The Return of the Wolf

Effects on Prey, Competitors and Scavengers

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Cover: The photographs show, from top left to lower right, wolf, raven, moose, golden eagle, pine marten, red fox, hunter (or more precise a boot that likely belongs to a hunter) with hunting dog, and goshawk.
(photo: movement-triggered cameras (STC-WD2-IR, Stealth Cam)

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Abstract

Apex predators may have both direct and indirect effects on other species through predation and competition. I investigated the effects of wolves (*Canis lupus*) on prey species, competitors (including humans) and the scavenging guild after the re-colonization by wolves of the Scandinavian Peninsula. Field methods included telemetry, snow-tracking, age determination, and camera monitoring.

Human extermination of wolves at the end of the 19th century in combination with the extent and mode of hunter harvest has caused moose (*Alces alces*) to become predator-naïve. This has resulted in high hunting success rates and short chase distances by wolves hunting moose, compared to areas in North America where moose have been continuously exposed to wolf predation. The high kill rate by wolves on moose, in combination with mainly additive wolf predation resulted in exploitation competition between wolves and hunters, leading to reduced hunter harvest of moose within wolf territories. In contrast, neither exploitation competition nor interference competition were evident between wolves and Eurasian lynx (*Lynx lynx*), which was most likely a result of wolves and lynx having different main prey species, a high density of the shared prey species and low densities of both predator species.

The largest food source for scavenging species regarding the annual amount of available biomass was remains after hunter harvest of moose in autumn. Presence of wolves slightly reduced available biomass to scavenging species, but more important, wolves reduced the high seasonal variation of available biomass by providing carcasses all year round. The red fox (*Vulpes vulpes*), common raven (*Corvus corax*), European pine marten (*Martes martes*), and northern goshawk (*Accipiter gentilis*) may benefit from the return of wolves, due to their high utilization of wolf-killed moose in spring when the presence of wolves increased the availability of carcasses.

In summary, apex predators will have relatively little influence on other species in areas where human activities have a large impact on animal densities, such as in the wolf and moose system on the Scandinavian Peninsula.

Keywords: apex predator, re-colonization, behavior change, competition, scavenging, wolf, moose, lynx, hunter harvest, Scandinavian Peninsula.

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To Isabell & Anders

Anything that happens, happens. Anything that, in happening, causes something else to happen, causes something else to happen. Anything that, in happening, causes itself to happen again, happens again. It doesn't necessarily do it in chronological order, though.

Douglas Adams

Dissertation

Time:	November 18, 2011, 10:00 am
Place:	Loftets hörsal, Ultuna, Uppsala
Chairman:	**Lena Gustafsson**, Swedish University of Agricultural Sciences (SLU)
External examiner:	**Douglas Smith**, Yellowstone Center for Resources
Evaluation committee:	**Anders Angerbjörn**, Stockholm University **Ilpo Kojola**, Finnish Game and Fisheries Research Institute **Susanne Åkesson**, Lund University **Åsa Berggren** (reserve), Swedish University of Agricultural Sciences (SLU)
Main supervisor:	**Olof Liberg**, Swedish University of Agricultural Sciences (SLU)
Assistant supervisor:	**Roger Bergström**, Forestry Research Institute of Sweden **Håkan Sand**, Swedish University of Agricultural Sciences (SLU)

Contents

List of Publications

My thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Sand, H., Wikenros, C., Wabakken, P. & Liberg, O. (2006). Cross-continental differences in patterns of predation: will naïve moose in Scandinavia ever learn? *Proceedings of the Royal Society B: Biological Sciences* 273, 1421-1427.

II Wikenros, C., Sand, H., Wabakken, P., Liberg, O. & Pedersen, H.C. (2009). Wolf predation on moose and roe deer: chase distances and outcome of encounters. *Acta Theriologica* 54, 207-218.

III Wikenros, C., Sand, H., Bergström, R. & Liberg, O. Effects of wolf predation on hunter harvest of moose in Sweden – an empirical approach. (Manuscript).

IV Wikenros, C., Liberg, O., Sand, H. & Andrén, H. (2010). Competition between recolonizing wolves and resident lynx in Sweden. *Canadian Journal of Zoology* 88, 271-279.

V Wikenros, C., Sand, H., Ahlqvist, P. & Liberg, O. Alteration of biomass flow to scavengers after re-colonization by wolves of the Scandinavian Peninsula. (Manuscript).

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1 Introduction

After being almost absent for about 100 years, the wolf (*Canis lupus*) has recently re-colonized the Scandinavian Peninsula. The return of a large predator to an ecosystem will affect many other species, including humans, in different ways because the presence of apex predators is an important factor shaping ecosystem processes (Hairston *et al*., 1960; Estes *et al*., 2011).

Re-colonization and reintroduction of apex predators to an ecosystem can have effects on other species through predation (Smith *et al*., 2003; Sand *et al*., 2005, 2008), behavioural changes of prey species (Lima and Dill, 1990; Berger, 1999; Berger *et al*., 2001b; Laundré *et al*., 2001), competition with other predators (Palomares and Caro, 1999), suppressing populations of meso-predators giving positive effects on smaller prey species (Crooks and Soulé, 1999; Elmhagen and Rushton, 2007; Ripple *et al*., 2011), alteration of the food base for scavengers (Wilmers *et al*., 2003a), density- or behaviourally-mediated indirect interactions on vegetation (McLaren and Peterson, 1994; Terborgh *et al*., 2001; White *et al*., 1998; Post *et al*., 1999), or changes of the intensity of herbivory which in turn might increase species richness and nesting density of breeding birds (Berger *et al*., 2001a), as well as beaver (*Castor canadensis*) density (Hebblewhite *et al*., 2005).

In my thesis I focus on the alteration of prey behaviour and competition with other predators, including humans, as well as the beneficial effects on the scavenging guild, after the return of wolves to the Scandinavian Peninsula (Figure 1).

1.1 Predator-prey interactions

Predators can limit or regulate the densities of their prey species (see review in Salo *et al*., 2010) and the impact of predation on prey population dynamics depends partly on the degree of compensatory mortality (Fretwell, 1987).

Besides direct lethal consequences for prey individuals, predation can also alter the behaviour of prey (Harvey and Greenwood, 1978). Trade-offs in prey can for example involve reduced foraging activity to increase vigilance (Abrams, 1984; Elgar, 1989; Lima and Dill, 1990). As a consequence, isolation from apex predators could result in a selection against costly anti-predator behaviour (Magurran, 1999). It has been shown that elk (*Cervus elaphus*) and bison (*Bison bison*) increased their vigilance level after the reintroduction of wolves in Yellowstone National Park, USA (Laundré *et al*., 2001). The authors suggested that these behavioural changes may influence elk and bison ecology more than direct predation by wolves. Also, the extinction of apex predators has resulted in a behavioural change in moose (*Alces alces*). When predation was relaxed, moose no longer responded to the sounds of the common raven (*Corvus corax*), previously associated with predation risk from wolves (Berger, 1999). However, herbivores are able to quickly adjust their behaviour in order to decrease predation risk after a re-colonization of an apex predator (Berger *et al*., 2001b). Consequently, the history of predator-prey interactions shapes the behaviour and interactions between current prey species and their predators.

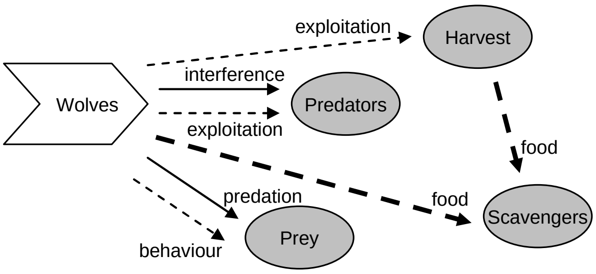

Figure 1. Expected interactions between re-colonizing wolves and other species, including humans, on the Scandinavian Peninsula. Filled arrows denote direct interactions (predation and interference competition); dashed arrows denote indirect interactions (behaviour alterations, exploitation competition and food provision); thin arrows denote negative effects; thick arrows denote positive effects.

