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THE World of Wolves

NEW PERSPECTIVES ON ECOLOGY, BEHAVIOUR AND MANAGEMENT

Edited by

MARCO MUSIANI,
LUIGI BOITANI,
AND PAUL C. PAQUET

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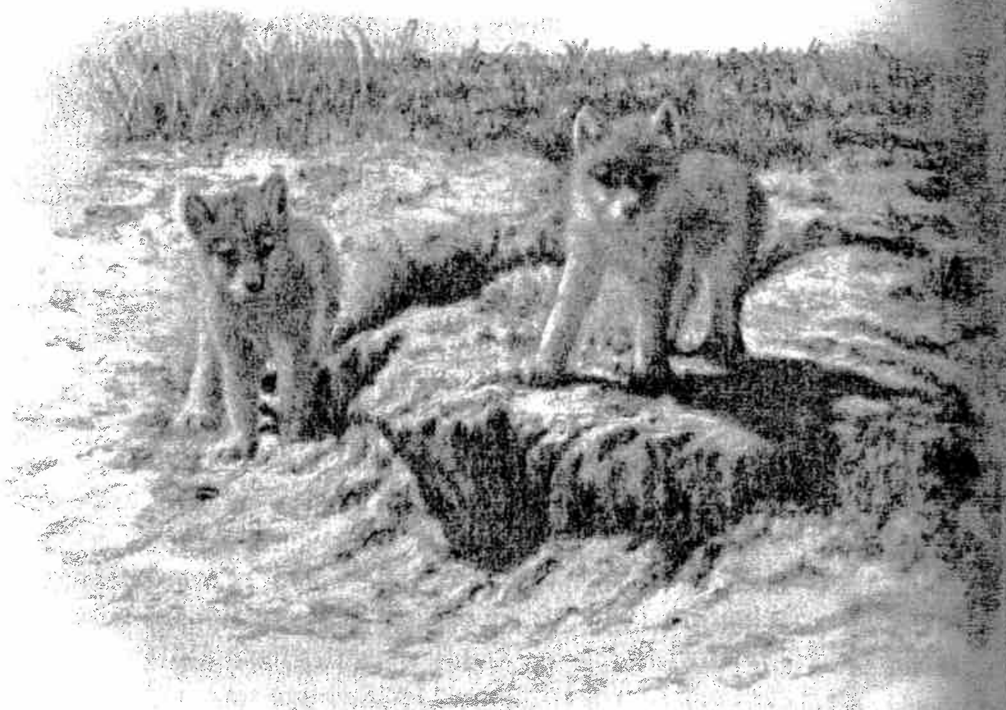

2.2 The Recolonizing Scandinavian Wolf Population: Research and Management in Two Countries

Olof Liberg, Åke Aronson, Scott M. Brainerd, Jens Karlsson, Hans-Christian Pedersen, Håkan Sand and Petter Wabakken

INTRODUCTION: TWO COUNTRIES WITH SIMILAR NATURAL BUT DIFFERENT CULTURAL, ECONOMIC, AND POLITICAL PRECONDITIONS FOR WOLVES

After a long period of persecution, the wolf (*Canis lupus*) has made a remarkable comeback in North America and Europe during the past few decades (Boitani 2003). An instrumental factor in this recovery has been an improvement in human attitudes toward wolves (Mech 1995). However, there is still a wide gap between the attitudes of urban and rural inhabitants toward this species (Skogen & Haaland 2001; Williams et al. 2002). The new challenge in wolf conservation is in striking a balance between both wolf and human interests, acceptable also to local people living with wolves and people living in cities (Mech & Boitani 2003a). This issue is especially critical in Europe, where there are no wilderness refuges large enough to harbour viable populations of large carnivores (Linnell et al. 2005a). Thus, wherever wolves settle on this continent, they will have to interact with humans (Promberger & Schröder 1993). If Europe is to accommodate its expanding wolf populations, we must find strategies that allow wolves and man to coexist (Linnell et al. 2001). Scientific research

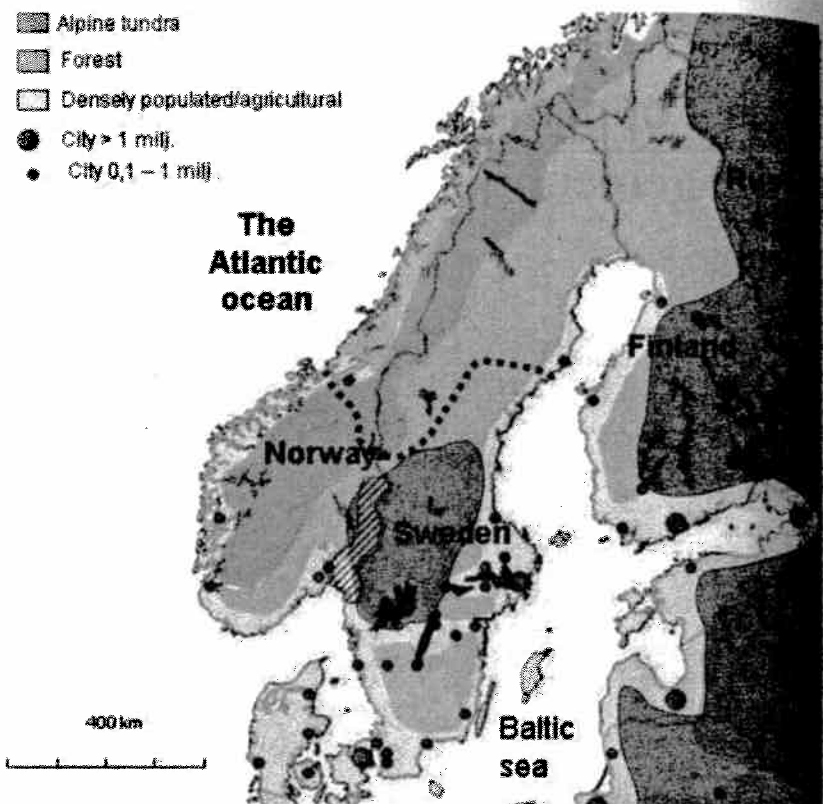

Figure 2.2.1. The Scandinavian Peninsula, with habitats and present distribution of the breeding wolf units (dark grey). The western portion of the range for the Finnish–eastern European wolf population is also indicated (in dark grey). The southern boundary of the reindeer grazing range in Scandinavia is indicated with dashed line. The Norwegian wolf zone is indicated by striped area.

has a key role in this process by providing a rational common ground for making difficult management decisions. However, this option has been poorly exercised thus far in Europe (Mech & Boitani 2003a).

Scandinavia and continental Europe share many common challenges regarding wolf recovery, although some aspects differ. Controversies with wolves and other large carnivores generally get worse in areas where they have been absent for extended periods before they return (Zimmermann et al. 2001), and this is also the case with Scandinavia (Wabakken et al. 2001; and see below). The Scandinavian Peninsula, shared by Norway and Sweden, might at a first glance seem well-suited for wolves. The human population density is low and there is a rich supply of wild ungulate prey and suitable habitat with forests comprising almost 60%, and alpine tundra another 25% of the Peninsula (Fig. 2.2.1).

However, most of these vast expanses are claimed by various stakeholders with potential or existing conflicts with wolves (Swenson & Andrén 2005).

