrations of the individual elements are below their known thresholds for toxicity.

Other essential elements: There are several other nutritionally essential elements, such as calcium (Ca), chloride (Cl), cobalt (Co), magnesium (Mg), phosphorus (P), potassium (K), sodium (Na), and sulfur (S). In addition, mammalian and avian blood and tissues contain trace amounts of numerous other elements because they exist in Earth’s crust and are found in soil, water, or food. Many of these elements have either no known biological function or the evidence for any physiological role is inconclusive. Others may occasionally show up at increased concentrations in wildlife due to contamination, e.g. cesium (Cs) from atmospheric fallout.

Lead (Pb) and other heavy metals in the Scandinavian bear population

Lead levels are high in the Scandinavian brown bear population. The mean blood lead concentration in bears was 96.6 µg/L (range: 38.7–220.5 µg/L) (Fuchs et al. 2021). Importantly, both the mean and range are well above established threshold concentrations for developmental neurotoxicity (12 µg/L), increased systolic blood pressure (36 µg/L) and prevalence of chronic kidney disease in humans (15 µg/L) (Fuchs et al. 2021). Interestingly, lactating females had higher lead blood concentrations compared to younger, non-lactating females. Blood lead concentrations of dependent cubs were correlated with their mother’s blood lead concentration, which in turn was correlated with the lead concentration in the milk. The mean lead concentration during hibernation (111.5 µg/L) was significantly higher than during the active state (69.5 µg/L), potentially posing a higher risk of health effects in hibernating animals (Hydeskov 2023).

Bears in Scandinavia also have other heavy metals in their system, including mercury, arsenic, and cadmium (Fuchs et al. 2023). A recent study comparing heavy metals in bears in Scandinavia and Alaska suggests that cadmium and lead blood concentrations were higher in Scandinavian bears than in Alaskan bears (Fuchs et al. 2023). However, Alaskan bears consuming salmon and other marine foods had higher mercury and arsenic blood concentrations compared to Scandinavian bears feeding on berries, ants, and moose (Fuchs et al. 2023). Blood concentrations of cadmium, lead, and arsenic in female bears increased with age, while arsenic and mercury concentrations in male bears appeared to decrease with age (Fuchs et al. 2023).

Despite the high levels of heavy metals, including lead, in the bear population in Scandinavia, the effects of these toxins on individual and population health remain unknown. Recent research suggests that three blood measurements indicative of chronic kidney disease (hemoglobin, hematocrit and creatinine) were correlated with lead (Hydeskov 2023). Lead was present in all brown bear tissues analyzed and the results suggest a body distribution similar to humans (three-compartment model) (Hydeskov 2023). However, no histopathological changes were identified in liver, kidney, or spinal cord tissues, so the definite health effects of lead in brown bears are still undetermined (Hydeskov 2023).

So where does the lead come from? The main sources of lead seem to come from human activities; mainly lead-based ammunition, leaded gasoline, and industrial activity. Environmental lead concentration is the main predictor of blood lead levels in bears (Brown et al. 2023a). Furthermore, moose harvest distribution and scavenging on slaughter remains was an additional source of lead exposure in bears (Brown et al. 2023a).

Caution when consuming

Edible tissues from hunted Scandinavian bears pose a risk to human health if consumed (Hydeskov 2023). Most samples exceeded the maximum allowable lead concentrations in meat and offal from domestic livestock. Again, the mean blood lead concentration in bears was 96.6 µg/L (range: 38.7–220.5 µg/L) (Fuchs et al. 2021). Importantly, both the mean and range are well above established threshold concentrations for developmental neurotoxicity (12 µg/L), increased systolic blood pressure (36 µg/L) and prevalence of chronic kidney disease in humans (15 µg/L) (Fuchs et al. 2021). Additionally, 98% of the bears hunted were shot with lead-based ammunition, further increasing contamination of bear meat products with lead.

6.3 Bear physiology and human health

KEY POINTS

- The distinct physiology of hibernating brown bears makes them a compelling translational model for medical research.
- Brown bear physiology provides unique insights for developing novel treatments in metabolic and cardiovascular human diseases.
- Bears undergo dramatic cardiac changes while hibernating, which has implications for understanding heart failure and myocardial infarction in humans.
- Hibernating brown bears display ‘antithrombotic mechanisms’ without increased bleeding risk, suggesting new avenues for human clot prevention.
- Bears avoid clogged arteries despite high cholesterol levels.
- Hibernating bears resist muscle atrophy and maintain bone health, offering insights for human muscle preservation and osteoporosis treatment.
- Hormonal shifts in hibernating bears offer insights for human endocrine and metabolic disorders.

