

**THE ECOLOGY OF AN INCREASING BROWN BEAR POPULATION:
MANAGING A SUCCESSFUL RECOVERY**

Jon E. Swenson

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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, Funk, Macdonald & Wayne 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, Herrero & Peyton 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, Dahle, Swenson & Gerstl 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, Gubar, Sokolov & Lobachev 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). It is interesting to note that brown bears have not been released 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, Swenson & Miller in press).

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 brings new problems to new areas, because the species predated on domestic livestock, predated on moose, thus competing with hunters, and cause fear because bears can be dangerous to people (Swenson, Sandegren, Bjärvall & Wabakken 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, Wabakken, Sandegren, Bjärvall, Franzén & Söderberg 1995). Because of this, there was a need for general knowledge about the ecology of the brown bear and managers needed specific knowledge about population dynamics, the mechanisms of population expansion, conservation genetics, the effects of hunting, and the bear as a predator on sheep and predator on moose. To meet these needs, a study of the brown bear has been conducted since 1984 in two study areas in Scandinavia, near the northern edge of the species' range, in the county of Norrbotten in Sweden, and near the southern edge of its range, in the counties of Dalarna and Gävleborg in Sweden and Hedmark in Norway (Fig 1).

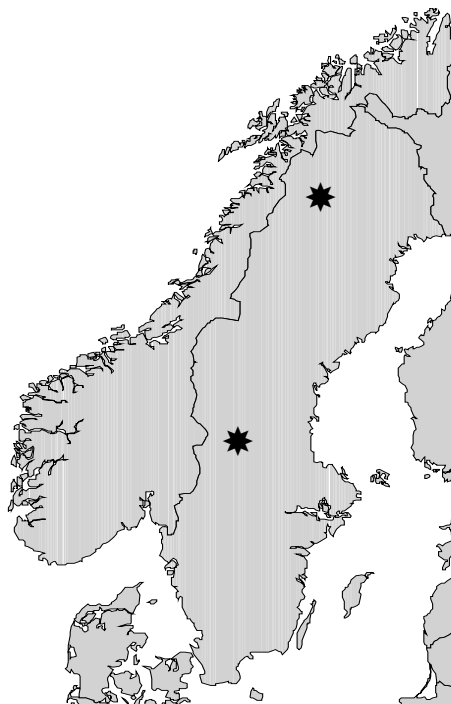


Fig. 1. Map of Sweden and Norway showing the centers of the northern and southern study areas of the Scandinavian Brown Bear Research Project.

This habilitation thesis is a summary of this work. It includes 24 scientific papers, which are organized into seven chapters, each of which describes an aspect of the ecology or management of brown bears in Scandinavia. There is a summary of each chapter following this introduction. The papers follow after the chapter summaries. They are referred to by bold numbers according to the list given below. The chapters and papers are:

I. The colonization of Scandinavia by brown bears

1. Taberlet, P., Swenson, J.E., Sandegren, F. & Bjärvall, A. 1995: Conservation genetics of the brown bear (*Ursus arctos*): localization of a contact zone between two highly divergent mitochondrial DNA lineages in Scandinavia. - *Conservation Biology* 9:1255-1261.

II. The decline and subsequent recovery of brown bears in Scandinavia

2. Swenson, J.E., Wabakken, P., Sandegren, F., Bjärvall, A., Franzén, R. & Söderberg, A. 1995: The near extinction and recovery of brown bears in Scandinavia in relation to the bear management policies of Norway and Sweden. - *Wildlife Biology* 1:11-25.
3. Swenson, J.E., Sandegren, F., Bjärvall, A., Söderberg, A., Wabakken, P. & Franzén, R. 1994: Size, trend, distribution and conservation of the brown bear *Ursus arctos* population in Sweden. - *Biological Conservation* 70:9-17.
4. Swenson, J.E., Sandegren, F. & Söderberg, A. 1998: Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. - *Journal of Animal Ecology* 67:819-826.