In the north, the Sámi people continue their traditional rights to graze semi-domesticated reindeer (*Rangifer tarandus*) on 40% of the Peninsula, and claim that wolves are not compatible with this practice. In the west, Norwegian farmers release over two million sheep each spring to graze on the open range, with significant losses to predators (Swenson & Andrén 2005). Furthermore, most of the land in Scandinavia is private, with associated hunting rights of economic and social importance. Moose (*Alces alces*), the favoured prey of Scandinavian wolves (Olsson et al. 1997), is also the most important game species. Approximately 140,000 moose are harvested annually in Norway and Sweden (Lavsund & Sandegren 1989; Solberg et al. 2003), and the annual moose hunt is rivalled only by Christmas as the largest event of the year in rural communities. There is a conflict between hunters and wolves already around the competition for moose (Kojola 2000; Sand et al. 2006a), but the worst conflict is caused by the fact that wolves kill hunting dogs (Karlsson & Thoresson 2000; Ericsson & Heberlein 2003), as was found also in Finland, although there attacks on dogs were even more frequent near human residences (Kojola et al. 2004). Dogs for more than 100 years constituted a central part of the Scandinavian hunting traditions, and 10–20 dogs have been killed annually by wolves in recent years. This is not only an economic loss to the owner, but also an emotional. The violent death of what often is regarded as a dear family member, and in some cases a valuable hunting champion, is understandably a traumatic event.

Another important factor that influences the attitudes of rural inhabitants is the fear for human safety (Linnell et al. 2002; Skogen & Krange 2003). The mere presence of wolves has increased anxiety for the safety of women and children in particular. Today, many local inhabitants in the wolf range consider that the return of the wolf has seriously reduced their overall quality of life (Skogen & Krange 2003; Sjölander-Lindqvist 2006).

Scandinavian wolf management is further complicated by the fact that Norway and Sweden have rather different political and economic situations. Sweden is highly industrialized, and farming is strongly rationalized in large units, and rural society is proportionately small and thus of less political influence. Norway, on the other hand, has pursued a long-term policy of preserving and promoting its rural communities and culture by subsidies for small-scale agricultural practices. As a result, a greater proportion of the Norwegian population inhabits rural areas, and consequently is more politically empowered relative to its Swedish counterpart. In addition, Sweden is a member of the European Union and is bound to its strongly protective legislation for large carnivores, whereas Norway is not. Consequently, Norwegian wolf policy is more influenced by rural interests and less by those of nature protectionists as compared with Sweden.

These different situations in the two countries have led to different large predator policies. The Swedish wolf management policy is regulated by the Predator Act "En sammanhållen rovdjurspolitik" passed by the Parliament in 2001 (Swedish Ministry of Environment 2000). The Act states that a preliminary national goal is to reach a minimum of 20 breeding packs, and before this goal is reached, control of wolves (e.g., to reduce depredation or mitigate conflicts in other ways) should be kept to a minimum. Wolves shall be allowed to occur all over the country wherever there is suitable habitat, but with a restriction that breeding packs must not be tolerated in the reindeer summer grazing range (mainly the alpine areas). Norwegian predator policy is regulated by the Predator Act "Rovvilt i Norsk Natur" (Norwegian Ministry of the Environment 2003), passed by the parliament in 2004. The Act states that wolves primarily shall be tolerated within a specified "wolf zone" in southeastern Norway, along the Swedish border (Fig. 2.2.1). Within this zone there shall be allowed a minimum of three breeding packs, not including packs that partly use Swedish territory. When this goal is reached, control of additional wolves in the zone might be allowed if local authorities find it necessary to mitigate conflicts. Outside the zone, local governments may allow removal of wolves after they have received complaints, irrespective of whether the goal inside the zone is reached or not.

Because both countries share the same wolf population, these different policies have at times led to some political tension between the countries. On top of this, biological restrictions, including small population size (roughly 150 animals in spring 2006) and genetic vulnerability of this isolated wolf population, limit options available to managers.

In spite of these political differences, we have been fortunate to achieve a very close scientific co-operation between Norway and Sweden, which has been formalized through project SKANDULV. In this chapter we will first provide an overview of the results from our biological research on the Scandinavian wolf population, and then describe the efforts made to integrate these results into management of this population. There is also an extensive social science research on large carnivore issues in Scandinavia (e.g., Andersson et al. 1977; Bjerke et al. 1998; Kaltenborn et al. 1999; Skogen & Haaland 2001; Williams et al. 2002; Ericsson & Heberlein 2003; Skogen & Krange 2003; Sjölander-Lindqvist 2006), to which we refer whenever needed, but a separate treatment of this research is beyond the scope of this paper.

RESEARCH STRATEGY AND METHODS

The small Scandinavian wolf population has been continuously monitored by snow tracking since the first solitary wolves were detected in the late 1970s, at first by volunteers and later by professional field personnel (Wabakken et al. 2001). The need for close coordination of research activities in Norway and Sweden resulted in the establishment of the Scandinavian Wolf Research Project (SKANDULV) in January 2000, two years after scientific research was first initiated. SKANDULV is a consortium of independent projects based at seven universities in Sweden and Norway. A research coordinator facilitates close co-operation and the flow of information internally and externally. Field efforts are closely coordinated and all data are shared within the consortium. One Swedish and two Norwegian ecological projects comprise the core of SKANDULV, along with associated projects focusing on genetics, population modelling, veterinary medicine and pathology, sociology, and depredation. SKANDULV also has close co-operative ties with Finnish wolf researchers (Aronson et al. 1999; Pedersen et al. 2005; Wabakken et al. 2006).

Each winter 10–20 wolves are captured and equipped with radio-collars. Wolves are located by ground tracking on snow and then darted from a helicopter. Between 1998 and 2006 we have instrumented a total of 76 wolves, representing 110 "wolf years" (number of years each wolf was instrumented summed up for all wolves). The first wolves were fitted with VHF transmitters; however, we have exclusively used GPS transmitters since 2003. We have programmed GPS transmitters to record a minimum of 1–6 positions/day, and up to 54 positions/day for intensive predation studies. For genetic analyses, we have taken blood and tissue samples from live-captured wolves and from retrieved dead wolves, and faeces found during tracking (Liberg et al. 2005). We use telemetry and snow-tracking as primary methods in our research, including the annual population estimates. Analysis of mortality, movements, and predation is based on radio-telemetry (for details see Wabakken et al. 2001; Liberg et al. 2005; Sand et al. 2005, 2006a; Zimmermann et al. 2007).

MONITORING

Monitoring of wolf numbers and distribution is based on snow tracking (3000–4000 km each year), since 1998/99 complemented with telemetry, and since 2002/03 with DNA-analyses of primarily scats (Liberg et al. 2005; Wabakken et al. 2006). Snow tracking has been performed each winter from 1978/79 to present. This work started as a purely voluntary effort, and gradually became more organized and official with co-operation between Norway and Sweden beginning in 1981. In both countries, monitoring efforts have been financed by the governments. In Sweden, since 2002 the regional county boards (Sw. "länstyrelserna") have been officially responsible for these counts in their respective jurisdictions. In Norway, Hedmark University College has been subcontracted by the Norwegian Institute for Nature Research to census stationary wolves while personnel of the Norwegian Nature Inspectorate record non-stationary wolves.

