THE SCANDINAVIAN BROWN BEAR
SUMMARY OF KNOWLEDGE AND RESEARCH NEEDS

Skandinaviska Björnprojektet

Report to the Wildlife Research Committee,
Swedish Environmental Protection Agency

Scandinavian Brown Bear Research Project Report 2007-1

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PREFACE

The Wildlife Research Committee, Swedish Environmental Protection Agency, is developing a research program from 2008 to 2013 or 2018. As a basis for this work, they have asked for a summary of our knowledge and future research needs for a number of species and themes. This report addresses these questions for the Scandinavian brown bear.

INTRODUCTION

The conservation and management of large carnivores is often difficult and controversial, because they often occur in low densities, have large home ranges, conflict with many human interests, and are expensive to study (Gittleman et al. 2001). This is also true for brown bears (*Ursus arctos*), and throughout the world, many brown bear populations are declining and becoming fragmented and isolated, due to commercial overexploitation, excessive mortality, habitat degradation and destruction, and natural resource development (Servheen 1990, Servheen et al. 1999). Therefore, most management actions regarding brown bears are aimed at saving small and isolated populations (Knight & Eberhardt 1985, Mattson & Reid 1991, Naves & Palomero 1993, Servheen et al. 1999, Zedrosser et al. 2001).

In spite of a generally pessimistic picture, especially in much of central Asia and western Europe, brown bears are increasing in numbers and distribution in several areas, particularly in northern and eastern Europe (Swenson 2000). This has been reported in several populations in Europe, including Russia with adjacent Finland and northeastern Norway, in the Carpathian Mountains, the northern parts of the Alps-Dinaric-Pindos mountain complex, and in Scandinavia (Chestin et al. 1992, Wikan 1996, Servheen et al. 1999, Zedrosser et al. 2001). In addition, brown bears have been released in areas in Europe where they have disappeared or where only very small populations exist. This has occurred as early as the 1500's in Germany and Poland and, most recently, Austria, France and Italy (Niethammer 1963, Buchalcyzk 1980, Rauer & Gutleb 1997, Zedrosser et al. 2001**,** Clark et al. 2002). It is interesting to note that brown bears have not been reintroduced into any areas from which they had disappeared in North America, although it has been proposed, and only one small population has been augmented (Servheen et al. 1999, Schwartz et al. 2003c).

The goal of conservation programs is usually to stop the decline in size and distribution of threatened or endangered populations, to find out why they are declining and, ideally, to allow the populations to increase to a size that is viable over long time periods (Caughley 1994). However, for a species such as the brown bear, attaining this goal by allowing small or reintroduced populations to increase and expand also causes problems, because the species depredates on domestic livestock, predates on moose, thus competing with hunters, and causes fear because bears can be dangerous to people (Swenson et al.1998). It can be particularly difficult for people to accept the return of a large carnivore after it has been gone for many decades (Boitani 1995).

The brown bear population was almost exterminated in Scandinavia at the end of the 19th century, but conservation efforts initiated by the Swedish government were successful and the population is increasing in size and distribution (Swenson et al. 1995). Because of this, there was a need for general knowledge about the ecology of the brown bear and managers needed specific information about many aspects of the ecology and population dynamics of the species to successfully manage this population recovery.

THE SCANDINAVIAN BROWN BEAR RESEARCH PROJECT

History. To better understand the brown bear, especially for a knowledge-based management, a study of brown bears using radiotelemetry was started in Sweden. The start of the Scandinavian Brown Bear Research Project (SBBRP) is "officially" stated to be 1984, when the first bear was captured and equipped with a radiocollar. This was "Rapahonan", who was captured as a yearling in Rapadalen in Sarek National Park and who has been followed by the (SBBRP) since then. This project was started as an extention of a research project about reindeer and their predators, conducted by the research branch of the Swedish Environmental Protection Agency (NV) during 1982-86 and led by Anders Bjärvall (Bjärvall et al. 1990). In 1985, the research branch of the Swedish Association for Hunters and Wildlife Management (SJF) started a bear project under the leadership of Finn Sandegren, when three bears were captured and radiomarked in Dalarna. These two projects were consolidated into one project already in 1985 (Bjärvall & Sandegren 1987). In 1987, these two project leaders and Petter Wabakken proposed that Norway be included, and it became an international cooperative project. In 1994 the project was named the Scandinavian Brown Bear Research Project. The study has continued in the two study areas since its start (Fig. 1).

Fig.1. Map of the northern and southern study areas of the Scandinavian Brown Bear Research Project showing the areas where bears are captured and marked (light red) and the area within which male bears marked by the project have immigrated (red lines).

Structure, cooperators and financing organizations. Today, the project consists of one full-time field supervisor (Sven Brunberg), a part-time data manager, who is also responsible for the biological samples (Arne Söderberg), a part-time field assistant in the northern study area (Peter Segerström), and a project leader (Jon Swenson). In addition, there are about 20 volunteers who help us locate the radiomarked bears in the southern study area and who gather other important field data. The core of our research is the work of our international team of PhD students (see list at the end of this section) and postdoctorate researchers. Because they work in several different universities, the project personnel meet twice yearly. Ole-Gunnar Støen, Andreas Zedrosser, and Jonna Katajisto received their PhD degrees with the SBBRP and work as postdoc researchers in the project with funding from Sweden (Adaptive Management Program at SLU, Umeå), Norway (Research Council of Norway), and

Finland (Academy of Finland #213457), respectively. Earlier L. Waits worked as a postdoc with NATO funding obtained by Pierre Taberlet.

The study is based on international cooperation, not only in fieldwork (the ~60 students and student volunteers in the project represent 15 citizenships) and funding, but also regarding participating researchers and students. Three academic organizations have prioritized cooperation with the SBBP in their research to the degree that they provide not only free researcher time, but also have obtained funding for PhD students and postdoc positions to work with us: Laboratoire d'Ecologie Alpine (CNRS and Université Joseph Fourier, Grenoble), the Metapopulation Research Group (University of Helsinki), and Institute of Wildlife Biology and Game Management, University of Natural Resources and Applied Life Sciences, Vienna (BOKU). We cooperate with the following researchers: Dr. Pierre Taberlet and Dr. Eva Bellemain, Centre National de la Recherche Scientifique, Grenoble (genetics); Prof. Jon M. Arnemo, Norwegian School of Veterinary Science (immobilizing, physiology); Prof. Stéphanie Manel, Université Joseph Fourier (spatial modeling of genetic structure); Dr. Göran Ericsson, Swedish University of Agricultural Sciences (SLU) (monitoring, human dimensions); Prof. Nigel Yoccoz, University of Tromsø (life histories, statistics); Dr. Atle Mysterud, University of Oslo (life histories); Dr. Solve Sæbø, Norwegian University of Life Sciences (UMB) (statistics); Dr. Jon Olav Vik, University of Oslo (modeling); Dr. Christian Nellemann, NINA (habitat studies); Dr. Bjørn Dahle, University of Oslo (reproductive strategies); Prof. Klaus Hackländer, BOKU (analysis of reproductive tracts), Dr. Frank Rosell, Telemark University College (chemical communication) and Prof. Marco Festa-Bianchet, Univ. Sherbrooke (life histories). In addition, we have ongoing or planned cooperation on bear research with Dr. Ilpo Kojola, Finnish Game and Fisheries Research Institute, Prof. Djuro Huber, University of Zagreb, Prof. Miha Adamič, University of Ljubljana, Prof. Andrew Derocher, University of Alberta, Dr. Charles Schwartz, Yellowstone Grizzly Bear Project, Jon Aas, Norwegian Polar Institute, Dr. Douglas Smith, Yellowstone Wolf Project, and Harry Reynolds, Alaska Dept. Fish and Game. In addition, the SBBRP cooperates with the lynx and wolverine projects in the northern study area. The SBBRP has cooperation with the National Veterinary Institute of Sweden (SVA), primarily through Arne Söderberg, who works there and with the SBBRP on data base management and curator of the biological samples. Åsa Fahlman, who is a PhD student in the project, also works at SVA.

Since the beginning of the project, the major financing agencies have been NV and SJF. Since 1987, the Norwegian Directorate for Nature Management (DN) has been an important financing agency. WWF-Sweden has also been a long-term financer of the project, and the Norwegian Institute for Nature Research (NINA) contributed to the project in the 1990s. Regional management agencies, especially the County Govenors in Hedmark, Dalarna and Norrbotten have provided financing for the project. Several private foundations, including the Olle and Signhild Engkvists stiftelser, Wallenberg Foundation, Carl Tryggers Foundation, WWF-Norway, Stora, Älvdalens Community Forest, Korsnäs, Iggesunds Bruk, Volvo, Norma, Vattenfall Norrbotten, Ockelbo, and some other foundations and companies have given support to the project. During many years, the project received support from Orsa Communal Forest, in the form of a field station and office. In 2006 a private person donated a house to the project to use as a field station. For the last several years, the budget of the SBBRP has averaged about SEK 2,500,000-3,000,000. Depending on the year, about 50% or more of these funds come from Swedish sources.

As of the end of 2006, 7 students have defended PhD-level theses within the SBBRP (see list of publications) and in addition 6 are active in the SBBRP. The status as of the PhD students and postdoctorate fellows as of 1 March 2007:

PhD students:

Jonas Kindberg, SLU, part-time student with funding from SBBRP, the SJF, and SLU, population monitoring, the effects of forestry on bears and their habitat, human dimensions of bears and bear management. Will finish in 2008.

Jodie Martin, dual doctoral program at UMB and Université Claude Bernard, Lyon, grant from the Office national de la chasse et de la faune sauvage, techniques to study habitat selection considering biological constraints, identifying important habitats of European brown bears (France, Scandinavia, Croatia), factors associated with population expansion and contraction. Will finish in 2007 or 2008.

Alice Valintini, dual doctoral program at Università degli Studi della Tuscia, Viterbo, Italy, and Université Joseph Fourier, Grenoble, univ. fellowship, genetics paternity studies, the contribution of individuals to population growth, genomics of brown and polar bears. Started in 2005

Richard Bischoff, UMB, university fellowship given as part of the prize received by the project leader, Harvesting as a selective pressure in life history. Started in late 2006.

Andrés Ordiz, dual doctoral program at Universidad de León and UMB with a grant from a Spanish NGO interested in bears. Methods of monitoring bear populations using observations of females with cubs, bear-human relationships. Started in 2006.

Åsa Fahlman, SLU/SVA, Uppsala. Effects of capture and immobilization on large carnivores. Started in 2006.

Postdoctorate fellows:

Ole-Gunnar Støen, SLU, Umeå, 50% postdoctorate position for 4 years studying human-bear interactions, funded by the Adaptive Management Program, Swedish Environmental Protection Agency.

Jonna Katajisto, University of Helsinki, 100% postdoctorate position for 1 year (with an application for an extension pending) to work on a spatially explicit population model for brown bears, funded by the Academy of Finland.

Andreas Zedrosser, UMN, 100% postdoctorate position for 3 years to study life-history strategies in large carnivores in relation to management, funded by the Research Council of Norway.

The International Review Committee. The Wildlife Research Committee commissioned an international review committee to examine the wildlife research projectes funded by NV and SJ during 1997-2001. This committee was satisfied with the SBBRP, calling it “outstanding” (Boyce et al. 2002). Nevertheless, they made several general recommendations for improving wildife research projects and we have encorporated them into our project:

1) Perform large-scale adaptive management experiments. When the NV decided to increase the harvest of brown bears in Dalarna, the SBBRP recommended a level of harvest that should stop the population growth and requested that this level be maintained for at least 5 years. This was done, and we will now compare the effects of two levels of harvest over periods of ca 10 years each and determine whether the predicted goal was achieved.

2) Harvesting populations in an uncertain world. As the committee recommended, we have included uncertainty into harvesting models (Sather et al. 1998, Katajisto 2006) and we are now working on spatial harvest models (see above).

3) Encourage the involvement of statisticians, mathematicians, social scientists and others into research consortia. The description of the structure and collaborators in the SBBRP, given above, shows that we have implemented this recommendation.

4) Support research careers of young scientists and wildlife managers. By including so many MSc and PhD students and postdoctorate fellows in the project, the SBBRP has contributed substantially to the recruitment of young scientists and managers in Sweden and Norway. Several of our MSc students have continued to PhD programs, five of our former PhD students have received postdoctorate fellowships, and many MSc students are now working at the county and national levels as wildlife managers.

Data and the database. Since the first bears were captured, the SBBRP has maintained radiomarked bears in both study areas. As this is a long-term project, and is the basis for PhD and postdoc studies, we have not made major changes in our major goals or methods. In this way, we have secured the long-term (23-year) individual-based data series. The major method has been to maintain radio contact with a large proportion of the adult females and their female offspring in both areas. Beyond this, the type of data gathered has changed somewhat over time, often in response to specific needs from managers (Table 1). The most important change in methods came in 1998, when it was decided to reduce the collection of data from bears in the north and only follow them closely enough to determine reproductive success and survival. This was done because there was not enough capacity to conduct intensive field work on all three species of large carnivores in the north.

Between 1984 and 2006, the SBBRP has captured 525 bears totally 1251 times. Except for a few in the beginning of the project, these were individually marked (tatoo, eartag and identification chip), weighed, measured and various samples were taken (tissue for DNA studies, hair, blood, etc.) and 381 have received a radiotransmitter. Those that were not radiomarked were primarily yearling males later in the project and some males captured during the breeding season in the south, when we were trying to capture females. We routinely capture the bears in the spring using a helicopter. Our goal has been to have radiotransmitters on all of the females and adult males in the northern area and a high proportion, >50%, of the females marked in the southern study area. We have maintained the goal in the north until 2004, when we had to reduce the number of marked males due to budget constraints. As a result, we have had 90-120 radiomarked bears after the marking season since 1996 (Fig. 2).

Radiomarked females with yearlings are all captured, although rarely a yearling escapes, and the female yearlings are radiocollared. Thus, we have built a data base consisting of many pedigrees, consisting of up to five generations. We know the mothers of 79% of our study animals (69% from field observations and 10% from DNA analyses) and the fathers of 61% (DNA analyses). This data set is the largest for brown bears in the world and the only one that is based on multigenerational pedigrees. In fact, the data set is almost unique for studies of large carnivores. In addition we have developed an individually based density index (Zedrosser et al. 2006), which allows us to examine density dependence on important life history characteristics, which has never been done before in bears (Taylor 1994) or most other large carnivores.

The data are kept in a Microsoft Access database at SVA, the field station, and with several of the project researchers. The GPS database is stored at the Swedish University of Agricultural Sciences in Umeå. Arne Söderberg, SVA, is responsible for the database, but in 2007 Andreas Zedrosser, postdoctoral fellow in the SBBRP will update the database. This is due to the SBBRP’s present economic situation.

Table 1. Summary of data gathered by the Scandinavian Brown Bear Research Project, 1986-2006. The bears captured in 1984 and 1985 are not included here, because this was a start-up phase. Active data gathering (involving capturing and following bears) is indicated with an upper-case letter and indirect data gathering with a lower-case letter. ”N” indicates the northern study area, ”S” the southern study area, and ”X” outside the study areas.

	Year																				
Data	**86**	**87**	**88**	**89**	**90**	**91**	**92**	**93**	**94**	**95**	**96**	**97**	**98**	**99**	**00**	**01**	**02**	**03**	**04**	**05**	**06**
Capture, marking	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Implanted radios												NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
GPS telemetry																	s	s	S	S	S
Survival	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Reproduction			NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Home range	S	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	S	S	S	S	S	S	S	S
Habitat use	S	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	S	S	S	S	S	S	S	S
Male emigration			NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	ns	ns	ns	ns	ns	ns	ns	ns
DNA captured	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
DNA shot bears					X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Samples (shot)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Moose predation			S						S	S	S	S	S							S	S
Sheep predation	x	x	x	x	X	X	X	X	x	x	x	x	x	x	x	x	x	x			
Population trend													X	X	X	X	X	X	X	X	X
Population size			NS	NS	N	N		S								S	S				
Denning times	S	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	S	S	S	S	S	S	S	S
Den sites	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
Food habits									S	S	S					S	S		S		S
Activity					S	S	S	S					S	S				S	S	S	S
Humans-bears	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	S
Virus infection										N											
Parasites																S					
Physiology																			NS	NS	NS
Human attitudes																			X	X	X

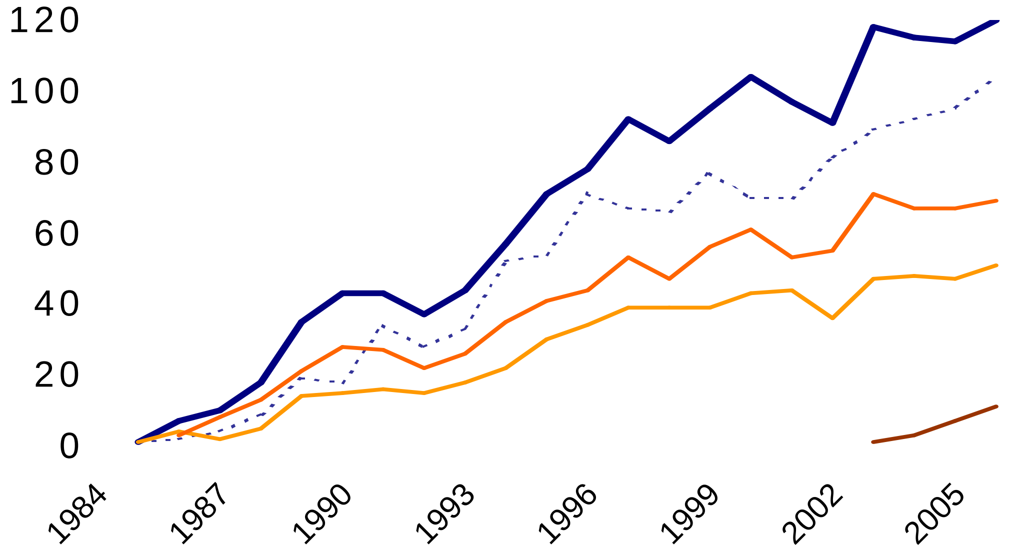

Fig. 2. The number of radiomarked brown bears in the Scandinavian Brown Bear Research Project. The solid blue line is the total number at the end of the marking season, dotted blue line is the total number at the end of the year, orange and yellow are number of marked bears at the end of the marking season in the south and north, respectively, and brown is the number of bears with GPS radios.