The brown bear as a translational model in medical research

The brown bear is a remarkable animal, exhibiting unique physiological adaptations that allow it to survive in a wide variety of environments. These adaptations are particularly evident during hibernation, a period when the bear undergoes significant changes in metabolism, cardiovascular function, and other physiological processes. Interestingly, despite the drastic physiological changes and the challenges of prolonged inactivity and fasting, the bear emerges from hibernation in a healthy state each spring. This ability to withstand physiological extremes has led researchers to propose using the brown bear as a translational model for understanding human health and disease. Even though they are not closely related, brown bears may be more physiologically similar and therefore relevant to humans than mice and rats, the conventional model animals in medical research. Unlike typical hibernators that lower their body temperature to near-ambient levels, brown bears maintain a moderate hibernation temperature between 33 and 35°C (Evans et al. 2023). This feature positions them as an interesting translational model for medical research.

One of the most intriguing aspects of bear physiology is their ability to tolerate obesity and a 'sedentary lifestyle' during hibernation and emerge from the den metabolically healthy in spring. This circular metabolic plasticity is in stark contrast to the linear path to worsening health seen in humans with ‘metabolic syndrome’, a condition characterized by a cluster of conditions that increase the risk of heart disease, stroke, and type 2 diabetes. Understanding the mechanisms underlying the bear's metabolic plasticity could provide valuable insights into the prevention and treatment of metabolic syndrome and other lifestyle-related diseases in humans (Fröbert et al. 2020).

The impact of hibernation on cardiovascular health

Heart failure: When brown bears hibernate, their cardiac function undergoes significant changes. Using small implantable biologgers, we have been able to monitor heart rate, respiratory rate, and body temperature in bears (Laske et al. 2018). We observed markedly low winter heart rate in bears, dropping to as few as 10 beats per minute, along with extremely slow blood flow (observed via ultrasound). These findings raise intriguing questions about their ability to evade blood clot formation when they are immobile and provide insights into potential applications for understanding human cardiac conditions like heart failure (the inability of the heart to efficiently pump blood around the body).

> Behind the scenes: By comparing cardiac structural and functional measures in hibernating and active bears using cardiac ultrasound, we found that during hibernation, bears exhibit a lower heart rate and decreased left ventricular systolic and diastolic measures, including ejection fraction and global longitudinal strain. These findings suggest that hibernating bears undergo cardiac adaptation characterized by reduced myocardial velocities (Jørgensen et al. 2020, Jørgensen et al. 2016).

Heart attacks: In humans, myocardial infarctions, or heart attacks, usually occur when a coronary artery becomes occluded or obstructed, resulting in a loss of blood supply to the heart. Even after reopening the artery in the hospital using balloon angioplasty, the reestablishment of blood flow can cause additional damage to the heart, known as reperfusion injury. Interestingly, our research suggests that blood serum from brown bears may offer a solution and may serve as a promising new avenue for the development of therapies to treat myocardial infarction.

> Behind the scenes: When mouse cardiomyocytes (cells responsible for contracting the heart) were treated with winter bear blood serum (as opposed to summer blood serum), there was a significant reduction in cell death compared to controls (Givre et al. 2021). In another cross-species experiment, we investigated the effects of bear blood serum on human adipose-derived mesenchymal stem cells (ADSCs). We found that ADSCs from patients with ischemic heart disease (coronary heart disease) treated with hibernating bear blood serum showed downregulation of genes linked to inflammation and upregulation of genes associated with cardiovascular development. Blood serum from both hibernating and active bears led to the downregulation of certain genes related to cell growth and differentiation. This suggests that plasma from hibernating bears has the potential to suppress inflammation and promote cardiovascular development in human ADSCs, offering possible therapeutic applications (Berg von Linde et al. 2021).

Blood clotting – a first breakthrough: Platelets are small, colorless cell fragments in the blood that play a crucial role in blood clotting and wound healing. Brown bears show a notable decrease in platelet aggregation, or clotting, when they hibernate compared to when they are up and active. This reduction in platelet aggregation may serve as a protective mechanism to prevent the formation of blood clots (thrombi) during the periods of reduced blood flow, which are common during hibernation (Arinell et al. 2018). Humans that experience illnesses or injuries that leave them immobile for short periods of time have increased risk of venous thromboembolism (VTE). VTE is characterized by the formation of blood clots in the deep veins of the legs (deep vein thrombosis) that can travel to the lungs (pulmonary embolism) which can be life threatening. Interestingly, both hibernating brown bears, which remain immobile for months, and humans with paralyzed spinal cord injuries are protected from VTE. This has important implications for the prevention and treatment of thrombotic diseases in humans such as deep vein thrombosis and pulmonary embolism.

> Behind the scenes: Our recent research suggests the mechanism behind this is the downregulation, or decreased production, of a certain heat shock protein (HSP) called HSP47. HSPs are proteins that are produced in higher quantities when the body is exposed to stressful conditions. Downregulation, or decreased production, of HSP47 decreases immune cell activation as well as something called ‘neutrophil extracellular trap formation’. The result is that the downregulation of HSP47 offers protection from thrombosis and VTE for both hibernating bears and paralyzed humans. This appears to be an evolutionarily conserved mechanism that protects hibernating bears from thrombosis while not elevating the risk of bleeding. Importantly, this sets it apart from most conventional anticoagulants used for clot prevention in humans (Thienel et al. 2023). Following a recent major research grant, we are now investigating the role of HSP47 in patients with VTE and other types of blood clots with the hope of developing a new type of anticoagulant.

