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Report 2018-1 from the Scandinavian Brown Bear Research Project

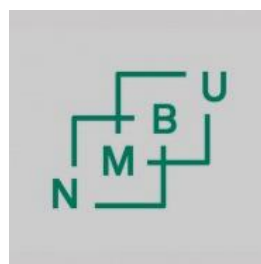


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Sammanfattning

Rapporten sammanfattar de viktigaste resultaten från det skandinaviska björnprojektet (SBP) under 2015-2017. SBP är ett långsiktigt, individbaserat björnforskningsprojekt. Vi bedriver ekologisk forskning med fokus på att ge förvaltningen i Sverige och Norge en solid vetenskapligt baserad kunskap som är relevant för att möta dagens och framtidens utmaningar i förvaltningen av den skandinaviska brunbjörnspopulationen. Under 2015-2017 producerade SBP 125 publikationer, varav 67 internationella vetenskapliga artiklar (inklusive 3 publicerade i 2018 och 4 in press), 1 bok kapitel, 14 doktorsavhandlingar, 15 magisteruppsatser, 1 kandidatexamen, 20 rapporter till förvaltningen och 10 populärvetenskapliga artiklar. Av SBP totalt 250 vetenskapliga artiklar har 55% varit direkt relevanta för förvaltningen och SBP är därmed ett av världens mest produktiva viltforskningsprojekt.

Vi ger i rapporten en kort beskrivning av våra resultat för varje arbetspaket som fanns i vår ansökan för denna studieperiod. Det som vi tror är mest relevant av produktionen under denna period är vår utvärdering av svensk förvaltnings förmåga att nå de mål för björnpopulationen som man haft under 5 perioder, under de senaste 70 åren. Denna utvärdering har visat att förvaltningen misslyckades med att nå de angivna målen i fyra av dessa perioder och att en adaptiv förvaltning inte förefaller användas i björnförvaltningen i Sverige trots att det har varit ett direktiv. En annan viktig kunskap är de faktorer som är inblandade när människor skadas eller dödas av björnar.

Vi har dokumenterat förekomsten av infanticid (Sexual Selective Infanticide, SSI) i den skandinaviska björnpopulationen, mekanismen (att hanar möter honor som de inte har parat sig med efter förändringar i hanarnas sociala organisering då en vuxen hanbjörn dödats), effekten (13-14% av variationen i björnpopulationens tillväxthastighet förklaras av jaktinducerad SSI) och honornas motstrategier under parningstiden, tex rör sig på små områden, val av habitat som skiljer sig från vuxna hanars, söker sig närmre människor och bebyggelse för att skydda sina ungar och att de parar sig med flera hannar för att skapa osäkerhet om faderskap. Vi har funnit att den nuvarande höga jakten påverkar populationens storlek och trender, populationsstruktur, åldersspecifik dödlighet, selektion av livshistorieegenskaper, förändrat beteendemönster vid olika tider på dygnet och vid födosök.

Våra studier av björn-varg interaktioner har gett överraskande resultat om flerartssystem med två olika rovdjur och deras predation på älg. Förekomst av vargar i ett landskap med björnar och älg verkar inte resultera i en enkel additiv effekt på älgpredationen. Genetiska studier har dokumenterat lågt genflöde mellan den nordliga delpopulationen i Sverige och närmaste delpopulationer i Finnmark i Norge och Finland/ Ryssland men också mellan den sydligaste delpopulationen i Sverige/Norge (Dalarna/Gävleborg/ Hedmark) och delpopulationerna längre norrut.

Summary

This report summarizes the main results gained by the Scandinavian Brown Bear Research Project (SBP) during 2015-2017. The SBP is a long-term, individual-based project that conducts ecological research focusing on providing managers in Sweden and Norway with solid, scientifically based knowledge that is relevant to meet present and future challenges presented by managing the population of brown bears. During 2015-2017, the SBP produced 125 publications, including 67 international scientific papers (which includes 3 published in 2018 and 4 in press), 1 book chapter, 14 PhD theses, 15 master's theses, 1 bachelor's thesis, 20 reports to management agencies, and 10

popular articles. Of the SBP's 250 scientific papers, 55% have been directly relevant for management. The SBP is one of the world's most productive wildlife research projects.

We provide a short description of our findings for each of the work packages that were in our application for this study period. Perhaps the most relevant issue for management that we have produced during this study period is our evaluation of the ability of Swedish management to reach the brown bear population goals that have been set during 5 periods during the past 70 years. This evaluation has shown that management failed to reach the specified goals in 4 of these periods and that adaptive management does not appear to be used in bear management in Sweden, even though its use is required by Parliament. Another important finding is the documentation of factors involved when humans are injured or killed by brown bears.

We have documented the occurrence of selected infanticide (SSI) in the Scandinavian brown bear population, the mechanism (males meeting females that they have not mated with following reshuffling of the male social organization after the death of an adult male), the effect (13-14% of the variation in the bear population's growth rate is explained by hunting-induced SSI), and female counterstrategies during the mating season, including reduced movements, selecting habitats not selected by adult males, seeking out human habitation to protect their cubs, and mating with many males to confuse paternity. We have found that the present high level of hunting is affecting population size and trends, population structure, age-specific mortality rates, selection for life-history traits, diurnal behavior patterns, and foraging behavior.

Our studies of bear-wolf interactions have given surprising results about this two-predator system and their predation on moose. The addition of wolves to a landscape with bears and moose does not seem to result in a simple additive effect on moose predation. Our genetics studies have documented low gene flow, particularly between the northern subpopulation in Sweden and the closest subpopulations in Finnmark, Norway and Finland/Russia, but also between the southernmost subpopulation in Sweden/Norway (Dalarna/Gävleborg/Hedmark) and the subpopulations farther north.

Introduction

The Scandinavian Brown Bear Research Project (SBP) is a long-term, individual-based project that conducts ecological research focusing on providing managers in Sweden and Norway with solid, scientifically based knowledge that is relevant to meet present and future challenges presented by managing the population of brown bears.