SYNTHESIS OF PRESENT KNOWLEDGE

The colonization of Scandinavia by brown bears

Brown bears in Europe are divided into two major genetic lineages, based on mitochondrial DNA (mtDNA). These eastern and western lineages were estimated to have diverged about 850,000 years ago (Taberlet & Bouvet 1994), although new molecular clock data suggest that they may have arisen from an ancestral population in the Carpathian Mountains about 70,000 and 25,000 years ago, respectively (Saarma et al. 2007). The western lineage is organized into two clades that probably originated from two ancestral refugia. Thus, the brown bears of Europe consist of three potential conservation units, based on mtDNA: 1) populations of the western lineage from the Iberian refugium, 2) populations of the western lineage from the Balkan refugium, and 3) populations of the eastern lineage from Russia (Taberlet & Bouvet 1994).

Bears from both the Iberian clade of the western lineage and the eastern lineage occur in Scandinavia (Taberlet & Bouvet 1994), with a clear and distinct contact zone between them. In 1994 we identified four female concentration areas in Scandinavia, based on the location of hunter-killed females (Swenson et al. 1994); the two female southernmost concentration areas were separated by a >100-km wide mtDNA contact zone with low bear densities. No females were found to cross the mtDNA contact zone, which was separated by a distance that was much greater than the dispersal distances observed for radio-marked females (Taberlet et al. 1995). However males crossed the contact zone. As mtDNA is maternally inherited, we concluded that they had dispersed from the other female concentration area, and that there was no mtDNA introgression in this contact zone. That this contact zone corresponds well with those of three other mammals that colonized Scandinavia from the south, *Sorex araneus*, *Microtus agrestris*, and *Clethrionomys glareolus* (Fredga & Nawrin 1977, Tegelström 1987, Fredga & Jaarola 1989) suggests that a common biogeographic event was responsible. We concluded that bears in Scandinavia colonized the peninsula after the last Ice Age from two directions, with bears of the Iberian clade of the western lineage coming from the south and those of the eastern lineage from the east (Taberlet et al. 1995).

Kohn et al. (1995) also found that bears of both lineages were found in several sites in Romania, suggesting a greater mixing of lineages there than in Scandinavia. They did not have enough samples to adequately describe the contact zone. However, the genetic status of brown bears in Romania is complicated by the fact that young bears were captured in the wild, raised, and then released in areas with lower densities of bear during the Ceauşescu regime (O. Ionescu, pers. comm.). Matsuhashi et al. (1999) documented a clear geographic structuring of brown bears on Hokkaido Island. Three distinct mtDNA lineages were found, which showed almost no overlap in distribution, similar to the situation we found in Scandinavia. Thus, brown bears seem to form rather distinct boundaries between mtDNA lineages when they meet, perhaps due to limited female dispersal into areas with high female bear densities (Støen et al. 2006a). This phenomenon was an early indication of the female social organization that the SBBRP later documented (Støen et al. 2005).

The decline and subsequent recovery of brown bears in Scandinavia

Originally, bears were found throughout Scandinavia (Collett 1911-12, Lönnberg 1929). Based on records of bountied bears by county, we estimated that there were 4,700-4,800 bears in Scandinavia around 1850; about 65% of these were in Norway (Swenson et al. 1995). An enormous number of bears were killed, 2,605 in Sweden and 5,164 in Norway during 1856-93, and the populations declined quickly, about 4.8% annually in Sweden and 3.2% in Norway. The greater decline in Sweden with lower harvest strengthens our conclusion that there were more bears in Norway at that time. Bears survived only in a few mountainous areas in northern and central Sweden. The low point for the brown bear population was about 1930, when about 130 bears were left in four populations that survived.

At the end of the 1800s and beginning of the 1900s, many realized that the situation was critical for brown bears in Norway and Sweden and, at that time, both the Swedish Hunters' Association and the Swedish Royal Academy of Sciences called for saving the species. All bounties were eliminated in Sweden in 1893, but this did not happen in Norway before 1973, 80 years later (Swenson et al. 1995). The number of bears in Sweden had increased enough by 1943 that a conservative hunting season was initiated. Since then, the number of bears has increased while being hunted (Swenson et al. 1994). The brown bear was exterminated as a reproducing species in Norway, with the last Norwegian population disappearing in the 1980s (Bækken et al. 1994). Immigration from the increasing and expanding Swedish, Russian and Finnish populations have led to a recolonization of Norway, as evidenced by both temporal and spatial patterns of bear occurrence in Norway (Swenson et al. 1995). Unfortunately, the reappearance of immigrating bears in Norway resulted in a vastly overestimated population size, based on public reports of bears. The estimate was a minimum of 130-194 bears in 17 populations in 1978-82 (Kolstad et al. 1986). The SBBRP updated a previous estimate of 620 bears for all of Scandinavia (Swenson et al. 1994) with some new data, and estimated the Scandinavian population to be about 700 bears in the early 1990's, of which about 2% were in Norway (Swenson et al. 1995), and about 30% of these were in the Pasvik Valley on the Russian and Finnish borders (Swenson & Wikan 1996). The latest estimate of bears in Scandinavia was about 2550 (2350-2900) in 2005 (Kindberg & Swenson 2006).

The population also increased in distribution (Swenson et al. 1995). We found that the increase in relative density from the edge of a female concentration area toward the center was quite steep, averaging a doubling in density every 24 km. There was a preponderance of males (75%) outside of the female concentration areas, compared with inside (50%). In Norway 87% of the killed bears were males during 1973-93 and 71% of those were in the age of active dispersal, 2-4 years. These frequencies were significantly greater than those found in female concentration areas in Sweden (Swenson et al. 1998c), which confirmed our earlier conclusion (Swenson et al. 1995), that the bears in Norway are a peripheral part of the Swedish population. A surprising finding was that female bears were not found significantly closer to the edge of the female concentration area than males, suggesting some long-range female dispersal, up to 80-90 km (Swenson et al. 1998c). This was later also found in Finland, where the distribution also is expanding (Kojola & Laitala 2000). We found, for the first time for bears, that female bears were dispersing from the female concentration areas before carrying capacity had been reached and while the population was increasing in size. How a brown bear population expands in distribution had not been documented prior to our study (Swenson et al. 1998c), nor had female dispersal been documented in any bear species (Støen et al. 2006 a).

Present population size and trend

We know that there is a high error rate in reports of bear observations and sign from the public (Elgmork et al. 1976), and that population estimates based on such observations can give gross overestimates (Swenson et al. 1995). Nevertheless, we compared reports of whether Swedish hunters considered the bear population to be increasing, stable, or decreasing in the various counties with the calculated harvest rate, and found a high correlation (r^2 = 83%) (Swenson & Sandegren 1996a). However, the high correlation between hunters' impressions and harvest rate was with time lags of 6-14 years (Swenson & Sandegren 1996a). This was not unexpected, because it takes 10-15 years for a bear populations' structure to stabilize following a change in harvest rate (Harris & Metzgar 1987) and because bears reproduce slowly (Miller 1990). Although our results indicated that hunters accurately observed and reported population changes, the long time lag make these observations unsuitable for routine management decisions (Swenson & Sandegren 1996a).

We compared three methods of population estimation on our southern study area of ~7000 km^2 in 2001 and 2002. We knew the minimum size of the population there, because of our intensive research efforts. The methods were: 1) using reports of females with cubs from the public, 2) a capture-mark-recapture (CMR) method using radiomarked adult males to locate marked and unmarked adult females during the breeding season, and 3) several CMR methods to analyze the results of individuals identified using DNA in scats collected by moose hunters. It is becoming increasing popular to use noninvasive genetic methods to census elusive species (Taberlet et al. 1999), including bears (eg. Boulanger et al. 2002). Our results showed that using the computer program MARK to analyze the DNA data from scats was an effective and relatively accurate method appropriate for Sweden, where bears occur at low densities and inhabit large areas (Solberg et al. 2006). We also used this method to estimate that there were 550 (482-648, 95% C.I.) bears in Dalarna and Gävleborg counties in 2001 (Bellemain et al. 2005), 159 (148-180) in Västernorrland in 2004 (Bellemain & Taberlet 2005), and 272 (254-299) in Västerbotten in 2004 (Kindberg & Swenson 2006b). We have used these estimates and results from the effort-corrected observations of bears by moose hunters from throughout the country (see below) to estimate that there were about 2550 (2350-2990) brown bears in Sweden in 2005 (Kindberg & Swenson 2006b).

Observations of bears and other large carnivores be included in the Swedish moose observation scheme since 1998. A comparison of local densities based on the DNA census and bear observations per 1000 hunter hours show very good relationships, although the slopes of the linear relationships vary among areas (Kindberg et al. unpubl.). Thus, this method seems to be appropriate to estimate the trends of bear populations at the county level in Scandinavia (Kindberg et al. 2004). Research is ongoing on this important subject for managers.

The demographic and genetic viability of the Scandinavian brown bear population
Knowledge of the viability of a given population is of utmost importance for managers, especially when the species is hunted, and it introduces a quantative element into risk assessment (Boyce 1992). However, these predictions are often very uncertain (Caughley 1994). We investigated both the demographic and genetic viability of the Scandinavian brown bear population (Sæther et al. 1998, Waits et al. 2000).

Demographic viability was evaluated using long-term, individual-based data from both of our study areas and a diffusion approximation in age-structured populations with demographic and environmental stochasticity (Sæther et al. 1998). For the model, we assumed no density-dependence, because we were concentrating on the minimum viable population size in Norway, where the species is an important depredator on domestic livestock, and densities are very low. In addition, the high growth rates we documented suggested that the populations were well below carrying capacity even in Sweden. The populations in both study areas showed high population growth rates ($r = 0.13$ or $\lambda = 1.14$ in the north and $r = 0.15$ or $\lambda = 1.16$ in the south) due to a combination of high survival rates and high reproductive rates. The Scandinavian brown bear populations showed the highest population growth rates yet recorded for brown bears (Sæther et al. 1998), in addition to the highest reproductive rates yet recorded for brown bears. We estimated that these bears reproduced at about 80% (south) and 70% (north) of a hypothetical maximum rate (Swenson & Sandegren 2000). The variance around r was partitioned into demographic variance, which was relatively large, an estimated $s^2_d = 0.180$ in the north and 0.155 in the south, and environmental variance, which was small, $s^2_e = 0$ in the north and 0.003 in the south. If we defined a population as viable when the chance of population survival was greater than 90% over 100 years, a minimum of 8 females ≥ 1 year old must be present in the north, and 6 in the south. However, these estimates are very sensitive to mortality rates, and a small increase in mortality rates will strongly reduce the viability of even relatively large brown bear populations.

The studies of mtDNA in Scandinavian bears found only one haplotype in each lineage (Taberlet & Bouvet 1994, Taberlet et al. 1995), which suggested low genetic heterozygosity. Other small and isolated European brown bear populations that have suffered a bottleneck in size also have shown monomorphic and fixed mtDNA haplotypes (Randi 1993, Randi et al.1994). Loss of genetic variability can have negative effects on fitness, such as lowered litter size, which has been correlated with inbreeding in captive brown bears (Laikre et al.1996). However, European brown bears in Carpathian Mountains in Slovakia, which had experienced a bottleneck in size, had normal allelic variation (Hartl & Hell 1994).

To determine the genetic status, genetic diversity and gene flow in Scandinavia, we used nuclear DNA microsatellites from 380 bears sampled from throughout the peninsula and from all the four female concentration areas (subpopulations, as determined by Swenson et al. 1994). Overall average and expected heterozygosities were 0.665 and 0.709, respectively, varying from 0.656 to 0.664 per subpopulation (Waits et al. 2000). The two subpopulations located in the middle of the four subpopulations differed significantly from Hardy-Weinberg allelic equilibrium, perhaps due to immigration from and emigration to adjacent subpopulations. Nuclear genetic diversity did not differ among the four subpopulations. Surprisingly, genetic diversity was in the upper end of reported diversities for brown bears in North America. Diversity was not significantly different from several populations that had not experienced known population bottlenecks. This was a very different result than was obtained from the analysis of mtDNA, but the reason is still unclear. Also, nuclear DNA genetic differentiation, as measured by microsatellite loci, was not consistent with mtDNA phylogeographical groupings, perhaps due to male-mediated gene flow over the mtDNA contact zone.

Our results documented that the Scandinavian brown bear population is demographically and genetically healthy, with the highest documented growth rate for any brown bear population and levels of genetic diversity that are similar to large North American populations without a history of population bottleneck (Sæther et al. 1998, Waits et al. 2000). The fact that the bears survived in four areas may be partly responsible for this. Four independent genetic drift effects may have randomly preserved different combinations of alleles in each subpopulation. We recommended that managers consider the Scandinavian brown bear population to consist of four genetically different subpopulations, with male-mediated gene flow among them. However, the two northernmost subpopulations were more similar to each other than to the other subpopulations (Waits et al. 2000).

To determine if our *a priori* assumption that the bear population was structured into four subpopulations, we reanalysed multilocus genotypes data without any prior presumption about the spatial structure using two independent methods (neighbour-joining trees and Bayesian assignment tests) (Manel et al. 2004). The result was that the population consisted of three genetic subpopulations (with the two formerly identified subpopulations in Norrbotten combined into one), which matched the three geographical clusters of individuals present in the population. Our results underline the importance of determining genetic structure from the data, without presupposing a structure, even when there seems to be good reason to do so. Even though the population shows a relatively high level of heterozygosity, there seems to be a low rate of gene flow between the southernmost subpopoulation and those farther north (Tallmon et al. 2004), which is might be a concern for management in the future. Also, the two northern subpopulations now appear to be growing together (Sahlén et al. 2006).

Behavioral ecology and life history

Surprisingly little is known about the social organization of bears. In fact, it is hardly mentioned in a recent review of the knowledge of grizzly bears (Schwartz et al. 2003b). Our results show that female brown bears are more social than previously assumed, but that both males and females show evidence of territorial behavior. The home range size of adult male and female brown bears is inversely related to population density (Dahle et al. 2003a), suggesting some form of territoriality. One study of American black bears (*U. americanus*) reported a relationship between female relatedness and spatial proximity (Rogers 1987), but another one did not find evidence of such a relationship (Schenk et al. 1998). In an analysis of the genetic spatial structure of the Scandinavian brown bear population, Manel et al. (2004) identified local clusters of related individuals, which suggested a kin-related social structure. Støen et al. (2005) confirmed kin-related social structure among female brown bears using the long-term and large-scale data series that combine field data with molecular techniques in the SBBRP. Thus, we can conclude that most female brown bears live in multigenerational matrilinear assemblages and apparently show some form of territorial behavior against unrelated females. Dahle et al. (2006a) found that the home-range size of subadult female brown bears decreased less with increasing population density than for subadult males, which is also consistent with the occurrence of matrilinear assemblages. There appears to be some resource competition due to hierarchial system among the related females in these matrilinear assemblages, because reproductive suppression is evident among young females that overlap home ranges with their mothers (Støen et al. 2006b). This is the first time this has been documented in a mammal that is not group living. There also seemed to be a dominance hieriarchy and a competition for philopatry among female siblings, with the smallest sibling staying farthest from the mother before dispersal and having the highest probability of dispersing (Zedrosser et al. in press).

Female dispersal has been considered to be rare in bears, and never documented (Rogers 1987, Schwartz & Franzmann 1992, Reynolds 1993). The documentation of how a brown bear expands showed that females do disperse and presented evidence that female dispersal might be inversely density dependent. However, there is considerable controversy in the literature about the presence of density dependence in dispersal (Lambin et al. 2001). Nevertheless, Støen et al. (2006a) found that in Scandinavian bears, 32-46% of the females dispersed from their natal home range, both females and males dispersed farther than had been documented in North America, and, for the first time, that natal dispersal probability and distances are inversely related to population density in a large carnivore.

Brown bears have a promiscuous mating system (Schwartz et al. 2003b). Beyond this general description, it is surprisingly poorly documented. Dahle & Swenson (2003) found that both males and estrous females roamed during the breeding season, supposedly to seek mates. The females had larger home ranges during the breeding season in the north, where there were fewer available males. This is the first time an effect of estrus on home range size has been reported for female carnivores. This roaming implies that the females are selecting mates. We investigated this more closely with our extensive paternity database. We found that females chose the largest, most heterogygous and less inbred males of those around them

(Bellemain et al. 2006b). The results also suggest that females might exercise a post-copulatory cryptic choice of the father of her young (Bellemain et al. 2006b).

With our paternity data base, we could also estimate annual reproductive success in male bears, using the number of genetically determined yearlings born to our marked females as the indicator of reproductive success. Older and larger males had higher annual reproductive success, but size was more important in the north, where there were fewer males per female and therefore less competition among males (Zedrosser et al. 2007). Also, less inbred males were more successful. As expected, males with a higher density of females around them had a higher annual reproductive success (Zedrosser et al. 2007).

