Léa Baronnat

Selection of roe deer (*Capreolus capreolus*) by predators during winter

A comparison between wolf (Canis lupus), lynx (Lynx lynx) and human predation

Supervisor :
Håkan Sand

Co-supervisor :
Camilla Wikenros

SKANDULV
Grimsö Wildlife Reseach Station
Department of Ecology, SLU
 730 91 Riddarhyttan
Sweden

Master "Ecological Engineering and Biodiversity Management"
University of Montpellier II, France
1st March - 30th September 2012

SKANDULV · GRIMSÖ WILDLIFE RESEARCH STATION · SVERIGES LANTBRUKSUNIVERSITET · S L U · UNIVERSITÉ MONTPELLIER 2 SCIENCES ET TECHNIQUES · IEGB

Abstract:

Predator-prey interactions are a key component in ecology. Because of top-down effects, predators' influence the dynamic of prey populations, such as roe deer. Predation behaviors are shaped by a suite of factors: in order to balance the cost-benefits predators have to select the most vulnerable prey. Thus lead to develop different hunting strategies. Indeed wolves are known to be coursing predators whereas lynx are stalking predators. The aim of recreational hunting is to provide game meat or a trophy. All these different strategies allow predators to select prey with different age, sex or body condition attributes. Understanding how these patterns would affect roe deer populations is a crucial issue for management. This study described wolves' selection patterns toward roe deer during winter, regardless age, sex and body conditions categories. Then this pattern was compared to lynx and human harvesting patterns. Results showed that wolves exert a low selection towards fawns, adults and females, which tend to be proportional to roe deer availability in the population. This could be linked to the opportunistic behavior of wolves, and because adult roe deer are not costly prey to prey on. Lynx seemed to be the less selective and prey upon all categories equivalently, as all stalking predators. The comparison of the different predators' patterns highlighted patterns' similarities between wolves and hunters, which reveal an additive effect of wolf predation on roe deer human-related mortality.

TABLE OF CONTENT

I.   Introduction

Predation is an important top-down regulatory force, and is a key factor shaping the structure of prey populations and communities (Krebs 1973, Sih 1987, Lima & Dill 1990, Huggard 1993). Predation impact on prey populations is also dependent on the compensatory nature of predation mortality (Caughley 1977). Predation behaviors are shaped by a suite of factors, including predator and prey behavior and interactions, morphology, and habitat requirements related to hunting or escape (Bakker 1983, Kruuk 1986), and thus ultimately determine prey selection patterns (Pastorok 1981; Sih and Moore 1990; Litvak & Legget 1992). In multi-predator systems it is expected that predation foraging behavior differ between predators (Kruuk 1986).

Predators evaluate the risk involved with obtaining their prey and must balance the cost-benefits of the act (Sunquist & Sunquist 1989). As a result, predators often attempt to select the most vulnerable prey (Errington 1946; Mech 1970; Curio 1976; Pole *et al.* 2003). Studies have shown that predation is not a random sample of available prey (Huggard 1993). Selection of vulnerable individuals with respect to age, sex and body condition of a particular prey species is sometimes related to the hunting strategy used by predator to capture individuals or environmental factors. Environmental conditions such as visibility, habitat cover (Lima and Dill, 1990), and snow depth (Peterson 1977) might affect prey vulnerability and the chances to escape. Actually, vulnerability has been shown to increase in open habitats, or with greater snow depth, or with harsh winters, during which body condition can deteriorate.

Hunting strategies influences prey selection, and is expected to differ between stalking and coursing predators. Coursing predators, such as wolves (*Canis lupus*, L. 1758), typically exhibit prolonged pursuit of prey through relatively open fields (Estes & Goddard 1967, Kruuk 1972, Schaller 1972). Because wolves chase swift prey, capture success tends to be low and depredated individuals are disadvantaged in some way (Pimlott 1967, Schaller 1972, Ewer 1973, Kunkel *et al.* 1999). Studies have shown that wolves select weak and vulnerable prey in higher proportion than healthy individuals (Mech 1970; Fritts & Mech 1981; Peterson, *et al.* 1984; Ballard *et al.* 1987; Temple 1987; Mech *et al.* 1995, Sand *et al.* 2012) based on characteristics such as sex and age (Sand *et al.* 2005, 2008). In this case, young and senescent individuals and animals in poor condition are overrepresented in prey choice compared to prime age animals (Fuller & Keith, 1980). In contrast, stalking predators, such as lynx (*Lynx lynx*, L. 1758) generally stalk prey and rely more upon cover to remain hidden right before a

chase. The absence of a prolonged pursuit could explain less prey selectivity and should favor a more random choice of individuals (Rosenzweig 1966; Estes & Goddard 1967; Kleiman & Eisenberg 1973; Caro & Fitzgibbon 1992, Husseman 2003). In areas where canids and felids hunt the same prey species, such as in Sweden, it can therefore be expected that these predators should select prey with different physical attributes. Moreover, despite the fact that humans are the dominant ungulate predator in most temperate ecosystems (McCullough 1979; Bartmann *et al.* 1992), there have been few attempts to compare their selectivity with those of other predators within the same ecosystem (Andersen *et al.* 2007). Modern recreational hunters are known to be strongly selective in terms of age and sex of ungulates, usually for large male trophy hunting (Cederlund & Liberg 1995). As there is an increasing interest in multi-predator systems (Kunkel *et al*. 1999; Gustine *et al*. 2006; Griffen & Byers 2006; Griffin *et al*. 2011), the Swedish predator-prey system exerts a perfect case study of large predator recovery's and their consequences for prey populations.

The European roe deer (*Capreolus capreolus*, L. 1758) is the most widespread wild ungulate in Europe, and occurs in areas where large mammalian predators are presently absent as well as in areas re-colonized by predators. In Sweden, the roe deer population has increased dramatically from 100000 to 375000 individuals during 1955 to 2008 (Swedish Hunters Association's Wildlife Monitoring website). The Swedish roe deer population is considered as an important resource among hunters with great economic value. In Sweden, which include more than 300 000 hunters, sale of hunting meat can generate an estimated budget of 40 to 50 million $US (Cederlund & Liberg 1998; Swedish Hunters Association's Wildlife Monitoring, www.jagareforbundet.se). In Scandinavia, roe deer is mainly prey upon by foxes (*Vulpes vulpes*, L. 1758, Nordström 2010), lynx (Jedrzejewski *et al*. 1993) and wolves (Gazzola *et al*. 2007), in addition to human harvest.

After 100 years on the brink of extinction, the gray wolf became a protected species in 1966 (Persson and Sand 1998), thus allowing wolves to reclaim their place as large predators in the Swedish fauna (Wabakken et al. 2001).Wolves successfully reproduced in south-central Scandinavia (Wabakken *et al*. 2001) for the first time in 1983. The population did not grow until 1991, but has increased since then with an approximate average of 25-29% per year (Persson *et al.* 1999; Wabakken *et al.* 2001; Aronson *et al.* 2003). Wolves are now re-colonizing southern Sweden (Wikenros *et al.* 2010) and habitats which are mostly characterized by high densities of roe deer. In south-central Sweden, the main prey of wolves are moose (*Alces alces*, L. 1758), and roe deer (Sand *et al*. 2005, 2008). Olsson *et al*. (1997) showed that wolves killed roe deer three times more often than moose when compared to their

relative densities. With the growing wolf and lynx populations in Sweden, knowledge on how predators influence prey populations, such as moose and roe deer, is a crucial issue for an effective management of wolves and their prey populations.

Objectives

I here test the hypothesis that wolves would show a strong selection towards weak individuals of roe deer (Mech 1970; Mech *et al*. 1995; Mech 2001). So, according to a gradient, I expect that (*i*) wolves prey mainly on fawns, senescent or sick individuals, followed by adult females, yearlings and in a lesser extent adult males. Moreover, (*ii*) I expect that wolves would select prey in poor or extremely poor body condition. Because lynx and wolves are known to have different hunting behaviors, (*iii*) I expect that stalking predators, such as lynx, show a lower selectivity for vulnerable roe deer than a coursing predator, such as wolves (Okarma *et al*. 1997; Molinari-Jobin *et al*. 2002). In contrast, human hunting are not only targeting prey for meat consumption, but also for trophies. Moreover, males' antlers size could be related to body condition (Vanpé *et al*. 2007). Therefore, I predict that (*iv*) prime age males, in good body condition, should be strongly selected for by hunters, if hunting pressure is directed towards trophies'. Then, because hunters and wolves are expected to prey upon different types of prey and seem to have complementary preferences, (*v*) I expect that, wolf predation would be largely compensatory to human harvest.