During the research period, we focused on what we considered to be the most relevant subjects for bear management in the coming years (see below). Most of these are covered in the Swedish Environmental Protection Agency's (SEPA) research strategy "Viltet och viltförvaltningen", and the "Åtgärdsprogram för bevarande av björn". Knowledge gained by the SBP has been important for the present policy, monitoring, and management of bears in Sweden, Norway, and abroad.

Basic methods

In our application for 2015-2017, we proposed to continue gathering and analyzing long-term, individually-based data on bears with a main goal of following females from birth to death. The SBP worked in 4 ways concurrently: 1) research on population dynamics, life-history strategies, and general ecology using the 33-year dataset of individually marked bears (the base project) and;

2) management-relevant research. In addition, it provided infrastructure and marked bears for 3) practical activities important for management, such as training and testing tracking dogs, and 4) associated research projects, such as veterinary science and human physiology.

During the report period, most of our data were collected from about 60 radio-collared bears at the beginning of each season. Each spring, yearlings with radio-collared mothers were captured and the female yearlings received implanted transmitters. We also conducted fieldwork for some specific studies each season. This fieldwork was usually conducted by PhD and Master's students, with help from volunteers.

Results—publications

During 2015-2017, the SBP produced 125 publications, including 67 international scientific papers (which includes 3 published in 2018 and 3 in press), 1 book chapter, 14 PhD theses, 15 master's theses, 1 bachelor's thesis, 20 reports to management agencies, and 10 popular articles. Since 1984, the SBP has produced 653 publications, including 250 international scientific papers, 23 books/book chapters, 22 proceedings papers, 32 PhD theses, 89 master's theses, 10 bachelor's theses, 142 reports to management agencies, and 90 popular articles. This makes the SBP the world's most productive carnivore research project, measured in scientific articles or PhD theses, and one of the most productive wildlife research projects, based on marked individuals, worldwide (Fig. 1). One reason for the high productivity is that the project has systematically collected individual-based data for 33 years.

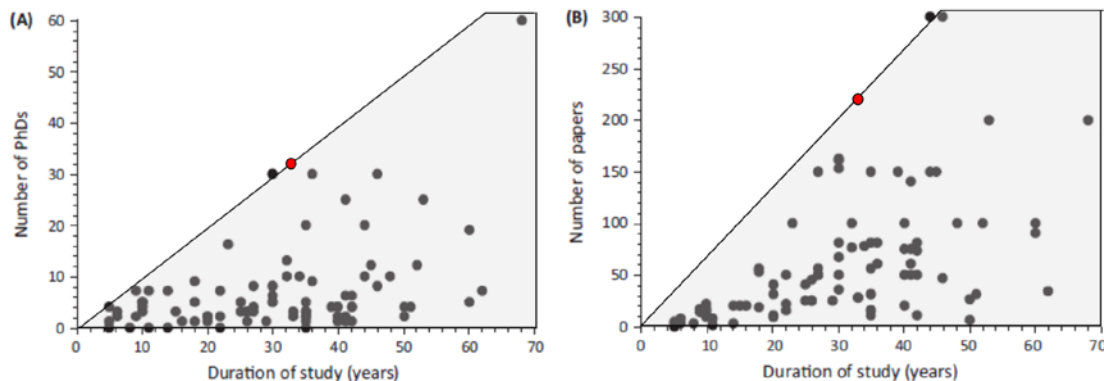


Fig. 1. Number of PhDs (A) and scientific papers (B) produced by 91 long-term, individual-based field studies of birds and mammals worldwide in relation to the length of the study (black circles, figure from Mills et al. 2015, Trends in Ecology and Evolution 30:581-589) and those of the SBP (red circles). Studies that are outside of the gray-shaded areas would be more productive than the SBP, in terms of PhD theses and scientific papers produced, respectively.

To exemplify the management relevance of all the scientific publications produced by the SBP, we rated papers on management; population and trend estimation, effects of hunting, human-bear relations, population ecology, predation, genetic status, habitat use, and population expansion to be directly relevant for management. A total of 137 (55%) of the 250 papers focused on these topics. An additional 13 (5%) were about the effects of capture and marking and 17 (7%) described biochemical studies with potential value for human medicine. Of course, papers on basic ecological or behavioral topics that do not seem to be directly applicable to management today might become valuable and relevant to management in the future.

Results and discussion for each Work Package

Here we provide a description of the major results from 2015-2017 in the same format as our application, and list the relevant publications. These publications are available on the SBP website, www.bearproject.info. Because we did not receive the entire funding we applied for, we could not work on all of the topics we had proposed. However, we have published findings from most topics.

1.1 Tools for wildlife management; methods for wildlife monitoring

The “observed bear” monitoring method (Large Carnivore Observation Index, LCOI). This is the method that is used in Sweden to follow the trend of the bear population. We tested the LCOI index against population estimates in Västerbotten, Jämtland, Västernorrland, and Norrbotten and found that it performed well. Nevertheless, the method’s predictive ability might be improved by correcting for sources of annual variation, such as environmental conditions, bears killed before the moose hunt and by managers, and proportion of females with young. We were not able to complete our research on this subject, but we did determine that the proportion of females giving birth was greater following years of high bilberry abundance. Thus, a higher bear observation index may follow a good berry year, because the hunters would observe more family groups, which are protected and therefore would have a higher probability of being observed repeatedly. We found that variations in berry abundance did not affect movement or diurnal behavior patterns, so the berry abundance in itself is probably not an important source of variation affecting the bear observation index.

We also developed a method to produce annual estimates of bear reproductions in Norway, correcting for the time they are in Sweden. The Norwegian management goal for brown bears is expressed in annual reproductions and this method is now used annually in Norway to calculate the number of reproductions at the level of Large Carnivore Management Region.