An organism's life history is its lifetime pattern of growth, reproduction and mortality. Life-history theory deals directly with natural selection, fitness, adaptation, and constraint, and is needed to understand the action of natural selection and how genetic variation is expressed (Stearns 1992). Empirical tests of life-history theories are rare in large mammals, because they require relatively large, long-term, individual-based datasets, such as the SBBRP has obtained for brown bears. Age of primiparity and reproductive senescence are important life-history parameters. In the southern study area, females were primiparous at ages 4, 5, and 6, but in the north, all were primiparous at age 5 (Støen 2006, Zedrosser 2006). Primiparous females had smaller litters, but not smaller young, and lost more cubs than multiparous females (Støen 2006, Zedrosser 2006). It is much more difficult to document age of senescence, because all studies have few bears in the oldest age classes. We participated in a cooperative study of 20 studies of brown bears and found that senescence occurs around the age of 28-29 years (Schwartz et al. 2003a).

Body size is one of the most important parameters affecting an individual's fitness. We have investigated the effects of body size (rather than body mass, which is extremely variable seasonally in bears) on a number of important life-history parameters. The results show that body size is very important in bears. For example, home range size is positively correlated with body size in subadults (Dahle et al. 2006a) and annual reproductive success is positively correlated with body size in adult males, especially in the study area with more competitors (Zedrosser et al. 2006). The size of yearlings is positively related to maternal size and negatively related to the number of siblings in the litter and population density (Dahle et al. 2006b). There was also a cohort variation in body size in yearlings, perhaps due to the effect of food abundance. Although larger mothers produced larger yearlings, size as a yearling was not related to size as an adult for females (Zedrosser et al. 2006). Adult female size was positively related to food availability during the subadult period and negatively related to population density (Zedrosser et al. 2006). Brown bear mothers may stay with their young for 1.4 or 2.4 years in Scandinavia, and body size of the yearlings influences the length of maternal care. Dahle & Swenson (2003d) found that the probability of staying with the mother to the age of 2.4 years was greater for small yearlings, especially those in a litter of two. Yearlings staying with their mother an extra year grew faster than those that did not, and the effect was greatest for young in a litter of two. Dahle & Swenson (2003d) concluded that, if large offspring body mass positively affects later offspring survival and reproduction, mothers may be able to optimize the length of maternal care according to the litter size and the size of their yearlings. Later, Dahle et al. (2006b) demonstrated that larger yearlings had a higher survival rate, using only natural causes of death.

Our studies have identified sexually selected infanticide (SSI) in brown bears for the first time (Swenson 2003, Swenson et al. 1997b, 2001a, b, Bellemain et al. 2006a, b). Infanticide is the killing of dependent offspring, either before or after it is born (Hrdy & Hausfater 1984). Infanticide is adaptive and termed “sexually selected” if the following requirements are met: 1) infanticidal males should not kill offspring they have sired, 2) infanticide should shorten the interbirth period of the victimized females, and 3) infanticidal males should mate with the mother of the dead infant and sire her subsequent offspring (Ebensperger 1998). We have examined this phenomenon in several papers. The number of adult males dying 1.5 years previously was correlated negatively with cub survival in the south. In the north, no factors correlated with temporal patterns of cub loss, but loss of adult males in these areas 0.5-1.5 years previously was the best explanatory variable among those tested. In the north, the few males present were young, and a greater proportion first bred successfully at young ages (3-6) than in the south (Zedrosser et al. 2007), when they are possibly not large or experienced enough to kill cubs that are defended by their mothers. We concluded that males kill cubs as predicted by the SSI hypothesis and that primarily immigrating males were responsible (Swenson et al. 2001c). We have continued our investigations about this phenomenon, followed females with cubs intensively in 1998-1999 and expanded our studies using DNA fingerprinting. We tested some of the requirements for SSI, specifically that infanticidal males should not kill offspring they have sired and that infanticidal males should mate with the mother of the dead infant and sire her subsequent offspring and found support for both of them (Bellemain et al. 2006a). In addition, we found that resident adult males are also infanticidal in a manner consistent with SSI.

We also studied females with cubs to determine whether they showed counterstrategies to infanticide, as would be expected if SSI were an important factor affecting female reproductive success (Ebensperger 1998). We found support for several counterstrategies (Swenson 2003, Bellemain et al. 2006a): 1) during the breeding season, females with cubs were less active than males and females without cubs, and most active when adult males were least active, 2) females with cubs moved less than either males or females without cubs during the breeding season, which is not only because cubs restrict female movement (Dahle & Swenson 2003a), 3) females with cubs used different habitats during the breeding season than those without cubs, and 4) females also mated promiscuously, because several litters had mixed paternity (Bellemain et al. 2006a), as has also been observed in Alaska (Craighead et al. 1995b). In Yellowstone, females have been observed to mate with up to 8 males during a breeding season (Craighead et al. 1995a). In conclusion, our results show that the three requirements for SSI are met in brown bears. In addition, females with cubs showed three or four of the proposed counterstrategies; aggressive physical defense (Craighead et al. 1995a), avoiding males, promiscuity, and perhaps postconception mating. Aggressive physical defence of cubs is well documented in brown bears (Craighead et al. 1995a), but our results show that the size of the litter influcences females’ willingness to defend them; singleton litters are least defended, perhaps because there is a lethal risk to defend cubs from a male (Zedrosser 2006). In addition, it seems that the primiparous females are less able to defend their cubs, especially those that are 4 years old (Zedrosser 2006).

SSI seems to also affect the mating system of brown bears. Because neighboring males are potentially infanticidal, polyandry is a counterstrategy (Bellemain et al. 2006a). As expected, fathers are chosen from among the spatially closer males, but among them, the females select the largest, most heterogygous and less inbred males (Bellemain et al. 2006b).

Sexually selected infanticide is promoted by the disruption of the male social organization when resident adult males die, thus allowing new males into an area or perhaps allowing other resident males to realign their home ranges. It has a solid and well-documented theoretical basis and should be expected in many species of large carnivores. In species exhibiting SSI, hunting adult males can promote it. According to the precautionary principle, wildlife managers should consider SSI when managing the hunting of large carnivores. Because there may be geographical or population differences in the occurrence of SSI, however, much more research is required before we can reliably apply knowledge of SSI to carnivore hunting management. The effects of hunting on the behavior of the hunted animals should receive increased attention from behavioral ecologists and wildlife biologists (Swenson 2003). Nevertheless, it is important to point out that this is a controversial subject. Several North American bear experts do not accept its occurrence, at least in brown bear populations in North America (Miller et al. 2003). One potential reason for the apparent difference in occurrence of SSI between the continents is that primiparous females seem to be most susceptible to SSI, with susceptibility increasing with decreasing age of first birth (Zedrosser 2006). Scandinavian brown bears give birth earlier than those in North America (Zedrosser 2006).

Foraging ecology

An important aspect of a species' ecology is its diet. Prior to our studies, the diet of Scandinavian bears had only been studied in southern Norway, where the now-extinct study "population" may have consisted of only one female bear (Elgmork & Kaasa 1992, Bækken et al. 1994) and in Sweden, consisting of a qualitative description of spring food (Haglund 1968). In Europe, brown bears in the north are more carnivorous than those in the south (Elgmork & Kaasa 1992). This has potentially important life-history consequences, as the amount of meat in the diet of brown bears in North America was found to be highly and positively correlated with female body size and litter size (Hilderbrand et al. 1999). Thus, knowledge of the diet of bears might help us understand the high population growth rate of Scandinavian brown bears (Sæther et al. 1998). We studied the diet of brown bears, based on scat contents, in south-central Sweden (unpublished), central Sweden-central Norway (Dahle et al. 1998), and far northeastern Norway (Persson et al. 2001). In central Sweden-central Norway, we compared the diet of bears on both sides of the border, with access to unguarded free-ranging sheep in Norway and without access to sheep in Sweden.

We estimated digestible energy from scat contents based on published conversion factors. In terms of digestible energy, ungulates, mostly carrion, were most important in both Norway and Sweden in central Scandinavia during the spring (Dahle et al. 1998). During summer, ants, forbs, and ungulates (reindeer *Rangifer tarandus* and moose *Alces alces*) were the most important food items in Sweden. In Norway, however, sheep was the most important item. In autumn, berries were most important in Sweden and sheep and berries in Norway. The most important berries were *Empetrum nigrum* and *Vaccinium myrtillus*. We estimated that Swedish bears obtained 44-46% and 14-30% of their annual energy intake from berries and ungulates, respectively. In Norway, it was 6-17% from berries and 65-87% from ungulates, primarily sheep. To gain body mass prior to denning, brown bears in Norway selected lipid-rich and easily obtainable sheep in summer and autumn, whereas in Sweden, they relied on carbohydrate-rich berries in autumn.

In the Pasvik Valley of northeastern Norway, we found that bears ate mostly the same items as farther south, but in different proportions. Ungulates, primarily moose, contributed about 85% and 70% of the estimated dietary energy content of the diet in spring and summer, respectively. In autumn, berries were most important (49%), but ungulates were still important (30% of dietary energy content) (Persson et al. 2001). There were only very few sheep in this area during the study. Adult ungulates were much more important in the bears' diet in the far north than in central Scandinavia (Dahle et al. 1998) or in southern Norway (Elgmork & Kaasa 1992). This has also been reported in European Russia (Danilov 1983) and Siberia (Krechmar 1995). Contributing reasons might be the lack of alternate prey in the early spring, the simpler northern ecosystem, weaker moose after the longer northern winters, and snow conditions that are more often favorable for predatory behavior by bears (Dahle et al. 1998).

We have so far only published the portion of our studies of the diet of bears in south-central Sweden that deal with myrmecophagy, i.e. predation on ants (Swenson et al. 1999a). We found that ants were an important food item for the bears, providing an estimated 20% of the total annual digestible energy. Ants were abundant (an estimated 9.6 kg/ha or 30.5-38.5 tons per bear) and comprised 12, 16, and 4% of the fecal volume in spring, summer, and autumn, respectively. Red forest ants (*Formica* spp.) were consumed most frequently in spring, and bears excavated on average 23% of the mounds annually, often several times. Bears consumed 4,000-5,000 ants for each mound they opened during the spring. In relation to availability, bears preferred carpenter ants (*Camponotus herculeanus*) during every season. This preference might be related to the nutrient contents of the ants. Carpenter ants had 71% more fat, one-fourth as much formic acid, and about one-half as much dietary fiber as red forest ants, and thus had a higher predicted digestibility. They are also larger and slower than the red forest ants, even though they live in small colonies in dead wood and are thus more difficult to obtain. Whereas ants are relatively important to Eurasian brown bears, they are much less important to brown bears in North America. The reason for this is not clear, although red forest ants that build large mounds are more common in Eurasia than North America.

Although we now have a rather good knowledge of the food habits and foraging ecology of Scandinavian brown bears, we cannot conclude that the exceptionally high reproductive rate of Scandinavian bears is due to a better diet than other studied populations of brown bears, because brown bear populations on the Pacific coast of Alaska with access to enormous amounts of spawning salmon (*Oncorhynchus* spp) are less productive than the Scandinavian brown bears. The reason for the high productivity in Scandinavian bears is still not completely understood. However, Zedrosser (2006) has suggested that the reason might be human-induced, because brown bear populations with a long history of human persecution (such as the Scandinavian population) show a greater reproductive investment relative to body mass than populations with a shorter persecution history. As a result, the populations with a long persecution history might be the most productive.

Bear-human conflicts

We have identified three major areas where brown bears cause conflicts with human interests in Scandinavia: predation on moose, depredations on livestock, especially sheep, and danger to human safety (Swenson et al. 1998b). Additionally, bears cause other problems, such as depredation on semidomestic reindeer in northern Scandinavia (mostly calves, Swenson & Andrén 2005). However, the importance of bears as a predator on reindeer has not been documented adequately. Bears also destroy beehives, but they can be protected quite adequately with electric fences.

<u>Predation on moose</u>. Earlier studies in Scandinavia have documented that bears kill moose (Haglund 1968, Wikan 1996), but is was difficult to estimate the magnitude of this predation, although Haglund (1968) concluded that the number of adult moose killed by bears in Sweden was less than 1-2% of the moose killed by hunters in the 1960's. Haglund (1968) mentioned that bears killed moose calves in Sweden, but he could not estimate the magnitude of this predation. Recently Ballard & Van Ballenberghe (1997) summarized studies from North America showing that brown bears killed 3-52% of the available moose calves and that each adult brown bear killed on average 0.6-4 adult moose per year in various study areas. The brown bear population in

Sweden has increased by several times since Haglund's (1968) study (Kindberg & Swenson 2006a) and moose hunting generates important revenues for landowners. Most Scandinavian hunters had been accustomed to harvesting moose in generally predator-free environments (Cederlund & Sand 1991). Consequently, many landowners have been concerned that the moose harvest, and thereby income from hunting, will decline with the increase in bear numbers (Swenson et al. 1998b). We studied bear predation on moose for six years using radio-collared moose in our southern study area and compared our results with four similar studies of radio-marked moose calves. Our results about predation on calves are in press (Swenson et al. in press b); the rest are yet only published as a Norwegian-language report (Swenson, et al. 2001b).

Our study was the first where brown bears are the only predator on moose calves. Bears killed about 26% of the calves and 92% of the predation took place when the calves were <1 month old. Bear predation was probably additive to other natural mortality, which was about 10% in areas both with and without bears (Swenson et al. 1999c, in press b). Females that lost their calves in spring produced more calves the following year (1.54 calves/cow) than females that kept their calves (1.11 calves/cow), which reduced the net loss of calves due to predation to about 22% (Swenson et al. in press b). The predation rates we observed in our southern study area, combined with our calculated rate of sustainable off take of the bear population, suggested that hunters lost the opportunity to harvest 10-15 calf moose for every bear they were able to harvest (Swenson et al. 2001b).

We found that bears in the southern study area only killed about 1% of the available adult moose annually (Swenson et al. 2001b). However, in many areas that bears were recolonizing, hunters reported that many adult moose had been killed. We investigated the possibility that bears could more easily kill naïve moose at the colonizing fronts than in the areas where bears and moose had lived together for a longer time in three areas in Scandinavian and two areas in North America (Berger et al. 2001). The results showed that naïve moose were less vigilant when confronted with smells and sounds of predators (bears and wolves *Canis lupus*) and were more easily killed by bears after bear-free periods of 50-130 years than those that were constantly exposed to predators. However, moose cows that lost their calves to predators became rapidly hypersensitive to smells and sounds of predators. Thus, there appeared to be rapid adaptive learning, particularly by the mothers when calves were killed, even as quickly as one generation. This rapid learning should reduce the chance that recolonizing predators would exterminate populations of naïve prey (Berger et al. 2001).

<u>Depredation on sheep</u>. The most difficult aspect of bear presence in Norway is that it is an important depredator on the >2 million free-ranging, unguarded domestic sheep. Each bear in Norway kills on average an estimated minimum of 50 sheep annually (Swenson & Andrén 2005). This is in great contrast to the situation in Sweden, where sheep are kept within electric fences in areas with bears, and there are very few losses. The Norwegian Parliament decided in all three Large Predator Policies that the number of bears should increase and that depredation losses should decrease (Miljøverndepartement 1992, 1997, 2004, Energi- og miljøkomitéen 1997). Is this realistic? We compared the trend of loss of ewes in two areas with sheep losses to bears near the border to Sweden with the trend in the number of bears in adjacent Sweden. We had a control area, with no documented sheep loss to bears, near each area with known loss to bears. In addition, we examined the effect of killing depredating bears on the level of loss of ewes the following year. We confined our analysis to ewes, because bears prefer to kill ewes (Aanes et al. 1996). We found highly significant relationships between loss of ewes and bear numbers in both areas with documented bear loss, but not where there was no documented bear loss (Sagør et al. 1997). In addition, the killing of depredating bears had no significant loss-reducing effect the

following year, indicating that it was not an effective method to reduce losses the following year, presumably because of high rates of immigration from Sweden (Sagør et al. 1997). Of course, overall losses could have been higher if bears had not been killed. This conclusion was very controversial and opposed by the sheep farmers. Recently, we have repeated the analysis, using the same areas, but with the years following the study referred to above. Our second study gave the same results (Swenson et al. 2003). We concluded that bears and the present method of sheep husbandry in Norway are incompatible and that obtaining the dual political goals of more bears and fewer losses of sheep to bears could only be reached by changing the method of sheep husbandry or separating sheep and bears geographically (Sagør et al. 1997).

Fear of bears. The brown bear is a powerful carnivore that has hurt and killed people (Herrero 1985), and studies show that many people in Scandinavia are afraid of bears (Norling et al. 1981, Dahle et al. 1987, Zimmermann et al. 2001, Røskaft et al. 2003, Havula 2006). We analyzed 114 encounters between bears and researchers in Scandinavia and searched the historical and recent literature for reports about people who had been injured or killed by bears (Swenson et al. 1999b). We found that bears usually left the area after encountering a person. There were no attacks during the 114 meetings, but bluff charges occurred in 4% of the meetings. When combining all similar studies in Eurasia, we found that no personal injuries had occurred in 818 encounters with bears by research personnel. Blowing and growling were apparently warning behaviors associated with the presence of cubs or carcasses. Although these are factors that apparently increase bear aggression, we only identified one factor that was truly dangerous: a wounded bear. The records suggest that more people were injured previously in Scandinavia than today. There were more bears, and more people working in bear habitat, but there were probably also many more wounded bears because of the use of ineffective weapons and set guns. We conclude that the Scandinavian bear is generally not aggressive, although females with cubs and bears defending carcasses are more prone to act aggressively. The most dangerous bear is a wounded bear (Swenson et al. 1999b). We are continuing our studies of this subject, and are now documenting how bears react to close encounters with humans in the forest.

Human disturbance of bears and their avoidance of humans

Another aspect of bear-human interactions is the degree to which humans might disturb bears or cause them to avoid otherwise suitable habitats. This has been studied intensively in North America, where brown bears have been found to be very sensitive to human presence, even to the degree that they avoid suitable habitats (Gibeau et al. 2002, Apps et al. 2004). Preliminary results from the southern study area suggested that Scandinavian bears avoid human habitation and roads (Swenson et al. 1996a).