In order to test these hypotheses I will:

(1) Describe the pattern of prey selection by wolves on roe deer in relation to individual attributes (sex, age, and body condition).

(2) Compare selection of roe deer by wolves and hunters according to body condition in term of bone marrow fat (BMF).

(3) Compare the prey selection pattern of wolves, lynx, and hunters on roe deer.

II.   Methods

1. Study area

Sweden covers an area of 449 964 km², of the Scandinavian Peninsula, hereafter referred to as south-central Sweden (59°05′N 14°39′E, 62°02′N 14°21′E). Grimsö Wildlife Research Area (GWRA) (130 km²) and Koberg area are also included in south-central Sweden (59°40'N, 15°25'E). All wolf territories studied were within the boreal forest zone and dominated by coniferous forests of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). Deciduous species consisted mainly of birch (*Betula pendula* and *B.pubescens*),

aspen (*Populus tremuloides*), alder (*Alnus incana and A. glutinosa*), and willow (*Salix spp*.). Snowfall mainly occurs from November through April in south-central Sweden each year, with temperatures mainly below 0°C and snow depth commonly ranges between 0–120 cm in the area (SMHI 2012, www.smhi.se). Prey species available within the territories are moose, roe deer, beaver (*Castor fiber*), mountain hare (*Lepus timidus*), capercaillie (*Tetrao urogallus*), and black grouse (*Tetrao tetrix*).

Wolf population development

During winter of 2010-2011, a total of 289-325 wolves were estimated on the Scandinavian Peninsula, of which 183-189 wolves belonged to 31 packs, and 57-61 wolves to 27-30 scent-marking pairs (alpha pair). Most of the wolves (235-266), were located in Sweden (Wabakken *et al.* 2011) (Fig.1). In this study, analyses were conducted for 15 wolves' packs in south-central Sweden (Table 1). Number of individual among the different packs ranged between 2 to 9 wolves. Different types of packs were registered such as "family group", "territory-marking pair" and "other stationary wolves" (Table 1) (Wabakken *et al.* 2011).

Table 1: These are the fifteen wolf territories that I included in my study. Packs structure and location in south-central Sweden. *"Family group" means at least three animals (including an alpha pair), which move within the territory and at least one wolf marks the territory regularly. Then we also observed "territory-marking pair", which is defined as two stationary wolves (male and female), who marks territory together. The "other stationary wolves" mean in most cases, single wolves that scent mark regularly.*

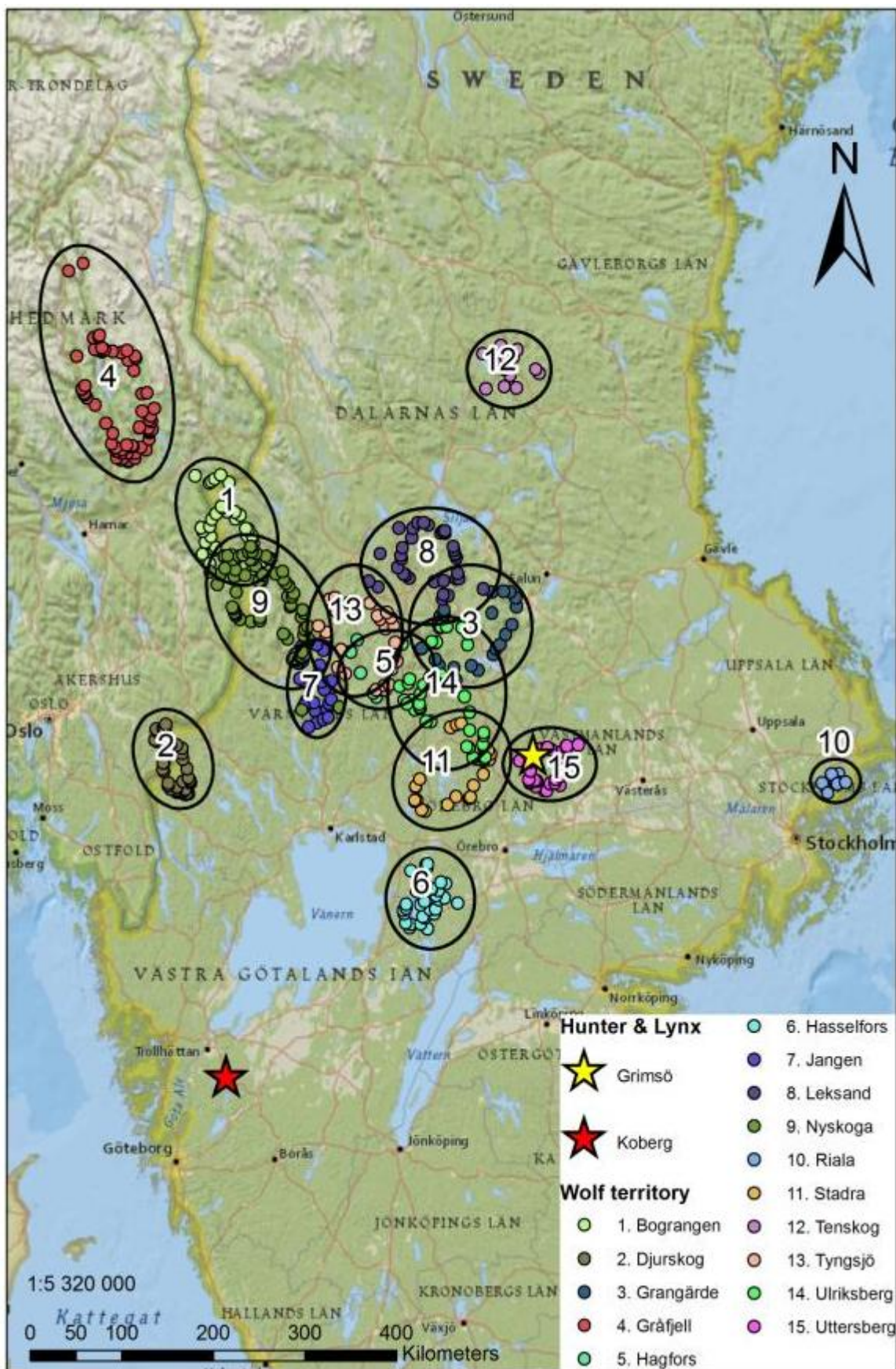| Name of the territory	District	Monitoring	Pack' status	Number of individual	Year of monitoring
Bograngen	Värmland	GPS	Family group	3	2003
Djurskog	Värmland	GPS	Family group	6	2001 + 2004
Gråfjell	*Norway*	*GPS*	*Family group*	*6*	*2001 + 2003*
Grangärde	Dalarna	VHF	Family group	5	2000 + 2001
Hagfors	Värmland	VHF	Other stationary wolves	2	1999 + 2001
Hasselfors	Örebro	GPS	Family group	5	2003
Jangen	Värmland	GPS	Territory marking pair	2	2004
Kloten	Örebro	GPS	Family group	7	2008
Leksand	Dalarna	VHF	Territory marking pair	2	2000 + 2001
Nyskoga	Värmland	VHF	Family group	8	2001 + 2002
Riala	Stockholms	GPS	Family group	5	2010
Stadra	Örebro	GPS	Territory marking pair	2	2003
Tenskog	Gävleborg	GPS	Territory marking pair	2	2010
Tyngsjö	Värmland	GPS	Other stationary wolves	2	2002
Ulriksberg	Dalarna	GPS	Territory marking pair	2	2006
Uttersberg	Örebro	GPS	Family group	9	2006