1.2 Competition between species

Interactions between predators may take the form of both interference and exploitation competition. Exploitation competition occurs indirectly through differing efficiency in obtaining the same food resource. The effect is greatest when resources are limited and may result in an avoidance of the dominant species by inferior competitors with, for example, habitat shift or reduction in food intake as a consequence (Creel, 2001; Palomares and Caro, 1999). In contrast, interference competition occurs directly via aggression (Rosenzweig, 1966) and may in the more extreme cases result in intra-guild predation (Polis and Holt, 1992). Intra-guild predation may lead to population decline or even cause local extinction of the inferior species. Interference competition can occur even if resources are not limited. One example of interference competition is the negative relationship between wolf and coyote (*Canis latrans*) densities in Yellowstone, and the fact that wolves generally kill coyotes scavenging remains after ungulates killed by wolves (Smith *et al*., 2003; Murray Berger and Gese, 2007). In contrast, Creel and Creel (1996) suggested that the negative correlation between densities of African wild dogs (*Lycaon pictus*) and spotted hyenas (*Crocuta crocuta*) was a result of exploitation competition due to a highly overlapping diet.

Competition between species differs depending on the species involved, habitats, geographical location, and the densities of the competitors and their prey (Creel, 2001). Also the difference in body size between predators affects the intensity of competition (Donadio and Buskirk, 2006). The type of social system may affect the outcome of competition with group-living species having an advantage over solitary species (Palomares and Caro, 1999). Competition may be weak between species even though they have the same preference of prey species if they select differently according to age and sex (Husseman *et al*., 2003). Also, avoidance in time or space for species with overlapping home ranges may minimize competition (Carothers and Jaksić, 1984).

Humans have caused the extinction of apex predators in many areas (Ray *et al*., 2005), including wolves on the Scandinavian Peninsula (Haglund, 1968). One reason for the extermination of large predators by humans is competition over the same food resources. Humans play a key role in ecosystem processes through fishing (Steneck, 1998) and hunting (Fryxell *et al*., 2010). In many ungulate populations, predation by apex predators has been the main mortality factor, often with a regulating effect (Gasaway *et al*., 1983; Messier, 1994; Hayes and Harestad, 2000). Through reduction or extermination of apex predators, human hunters have gradually taken over the role as the main regulator of ungulates (Solberg *et al*., 1999; Coulson *et al*., 2004). However, this means that hunters have had to reduce their harvest after the return of apex predators preying on the same ungulate populations (Nilsen *et al*., 2005). In boreal ecosystems where moose are preyed upon by several predator species, prey density typically declines with each additional predator species, including hunter harvest (Gasaway *et al*., 1992).

In ungulates, the contribution to population growth generally differs between age and sex classes (Coulson *et al*., 2004). As human hunters often select differently than predators regarding body condition, age structure and sex of the killed individuals, their respective impact on prey population growth might differ even if they remove a similar number of prey individuals (Solberg *et al*., 2000; McCullough, 2001).

1.3 Predators as food-providers to scavenging species

Scavenging is a common phenomenon among terrestrial vertebrates (see review in DeVault *et al*., 2003). Predators may have a strong influence on the scavenging community through their supply of carcass remains from their prey (Wilmers *et al*., 2003a; Mattisson *et al*., in press). Utilization of carcasses during periods of prey shortage, in stressful environmental situations, or as an alternative food resource may have substantial impacts on population dynamics and thus on the structure of scavenging communities (DeVault *et al*., 2003). In Yellowstone, winters are becoming shorter as a consequence of climate change, resulting in fewer ungulates dying of starvation (Wilmers and Getz, 2005). This has led to less food being available for scavenging species. The return of the wolf has compensated for the decrease of winter carcasses by providing wolf-killed prey remains with a reduced seasonal and year-to-year variation compared to remains after hunter harvest (Wilmers *et al*., 2003b) and winter starvation in ungulates (Wilmers and Getz, 2005).

Scavengers may adjust their behaviour to locate carcass remains after establishment of an apex predator. The raven associates with wolves during winter as a foraging strategy to discover carcasses at an early stage (Stahler *et al*., 2002). The red fox also seems to use wolves as guides to find kill remains by following their tracks in the snow (Jędrzejewski and Jędrzejewska, 1992). However, scavenging kills by large predators is also a risky behaviour due to intra-guild predation (Palomares and Caro, 1999). Wolves often return to old kills (Huggard, 1993) where they might surprise scavengers and kill them. In addition, predator kills are often consumed to a large extent by the predator itself (Houston, 1979), forcing scavengers to rely more on animals that have died from other causes than predation (DeVault *et al*., 2003). Also humans provide food for scavengers through hunting and wildlife-vehicle collisions. These sources of biomass have large temporal and spatial variations. Remains from hunter harvest are generally available only for a few months during the hunting season in autumn (Wilmers *et al*., 2003b), and road density will affect the number of ungulate-vehicle collisions (Seiler, 2004). Consequently, the temporal and spatial distribution of carcasses to scavengers will depend on the predominant cause of mortality in ungulate populations (DeVault *et al*., 2003).

2 Objectives

The aim of my thesis was to study how the reestablishment of an apex predator in a forest-dominated landscape affected other species, including humans. Both indirect effects through behavioural changes in prey and direct effects through limitation or regulation of prey numbers may occur after the re-colonization by wolves of the Scandinavian Peninsula. A decline in prey populations may be followed by competition between wolves and other predators, as well as between wolves and human hunters, when sharing the same prey species. The remains after prey killed by wolves may influence the food base for scavenging species. My main questions were:

Paper I	Has the re-colonization of wolves resulted in behavioural changes (i.e. re-adapting anti-predator behaviour) in its main prey species, the moose?
Paper II	Are chase distances, hunting success and prey defence behaviour during wolf encounters with moose and European roe deer (*Capreolus capreolus*) reflected by predator-prey history?
Paper III	Has the reestablishment of a wolf population resulted in exploitation competition with hunter harvest of moose?
Paper IV	Has the re-colonizing wolf population resulted in exploitation or interference competition with a sympatric medium-sized predator, the Eurasian lynx (*Lynx lynx*)?
Paper V	Has the presence of wolves altered the resource flow to scavengers and which scavenging species may benefit from the presence of wolves?

3 Study area

3.1 General description

The study area for my thesis was located in the south-central part of the Scandinavian Peninsula (south-central Sweden and adjacent eastern part of Norway). The area in Sweden contained the entire, or parts of the counties of Dalarna, Gävleborg, Värmland, Örebro (all papers), Västmanland (Paper III-V), and Västra Götaland (Paper III). In Norway, the counties of Hedmark (all papers), Akershus and Østfold (Paper IV) were partly included (Figure 2).

The study area was situated in the boreal vegetation zone (Esseen *et al.*, 1997) which was dominated by managed coniferous forest. The intensive forest management includes clear-cutting regeneration resulting in a mosaic of conifer stands in different age classes and an extensive network of forest roads. The dominating trees species were Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), mixed with downy birch (*Betula pubescens*), European white birch (*Betula pendula*) and European aspen (*Populus tremula*). Snow covered the study area for three to six months each year. Human population density in Sweden averages 20/km^2, but large parts of the study area had a density of < 1/km^2 (Swedish National Atlas 1991).