Katajisto (2006) used utilization distributions estimated with the kernal method for home ranges of 73 radiomarked adult female bears in both study areas to build a quantative habitat model. The resulting model was tested with the distribution of hunter-killed bears, which showed a high correlation with predicted habitat suitability and increased our confidence in the model. The model showed that bears were found in forest habitats with a low level of human influence, especially human settlements. Katajisto (2006) estimated that about 120,000 km^2 of suitable habitat was available for bears in Scandinavia. Nellemann et al. (in press) analyzed the habitat use of 106 radiomarked bears in the southern study area in relation to distance to resorts and towns, terrain ruggedness, sex and age of bears. In addition, distributions of 145 individual bears were derived from DNA analyses of bear scats collected independently by hunters (Bellemain et al. 2005). Both data sets revealed similar results. Bear presence was significantly greater in rugged terrain and far from towns and resorts. More than 74% of all female bear locations were in the 29% of the terrain classified as "rugged" and located >10 km from any town or resort, whereas similar habitat closer to towns or resorts was avoided. Interestingly, sub-adult bears (<4 years) comprised up to 52% of all bear use within 10 km from resorts and settlements, likely representing exploratory dispersing individuals. These areas, however, contained only 8% of the old males (>7 years) (Nellemann et al. in press). These findings are consistent with recent research in North America, suggesting that some categories of bears may use areas near humans, because it is a "refuge" from adult males (Rode et al. 2006).

Another effect of humans is disturbance of bears in winter dens. Teitje & Ruff (1980) reported that American black bears (*Ursus americanus*) that changed dens had a greater loss of body mass (25%) than those that did not (16%). We found that an average of 9% of the bears abandoned their den and dug a new den during a given winter and that there was no effect of age or sex (Swenson et al. 1997a). People, hunters, forestry workers, fishermen and skiers, appeared to have caused a minimum of 67% of these cases of den abandonment. We were the first to document a fitness effect of changing dens; pregnant females that had changed dens lost young significantly more often (60%) than those that did not change dens (6%) (Swenson et al. 1997a).

The management of bear hunting

The hunting of bears has a long tradition in Scandinavia, and the population in Sweden has been hunted continuously since 1943 (Swenson et al. 1995). According to European Union regulations under the Habitat Directive, bears can only be killed to prevent serious damage to culture and livestock, public health, sanitary and safety reasons and only if this has no negative impact on the preservation of the species (Zedrosser et al. 2001). The threats bears pose to humans and their interests were discussed above. It is obvious that the hunting carried out in Sweden has not been detrimental to the preservation of the species, as bear numbers and distribution have increased dramatically since hunting was reinstated (Swenson et al. 1994, 1995, Sæther et al. 1998, Kindberg & Swenson 2006a). However, it is both biologically and ethically important to have a good understanding of the effects of hunting on a bear population. In addition, kill permits are often issued in Norway to remove bears that have killed sheep (Hustad & Swenson 2001).

We have modeled how a bear population could be harvested to keep it at the lowest possible level, yet still demographically viable. This might be a management strategy in areas where conflicts are high, such as in Norway (Tufto et al. 1999). Using the demographic values reported in Sæther et al. (1998) and the criterion that the probability of extinction over the next 100 years is less than 10%, we found that all bears could be harvested above a threshold number of 34 female bears ≥ 1 year old (Tufto et al. 1999). However, this number could be lower if one harvested a proportion of the bears above a threshold number (Lande et al. 1995a, b). Then 35% of the bears exceeding a threshold population of 12 female bears ≥ 1 year old could be harvested and a viable population would be maintained. Using this strategy, the population would be expected to stabilize at about 20 female bears. The relatively low estimate for viable, harvested populations is due to the high intrinsic growth rate of the population. However, if this growth rate were reduced by only ca 3%, the threshold must, under some conditions, be doubled. An additional problem is uncertainty associated with population estimation. As this uncertainty increases, the threshold must be raised considerably to assure that extinction is avoided, given the prescribed population survival probability. This is a relevant finding for management, because bears are notoriously difficult to census and monitor (Eberhardt et al. 1986). Other factors that are important to consider when evaluating these results are that the IUCN criteria we used allow a quite high rate of extinction (10% in 100 years), perhaps higher than desired (Tufto et al. 1999). In addition, genetic drift results in loss of variability at such low numbers and the population may loose the ability to track changes in the optimal phenotype and thus avoid extinction (Lande & Shannon 1996).

Katajisto (2006) has also modeled the more realistic scenario of the large population of brown bears in Sweden using individual-based models and data from the SBBRP. She concludes that the population is quite robust to changes in harvest policy and could sustain a doubling of the present rate of harvest. However, under some harvest scenarios, especially increasing the harvest of trophy bears (adult males), there would be a time-lag effect that is significantly greater than the short-term effect on population growth. Thus, constant monitoring of the population trend is important (Katajisto 2006).

Beyond the actual killing of individuals, and the effect that this has on population change, there are other, more indirect, effects on the population. One effect is the orphaning of cubs when their mother has been killed. Although it is illegal to kill bears in a family group in Sweden, this happens occasionally when the hunter does not see the other bears. In such cases, the cubs have often been captured and taken into captivity. We were the first to document the survival, growth and subsequent reproduction of orphaned brown bear cubs, although it was only 5 cubs from 2 litters. Our results showed that cubs can survive well from about midsummer and for those surviving beyond their yearling year, we did not find that loosing their mother had a negative effect on growth, survival or reproduction. We concluded that it was ethically acceptable to leave orphaned cubs to fend for themselves after midsummer (Swenson et al. 1998a), and this is now done in Sweden.

One indirect effect of hunting that is often considered desirable is that hunted bears are thought to be more wary of people. Although this is widely believed, there is very little scientific evidence to support or refute this impression. A review of the literature from Eurasia cannot be considered to be strong scientific evidence, due to the nature of the studies that were compared, but some consistent patterns emerged. It appears that hunted populations of bears are in fact more wary of people than those that are not hunted, but only if human-derived foods are not available (Swenson 1999). Fear of people can apparently be learned quickly when people begin to hunt bears and this fear can be maintained over a long time, even after hunting has been banned. However, the availability of human-derived foods appears to be more important in shaping the shyness of bears than hunting (Swenson 1999).

Our studies have yielded yet another example of an indirect effect of hunting on bear populations, the promotion of sexually selected infanticide (SSI) (Swenson 2003, Swenson et al. 1997b, 2001a, b, Bellemain et al. 2006a, b), which is described in more detail above. We concluded that killing an adult male would disrupt the male social organization for 1.5 years, that it decreased the population growth rate (λ) by 3.4%, and that killing an adult male in our southern study area led to a loss of reproductive output that was equivalent to killing 0.5-1 adult females (Swenson et al. 1997b). The time lag we recorded does not seem unreasonable for brown bears if the loss of cubs is primarily caused by infanticide by immigrating males that establish a home range on the study area after the death of a resident adult male. Bears are generally killed during the fall, when fattening for winter denning is important. The breeding season starts in the spring not long after den emergence and continues to midsummer.

We also looked at the bear-caused deaths of subadult bears (1-4 years old) in relation to the death of adult males (Swenson et al. 2001a). Most yearlings separated from their mothers in May. Other bears killed no subadult females older than yearlings, but males were killed as 1-, 2-, and 3-year-olds. Neither population density nor food abundance influenced rates of intraspecific predation on yearlings, but intraspecific predation on yearling females increased with the number of adult males that had died 2.5 years previously and whether any adult male had died 1.5 years previously. Because we found a similar pattern for intraspecific predation on yearling females as we had found for cubs, we speculated that infanticidal males might be prone to kill subadult bears, although this is clearly not SSI (Swenson et al. 2001a). Intraspecific predation on subadults was highest during the breeding season, as it was for cubs and was also reported by Mattson et al. (1992). Combining the results of our studies (Swenson et al. 2001a**,** c) and calculated population growth using a standard deterministic model (Ferson & Akçakaya 1990), the loss of adult male(s) was associated with a 4.5% reduction in the population growth (Swenson 2003). However, one could counter that the effects of SSI would be compensated somewhat, because of the shortened litter interval, because females usually breed soon after they loose their young, and therefore give birth the next year (a requirement of SSI). Katajisto (2006) did not observe this in an individual-based model, however, probably because the males often fail to kill the entire litter, which would be required to shorten the litter interval. Apparently the females' anti-SSI strategies are relatively successful.

We tested the hypothesis that an increase in harvesting adult male bears would increase cub mortality. After we reported that the southern population showed a 16% annual growth rate in 1985-95 (Sæther et al. 1998), harvest quotas were increased markedly. We predicted that the increased harvest rate of adult males would increase cub mortality through SSI. In the counties encompassing the southern study area, the annual number of harvested bears increased six-fold after 1995, the annual number of harvested adult ($\geq$ 5 years old) males increased 35-fold, and the total annual mortality of radio marked adult males doubled, as did mortality of cubs accompanying radio marked females. Thus, the results supported the SSI hypothesis (Swenson 2003).

Sexually selected infanticide seems to be promoted by the disruption of the male social organization when resident adult males die, thus allowing new males into an area or perhaps allowing other resident males to realign their home ranges. It has a solid and well-documented theoretical basis and should be expected in many species of large carnivores. In species exhibiting SSI, hunting adult males can promote it. According to the precautionary principle, wildlife managers should consider SSI when managing the hunting of large carnivores. Because there may be geographical or population differences in the occurrence of SSI, however, much more research is required before we can reliably apply knowledge of SSI to carnivore hunting management. The effects of hunting on the behavior of the hunted animals should receive increased attention from behavioral ecologists and wildlife biologists (Swenson 2003). Nevertheless, it is important to point out that this is a controversial subject. Several North American bear experts do not accept its occurrence, at least in brown bear populations in North America (Miller et al. 2003). One potential reason for the apparent difference in occurrence of SSI between the continents is that primiparous females seem to be most susceptible to SSI, with susceptibility increasing with decreasing age of first birth (Zedrosser 2006). Scandinavian brown bears give birth earlier than those in North America (Zedrosser 2006).

The development and testing of field and laboratory methods

The SBBRP feels it is important to contribute to the development of research and laboratory methods, both to promote more effective field work in the project, but also to allow researchers to use our data set to develop and test new methods.

The project has therefore participated in the "Technique Project" (Teknikprojektet), which was an EU-financed project with the goal of constructng GPS collars and developing the technology for wildlife research. This participation has been important to develop competence within this area in the SBBRP. We have also contributed to developing the GPS data base at SLU, Umeå. We maintain an ongoing dialog with GPS manufacturer to assist in the development of products that meet our damands at a reasonable cost. We have also conducted studies in Orsa Grönklitt Bear Park to interpret the activity data that we received from our GPS collars (Genovesi et al. 2006). We have used bears in bear parks to develop the dosages of immobilizing drugs that we use in the field. We work continually on improving the methods we use in our field studies. We also work with captive bears to test the doses of the immobilizing drugs we use (Arnemo et al. 2003).

The geneticists cooperating with the SBBRP have developed improved software for parentage analysis (Cercueil et al. 2002) and, while working with the DNA from feces for population estimation, have made several important improvements in the techniques (Bellemain & Taberlet 2004, Piggot et al. 2004). The work with the fecal DNA also led to their work on the importance of tracking and assessing genotyping errors (Bonin et al. 2004, Miquel et al. 2006). Our data on the spatial genetic structure of the brown bear population in Sweden was used to develop a new method to identify genetic discontinuities in natural populations (Manel et al. in press).

Other analytical advancements made by cooperators in the project include a method to analyse home range sizes using the kernel method and locations with irregular time intervals, which is the type of VHF-telemtry data we have gathered (Katajisto & Moilanen 2006). A further application of this method is how to estimate kernel home ranges while accounting for habitat boundaries (Katajisto 2006).

Brown bears as a model for large carnivore conservation in human-dominated landscapes
As the application of conservation biology to real world situations involves public relations and politics as much as, or more than, science, conservationists have recognized the need to develop "sales strategies" to capture the public's imagination (Linnell et al. 2000). This often involves using a single charismatic focal species, a "flagship", to engage the public emotionally and anchor a conservation campaign (Simberloff 1998) or focusing on conserving a single species in order to conserve the rest of the biodiversity in the area in question. This requires that the single species in question can be regarded either as an "indicator" of important biodiversity (its presence, reproduction, density, etc. is used as an index of a multitude of attributes for other species or environmental conditions of interest, Landres et al. 1998), an "umbrella" (a species requiring such large tracts of habitat that saving it will automatically save many other species, Simberloff 1998), or a "keystone" species (a species that impacts other species far beyond what might be expected from its biomass or abundance, Simberloff 1998). The large carnivores in Scandinavia and the rest of Europe occur in man-dominated landscapes and the attitudes of many rural people are negative to large carnivores due to their depredations on livestock and semidomestic reindeer and predation on ungulates (Sagør & Aasetre 1996, Breitenmoser 1998). Therefore, it does not seem logical to choose a flagship that attracts such polarized and emotional viewpoints, although the opposition to bears seems to be lower in Sweden than in Norway. In addition, although bears and other large carnivores in Scandinavia use very large areas, they are habitat generalists and do not seem to be very negatively impacted by the extremely intensive forestry practices in Scandinavia that are endangering large numbers of other organisms (Linnell et al. 2000). Thus, although they are appropriate as "umbrellas" indicating the presence of large blocks of habitat, this habitat is not suitable for most threatened or endangered species. For the same reason, they are not good

indicators of biodiversity. To what degree these predators are keystone species is still unknown, but there is no question that they can be important predators on native ungulates (Linnell et al. 1995, Swenson et al. in press b). This is a problem, because the hunting of wild ungulates, such as moose and roe deer (*Capreolus capreolus*), is an important recreational activity and is a substantial source of income for forest owners (Cederlund & Bergström 1996). Thus, we conclude that carnivore conservation in Scandinavia, and probably much of the rest of Europe, is so filled with specific problems that it requires special conservation planning, and cannot ride on the back of, or carry, other conservation initiatives (Linnell et al. 2000).

So, what is the future of large carnivore conservation in Europe? Woodroffe (2000) presented a very pessimistic view, showing that large carnivore extinction probabilities were closely and positively related to human population density. With increasing human densities throughout the world, this does not bode well for large carnivores. However, Woodroffe's (2000) analysis was based on data from Africa and historical data from North America. We examined these patterns using present data from North America and Europe, to determine whether populations of large carnivores could be conserved even at high human densities if a favorable and effective management policy was in place (Linnell et al. 2001). The results showed clearly that today, with modern and almost universal favorable large carnivore management in the areas we investigated, populations of large carnivores are mostly stable or increasing, and the status of the populations are not correlated with human density. We have a more optimistic view than Woodroffe (2000), and suggest that the existence of effective wildlife management structures is more important than human density *per se* in large carnivore conservation (Linnell et al. 2001).

Thus, managers can conserve and are conserving the brown bear in human-dominated landscapes in Scandinavia and many other parts of Europe. The purpose of our studies has been to understand the ecology of the species in such landscapes and to give managers the knowledge they require to ensure that bears and people can coexist there. Although the boreal forests of Scandinavia are quite different from those of Central Europe, it appears that the results of our studies have more relevance to understanding and managing brown bears in Central Europe than to those in North America. One important factor is that brown bears show similar autumn body masses in Scandinavia and the Dinara Mountains of Slovenia and Croatia (Swenson et al. in press a). As reproductive parameters are correlated with autumn body mass of adult females (Hildebrand et al. 1999), we can conclude that the reproductive parameters we have documented can be used in modeling population dynamics of Central European bears. Mortality rates are site specific, but it is easier to document mortality rates than reproductive rates in bear populations. In addition, brown bears have survived in many human-dominated landscapes for thousands of years, despite eradication campaigns, in contrast to the situation in North America. This may have changed life-history strategies in European brown bears, making them more productive and thus easier to conserve (Zedrosser 2006). We hope that our research contributes to management and conserving brown bear populations not only in Scandinavia, but also elsewhere in Europe.

FUTURE RESEARCH NEEDS

The Wildlife Research Committee has asked the SBBRP to give them our assessment of future research needs regarding brown bears in Scandinavia. There are two major types of needed future research; applied research for managers and fundamental research. The need for applied research will be quite large in the future, because the brown bear population is increasing quite rapidly (5.5% annually at the present, Kindberg et al. 2004, which implies a doubling time of about 13 years). This means that the area of bear distribution will continue to increase, and now more than before into areas with higher human density. As more and more people come into contact with bears, there is now and will be even a greater need in the future to understand better both how bears react to humans and humans to bears. A better understanding of bear social organization and communication will be required to be able to hinder bears from coming into areas near human habitation. This increase in the bear population will increase demands from the public to increase harvest levels to stop population growth. This might be difficult in a species with such great demographic variance in reproductive rates. A risk analysis of various harvest rates and knowledge about hunter selection in relation to age, sex and individual quality is necessary. Also, we are only beginning to study bear social organization, which is a requirement to predict how various degrees of harvest will affect population trends. At the same time, human use of forested areas for recreation and recreational development is increasing, which probably negatively affects area use by bears. Brown bear populations are increasing similarly in much of northern, eastern, and southeastern Europe, which means that research-based knowledge that can be obtained in Scandinavia will be useful in many other European countries.

The SBBRP has amassed an individual-based data set, including pedigrees, which is quite unique for large carnivores. These data can be used to explore fundamental questions about the population dynamics, social organization, and life history traits of large, long-lived carnivores. The results can be interesting for both management and development of scientific theory. Because we regularly capture individuals to change radiocollars, we have a series of measurements of size and mass for them. The long-term brown bear project that is most natural to compare with, the grizzly bear study in the Greater Yellowstone Ecosystem in USA, has data on roughly half as many bears as we do (since 1983), they have a much lower proportion of the population marked, they have not captured and measured the individuals regularly, and they do not work on subjects such as social organization and life history traits (Schwartz et al. 2006). Our genetics data from a large proportion of the population over its entire range, obtained from hunter-killed bears, scats collected during the DNA-based censuses, and all captured bears, is also quite rare, and allows studies of genetic structure, “landscape genetics”, paternity studies and the effects of heterozygosity, inbreeding, and outbreeding on life history traits. Our mortality and survival data allow further analysis of population dynamics and risk assessment. The amount of data has recently reached a level that has allowed us to begin answering some of these questions, and produce new fundamental knowledge about this species, much of it relevant to other species of bears and large carnivores.