- Bischof et al. 2016. Wildlife in a politically divided world: insularism inflates estimates of brown bear abundance. *Conservation Letters* 9:122-130.
- Hertel, et al. 2016. Temporal effects of hunting on foraging behaviour of brown bears: Do bears forego foraging when risk is high? *Oecologia* 182: 1019-1029.
- Hertel, et al. 2018. Berry production drives bottom-up effects on body mass and reproductive success in an omnivore. *Oikos* 127:197–207.
- Kindberg & Swenson. 2015. Björnstammens storlek i Västerbotten 2014. Rapport 2015:6 from the Scandinavian Brown Bear Research Project.
- Hertel, A. 2017. Movement activity of Scandinavian brown bears in relation to variation in bilberry and lingonberry production between 2006-2015. Report 2017–4 from the Scandinavian Brown Bear Project.
- Kindberg & Swenson. 2017. Björnstammens storlek i Jämtland och Västernorrland 2015. Rapport 2017-2 från det Skandinaviska björnprojektet.
- Kindberg & Swenson. 2017. Björnstammens storlek i Norrbotten 2016. Rapport 2017-3 från det Skandinaviska björnprojektet.

1.2 Tools for wildlife management; measures to regulate populations and prevent damage

Human injuries. We have interviewed all of the surviving people who were injured by bears in Scandinavia since 1977 and conducted over 500 approaches of radio-marked bears. Our analysis of bear-injured people is complete and a manuscript has been submitted for publication. Hunters are most prone to attacks and the annual number of injured/killed hunters has increased with bear population size. In contrast, we found no correlation with the number of nonhunters injured by bears and the bear population size. The analysis also suggests that the bear-hunter education courses may have resulted in fewer injuries among hunters, but the number of injuries is too low to document a significant result. We also found that the increase in attacks around the onset of the

denning period in October may be due to bears being in a lethargic state, which may prevent them from fleeing from humans, as they normally would, perhaps increasing the chance of an attack when they encounter a human.

There is an increase in bear occurrence near human habitation during the spring and early summer, which is the bear's breeding season. These bears are primarily females with young and subadult bears that appear to be avoiding dominant adult males, rather than seeking out humans or their food. In fact, the young of females that show this behavior survive better than those that do not remain near settlements during the breeding season. Thus, this behavior should be viewed as natural, from the bears' perspective.

Sahlén, et al. 2015. Behavioural differences between single Scandinavian brown bears (*Ursus arctos*) and females with dependent young when experimentally approached by humans. PLoS ONE 10(4): e0121576.

Sahlén, et al. 2015. Den entry behavior in Scandinavian brown bears: implications for preventing human injuries. Journal of Wildlife Management 79:274–287.

Penteriani, et al. 2016. Human behaviour may trigger large carnivore attacks in developed countries. Scientific Report 6:20552.

Steyaert, et al. 2016. Human shields mediate sexual conflict in a top predator. Proceedings of the Royal Society B 283:20160906.

Nina Emilie Stenset. 2016. Norwegian University of Life Sciences, Master Thesis. Behaviour of brown bears (*Ursus arctos*) when repeatedly approached by humans on foot.

Elfström & Støen. 2015. Occurrence of large carnivores near settlements: a review of mechanisms and preventive measures. Rapport 2015:4 from the Scandinavian Brown Bear Research Project.

Summer farms. An experimental test found that the smell of bear feces did not decrease the milk production of dairy cows, as has often been speculated.

Christin Beate Johnsen. 2017. University College of Southeast Norway, Bø. Master Thesis: Naïve dairy cattle do not produce less milk in response to brown bear (*Ursus arctos*) fecal odor.

Hunting mortalities on the landscape level. We found that mortality risk for bears was significantly associated with human presence, especially for management-killed bears, and that oat fields are ecological traps for bears, because they are attracted to oat fields and are often killed there. Also, we found that bears in the mountain national parks of northern Sweden, where they are protected, had significantly higher mortality than those in the adjacent lands, where they are hunted. This was due to higher levels of poaching in the national parks. The same results were found for the other large carnivores in the area (Eurasian lynx and wolverine).

Bischof. 2015. Approaches for assessing illegal hunting of brown bears and other large carnivores in Sweden. Rapport 2015:5 from the Scandinavian Brown Bear Research Project.

Rauset, et al. 2016. National parks in northern Sweden as refuges for illegal killing of large carnivores. Conserv. Lett. 9:334–341.

Steyaert, et al. 2016. Ecological implications from spatial patterns in human-caused brown bear mortality. Wildl. Biol. 22:144–152.

Penteriani V., M. M. Delgado, M. Krofel, K. Jerina, A. Ordiz, F. Dalerum, A. Zarzo-Arias, and G. Bombieri. In press. Evolutionary and ecological traps for brown bears in human-modified landscapes. Mammal Review.

Hunting methods. We did little work on this topic, although Steyaert et al. (see topic above) found that the banning of baiting as a hunting method did not alter the spatial distribution of mortalities. Also, we contributed to a review of the consequences for bears of bear viewing tourism.

Penteriani, et al. 2017. Consequences of brown bear viewing tourism: a review. Biol. Conserv. 206:169–180.

Brunberg. 2015. Studien om överlevnad av ensamårsungar 2014. Rapport 2015:1 from the Scandinavian Brown Bear Research Project.

Rapid changes in bear harvest. The level of bear harvest has increased rapidly during the life of the SBR. This has allowed us to evaluate the effects of high harvest levels, compared to the effects of the previously low harvest levels. The low harvest levels allowed the bear population to increase rapidly and the present high levels have resulted in stable or declining populations. We have documented that the high level of harvest also has disrupted the interplay between age-specific survival and environmental factors, altered the consequences of reproductive strategies, and changed reproductive values and life expectancy in the Swedish bear population. The regulation that protects family groups from hunting may have selected for mothers that keep their young for an additional year, thus providing protection to the family, but reducing the number of litters a mother can produce in her lifetime. Thus, harvest level influences much more than population size and all aspects should be considered by those setting the quotas.

Increased harvest affects the sociospatial relationships of both males and females. We also evaluated if harvest data could be used to detect changes in the population structure and life-history traits of bears. We found that harvest data could be used for detecting changes in the ratio of yearlings to adult females in the population, but is less reliable to detect changes in body mass.