III. The demographic and genetic viability of the population

5. Sæther, B.-E., Engen, S., Swenson, J.E., Bakke, Ø. & Sandegren, F. 1998: Assessing the viability of Scandinavian brown bear, *Ursus arctos*, populations: the effects of uncertain parameter estimates. - *Oikos* 83:403-416.

6. Waits, L., Taberlet, P., Swenson, J.E., Sandegren, F. & Franzén, R. 2000: Nuclear DNA microsatellite analysis of genetic diversity and gene flow in the Scandinavian brown bear (*Ursus arctos*). - *Molecular Ecology* 9:421-431.

IV. Foraging ecology

7. Persson, I.-L., Wikan, S., Swenson, J.E. & Myrsterud, I. 2001: The diet of the brown bear in the Pasvik, Valley, northeastern Norway. - *Wildlife Biology* 7: 27-37.
8. Dahle, B., Sørensen, O.J., Wedul, E.H., Swenson, J.E. & Sandegren, F. 1998: The diet of brown bears *Ursus arctos* in central Scandinavia: effect of access to free-ranging domestic sheep *Ovis aries*. - *Wildlife Biology* 4:147-158.
9. Swenson, J. E., Jansson, A., Riig, R. & Sandegren, F. 1999: Bears and ants: myrmecophagy by brown bears in central Scandinavia. - *Canadian Journal of Zoology* 77:551-561.

V. Conflicts with human interests

10. Berger, J., Swenson, J.E. & Persson, I.-L. 2001: Recolonizing carnivores and naïve prey: conservation lessons from Pleistocene extinctions. - *Science* 291:1036-1039.
11. Swenson, J.E., Wallin, K., Ericsson, G., Cederlund, G. & Sandegren, F. 1999: Effects of ear tagging on survival of moose calves. - *Journal of Wildlife Management* 63:354-358.
12. Sagør, J.T., Swenson, J.E. & Røskaft, E. 1997: Compatibility of brown bear *Ursus arctos* and free-ranging sheep in Norway.- *Biological Conservation* 81:91-95.
13. Swenson, J.E., Sandegren, F., Söderberg, A., Heim, M., Sørensen, O.J., Bjärvall, A., Franzén, R., Wikan, S. & Wabakken, P. 1999: Interactions between brown bears and humans in Scandinavia. *Biosphere Conservation* 2:1-9.

VI. The management of bear hunting: not as easy as it seems

14. Tufto, J., Sæther, B.-E., Engen, S., Swenson, J.E. & Sandegren, F. 1999: Harvesting strategies for conserving minimum viable populations based on World Conservation Union criteria: brown bears in Norway. - *Proceedings of the Royal Society of London B* 266:961-967.
15. Swenson, J.E. & Sandegren, F. 1996: Sustainable brown bear harvest in Sweden estimated from hunter-provided information. - *Journal of Wildlife Research* 1:228-231.
16. Swenson, J.E., Franzén, R., Segerström, P. & Sandegren, F. 1998: The age of self-sufficiency in Scandinavian brown bears. - *Acta Theriologica* 43:213-218.
17. Swenson, J.E., F. Sandegren, S. Brunberg, and P. Wabakken. 1997: Winter den site abandonment by brown bears *Ursus arctos*: causes and consequences. *Wildlife Biology* 3:35-38.
18. Swenson, J.E. 1999: Does hunting affect the behavior of brown bears in Eurasia? - *Ursus* 11:157-162.
19. Swenson, J.E., Sandegren, F., Söderberg, A., Bjärvall, A., Franzén, R. & Wabakken, P. 1997: Infanticide caused by hunting of male bears. - *Nature* 386:450-451.
20. Swenson, J.E., Sandegren, F., Brunberg, S. & Segerström, P. 2001: Factors associated with loss of brown bear cubs in Sweden. - *Ursus* 12: 69-80.
21. Swenson, J.E., Dahle, B. & Sandegren, F. 2001: Intraspecific predation in Scandinavian brown bears older than cubs-of-the-year. - *Ursus* 12: 81-92.
22. Swenson, J.E. 2003. Implications of sexually selected infanticide for hunting of large carnivores. – Pages 171-189 in M. Festa-Bianchet and M. Apollonio, eds. *Animal Behavior and Wildlife Management*. Island Press, Washington, D.C.