The SBBRP has always had a goal of combining fundamental and applied reseach, which the International Review Committee recognized and commented favorably upon (Boyce et al. 2002). The SBBRP recommends a continuation of gathering long-term individually based data on brown bears in both study areas. This will allow us to continue to increase our fundamental knowledge about the species on a broad front, focusing on population ecology, social organization, life-history strategies, and spatial aspects (with genetics as an important tool in most of these areas of research). At the same time, we will continue to answer the many pressing management questions regarding brown bears. The following are immportant needs for future research about the Scandinavian brown bear, in our view. Both applied and fundamental questions are given under each category:

Population estimation and monitoring
A reliable method of population monitoring is essential for the future management of the bear population. The SBBRP has estimated bear population size using DNA from scats collected by hunters over large areas (Bellemain et al. 2005, Solberg et al. 2006). Managers and hunters are enthusiastic about this method and scat collections have now been carried out in Dalarna, Gävleborg, Västernorrland, Västerbotten, and Jämtland counties. Although this

method has great promise, the hunters find the scats opportunistically, so the sampling has not been carried out in a systematic manner. We are aware of some biases, such as an estimated sex ratio that differs from the actual sex ratio of the population (Bellemain et al. 2005). It would be valuable to document spatial patterns of defecation rates in relation to habitats, day or night beds, etc. from following the trails of GPS-marked bears using dogs. With these results, we could model the effects of various collection schemes to determine whether or not the lack of systematic collection is a problem and, if so, how much and in which direction is the bias. We could also use the maps of the sampled scats from the five counties to test the hypothesis that scats are gathered randomly. The results would be applicable to other large-scale population census efforts of elusive mammals using volunteers to collect scats.

The DNA-based censuses are costly in terms of time and money. Therefore, we have used the census results from the different counties to test the Large Carnivore Observation Index (LCOI), based on observations of bears, corrected for hunter effort, during the first week of the moose hunt. Preliminary results (Kindberg et al. unpubl.) show high correlations between minimum density and the observation index, but the slopes of this relationship seems to vary among areas for bears, as it does for moose (Ericsson & Wallin 1999). We should therefore conduct further tests when results are available from other areas with various degrees of forest openess. This will also allow us to calculate a national population estimate for Sweden, as is prioritized in NV's "Åtgärdsprogram".

In many parts of the world, observations of female brown bears with cubs are used as to estimate population size and monitor populations (Keating et al. 2002). This method might also be useful in Scandinavia at the edge of the species range (such as in Norway) or where it is important to document population trends in a relatively small area. The SBBRP can now easily gather detailed data on the movements of females with cubs to evaluate the assumptions of this method and how they influence the population estimate, which may be useful in other parts of the world.

Harvesting bear populations

The Scandinavian brown bear population shows high demographic variance, low environmental variance, and rates of infanticide that are correlated with harvest rates for adult males (Swenson et al. 1997b, 2001a, 2001c, Sæther et al. 1998, Swenson 2003, Zedrosser 2006). With these demographic characteristics, it is important to understand the effects of hunting on population growth. We should continue the modeling of the risks of various harvest strategies on bears given these and other uncertainties (harvest selection, spatial variation, etc.), as recommended by the International Review Committee and started by Katajisto (2006). The mechanism behind the harvest of adult males seemingly leading to more infanticide is has not been confirmed. We should therefore investigate how the harvest on adult males influences their social organization and how this influences the probability of infanticide. This is important for the future setting of harvest quotas and in understanding the general relationship between killing males and infanticide, because evidence of this is now available from several species of large solitary carnivores (Swenson 2003).

An important ethical question is whether harvesting is an unnatural selective pressure on life-history evolution (Festa-Bianchet 2003). This has been documented in many harvested fishes (e.g. Jennings et al. 1999) and a few large mammals with obvious trophy-related attributes that hunters can base selection on (eg. Coltman et al. 2003). This could be operating for bears, as 88% of all mortality of bears >1 year old is due to human causes, almost exclusively hunting, and hunting mortality is different from natural mortality, which is concentrated on very young and very old bears (Festa-Bianchet 2003, Sahlén et al. 2006). To adequately study this phenomenon, one needs a long-term data set and data on maternity and paternity to calculate heritability (Coltman et a. 2003). The SBBRP has this for bears, in addition to data from different harvest regimes during the course of our study. We should use data on marked and hunter-killed bears to document whether hunters select bears in relation to life-history attributes and estimate the heritability of life-history traits. We should also document the spatial and temporal variation in harvesting pressure and selectivity and use individual-based modeling to estimate how harvesting might affect the mean and variance in reproductive success and whether management regimes might act as a selective agent in brown bears. The question of the long-term effects of hunting is certainly one that managers will have to face in the near future, as public awareness of this phenomenon grows.

Genetics

The genetics studies conducted by the SBBRP have been important to managers. We have shown that Scandinavia was colonized by bears from the south and the east (Taberlet et al. 2005), there are three genetic subpopulations (Manel et al. 2004), that the genetic status is good, based on nuclear DNA (Waits et al. 2000), but there is little gene flow between the middle and southern subpopulations (Tallmon et al. 2004). The genetics studies have been essential to answer many fundamental questions. We have identified the male attributes used by females during mate choice (Bellemain et al. 2006b) and evaluated the factors determining male reproductive success (Zedrosser et al. 2007). We should continue to determine the paternity of our bears to document correlates with lifetime reproductive success in males. We also want to analyze microsatellites and Major Histocompatibility Complex (MHC) genes using our extensive long-term data on body size, growth, age of reproduction, long-term reproductive success, survival of offspring, home-range size, social organization, mortality, etc. to determine whether life-history traits are correlated with MHC compatibility, genetic heterozygosity, inbreeding and/or outbreeding, odor signals, and whether MHC compatibility is a factor in mate choice and kin recognition. Studies of this type are providing exciting new insights in understanding the genetic components of fitness (Coltman et al. 1998, Kruuk, et al. 2000, Penn 2002). If we find correlates with reproductive success, we will use this in our study of harvest-induced selection.

Until now, most of our research has been on “population genetics”, but we would like to expand our research to include “population genomics”. This involves the analysis of hundreds of markers for many individuals (genome scan), and discerning neutral markers from “outlier” markers, which are potentially under selection. This emerging discipline aims to assess the role of evolutionary forces (such as mutation, gene flow or natural selection) implied in the variability of genomes and populations (Luikart et al. 2003). One of the applications of genome scans concerns the study of the genetic basis of speciation to understand how species evolve to become distinct phenotypically, and which genes are involved in this process. Brown bears and polar bears constitute an excellent model for studying speciation, as those two species diverged recently (about 300,000 years ago; Talbot et Shields 1996) and show well marked adaptations (such as size, hair color, structure, and feeding habits). We will sample different population of polar and brown bears across Europe and the United States. Genomic tools will allow searching for chromosomical regions differentiating those two species and test whether those differences are concentrated in a few regions, as suggested by Wu & Ting (2004).

Density-dependent effects on brown bear population ecology and life-history traits

Bear researchers have advised managers not to assume density dependency in their models, because density-dependent reproduction has not been documented for bears (Miller 1990), although it has recently been suggested to affect both reproduction and subadult survival, in a comparison of bears in two adjacent areas (Schwartz et al. 2006). As stated earlier, only the SBBRP has estimated the density experienced by each individually marked bear. We have found that density is an important factor affecting home range size (Dahle et al. 2003a, 2006a), body growth (Dahle et al. 2006b, Zedrosser et al. 2006), propensity to disperse (inverse effect) (Støen et al. 2006a) and male reproductive success (Zedrosser et al 2007). We should now analyze the effects on reproduction and survival and the shape of the relationships between these parameters and density. This is important to know the effects of harvest, because the ability of the bear population to sustain harvest will probably depend on its density and the harvest models carried out so far have assumed no density dependence (Sæther et al. 1998, Katajisto 2006). Therefore, it is essential for managers to know the pattern of density dependency in reproduction and mortality in bears.

We propose to use our extensive long-term data on body size, age of reproduction, long-term reproductive success, survival of offspring, home-range size, mortality, individual density, etc. to study the relationships among life-history traits and trade-offs among them. This is the key to understanding population dynamics and evolution in a species (Stearns 1992) and this is a golden opportunity to significantly increase our fundamental knowledge in this area, particularly for large mammals. This has obvious ramifications for management.

Factors promoting and hindering population expansion

The increasing brown bear population will certainly continue to expand into suitable habitat. Based on habitat use by radio-marked females, Katajisto (2006) modeled suitable brown bear habitat in Scandinavia, showing that they are mostly occupied in Sweden (except Bohus län and Småland) and mostly unoccupied in Norway. The next question is where and how quickly the bears will arrive in an area. We should model the change in the distribution of female concentration areas since 1981, based on the locations of hunter-killed females, and include habitat aspects, such as forest cover, productivity, type, terrain ruggedness, and human influences, such as roads, habitation, cities and towns, recreational developments, agricultural areas, and reindeer husbandry, to create a model that mimics the observed pattern of expansion and contraction of the female concentration areas. We could then predict how changes will occur from the present female distribution.

Modern forestry appears to be primarily negative for brown bears in North America (McLellan & Hovey 2001), yet the Scandinavian population shows the highest reproductive rates yet documented for the species (Sæther et al. 1998) and it lives in the most forestry-influenced boreal forest. With an ecosystem approach, as recommended by the International Evaluation Committee, the SBBRP has documented the habitat relationships of all of the major bear foods; berries, moose calving grounds, *Formica* and *Componotus* ants, in addition to selected habitats for day and night beds. We should use data from our radio-marked bears, satellite imagery and GIS software to build a model to predict the influence of modern forestry on bear habitat and examine the effects of habitat on reproductive performance and size of adult female bears. One bias to habitat selection studies is overlooking the potential effects of biological constraints. If an individual is unable to visit all of the habitats randomly, due to constraints on movement, for example, the true availability of habitats might be different than assumed. We should analyze this effect, based on known movements of our bears, and compare the results with traditional analyses. Unfortunately, our VHFbased daytime locations are biased to daybed habitats (Moe et al. submitted ms). To adequately document habitats used by bears for foraging, we must use GPS transmitters. We can also use spatially explicit population models to examine how landscape composition and physiognomy are important for bear population dynamics (Wiegand et al. 1999, Boyce et al. 2001).

Brown bears were previously assumed not to be territorial, but we have found that females form matrilineal assemblages consisting of related females with inter-overlapping home ranges occupying exclusive areas. Generally, related females overlap more extensively than unrelated females (Støen et al. 2005), which probably means that some areas will have higher bear densities than others, due primarily to female social organization. To understand how bear density is related to habitat variables, we should document how habitat resources are distributed between the exclusive parts (core area) and overlapping parts (peripheral area) of female home ranges, and if resource sharing within and among the matrilineal assemblages is related to kinship. This will help us understand where, how and why brown bears are territorial. This is important knowledge for managers because territorial and nonterritorial species react differently to harvest and population density changes, and if some habitats promote the formation of matriarchial assemblages, it will be possible to have higher densities of bears there.

The use of habitats and areas by bears could also be studied in more detail, by following the movements of GPS-marked bears through real landscapes. This should allow the documentation of how bears use a typical boreal landscape with high road density and some human habitation. Modeling could tell us what habitats are preferred, preferred but underused because of human or other influences, and how bears would move through a fragmented landscape when dispersing. The results from this modeling effort could be used to predict areas that would receive especially high numbers of dispersing bears, even if they are far from the female concentrations. With this knowledge, managers could prepare in advance for the arrival of these bears.

Bear-human conflicts when a bear population expands

Besides knowing when and where to expect bears, managers also have to deal with human reactions. Dr. Göran Ericsson and Jonas Kindberg (SLU, Umeå) have cooperated with the SBBP to interview people living in areas with varying and known bear densities, as determined by the LCOI and the scat censuses. The locations of the homes of the respondents and nonrespondents are also known. This is the first study of its kind, and should help managers to understand human behavior in relation to the length of time bears have been in an area and their density. It would be especially important to document which conflicts are transient when bears expand into an area, and which are more permanent.

People often fear bears, because people can be injured or even killed by bears. The SBBRP is studying the behavior of bears when a person approaches them, using GPS transmitters on both the bear and the person (Støen et al. unpubl.). It would also be important to interview people who have been injured by bears to learn more about the circumstances involved

Bears sometimes use areas near human habitation, often without the people being aware of it. Using GPS-marked bears, we could also document how bears avoid or react to human habitation, humans themselves, slaughter remains, roads, etc. When more is known about the bear-human interface, we should conduct a questionnaire survey to learn how much people are willing to change their lifestyle to accommodate bears in their surroundings.

Another human dimension related to bears is economy. Bears can be a negative economic factor for the owners of hunting rights, because they can kill a considerable proportion of the available calves (Swenson et al. in press b). This reduces the value of the terrain for moose hunting, because few calves are available for the hunters. However, the bear is also a positive economic factor, because the owner of the hunting rights can sell rights to bear hunting and take a payment for each harvested bear. Both the moose calves that the hunters are not able to shoot due to bear predation and the bears that they are able to shoot have a direct (meat, hide) and recreational value to the hunter. We do not know whether this economic equation favors the bear or the moose, but it would be important to the large-carnivore debate to find out.

Although we now understand the effects of bear predation on moose quite well (Swenson et al. 1999c, in press b), relatively little is known about the effects of bear predation on reindeer, especially reindeer calves. A documentation of this effect is important for the Swedish compensation system for damage caused by large carnivores. A recent methodological advance developed by Rauset (2006), using a GIS analysis of the GPS-generated locations of radiomarked bears, has proven successful to estimate rates of bear predation on moose calves on the southern study area. This method could also be used in a reindeer management area.

The phenomenon of “problem bears”, ie those showing “unnatural” behavior and using areas near human habitation, occurs whereever bears and humans coexist. This problem will certainly increase as the bear population increases in size and distribution, and results in many killed problem bears (eg. Gunter et al. 2004). We have already shown that moving them is not a viable management option (Linnell et al. 1997). Research we have conducted (Nellemann et al. in press) and new research results from North America (eg. Rode et al. 2006) suggest that the bears that come in to human habitation might really be trying to avoid adult males, which show a strong avoidance of human habitation. This is an important point, because managers might have been treating a symptom without understanding the cause. It is important to document which categories of bears visit human habitation and when, to determine if the pattern fits one of vulnerable categories of bears avoiding large males at times when conflict with large males is greatest. A preliminary literature search has revealed that virtually nothing is known about the chemical communication system of bears, with the exception of the giant panda (*Ailuropoda melanoleuca*) (Swaisgood et al. 2004). If it were possible to identify how and with which chemicals adult male bears signal their presence in an area, it may be possible to artifically produce these chemicals and keep bears seeking to avoid adult males away from human habitation. This could provide managers an option to scaring and killing bears. To do this, we must understand how bear populations are organized socially and how they communicate with each other.

Bears as part of a large-carnivore community

The brown bear is one of four large carnivores in the Scandinavian ecosystem. Using available data, and preferably GPS-generated data, researchers in the bear, lynx (*Lynx lynx*) and wolverine (*Gulo gulo*) projects could analyze and compare the use of area and habitats by all of these species in the northern study area. Besides the scientific interest of understanding how the predator community uses space in relation to each other, the results would be important for managers to estimate the problems the species could cause for reindeer husbandry (especially if data on reindeer distribution were also available) and to understand how to form reserves that would best protect all the species, if this were a goal. Such an analysis has been started in the western part of the southern study area (Hedmark County, May et al. unpubl.).

There is some evidence from North America that brown bears and wolves in concert can have a major and population regulating effect on moose populations, although these conclusions are controversial (Gasaway et al. 2002, Orians et al. 1997). Our study of brown bear predation on moose calves is the first in the world in an area with only brown bears present (Swenson et al. in press b). Now wolves are starting to become established at the edge of the southern study area. When they become established within the study area, this will give a golden opportunity to repeat the calf predation study and perhaps answer the very important question; can wolf and bear predation together drive a moose population into a predator pit (Gasaway et al, 2002)? We could also investigate some of the ecological roles that bears play, such as seed dispersal, etc.

The effects of capture, immobilization, and implanted transmitters on brown bears
The ethical treatment of wild animals used in scientific research is an important topic that will only gain in importance. The SBBRP feels a responsibility to the bears, the public and the financing agencies to know how our research is affecting our study subjects. Our commitment to ethical treatment of our study animals has resulted in a 10-fold reduction in capture mortality during our study (Arnemo et al. 2006), but we still have much to learn about the effects of capture, immobilization, and implanted transmitters. We are taking a leading role in this respect. For example, implanted transmitters have been used in mammals since the 1970s, but our ongoing project is the first to examine their long-term effects.

HOW HAVE THE RESEARCH RESULTS BEEN USED IN MANAGEMENT?

The goal of the SBBRP has been to produce scientifically sound results that would advance our knowledge of the ecology of the Scandinavian brown bear and at the same time provide this knowledge for the practical management of the species and the conflicts surrounding it. This was recognized by the international evaluation of Swedish wildlife research in 2001 (Boyce et al. 2002). In their report they stated the following about the SBBRP: "This outstanding project has most successfully brought science and management together in a very productive and visible way. The publication rate has been excellent showing that applied and fundamental research by no means is mutually exclusive." Results from the SBBRP have been used actively as a basis of knowledge for the formation of large-carnivore policy in both Sweden and Norway. In addition to this, the project has provided specific research-based knowledge to managers in both countries in response to management questions, or in anticipation of coming management questions. These specific results are expanded upon below.