Leclerc, et al. 2016. Can hunting data be used to estimate unbiased population parameters? A case study on brown bears. *Biol. Lett.* 12:20160197.

Bischof, et al. 2018. Regulated hunting re-shapes the life history of brown bears. *Nature Ecol. Evol.* 2:116–123.

Frank, et al. 2018. Sociodemographic factors modulate the spatial response of brown bears to vacancies created by hunting. *J. Anim. Ecol.* 87:247–258.

Van de Walle, J., G. Pigeon, A. Zedrosser, J. E. Swenson, and F. Pelletier. In press. Hunting regulation favors slow life histories in a large carnivore. *Nature Communications.*

1.3 Tools for wildlife management; harvest models

Sexually selected infanticide (SSI). We documented that the removal of an adult male causes the reorganization of the surviving males' sociospatial structure. This drives SSI and explains the 1.5-year time lag that our previous results suggested. Also, we found that hunting-induced SSI explains 13.6% of the variation in the bear population's growth rate. Thus, we recommend that SSI be considered when evaluating the effect of hunting on a bear population.

We also wrote two reviews about the indirect effects of bear hunting, showing that the start of the hunting season affects bears' habitat use and daily activity patterns and evaluating several other potential, but undocumented, indirect effects of hunter harvest. One important, long-term effect is hunting-induced selection on life-history and morphological traits.

Gosselin, et al. 2015. The relative importance of direct and indirect effects of hunting mortality on the population dynamics of brown bears. *Proc. Roy. Soc. B* 282: 20141840.

Gosselin, et al. 2017. Hunting promotes sexual conflict in brown bears. *J. Anim. Ecol.* 86:35-42.

Leclerc, et al. 2017. Hunting promotes spatial reorganization and sexually selected infanticide. *Sci. Rep.* 7:45222.

Leclerc, et al. 2017. Harvesting as a potential selective pressure on behavioral traits. *Journal of Applied Ecology* 54:1941–1945.

Frank, et al. 2017. Indirect effects of bear hunting; an important topic for managers. *Ursus* 28:150-181.

Shane Carl Frank. 2017. University College of Southeast Norway, Bø. PhD thesis: The effects of harvest on the sociospatial and genetic structure of a solitary-living large carnivore, the brown bear *Ursus arctos*.

Density and social organization and Density dependence. Due to reduced funding, we did little work on density dependence, although we have started analyzing our data. Regarding social organization, we found that male home ranges overlapped more at higher densities, thus resulting in a lower degree of social reorganization following the death of an adult male at higher densities.

Leclerc, et al. 2017. Hunting promotes spatial reorganization and sexually selected infanticide. *Sci. Rep.* 7:45222.

2 From one- to several-species management

Bear and wolf predation on moose. During the project period, we have cooperated with the Skandulv project to evaluate the effects of bear and wolf predation on moose. Our results were surprising, because we found that the kill rate of wolves actually was less in areas with bears than without bears in both in Scandinavia and the Yellowstone Ecosystem in North America. We should continue to work on this subject, to determine the mechanism behind these counterintuitive results. Nevertheless, this suggests, that moose harvest models that have included additive wolf and bear predation may have overestimated the importance of large carnivore predation.

We have also evaluated bear predation on reindeer. We found that bears are important predators on reindeer calves, but only during the peak of calving during the last three weeks of May. Female reindeer did not change their habitat selection during the calving season in response to the presence of bears. Thus, it appears that habitat or space use by bears was the primary factor influencing how many reindeer calves were preyed upon.

Sivertsen, et al. 2016. Reindeer habitat selection under the risk of brown bear predation during calving season. *Ecosphere* 7(11): e01583.

Tallian, et al. 2017. Competition between apex predators? Brown bears decrease wolf kill rate on two continents. *Proc. Roy. Soc. B* 284:20162368.

Therese Sivertsen. 2017. Swedish University of Agricultural Sciences, Uppsala. PhD thesis: Risk of brown bear predation on semi-domesticated reindeer calves – Predation patterns, brown bear-reindeer interactions and landscape heterogeneity.

Aimee Tallian. 2017. Utah State University, Logan. PhD thesis: The behavior and ecology of cursorial predators and dangerous prey: integrating behavioral mechanisms with population-level patterns in large mammal systems.

Støen, et al.. 2016 En vurdering av brunbjørnens potensielle predaasjon på tamrein i Norge. Report 2016 – 1 from the Scandinavian Brown Bear Project

Swenson, and Kindberg. 2015. Effects of combined predation by brown bears and gray wolves on moose population dynamics; what more do we need to know? Bidrag till Norsk institutt for naturforskning (NINA) för arbete inom Skandinaviska björnprojektet säsong 2014 (NV-04578-14). Report from the Scandinavian Brown Bear Project.

Sand, et al. 2017. Forekomst av björn påvirker ulvens predaasjon på elg. *Rovdyrviten* 5:8-9.

Bear—wolf interactions. We also evaluated bear-wolf interactions, focusing on the effect of the presence of bears on wolf territory establishment. We found that the presence of bears negatively affects the probability of wolves establishing territories in an area. We have started the analyses of bear-wolf interactions at kill sites, but we do not have any results to report at this time. We also cooperated on a study of "legacy risk effects", which showed that three species of ungulates in an area that has not had bears for 170 years all used more open areas when confronted with bear scent.

Ordiz, et al. 2015. Wolves, people, and brown bears influence the expansion of the recolonizing wolf population in Scandinavia. *Ecosphere* 6(12): article 284.

Sahlén, et al. 2016. Phantoms of the forest: legacy risk effects of a regionally extinct large carnivore. *Ecol Evol.* 6: 791-799.

Ellinor Sahlén, 2016 Swedish University of Agricultural Sciences, Umeå. PhD thesis: Indirect effects of predation in human-modified landscapes.