VII. On managing large carnivores in human-dominated landscapes

23. Linnell, J.D.C., Swenson, J.E. & Andersen, R. 2000: Conservation of biodiversity in Scandinavian boreal forests: large carnivores as flagships, umbrellas, indicators, or keystones? - *Biodiversity and Conservation* 9: 857-868.

24. Linnell, J.D.C., Swenson, J.E. & Andersen, R. 2001: Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. - *Animal Conservation* 4: 345-349.

I. 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 may have diverged about 850,000 years ago (7% differences in control-region sequences, Taberlet & Bouvet 1994). Moreover, 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). We analyzed the pattern of occurrence of mtDNA more closely and found that there was a very clear and distinct contact zone between these two lineages. There are four female concentration areas in Scandinavia, based on the location of hunter-killed females (3), and the two female concentration areas separated by the mtDNA contact zone were 134 km apart. Bear densities are very low in this zone. No females were found to cross the mtDNA contact zone, which was separated by a distance that was much greater than the 95th-percentile dispersal distance observed for radio-marked females (1). However four males had crossed the contact zone, two from each lineage, although all were located within the 95th-percentile dispersal distance from the female concentration area where they supposedly originate. 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 agrestis*, 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 (1).

At about the time we published our results, Kohn, Knauer, Stofella, Schröder & Pääbo (1995) reported 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, fed, and then released in areas with lower densities of bear during the Ceaușescu regime (O. Ionescu, pers. comm.). If many of these survived and reproduced, it would in itself cause a geographic mixing of mtDNA lineages. Recently, Matsushashi, Masuda, Mano & Yoshida (1999) documented a clear geographic structuring of brown bears on Hokkaido Island. Three distinct lineages were found, which diverged from each other perhaps 0.5-1.0 million years ago, depending on the rate of molecular change that is used (mean genetic distances of the mtDNA control region of 2.0% and 3.7%). These lineages showed almost no overlap in distribution, similar to the situation we found in Scandinavia. Thus, the evidence to date suggests that brown bears form rather distinct boundaries between lineages when they meet, perhaps due to limited female dispersal into areas with high female bear densities (1). This phenomenon should be evaluated elsewhere where lineages meet and by intensive study of dispersal of individual females in relation to population density.

II. 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 (2). 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 disappeared first from the lowlands, and 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 1800's and beginning of the 1900's, 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. The effective efforts to save the bear from extinction were those related to the economics of killing bears by removing bounties and declaring all dead bears to be the property of the Crown (Sweden) (2). 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 (3). The brown bear was exterminated as a reproducing species in Norway, with the last Norwegian population disappearing in the 1980's (Bækken, Elgmork & Wabakken 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 (2). 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, Mysterud, Kvam, Sørensen & Wikan 1986). We updated a previous estimate of 620 bears for all of Scandinavia (3) 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 (2). The 1996 estimate was about 1000 bears in Scandinavia (Swenson & Wikan 1996).

Four population estimates in Sweden from 1942-1991 suggested an average population growth rate of 1.5% annually. In addition, the annual legal harvest was about 5.5% of the estimated population (3). This increase in population size was associated with an increase in distribution (2). How a brown bear population expands in distribution had not been documented prior to our study (4). In fact, female dispersal, which is necessary for an increase in distribution, has been considered to be rare in bears, at least in populations that were not increasing (Rogers 1987, Schwartz & Franzmann 1992, Reynolds 1993). 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%), which confirmed earlier results that males are the dispersing sex in bears. We used this finding to test the status of the bears in Norway. We found that in Norway 87% of the bears killed were males during 1973-93 and that 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 (4). This confirms our earlier findings (2), 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 (4). This was later also found in Finland, where the distribution is expanding (Kojola &

Laitala 2000), and distances of this magnitude have now been confirmed with radio telemetry (Swenson, et al. unpublished data). 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. Interestingly, a review of European brown bear populations showed that dispersal was rare in stable populations but common in increasing populations (4).