Besides Scandinavia, the SBBRP has provided comments, recommendations and results as requested by national governmental agencies, the European Commission, the Council of Europe, and nongovernmental organizations to help with the management of and research on brown bears in Bulgaria, Estonia, Finland, France, Georgia, Italy, Japan, Pakistan, Poland, Spain, Slovakia, Slovenia, the United States (Greater Yellowstone Ecosystem grizzly bear population), and in Europe generally (Swenson et al. 2000). We have found that brown bears have similar growth patterns and reach similar body mass throughout Europe (Swenson et al. in press a). Because female body mass is correlated with reproductive potential (Hilderbrand et al. 1999), our results will be useful for population modeling in other parts of Europe. We have also given recommendations to a research study of sloth bears (*Melursus ursinus*) in Sri Lanka, and one of our PhD students (M.A. Nawaz) mainly works on the population of Deosai National Park, Pakistan. Therefore, the SBBRP is an important source of information and recommendations for brown bear management and conservation in Europe and Asia.

Determination of population status and subpopulation structure
One of the greatest concerns that managers have when managing a large carnivore population, especially one that has experienced a major population bottleneck, is its conservation status. In fact, knowing whether a population is in “favorable conservation status” is an important point in EU’s Habitat Directive. The SBBRP has clearly documented the positive conservation status of the brown bear, but also identified some areas of concern. The project has investigated both the genetic and demographic status of the population.

Genetics. Our results regarding the genetic status of the population have changed somewhat with time, reflecting the development of new methods, in addition to changes in the bear population. The first study, using mitochondrial DNA (mtDNA), showed extremely low mtDNA variation (Taberlet et al. 1995), but a study using nuclear DNA (19 microsatellites) showed a high level of genetic diversity (Waits et al. 2000).

Based on the study of mtDNA, Taberlet et al. (1995) recommended considering two populations as separate conservation units until more information was available. Based on the first results of nuclear DNA, Waits et al. (2000) proposed considering the Scandinavian brown bear population as one evolutionary unit and four management units, which were the four female concentratation areas that were identified earlier (Swenson et al. 1994). In a later study, we did not presuppose any genetic structure, and found that the genetic data grouped most naturally into three subpopulations, with the two previously identified subpopulations in Norrbotten forming one group (Manel et al. 2004). A study of gene flow between the southern subpopulation and those farther north revealed a low immigration rate (Tallmon et al. 2004). This should be monitored, because it is a cause of concern for the future genetic status of this subpopulation.

Thus, the population shows a relatively high level of heterozygosity and is structured into three somewhat different genetic groups, with adequate gene flow among them, except for the southernmost group (Dalarna, Hälsingland, Härjedalen), which receives limited gene flow. The two northern subpopulations now appear to be growing together (Sahlén et al. 2006).

Population dynamics. A population viability analysis was conducted using data collected during 1984-1995 in both study areas (Sæther et al. 1998). This was a period with relatively low harvest rates. The results showed annual population growth rates of 14% in the north and 16% in the south, which are the highest ever reported for a brown bear population. The populations had a very high viability, with extremely low probability of extinction, given the reproductive and mortality rates that were documented during the study. Based on modeling of the data, however, Sæther et al. (1998) found that the viability of the Scandinavian brown bear population was very sensitive to mortality rates, and that even a relatively small increase in the mortality could strongly reduce the viability of even relatively large populations. Since 1995, harvest levels have increased considerably. We are now conducting population modeling with the present harvest and demographic rates (Katajisto 2006).

Population estimation and monitoring
The management of a wildlife population requires knowledge about the population trends and numbers, especially if the population is hunted. It is well known that bear populations are sensitive to harvest, especially the killing of adult and subadult females (Miller 1990, Eberhardt et al. 1994, Boyce et al. 2001).

The SBBRP has evaluated several methods for estimating the numbers of bears, and has concluded that estimates using capture-recapture models based on the “capture”of individual bears identified from DNA in scats collected by big-game hunters is the most appropriate for Sweden, where bears occur at low densities and inhabit large areas (Bellemain et al. 2005, Solberg et al. 2006). After using Dalarna and Gävleborgs counties as a test area, the SBBRP has prepared guidelines for other counties to conduct DNA-bases censuses (Brunberg & Swenson 2006) and assisted actively with population censuses in Västernorrland, Västerbotten and Jämtland (Bellemain & Taberlet 2005, Kindberg & Swenson 2006b). These censuses are very popular among the hunters and local people, perhaps because they participate in collecting the samples. This gives the results legitimacy, which is important for managers.

The DNA-based population censuses are expensive in time, money and administration. The SBBRP recommended in 1997 that observations of bears and other large carnivores be included in the moose observation scheme. This was accepted and put into practice in 1998. A comparison of local densities based on the DNA census and bear observations per 1000 hunter hours show very good relationships, although the slopes of the linear relationships vary among areas (Kindberg et al. unpubl.). Thus, this method seems to be appropriate to estimate the trends of bear populations at the county level in Scandinavia (Kindberg et al. 2004). In other parts of the world, observations of females with cubs are often used to estimate the size of and monitor the trends of brown bear populaitons. The SBBRP has cooperated with almost all brown bear projects in Europe to develop movement-based rules for deciding, at a given probability, whether two observations of females with cubs might be the same family (Ordiz et al. in press).

Using the DNA-based censuses and trend results, the SBBRP has made two recent national population estimates for Sweden (Kindberg et al. 2004, Kindberg & Swenson 2006a). Another estimate will be made after the results from Jämtland are available.

The national population goals for bears are expressed in annual reproductions, both in Sweden and Norway. This can be a difficult concept, because most people think of goals in numbers of animals. The SBBRP has determined what an annual reproduction means in terms of population size, and has found that it varies by period, area and time of year that the reproductions are documented (Swenson & Katajisto 2005).

Recommendations about hunting seasons and quotas

The SBBRP has actively provided the Swedish Environmental Protection Agency and some county managers with information and recommendations about hunting seasons and quotas to meet stated objectives. This has included recommendations about management areas for quotas and quota restrictions, such as use of female quotas (Swenson & Sandegren 1996b). The project is currently evaluating the effects of female quotas, the baiting ban, and hunting method on the age and sex of shot bears. The project has modeled the effects of hunting on population growth (Sæther et al. 1998, Tufto et al. 1999, Katajisto 2006) and is continuing this research. In addition, we have estimated the degree of illegal hunting in Sweden (Swenson & Sandegren 1999). Our research in this area is ongoing.

Cubs-of-the-year are sometimes found by members of the public. Formerly, they were taken from the wild, but there are few available places for more bears in zoos. We have found that these cubs do have a possibility to survive, develop normally, and reproduce if they become alone after midsummer, so they may be left in the wild then (Swenson et al. 1998a).

The danger of bears to people

The question of how dangerous bears really are and how people should react around bears is very important to managers. The SBBRP has analyzed the available data on injuries and deaths caused by bears, going far back in time, and bear behavior when meeting people. These results have been published scientifically (Swenson et al. 1996b, 1999b) and in brochures for the public in several languages (Brunberg 2000a, b, c, Olsson 2000, 2001a, b, 2003, 2004). Managers at the national and county level in both Sweden and Norway have used this information to prepare locally adapted educational materials. Our research on this subject is ongoing, including the behavior of bears in the vicinity of habitation, use of sites of slaughter remains, and bear behavior when humans approach them at close distances in the forest (Sahlén 2006).

Bear depredations on domestic livestock and moose

Bear depredation on sheep is the major source of conflict between people and bears in Norway. This is a minor problem in Sweden, probably because sheep in Norway graze mostly unguarded in the mountains and forests (Swenson & Andrén 2005). The SBBRP has conducted research on this topic in Norway and has made literature reviews to give reliable recommendations about effective protective measures (Wabakken & Maartmann 1994, Aanes et al. 1996, Linnell et al. 1996a, b, Mysterud et al. 1996, Sagør et al. 1997, Dahle et al. 1998, Linnell et al. 1999, Smith et al. 2000a, b). At the present, we are studying the behavior of bears near summer farms (fäbodar) in Sweden.

As mentioned above, the SBBRP has studied the effects of bear predation on a moose population in Sweden (Swenson et al. 2001b, in press b). The results show that bears only have an important effect on calf survival and that this effect varies with the moose-bear ratio in the area. The SBBRP is now studying the economic effects of having huntable populations of moose and bears on hunters and owners of the hunting rights. If wolves become established in our southern study area, it will provide a unique opportunity to document the effects of two major predators on a moose population in an area where the effect of one of the predators alone has been documented earlier.

Bear predation on domestic reindeer is another source of conflict, especially in Sweden and some areas of Norway. The SBBRP have not conducted research on this topic, but has assisted in a pilot project conducted by the managers in Norrbotten County. The SBBRP anticipates starting research on this topic in the future.

The effects of humans on use of space by brown bears

There is a large body of evidence documenting that humans and human habilitation has a negative effect on the use of space and habitats by grizzly bears in North America (Gibeau et al. 2002, Apps et al. 2004). Our results show that this is also true for the brown bear in Scandinavia. At the home-range scale, human habilitation and roads affect the use of space by bears during the active period and den placement (Swenson et al. 1996a, Katajisto 2006, Yri 2006, Elfstöm et al. in press). On the landscape scale, this results in areas that are actively avoided around towns and tourist developments, with both categories having equal effect (Katajisto 2006, Nellemann et al. in press). Thus, the occurrence of humans, in addition to habitats, is very important in determining where bears will establish in the future (Katajisto 2006). Managers should also be aware of the great impact that tourist developments have on bear distribution (Nellemann et al. in press).

The ethical aspects of conducting research on large carnivores
Management authorities and ethical committees give the permission to conduct research on free-living wild carnivores. Thus, it is in their interest to see that this research is conducted as ethically as possible and to know the effects that capture and research methods have on the animals. The SBBRP has participated in the development of a capture protocol for bears (Arnemo et al. 2005) and the testing of new immobilization drugs and doses (Arnemo et al. 2001, 2003). The SBBRP has prioritized efforts to make the capture of bears as safe as possible. These efforts have been successful, as the mortality rate during capture as declined from 3.8% prior to 1992 to 0.3% since 1992 (Arnemo et al. 2006). The SBBRP is currently conducting research on the physiological effects of capture and immobilzation and the long-term effects of surgically implanted radiotransmitters.

Practical help for managers in the field
The SBBRP has always been available to managers to provide practical help in the field, such as helping scaring away bears near habitation in both Sweden and Norway and giving courses for people involved in practical bear management, including those that examine shot bears. In addition, the SBBRP has assisted managers in both Sweden and Norway in the training of hunters and their dogs to follow the tracks of radiomarked bears (Kristoffersson et al. 2001). It is important that well trained tracker-dog teams are available to track down bears that are wounded by hunters or hurt in traffic accidents. Much of this practical work has been conducted in cooperation with the Swedish Wildlife Damage Center at Grimsö Research Station.

General information to the public
The members of the SBBRP spend a great deal of time informing the public about bears through lectures, interviews for the media, cooperating with journalists and film-makers, etc. The SBBRP has also published a large number of publications and reports in Swedish and Norwegian, including a booklet about bear ecology in Swedish (Sandegren & Swenson 1997). A popular-scientific book in Swedish and Norwegian is planned. The SBBRP maintains a website (www.bearproject.info) that gives much information in Swedish, Norwegian, and English. It receives about 700 visits per month. It is our impression that there is a great interest among the public about our results, and not only the results with practical application. The public seems also to be interested in bear social organization, sexually selected infanticide, denning behavior and physiology, colonization after the last Ice Age, etc. This seems to improve the acceptance of the bear by people, although we have no data to support our impressions. The project has also participated in producing an information compendium about the European brown bear (Linnell et al. 2002). The SBBRP plays an important role in the education of future large carnivore managers and researchers, as recommended by the International Review Committee (Boyce et al. 2002). To date, 47 Master-level theses and 7 PhD-level theses have been produced within the SBBRP. Many of these students are employed in positions of active large carnivore management in Sweden, Norway, and Italy. Others work in positions where they provide the public information about large carnivores. Five of the PhD students received postdoctorate positions to continue their research careers (the other two did not apply).

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THE SCANDINAVIAN BROWN BEAR RESEARCH PROJECT
Complete publication list to 15 March 2007

Summary:
A) Publications in peer-reviewed journals (74)
B) Books and book chapters (10)
C) Papers in nonrefereed publications (20)
D) Completed student theses (55)
E) Rapports to management agencies, etc. (63)
F) Popular publications (57)
G) Websites for the public (6)
H) Posters presented at proceedings (16)
In total, 300 entries

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Arnemo, J. M., P. Dypsund, F. Berntsen, S. J. Wedul, B. Ranheim & L. Lundstein. 1998. Bruk av implanterbare radiosendere på store rovdyr. **Norsk Veterinærtidsskrift** 110:799-803. (Use of implantable radio transmitters in large carnivores. In Norwegian)

Andersen, R. & J. Swenson. 1999. Wildlife and nature conservation in Scandinavia with special regard to large predators. Pages 59-67 in Natura 2000 Eine Chance für den Naturschutz Europas/A chance for nature conservation in Europe. **Schriftenreihe des Bundesministerium für Umwelt, Jugend und Familie,** Band 14/1999. Vienna.

Swenson, J. & F. Sandegren. 1999. Den svenske bjørnebestandens levedyktighet. Pages 85-90 in T. Ebenhard & M. Höggren, eds. Livskraftiga rovdjurstammar. **Centrum för biologisk mångfold, Skriftserie** 1. Uppsala, Sweden. (The viability of the Swedish brown bear population. In Norwegian)

Swenson, J. E. and F. Sandegren. 2000. Conservation of European brown bear populations: experiences from Scandinavia. Pages 111-116 in J. F. Layna, B. Heredia, G. Palomero and I. Doadrio, editors**. La conservación del oso pardo en Europa: un reto de cara al siglo XXI. Serie encuentros I.** Fundación Biodiversidad, Ministerio de medio ambiente, Madrid, Spain.

Dahle, B. 2000. Extensive illegal killing of brown bears in Sweden. **Intern. Bear News** 9(2):7.

Dahle, B. 2000. Large-carnivore white paper presented in Sweden. **Intern. Bear News** 9(2):8.

Arnemo, J. M. 2001. Reversible anaesthesia in brown bears. **DDA News** 2:8.

Swenson, J. E. 2001. Bjørnens tilbakekomst. **Det norske videnskaps-akademi, Årbok** 2000: 463-470. (In Norwegian: The return of the brown bear)

Arnemo, J. M., S. Brunberg, P. Ahlqvist, R. Franzén, A. Friebe, P. Segerström, A. Söderberg, and J. E. Swenson. 2001. Reversible immobilization and anesthesia of free-ranging brown bears (Ursus arctos) with medetomidine-Tiletamine-Zolazepam and Atipamezole: a review of 575 captures. **Proceedings of the American Association of Zoo Veterinarians, American Association of Wildlife Veterinarians, Association of Reptilian and Amphibian Veterinarians, and National Association of Zoo and Wildlife Veterinarians Joint Conference.** 2001:234-236.

Zedrosser, A. & B. Dahle. 2002. Brown bear attack in central Sweden. **Int. Bear News** 11:9.

Bjärvall, A. 2003. Stora rovdjur—samspel mellan forskning och förvaltning med björnen som exempel. Pages 13-20 *in* L. Terenius, Chefsredaktör. Icke-traditionella försöksdjur I forskningen. **Centrala försöksdjursnämnden, Skriftserie Nr. 48. Stockholm.**

Swenson, J. And F. Sandegren. 2003. A summary of results from the Scandinavian brown bear research project. Pages 186-189 *in* P. I. Danilov and V. B. Zimin, editors. **Dynamics of game animals populations in Northern Europe—Proceedings of the third international symposium**. Karel'skii Nauchnyi Tsentr RAN, Redaktsionno-izdatel'skii Otdel, Petrozavodsk, Russia.

D) Completed student theses (55)

(* indicates theses that have resulted in a publication, (*) indicates that work on a manuscript is underway or the manuscript has been submitted)

Doctorate level theses (7)

2003 * Bjørn Dahle, Norwegian University of Science and Technology, Trondheim. Dr. scient. (PhD) thesis: Reproductive strategies in Scandinavian brown bears.

2004 * Jon E. Swenson, Institut für Wildbiologie und Jagdwirtschaft, Universität für Bodenkultur Wien, Vienna, Austria. Habilitation (Dr.habil.) thesis: The ecology of an increasing brown bear population: managing a successful recovery.

2004* Alain Cercueil, Laboratoire des Techniques de l'Imagerie, de la Modélisation et de la Cognition & Laboratoire d'Ecologie Alpine, Université Joseph Fourier, Grenoble, France. Thèse d'université (PhD thesis): Contributions statistiques en génétique des populations.

2004 * Eva Bellemain, Agricultural University of Norway, Ås (PhD) and Université Joseph Fourier, Grenoble (Docteur); joint (co-tutelle) degree program. PhD thesis/thèse d'université: Genetics of the Scandinavian brown bear: implications biology and conservation.

2006 * Ole-Gunnar Støen, Norwegian University of Life Sciences, Ås. PhD thesis: Natal dispersal and social organization in brown bears.

2006* Andreas Zedrosser, Norwegian University of Life Sciences, Ås and University of Natural Resources and Applied Life Sciences, Viena. PhD thesis: Life-history strategies of brown bears.

2006* Jonna Katajisto, University of Helsinki. Dr. scient. (Doctor of Science) thesis: Habitat use and spatial population dynamics of brown bears (*Ursus arctos*) in Scandinavia.