Figure 1 : Map displaying subset from wolf GPS locations, with approximate estimations of pack locations. (Modified from: Wildlife Damage Center (www.viltskadecenter.com)

Wolves were captured by darting from a helicopter, between 1998 and February 2010 (Fig.2). All wolves were measured, and weighed. Biological samples were collected, according to standard procedures for free-ranging wolves (Arnemo *et al*. 2004). In order to monitoring individuals, wolves were radio-collared, with either a GPS collar (Simplex, Televilt International, Lindesberg, Sweden and Vectronic GPS-plus collars, Berlin, Germany) in eleven territories; or a conventional VHF radio-collar (Telonics Mod. 500, Mesa, Arizona, U.S.A.) in four territories (Table 1).
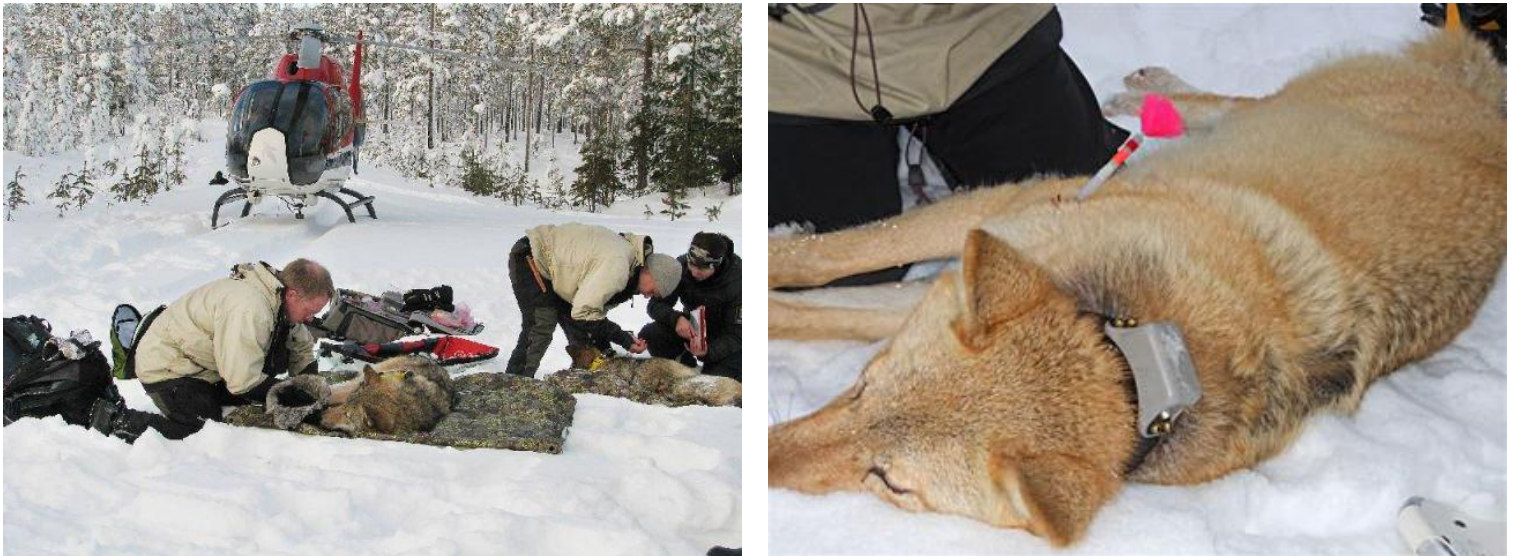

Figure 2: Wolf capture during winter 2011, and radio collared with GPS collars. *(Sources: lst.se)*

Clustering process and detection of killed-prey

Predation was studied in winter period, from 1999 to 2010. A total of 21 intensive study periods were distributed in 15 different wolf territories (11 based on GPS and 4 based on VHF). Prey kill-sites were delimited by snow-tracking combined with wolves' radio-tracking (for VHF collars), but also thanks to GIS analyses in order to identify clusters of GPS position (for GPS collars). GPS-clusters were located and searched for kill sites by using a handheld GPS-unit (GARMIN GPS 12/12XL, accuracy: 15 meters). Kill sites were characterized by remains from carcasses and sometimes tracks from a wolf attack and heavy bleeding or fresh blood from prey.

Lynx-killed roe deer data were gathered following the same predation study protocol, in GWRA, between 1994 and 2007. Moreover, in the GWRA and Koberg area, roe deer were harvested throughout fall and winter, thereby providing data on roe deer that could be used for comparison of age, sex, and marrow fat content with roe deer killed by wolves during winter.

Lynx and wolf-kills were mainly collected during late winter (February-April) (n=24 and 129, respectively), and only few were collected during early winter (November-January). In contrast, most harvested roe deer were registered during early winter (n=530 kills against 61 during late winter).

Estimation of age of predator-killed and harvested animals

Carcasses found during field search were examined in order to identify species and sex. Sex was determined by the sexual organ or by presence of antlers or antler pedicels. Age was determined by comparing tooth eruption of mandibles from wolf-killed roe deer with tooth eruption of mandibles from roe deer of known age (Cederlund and Liberg 1995). Roe deer were classified in four age categories as commonly used for roe deer (Gaillard *et al*. 1993b; Loison *et al*. 1999): such as fawns (< 1 year), yearlings (1-2 years), prime age adults (2-7 years), and senescent (> 7 years).

Estimation of body condition of predator-killed and harvested roe deer

One commonly used measure of body condition for ungulates is bone marrow fat (BMF) content in various bones (Cheatum 1949; Neiland 1970; Franzmann & Arneson 1976; Ratcliffe 1980; Fong 1981; Fuller *et al.* 1986, Sand *et al.* 2012), which represent the last resources to be metabolized during times of food starvation (Dauphine 1971; Mech & DelGiudice 1985). Low marrow fat levels (<25%) indicate individuals in very poor condition (Franzmann and Arneson 1976; Ballard *et al.* 1987; Mech *et al.*1995). In order to estimate the bone marrow fat content, mandibles and different leg bones were collected from wolf-killed and harvested roe deer. Estimation of BMF from a subsample of only wolf-killed and harvested roe-deer was performed using the Neiland (1970) method with bone marrow weighed and dried at 70 °C for 14 days, then weighed again, and fat content calculated as the ratio of dry and wet mass. Quantitative estimates of fat content were combined classifying marrow fat in 4 categories according to Peterson's classification (1977): good (fat content over 75%), fair (fat content ranging between 50-75%), poor (fat content ranging between 25-50%), and extremely poor (fat content less than 25%). Because bone marrow fat can vary between proximal and distal bone during the year (Okarma, 1991), I decided to use only data from the mandibular.

For ungulates in temperate regions body condition tends to decline through winter (Ballard 1981). In order to avoid this bias, wolf-killed and harvested roe deer were compared between early (November-January) and late winter (February-April), using a Chi-square

goodness-of-fit test. As I did not find any significant difference between the two different periods (χ^2= 2.2891; p-value= 0.515) I pooled all data for further analyses.

2. Roe deer population

Standing age and sex distribution of a roe deer population

I characterized the structure of a standing roe deer population by using data on sex and categories determined by roe deer's monitoring in GRWA. Roe deer were captured every winter using trap boxes near feeding sites, or as newborns. Age and sex were identified during captures. I used these capture data as representing the standing winter population regarding age and sex distribution. This standing population was used as a control to compare with wolf- and lynx-killed roe deer. I analyzed data from 1973 until 1996, which is the year of the first reproductive event of lynx in GWRA. Wolves recently settled in GWRA in 2003 (Wabakken *et al*. 2004).

Estimation of density of roe deer populations

An average estimate of population densities of roe deer were obtained through pellet-count survey within the fifteen wolf territories (Table 1) (Pehrson 1997).

In GWRA and Koberg area, roe deer densities were estimated by combining, the Petersen-Lincoln estimate (Caughley 1977) and pellet count survey. Indeed, the capture-mark-recapture leads to a ratio of marked/unmarked animals in a population. This combination allows us to get an estimate on roe deer density.

3. Analyses of the prey selection pattern

Prey selection patterns were tested using three different approaches, including prey age and sex distribution analysis, a trophic niche analysis, and finally with different set of models (Table 2).