An effort is made to find and distinguish all wolves in the population through the tracking work, but with an emphasis on stationary wolves. Over 100 field personnel, employed both full-time and part-time, search actively for wolf tracks on snow during the census period (1 October–28 February), and follow several thousand kilometres of wolf tracks each season. These are also assisted by volunteers and aided by reports from hunters and from the general public. Wolves are classified either as family groups (packs), scent-marking pairs, solitary stationary wolves, or solitary non-stationary (vagrant) wolves. We count the total number of wolves in each pack, and infer reproduction through the presence of pups. We employ DNA and telemetry techniques to distinguish between wolves in adjacent territories. Census data are entered into a government owned data base in Norway ("Rovbasen") and Sweden ("Rovdjursforum") respectively. In co-operation with SKANDULV, the monitoring institutions in each country have produced annual Scandinavian wolf status reports since 1999 (e.g., Aronson et al. 1999; Wabakken et al. 2006). Through co-operation with colleagues in Finland, data on Finnish wolf packs also were included in these reports.

GENETICS AND BREEDING HISTORY OF THE POPULATION

Breeding history and the construction of a pedigree

The Scandinavian wolf population is small and isolated, with a gap of 800 km between it and the nearest neighbouring wolf population in eastern Finland (Liberg 2005; Linnell et al. 2005; Fig. 2.2.1). These are typical preconditions for genetic problems (Shaffer 1981; Ebenhard 2000). Genetics thus have been central within this study from its start. Fortunately the DNA-technique was already well developed at that time. One of the first tasks of SKANDULV was to track the kinship relations of the population. Unfortunately, DNA-material from the early days of wolf re-colonization in the 1980s was scant. However, we combined records from snow tracking and other field data with DNA-profiles from the few wolves that were sampled during that era. Only one of these early samples belonged to a breeder, and the genotypes of the other breeders were reconstructed with aid of DNA from putative offspring. Thus, we reconstructed the breeding history of the population, starting from the first founders to present (Liberg et al. 2005). The result was one of the first complete pedigrees of a wild mammal population ever constructed (Fig. 2.2.2).

Wolves disappeared from the Scandinavian Peninsula by the end of the 1960s or early 1970's (Wabakken et al. 2001). The last confirmed breeding occurred in 1964, in northernmost Sweden. However, in the end of the 1970s there were persistent reports of wolves from the south-central part of the Peninsula, and in 1983 biologists recorded the first litter here. DNA analyses later revealed that both wolves in the breeding pair were immigrants from Finland/Russia (Vilà et al. 2003a; Liberg et al. 2005). The same pair continued to produce litters until 1985, when the female was killed by a sheep farmer. She is the only breeding wolf born before 1995 for which DNA material was preserved and later genotyped (Fig. 2.2.2). Her mate, whose tracks were distinguishable due to a deformed paw, disappeared the following spring. However, wolves again reproduced in this territory two years later, and genetic evidence implies that these breeders were siblings, offspring from the first breeding pair. Incestuous breeding by a sequence of various constellations of wolves continued within this pack until 1991, when we observed the first mating outside the original territory. A female, descended from the original pair, had dispersed northeast 250 km in 1985 (almost half the distance to the Finnish population), settled there and finally mated and bred there with an unrelated male ("Gh" in Fig. 2.2.2). We were able to reconstruct the genetic make-up of the two breeding wolves from DNA obtained from their offspring, and determined that the male in this pair was a new immigrant from the east

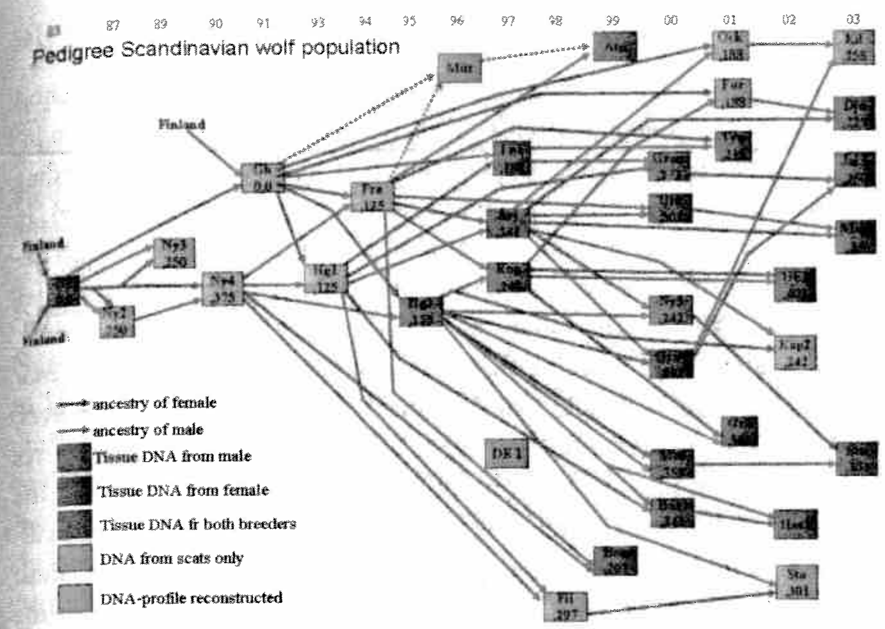

Figure 2.2.2. Pedigree of the Scandinavian wolf population. Abbreviations inside squares indicate the identity of the pair, figures indicate inbreeding coefficient (F) for the offspring of that pair. Arrows indicate the ancestry of the male and female in each breeding pair. Dashed lines indicate less secure ancestries. Arrangement of breeding pairs according to the time scale on top indicates first year of breeding for each pair. This figure and findings by Liberg et al. are also described by Wayne (see this volume, page 24).

(Liberg et al. 2005). He was the last wolf from the outside taking part of the Scandinavian breeding population. Thus, the Scandinavian wolf population is composed of the genes from only three founders, all from the larger Finnish/Russian population (Vilà et al. 2003a; Liberg et al. 2005). From this point onward, the number of breeding pairs increased rapidly (Fig. 2.2.2), although we so far have not been able to confirm any new immigrants (Liberg et al. 2005).

From 1998, when the wolf marking programme started, we got DNA directly also from breeders (Fig. 2.2.2). Four years later we started extracting DNA also from scats. This latter source has proven to be a very valuable tool that has enabled us to continually update the pedigree by genotyping almost every new breeder in the population.

Inbreeding depression

From the pedigree we have calculated inbreeding coefficients for almost all litters born, and documented a strong negative correlation between inbreeding coefficients and litter sizes (Liberg et al. 2005). This inbreeding problem is already limiting the growth of the population (see below). In addition to this, Scandinavian wolves tend to display an unusual high degree of presumably inherited malformations in the population (Räikkönen et al. 2006), although these have not been directly linked to inbreeding. Refined analysis have revealed that there is a strong selection (i = 0.245/generation; Lande & Arnold 1983) against the most homozygous wolves, such that for each level of inbreeding it is the most heterozygous wolves that are recruited into the breeding population (Bensch et al. 2006). The conclusion of this study is that this mechanism will retard the deteriorating effects of inbreeding, but not prevent them (Bensch et al. 2006). Thus, eventually there will be a need for further immigration of wolves from the Finnish/Russian population to our own. Although the distance is great (see above), we have recorded several dispersals matching the gap, including an 1100 km dispersal of a Scandinavian female to northern Finland near the Russian border. A significant barrier to interchange between these populations is the reindeer husbandry zones in Fennoscandia, since national policy in Norway, Sweden, and Finland and local cultures do not tolerate their presence or establishment due to depredation risks (Swedish Ministry of Environment 2000; Norwegian Ministry of the Environment 2003). We have identified several immigrants in northern Scandinavia by DNA analysis of scats and tissue samples, but so far all of these disappeared within a short time, most likely poached, before they could contribute to our gene pool. However, lethal control sanctioned by the government has also removed potential immigrants. In 2005, an immigrant wolf was killed by the Swedish management authorities only 200 km north of the current Scandinavian wolf breeding range. A possible remedy to this stalemate is by trans-locating wolves from Finland to Scandinavia – however, this is a controversial issue and is presently the subject of hot debate in Sweden.