Master of Science level theses (41)

1990 Marie Dahlström, Stockholm University. Undergraduate thesis (20 points): Licensjakten på björn 1981-89—en sammanställning. (License hunting of bears, 1981-89—a summary)

1993 Caroline Paulson, Veterinary College, Swedish University of Agricultural Sciences, Uppsala. Thesis. Immobilisering av brunbjörn. (Immobilization of brown bears)

1995 * Jens Thomas Sagør, University of Trondheim. Cand. scient. (Master of Science) thesis: Et studie av konflikten mellom bjørn og sau i perioden 1981-1993. (A study of the conflict between bears and sheep in the period 1981-1993).

1996 * Bjørn Dahle, Norwegian University of Science and Technology, Trondheim. Cand. scient. (Master of Science) thesis: Nutritional ecology of brown bears (*Ursus arctos*) in Scandinavia with special reference to moose (*Alces alces*)

1996 * Raili Ytterberg, Stockholm University. Undergraduate thesis (10 points): Do ants support the high reproductive rate in the Scandinavian brown bear (*Ursus arctos*) population?

1997 * Anna Jansson, Swedish University of Agricultural Sciences, Uppsala. Undergraduate thesis (20 points): Can a high protein availablility explain the high reproductive rate in the Scandinavian brown bear (*Ursus arctos*)?

1997 * Thomas Johansen, Norwegian University of Science and Technology, Trondheim. Cand. scient. (Master of Science) thesis: The diet of the brown bear (*Ursus arctos*) in central Sweden.

1998 * Inga-Lill Persson, University of Oslo. Cand. scient. (Master of Science) thesis: Brown bear *Ursus arctos* predator upon adult moose in Scandinavia: a study at two levels of scale.

1998 * Ole Opseth, Norwegian University of Science and Technology, Trondheim. Cand. scient. (Master of Science) thesis: Brown bear (*Ursus arctos*) diet and predation on moose (*Alces alces*) calves in the southern tiaga zone in Sweden.

1998 * Helena Busk, Swedish University of Agricultural Sciences, Uppsala. Undergraduate thesis (20 points): Brown bear (*Ursus arctos*) predation on moose (*Alces alces*) calves in a Swedish boreal forest.

1999 * Line Stabell, University of Oslo. Cand. scient. (Master of Science) thesis: Use of ungulates by brown brown bears *Ursus arctos* in Scandinavia: effects of area, season, sex, age, and individual.

2000 Torleiv Yli Myre, Agricultural University of Norway, Ås. Cand. agric. (Master of Science) thesis: Strategies for female brown bear (*Ursus arctos*) to avoid infanticide: activity patterns.

2000 * Andrea Friebe, Johann-Wolfgang Goethe Universität, Frankfurt am Main, Diplomarbeit (Master of Science) thesis: Das Winterverhalten und die täglichen Wanderungen von weiblichen Braunbären (*Ursus arctos*) in Zentralschweden.

2000 * Håkon Hustad, Agricultural University of Norway, Ås. Cand. agric. (Master of Science) thesis: The issuing of kill permits for brown bears in response to domestic sheep depredation in Norway, 1989-99.

2000 Beverly Ann Wilson, University of Stirling, UK. Master of Science thesis: Conservation management of the brown bear , *Ursus arctos*, in Scandinavia: using GIS and a habitat quality index to explain the temporal and spatial variation in sub-population core areas.

2000 Christer Zakrisson, Swedish University of Agricultural Sciences, Umeå. Undergraduate thesis (20 points): Do brown bear (*Ursus arctos*) females with cubs alter their movement pattern in order to avoid infanticidal males?

2000(*) Rikako Fujita, Swedish University of Agricultural Sciences, Uppsala. Undergraduate thesis (20 points): Bait-hunting for brown bear in Sweden: temporal and spatial occurrence and potential effects on the population.

2001 Wiebke Neumann, Universität Osnabrück, Osnabrück, Diplomarbeit (Master of Science) thesis: The brown bear *Ursus arctos* and berries in the Swedish boreal forest: exploiting a temporarily and spatially variable resource.

2001 Oddmund Rønning, Agricultural University of Norway, Ås. Cand. agric. (Master of Science) thesis: Spatial and temporal supply of berries and their use by brown bears in south-central Sweden.

2001 Valgerður Bjarnadottír, Swedish University of Agricultural Sciences, Uppsala. International Master of Science thesis: Brown bear (*Ursus arctos*) use of three berry species in central Sweden: do bears choose foraging plots based on the densities of berries?

2001 Kristin Høivik Fossum, Agricultural University of Norway, Ås. Cand. scient. (Master of Science) thesis: Brown bears (*Ursus arctos*) and berries: use of a spatially and temporally variable resource by bears of different age and sex.

2001 Jonna Katajisto, University of Helsinki, Helsinki. Master of Science thesis: Bed site selection of female brown bears (*Ursus arctos*) as a counter-strategy to avoid sexually selected infanticide by males.

2001 * Eva Bellemain, Université Claude Bernard, Villeurbanne, France. Master of Science thesis: Etude du système d'appariement de l'ours brun de Scandinavie. (Study of the Scandinavian brown bear mating system) (In Franch and English).

2001 Ander Larunbe Anderson, University of Stirling, UK. Master of Science thesis: Use of GIS to study brown bear, *Ursus arctos*, distribution in relation to habitat and traditional reindeer (*Rangifer tarandus*) herding in Scandinavia.

2002 Solveig Kristoffersen, University of Oslo, Oslo. Cand. scient. (Master of Science) thesis: Restricting daily movements as a counterstrategy against sexually selected infanticide in brown bears (*Ursus arctos*).

2002 Paul Antoni Nilsen, Agricultural University of Norway, Ås. Cand. scient. (Master of Science) thesis: Scandinavian brown bear (*Ursus arctos* L.) foraging on tempory and spatially variable berry resources in the boreal forest.

2002 Jessica Åsbrink, Swedish University of Agricultural Sciences, Uppsala. Undergraduate thesis: Parasites and metals in the Scandinavian Brown Bear (*Ursus arctos*). Study project from the Department of Pathology, No. 30.

2002 Lars Plahn, Swedish University of Agricultural Sciences, Uppsala. Undergraduate thesis (20 points): Avoidance of potentially infanticidal males by female brown bears (*Ursus arctos*): patterns of diel activity.

2003 Patrik Jigsved, Umeå University, Umeå. Undergraduate thesis (30 ECTS): Utilisation of berries by brown bears in the Scandinavian boreal forest.

2003* Knut Håkon Solberg & Ola-Mattis Drageset, Agricultural University of Norway, Ås. Cand. scient. (Master of Science) thesis: A test of methods to estimate brown bear (*Ursus arctos*) population size.

2004 Insa Bauhaus, Albert-Ludwigs-Universität, Freiburg, Germany. Diplomarbeit thesis: Factors for the use of carpenter ants (*Campanotus* spp.) on clear-cuts by Scandinavian brown bears (*Ursus arctos* L.).

2004 Eskil Nerheim, Agricultural University of Norway, Ås. Master of Science thesis: Futility of shooting brown bears *Ursus arctos* to stop sheep loss in Norway is confirmed.

2004* Marcus Elfström, Umeå University, Umeå. Undergraduate thesis (30 ECTS): Denning ecology of Scandinavian brown bears.

2004 Knut Madslien, Norwegian School of Veterinary Sciences, Oslo. Student thesis: Use of intraperitoneal radiotransmitters in yearling female brown bears; anesthetic and surgical procedures.

2005(*) Ingela Jansson, Swedish University of Agricultural Sciences, Umeå. Undergraduate thesis (20 points): A pilot study of brown bear (*Ursus arctos*) habitat use in central Sweden using GPS.

2005 Hanna Barck, Swedish University of Agricultural Sciences, Uppsala. Undergraduate thesis (20 points): Factors affecting foraging by brown bears *Ursus arctos* on carpenter ants, *Camponotus herculeanus*.

2005 Claudio Signer, University of Basel, Switzerland. Multi-level habitat analsis of female brown bears (*Ursus arctos*) in central Sweden.

2005(*) Therese Fosholt Moe, Norwegian University of Life Sciences, Ås. Master of Science thesis: Diel variation in habitat selection of female Scandinavian brown bears (*Ursus arctos*) in relation to resting and foraging behavor.

2006 Veronica Sahlén, University College London. Master of Science thesis: Female brown bear *Ursus arctos* use of an anthropogenic food source: a study from south-central Sweden

2006 Geir Rune Rauset, Norwegian University of Life Sciences, Ås. Master of Science thesis: Estimating individual kill rates on moose calves by brown bears based on GPS technology and GIS cluster analysis.

2006 Inger Marie Yri, Norwegian University of Life Sciences, Ås. Master of Science thesis: Seasonal and diel variation in road avoidance behaviour of female Scandinavian brown bears.

Bachelor of Science level theses (8)

1988 Paul Klute & Tom Erik Ness, Statens skogskole, Evenstad. Undergraduate report. Älvdalsbinna - arealbruk, forflyttninger og habitatbruk 1987. (Älvdalsbinna—use of area, movements and habitat use in 1987).

1989 * Arne Söderberg, Öster-Malma jaktvårdsskola. Undergraduate final reseach report: Mortalitet hos älgkalvar under sommaren. (Moose calf mortality in summer; In Swedish)

1992 Mats Ola Johnsson, Klarälvdalens Folkhögskola. Undergraduate two-year school final research report. Brunbjörn. En ankät undersökning över björnförekomst i Värmlands norra delar. Samt en sammanställning av det Svensk - Norska björnprojektet. (A questionnaire study of the occurrence of bears in northern Värmland and a description of the Swedish-Norwegian Brown Bear Project).

1995 * Andreas Norin, Klarälvdalen Folkehögskola. Undergraduate two-year school final research report. Studier av näringsval och rörelsemönster hos radiomärkta brunbjörnar (Studies of food selection and movement patterns of radio-market brown bears; In Swedish)
1997 Paul Anzjøn & Johan Henrik Castberg, Regional College in Nord-Trøndelag, Steinkjer, Norway. Undergraduate thesis: Omtalen av bjørn (*Ursus arctos*) i media i 1995. (Reporting about brown bears in the Norwegian media in 1995; In Norwegian).
1998 Pilivi Vaajakari, Omnivet. Undergraduate final report: Reproduktionen hos brunbjörnar i Sverige. (Reproduction into Brown bear in Sweden. In Swedish)
1999 Carina Sisell, Älvdalens naturbruksgymnasium. Undergraduate final report: Björnen, människan och turismen—går de att förena? (Bears, people and tourism—is it possible to combine them? In Swedish)
2005 Kent Ove Moren, Høgskolen i Hedmark Bachelor thesis: Brun björnens (*Ursus arctos*) habitatvalg:kantsoner og habitatdiversitet. (Habitat selection in brown bears (Ursus arctos): edges and habitat diversity. In Norwegian)

E) Rapports to management agencies, etc. (63)

Bjärvall, A., F. Sandegren, & P. Wabakken. 1988. Rapport 1 från det svensk-norska björnprojektet. **Rapport Svenska Jägareförbundet och Naturvårdsverket**. (Report 1 1988 from the Swedish-Norwegian Brown Bear Project. In Swedish)
Bjärvall, A., F. Sandegren, & P. Wabakken. 1988. Rapport 2 från det svensk-norska björnprojektet. **Rapport Svenska Jägareförbundet och Naturvårdsverket**. (Report 2 1988 from the Swedish-Norwegian Brown Bear Project. In Swedish)
Bjärvall, A., F. Sandegren, & P. Wabakken. 1989. Rapport 1 från det svensk-norska björnprojektet. **Rapport Svenska Jägareförbundet och Naturvårdsverket**. (Report 1 1989 from the Swedish-Norwegian Brown Bear Project. In Swedish)
Bjärvall, A., F. Sandegren, & P. Wabakken. 1990. Rapport 1 från det svensk-norska björnprojektet. **Rapport Svenska Jägareförbundet och Naturvårdsverket**. (Report 1 from the Swedish-Norwegian Brown Bear Project. In Swedish)
Bjärvall, A., F. Sandegren, & P. Wabakken. 1990. Rapport 2 från det svensk-norska björnprojektet. **Rapport Svenska Jägareförbundet och Naturvårdsverket**. (Report 2 from the Swedish-Norwegian Brown Bear Project. In Swedish)
Bjärvall, A., F. Sandegren, & P. Wabakken. 1990. Rapport 3 från det svensk-norska björnprojektet. **Rapport Svenska Jägareförbundet och Naturvårdsverket**. (Report 3 1990 from the Swedish-Norwegian Brown Bear Project. In Swedish)
Franzén, R., F. Sandegren, & P. Wabakken. 1991. Årsrapport från det svensk-norska björnprojektet. **Rapport Svenska Jägareförbundet och Naturvårdsverket**. (Report of the year 1991 from the Swedish-Norwegian Brown Bear Project. In Swedish)
Söderberg, A., F. Sandegren. 1992. Rapport 1 från det svensk-norska björnprojektet. Våra **Rovdjur Nr.2, Årg.9**. (Report 1 1992 from the Swedish-Norwegian Brown Bear Project. In Swedish)
Franzén, R., F. Sandegren, & P. Wabakken. 1992. Rapport 2 från det svensk-norska björnprojektet. **Rapport Svenska Jägareförbundet och Naturvårdsverket**. (Report 2 1992 from the Swedish-Norwegian Brown Bear Project. In Swedish)
Wabakken, P. A. Bjärvall, R. Franzén, E. Maartmann, F. Sandegren, & A. Söderberg. 1992. Det svensk-norske bjørneprosjektet 1984-91. **Norwegian Inst. Nature Res., Oppdragsmelding** 146. (The Swedish-Norwegian Bear Research Project 1984-91. In Norwegian)
Franzén, R., F. Sandegren, & P. Wabakken. 1993. Rapport 1 från det svensk-norska björnprojektet. **Rapport Svenska Jägareförbundet och Naturvårdsverket**. (Report 1 1993 from the Swedish-Norwegian Brown Bear Project. In Swedish)

Wabakken, P. & E. Maartmann. 1994. Slutrapport for bjørn-sauprosjektet i Hedmark 1990-93. **Norwegian Inst. Nature Res., Forskningsrapport** 58. (Final report for the bear-sheep project in Hedmark, 1990-93. In Norwegian)

Swenson, J. E., F. Sandegren, P. Wabakken, A. Bjärvall, A. Söderberg and R. Franzén. 1994. Bjørnens historiske og nåværende status og forvaltning i Skandinavia. **Norwegian Inst. Nature Res., Forskningsrapport** 53. (The historic and present status and management of the brown bear (*Ursus arctos* L.) in Scandinavia; in Norwegian with English summary).

Swenson, J. E., F. Sandegren, & P. Wabakken. 1994. Rapport 1 från det Skandinaviska Björnprojektet. **Rapport Svenska Jägareförbundet och Naturvårdsverket**. (Report 1 1994 from the Scandinavian Brown Bear Project. In Swedish)

Swenson, J. E., F. Sandegren, & P. Wabakken. 1994. Rapport 2 från det Skandinaviska Björnprojektet. **Rapport Svenska Jägareförbundet och Naturvårdsverket**. (Report 2 1994 from the Scandinavian Brown Bear Project. In Swedish)

Swenson, J. E., F. Sandegren, & P. Wabakken. 1994. Årsrapport från det Skandinaviska Björnprojektet. **Rapport Svenska Jägareförbundet och Naturvårdsverket**. (Report of the year 1994 from the Scandinavian Brown Bear Project. In Swedish)

Sagør, J. T., J. E. Swenson, and E. Røskaft. 1995. Bjørn og sauehold: Er det mulig å nå Rovviltmeldingenes målsettingene? (Bears and sheep husbandry: Is it possible to reach the goals in the Large Predator White Paper? In Norwegian). **Norwegian Inst. Nature Res., Fagrapport** 14.

Swenson, J. E., F. Sandegren. 1995. Årsrapport från det Skandinaviska Björnprojektet. **Rapport Svenska Jägareförbundet och Naturvårdsverket**. (Report of the year 1995 from the Scandinavian Brown Bear Project. In Swedish)

Swenson, J. E. 1995. How can research be an effective part of wildlife management?. Wirkungsvoller Naturschutz – Welche Rolle kann die SGW übernehmen? **Jahrestagung der Schweizerischen Gesellschaft für Wildtierbiologie (SGW) 1995**. S 4-9

Sandegren, F., S. Brunberg, J. Swenson & A. Söderberg. 1996. Rapport angående arbetet med björnhonan Koska och hennes ungar. **Rapport till länsstyrelsen i Dalarna**. 3 pp. (Report about work with the bear female "Koska" and her young. In Swedish)

Swenson, J. E., F. Sandegren. 1996. Björnlakten i Sverige – Några rekomendationer. **Rapport till Naturvårdsverket**.

Swenson, J. E., F. Sandegren & A. Söderberg. 1996. Utvärdering av björnobsen. **Rapport till Svenska Jägareförbundet**.