Table 2: Summary of the data that I used in my report, with the analyses performed in order to explore my main questions

	Variables	Tests					
Wolf/Lynx/Hunt monitoring	*Cause of death*	Relative occurrence of frequencies (+ Ternary Plot for Age class)	χ²	Multinomial logistic regression	Jacobs' index	Levin's index	Pianka's index + dissimilarity matrix
	Age						
	Sex						
	Bone marrow fat content						
	Month of kill						
Pellet count	*Prey density*		T-test				
Roe deer capture in GWRA (1973-1996)	*Age (control)*	Relative occurrence of frequencies			Jacobs' index		
	Sex (control)						
Questions	**1**	***Wolf selection pattern on roe deer***		***Wolf selection pattern on roe deer***			
	2			***Compare body conditions of wolf- killed and harvested roe deer***			
	3	***Compare prey selection patterns of wolves, lynx and hunter harvest on roe deer***					

Frequency of occurrence of food item

Frequency of occurrence (FO) for each food item (age class, sex) was calculated for wolf, lynx and hunters, given as:

$$FOij = \frac{\Sigma Nij}{\Sigma Nj} \times 100$$

where:

N_{ij} is the number of occurrence of i^{eth} food item in the diet of the species j, and,

N_j is the number of occurrence of all food items in the diet of species j.

Chi-square goodness-of-fit test were performed on the data of age, sex and body condition of prey species, in order to determine if a specific prey category was preferred or not for wolves, lynx and hunters, (to identify significant differences between the diet of wolf, lynx and hunters). Next, the same tests were implemented in order to compare the age distribution between predators-killed and the standing population.

Finally, I used ternary, or triangle, plot in order to display prey selection of the three different predators, depending on the different prey category' proportions. This representation identified which prey categories are the most represented in the diet. Technically, each triangle' summit is associated to a prey category: fawns, yearlings and adults roe deer. Then each predator is characterized by three proportions, one of every prey categories, and plotted within this triangle.

Trophic niche analysis: breadth and overlap

A trophic niche can be defined by how species use all available food resources in the environment (Polechová & Storch, 2005). The trophic *niche breadth*, will allow me to explore the diversity/richness of prey categories predated by wolves, lynx and hunters (*i.e.* the number of food item such as age and sex categories). Standardized Levins' index, B', (Krebs, 1998) was used as an exploratory measurement of niche breadth, given as:

$$B' = \frac{B-1}{n-1} \quad with \quad B = \frac{1}{\sum pi^2}$$

where:

B' is the standardized Levins index by the number of food items, such as age or sex categories

pi is the frequency of the item on the total number of prey killed.

Values of B' close to 1 indicate that the resources are used in similar frequencies (equidistributed), while diet for strongly selective predator will generates B' values close to 0.

The trophic *niche overlap* was calculated using the total number of items identified in the diet of wolves and lynx and in the harvested roe deer. Pianka's index, R, (Pianka, 1974; Krebs, 1998) is given as:

$$R = \frac{\sum p_{ij} \times p_{ik}}{\sqrt{(\Sigma p_{ij}^2 \times \Sigma p_{ik}^2)}}$$

where:

pi is the frequency of the ith food item (categories) used by species j and k .

This index was used as a measure of overlap and is in fact a correlation between species along the abundance of food categories in the prey population. This index ranges between 0 when trophic niches between two predators present have no overlap and 1 when the two trophic niches are completely overlapped. Pianka index leads to identify species with similar food diet in term of age, sex and body condition of prey. A clustering hierarchic analysis was used to plot, on a dendrogram, the degree of overlap among the three different predators' trophic niche. A dissimilarity matrix was built using Pianka's index values previously calculated and transformed as $(\sqrt{1-R})$. Dissimilarity distances were calculated, and predators where grouped in pairs, through an aggregation criterion (mean link).

Predator' selectivity for age and sex

Unlike Pianka or Levins' indices, Jacob's index, D, (Jacobs, 1974) is weighted by the prey category availability as–obtained from the standing population- and show the strength of the prey selectivity for all prey age and sex categories:

$$D = (n - p) \times (n + p \times 2np)$$

where:

n is the proportion of the food item in the diet,

p is the proportion of the food item in foraging areas. The index ranges from -1 (total avoidance of a food item by the predator) to +1 (maximum selection of a food item). Values close to 0 indicate selection of a food item proportional to availability.

Identification of factors influencing prey selection

In order to determine which variables (Table 3) may explain the selection pattern, I implemented two different set of models, using an inferential approach.

(1) First, in order to explore wolf selection among roe deer age, sex and body condition categories, I performed three different models with three different response variables which are: (*i*) age, (*ii*) body condition and (*iii*) sex (Table 4). Because I used four different age

categories, I used (*i*) a multinomial logistic regression. Regardless of body condition, because individuals in poor or extremely poor condition were in small numbers I pooled them together. Because only one roe deer was in good body condition I also pooled roe deer in good and fair body condition. As a result, body condition (*ii*) and sex (*iii*) were used as a binomial response and therefore generalized linear models with binomial distribution error and link logit for body condition and sex categories were used (Table 4).

(2) Secondly, in order to investigate wolf and hunters selection among prey of different body condition I used a generalized linear model with binomial distribution (Table 4), with cause of death as the response variable (hunter or wolf).

For all the performed models I wanted to evaluated the effect of the fixed factors such as the winter period, pack structure, and roe deer densities for the different wolf' territories. All models and tests have been carried out using statistical packages of Program R (version 2.14.2, *R Core Team*, Vienna, Austria).

Table 3: All the different variables used in the sets of models, in order to identify which factors will influence the prey category selection.

Variable	*Category*
Cause of death	Wolf
	Lynx
	Hunter
Age	Fawn (0-1 yr)
	Yearling (1-2 yr)
	Prime-age adult (2-7 yr)
	Senescent (>7 yr)
Sex	Male
	Female
Winter period	Early winter (november-january)
	Late winter (february-april)
Pack Structure	Family group
	Territory marking-pair
	Other stationnary wolves
Roe deer density	continuous variable

Table 4 : Model used in order to explore a) wolf selection patterns, 2) wolf and hunters patterns among roe deer of different body condition.

	n	Model	Variables	k
Wolf- *Age*	65	MWage *(multinomial)*	*Age categories* ~ Winter period + Roe deer density + Pack Structure	3
Wolf- *Body condition*	19	MWbmf *(glm)*	*Body condition categories* ~ Roe deer density + Pack Structure	2
Wolf-*Sex*	9	MWsex *(glm)*	*Sex categories* ~ Winter period + Roe deer density + Pack Structure	3
Body condition exploration	16	Mbmf *(glm)*	*Cause of death* ~ body condition categories	1

III.   Results

1. Clustering process and detection of prey killed: Sample size and distribution

In total, for all predation studies on wolves 144 roe deer kills events were registered. For only a minor part were we able to identify the sex, including females (n=17) and males (n=11). The sample included fawns (n=26), yearlings (n=4), prime age adults (n=32) and senescent individuals (n=3). In parallel, 591 harvested roe deer have been recorded between 1973 and 2010, in Grimsö (n=576) and Koberg (n=15) area, including females (n=261) and males (n=317) (Appendix I, Table 1.b). All the age categories were represented with fawns (n=238), yearlings (n=37), adults (n=278) and senescent individuals (n=22) (Appendix I, Table 1.a). Moreover, lynx monitoring lead resulted in 40 events of lynx-killed roe deer, including 25 females and 15 males distributed on all age categories. In total, 39 jaw bones were analyzed in order to estimate body condition ($n_{Wolf-killed}$=24, $n_{Hunter-killed}$=15) (Appendix I, Table 1.c).

2. Roe deer population

Standing age and sex distribution of a roe deer population

During the 23 years' period, 689 roe deer were trapped in total, consisting of 354 males (51%) and 335 females (49%) (Appendix I, and Table. 2). Fawns and yearlings were more represented than adults (%$_{Young}$=58 and %$_{Adults=}$ 38). Senescent individuals (more than 7 years) are less present in the population (4% of the total population).Estimation of density of roe deer populations.