Maintaining oxygen supply: Bears sustain efficient oxygen delivery to the tissues in their body during hibernation without elevating their metabolic rate, a phenomenon that could have applications in human metabolic and respiratory medicine.

> Behind the scenes: Oxygen consumption and blood oxygen affinity, two crucial aspects of respiratory function, also change in brown bears during hibernation. Hibernating bears exhibit a significant reduction in basal oxygen consumption rate (about 25% of that compared to during the active time of year) and a moderate decrease in body temperature. This suggests a temperature-independent aspect of their metabolic depression. Interestingly, despite the decrease in oxygen consumption, hibernating bears exhibit higher blood oxygen affinity, attributed to lower levels of a certain red blood cell (Hb-cofactor 2,3-diphosphoglycerate, or DPG) during hibernation. This decrease in DPG is crucial for maintaining tissue oxygen tension during hibernation without significant upregulation of glycolysis, the metabolic pathway that converts glucose into pyruvate and generates energy (Revsbech et al. 2013).

Hibernation and lipid metabolism, diabetes, and atherosclerosis

Avoidance of diabetes - lipids and the gut: Fatty acid metabolism is another area where bears exhibit unique adaptations during hibernation. We investigated how free-ranging brown bears manage to gain weight before hibernation without developing issues like insulin resistance. Insulin resistance is an impaired response to insulin by the body that results in elevated levels of blood sugar (glucose), which is a key component of type 2 diabetes and often a problem related to human obesity. We also explored whether gut microbiota (the microorganisms that live in the digestive tract) help bears adapt to hibernation. Our results suggest that gut microbiota play an important role in bear metabolic adaptations and cardiovascular health. This information could potentially offer insights into novel treatments for lifestyle diseases like chronic kidney disease, which is often associated with cardiovascular disease (Ebert et al. 2020).

> Behind the scenes: The first example study focused on the expression of proteins associated with lipid (fat) breakdown, or lipolysis, in the bears' adipose tissue (body fat). This study found that while the expression of Adipose Triglyceride Lipase (ATGL) remained constant across seasons, there was a significant increase in the expression of proteins that inhibit the breakdown of lipids, or fats, during the summer. This suggests that bears naturally regulate the breakdown of fat in a way that preserves insulin sensitivity even as they gain weight, potentially offering options for human therapies (Jessen et al. 2016).
>
> Both brown bears and garden dormice show consistent changes in fatty acid profiles between hibernation and summer, including reduced levels of certain fatty acids (alpha-linolenic acid and eicosapentaenoic acid), and increased levels of others (docosapentaenoic acid which is an omega-3 fatty acid). Interestingly, dietary differences affect these profiles, with high intake of linoleic acid, an omega-6 fatty acid, unexpectedly boosting the transformation of omega-3 fatty acids. These findings suggest a link between fatty acid patterns and the hibernation phenotype, highlighting the complex connections between diet, fatty acid metabolism, and hibernation (Strandvik et al. 2023).
>
> In a study of gut microbiota of brown bears, we explored how they maintain metabolic health despite seasonal obesity. We found distinct changes in the microbial composition and diversity of gut microbes between active and hibernating states, accompanied by shifts in lipid metabolism markers like cholesterol and triglycerides. When these gut microbes were transplanted into germ-free mice, the bear microbiota induced some of these seasonal metabolic changes. Mice transplanted with summer microbiota became obese, whereas those with winter microbiota remained lean; notably, both groups evaded insulin resistance - a prominent characteristic of obesity and a precursor to diabetes (Sommer et al. 2016). These findings imply a functional role for gut microbiota in the bear's metabolic adaptations.

Gut metabolites (substances produced by the gut microbiota) also play a crucial role in the bear's cardiovascular health during hibernation. In a study comparing the levels of the gut metabolites betaine, choline, and trimethylamine N-oxide (TMAO) in human chronic kidney disease and various animal species, including hibernating brown bears, we found that these metabolites are associated with kidney function in humans. In contrast, free-ranging brown bears exhibit a unique pattern during hibernation, with increased betaine and choline levels but undetectable TMAO (Ebert et al. 2020).