III. 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 quantitative element into risk assessment (Boyce 1992), although we must recognize that these predictions are often very uncertain (Caughley 1994). We investigated both the demographic and genetic viability of the Scandinavian brown bear population (5, 6).

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 (5). 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 predator 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 (5), 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, 1), 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, Gentile, Boscagli, Huber & Roth 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, Andr en, Larsson & Ryman 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 (6). Overall average and expected heterozygosities were 0.665 and 0.709, respectively, varying from 0.656 to 0.664 per subpopulation. Most partitioning of genetic diversity was attributed to diversity among individuals (93.3%). Diversity among subpopulations (2.0%) and between mtDNA phylogenetic lineages (2.7%) were relatively unimportant (6). 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 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 (5, 6). 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 (6), and recent work suggests that they should not be differentiated in management (S. Manel et al. unpublished results).

IV. 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 a comparison of European populations, Elgmork & Kaasa (1992) concluded that northern populations were more carnivorous than southern populations. 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, Schwartz, Robbins, Jacoby, Hanley, Arthur & Servheen 1999). Thus, knowledge of the diet of bears might help us understand the high population growth rate of Scandinavian brown bears (5). We studied the diet of brown bears, based on scat contents, in south-central Sweden (unpublished), central Sweden-central Norway (8), and far northeastern Norway (7). 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 (8). 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) (7). There were only very few sheep in this area during the study. Adult ungulates that were killed by bears were much more important in the bears' diet in the far north than in central Scandinavia (8) or in southern Norway (Elgmork & Kaasa 1992). This geographical difference in the importance of ungulates in the diet of bears has also been reported in European Russia (Danilov 1983) and Siberia (Krechmar 1995). Contributing reasons for this 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 (8).

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 by bears (9). 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. Among mound-building red forest ants, bears preferred the *F. aquilonia/polycytena* complex over *F. exsecta* and *F. lugubris*, perhaps because *F. aquilonia/polycytena* had larger mounds. Bears consumed 4000-5000 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.

V. Conflicts with human interests

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. 1998). Additionally, bears cause other problems, such as depredation on semi domestic reindeer in northern Scandinavia, destruction of beehives, etc. However, the bear is apparently a relatively unimportant predator on reindeer, taking mostly calves (Swenson and Andrén in press), and beehives can be protected quite adequately with electric fences. Also, the subjects mentioned first are those that seem to be most important in influencing the public's attitude towards bears.

Earlier studies in Scandinavia have documented that bears kill moose (Haglund 1968, Wikan 1996), but it 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 more than three times since Haglund's (1968) study (2, 3, Swenson & Wikan 1996) 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. 1998). We studied this bear predation on moose, using radio-collared moose in our southern study area for six years and compared our results with four other similar studies of radio-marked moose calves. Most of our results are yet only published as a Norwegian-language report (Swenson, Dahle & Sandegren 2001). However, we have compared the mortality of 175 control calves (unmarked) in two areas with bears and three areas without bears in Sweden and found a highly significant difference in mortality. In areas with bears, the calf mortality averaged 41%, compared with 11% without bears (11). Thus, we conclude that, in two areas with high densities of bears, the net loss due to bears was about 30% of the available calves.

We found that bears in the southern study area only killed about 1% of the available adult moose annually (Swenson et al. 2001). 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 (10). The results showed consistently and significantly 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 (10). 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. 2001).