DEMOGRAPHY

The Scandinavian wolf population is expanding in an environment that is favourable concerning resources (space and prey) but hostile concerning human tolerance. These aspects, as well as genetic problems, strongly influence its demography.

Reproduction and pack sizes

Number of reproducing packs per year has increased from one in 1990 to 15 in 2005 (Wabakken et al. 2006). Litter sizes are recorded on snow during winter. We limit our estimates to first-born litters only as it is impossible to differentiate between pups of the year and older siblings from tracks (Wabakken et al. 2001). For the whole study period 1983–2005 the average winter litter size was 3.9 (range 0–8). During 1991–1997 the average winter litter size was 4.2, which is in the lower part of the range reported in the literature (Fuller et al. 2003). Thereafter, the average litter size however has declined, to 3.9 during 1998–2001, and later to 3.4 for the period 2002–2005. This decline is most likely the result of ongoing inbreeding depression (Liberg et al. 2005). Winter pack sizes have averaged 6.1 wolves (range 3–11, pairs not included) for the entire study period, which corresponds well to the average reported for a large number of North American wolf populations living on deer and moose (Fuller et al. 2003), but is well above the level reported for another newly established expanding wolf population (Wydeven et al. 1995).

Survival

Our survival estimates are based on 76 wolves that we have radio-marked since December 1998. Overall annual survival was 0.67 for the period 1999–2006 (n = 110 "wolf years"). This does not include pup survival between birth and the winter marking period in January–March. Territorial animals had a survival rate of 0.78, while subordinate adult pack members had a survival of 0.61 and survival of dispersing animals was as low as 0.22. Poaching was the strongest single mortality factor, causing

58% of total mortality, while legal killing comprised 14%, traffic 11% and natural causes (disease, age, trauma) another 17% of total mortality. We could not find any time trend in the survival estimates during the period 1999–2006. However, based on annual population and recruitment estimates, we could deduce an annual overall survival rate for the pre-marking period of 1991–1999. For this early period we cannot differentiate between mortality factors, but the total survival of 0.79 was clearly higher than the 0.67 as estimated for the radio-monitoring period 1999–2006. The former figure is typical for a non-harvested wolf population, (Ballard et al. 1987; Hayes & Harestad 2000), while the latter corresponds well to the average for many wolf populations in North America (Fuller 1989a; Fuller et al. 2003), although well above the level typical for declining populations (Ballard et al. 1987).

Population Growth

The winter population size has grown from 2–4 animals in 1982/83 to 150 animals in 2005/06 (Fig. 2.2.3). For our calculations of annual growth rate, we have not included the period 1983–1990, when only a single family existed and the population was stagnant. After the second pair bred in 1991, the wolf population grew nearly continuously with an average annual lambda over the whole period of 1.17. During the 1991–97 period this rate was 1.31 but declined to 1.16 during 1997–2002 and further to 1.12 during 2002–2006. Considering the situation of this wolf population, with adequate prey and large tracts of unoccupied habitat (Wabakken et al. 2001; Sand et al. 2006b), a steadier increase in growth rate could be expected. We believe the main reason is a combination of the reduced survival rate due to illegal killing, and declining litter sizes due to the progressing inbreeding (see above). However, preliminary population simulations, based on these data, predict continued positive population growth over the next 30–40 years if no additional problems occur, e.g., an increase in the rate of illegal killing, or more inbreeding effects than those already accounted for (Forslund et al., unpublished data).

DISPERSAL – TERRITORY ESTABLISHMENT

Typically, Scandinavian wolves disperse at an early age and may disperse long distances. By May 2005, we had radio-collared 17 pups for which we also have information until 3 years of age. Out of these 17 young wolves, 15 (88%) dispersed, all of them as pups (13%) or yearlings (87%) (Fig. 2.2.4). Nine (60%) of these 15 dispersed from their natal territory as 10–14 months old, i.e., during March–June. The two non-dispersers (female siblings) budded as yearlings from their natal pack after their father was illegally killed and their mother failed to hold the territory without a new partner. Dispersal ages of Scandinavian wolves are similar to what was found for dispersing wolves in Finland (Kojola et al. 2006) and north-eastern Minnesota (Gese & Mech 1991), but are lower than reported in most North American studies, where the average dispersal age ranged between 2.5 and 3 years (Mech & Boitani 2003b).

A record straight-line dispersal distance of nearly 1100 km was set by a female wolf which traversed across Fennoscandia from southeastern Norway to the northeast part of the Finnish-Russian border. However, long range dispersers (> 300 km; N=23) were predominately males (87%), and most of them did not succeed to reproduce. Among 68 successful breeders (even sex ratio), there was no significant difference in dispersal distance between females (130 km, range 15–345 km) and males (167 km, 34–422 km). The low dispersal age and the long distance dispersals of Scandinavian wolves may be explained by low wolf densities, good supply of ungulate prey, and large expanses of vacant habitat (Wabakken et al. 2001).

So far, no group dispersal is confirmed, and no disperser has been verified to join an already established pack in Scandinavia. An individual disperser settles in a vacant area or a territory already established by an individual of opposite sex. In most cases, the female settles before the male.

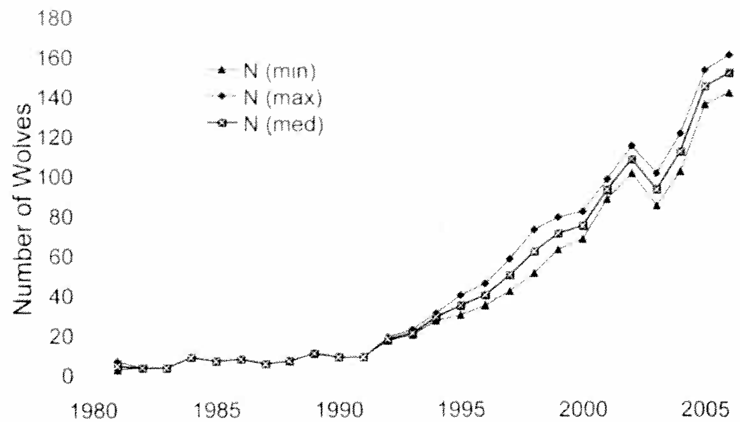

Figure 2.2.3. Dynamics of the Scandinavian wolf population 1981–2006. Data show number of wolves counted during winter.

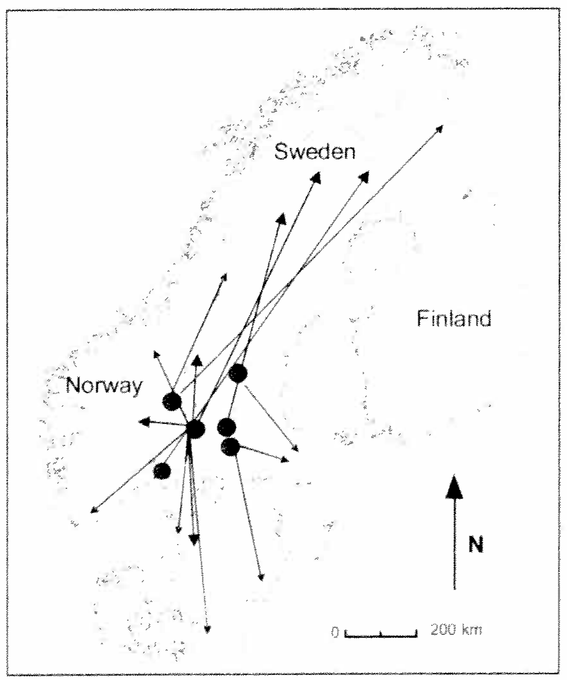

Figure 2.2.4. Long range dispersals in 15 wolves during 1984–2004 in Scandinavia. Black circles indicate natal territories. Arrows indicate the place where the wolf was found dead or where faeces were found that could be identified with aid of DNA-analyses.