Estimation of density of roe deer populations

Population density of roe deer was relatively high in only two wolves' territories: Uttersberg and Riala, with 1.5 and 4 roe deer/km², respectively (H. Sand, unpublished data). In the other wolf territories, densities were much lower and ranged between 0 and 0.9 roe deer/km².

In GWRA, roe deer's density is high compared to within the wolf territories, with 10 roe deer /km², during the 1990's with a successive decrease up to 2010. Annual pellet counts (Pehrson 1997) since 1976 reveal a steady decline over the last years and reasons for this recent decline remain unclear. So, after 2010, roe deer population densities were estimated at 1.2 roe deer /km².

3. Analyses of the prey selection pattern

Frequency of occurrence of food item

- Age categories

Fawns (%$_{wolf-killed}$=40, %$_{Lynx-killed}$= 32.5 and %$_{Hunter-killed}$= 41.4) and adults (%$_{wolf-killed}$=49.2, %$_{Lynx-killed}$=45.0 and %$_{Hunter-killed}$=48.3) were consumed in higher quantities out of all killed roe deer (Fig.3). Lynx seemed to prey upon yearlings and senescent individuals (%$_{Yearlings}$=15 and %$_{Senescent}$=7.5) twice as frequently as wolves (%$_{Yearlings}$=6.2 and %$_{Senescent}$=4.6) and hunters (%$_{Yearlings}$=6.4% and %$_{Senescent}$=3.8). When proportions of roe deer killed in each age class were compared between hunters and wolves, predation on fawns and adults had similar distributions for the two predators (Fig.4). However, a Chi-square goodness-of-fit tests did not show any significant differences in age selection of roe deer among the three predators (χ^2 = 6.1354; p-value = 0.408). In addition, only the age distribution of wolf-killed (χ^2= 13.634; p-value = 0.003) and harvested roe deer (χ^2= 91.904; p-value $< 2.2^{-16}$) were significantly different from the standing population.

The average position in ternary plot (Fig.5, black point and solid line) illustrated the proportions of each age category killed by all predators combined. Here 40 % of fawns, 50% of adults and 10% of yearlings were killed by wolf, lynx and hunters, in total. Senescent individuals are not represented on this diagram because they represent an average of 5% percent of the prey. Because of their position in the diagram, I can distinguish two categories of predators. A first group composed of wolves and hunters that mainly foraged upon fawns and adult roe deer. A second group, represented by lynx, was discriminated in comparison with other predators, mainly because they feed on yearlings in higher proportion (Fig. 3).
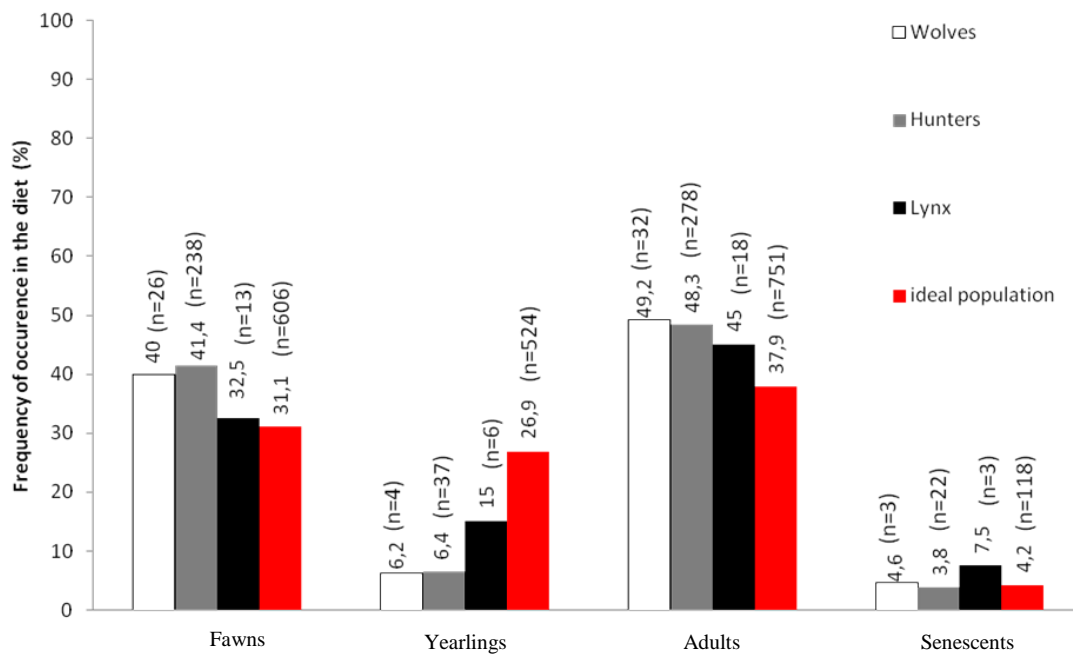
Figure 3: Proportions of roe deer killed by wolves, lynx and hunters, for each age category: fawns, yearlings, adults and senescent individuals. In red are the proportions of roe deer in each age category in the model population, used as a control of predation study.
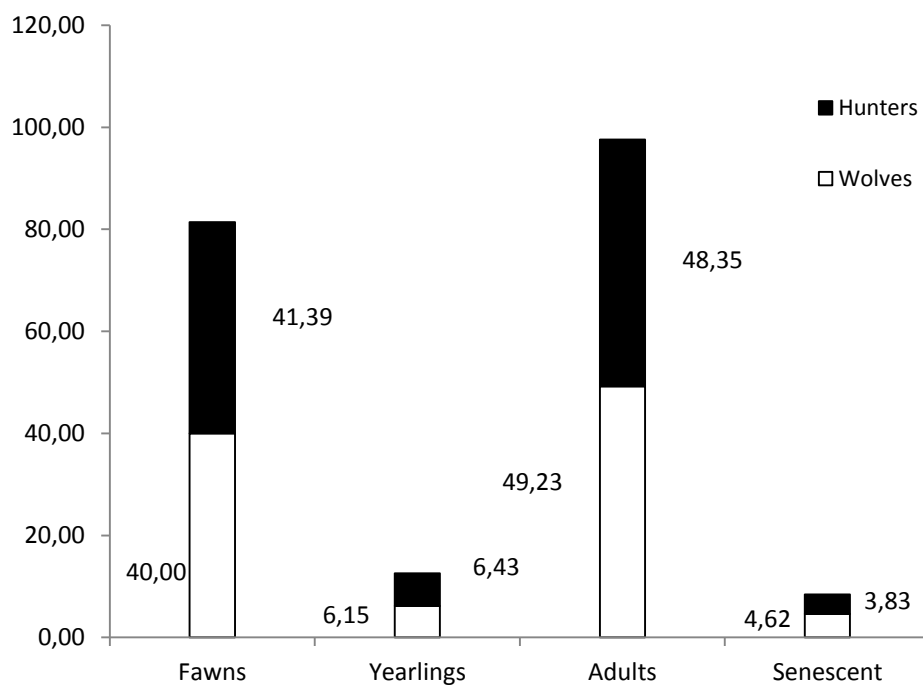

Figure 4: This graphic is focus on the presentation of proportions of roe deer killed by wolves and hunters.
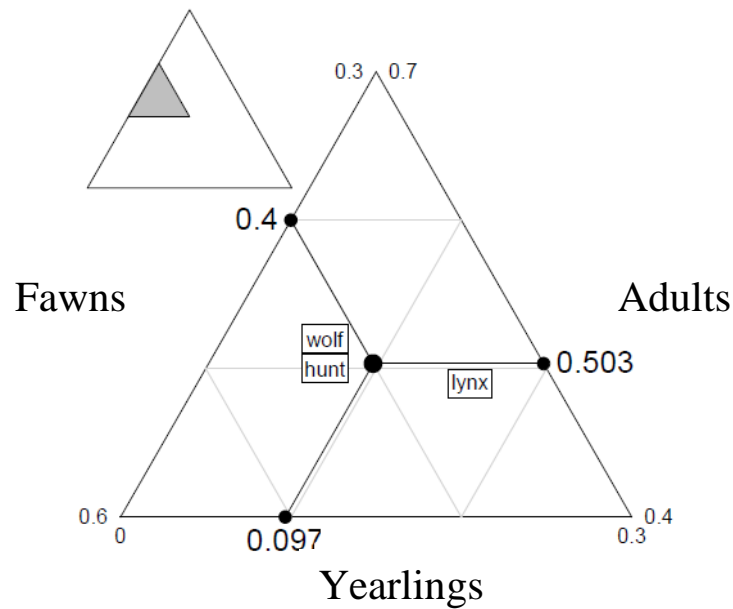
Figure 5: Ternary plot presenting wolf, lynx and hunters' prey composition of fawns, yearlings and adults.