Atherosclerosis – clogged arteries: Despite the large lipid (fat) fluxes during hibernation, brown bears do not develop atherosclerosis. Atherosclerosis a condition characterized by the buildup of fats, cholesterol, and other substances in and on the artery walls which results in clogged arteries. This is in contrast to humans and non-hibernators, who often develop clogged arteries and related cardiovascular diseases in response to high cholesterol levels and other metabolic problems. Our research suggests that brown bears may serve as a model for studying atherosclerosis resistance and related cardiovascular diseases in humans (Arinell et al. 2012)

Behind the scenes: We analyzed lipid profiles and arterial histopathology in free-ranging brown bears during hibernation and active periods. Despite elevated lipid levels during hibernation, bears showed no signs of clogged arteries, suggesting brown bears may serve as a model for studying atherosclerosis resistance (Arinell et al. 2012). Another, contributing mechanism shielding bears from heart attack was found when we studied two antibodies (known as anti-PC and anti-MDA) in brown bears during hibernation and active periods. Elevated levels of certain anti-PC antibodies were found in hibernating bears, potentially serving as a natural defense against heart issues like atherosclerosis (Samal et al. 2021).

One of the mechanisms underlying the bear's resistance to clogged arteries is the management of lipid fluxes through changes in the composition of high-density lipoproteins (HDL), the so-called 'good' cholesterol. For instance, bears exhibit higher levels of inflammatory metabolites (such as 7-ketocholesterol and 11ß-prostaglandin F2α) during hibernation, which correlate inversely with cardioprotective HDL proportions and HDL sizes. Additionally, greater plasma antioxidant capacities in hibernating bears prevent excessive lipid-specific oxidative damages in plasma and muscles (Giroud et al. 2021). These findings suggest that modulation of lipid metabolism and antioxidant defenses could be a promising strategy for preventing atherosclerosis and related cardiovascular diseases in humans.

In another study we examined plasma lipoproteins across winter and summer in 10 bears, focusing on LDL cholesterol (so-called ‘bad cholesterol) binding to arterial proteoglycans and cholesterol efflux capacity (CEC) (Pedrelli et al. 2021). We found that bear LDL, which is larger and richer in triglycerides, binds less to arterial proteoglycans than human LDL and that bears have higher plasma CEC, particularly in the HDL cholesterol (‘good cholesterol’) fraction. This suggests the bears' resistance to early atherosclerosis may also be due to these unique lipid transport properties in their blood.

Hibernation and muscle and bone

Muscle preservation and protein regulation: Muscle atrophy, or the wasting away of muscle tissue, is a major health challenge in humans, particularly for people with prolonged immobility or certain diseases. Interestingly, hibernating brown bears are able to resist muscle atrophy despite the prolonged period of inactivity during hibernation. Remarkably, human muscle cells exposed to winter bear blood serum showed reduced protein turnover and inhibited proteolysis, resulting in increased muscle cell protein content (Chanon et al. 2018). Thus, research on hibernating bears has important implications for the prevention of muscle loss in humans with medical conditions that leave them immobile for extended periods of time.

Behind the scenes: Halofuginone, a pharmacological agent, activates Activating Transcription Factor 4 (ATF4)-regulated genes associated with muscle atrophy. Interestingly, it also

> inhibits Transforming Growth Factor-beta (TGF-β) signaling while promoting Bone Morphogenetic Protein (BMP) signaling, leading to reduced muscle atrophy under hindlimb suspension conditions. These regulatory patterns are similar to those observed in the muscles of hibernating brown bears, which are resistant to atrophy. The data suggest that activation of ATF4 does not invariably result in muscle atrophy and that modulation of TGF-β/BMP signaling may present a novel approach for preventing muscle loss (Cussonneau et al. 2022). Another potential musculo-protective mechanism in bears involves increased expression of cold-inducible proteins and downregulation of components in mitochondrial electron transfer, reducing reactive oxygen species production (Chazarin et al. 2019).

<u>MicroRNAs and the endocannabinoid system in muscle atrophy resistance:</u> Our research suggests that microRNAs (small non-coding RNAs that regulate gene expression) also play a crucial role in the bear's resistance to muscle atrophy during hibernation.

> <u>Behind the scenes:</u> A study using quantitative reverse transcription PCR (RT-qPCR) found that several microRNAs associated with skeletal muscle development, metabolism, and regeneration are upregulated in the vastus lateralis, a muscle in the thigh, of hibernating brown bears. These include miR-1 and miR-206, which are controlled by the transcription factor MEF2A and promote muscle maintenance by downregulating the genes pax7 and id2. Additionally, several metabolic microRNAs, including miR-27, miR-29, and miR-33, are increased during hibernation, suggesting metabolic suppression (Luu et al. 2020). These findings highlight the complex interplay between microRNAs and other regulatory molecules in the bear's resistance to muscle atrophy during hibernation.
>
> The endocannabinoid system (ECS), a complex cell-signaling system that plays a crucial role in regulating a wide range of physiological processes. During hibernation in brown bears, the ECS undergoes marked changes, such as decreased concentrations of 2-arachidonoylglycerol in adipose and muscle tissues and reduced mRNA levels for CB1 and CB2 receptors. These alterations facilitate fatty acid mobilization and carbohydrate metabolism in muscle, likely playing a pivotal role in sustaining hibernation. Elevated levels of the endocannabinoid-like compound N-oleoylethanolamide may support lipolysis and fatty acid oxidation, while also conserving anorexigenic signals (Boyer et al. 2020).