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 in press). 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. As the Norwegian Parliament has decided in the first Large Predator Policy that the number of bears should increase and that depredation losses should decrease (Miljøverndepartement 1992, reiterated in the Second Large Predator Policy by Energi- og miljøkomitéen 1997, Miljøverndepartement 1997), we asked how realistic this was. 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, Swenson & Linnell 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 (12). 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 (12). 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, Dahle, Arnemo, Brunberg, Hustad, Nerheim, Sandegren, Solberg & Söderberg 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 (12).

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, Jägnert & Lundahl 1981, Dahle, Solberg & Sødal 1987). 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 and the circumstances of the attack (13). We found that bears usually left the area when meeting 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 (12).

VI. The management of bear hunting: not as easy as it seems

The hunting of bears has a long tradition in Scandinavia, and the population in Sweden has been hunted continuously since 1943 (2). 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 negative to the preservation of the species, as bear numbers and distribution have increased dramatically since hunting was reinstated (2, 3, 5). 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 kill bears that have killed sheep (12).

We are presently concluding a study of the rate of harvest that the Scandinavian brown bear population can sustain and still remain stable. However, 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 an area where conflicts are high, such as in Norway (14). Using the demographic values reported in (5) 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 of 34 female bears ≥ 1 year old (14). However, this number could be lower if a threshold harvesting strategy were used (Lande, Engen & Sæther 1995, Lande, Sæther & Engen 1997). Then 35% of the bears exceeding a threshold population of 12 females 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 estimates 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, Knight & Blanchard 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 wanted (14). In addition, genetic drift results in loss of variability at such low numbers and the population may lose the ability to track changes in the optimum phenotype and thus avoid extinction (Lande & Shannon 1996).

We know that there is a high error rate in reports of bear observations and sign from the public (Elgmork, Brekke & Selboe 1976), and that population estimates based on such observations can give gross overestimates (2). 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 ($r^2 = 83\%$) (15). The harvest rate that would stabilize the population, calculated from the regression equation, was similar to that obtained from other methods. However, the high correlation between hunters' impressions and harvest rate was with time lags of 6-14 years (15). It was not unexpected to find such a time lag, because it takes 10-15 years for a bear population's 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 (15).

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 the cubs survived well from about midsummer and for those surviving beyond their yearling year, we did not find that losing 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 (16), and this is now done in Sweden. Another indirect effect of hunting is disturbance of bears in winter dens by hunters after other game than bears during the winter. 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 (17). A minimum of 67% of these cases of den abandonment were caused by people, either hunters, forestry workers, fishermen or skiers. 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%) (17).

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. I undertook a review of the literature from Eurasia to examine this phenomenon. The results can not 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 (**18**). Fear of people can apparently be gained 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 (**18**).

Our studies have yielded yet another example of an indirect effect of hunting on bear populations, sexually selected infanticide (SSI) (**19-22**). 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. We used data from 1985-95 to test the following predictions arising from the SSI hypothesis retrospectively: 1) premature loss of cubs would shorten the interval to the subsequent estrus, 2) cubs would disappear (presumably die) during the breeding season, 3) cub survival would be lower following the killing of adult (≥ 5 years) males in the south, where hunters killed males during 1985-95, and 4) cub survival would be high in the north, where no males had been killed by hunters. Unmarked cubs were monitored by following their radio marked mothers. All the predictions were met (**19**). Time lags of 0.5 and 1.5 years were found between the killing of an adult male and elevated cub mortality. They were not whole numbers because males were killed in the fall and cub loss occurred the following spring. 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 (**19**). 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. Thus, there is a relatively short time for an immigrating male to become established in a vacancy from the dead adult male and to breed (**20**). In addition, a young male will probably have difficulty killing defended young, but can become more effective with increasing age.