- Sex categories

In general, females were slightly more represented among the prey killed by wolf, lynx and hunters (Fig. 6). We can distinguish two group of predators, first, wolves and lynx which show similar proportions of females (%$_{Wolf-killed}$=61 and %$_{Lynx-killed}$=62.5) and similar proportions of males (%$_{Wolf-killed}$=39 and %$_{Lynx-killed}$=37.5%). Hunters, seemed to kill slightly less females (54%) than wolf and lynx (%$_{Wolf-killed}$=61 and %$_{Lynx-killed}$=62,5%), and more males (%$_{Hunter-killed}$=46% versus %$_{Wolf-killed}$=39 and %$_{Lynx-killed}$=37,5%). However, although I found differences in the preys' sex categories frequencies of occurrence, a Chi-square goodness-of-fit tests did not show any significant differences among the three predator (χ^2 = 1.2015; p-value = 0.548). In addition, there is no difference in the proportion of sex of roe deer between predator-killed and the standing population.
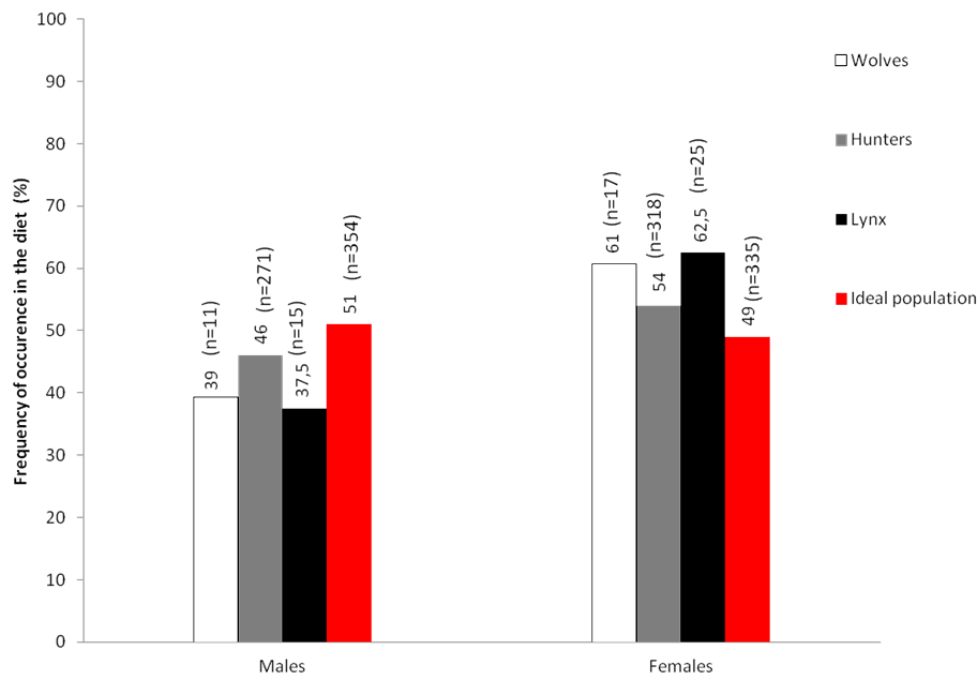

Figure 6: Proportions of roe deer killed by wolves, lynx and hunters, for each sex category. In red are the proportions of roe deer in the model population, used as a control to the predation studies.

16

For hunters (%$_{\text{Extremely-Poor}}$=13% and %$_{\text{Poor}}$=7%), and in a lesser extent for wolves (%$_{\text{Extremely-Poor}}$=17% and %$_{\text{Poor}}$=17%) individuals in poor or extremely poor body condition were low (Fig.7). Wolves and hunters seemed to kill mainly roe deer in fair body condition. Indeed, roe deer in fair body condition represented 63% for wolves and 80% for hunters of the prey killed. As for other prey categories, a Chi-square goodness-of-fit test did not show any significant differences among the two predator (χ^2= 2.5458; p-value = 0.467).
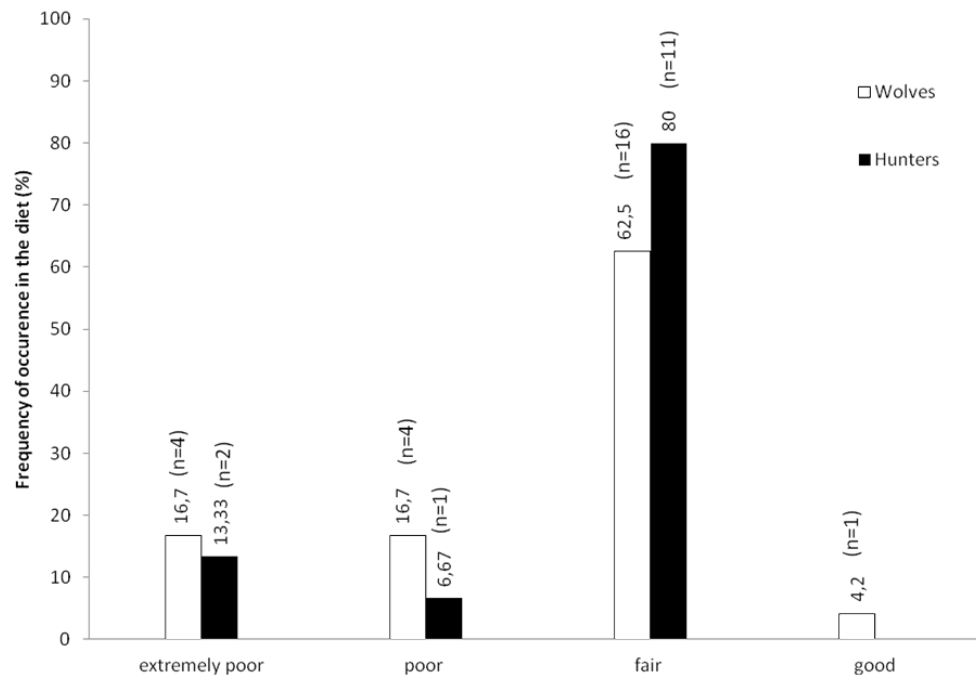

Figure 7: Proportions of roe deer killed by wolves, lynx and hunters, for each body condition category: extremely poor, poor, fair and good body condition.