<u>Bone health and vitamin D metabolism:</u> Bone health is another area where bears exhibit unique adaptations during hibernation. In addition to muscle loss, humans also experience bone loss during prolonged periods of immobility or inactivity. However, bears do not lose bone mass during hibernation. Understanding the mechanisms underlying the bear's preservation of bone health during hibernation could provide valuable insights into the prevention and treatment of osteoporosis and other bone diseases in humans (Vestergaard et al. 2011).

> <u>Behind the scenes:</u> We examined 25-hydroxy-vitamin D (25OHD) levels and bone markers in hibernating and active bears found that levels of 25OHD, a measure of vitamin D status, are higher in summer than in winter. Despite this seasonal variation in 25OHD levels, bears do not lose bone mass during hibernation (Vestergaard et al. 2011).

Hormonal changes and their impact on metabolism during hibernation

<u>Hypothyroidism:</u> Hibernating bears are hypothyroid, meaning the thyroid gland is making less thyroid hormone when bears are hibernating compared to active. This hypothyroid state is associated with several physiological features that are also seen in hypothyroid humans, including decreased basal metabolic rate, bradycardia (slow heart rate), hypothermia (low body temperature), and fatigue (Frøbert et al. 2023). Further research on bear thyroid function could offer insights into human endocrine and metabolic disorders.

> Behind the scenes: Hibernating bears have levels of thyroid hormones thyroxine (T4) and triiodothyronine (T3) reduced to less than 44% and 36%, respectively, of those measured during their active period.

The role of steroid hormones: Shifts in hormones may contribute to the bear's ability to survive the prolonged period of inactivity and fasting during hibernation. This presents another interesting avenue for research linking bear physiology to human medicine.

> Behind the scenes: In brown bears during hibernation, total plasma protein concentrations increase, even though most individual plasma proteins decrease. Notably, there is a striking 45-fold increase in Sex Hormone-Binding Globulin (SHBG) (Frøbert et al. 2022a, Welinder et al. 2016). This increase in SHBG could potentially dampen the activity of reproductive hormones, thereby contributing to the bear's ability to survive the prolonged period of inactivity and fasting during hibernation (Frøbert et al. 2022b). The protein adaptations are likely facilitated through three key mechanisms: dehydration, which augments protein concentration without new synthesis; reduced protein degradation, due to a moderate drop in body temperature and lowered protease activity; and strategic de novo synthesis of select vital proteins.

Conclusion

Brown bear physiology serves as a novel translational model for advancing our understanding of human metabolic and cardiovascular disorders. The bear's distinctive anti-thrombotic mechanisms hold significant promise, offering insights that could lead to the development of safer and more effective anticoagulant therapies. The unique metabolic adaptations observed in hibernating bears could guide the creation of novel interventions for human conditions such as insulin resistance and obesity. Moreover, bears display intriguing cardio-protective and anti-inflammatory properties, suggesting new therapeutic possibilities for managing ischemic heart disease. Collectively, our findings have the potential to transform both the prevention and treatment of a wide array of human diseases.

7 Research Tools and Ethics

7.1 The leading edge of brown bear capture-anesthesia methodology

KEY POINTS

- The current anesthetic drug combination for free-ranging brown bears has been used since 1992.
- The anesthetic protocol (SOP) has been refined and improved based on numerous scientific studies. A new version is now available (Græsli et al. 2024).
- Anesthesia, analgesia, monitoring, supportive care, and surgery follow best practice guidelines established in veterinary medicine.
- From 1992 through 2023, 2,325 helicopter-based captures were carried out between April and June on 906 individuals. The mortality rate during capture and the following 3 days was 0.7% (n=15).
- From 2010 through 2023, 79 captures of 59 hibernating subadult bears were captured in their dens between February and March using a modified anesthetic protocol. There was no mortality.

History of the SBBRP anesthetic protocol

<u>1984-1991 (etorphine – helicopter darting):</u> From 1984 through 1991, bears were immobilized from a helicopter mainly with etorphine. An alternative combination, medetomidine-ketamine, was tested in a limited number of animals. Seven capture-related deaths (4.0 %) occurred in 174 captures. Six of these deaths occurred when bears were immobilized with etorphine: three due to stress, hyperthermia and/or respiratory depression (one of these animals had only one functional lung), two due to drowning, and one due to dart trauma (pneumothorax). In addition, one bear immobilized with medetomidine-ketamine was shot for human protection after a spontaneous recovery from anesthesia.

<u>1992-2023 (medetomidine-tiletamine-zolazepam – helicopter darting):</u> From 1992 through 2023 a total of 2,325 captures on 906 individuals were carried out from a helicopter with medetomidine-tiletamine-zolazepam. Ten bears (0.5 %) died during the capture event using this protocol: three because of shock/circulatory failure, five due to drowning, and two due to dart trauma (penetration of the thoracic cavity). Five bears (0.2 %) died within 3 days of capture due to unknown causes (inconclusive necropsies).