3.2 The wolf population

In the mid-19th century the wolf population at the Scandinavian Peninsula probably comprised more than 2000 individuals (Persson and Sand, 1998). Wolves were extirpated from the study area and from most of the Scandinavian Peninsula at the end of the 19th century and were functionally extinct from the entire peninsula by the 1960s (Haglund, 1968). Wolves returned to the study area in the early 1980s through natural re-colonization from the large Finnish-

Russian population in the northeast, and the first reproduction occurred in 1983 (Wabakken *et al.*, 2001). During the 1990s the wolf population increased both in numbers (29% average annual increase) and range (Wabakken *et al.*, 2001). In the winter of 1994/1995 the wolf population consisted of three packs and one pair (Wabakken *et al.*, 2001) and in the winter of 2009/2010 of 28 packs and 21-24 pairs (252-291 wolves, Wabakken *et al.*, 2010). During the last winter of the study period (2009/2010), wolves were managed with the objective of maintaining the population at 210 individuals. The major part of the wolf population was located in Sweden and within the study area. Pack size (≥ 3) averaged six wolves with a maximum of eleven (Sand *et al.*, 2007). The wolf is an endangered species in Sweden (Gärdenfors, 2010).

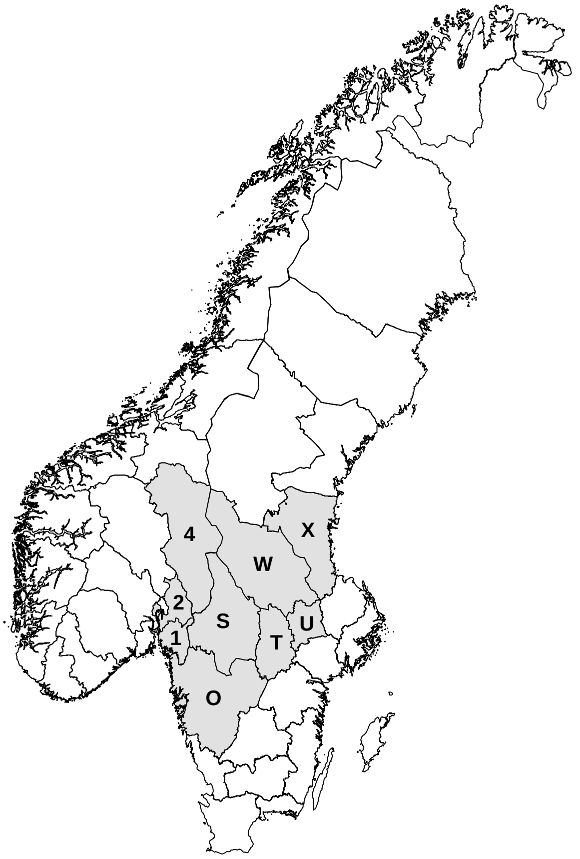

Figure 2. Location of the counties on the Scandinavian Peninsula (Sweden and Norway) in which the study was done. The study area includes entirely, or partly the counties (here shown in grey) of Dalarna (W), Gävleborg (X), Värmland (S), Västmanland (U), Västra Götaland (O), and Örebro (T) in Sweden, as well as the counties of Akershus (2), Hedmark (4) and Østfold (1) in Norway.

3.3 The prey species

Moose were the main prey of wolves in the study area (Olsson *et al.*, 1997; Sand *et al.*, 2005, 2008). The moose population increased during the 20th century and peaked during the 1980s (Lavsund *et al.*, 2003). The increase was due to regulation of hunting laws, altered forest management that resulted in more favourable habitats for the moose, absence of large predators, and a decrease of free-ranging livestock (Liberg *et al.*, 2010). Wolves also prey on roe deer (Olsson *et al.*, 1997; Sand *et al.*, 2005, 2008). The roe deer population was considered almost extinct in the 1820s, but recovered (due to the same reason as the moose population) and reoccupied south-central Scandinavia during the early 1900s (Liberg *et al.*, 1994). Within the wolf territories, winter densities ranged between 0.6-2.5 moose/km^2 and 0.01-3.5 roe deer/km^2, following estimates from pellet group counts and aerial censuses (Sand *et al.*, 2006a, unpublished data). Other potential prey species for wolves were the European badger (*Meles meles*), beaver (*Castor fiber*), mountain hare (*Lepus timidus*), brown hare (*Lepus europaeus*), western capercaillie (*Tetrao urogallus*), and black grouse (*Lyrurus tetrix*, Sand *et al.*, 2005, 2008).

3.4 Hunter harvest

Moose and roe deer have for a long time been harvested by humans on the Scandinavian Peninsula. The moose population has been one of the most extensively harvested moose populations in the world since the 1960s (Lavsund *et al.*, 2003). Approximately 100 000 moose or 25-30% of the pre-harvest population were harvested annually at the beginning of the 21st century (Lavsund *et al.*, 2003). The harvest of roe deer peaked at almost 400 000 individuals during the 1990s but decreased to 100 000 individuals at the beginning of the 21st century. There are several modes of moose and roe deer hunting, for example using a team of hunters, stalking, and using hunting dogs (Liberg *et al.*, 2010). One example is the use of baying dogs during the moose hunt. A moose-searching dog is released and when it finds a moose it tries to keep it at bay by barking, allowing the hunter to locate it and stalk the moose. Moose hunting has both great economic and recreational value (Storaas *et al.*, 2001) and provides a considerable amount of meat and income to landowners. There are also costs associated with high ungulate densities (mainly moose) through damage to agricultural crops and forest trees (Liberg *et al.*, 2010) and ungulate-vehicle collisions (Seiler *et al.*, 2004).

3.5 The lynx population

The lynx reoccupied south-central Sweden at the beginning of the 1950s after a 60-year period when the species was limited to a small area in northern Sweden. In the early 1980s the lynx population was estimated at approximately 700 individuals (Liberg, 1998) and by 2002/2003 it had increased to between 1300 and 1600 and was established in the entire study area (Liberg and Andrén, 2006). The lynx is a near threatened species in Sweden (Gärdenfors, 2010). The main prey of lynx within the study area was roe deer (Aanes *et al*., 1998).

3.6 The scavenging guild

Large and medium-sized mammal scavenging species in the study area were the brown bear (*Ursus arctos*), red fox (*Vulpes vulpes*), European badger (*Meles meles*), and European pine marten (*Martes martes*). According to a carcass utilization study in Poland (Selva *et al*., 2005), the most common avian scavengers were the Eurasian jay (*Garrulus glandarius*), raven, common buzzard (*Buteo buteo*), and white-tailed eagle (*Haliaeetus albicilla*). All these species occurred in the study area, although the density of white-tailed eagles was low (Gärdenfors, 2010).

4 Methods

My thesis is part of an ongoing wolf research project (SKANDULV [http://skandulv.nina.no]), and many people have been involved in collecting data during the period used in this study (1983-2010). In my thesis I have used data obtained both from several different field methods, and from different kinds of statistical databases kindly provided by a number of organizations. I here present the different methods used in paper I-V, and briefly discuss the pros and cons of the methods.

4.1 Telemetry

Wolves and moose were immobilized with darts from helicopters (see Sand *et al.* [2006b] for a detailed description of the method used for catching wolves and Cederlund *et al.* [1989] for capture of moose). Lynx were captured using box traps or trained dogs (Andrén *et al.*, 2006). The animals were captured during winter and fitted with neck-collars (VHF or GPS). Capture, handling and collaring of wolves, lynx, and moose fulfilled the ethical requirements of the Swedish Animal Welfare Agency and the Norwegian Experimental Animal Ethics Committee (only for wolves).

Locations from the collars were used for determining territory borders of wolves (Paper III and IV) and lynx (Paper IV), finding prey killed by wolves (Paper I, III, IV and V) and lynx (Paper IV), as well as for capture of moose calves (Paper I) and lynx kittens (Paper IV). Locations from collared lynx were provided by the lynx research project (SCANDLYNX) and locations from collared moose from the moose research project at Grimsö Wildlife Research Station. The annual number of moose killed by wolves (Paper III and V) was based on data involving > 500 wolf-killed moose all year round and in areas with different moose densities and wolf pack sizes.