Later we reanalyzed our data using all adult male deaths, not just hunting kills, and extended the period to 1998. We changed the study area definition from a composite area containing all females with cubs for all years to an area containing the home ranges of females with cubs for each individual year. We made spatial and temporal comparisons to examine whether nutritional, social (SSI), or den disturbance factors best explained the observed variation in cub survival (**20**). The loss of cubs at both the spatial and temporal levels of comparison was best explained by social factors. Nutrition did not seem to be important, because in both studies, cub loss was greater in years when the body mass of adult females and cubs (as inferred from yearling body mass in spring) was highest, contrary to what we expected (**19**,

20). Disturbance was only evaluated in the south and explained some variation in cub survival. In the north, few adult males died and 3 adult males lost early in the study were not replaced for many years, presumably due to little immigration of new males. In the south, 5 times as many males died annually, and in years with recorded adult male mortality, an average of 20% of the adult males died. The estimated number of adult males remained stable on the study area during this period, presumably due to immigration. The number of adult males dying 1.5 years previously in the area containing all radio marked females with cubs in a given year 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 most first bred successfully as 3-year-olds, 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 (**20**).

We also looked at the bear-caused deaths of subadult bears (1-4 years old) in relation to the death of adult males (**21**). Most yearlings separated from their mothers in May. We found area differences in the rates of intraspecific predation only for yearling females, which was higher in the south than in the north. 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 (**21**). Intraspecific predation on subadults was highest during the breeding season, as it was for cubs and was also reported by Mattson, Knight & Blanchard (1992). When I combined the results of our studies (**20**, **21**) and calculated population growth using a standard deterministic model (Ferson & Akçakaya 1990), I found that the loss of adult male(s) was associated with a 4.5% reduction in the population growth (**22**).

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 (**22**). In addition, we found that resident adult males are also infanticidal in a manner consistent with SSI. We tested the hypothesis that an increase in harvesting adult male bears would increase cub mortality. Because the southern population showed a 16% annual growth rate in 1985-95 (**5**), 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 (≥ 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 (**22**). Finally, 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 (Esbensperger 1998). We followed adult males and females with and without cubs intensively to determine whether the females with cubs exhibited any of the following counterstrategies to avoid meeting males: 1) avoiding males by a) different activity rhythms

than males, b) less movement during the breeding season, c) different use of habitat, and 2) by mating promiscuously. We found support for the hypothesized counterstrategies (22): 1a) 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. 1b) Females with cubs moved less than either males or females without cubs during the breeding season. One could argue that this is because cubs restrict female movement, but home range sizes of females with cubs were negatively correlated with population density (Dahle & Swenson in press). Thus, it is not only the cubs causing females with cubs to move less. 1c) Females with cubs used different habitats during the breeding season than those without cubs. Bed sites for females with cubs were located in areas with better visibility and more large Scots pine (*Pinus sylvestris*) trees. We observed several cubs that were saved from infanticide by climbing large pine trees, and that males killed cubs more often than expected in areas without large pine trees. 2) The females also mated promiscuously, because several litters had mixed paternity, as was also observed in Alaska (Craighead, Paetkau, Reynolds, Vyse & Strobeck 1995b). In Yellowstone, females have been observed to mate with up to 8 males during a breeding season (Craighead, Sumner & Mitchell 1995a). In conclusion, our results show that the three requirements for SSI are met in brown bears. Also 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. However, they do not use pregnancy block, as far as we know, group defense, or territoriality as counterstrategies.

Sexually selected infanticide is promoted by 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 (22).

VII. On managing large carnivores in human-dominated landscapes

I conclude this Habilitationsschrift on a philosophical note, with two papers dealing with the conservation of bears and other large predators in Scandinavia and Europe. 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 (23). This often involves using a single charismatic focal species, a “flagship” such as the brown bear, 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, Verner & Thomas 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 (species that impact other species far beyond what might be expected from a combination of their 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 semi domestic 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. 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 (23). 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, Aanes & Andersen 1995). 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 (23).

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 (24). 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 (24).

I believe that we can conserve the brown bear in human-dominated landscapes in Scandinavia and many other parts of Europe. The purpose of our studies have 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, Adamič, Huber & Stokke, in prep). 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 human-dominated landscapes for thousands of years, in contrast to the situation in North America. I hope than our research results will be useful to those managing and conserving brown bear populations elsewhere in Europe.

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