- Cyril Milleret. 2016. Hedmark University of Applied Sciences, Evenstad. PhD thesis: Spatial ecology of wolves in Scandinavia – from spatio-temporal dynamics of wolf pairs to wolf population dynamics.
- Juan Romairone. 2015. Pablo Olavide University, Seville, Spain. Master of Science thesis in Biodiversity and Biology of Conservation. Habitat characteristics between different clusters of wolf (*Canis lupus*) activity before and after brown bear (*Ursus arctos*) emergence in Central Sweden.

Regional variation in bear density and moose recruitment. Due to reduced funding, we have only started analysis of this subproject and do not have results to report at this time.

3 Future wildlife management

History and Adaptive management. These two topics have been combined. We documented the history of bear management in Sweden since 1943 and especially examined whether managers met their goals during 5 identifiable management periods. It seems that this usually did not happen in the past. In fact, adaptive management, which is required by law to be used for bear management in Sweden, does not seem to be working as the management tool it is envisioned at the present. Although we recognize that a collaborative approach to bear management probably is most conducive to public support, it seems that the present system must be revised to incorporate adaptive management, which is legally required.

Redpath, et al. 2017. Don't forget to look down - collaborative approaches to predator conservation. *Biological Reviews* 92:2157-2163.

Swenson, et al. 2017. Challenges of managing a European brown bear population; lessons from Sweden, 1943-2013. *Wildl. Biol.* 2017:wlb.00251.

Attitudes towards bears in relation to local conditions. Because we received less funding than we applied for, we were not able to address this topic. However, we have participated in a project to document human fear of bears, evaluate whether this fear can be mitigated through increased knowledge of bears, and how people should behave when meeting a bear. Experimental meetings with bears were carried out by volunteers accompanying a member of the SBP into the field to walk by a radio-marked bear in its nearby daybed. The results indicate that human fear is reduced with increased knowledge and guidance in how to cope with bears. This test would not have been possible to do without the SBP infrastructure provided by the base project. In addition, we have contributed to a review paper on local attitudes and predator management.

Johansson, et al. 2015. Interventions targeting human fear of large carnivores – many ideas but scarce data. Rapport 2015:3 from the Scandinavian Brown Bear Research Project.

Johansson, et al. 2016. Targeting human fear of large carnivores — Many ideas but few known effects. *Biol. Conserv.* 201:261–269.

Johansson, et al. 2016. Exposure as an intervention to address human fear of bears. *Human Dimen. Wildl.* 21:311-327.

Johansson, et al. 2017. An evaluation of information meetings as a tool for addressing fear of large carnivores. *Soc. & Nat. Resour.* 30:281-298.

Støen & Johansson. 2016. Rapportering av aktivitet i 2015 fra prosjektet: Brown bear behavior and human perceptions - continued. Kontraktnr: 15040049. Report 2016–3 from the Scandinavian Brown Bear Project.

Støen & Johansson. 2017. Rapportering av aktivitet i 2016 fra prosjektet: Brown bear behavior and human perceptions - continued. Kontraktnr: 15040049. Report 2017–1 from the Scandinavian Brown Bear Project.

4. Other upcoming important topics

Ethics of research methods. We have continued our important work to improve the ethical handling of our research bears during the capture of free-ranging and denning bears. This included testing mixtures of the drugs used to immobilize the bears and developing and testing methods to document capture stress. Improved capture and handling methods improve the condition of the

captured bears, and by extension, the quality of the results obtained for all of our research. Our results should improve the ethical handling of bears animals in research projects worldwide.

- Ozeki, et al. 2015. Effect of active cooling and α 2-adrenoceptor antagonism on core temperature in anesthetized brown bears (*Ursus arctos*). *J Zoo Wildl. Med.* 46:279-285.
- Græsli, et al. 2015. Seasonal variation in haematological and biochemical variables in free-ranging subadult brown bears (*Ursus arctos*) in Sweden. *BMC Vet. Resear.* 11:301.
- Esteruelas, et al. 2016. Leukocyte coping capacity as a tool to assess capture- and handling-induced stress in Scandinavian brown bears (*Ursus arctos*). *J. Wildl. Diseases* 52:S40-S53.
- Evans, et al. 2016. Physiological reactions to capture in hibernating brown bears. *Conserv. Physiol.* 4(1):cow061.
- Esteruelas, et al. 2017. Double-blinded, randomized comparison of medetomidine-tiletamine-zolazepam and dexmedetomidine-tiletamine-zolazepam anesthesia in free-ranging brown bears (*Ursus arctos*). *PLoS ONE* 12(1): e0170764.
- Alina Lynn Evans. 2016. Hedmark University College. PhD thesis: Ecophysiology of brown bears; basic physiology and effects of hibernation, pregnancy, body mass, and capture.
- Núria Fandos Esteruelas. 2017. Inland Norway University of Applied Sciences, Evenstad. PhD thesis: Short and long-term physiological effects of capture and handling on free-ranging brown bears (*Ursus arctos*).
- Arnemo, et al. 2017. Døde forsøksbjørner i Norrbotten 2016. Report from the Scandinavian Brown Bear Research Project

Landscape of fear. Our research continues to document how bears avoid humans and their infrastructure. We found that bears reduced their foraging activity and efficiency and foraged on sites with fewer and poorer quality berries during the morning hours of the hunting season, when mortality risk is highest. There was no effect of hunting on afternoon foraging, when mortality risk was lower, but the bears did not compensate for the loss of foraging opportunities they experienced in the morning. We documented that bears changed their foraging behavior to avoid high-risk habitats after the hunting season had started. Measures of heart rate variability showed that bears were more stressed when near settlements, especially during the fall, when more humans, including hunters, are present in the forest.

- Støen, et al. 2015. Physiological evidence for a human-induced landscape of fear in brown bears (*Ursus arctos*). *Physiol. Behav.* 152A:244-248.
- Hertel, et al. 2016. Temporal effects of hunting on foraging behavior of an apex predator: Do bears forego foraging when risk is high? *Oecologia* 182:1019-1029.
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- Ordiz, et al. 2017. Staying cool or staying safe in a human-dominated landscape: which is more relevant for brown bears? *Oecologia* 185:191–194.
- Anne Gabriela Hertel. 2017. Norwegian University of Life Sciences, Ås. PhD thesis: The effect of berry abundance and mortality risk on behavior and life history in Scandinavian brown bears.
- Henriette Wathne Gelink. 2015. Norwegian University of Life Sciences. Master Thesis: Risky berry business? Brown bear (*Ursus arctos*) foraging behaviour in a landscape of fear.
- Hanna Kavli Lodberg-Holm. 2015. Norwegian University of Life Sciences. Master Thesis: When the hunter becomes the hunted: Impacts of hunting on the foraging behavior of the brown bear (*Ursus arctos*) in Sweden.