<u>2010-2023 (medetomidine-ketamine-tiletamine-zolazepam – ground darting):</u> During February and March 2010-2023, a modified anesthetic protocol based on medetomidine-ketamine-tiletamine-zolazepam was used to conduct 73 captures of 59 individuals hibernating subadults with no mortalities (Evans et al. 2012).

Development of the SBBRP anesthetic protocol

Initially, anesthetic monitoring was very limited and only vital signs (pulse rate, respiratory rate, and rectal temperature) were assessed and recorded. In the 1990s, a portable pulse oximeter was introduced for routine monitoring of blood oxygenation. After 2000, however, the SBBRP anesthetic protocol was significantly improved based on numerous scientific studies carried out as part of the project. This includes more frequent recording of vital signs, supplemental oxygen delivery in all bears, administration (if needed) of intravenous fluids and analgesics and best-practice guidelines for invasive sampling and surgical procedures. For example, in 2006 we began providing supplemental oxygen to anesthetized bears which reduced their chances of hypoxemia (low oxygen concentration in the blood) during capture (Fahlman et al. 2012, Fahlman et al. 2010).

We have since continually evaluated the effect of our capture methodologies, assessing bears physiological responses to anesthesia and capture protocols, and providing recommendations for future monitoring and methodologies within our project and to other brown bear capture and monitoring projects around the world (Fahlman et al. 2011, Fandos Esteruelas et al. 2017, Fandos Esteruelas et al. 2016, Gandolf et al. 2010, Jørgensen et al. 2014, Jørgensen et al. 2020, Morelli et al. 2020, Ozeki et al. 2015, Ozeki et al. 2014, Painer et al. 2012). For example, we have provided in-depth guidelines on brown bear capture best-practices. This includes recommendations to use “experienced professional capture teams, 2) developing and following a capture protocol specific to each species, and 3) requiring that a mortality assessment be undertaken after any capture-related death” (Arnemo et al. 2006). A new and extensive biomedical protocol for Scandinavian brown bears is now available (Græsli et al. 2024)

7.2 Effects of capture on Scandinavian brown bears

KEY POINTS

- The utilization of wild animals for research requires evaluation of the effects of capture and invasive sampling. Determining the severity and duration of these interventions on the animal’s physiology and behavior allows for refining study methodology and for excluding or accounting for biased data.
- Human disturbance, including research efforts, can affect animal life history and even population dynamics. However, the consequences of these disturbances are difficult to measure.
- Hibernating animals are highly vulnerable to disturbance, because hibernation is a process of major physiological changes, involving conservation of energy during a resource-depleted time of year.
- Both body temperature and heart rate increased during winter capture and returned to hibernation levels after 15–20 days. We showed that bears required 2–3 weeks to return to hibernation levels after winter captures, suggesting high metabolic costs during this period.
- Movement rates of bears captured in winter were affected from den exit until hyperphagia phase
- The wax coating of Telonics transmitters, used for VHF tracking, was not biocompatible, and the technical quality of the devices was poor, thus these implants should not be used in brown bears.

Research on wild animals often necessitates the capture, immobilization, and tagging of individuals, often with GPS or radio collars or tags. Although already intrusive, tagging procedures may include even more invasive methodologies such as pulling teeth or hair, drawing blood, muscle biopsies, or surgery, depending on the goal of the scientific study. How these procedures affect the subsequent physiology and behavior of the study species is a central question in wildlife ecology. This is because capture-induced shifts in behavior may cloud our understanding of the actual behavioral patterns we are attempting to measure in the first place. Furthermore, animal models serve as vital tools in translational medicine, bridging scientific discoveries to practical applications for human health (see Section 6.3 Bear physiology and human health). However, ethical considerations demand a careful balance between societal benefits and the welfare of research animals, particularly when utilizing wild animals and employing invasive sampling methods. Studies involving Scandinavian brown bears captured both in the dens during hibernation and via helicopter revealed altered behavior and physiology post-capture and surgery (Evans et al. 2016b, Thiel et al. 2023). This underscores the need for cautious interpretation of data collected from animals after subjecting them to invasive techniques.

Effect of captures during summer

Here, we explored the effect of invasive capture procedures (captures that included abdominal surgery or muscle biopsy) on bear behavior in the days, weeks, and months following the capture event. Subadult bears captured in summer showed reduced movement and body temperature for at least 14 and 3 days, respectively, with an 11% decrease in hourly distance, compared to pre-capture levels, but did not differ in the timing of hibernation onset (Thiel et al. 2023). We reveal that brown bear behaviour and physiology can be altered in response to capture and surgery for days to months, post-capture (Thiel et al. 2023). This has broad implications for the conclusions of wildlife studies that rely upon invasive sampling. Currently ongoing research is evaluating the short-term effects of capture during spring on Scandinavian brown bears.