The use of collared animals gave highly accurate locations (especially when using GPS collars) all year round. However, the difficulty of catching and especially re-catching these large mammals reduced the possibility of obtaining long time series for individual animals. Even more crucial were the technical problems with collars that, too often, resulted in them completely failing to function. This resulted in a great variation in the number of locations available for determination of territory borders between years and territories.

4.2 Snow-tracking

Wolves were snow-tracked to detect new wolf establishments (Paper III) and determine approximate size of territories (Paper III and IV) by personnel from the County Administrative Boards that are responsible for the annual estimation of wolves on the Scandinavian Peninsula. Additional snow-tracking was also done as part of the SKANDULV wolf research programme. DNA analyses (faeces, blood or hair) were done by the Wildlife Damage Centre to distinguish between lone wolves, scent-marking pairs and wolf packs (Paper III and IV). The yearly amount of snow-tracking performed varied between years and was largely dependent on the duration and quality of snow cover. To correct for less accurate wolf territory borders due to low numbers of locations and the small amount of snow-tracking data available, we also used artificially created wolf territories (Paper IV).

Data from national censuses of the number of lynx family groups (Paper IV) were based on snow-tracking and were received from the County Administrative Boards and the Swedish Association for Hunting and Wildlife Management, in collaboration with the Wildlife Damage Centre. These censuses did not result in an annual population size as they did not cover all areas and the coverage also differed between years. Therefore it was not possible to analyse the effect of wolf presence on the number of lynx. Instead, the data were used to look for spatial distribution of lynx in relation to wolf territories.

Snow-tracking was also used to obtain detailed data that could not be obtained using locations from collared animals alone. Specifically, data on failed hunts by wolves on moose (Paper I), chase distances by wolves on moose and roe deer and outcome of encounters (Paper II), estimations of the number of lynx kittens during winter (Paper IV), and registration of tracks of scavenging species at carcass sites at the time of detection of wolf-killed prey (Paper V) were obtained through snow-tracking. Also, wolf-killed moose in territories without collared wolves (Paper I, II and V) were found using the snow-tracking method.

Snow-tracking was the only available method to obtain detailed data of animal behaviour in our study area. An alternative method using direct observations of animals was not possible due to dense vegetation and high canopy cover. The snow-tracking method is restricted to the winter period, which is why we could not obtain all year round behaviour data.

4.3 Age determination

Wolf age (Paper II) was determined by a combination of three methods and ranked in order of accuracy: (1) known age of captured animals classified as pups at first capture by the presence of a growth zone in the tibia (Rausch, 1967), (2) pedigree construction of birth year based on DNA analyses for non-collared wolves (Liberg *et al.*, 2005), and (3) tooth wear of captured adults (Gipson *et al.*, 2000). The age of wolf-killed moose (Paper II, III, and V) was determined from mandibles by their ontogenetic development (Markgren 1969). For roe deer (Paper II), age was determined by comparing tooth eruption of mandibles from wolf-killed roe deer with roe deer of known age (Cederlund and Liberg, 1995).

4.4 Camera monitoring

Movement-triggered cameras were used to monitor the number of visits by scavenging species (mammals and birds, Figure 3) to wolf-killed moose and remains from hunter harvest (Paper V). The use of cameras enabled recording throughout the year at carcasses that remained for several months. The dense vegetation in the study area made visual observations difficult and this was an unrealistic method to use both day and night over long periods of time.

The camera technique requires supervision at irregular intervals depending on weather conditions, temperature, and frequency of visits by scavengers and wolves at the carcass sites. The function of the cameras may vary both between and within different trademarks. We used three different types of cameras all from the same trademark, but due to the small sample size for two of the cameras it was not possible to control for this potentially confounding factor. Besides photographs of visiting animals at carcass sites, cameras also took photographs that contained no visitors. In our study (Paper V), photographs without visitors were most likely caused mainly by animals being inside the movement detector range but outside the camera range, as the number of photos with no scavengers was positively related to the number of photographs with animals present.

Figure 3. Examples of photographs taken during camera monitoring of scavenging species at wolf-killed moose sites on the Scandinavian Peninsula. Date and time were registered on each photograph. The photographs show, from top left to lower right, red fox, common raven, European pine marten, northern goshawk, golden eagle, Eurasian jay, brown bear, and wolf.

The camera monitoring of scavenging species fulfilled the ethical requirements of the Swedish Animal Welfare Agency. Permission for camera monitoring was obtained from the County Administrative Boards in Sweden.

4.5 Additional data

Data on hunter harvest (Paper III and V) and hunting quotas of moose (Paper III) were kindly provided by the County Administrative Boards in Sweden. Hunters are obliged to register the number and category of harvested moose each year and therefore the data represented the actual harvest. Quotas allocated of moose were set by the County Administrative Boards.

The Swedish Association for Hunting and Wildlife Management kindly provided data of hunter observations (Paper III), hunter harvest of roe deer (Paper IV), harvest date of moose (Paper V), and the proportion of vehicle-killed moose meat suitable for human consumption (Paper V). It is voluntary for hunters to report these data but the lack of a structured data collection was compensated for by large sample sizes.

Data on the number of moose-vehicle collisions (Paper V) was available online from the National Wildlife Accident Council (2009). These data were the actual number of police-reported moose-vehicle collisions but due to the fact that all collisions are not reported, an adjustment of the number of moose involved in collisions on roads had to be made. This resulted in an uncertainty in the number of vehicle-killed moose and these numbers have to be interpreted with caution.

4.6 Data processing

Wolf territory sizes (Paper III and IV) and lynx home range sizes (Paper IV) were determined using the 100% minimum convex polygon method (MCP). This method was chosen as the sample size was not adequate for all individuals to allow for other home range estimations. An exception was the estimations of artificially created wolf territories (Paper IV) that were calculated using both 100% MCP and 95% kernel. All home range calculations were performed in ArcView version 3.2 (Environment Systems Research Institute (ESRI), Redlands, California, USA). The software ArcView was also used to select management units in relation to wolf territories (Paper III), generate random points (Paper IV), measure distances between wolf territories and either control areas (Paper III) or lynx family groups and random points (Paper IV), calculate home range overlap, and estimate the centre of wolf territories (Paper IV).

4.7 Statistical methods

We used inferential statistics, i.e. Spearman correlation (Paper I and V) and Kolmogorov-Smirnov test (Paper IV) for non-normally distributed datasets, as well as t-test (Paper II) and linear regression (Paper V) for normally distributed datasets. Pearson's chi-square test (Paper II and V) and binary logistic regression (Paper I and IV) were used for categorical data. We also conducted a statistical power analysis (Paper IV).

General linear models (univariate GLM) were used when data were normally distributed (Paper II and IV). Akaike's information criteria AIC (Burnham and Andersson, 2002) were used to evaluate model performance (Paper II). Repeated measures general linear models (repeated GLM) were used for data sets that besides having normal distribution were also measured at multiple times scales with available data for all time periods (Paper III and IV). When data points were missing we used a linear mixed model (LMM, Paper III). We used generalized linear mixed models (GLMM) for non-normally distributed datasets with repeated measurements of variables and non-complete datasets (Paper V). The distribution used for the dependent variable was either binominal or Poisson. All analyses were done in SPSS Statistics version 11.5, 17.0 or 19.0 (IBM SPSS Inc., Chicago, Illinois, USA).