Trophic niche analysis: breadth and overlap

Concerning age categories, lynx showed the broadest trophic niche (B'= 0.66, Fig.8), which could describe a consumption more equally distributed for all prey age categories compared to the other predators. Wolf and hunters had a similar lower index (B'= 0.48, Fig. 8), which was identified by a diet predominantly composed by two age categories of prey (*i.e.* fawns and adults, Fig. 3). Other prey categories were still present but in smaller proportions (Fig.3). Regarding sex, all predators presented very high indices (B'= 0.91, 0.98 and 0.88 respectively). That means that they tend to kill females in similar frequencies as males. Finally, concerning body condition categories (Fig.3), low indices showed that both wolf and hunters tend to mainly prey on individual in fair body condition (B'= 0.40 for wolf and 0.17 for hunters).
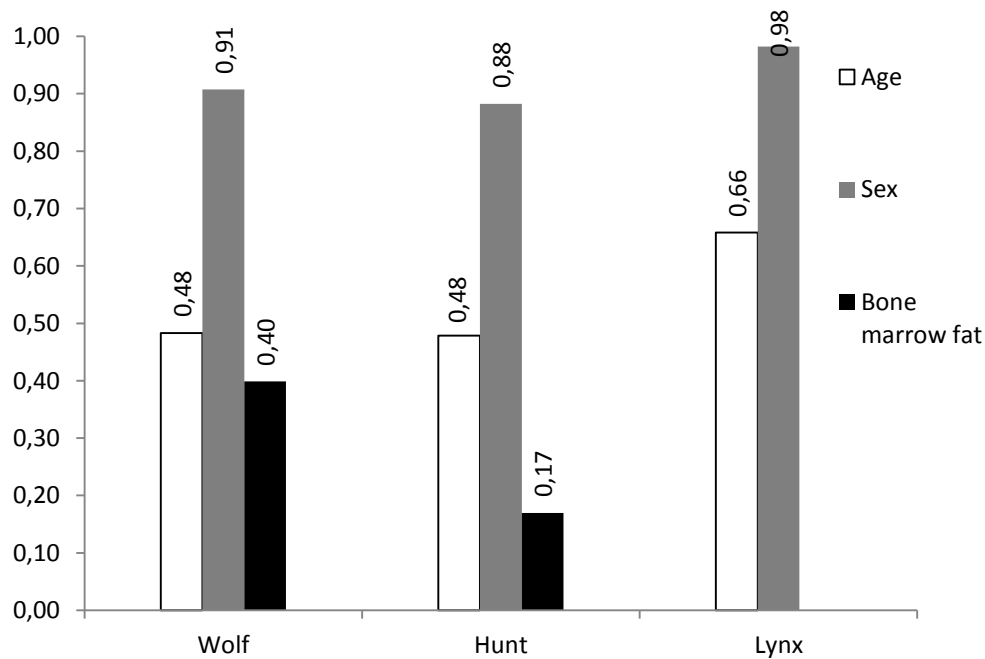
Figure 8: Standardized Levins' Indices: niche breadth for each age, sex and body condition of prey categories, killed by wolves, hunters and lynx.

Pianka's indices (Table 5) described the niche overlap between wolf, lynx and hunter harvest (diet similarities among pair of predators). Concerning age categories, it seemed that wolf, lynx and hunter harvest, resulted in a nearly complete overlap of their trophic niches, with indices ranging between 0.981 ($R_{Hunters-Lynx}$) and 0.999 ($R_{Hunters-Wolf}$). Then, for sex categories, indices were also very high, and they tend to range between 0.989 ($R_{Hunters-Lynx}$) and 0.999 ($R_{Lynx-Wolf}$). In all cases, indices were very high and almost equivalent to one, which indicated that the three predators had strong similarities in their prey choice regarding age and sex categories (mainly adults and fawns, and females). In addition, the niche overlap for body condition estimated for hunters and wolves was very high ($R_{Wolves-Hunters}=0.961$). This suggested that their patterns are very similar and both of them prey upon individual in fair body condition (Fig.7).

Table 5 : Pianka's indices: niches' overlap between the different predators.

		Hunt	*Wolf*	*Lynx*
	Hunt	0		
Age	*Wolf*	0.999	0	
	Lynx	0.981	0.983	0
	Hunt	0		
Sex	*Wolf*	0.995	0	
	Lynx	0.989	0.999	0
Bone marrow	*Hunt*	0		
fat	*Wolf*	0.961	0	

The dissimilarity matrix derived from Pianka's indices values, indicated differences between the different predators trophic niches for prey category preference. The resulting dendrogram allows me to make a distinction between different groups of predators for each prey category. For age categories (Fig. 9.a), I can distinguish lynx on the one hand, and wolf and hunt harvesting on the other. For sex categories (Fig. 9.b), hunters can be distinguished from wolf and lynx, because they are represented on a separated branch of the tree. However, distances separating all predators on trees are very small (<0.20), indicating important similarities in the selection for age and sex patterns of roe deer.

Figure 9: Dendrograms calculated with mean link aggregation criteria. These figures illustrate the niche overlap among predators concerning prey a) *age* categories and b) *sex* categories.

Prey selectivity for age and sex categories

Regardless of the age categories analysis, I obtained four selectivity indices for each predator, one for each age categories (Fig. 10). The first observation showed that all predators tend to select fawns ($D_{wolves}= 0.04$, $D_{Hunters}= 0.05$ and $D_{Lynw}=0.009$) and adults ($D_{wolves}=D_{Hunters}=0.05$ and $D_{Lynx}=0.003$), or under-select yearlings ($D_{wolves}= D_{Hunters}= -0.05$ and $D_{Lynw}=-0.03$). Concerning sex categories (Fig. 11), all three predators, tend to select females ($D_{wolves}= 0.11$, $D_{Lynx}=0.14$ and $D_{Hunters}= 0.06$), over males (indices < 0). In general, for all predators, and for age and sex categories, the entire indices are almost equivalent to 0 which indicates a very low degree of selection. Thus, selection seemed to be proportional to categories' availability in the prey population.
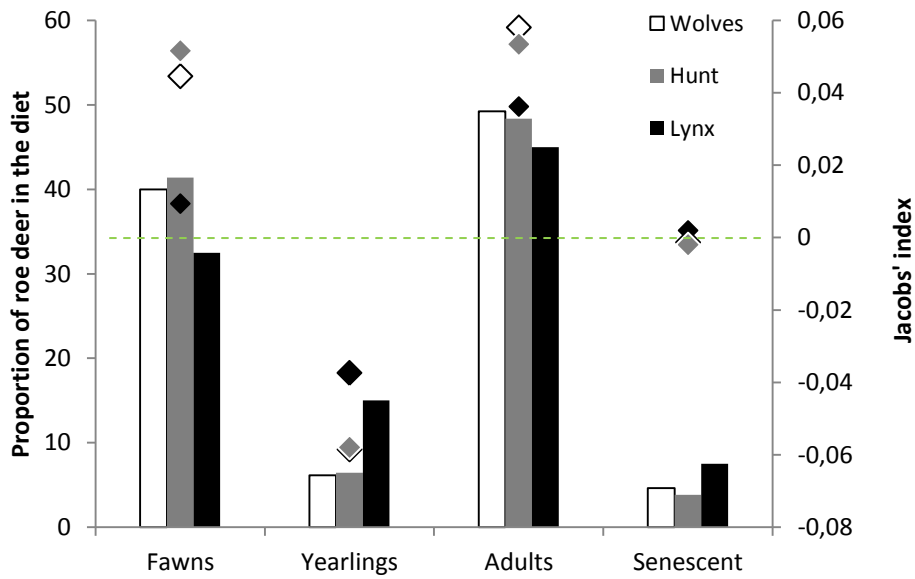
Figure 10: Jacob's selectivity index: selection of age categories. These indices show the preference and selection among the different predators for the different age categories of prey. Bar charts represent the proportion of roe deer killed by each predators (left scale), and points illustrate the Jacob's indices for each predator (right scale).

Figure 11: Jacob's selectivity index: sex categories selection. These indices show the preference and selection among the different predators for the different *sex* categories of prey. Bar charts represent the proportion of roe deer killed by each predators (left scale), and points illustrate the Jacob's indices for each predator (right scale).
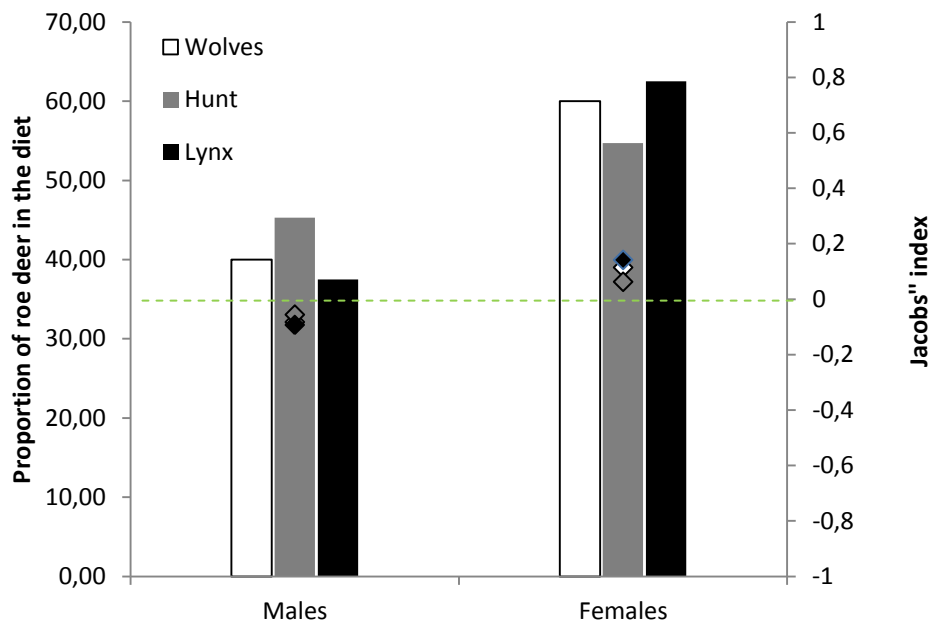
Identification of factors influencing prey selection

      For each performed model, over-dispersion was tested and was insignificant in all cases. That means that selected models were correctly adjusted to my datasets.