Preliminary results on the effects of captures in spring indicate that bear behavior is disturbed for about one week after capture.

Effect of captures during winter hibernation

Human disturbances can profoundly impact animal life history and population dynamics, especially for hibernating species vulnerable to disturbance-induced physiological changes. Research on subadult brown bears captured in winter showed increased body temperature and heart rate during captures (Evans et al. 2016b). These changes took 2-3 weeks to return to normal hibernation levels, suggesting high metabolic costs associated with the capture event (Evans et al. 2016b). In other words, the capture event altered the hibernating bears baseline physiology which likely resulted in increased energy expenditure, a high cost for hibernating bears. Winter captures resulted in delayed den emergence and reduced movement rates after den exit persisting into summer (Thiel et al. 2023), emphasizing the need for careful consideration of disturbance effects on hibernating wildlife populations (Evans et al. 2016b).

Effects of tagging equipment

Intraperitoneal VHF radio transmitters (very high frequency (VHF) radio transmitters placed with an animal’s abdominal cavity) are sometimes used as a marking device in free-ranging wild mammals, including brown bears. However, the quality and compatibility of the device with the species raises concerns over the long-term effects of implanting such devices. A comprehensive 19-year study assessing Telonics intraperitoneal VHF radio transmitters in brown bears highlighted significant technical issues (Arnemo et al. 2018). These included battery failures that lead to ‘foreign body reactions’ in about half of all study bears, and long-term effects that lead to the death of 2 individuals 10 to 13 years after implantation (Arnemo et al. 2018). Histopathological analysis indicated that the transmitters were of poor quality and had serious technical problems, ranging from metal corrosion, detachment of the end cap, and melting of the devices wax coating (Arnemo et al. 2018). These results emphasize the need to avoid using Telonics intraperitoneal VHF radio transmitters with brown bears (Arnemo et al. 2018).

8 Future Perspectives

8.1 The future of the SBBRP

KEY POINTS

- Continue long-term monitoring by maintaining a GPS-marked population of bears.
- Continue long-term monitoring in the core study area and include temporary study areas as needed (e.g., the arctic regions).
- Continue to refine our experimental design with respect to animal welfare.
- Core areas of future research and development include:
    - Developing instruments and methods to facilitate brown bear management in Scandinavia.
    - Facilitating collaboration and reducing conflict within the Scandinavian system.
    - Providing baseline understanding of multispecies interactions and ecology to facilitate multispecies management.
    - Understanding brown bear ecology in the context of future large-scale and system-wide changes.
    - Continuing to advance our understanding of how wildlife research methodologies effect animal welfare.
    - Furthering our understanding of bear physiology to help advance human medicine.

The long-term goal of the SBBRP is to continue to monitor the Scandinavian brown bear population and facilitate management decisions on multiple scales, contribute to the understanding of brown bear biology and ecology in the context of our changing world, and provide nature-based solutions based on brown bear physiology to the field of human medicine.

Our core goals

Continue long-term monitoring by maintaining a GPS-marked population of bears: The SBBRP aims to follow individuals for as long as possible, preferably from birth to death. Our goal is to maintain about 50 radio-tagged bears at the end of each year, after the hunting season in the fall, to get statistically reliable estimates of important population parameters. Research on bear ecology and demography is demanding because the species slow life history; they reach reproductive potential at an advanced age (4-7 years), give birth every 1-3 years, and can live to be 30 years old. If the number of study animals is reduced too much, the uncertainty in the parameters will be so great that it will be difficult to detect changes over time or differences between areas within the bear population.

Continue long-term monitoring in the core study area and include temporary study areas as needed: The core study area of the SBBRP, the so-called Southern Study Area, encompasses approximately 20,000 km^2 in Dalarna, Gävleborg, and Jämtland Counties in south-central Sweden (61°N, 15°E). We plan to continue long-term monitoring in this region and add other study areas as needed to conduct research on relevant ecological and management-related questions. For example, conducting research further north within the arctic may provide insight into climate change related questions and help facilitate local management decisions for bear populations in the area.

Continue to refine our experimental design with respect to the 3 Rs (replace, reduce, and refine): Because the goal of the SBBRP is to document the wild brown bear demographics and natural behavior, it is often difficult replace non-invasive methods for the capture and tagging of wild bears or reduce the number of bears needed in the study. However, information collected from GPS-collared animals are supplemented with non-invasive techniques such as observational studies, camera-trapping, and DNA analysis. Furthermore, while we may not be able to reduce the number of study animals to a large degree at this point, we can continue to reduce the impact of capture and sampling methods on our study animals.

Continue to extend our collaborative network outside of Scandinavia: Collaboration with other bear projects and researchers is important for comparison of results and development of methods. We already have several ongoing collaborations, and we will continue to focus on work with Finland as well of other parts of Europe and North America.