5 Results and discussion

5.1 Hunter harvest causes predator-naïve moose (Paper I)

Based on 3 400 km of snow-tracking in combination with telemetry data, we found that moose on the Scandinavian Peninsula lacked appropriate behaviour to escape wolf predation and were easier to kill (i.e. naïve) compared to moose in North America. Hunting success by wolves on moose based on the proportion of chased individuals killed was two to ten times higher on the Scandinavian Peninsula (n = 54) than in North America (n = 595, Mech, 1966; Peterson, 1977; Peterson *et al.*, 1984; Haber, 1977; Mech *et al.*, 1998). Also hunting success based on the proportion of successful hunts (independent of how many moose individuals were involved in each hunt) was higher by a factor of three to five on the Scandinavian Peninsula (n = 122) compared to North America (n = 83, Mech, 1966; Mech *et al.*, 1998, Table 1). Neither wolf pack size, wolf body size, moose body size, percentage of calves killed, percentage of adult females killed, percentage old (> 10 year) moose killed, moose population density, moose population age structure, percentage of wolf-killed calves with depleted marrow fat, snow depth, nor month of data collection explained differences in wolf hunting success between continents. Contrary to our prediction, wolves' hunting success did not decrease with time since wolf establishment (up to 21 years) in our study area, which is expected to occur within a moose generation if moose adjust their anti-predator strategies (Berger *et al.*, 2001b).

Moose behaviour during wolf attacks differed between the continents. Moose in North America were aggressive and took a stand against attacking wolves in 32-56% of the cases (Mech, 1966; Peterson *et al.*, 1984, Table 1), while the corresponding proportion for Scandinavian moose was only 8%. The same lack of defensive behaviour could be observed in Scandinavian moose cows during capture of their newborn calves (defensive behaviour was observed only twice during 131 captures) compared to North American moose (where defensive behaviour is common). On the Scandinavian Peninsula, moose calves were captured by hand with no special equipment to protect the personnel, whereas in North America helicopters were normally needed to separate the moose cows from their calves (Ballard *et al.*, 1979; Gasaway *et al.*, 1992; Franzman, 1998).

Table 1. *Differences between the Scandinavian Peninsula and North America (Alaska and Isle Royale) in hunting success, chase distances, and predation pressure by wolves hunting moose, as well as the extent and mode of hunter harvest, and moose behaviour, during the 20th century.*

	Scandinavian Peninsula	North America	
		Alaska	Isle Royale
Hunting success by wolves on moose (per individual)	26%	5-13%[a]	3-8%[b]
Hunting success by wolves on moose (per hunt)	43-61%	19%[c]	13%[d]
Chase distances in 78% of chases by wolves hunting moose	≤ 200 meters	-	< 800 meters[d]
Annual mortality due to predation from large predators	< 5%[e]	50-80%[f]	> 58%[g]
Annual hunter harvest of the moose population during the last 50 years	25-40%[h]	< 5%[f]	no harvest
Annual number of moose shot by the use of baying dogs	20-30%[i]	0%	no harvest
Moose fronting wolves during wolf attacks	6-8%	56%[j]	32-40%[b]
Moose cows aggressive towards humans at calf capture	rare	common[k]	no capture

[a]Haber, 1977; Peterson *et al*., 1984; Mech *et al*., 1998, [b]Mech, 1966, 1970; Peterson, 1977, [c]Mech *et al*., 1998, [d]Mech, 1966, [e]Swenson *et al*., 1994; Wabakken *et al*., 2001, [f]Orians *et al*., 1997; Ballard and Van Ballenberghe, 1998; Van Ballenberge and Ballard, 1998, [g]Peterson, 1977, [h]Markgren, 1969; Lavsund and Sandegren, 1989; Solberg *et al*., 2003, [i]Sand *et al*., unpublished data, [j]Peterson *et al*., 1984, [k]Ballard *et al*., 1979; Gasaway *et al*., 1992; Franzman, 1998.

We explained the differences in hunting success and moose behaviour between the two continents by a difference in predation pressure and hunter harvest intensity during the 20th century. In North America, moose have been continuously exposed to predation from wolves and brown bears in combination with a low rate of hunter harvest. In contrast, the extermination of apex predators and the very high harvest rate of moose on the Scandinavian Peninsula have resulted in predator-naïve moose. We explained the lack of adaptation of moose to the new situation with re-colonized wolves by the fact that hunter harvest still is the main mortality factor rather than wolf predation (Table 1).

Besides differences in predator-prey history and main mortality factors, the mode of moose hunting also differs between the two continents (Table 1). In North America, the use of dogs for hunting moose is prohibited. The hunting dogs used on the Scandinavian Peninsula are supposed to keep the moose at bay, thereby distracting it and disclosing its location to the hunter, who can then stalk the moose and shoot it. As a result of this hunting mode, the most successful anti-predator behaviour moose can use against wolves, being aggressive and fronting wolves (Mech, 1966, 1970; Peterson, 1977), is exactly the behaviour that has been selected against through a long tradition of using hunting dogs while hunting moose on the Scandinavian Peninsula.

5.2 Predator-prey history shapes ungulate behaviour (Paper II)

We registered a total of 316 hunts by wolves on moose and roe deer during 4 200 km of snow-tracking. Chase distances during successful hunts ranged from 0 m (moose and roe deer killed while lying down) to 1.7 km for moose and 2.3 km for roe deer. The longest unsuccessful chase lasted 5 km during hunts on moose and 13.7 km on roe deer. However, most chase distances were shorter than 400 m (90% of the hunts on moose and 69% on roe deer). Chase distances during all hunts were on average 68% shorter for moose (76 m) than for roe deer (237 m). Prey species was the single most important factor explaining the variance of chase distances. Short chase distances were associated with greater snow depth and successful hunts on moose but not on roe deer.

Differences in chase distances most likely depend on variation in vigilance between prey species due to different predator-prey history and anti-predator behaviour. Compared to moose, roe deer may be a less predator-naïve prey species since their main predator, the lynx, reoccupied the south-central part of the Scandinavian Peninsula 30-40 years before the return of wolves to this region. In contrast to the cursorial wolf, the lynx is a stalking predator probably forcing roe deer to adopt more vigilant behaviour, as compared to moose, in response to the return of the main predator.

Different prey defence strategies also explain the shorter chase distances by wolves on moose compared to roe deer where the larger moose are able to confront attacking wolves, an option not available for the smaller roe deer. Once wolves caught up with prey, roe deer were also easier to kill than moose. In 11% of the wolf attacks on moose at least one moose was injured without being killed (hair, blood or skin found along the tracking route) whereas no injured roe deer survived. Wolf hunting success did not differ between the prey species neither as the proportion of successful hunts (moose 43%, roe deer 47%) nor as the proportion of prey animals killed out of all prey animals involved in the hunts (moose 26%, roe deer 22%). Considering that roe deer are less predator-naïve than moose, the hunting success rate could be expected to be lower for roe deer compared to moose. However, in contrast to roe deer, not all moose are vulnerable to wolf predation. Wolves may terminate attacks on certain moose individuals (e.g. prime-aged individuals) resulting in a lower success rate when hunting moose. There also is less risk of wolves being injured when attacking roe deer compared to moose, which may result in them pursuing attacks on roe deer.

The short chase distances during wolf hunts of moose in our study compared to North American studies (Mech, 1966; Paquet, 1989), in addition to the high hunting success rate and the low proportion of moose that made a stand (Paper I), further support the conclusion that moose are a predator-naïve prey for wolves (Table 1). As also discussed in Paper I, this is probably a result of predator-prey history and hunter harvest as the main mortality factor for moose during the last century on the Scandinavian Peninsula.