Swenson, J. E., F. Sandegren, M. Heim, S. Brunberg, O. J. Sørensen, A. Söderberg, A. Bjärvall, R. Franzén, S. Wikan, P. Wabakken, and K. Overskaug. 1996. Er den skandinaviske bjørnen farlig? **Norwegian Inst. Nature Res., Oppdragsmelding** 404. (Is the Scandinavian brown bear dangerous? In Norwegian)

Andersen, R., J. Linnell, and J. Swenson. 1996. Hovedrapport—Regionfelt Østlandet. Tema hjortevilt og rovvilt. **Norwegian Inst. Nature Res., Oppdragsmelding** 405. (Final report—Regionfelt Østlandet. Ungulates and carnivores. In Norwegian)

Aanes, R., J. D. Linnell, J. E. Swenson, O. G. Støen, J. Odden, and R. Andersen. 1996. Menneskelig aktivitets innvirkning på klauvvilt og rovvilt. En utredning foretatt i forbindelse med Forsvarets planer for Regionfelt Østlandet, del 1. **Norwegian Inst. Nature Res., Oppdragsmelding** 412. (The effect of human disturbance on ungulates and carnivores: a study undertaken in connection with the proposal by the Department of Defense to establish a shooting range in southeastern Norway, part 1, in Norwegian)

Linnell, J. D. C., B. Barnes, J. E. Swenson, and R. Andersen. 1996. Hvor sårbare er bjørner for forstyrrelser i hiperioden? En utredning foretatt i forbindelse med Forsvarets planer for Regionfelt Østlandet, del 2. **Norwegian Inst. Nature Res., Oppdragsmelding** 413. (How vulnerable are denning bears to disturbance? a study undertaken in connection with the proposal by the Department of Defense to establish a shooting range in southeastern Norway, part 2, in Norwegian)

Swenson, J. E., T. M. Heggberget, P. Sandström, P. Wabakken, A. Bjärvall, A. Söderberg, R. Franzén, J. D. C. Linnell, and R. Andersen. 1996. Brunbjørnens arealbruk i forhold til menneskelig aktivitet. En utredning foretatt i forbindelse med Forsvarets planer for Regionfelt Østlandet, del 5. **Norwegian Inst. Nature Res., Oppdragsmelding** 416. (Use of area by brown bears in relation to human activity: a study undertaken in connection with the proposal by the Department of Defense to establish a shooting range in southeastern Norway, part 5, in Norwegian)

Mysterud, I., J. E. Swenson, J. D. C. Linnell, A. O. Gautestad, I. Mysterud, J. Odden, M. E. Smith, R. Aanes, P. Kaczensky. 1996. Rovvilt og sauenæring i Norge: kunnskapsoversikt og evaluering av forebyggende tiltak. **Report, Biological Institute, University of Oslo, Norway.** (Carnivores and sheep farming in Norway: a survey of the information and evaluation of mitigating measures. In Norwegian)

Aanes, R., J. E. Swenson, and J. D. C. Linnell. 1996. Rovvilt og sauenæring i Norge. 1. Tap av sau til rovvilt: en presentasjon av tapets omfang basert på brukeropplysninger. **Norwegian Inst. Nature Res., Oppdragsmelding** 434. (Carnivores and sheep farming in Norway. 1. Loss of sheep due to large predators: a presentation of the magnitude of loss based on information from sheep farmers. In Norwegian)

Linnell, J. D. C., M. E. Smith, J. Odden, P. Kaczensky, and J. E. Swenson. 1996. Rovvilt og sauenæring i Norge (Carnivores and sheep farming in Norway). 4. Strategies for the reduction of carnivore—livestock conflicts: a review. **Norwegian Inst. Nature Res., Oppdragsmelding** 443. (In English)

Linnell, J. D. C., M. E. Smith, J. Odden, P. Kaczensky, and J. E. Swenson. 1996. Rovvilt og sauenæring i Norge (Carnivores and sheep farming in Norway). 5. Strategier for å redusere rovdyr-husdyr konflikter: en litteraturoversikt. **Norwegian Inst. Nature Res., Oppdragsmelding** 444. (In Norwegian with English summary)

Sæther, B.-E., S. Engen, J. E. Swenson, Ø. Bakke, and F. Sandegren. 1997. Levedyktighetsanslyser av skandinavisk brunbjørn. **Norwegian Inst. Nature Res., Fagrapport** 25. (Population viability analysis for the Scandinavian brown bear. In Norwegian).

Swenson, J. E., F. Sandegren. 1997. Årsrapport från det Skandinaviska Björnprojektet. **Rapport Svenska Jägareförbundet och Naturvårdsverket**. (Report of the year 1997 from the Scandinavian Brown Bear Project. In Swedish)

Linnell, J. D. C., J. E. Swenson, A. Landa & T. Kvam. 1998. Methods for monitoring European large carnivores—a worldwide review of relevant experience **Norwegian Inst. Nature Res., Oppdragsmelding** 549.

Linnell, J. D. C., J. E. Swenson, A. Landa & T. Kvam. 1998. Metodikk for bestandsovervåking av store rovdyr—en litteraturgjennomgang. **Norwegian Inst. Nature Res., Oppdragsmelding** 550. (Methods for monitoring European large carnivores—a worldwide review of relevant experience. In Norwegian)

Brunberg, S., S. Nordlund & F. Sandegren. 1998. Rapport om björnen W9705 Björe. The Scandinavian Brown Bear Research Project, Unpubl. Rept. (Report about the bear W9705 Björe. In Swedish).

Swenson, J. E., F. Sandegren. 1998. Årsrapport från det Skandinaviska Björnprojektet. **Rapport Svenska Jägareförbundet och Naturvårdsverket**. (Report of the year 1998 from the Scandinavian Brown Bear Project. In Swedish)

Swenson, J. E., F. Sandegren, A. Bjärvall, P. Wabakken, R. Franzén & A. Söderberg. 1998. Bjørneungers oppvekstvilkår: hvilke faktorer er viktige for overlevelse av årsunger? Pages

180-184 in NINAs strategike instituttprogrammer 1991-95: Store rovdyrs økologi i Norge, Slutrapport. **Norwegian Inst. Nature Res., Temahefte 8.** (In Norwwegian)

Swenson, J. E., F. Sandegren, P. Wabakken, A. Bjärvall, A. Söderberg R. Franzén & P. Segerström. 1998. Bjørneungers spredningsdynamikk. Pages 185-188 in NINAs strategike instituttprogrammer 1991-95: Store rovdyrs økologi i Norge, Slutrapport. **Norwegian Inst. Nature Res., Temahefte 8.** (In Norwwegian)

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Swenson, J. & F. Sandegren. 1999. Mistänkt illegal björnjakt i Sverige. Pages 201-206 in Bilagor till Sammanhållen rovdjurspolitik; Slutbetänkande av Rovdjursutredningen. **Statens offentliga utredningar** 1999:146. Stockholm, Sweden (Suspected illegal hunting of bears in Sweden. In Swedish)

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Bjärvall, A. & P. Ahlqvist. 1985. Första björnen med radiosändare. **Svensk Jakt.** 123:278-281. (The first bear with a radio transmitter. In Swedish)

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Bjärvall, A. & F. Sandegren. 1988. Vi behöver veta mer om björnen. **Dalajägaren 40 år**. Pp. 82-92. (We must know more about bears. In Swedish)

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Bjärvall, A. 1989. Björnens vandringar klarnar. **Svensk Jakt** 127:902-904. (The wanderings of bears become more clear. In Swedish)

Sandegren, F. & A. Söderberg. 1989. Provtagning på björn. **Svensk Jakt** 127:878. (Taking samples from bears. In Swedish)

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Swenson, J. E. and F. Sandegren. 1995. Brunbjörnens genetik i Skandinavien. **Svensk Jakt** 1995(5):493-497. (The genetics of brown bears in Scandinavia. In Swedish)

Söderberg, A. and J. E. Swenson. 1996. Björn på villovägar? **ABC Jakt** 10:6-7. (Lost bears? In Swedish)

Sagør, J. T. and J. Swenson. 1996. Sau i bjørneland—kilde til konflikt! Pp. 8-23 in K. H. Brox (ed.). **Natur 96/97.** Tapir forlag, Trondheim, Norway. (Sheep in bear country—the source of conflict! In Norwegian, Invited chapter)

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Swenson, J. 1988. Forebyggende tiltak mot rovdyrskader. Pp. 374-379 in **Husdyrforsøksmøtet 1998**, Norwegian Agricultural University, Ås. 709 pp. (Mitigating measures against predator depredation. in Norwegian)

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Söderberg, A., F. Sandegren & J. Swenson. 1999. En ovanlig vandringsväg. **Våra Rovdjur** 2: 8-9. (An unusual dispersal route. in Swedish)

Sandegren, F. & J. Swenson. 2000. Björnen som älgjägare. **Svensk Jakt** 2000(2/3):62-65. (The brown bear as a moose hunter. in Swedish)

Olson, J. E. 2000. **Är björnen farlig**? Björnprojektet i Orsa, Orsa. 24 pp. (Is the brown bear dangerous? In Swedish)

Swenson, J. E. 2000. Rovdyr og rovdyrforvaltning. Pp. 325-329 in I. S. Kristiansen, chief editor. **Store Norske Årbok 2000**, Kunnskapsforlaget, Oslo, Norway. 543 pp. (Large predators and their management; in Norwegian)

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Brunberg, S. 2000. Om du möter en björn. **Broschyr från Viltskadecenter.**
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Sandegren, F. & J. Swenson. 2001. Åteljakt på björn—bra eller dåligt? **Svensk Jakt** 2001 (2/3):64-65. (Bait hunting for brown bears—good or bad? in Swedish)
Hustad, H. & J. E. Swenson. 2001. Tildeling av skadefellingstillatelser på bjørn som tar sau. **Sau og Geit** 2001(5):60-63. (Issuance of kill permits for bears that kill sheep; in Norwegian)
Swenson, J. E. 2002. Nå våkner bjørnen! **Villmarksliv** 29(4):56-59. (Bears are waking now!; in Norwegian).
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Olson, J. E. 2004. **Lórso bruno é pericoloso?** Björnprojektet i Orsa, Orsa. 24 pp. (Is the brown bear dangerous? In Italian)
Katajisto, J.K. 2004. Näin pärjäät karhun naapurina, **Tiede** 3/2004 (Having bears as neighbour, Finnish science magazine, in Finnish).
Swenson, J., J. Kindberg, E. Bellemain, S. Brunberg & G. Ericsson. 2004. Björnstammen är större än man trott. **Våra Rovdjur** 2004(3):14-15. (The population of brown bears is larger than previously thought; in Swedish).
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Zedrosser, A. 2005. Mord, Intrigen und Sex. - Über die Partnerwahl bei Braunbären. **Österreichs Weidwerk** 6: 60-61. (Murder, intrigue, and sex—On mate choice in brown bears; in German)
Zedrosser, A. 2005. Bäriges. **Österreichs Weidwerk** 8: 46-47. (About bears; in German)
Zedrosser, A. 2007. Kindesmord zu Fortpflanzungszwecken. **Wildbiologie** 1/2007: 1-12. (Infanticide for the purpose of reproduction; in German)

G) Websites for the public (6)

Söderberg, A., F. Sandegren & J.E. Swenson. 1999. En ung björnhanes ovanliga vandringsväg. http://www.jagareforbundet.se/forsk/projekt/granis.html (A young male brown bear's unusual dispersal route. In Swedish)
Franzén, R. 2002. Ursus arctos brunbjörn. (Rev. Sven Brunberg & Jon Swenson 2002). ArtDatabanken, SLU: 2002-11-25. Tillgänglig URL: http://www-umea.slu.se/MiljoData/webrod/Faktablad/ursu_arc.pdf (2002-11-27).
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H) Posters presented at proceedings (16)

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Wabakken, P., A. Bjärvall & F. Sandegren. 1988. The Swedish-Norwegian bear study progress report. **11th Nordic Congress on Game Research**, Espoo, Finland.

Wabakken, P., A. Bjärvall & F. Sandegren. 1989. Radio-tracking Scandinavian brown bears: study progress report. **12th Congress of the International Union of Game Biologists**, Trondheim, Norway.

Arnemo, J. M., P. Dypsund, F. Berntsen, J. Schultze, S. J. Wedul, B. Ranheim & L.G. Lundstein. 1998. Implantation of intraperitoneale radiotransmitters in brown bears (Ursus arctos), wolverines (Gulo gulo) and lynx (Lynx lynx): anesthetic and surgical procedures for field use. **47th Annual Conference of the Wildlife Disease Association,** Madison, Wisconsin, USA.

Friebe, A., J. E. Swenson & F. Sandegren. 1999. Daily movements and denning ecology of female brown bears (*Ursus arctos*) in central Sweden. **33rd International Congress of the International Society for Applied Ethology**, Lillehammer, Norway.

Bellemain, E., J. E. Swenson, D. Tallmon, S. Brunberg, P. Taberlet. 2004. Brown bear population size estimates using DNA from hunter-collected feces: A comparison of different methods. **15th International Conference on Bear Research and Management**. San Diego, California USA

Schoettler, A., S. Brunberg. 2004 Testing methods used in activity studies. **15th International Conference on Bear Research and Management**. San Diego, California USA

Katajisto, J., A. Moilanen, J. E. Swenson. 2004. Brown bear distribution in relation to habitats and humans. **15th International Conference on Bear Research and Management**. San Diego, California USA

Zedrosser, A., B. Dahle, J. O. Vik, J. E. Swenson. 2004. Offpring abandonment and maternal defense as reproductive strategies in European brown bears. **15th International Conference on Bear Research and Management**. San Diego, California USA

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Katajisto, J., A. Moilanen, J. E. Swenson. 2004. The effect of conspecifics on brown bear movement inside their home ranges. **15th International Conference on Bear Research and Management**. San Diego, California USA

Zedrosser, A., G. Rauer, L. Kruckenhauser. 2004 Early primiparity in brown bears. **15th International Conference on Bear Research and Management**. San Diego, California USA

Hodder, D.P., Rea, R.V., and Zedrosser, A. 2004. Does the establishment of den site buffer zones have significant impacts on forestry economics? **15th International Conference on Bear Research and Management**. San Diego, California USA

Katajisto, J., A. Moilanen, J. E. Swenson. 2005. Kernel-based home range metod. For data with irregulare sampling interval. **16th International Conference on Bear Research and Management**. Riva Del Garda, Trentino Italy

Madslien, K., J. M. Arnemo, J. E. Swenson. 2005. Use of intraperitoneal radiotransmitters in yearling female brown bears. Anesthetic and surgical procedures. **16th International Conference on Bear Research and Management**. Riva Del Garda, Trentino Italy

Schoettler, A., S. Brunberg. 2005. Shift from diurnal to nocturnal behaviour: Influence of minimum temperature on night activity. **16th International Conference on Bear Research and Management**. Riva Del Garda, Trentino Italy

PUBLICATION PLAN

This publication plan includes publications that are in various phases of publishing and planning. The "planned publications" include those which we can write with the data available within the SBBRP, those that can be written with data that are gathered routinely (assuming that the project continues), and some that can be written with data from side projects that have been applied for.

Second revision sent in, waiting for final decision

Zedrosser, A., Dahle, B., Vik, J.-O., and Swenson, J. E. Abandonment and reduced maternal care as reproductive strategies in European brown bears. Revised manuscript sent to **American Naturalist**.

Elfström, M., Swenson, J. E., and Ball, J. P. Selection of denning habitats by Scandinavian brown bears. **Wildlife Biology**

Moe, T. F., Kindberg, J., and J. E. Swenson. The importance of diel behaviour when studying habitat selection; examples from female Scandinavian brown bears (*Ursus arctos*)**. Canadian Journal of Zoology.**

Ordis, A., J. Naves, A. Fernández, D. Huber, P. Kazcensky, A. Mertens, Y. Mertzanis, A. Mustoni, S. Palazón, P. Y. Quenette, G. Rauer, C. Rodríguez, and J. E. Swenson. Movement patterns of female brown bears with cubs in Europe: application to population monitoring. **Ursus**

Katajisto, J. and Moilanen, A. Estimation of habitat-weighted kernel home ranges. **Journal of Applied Ecology**

Submitted manuscripts

May, R., van Dijk, J., Wabakken, P., Linnell, J. D. C., Swenson, J. E., Zimmerman, B., Odden, J., Pedersen, H. C., Andersen, R. and Landa, A. Habitat differentiation within the large-carnivore community of Norway's multiple-use landscapes.

Swenson, J.E., Zedrosser, A., and Gossow, H. Human induced life-history changes promote conservation of brown bears.

Bischof, R., Swenson, J.E., Fujita, R., Zedrosser, A., and Söderberg, A. Hunting patterns, the ban on baiting, and harvest demographics of brown bears in Sweden.

Katajisto, J., Moilanen, A. and Swenson, J.E. Landscape level habitat use by brown bears (Ursus arctos) in relation to human distribution in Scandinavia.

Zedrosser, A., B. Dahle, O.-G. Støen, and J. E. Swenson. Primiparity, litter size and cub survival in a species with sexually selected infanticide, the brown bear.

Katajisto, J., Ovaskainen, O. and Swenson, J.E. The role of sexually selected infanticide in the reproductive biology of the brown bear (*Ursus arctos*)

Katajisto, J., Moilanen, A., Wiegand, T. and Swenson, J.E. Effects of targeted harvesting on Scandinavian brown bears

Planned papers

<u>Genetics</u>

MHC polymorphism in the brown bear and its association with mate choice, lead author E. Bellemain

Testing the theory of speciation: brown bears and the polar bears as a case study, lead author E. Bellemain

Heritability of morphometric and life-history traits in brown bear populations, lead author A. Valentini

Genome scanning for inferring intra- and interspecific differentiation between polar and brown bears, lead author A. Valentini

Resolving bear phylogeny by using markers under selection, lead author A. Valentini
The genetic impact of males is larger in small populations of large carnivores, lead author A. Zedrosser

Life history
The relative contribution of individuals to population growth in two wild brown bear populations, lead author A. Valentini
Use of pedigrees to understand the importance of individuals in populations, lead author A. Valentini
Are self confident bears better mothers? lead author O.-G. Støen
Lifetime reproductive success of male brown bears, lead author A. Zedrosser
Lifetime reproductive success of female brown bears, lead author A. Zedrosser
Comparison of patterns of lifetime reproductive success in North American and European brown bears, lead author A. Zedrosser
Longevity in brown bear populations and the potential impacts of humans on brown bear life history, lead author A. Zedrosser
Differences in the patterns of life history traits and mating system between large carnivores and ungulates, lead author A. Zedrosser
Differences in the patterns of life history traits and mating system of large carnivores, lead author A. Zedrosser
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