Cascading effects. Due to reduced funding we have nothing to report from this topic.

Effects of climate change on bear populations. We approached this topic on two different scales. The first was the European scale during the past 12,000 years. Our results showed that the decline in brown bear distribution was driven by the expansion of humans, warming climate (which

reduced fecundity), and an interaction between climate and humans, as warming climate allowed humans to settle in areas that were once inhospitable. The start of their major decline in Europe occurred during the Roman Empire.

The second scale involved bilberries and bears in our study area. We found that temperature during plant dormancy and flowering and precipitation during fruit ripening influenced berry production in both bilberries and lingonberries. Bilberry, but not lingonberry, abundance was positively related to autumn weights of female bears and spring weights of yearling bears and resulted in an increased probability of reproductive success for low-weight females.

The survival of cubs of the year during their first spring is reduced after a severe winter. Weather also influences the vulnerability to harvest, at least for males. Harvest mortality is higher for males before mild winters, presumably because they den later at the start of mild winters, making them vulnerable to hunting for a longer period.

Albrecht, et al. 2015. How humans and climate change propelled the 12,000-year decline of the largest terrestrial carnivore. *Sci. Rep.* 7:10399.

Bischof, et al.. 2018. Regulated hunting re-shapes the life history of brown bears. *Nature Ecol. Evol.* 2:116–123.

Hertel, et al. 2018. Berry production drives bottom-up effects on body mass and reproductive success in an omnivore. *Oikos* 127:197–207.

Anne Gabriela Hertel. 2017. Norwegian University of Life Sciences, Ås. PhD thesis: The effect of berry abundance and mortality risk on behavior and life history in Scandinavian brown bears.

Habitat use/effects of forestry. We have documented several of the impacts that modern forestry has on bear habitat quality. Clearcuts increase the availability of carpenter ants, an important summer food. Bears forage in the fall in areas with a high abundance of berries, which occur primarily on clearcuts and in mature forest. Clearcutting also negatively influences the availability of denning sites, as few bears den in clearcuts. We have also started a cooperative study comparing the responses of brown bears to forest management practices in Sweden and Alberta, Canada. This project is in its initial stages, so we do not have any definitive results at this time.

Frank, et al. 2015. A "clearcut" case? Brown bear selection of coarse woody debris and carpenter ants on clearcuts. *Forest Ecol Manage.* 348:164–173.

Leclerc, et al. 2016. Quantifying consistent individual differences in habitat selection. *Oecologia* 180:697-705.

Hertel, et al. 2016. Bears and berries: species-specific selective foraging on a patchily distributed food resource in a human-altered landscape. *Behav. Ecol. Sociobiol.* 70:831-842.

Linda Nowak. 2015. University for Natural Resources and Applied Life Sciences, Vienna, Austria. Master thesis: Reproductive performance of Scandinavian female brown bears (*Ursus arctos*) in relation to the use of den-type.

Alja H. I. Mannaart. 2016. Norwegian University of Life Sciences, Ås. Master Thesis: Denning ecology of Scandinavian brown bears (*Ursus arctos*) in a dynamic landscape.

Genetics. We found that three genetic subpopulations of brown bears occurred in southern, central and northern Scandinavia, both in historical and modern times. Mitochondrial DNA diversity showed a major decline in haplotype numbers across the population bottleneck ~100 years ago. However, the loss of autosomal genetic diversity was less pronounced, although a significant decline occurred in the southern subpopulation. Male gene flow did not appear to contribute to the population recovery, as there was limited gene flow from the east, i.e., Finland and Russia. We also found evidence that the increase in population size and dispersal of individuals in the increasing Scandinavian population after the bottleneck did not lead to increased genetic connectivity within Scandinavia or with bears in Finland and Russia.

- Schregel, et al. 2015. Y chromosome haplotype distribution of brown bears (*Ursus arctos*) in Northern Europe provides insight into population history and recovery. *Mol. Ecol.* 24: 6041–6060.
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- De Barba, et al. 2017. High-throughput microsatellite genotyping in ecology: improved accuracy efficiency, standardization and success with low-quality and degraded DNA. *Mol. Ecol. Resour.* 17:492–507.
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- Schregel, et al. 2017. Sex-specific genetic analysis indicates low correlation between demographic and genetic connectivity in the Scandinavian Brown Bear (*Ursus arctos*). *PLoS ONE* 12(7): e0180701.
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- Schregel, et al. In press. Multi-level patterns in population genetics: variogram series detects hidden isolation-by-distance dominated structure of Scandinavian brown bears. *Methods Ecol. Evol.*
- Julia Schregel. 2015. Norwegian University of Life Sciences, Ås. PhD thesis: Genetic structure and gene flow in a continuously distributed large terrestrial carnivore – the brown bear (*Ursus arctos*) in Northern Europe.
- Anita J. Norman. 2016. Swedish University of Agricultural Sciences, Umeå. PhD thesis: Genomic studies of contemporary processes in wild populations, with the Scandinavian brown bear as a model.

5. Associated research topics that are dependent upon the base project

We cooperate with several research teams in human physiology, because the bears' physiological adaptations to hibernation have the potential to help treat several modern human ailments, such as heart attacks, osteoporosis, kidney failure, muscle loss due to inactivity, obesity, diabetes, etc. A project funded by the Norwegian Environment Agency used the physiology-instrumented bears to study experimentally how bears react physiological to encountering humans and being hunted with dogs. These associated projects cover the additional costs incurred by the SBP and contribute to the base project, which is essential for these cooperative studies. They published 6 scientific papers in the study period.