5.3 Competition between wolves and hunter harvest (Paper III)

Based on 31 827 harvested moose, we found a general reduction in hunter harvest during ten-year periods and the reduction was stronger within wolf territories than in control areas without wolves. In areas where we investigated the total number of harvested moose for five years before wolf establishment and for five years after the establishment ($n = 25$), the reduction in harvest was 44%. The corresponding reduction in harvest within control areas was 20%. The same pattern was shown for the number of harvested females (53% reduction in wolf territories and 22% in control areas). In contrast, there was no difference in numbers of harvested males or calves with time between wolf territories and control areas. In areas that had a history of continuous wolf presence during at least ten years ($n = 43$), the reduction in harvest with time for the total number of moose, females and calves was also more pronounced within wolf territories than in control areas. The reduction in harvest was dependent on wolf territory size, with a 53% reduction of the total number of harvested moose within small territories (range 520-830 km^2) compared to 29% in large territories (range 1 220-1 830 km^2) after the establishment of wolves. The same pattern was shown for all moose categories.

Hunters responded to the establishment of a new competitor by changing the composition of their hunting bags and shooting fewer females. Also, the reduction in the total number of moose harvested as well as the number of males harvested approximately matched the estimated number of moose killed annually by wolves, when accounting for the same change (numerical reduction) that occurred within the control areas. In contrast, the reduction in harvest of calves was less than the estimated number needed to compensate for wolf predation, while the opposite was shown for females. However, harvesting a high proportion of calves will not affect population growth in the same way as harvest of adult moose (Sæther *et al.*, 2001). In contrast, the reduction in hunter harvest in areas with wolf presence during at least ten years did not fully compensate for the estimated number of wolf-killed moose in all categories, despite there being fewer females and calves in the harvest bag compared to control areas (Figure 4).

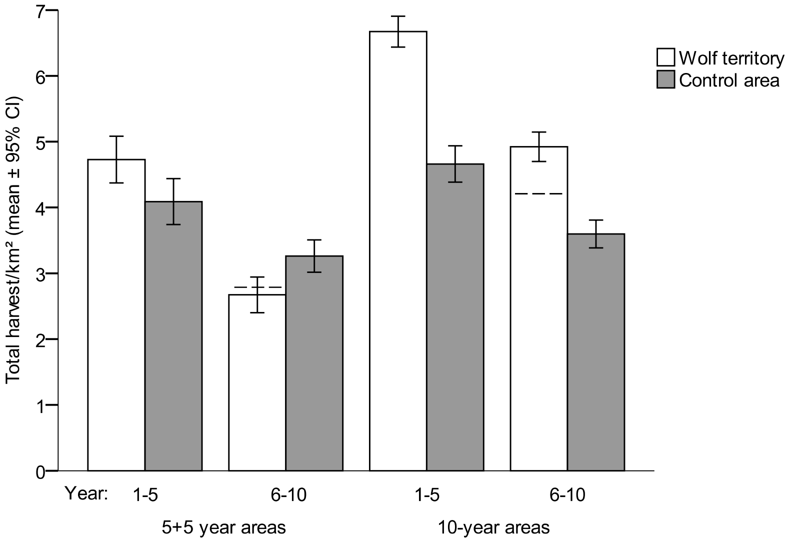

Figure 4. Total harvest of moose/10 km^2 during five-year periods in areas five years prior to wolf establishment and five years with wolf presence (5+5 year areas, n = 25), and areas with ten years of presence of wolves (10-year areas, n = 43), as well as their respective control areas, in south-central Sweden. Dashed lines indicate the calculated reduction in harvest within wolf territories if harvest had exactly compensated for the loss due to wolf predation, and assuming the same trend (numerical reduction) of moose harvest within wolf territories as in control areas.

An adaptive management strategy involving both managers and hunters was immediately implemented during the first hunting season after wolf establishment. This extremely quick behavioural response by managers and hunters after the establishment of a new predator contradicts the more common time-lagged response between harvest rate and fluctuations in ungulate population densities (Solberg *et al.*, 1999; Fryxell *et al.*, 2010). Therefore, the response to wolf establishment by managers and hunters was more likely solely a response to the awareness of an establishment of a new competitor rather than to a decline in moose density caused by wolf predation. However, this adaptive management was not observed in areas with a history of wolf presence during at least ten years. If harvest rates are not adjusted to lower levels in these areas, or the composition of the harvest bag changed, this will probably lead to a further decline in the moose populations (cf. Nilsen *et al.*, 2005). Besides taking into account the presence of wolves, knowledge of wolf territory size and prey density will be necessary to predict the impact of wolf predation on hunter harvest. Our study indicated that wolves established territories and remained in areas with initially relatively higher moose densities compared to control areas, but the cause of this observation requires further investigation.

5.4 No competition between wolves and lynx (Paper IV)

Despite a sympatric distribution, a shared prey species, and a size difference between wolves (35-50 kg) and lynx (15-25 kg) that suggest a potential for competition, we found no evidence that lynx suffered from competition with wolves. The spatial distribution of lynx family groups (i.e. breeding females with kittens, n = 378, Figure 5) over four winters (2003/2004-2006/2007) was

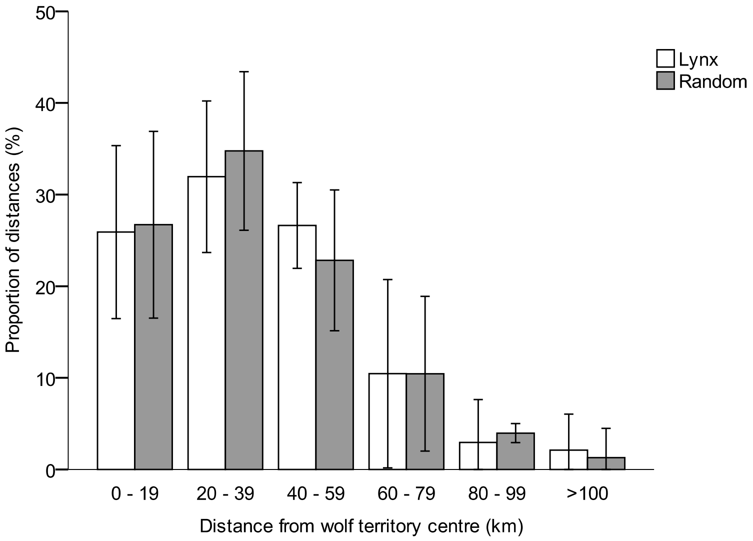

Figure 5. Distance of lynx family groups (n = 378) and random points from nearest wolf territory centre (where > 20 km is outside most wolf territories), in south-central Sweden during four winters (2003/2004-2006/2007).

not significantly affected by the expanding wolf population. Lynx did not prefer areas without wolf territories and home ranges of lynx overlapped extensively with wolf territories. Also, female lynx (n = 3) that were radio-tracked during a total of 25 lynx years before and after wolf establishment did not change their home ranges as a response to establishment of wolves. Annual home range size (n = 42) of lynx (n = 14) was not affected by wolf presence suggesting that wolves did not cause a decline in the roe deer population, as the home range size of lynx is shown to increase with decreasing prey density (Herfindal *et al.*, 2005). Finally, we found no evidence for scavenging or cleptoparasitism by wolves on roe deer killed by lynx. Consequently, the exploitation competition between lynx and wolves appeared to be minor despite the fact that both prey on roe deer.

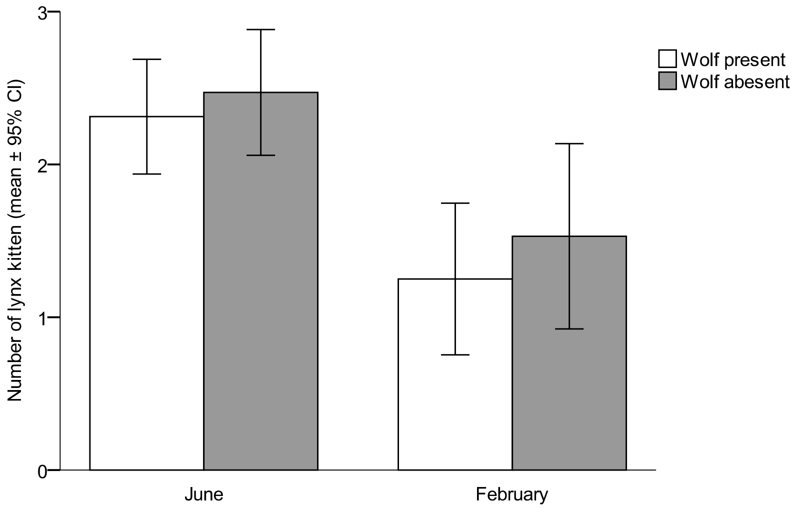

Figure 6. Number of kittens in June and February for female lynx with wolves present (n = 37) or absent (n = 42) in the lynx home range, in south-central Sweden.