PREDATION AND IMPACT ON WILDLIFE AND HUNTING

Prey choice

Several ungulate species are available for the wolf in Scandinavia. The moose (*Alces alces*) occurs in high densities (0.5–2.0 / km^2) over most of the Peninsula, whereas the roe deer (*Capreolus capreolus*) reaches high densities (2–10/ km^2) only in the southern half of it. Semi-domestic reindeer (*Rangifer tarandus*) only occurs in the northern third of the Peninsula, whereas the wild variant is limited to alpine habitats in southern Norway. Local populations of red deer (*Cervus elaphus*), fallow deer (*Dama dama*), and wild boar (*Sus scrofa*) are found in fragmented populations in southern Sweden, and red deer also occur on the west coast of Norway, all generally outside the present wolf range.

The moose constitutes the primary prey both in terms of numbers killed (>75%) and by kg biomass ingested (>95%) by wolves in Scandinavia (Olsson et al. 1997; Sand et al. 2005) (Fig. 2.2.5). The roe deer is the next most important ungulate prey and is the primary species consumed by wolves in territories where roe deer densities are high relative to those of moose. Wolves also consume small game species such as beaver (*Castor fiber*), badger (*Meles meles*), mountain hare (*Lepus timidus*), and capercaillie (*Tetrao urogallus*) and black grouse (*Tetrao tetrix*). In addition, wolves occasionally depredate livestock, primarily reindeer and domestic sheep (*Ovis aries*).

Moose calves comprise between 39% and 93% of all kills, depending on the pack sampled. Calf occurrence in diet was not correlated with the age distribution in the local moose population, which indicates that packs may learn different hunting strategies. The high proportion of calves in wolf kills during winter in Scandinavia compared with North American studies (13–56%; Mech 1966; Haber 1977; Peterson 1977; Peterson et al. 1984; Mech et al. 1998) may be explained by both a stronger selection for this age class and a higher proportion of calves in the living winter population (15–30%). Compared with human harvest, more calves, less prime-aged

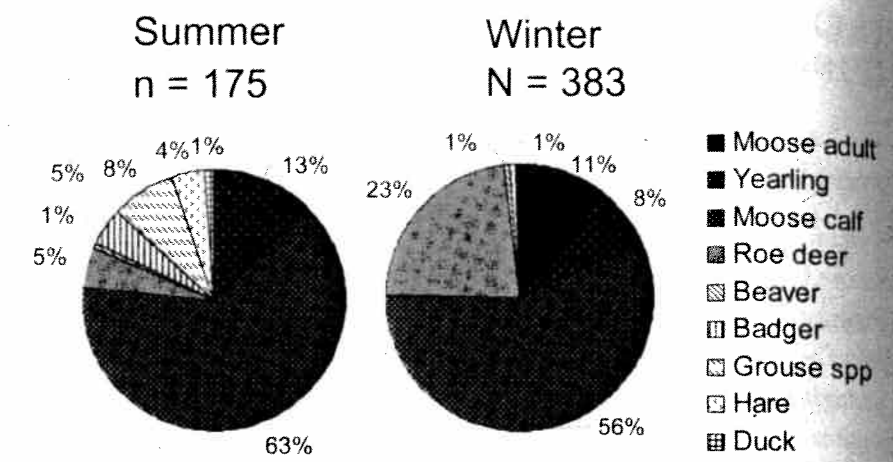

Figure 2.2.5. Number and type of wolf killed prey found during study periods in winter and summer 1999–2004 in Scandinavia.

(2–10 years), and older (≥11 years) moose were killed by wolves, whereas yearlings were killed in similar proportions by wolves and hunters. This pattern of age selection of moose by Scandinavian wolves corresponds well to results from North American studies (Mech 1970; Mech et al. 1998; Hayes et al. 2000).

Kill rates

We studied wolf predation behaviour in detail with the aid of GPS radio-transmitters in >15 packs in Scandinavia. We applied a novel technique based on combining downloaded GPS data with GIS analyses in order to find all ungulate kills during intensive study periods during both summer and winter by using a schedule of hourly (winter) or half-hourly (summer) positions.

Winter kill rates of moose in Scandinavia was almost two moose killed per week/pack or 4–5 moose killed/wolf/100 days, which roughly corresponds to 5–10 kg biomass meat available/wolf/day (Sand et al. 2005). This kill rate in terms of *number of moose* killed per time unit during winter is higher (30–110%) than generally reported in the American literature (Peterson et al. 1984; Ballard et al. 1987, 1997; Thurber & Peterson 1993; Messier 1994; Hayes et al. 2000). The higher kill rate in Scandinavia compared with North America may best be explained by the higher proportion of calves in the kill and thus a lower amount of consumable biomass per moose killed.

Few studies have reported wolf kill rates for the summer period (but see Jedrzejewski et al. 2002). By visiting the majority (>90%) of GPS positions received from one or both of the breeding wolves in various packs, and by using dogs in the field for finding prey killed, we were able to obtain data on kill rates for the summer period (June–Sept). During this season, wolves displayed an even higher preference (90%) for calves (1–4 month old) than during winter. Total kill rates were 56–73% higher than during winter, although decreasing with time as calves grew larger during the summer. Biomass available to wolves was on average of 5–6 kg/wolf/day. As a result of the high summer kill rate, as much as 40–50% of the total annual moose kill may occur during the 4-month period June–September. Since most calf predation during summer is additive in Scandinavia, this may be an important factor limiting moose population growth within wolf territories.

Interestingly, most moose carcasses were not totally consumed by wolves and were usually abandoned within 24–36 hours after killing (Sand et al. 2005). A total time of 1.25 days near their killed prey corresponds to approximately 10–70% of the average handling time reported for wolves preying on moose in North America (Fuller & Keith 1980; Messier & Crête 1985; Ballard et al. 1987, 1997; Hayes et al. 2000). Variation in pack size was not a likely cause to this variable pattern since the handling time of prey was not related to pack size in Scandinavia. Our GPS data indicated that the wolves tended to kill and feed upon larger prey such as moose mainly during the dark hours and that they normally rested during daytime several kilometres away from carcasses between feeding bouts. Thus, short handling time, incomplete consumption of carcasses, and resting far from killed prey is a typical pattern for wolves in Scandinavia. This may be an adaptation for minimizing encounters with humans in Scandinavia, previously and presently the main mortality factor of wolves. A dense forest road system (1–1.5 km/km^2) combined with a higher human population density makes wolf areas more accessible in Scandinavia compared with many wolf areas in North America. Alternatively, or additionally, this typical pattern may be caused by the high availability (density + behaviour) of their main prey species (see below). Several studies have shown wolves use carcasses less when prey is easy to kill (Carbyn 1983; Bobek et al. 1992).