Core areas of future research and development

Over the last 40 years, the SBBRP has made important scientific contributions to our understanding of a range of subjects including brown bear biology and ecology, animal welfare, and human health. The project has also contributed to the conservation and management of the Scandinavian brown bear population as well as to the world’s overall understanding of brown bear biology and ecology. We hope to maintain this level of impact moving forward, and have identified several core areas related to monitoring and research that we plan to focus on:

Develop instruments and methods to facilitate brown bear management in Scandinavia

- Refine noninvasive methods to facilitate population monitoring. These include cutting edge epigenetic methods to detect and evaluate population vital rates, distribution, gene flow, pedigrees, and population viability.

- Develop and refine models that can be used to assess the impact of management strategies on the bear population (e.g., harvest models), including integrated population models and projection models. This is very important in relation to the large increases in harvest quota in recent years.

- Evaluate current monitoring systems based on DNA, with data from our radio marked individuals, to better understand differences in capture probability in relation to habitat and categories of bears.

Facilitate collaboration and reduce conflict

- Continue the collaboration with managers and stakeholders to ensure that we are working on relevant topics and questions. Deep collaboration across multiple levels facilitates information flow, participation, and the incorporation of local knowledge.

- Develop and expand the involvement of personnel from Länsstyrelsen and SNO in different project areas to increase their experience with bears and facilitate exchange of knowledge. This includes the ongoing dog tracking project to support evaluation and training.

Provide baseline understanding of multispecies interactions and ecology to facilitate multispecies management

- Continue collaboration in the Ljusdal area in Sweden with the Scandinavian Wolf Research Project (Skandulv) and the Swedish University of Agricultural Sciences Moose

Research Project in Umeå (MRP). The current collaboration focuses on quantifying the combined impact of bears and wolves on moose and red deer populations and exploring behavioral interactions between all 4 species such predation and competition. Together, the SBBRP, MRP, and Skandulv envision a long-term collaborative effort in the Ljusdal Study Area with the aim of long-term multispecies monitoring and research to facilitate scientific advancement and adaptive wildlife management in Sweden.

Understand brown bear ecology in the context of future large-scale and system-wide changes

- Continue building our baseline understanding of bear ecology in Scandinavia so that shifts in their ecology in the context of future change can be predicted and understood. This includes a wide range of ecological topics including bear physiology, mating and reproduction, social organization, foraging behavior and diet, habitat use and movement, and denning behavior.

- Contribute to our understanding of how humans affect brown bears and their interactions within their ecosystem. This includes, for example, exploring how hunting, recreation, human infrastructure (e.g., villages and roads), and human industry (e.g., forestry and energy) affects bear population dynamics, bear behavior, and other biological processes such as trophic cascades.

- Begin to explore how future shifts in climate such as precipitation and temperature cycles will affect bear populations and human-wildlife conflict.

Continue to advance our understanding of how wildlife research methodologies effects animal welfare

- Future studies on the topic of wildlife research methodologies and their impact on animal welfare and scientific outcomes should focus on several key areas to address existing gaps in knowledge and improve research practices. There is a critical need for longitudinal studies that track the long-term effects of invasive sampling techniques and instrumentation on wildlife populations to fully evaluate welfare implications and potential population-level consequences.

Further our understanding of bear physiology to help advance human medicine

- Brown bear physiology provides unique insights for developing novel treatments in metabolic and cardiovascular human diseases. We are only at the beginning of our understanding of how bears physiologically adapt to prolonged inactivity and fasting during hibernation. There are a wide range of knowledge needs associated with this research, which includes:

    - Examining antithrombotic mechanisms in hibernating bears, focusing on HSP47 down-regulation, for human venous thromboembolism prevention.

    - Investigating bear serum's effects on reducing cell death post-myocardial infarction and modulating inflammation and cardiovascular development in human stem cells.

    - Studying cardiac adaptations in hibernating bears to inform heart failure management in humans.

  - Investigating bear lipid metabolism and gut microbiota for insights into human diabetes and cardiovascular health.

  - Studying dietary fatty acids and gut metabolites in bears to inform obesity and kidney disease treatments.

  - Exploring bear muscle preservation mechanisms for human muscle atrophy prevention.

  - Examining the preservation of bone mass in hibernating bears to identify potential targets for preventing osteoporosis.

  - Advocating for heightened awareness among funding agencies of the substantial human health benefits that could arise from supporting translational research on brown bears.

Future funding

- The main funding for the SBBRP has always come from Naturvårdsverket and Miljødirektoratet, and with the latest agreements with them we have secured funding for long-term viability of the base project. Several other sources of funding and support have been available including from the Swedish Association for Hunting and Wildlife Management, conservation organizations, and private funders. We plan to increase and diversify our funding from other sources to include more international funding as well as direct funding or support for specific sub-projects.

- NINA, together with the Swedish Association for Hunting and Wildlife Management, has created a non-profit foundation to facilitate our field station in Tackåsen with the potential to also get funding for research projects and support.

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