We found no support for interference competition regarding survival of lynx kittens until nine months of age as the survival rate did not differ between litters inside (54%) and outside (62%) wolf territories (Figure 6). Also, female lynx (n = 3) selected natal den sites (n = 19) in the same area (corresponding to 2-9% of their total annual home range) before and after wolf establishment. Further, there were no documented cases of lynx killed by wolves either during snow-tracking (> 15 600 km, Sand *et al.*, 2006a; Wabakken *et al.*, 2004, 2005, 2006, 2007, 2008) or during kill-rate studies using locations from GPS-collared wolves (429 kill-sites investigated, Sand *et al.*, 2005, 2008, unpublished data), and analysis of wolf scats (n = 2 091) revealed no occurrence of lynx hair (Knappwost, 2006; Müller, 2006). Together, these results point towards extremely low or no interference competition between lynx and wolves.

We suggest that the lack of exploitation and interference competition between lynx and wolves is a result of a combination of their different choice of main prey species (wolves preying mainly on moose), a high density of the shared prey species (roe deer), and low density of both predator species.

5.5 Wolves alter biomass flow to scavengers (Paper V)

In the study area, moose carcasses became available for scavenging species through wolf-kills, hunter harvest, vehicle collisions, and natural death (here defined as mortality not caused by humans or wolves). From wolf-killed moose (n = 117), approximately 30% of the available biomass was left for scavengers when wolves left kill sites. Despite the fact that wolves did not consume their killed prey entirely, the total annual amount of biomass available to scavenging species was slightly reduced (6%) in areas with wolves (22 814 kg per year within an annual average wolf territory of 900 km^2 compared to 24 289 kg in a similar sized areas without wolves). This reduction was a result of wolf predation being partly compensatory during winter, consequently leading to a reduced amount of available biomass from natural mortality. Wolf-kills contributed to approximately one-sixth of the total annual available biomass for scavengers within wolf territories. Remains after hunter harvest were the largest food source for scavengers as they made up 64% of available biomass within wolf territories. In areas outside wolf territories, where hunter harvest and natural mortality replaced wolf predation, the proportion of biomass from moose harvest was even higher (81%).

The largest amount of available biomass from moose carcasses for scavengers occurred in October due to the peak of moose hunting during that month (Figure 7a). This was evident both in areas with and without wolf presence. But more importantly from a scavenger's point of view, wolves reduced the high seasonal variation of carcass availability (Figure 7b). Presence of wolves increased available biomass each month (14-181%) except during the first part of the hunting season (from September to November) when biomass was reduced by 4-22% each month.

We found only minor differences between wolf-kills and remains after hunter harvest when comparing presence and number of visits by scavenging species. However, the presence of scavengers decreased faster with time at remains from hunter harvest compared to wolf-kills, which is most likely a result of the greater amount of biomass available from each wolf-kill compared to what remained after a harvested moose. This further increases the importance of wolf predation because remains from hunter harvest are not likely to be similarly available for scavengers during spring. The number of visits by scavengers to wolf-kills also increased the larger the amount of biomass available on the carcass. In addition, returns by wolves to old kill sites

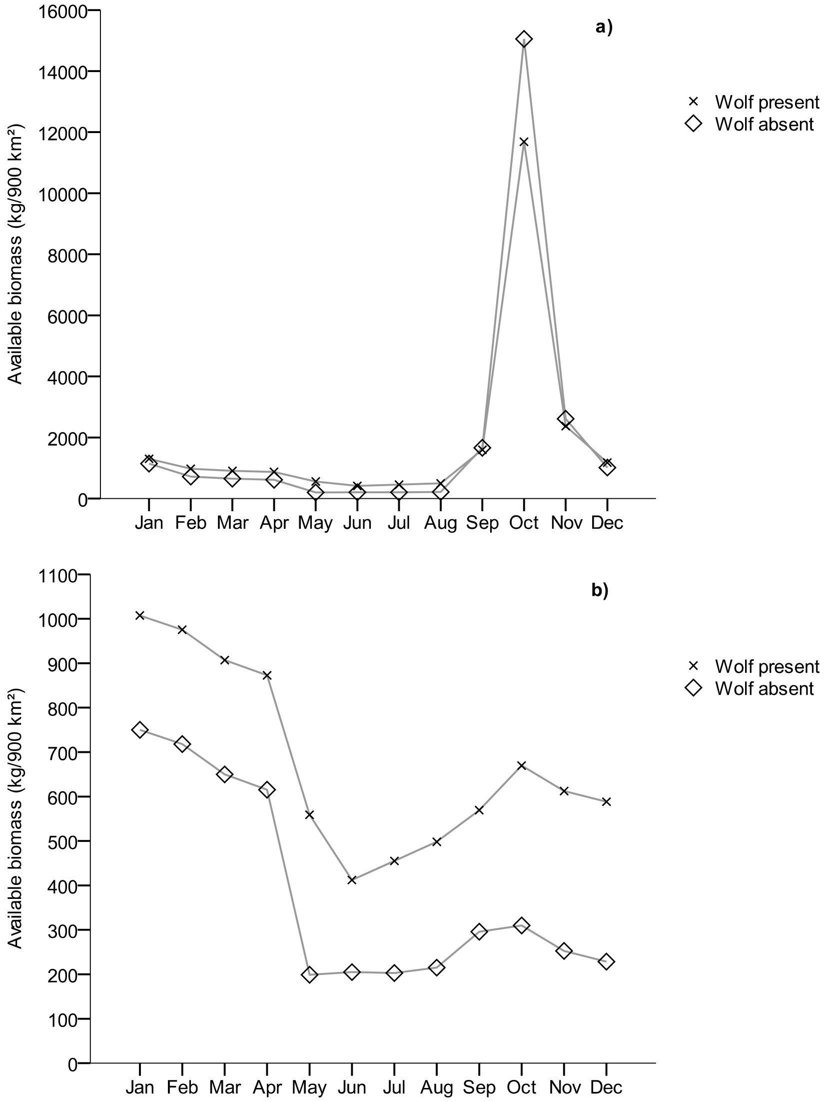

Figure 7. Total amount of biomass from wolf-kills, hunter harvest, vehicle collisions, and natural death for scavenging species in areas with and without presence of wolves. Hunter harvest is included in a), excluded in b), while wolf-kills are only included in "Wolf present". The biomass is calculated in an averaged wolf territory (900 km^2) on the Scandinavian Peninsula.

were associated with an increase in the number of visits by scavengers. This suggests that scavengers follow wolves to find carcasses and do not avoid carcasses when wolves are nearby.

The positive effect of the re-colonization by wolves on the scavenging guild was further shown by the lack of temporal correlation between the number of visits by scavenging species to wolf-killed moose and the total amount of available biomass. The greatest amount of available biomass occurred in autumn (from September to November) but the number of visits by scavengers at wolf-killed moose was instead highest during spring (from April to June) when most scavenging species rear their young. The increased availability of food from wolf-kills during spring may therefore lead to an increase in survival and/or reproductive success of scavenging species (Lindström and Hörnfeldt, 1994; Persson, 2005).