Communication efforts

As always, we have made great efforts to communicate our results. In addition, to the scientific publications, we have given many presentations and posters at several international scientific conferences, including the 24th International Conference on Bear Research and Management (IBA) in Alaska in 2016, and the 25th IBA conference in Ecuador in 2017. We have given numerous lectures to interested publics and interview about bears. We also respond whenever managers request information or recommendations. On 14-15 December 2016, we held a public symposium for bear managers and others from Sweden and Norway; 88 participants attended. We also wrote 20 reports for managers and 9 popular scientific articles aimed at the general public, including one for doctors in Swedish (see below).

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- Leclerc. 2015. Brown bear habitat selection personality. *Atlas of Science* <http://atlasofscience.org/brown-bear-habitat/>
- Sahlén. 2015. Når bjørn og menneske møtes. *Rovdyrviten* 3:14-15.
- Stenvinkel, et al. 2015. Biomimetik – att efterlikna naturen för att förebygga sjukdom. *Läkartidningen* 112:586-590.
- Støen, et al. 2015. Bjørnens predasjon på tamrein—og forebyggende tiltak. *Rovdyrviten* 3:40-41.
- Steyaert. 2015. Infanticide bij beren uitgeplozen. *Natuur.focus* 2015 (maart): 34-35.
- Swenson & Linnell. 2015. Bestandene av store rovdyr er økende i Europa. *Rovdyrviten* 3:42-43.
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Usefulness for management—conclusions and recommendations

Perhaps the most relevant issue for management that we have produced during this study period is our evaluation of the ability of Swedish management to reach the brown bear population goals that have been set during 5 periods during the past 70 years. This evaluation has shown that management failed to reach the specified goals in 4 of these periods. An evaluation of the ability of the Delegations for Game Management to reach their population or trend goals showed the same pattern, even though Parliament has stipulated that they shall use adaptive management. The SBP has developed and tested methods for estimating population size and trend that are very applicable for evaluating whether goals have been reached or not, using an adaptive management procedure. We recommend that the appropriate authorities start a discussion to decide how adaptive management can be incorporated into brown bear management. This may require cooperation with researchers, such as those in the SBP.

Another important finding that is relevant for management is the documentation of factors involved when humans are injured or killed by brown bears. The victims are greatly dominated by hunters and the number of incidents has increased with the increasing bear population and bear harvest. There has been no such increase for unarmed outdoor recreationists. Hunters, which are the most vulnerable group to being injured by bears, are an easy group to reach with relevant information. In fact, we have shown that the bear hunting course that many hunters take seems to have had a positive effect in reducing injuries.

Our research on sexually selected infanticide (SSI) has come far. We have documented its occurrence, the mechanism (males meeting females with cubs that they have not mated with following reshuffling of the male social organization after the death of an adult male), the effect (13-14% of the variation in the bear population's growth rate is explained by hunting induced SSI), and female counterstrategies during the mating season, including reduced movements little, selecting habitats not selected by adult males, seeking out human habitation to protect their cubs, and mating with many males to confuse paternity. Beyond SSI, we have found that the present high level of hunting is affecting population size and trends, population structure, age-specific mortality rates, selection for life-history traits, diurnal behavior patterns, and foraging behavior. Our studies of bear-wolf interactions have given surprising results about this two-predator system and their predation on moose. More research is needed, but it is becoming apparent that the addition of wolves to a landscape with bears and moose probably does not result in a simple additive effect on moose predation, as we had assumed in our previous modeling.

Our genetics studies suggest significant barriers to gene flow. The greatest barrier is between the northern subpopulation in Sweden and the closest subpopulations in Finnmark, Norway and Finland/Russia. However, there also appears to be an important barrier between the southernmost subpopulation in Sweden/Norway (Dalarna/Gävleborg/Hedmark) and the subpopulations farther north. Managers should be aware of this and seek methods to facilitate movement of bears across this barrier.

List of publications

Publications in peer-reviewed journals

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Completed doctorate level theses

- 2015 Andrea Friebe, Goethe-Universität in Frankfurt am Main. PhD thesis. Winter ecology of free-ranging brown bears (*Ursus arctos*) in central Sweden. Dissertation.
- 2015 Julia Schregel, Norwegian University of Life Sciences, Ås. PhD thesis: Genetic structure and gene flow in a continuously distributed large terrestrial carnivore – the brown bear (*Ursus arctos*) in Northern Europe.
- 2015 Marine Plumel, Institut pluridisciplinaire Hubert Curien, Strasbourg, France. PhD thesis: Optimization of quantitative proteomics analytical strategies: application to studying metabolic adaptive responses in various organisms.
- 2016 Inge G. Revsbech. Aarhus University. PhD thesis: Molecular mechanisms regulating oxygen transport and consumption in high altitude and hibernating mammals.
- 2016 Alina Lynn Evans. Hedmark University College. PhD thesis: Ecophysiology of brown bears; basic physiology and effects of hibernation, pregnancy, body mass, and capture.
- 2016 Anita J. Norman. Swedish University of Agricultural Sciences, Umeå. PhD thesis: Genomic studies of contemporary processes in wild populations, with the Scandinavian brown bear as a model.
- 2016 Ellinor Sahlén. Swedish University of Agricultural Sciences, Umeå. PhD thesis: Indirect effects of predation in human-modified landscapes. (Acta Universitatis agriculturae Sueciae, 1652-6880; 2016:116)
- 2016 Cyril Milleret. Hedmark University of Applied Sciences, Evenstad. PhD thesis: Spatial ecology of wolves in Scandinavia – from spatio-temporal dynamics of wolf pairs to wolf population dynamics.
- 2017 Aimee Tallian. Utah State University, Logan. PhD thesis: The behavior and ecology of cursorial predators and dangerous prey: integrating behavioral mechanisms with population-level patterns in large mammal systems.
- 2017 Therese Sivertsen. Swedish University of Agricultural Sciences, Uppsala. PhD thesis: Risk of brown bear predation on semi-domesticated reindeer calves – Predation patterns, brown bear-reindeer interactions and landscape heterogeneity.
- 2017 Anne Gabriela Hertel. Norwegian University of Life Sciences, Ås. PhD thesis: The effect of berry abundance and mortality risk on behavior and life history in Scandinavian brown bears.