Impact on moose population and harvest

The present knowledge of wolf predation on moose has mainly emerged from studies in North America (Ballard & Van Ballenberghe 1998). Wolf predation has been found to constitute everything from a slight (e.g., Ballard et al. 1987) to a major (Boutin 1992; Orians et al. 1997; Ballard & Van Ballenberghe 1998) limiting factor for moose populations. The varying impact may reflect a genuine variation among areas and years due to variation in moose density (e.g., Messier 1994), wolf pack size (Hayes et al. 2000), wolf/moose ratios (Vucetich et al. 2002), prey age structure (Peterson et al. 1984; Ballard et al. 1987), and varying supply of alternative prey (Messier & Crête 1985).

In most of Scandinavia, predation on moose by large carnivores (wolves and brown bears) has been absent during the last century. The lack of top-down limitation by large carnivores, combined with restrictive hunting regulations, resulted in a dramatic increase in the moose population during the twentieth century (Cederlund & Markgren 1987; Østgård 1987; Lavsund et al. 2003). Human harvest became the main limiting factor of moose during this time (Cederlund & Sand 1991; Solberg et al. 1999, 2003). Today the average density of moose in southern and central Scandinavia is >1 moose/km^2 with an annual population growth (λ) before harvest of 1.35–1.45 in most areas (Solberg et al. 2003).

The impact of wolf predation on the total Scandinavian moose population is at present very limited. In 2003 hunters harvested approximately 140,000 moose annually in Scandinavia. This represents about 25–30 % of the pre-hunt moose population (Solberg et al. 2003), which numbers about 450,000–500,000 moose. In 2005, 150 wolves distributed over 28 wolf territories were estimated to have killed approximately 3500 moose/year in Scandinavia, which corresponded to approximately 2.5% of the total annual human harvest. In comparison, estimated traffic mortality (automobiles and trains) corresponded to 4–5% of the annual harvest.

In Värmland, the province of highest wolf density in Sweden (7 wolf packs or pairs with 34 wolves over 17 000 km^2 = 2 wolves/1000 km^2), wolves killed approximately 840 moose in 2005 compared with 9200 moose killed by hunters and an additional 400 moose killed by traffic. If we conservatively assume that mortality from other causes, such as malnutrition, disease, and bears, is equal in size to traffic mortality (probably an underestimation), harvest accounted for 82.5 % and traffic for 3.9 % of moose mortality in Värmland that year, whereas wolf predation was responsible for 9.7 % of mortality (probably an overestimation).

For local moose management in Scandinavia with wolf territories patchily distributed it may be more relevant to estimate the effects of wolf predation within actual wolf territories than over larger areas. At this geographical level, depending on factors such as the local moose density (0.5–2.0 km^2) and productivity, as well as wolf territory size (500–1500 km^2), wolf predation *per se* may account for 15–100 % of the total annual growth (λ) in the moose population. However, even within most wolf territories current estimates of predation does not exceed 50% of the annual production of moose.

Based on predator-prey studies from Scandinavia, Europe, and North America we argue that the expected impact of wolves on moose in the future will continue to be low compared with other human activities (harvest, traffic mortality). This assumption may be explained by a low density of wolves far below saturation and with relatively large, non-contiguous territories, partly resulting from an active management regime currently aiming at controlling the wolf population far below their biological carrying capacity. The assumption of low impact of wolves on moose is also corroborated by the fact that the moose population in most parts of Scandinavia continues to have a high density and productivity. However, locally in areas with low density and productivity of moose coinciding with high densities (small territories) of wolves, the impact from wolf predation may turn out to be the dominating mortality factor, sometimes even exceeding the annual production of moose.

Hunting success

Scandinavian wolves are highly successful moose predators. Average hunting success was 50–60% counted on moose groups attacked, and 26% counted on number of individual moose involved in the attack (Sand et al. 2006a). This is roughly 3–4 times higher than reported in North America (Mech 1966; Haber 1977; Peterson 1977; Peterson et al. 1984; Mech et al. 1998) (Fig. 2.2.6). Furthermore, Scandinavian moose seldom stand their ground when attacked by wolves as compared with their conspecifics in North America. Chase distances in Scandinavia were short (average 50–100 m) with some moose even being killed while lying down. We have found no evidence that moose have adjusted to wolf presence by changing their anti-predator behaviour even in areas where wolves have occurred continuously for 10–20 years since their re-colonization. It seems that moose behaviour toward wolves, but also toward humans, in Scandinavia differs from North America. Aggressive behaviour toward humans has frequently been reported for North American calf-rearing female moose (Geist 1963; Mech 1966, 1970; Peterson 1977; Franzmann & Schwartz 1998; Mech et al. 1998). In Scandinavia, aggressive behaviour by calf-rearing females toward humans is extremely rare (Ekman et al. 1992; Sand et al. 2006a). We conclude that Scandinavian moose have not regained an efficient anti-predator behaviour toward recolonizing wolves as swiftly as has been seen in North America. We argue that the reason for this difference is the longer period of separation between the two species in Scandinavia, the longer and much more intensive human harvest of moose compared with any North American area, and perhaps even the use of baying dogs as a common hunting method in Scandinavia (Sand et al. 2006a). Whether this will just cause a delay in readjustment, or whether selection and/or drift have completely eliminated some of the genetic basis for this behaviour in the Scandinavian moose population remains to be seen.

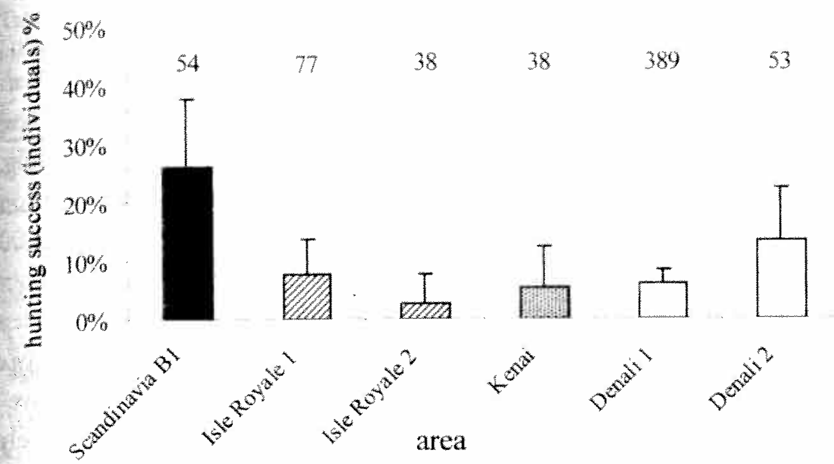

Figure 2.2.6. Wolf hunting success on moose (95% C.I.) based on the number of individual moose attacked in Scandinavia and North America; Isle Royale 1 (Mech 1966); Isle Royale 2 (Peterson 1977); Kenai (Peterson et al. 1984); Denali 1 (Haber 1977); Denali 2 (Mech et al. 1998). Sample size (*n*) for each study is given above bars.

DEPREDATION ON DOMESTIC STOCK AND DOGS

Conflicts between wolves and rural interests are directly related to land use practices in Sweden and Norway. Swenson and Andrén (2005) provided an excellent overview of the contrasting policies regarding rural communities, livestock and reindeer grazing, large carnivore management, and compensation schemes. The Norwegian situation is presented in detail in Andersen et al. (2003). Commonalities between Norway and Sweden include conflicts associated with depredation on dogs and semi-domesticated reindeer. The situation regarding other livestock, however, differs, with greater conflict and depredation on free-ranging sheep in Norway, where this activity is heavily subsidized by the government. In Sweden, this activity is not, and farmers must take measures to protect their livestock on fenced pastures near their homes.