Movement-triggered cameras revealed 17 different species that utilized wolf-killed moose (n = 49). However, birds smaller than jays and mammals smaller than pine martens did not trigger the movement detectors, and the utilization by these species remained unknown. The most common scavengers were the red fox, raven, pine marten, and northern goshawk (*Accipiter gentilis*). These species accounted for 90% of all visits to carcass sites. We suggest that these species, due to their high utilization of wolf-kills, are the ones most likely to benefit by the presence of wolves. For the rest of the scavenging guild monitored in this study, the return of wolves will probably have little impact as these scavenging species rarely visited wolf-kills. The exception may be the golden eagle (*Aquila chrysaetos*), a near threatened species in Sweden (Gärdenfors, 2010), and the most common scavenger after the four main scavenging species.

5.6 Concluding remarks

Effects of apex predators on other species have been documented worldwide in a range of terrestrial, freshwater and marine ecosystems (see appendix in Estes *et al.*, 2011). Estes *et al.* (2011) argued that human-caused extinction of apex predators, or introduction of exotic species can result in irreversible disappearances of ecological interactions. In Europe, human activities control densities of species to a large extent primarily through hunter harvest and habitat changes (e.g. through forestry and agriculture). This contrasts with large protected areas where humans have little impact on animal populations, and where instead the effect of predators on other species may be more pronounced. It has been argued that it is unlikely that the number of apex predators in Europe will reach the extent where they have an essential impact on the population densities of their prey species (other than locally), due to constraints on space, habitat and human tolerance (Linnell *et al*., 2005).

In areas with little to moderate human impact the return of an apex predator will most likely affect adjacent as well as non-adjacent trophic levels in the ecosystem. The strength of the predator-herbivore-plant interactions will vary with the number of predator levels in an ecosystem (Fretwell, 1987). When this number is odd (i.e. one or three levels of predators) the herbivore-plant interactions will be weak, whereas an even number of predator levels gives strong herbivore-plant interactions. An example of this was demonstrated by Estes *et al*. (1998) where marine kelp forests declined after an increase of herbivorous sea urchins, the main food source for the sea otter (*Enhydra lutris*), as a result of the entrance into the ecosystem of a new apex predator the killer whale (*Orcinus orca*), which increased predation on the sea otter. On the Scandinavian Peninsula, humans have played the role of the ultimate apex predator affecting all three levels (wolves-moose-forest) through intensive management. With the current management regime it is therefore not likely that the re-colonization of wolves will affect adjacent levels (moose, Figure 8) or non-adjacent trophic levels (forest) to a larger extent than human activities.

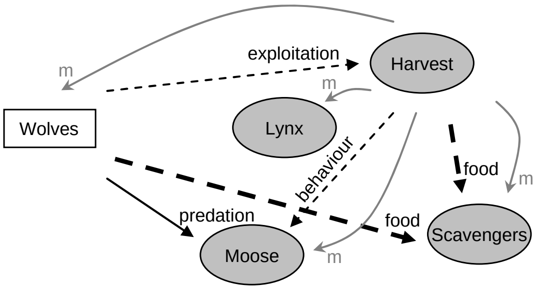

Figure 8. Interactions confirmed in this thesis between wolves and other species, including humans, on the Scandinavian Peninsula. Filled arrows denote direct interactions (predation); dashed arrows denote indirect interactions (behaviour alterations, exploitation competition and food provision); thin arrows denote negative effects; thick arrows denote positive effects. Also shown is the impact of management (m) through hunter harvest denoted by curved grey arrows.

The situation on the Scandinavian Peninsula contrasts with protected areas where the loss of apex predators has not been compensated for by predation from humans through hunter harvest (Figure 8). However, hunter harvest will probably not replace all the multi-faceted functions that apex predators may have in the ecosystem (Beschta and Ripple, 2009; Stenseth and Dunlop, 2009; Genovart *et al*., 2010). In my thesis I argue that by exterminating wolves, human harvest has replaced wolf predation as one of the major mortality factors in the moose population and has caused a loss of anti-predator behaviour in moose resulting in high hunting success rates by re-colonizing wolves. Our results support the notion that the influence on prey behaviour by apex predators is very important for prey ecology (Laundré *et al.*, 2001; Creel and Christianson, 2008). However, hunter harvest has had a greater effect on moose behaviour than wolves on the Scandinavian Peninsula because the extent and mode of hunter harvest prevented a re-adaptation to a more successful anti-predator behaviour. In areas with less impact from humans, reestablishment of apex predators will most likely result in a re-adaptation to the anti-predator behaviour of prey (Berger *et al.*, 2001b).

The high kill rate by wolves on moose (Sand *et al.*, 2005, 2008, 2011a), in combination with mainly additive wolf predation (Sand *et al.*, 2011b) intensified the competition with hunter harvest of moose and resulted in reduced hunter harvest within wolf territories. The extent to which the reduction in hunter harvest within wolf territories is a numerical effect of a reduced moose density caused by wolf predation, a response to the awareness of an establishment of a new competitor, or due to changes in hunting strategies (where for example the use of baying dogs inside wolf territories may decrease, due to the risk of dogs being killed by wolves, and thereby may reduce hunting efficiency) needs to be further investigated.

In contrast to the exploitation competition shown between wolves and hunters, neither exploitation competition nor interference competition was evident between wolves and lynx. Contrary to the intense competition between wolves and hunters, wolves and lynx did not share the same prey species (roe deer) to a similar extent as shown for wolves and hunters regarding the moose. The intensity of competition between wolves and lynx in other areas on the Scandinavian Peninsula where wolves prey mainly on roe deer remains to be investigated. I predict that it will be more intense than shown in our study area if predator densities increase. In areas where wolves prey mainly on roe deer exploitation competition between wolves and hunters regarding the moose will most likely decrease.

The high kill rate by wolves on moose has resulted in the total biomass from wolf-killed moose exceeding the wolves' energy requirements (Sand *et al.*, 2008). This was also evident during our study as wolves did not consume the entire moose carcasses before leaving kill sites. The impact of wolves on the scavenging guild may be significant due to the increased biomass from wolf-kills during the critical time in spring. This may benefit both common scavenging species like the red fox and raven but also near threatened species like the golden eagle (Gärdenfors, 2010). Also, occurrence of wolf-kills may promote colonization of wolverines (*Gulo gulo*) into the south-central parts of the Scandinavian Peninsula (van Dijk *et al.*, 2008). However, considering the total annual carcass availability, humans still made a larger contribution than wolves mainly through hunter harvest but also through moose-vehicle collisions on roads and railways. The dominance of hunter harvest on the Scandinavian Peninsula regarding provision of biomass for the scavenging guild is further illustrated by a comparison with Yellowstone. Here, available biomass to scavengers from wolf-killed elk corresponded to 40% of the biomass from hunter harvest (Wilmers *et al*., 2003b), while the corresponding proportion from wolf-killed moose on the Scandinavian Peninsula was only 17%.

In summary, apex predators will have less influence on other species in areas where human activities (hunter harvest and habitat changes) have a large impact on several trophic levels. The results from my thesis support the concept that the role of an apex predator differs between wolves and humans (Berger, 2005). Conservation of apex predators most likely promotes biodiversity even though this depends on the specific conditions and is not the case for all species and ecosystems (Sergio *et al*., 2008). An understanding of the effects caused by both apex predators and humans is required to provide the management tools necessary for restoration and sustainability goals (Pace *et al*., 1999).

The return of the wolf to the Scandinavian Peninsula is a challenging issue affecting not only other species but also human activities with a long tradition, such as hunting (especially the use of hunting dogs), livestock management, reindeer husbandry, and free-ranging livestock. The big challenge for management may be to compromise between the preservation of wolves and their role as an apex predator and sustainability of human activities that are affected by wolves.

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