- 2017 Shane Carl Frank. University College of Southeast Norway, Bø. PhD thesis: The effects of harvest on the sociospatial and genetic structure of a solitary-living large carnivore, the brown bear *Ursus arctos*.
- 2017 Annelies De Cuyper Ghent University. PhD thesis: Prey selection and digestive processing in terrestrial carnivorous mammals
- 2017 Núria Fandos Esteruelas. Inland Norway University of Applied Sciences, Evenstad. PhD thesis: Short and long-term physiological effects of capture and handling on free-ranging brown bears (*Ursus arctos*).

Completed Master of Science level theses

2015. Nina Emilie Stenset. Norwegian University of Life Sciences, Faculty of Environmental Science and Technology, Department of Ecology and Natural Resource Management. Master Thesis. Behaviour of brown bears (*Ursus arctos*) when repeatedly approached by humans on foot.
- 2015 Juan Romairone. Pablo Olavide University, Seville, Spain. Master of Science thesis in Biodiversity and Biology of Conservation. Habitat characteristics between different clusters of wolf (*Canis lupus*) activity before and after brown bear (*Ursus arctos*) emergence in Central Sweden.
- 2015 Linda Nowak. University for Natural Resources and Applied Life Sciences, Vienna, Austria. Master thesis: Reproductive performance of Scandinavian female brown bears (*Ursus arctos*) in relation to the use of den-type.
- 2015 Marion Lukkari Arnesen. Telemark University College, Bø. Master thesis: Use of experimental bait sites by wolverines.
- 2015 Henriette Wathne Gelink. Norwegian University of Life Sciences. Master Thesis: Risky berry business? Brown bear (*Ursus arctos*) foraging behaviour in a landscape of fear.
- 2015 Hanna Kavli Lodberg-Holm. Norwegian University of Life Sciences. Master Thesis: When the hunter becomes the hunted: Impacts of hunting on the foraging behavior of the brown bear (*Ursus arctos*) in Sweden.
- 2016 Alja H. I. Mannaart. Norwegian University of Life Sciences, Ås. Master Thesis: Denning ecology of Scandinavian brown bears (*Ursus arctos*) in a dynamic landscape.
- 2016 Jack D. Kleiner. Norwegian University of Life Sciences, Ås. Master Thesis: Selection of trees marked by rubbing by Andean bears in the Peruvian dry forest.
- 2016 Henry Anderson-Elliott. Peterhouse College, University of Cambridge. Master of Philosophy Thesis: The conservation of brown bears *Ursus arctos* in Scandinavia: Identifying hybrid wildlife in Anthropocene science.
- 2017 Christin Beate Johnsen. University College of Southeast Norway, Bø. Master Thesis: Naïve dairy cattle do not produce less milk in response to brown bear (*Ursus arctos*) fecal odor.
- 2017 Marte Olsen. Norwegian University of Life Sciences, Ås. Master Thesis: Predation-induced ungulate carcasses mediate vegetation composition in the boreal ecosystem.
- 2017 Bastien Desmecht. Liège université. Master Thesis: Impacts of power lines on brown bear movement in central Sweden.
- 2017 Tommy Virmaja. Karlstad University. Master Thesis: Skillnader i födoval mellan brunbjörnhonor (*Ursus arctos*) med och utan årsungar. (Differences in choices of food items between femal brown bears (*Ursus arctos*) with and without cubs of the year)
- 2017 Elke Stengeli. University for Natural Resources and Applied Life Sciences, Vienna, Austria. Master thesis: Large carnivore predation mediates chemical soil properties and the soil seedbank.
- 2017 Estrella Zirk. University for Natural Resources and Applied Life Sciences, Vienna, Austria. Master thesis: Endozoochorous plant seed dispersal by brown bears (*Ursus arctos*) in south-central Sweden.
- 2018 Matej Domevščik. Swedish University of Agricultural Sciences, Umeå. Master thesis: Resource distribution in disturbed landscapes – the effect of clearcutting on berry abundance and their use by brown bears

Completed Bachelor of Science level thesis

- 2017 Shotaro Shiratsuru, Nord University, Bodø, Norway. Bachelor thesis: Physical properties of excavated winter dens utilized by Scandinavian brown bears (*Ursus arctos*) in relation to energy conservation during hibernation.

Rapports to management agencies, etc.

- Linnell, J. D. C., O.-G. Støen, I. Hansen, S. Eilertsen, Ø. Flagstad, V. Gervasi, H. Brøseth, J. Swenson, J. & J. Odden. 2015. Utredning om endring i yngleområdene for jerv og bjørn i rovvilt region 6. **NINA Rapport** 1123. 36 s.
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- Bischof, R. 2015. Approaches for assessing illegal hunting of brown bears and other large carnivores in Sweden. Rapport 2015:5 from the **Scandinavian Brown Bear Research Project**.
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Popular publications

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- Swenson, J. E. & J. D. C. Linnell. 2015. Bestandene av store rovdyr er økende i Europa. **Rovdyrviten** 3:42-43.
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- Steyaert, S. 2015. Infanticide bij beren uitgeplozen. **Natuur.focus** 2015 (maart): 34-35.
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Financing

During 2015-2017, the SBP base project received SEK 3,800,000 from the Swedish Environmental Protection Agency with funds from the Viltvårdsfond. This was 44% of the total financing of the SBP base project during this period, which was NOK 10,744,129. Other important sources of funding were the Norwegian Environment Agency (48%), Örebro University Hospital (5%), and the French CNRS (3%). This amount does not include financing that was paid to the project to cover actual costs of housing for the bear-tracking dog teams sent by Swedish and Norwegian authorities or externally funded projects that were not administered by the SBP, such as the bear hunting dog project or the reindeer predation project.