Livestock

There are a total of 2.4 million domestic sheep and 236,000 cattle in Norway (Norwegian Ministry of the Environment 2003). About 2.1 million sheep are grazed annually on open range with little or no shepherding. Most other livestock, including 300,000 sheep, are grazed on pastures on or near farms. Total sheep mortality, due to all causes, averages 120,000 sheep/year (5%). During 1999–2006, the Norwegian government paid out on average €6.7 million per year in compensation for around 32,000 sheep killed annually by predators (golden eagle (*Aquila chrysaetos*), lynx (*Lynx lynx*), brown bear (*Ursus arctos*), wolverine (*Gulo gulo*), and wolf) (Norwegian Directorate for Nature Management 2005). Of these, approximately €202,000 was spent to compensate the loss of 995 wolf-killed sheep each year , or about 3% of total annual depredation loss in the country. On average, about 72% of all wolf-killed sheep occur in Hedmark county in southeastern Norway; however, most (nearly 90%) sheep in this county are killed by other predators such as brown bear, lynx, and wolverine (See Table 2.2.1). In 2008, the Norwegian government budgeted about €13.6 million for monetary compensation for livestock and reindeer depredation by large predators, in addition to about €6.7 million for measures aimed at reducing conflicts and preventing depredation (Norwegian Ministry of the Environment 2007).

In Sweden, there are approximately 500,000 sheep and 1.2 million cattle, of which the vast majority (99%) are grazed within fenced pastures. Livestock operations are generally small, and 92% of sheep farms have < 50 ewes. Between 100–200 sheep and 2–6 calves are killed by wolves each year. Since 1997, the government compensates for documented cases of depredation on livestock. This amounts to about €30,000 per year, with farmers receiving 1–2 times the market value for animals lost. In addition, the government invests about €100,000 annually on pro-active measures – aimed at reducing depredation by large carnivores, primarily through the construction of electric fences. In the core wolf area, wolves kill approximately 1% of the total number of sheep each year (Statistics Sweden 2006). Thus, wolf depredation on livestock is not considered to be critical for lamb producers in Sweden today.

Table 2.2.1. Number, species and age of ungulate prey found and classified as being killed (n=97), or probably killed (n=18), by wolves during five winter study periods in three wolf territories.

Type of prey	Tyngsjö 2002	Gråfjell 2001	Gråfjell 2002	Gråfjell 2003	Bograngen 2003	Total / Average
Moose adult	12	3	5	1	2	23
Moose calf	8	13	25	23	14	83
Moose of unknown age	0	0	2	0	0	2
Total moose	20–24	15–16	26–34	20–24	16–17	97–115
Roe deer	3	0	1	1	1	6
Total number of prey	23	16	33			72
Study period	84	70	133	62	62	411
No of days per moose	4.2–3.5	4.7–4.4	4.2	3.1–2.6	3.9–3.6	4.2–3.6

Semi-domesticated reindeer

In Norway, about 200,000 reindeer are grazed throughout the year on roughly 40% of the total land area, primarily in northern Norway. Although this area is outside the current boundaries of the breeding wolf population, wolves occasionally disperse into this region. On average, the government pays herders about €3.3 million for around 22,500 reindeer estimated to be taken by predators (mostly lynx and wolverine) each year. Herders received compensation for 213 reindeer killed by wolves during the seasons 1999/2000–2004/05. Wolf depredation varies greatly from year to year (0–114 animals), with compensation averaging about €8,500 annually (see Table 2.2.2).

In Sweden there are approximately 250,000 reindeer grazing year-round in the northern 40% of the country. As in Norway, there are no

Table 2.2.2. Depredation loss for domestic sheep in Norway, 1999–2004 (Source: Norwegian Directorate for Nature Management).

Year	Sheep depredation total	Sheep killed by wolves
1999	33109	622
2000	32034	837
2001	29891	788
2002	30920	1847
2003	31902	742
2004	30477	2408

resident wolves in this region. Dispersing wolves kill 50–200 reindeer annually. The government does not compensate for individual losses, but instead pays the Sámi villages for verified presence of wolves. Sámi villages receive €2,500 for confirmed wolf presence (tracks), and €50,000 for each established reproductive pair. About €10,000/year is paid to Sámi villages, primarily to cover costs associated with moving reindeer to areas with fewer predators.

Dogs

As the wolf population increased in Scandinavia, the incidence of wolf attacks on dogs increased concurrently (Fig. 2.2.7). During 1995–2005, 151 dogs (of which 80% were used for hunting) were classified as wolf-killed in both countries. In addition, many other dogs were either injured or suspected to have been killed by wolves. Norway has compensated owners for the actual value (as much as €5,000) of wolf-killed dogs since 1999. In Sweden, dog owners are compensated with €1,000, independent of the dog's actual value.

SKANDULV has actively co-operated with hunting organizations in both countries in testing and implementing various preventative measures. The most notable of these is the so-called "Wolf Telephone". This is a telephone answering machine which continually is updated with a very approximate position for the last radio location for each of our instrumented

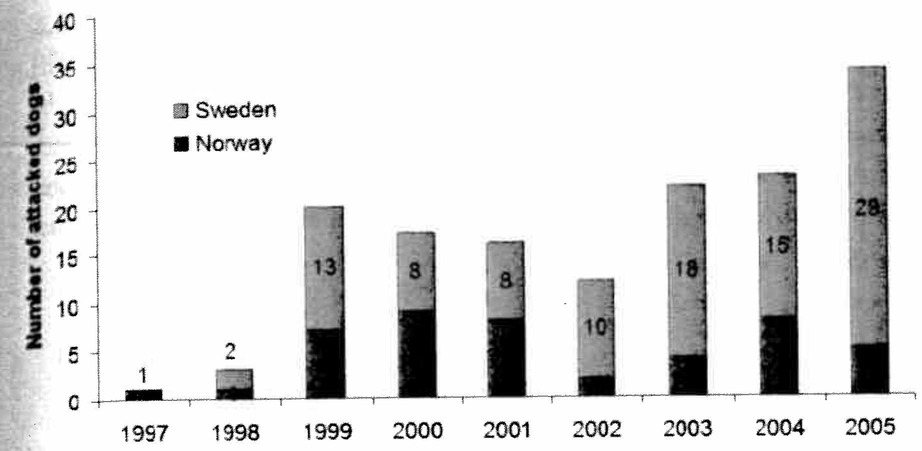

Figure 2.2.7. Wolf attacks on dogs in Sweden and Norway 1997–2005. Most of the attacks were fatal.

wolves during the hunting season. Hunters may then choose not to hunt in that area that day. The warning does of course not completely prevent wolf dog-encounters as wolves are very mobile and there usually are also non-instrumented wolves in the territory. So far we have not been able to detect any reduction in the number of wolf attacks in wolf territories with a "Wolf Telephone" compared with territories without a wolf telephone. This may however be due to an increased hunting frequency in territories with a "Wolf Telephone" as hunters might feel less worried for their dogs´ security there. In a survey of 500 hunters (with hunting dogs) in five wolf territories, on average 98% wished to keep the "Wolf Telephone" (J. Karlsson, unpublished data).

Extent of wolf depredation in relation to other predators

In general, wolf depredation on domestic livestock and semi-domesticated reindeer is minimal in Norway and Sweden relative to depredation by other species of large predators (Table 2.2.3). However, when it occurs, it generates strong controversy and negative sentiments among rural dwellers. Indeed, wolf zoning policy in Norway is based to a large extent on the density of grazing sheep in order to prevent greater depredation loss by wolves. Depredation on dogs is very controversial among hunters in both countries, and is difficult to mitigate. Effective mitigation and management measures are essential in both countries if wolves are to gain broader acceptance among rural dwellers in both countries.

INTEGRATING RESEARCH INTO WOLF MANAGEMENT

The wolf management in Scandinavia is facing several challenges. In the typical European manner, the Scandinavian wolf population is completely limited to a multi-use landscape which it is sharing with humans and their activities (Breitenmoser 1998; Linnell et al. 2005). This inevitably has led to a number of conflicts with humans, including competition for prey, depredation on domestic stock and dogs, and an increasing number of complaints from people that have had direct confrontations with wolves. At the same time the wolf population itself is facing growing problems and its long-term viability is far from secured. Although the population has developed well since it first established itself in the 1980s, a heavy toll from poachers and a progressing inbreeding depression now is reducing the growth rate and eventually threatens to turn it negative (see above). We will here try to line out how the research sector has been, or could be, used to improve the wolf management and conservation.

The most obvious way in which research can support management is by providing data and analyses critical for management decisions or policies (Mech & Boitani 2003a). The identification of the two main limiting factors for the Scandinavian wolf population, illegal killing and inbreeding depression, are research results of high relevance for the management. Our quantification of the amount of poaching has led to the Government decision to allocate more resources into anti-poaching activities in both Norway and Sweden. SKANDULV personnel have also been called to

Table 2.2.3. Depredation loss for semi-domesticated reindeer in Norway (1999/2000–2004/2005) (Source: Norwegian Directorate for Nature Management).

Year	Reindeer loss (total)	Reindeer killed by wolves
1999/00	19468	1
2000/01	20033	0
2001/02	11532	81
2002/03	10720	4
2003/04	10400	13
2004/05	11400	114

court trials to witness in cases concerning poaching. So far, these efforts have not led to any measurable decrease of illegal wolf killing, but we believe that recognition of the problem and information on its magnitude are necessary preconditions for it being solved.

The detection and quantification of the inbreeding depression of wolf litter sizes has had profound effects for the wolf debate in Scandinavia. At almost every occasion where wolf management and conservation is discussed in Scandinavia, this issue is brought up. It has led to a strong lobbying for actively bringing in more wolves, and although the governments and the managing authorities in the two countries so far are not prepared to take such a step, they are aware of the option and are discussing it. They are also carefully following our ongoing demographic and genetic monitoring of the wolf population. Continuous updating of our wolf population simulation model with new data is providing us with an important early warning device, should the wolf situation turn critical. Before an allowance is given to kill a wolf for damage prevention, the normal routine now includes a DNA analysis of the targeted offender (mainly by collecting faeces from it) to evaluate its genetic value.

Our data on predation rates and impact on the moose population are frequently used in the debate on how much wolves compete with hunters. Moose densities within most of the Scandinavian moose range typically is above 1/km^2, (Solberg et al. 2003). At such densities, there is moose enough for both wolves and hunters (Andrén et al. 1999). One complication is that several large forest companies within the wolf range want to reduce moose densities down to 0.4–0.5/km^2 because of claimed damages on young trees, especially pine (Bergström et al. 1995; Glöde et al. 2004). At such low densities the competition between hunters and wolves will be intense. Our data do not solve this conflict, but they give the factual baseline from which to reach compromises.

Contacts between managing agencies and research are not limited to reading reports. There is a continuous communication between the two through numerous channels both formal and informal, often on a personal level. The SKANDULV coordinator updates agencies regularly on our research results and field work, primarily by electronic newsletters, as well as by telephone and/or meetings with managers. The financers of large carnivore research in Norway, Sweden, and Finland, both government institutions and non-governmental organizations, together with representatives from central management authorities in all three countries have formed a committee for coordinating large carnivore research in the three countries, and personnel from SKANDULV are frequently invited to its meetings. Also, SKANDULV has taken the initiative in a regular series of annual conferences where during three days scientists and managers meet, preliminary research results are presented and planned management actions are discussed. This is one of the few forums where officials from central managing agencies in Norway and Sweden regularly meet and get opportunity to discuss matters of mutual interest.

SKANDULV also arranges special scientific workshops with invited researchers and managers (e.g., Liberg 2006), and major research results are often presented at special meetings with Scandinavian managers prior to publication. Often (but not always) scientific personnel from SKANDULV are asked for background facts before large decisions are taken by the central authorities. SKANDULV scientists have provided reports to both Norwegian and Swedish governments as part of the larger process of large carnivore policies formulations (Andrén et al. 1999; Pedersen et al. 2005).

Involvement of stakeholders, including hunters, farmers, foresters, conservationists, local politicians, and even policemen, is a very important part of large carnivore management (Decker et al. 1996). To this end, managing agencies in Norway and Sweden have organized in each country a national committee with representatives from concerned stakeholders which meet three or four times a year to discuss management actions and policies with responsible officials. No scientists are formally attached to these committees, but they are frequently invited to their meetings to give factual backgrounds.

However, through our work on the ground in the wolf areas, scientists and field assistants in SKANDULV meet local people almost daily, which also has led to a developed network of contacts with key persons in the local communities. In each wolf territory where we put transmitters on wolves, we also organize a contact group with representatives from local stakeholders and politicians, and with one representative from SKANDULV in each group. We hold regular meetings, usually on a monthly basis, where we inform about the wolf situation and discuss any matter brought up. These groups have turned out to be very important for dampening of irritations and conflicts. The so-called "wolf telephone" (see above) was started on the initiative of SKANDULV, to warn hunters where it might be risky to let dogs loose. Since the research project began we have striven to involve local people in our activities. During the first years, much of the monitoring work was performed by local volunteers with whom we co-operated. Recently much of the managing responsibility for large carnivore management has been delegated from central to regional agencies in both countries and SKANDULV closely co-operates with these. We are often invited to their meetings, and frequently asked for advice on a large host of topics, from their regional management plans to how to deal with specific problem wolves. These regional agencies have a number of field personnel employed in two main tasks: inspecting depredated domestic animals as a prerequisite for damage compensation, and annual monitoring of large carnivore populations. Often these are the same people that were earlier co-operating with us in SKANDULV, and our involvement with them is continuing through participation in training courses and through frequent informal contacts. SKANDULV personnel travel to more than 100 local meetings annually in both countries, to inform about and discuss wolf matters.

Finally, we think it necessary to point out that, although close involvement of research with management offers great opportunities, there are also risks involved. There are probably few fields of science where the separation and distinction between the roles of research and management are as easily confused as when working with large carnivores. Scientists can risk losing their credibility with stakeholders and with the general public by becoming too involved in management issues or by taking stands in conflict issues (Skogen and Haaland 2001). Managers, on the other hand, might be tempted to interfere in an unsound way with the research. There is also the risk of territorial disputes between management and research as to the proper borderline between the two. Also, irritation might occur when scientists fail to appreciate the political restrictions that limit management options or make their results comprehensible. Managers might annoy scientists by disregarding their results or advice, for prestige purposes or due to lack of understanding.

On the other hand, it is a privilege for researchers to work with an issue where the interest in their results is so intense and widespread, and it is a grand opportunity for managers to work so closely with science and be able to put brand new research results directly into practice. And if there is any area in resource management where there is a great potential for an adaptive approach, this is it. To successfully grasp the opportunities while avoiding the risks, both parties have to engage in a will to understand, a mutual respect for the professional skill of each other, and in frequent and open communication.

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