(1) Regardless exploration of wolf selection's patterns, the different models were relatively conclusive. The multinomial model, used to investigate selection among *i*) age categories, showed that roe deer densities within wolf territories can significantly explain variation in prey choice (Table 6, model MWage). Wolves seem to kill more fawns when roe deer's densities are low, whereas more adults are killed at high densities (Fig. 12). Moreover wolves' pack size, also tend to significantly explain the prey choice (Table 6, model MWage) with more young killed in small packs. The date of kill (late or early winter) does not seem significant. The generalized linear model, used to explore selection for *ii*) body condition categories, showed that roe deer densities within wolf territories and pack size was not important for the prey choice (Table 5, model MWbmf). The generalized linear model used in order to indentify choice among *iii*) sex categories revealed that only pack size was significantly related to the prey choice (Table 6, model MWsex). Larger wolf packs were associated with killing more male roe deer than smaller packs (Fig. 13).

(2) A generalized linear model showed that body condition of killed roe deer was not influenced by the cause of death (Table 6, model Mbmf).
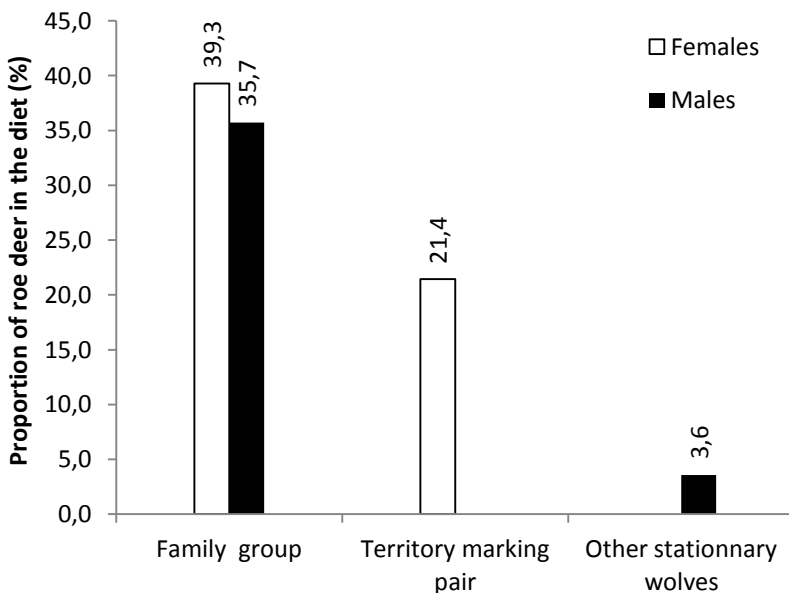

Figure 13 : Proportions of roe deer killed in each age categories related to different roe deer densities.
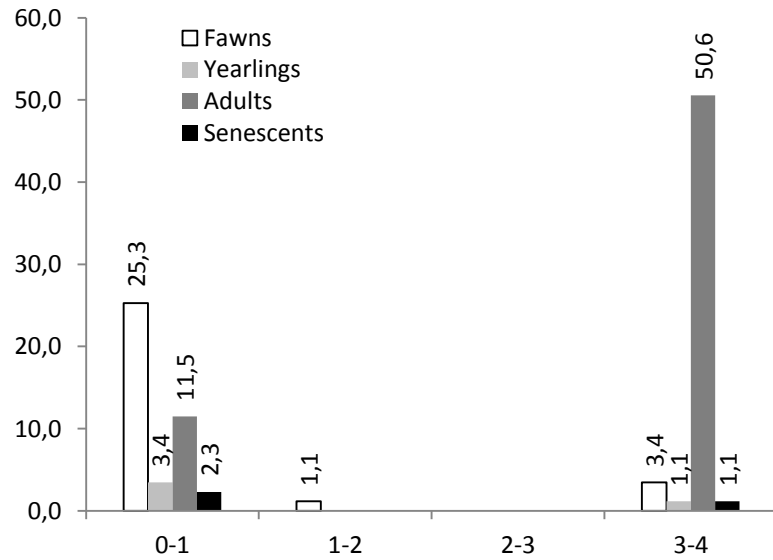
Figure 12 : Proportions of roe deer killed in each sex categories related to different wolf pack' status.

Tableau 2 : Parameters obtained for each factors

	Model	Response variable	Factors	LR Chisq	Df	Pr (>Chisq)
		Age	Winter period	4.1304	3	0.24772
	MWage		Roe deer density	9.1348	3	0.02755 *
			Pack structure	12.4595	6	0.05247 .
(1) Wolf selection patterns	MWbmf	Body condition	Roe deer density	2.6766	1	0.10183
			Pack structure	2.8293	1	0.09256 .
			Winter period	0.3164	1	0.573774
	MWsex	Sex	Pack structure	1.7181	1	0.006838 **
			Roe deer density	7.3150	1	0.189939
(2) Body condition selection	Mbmf	Cause of death	Body condition	2.9528	2	0.2285

IV. Discussion

1. Predation patterns analyses

Wolf selection's patterns among roe deer age and sex categories

Wolf predation patterns on roe deer *age* categories showed that wolf preyed significantly more upon fawns (0-1 year) and adults (2-7 years) compared to the standing population. Yearlings (1-2 year) and senescent (> 7 years) individuals were taken in lesser proportion than other categories (Fig.3). Jacob's index suggested that age categories are consumed according to their availability in the population only. Here the analyses show a statistical difference (cf. chi-square which biologically might be small). The high presence of fawns (40%) in the diet could be explained by the fact that it has been observed that predators preferentially select young or senescent animals because they are less able to escape predation (Mech 1970; Curio 1976; Karanth & Sunquist 1995). In addition, optimal foraging theory predicts that predators tend to choose the most profitable prey (MacArthur & Pianka 1966; Charnov 1976). For large predators the most profitable prey is the largest available they can safely kill (Sunquist & Sunquist 1989). Within the roe deer population, adults are the largest available prey that wolves can prey upon safely and, this could explain the unexpected high presence (49.2%) of adult roe deer in wolves' diet. Yearling's occurrence in wolf's diet was low (6.2%), as compared to the standing population (26.9%). This is opposed to Jacob's index suggestion (see above). I expected yearlings to be more hunted than prime age adults, because of their lack of experience or naive behavior facing predators. Although, during their first winter, fawns stay with the doe (Nordström, 2010), that allowed them to learn how to react to predator presence or attack. Additionally, fawns reach about 70% of adult body size during their first winter (Andersen *et al*. 1997), so they are strong enough to escape predation when they are yearlings and that could probably express the observed yearling occurrence in the diet.

Wolf predation patterns regarding roe deer *sex* categories showed that wolf selected 22% more females than males although it was not confirmed with the Jacob's index (D = 0.11, predation proportional to availability). It is difficult to explain the relatively high predation on females, because in contrast to the results, several studies among ungulate populations proved that predation is skewed towards males (Fitzgibbon 1990; Karanth & Sunquist 1995). This can be explained by the fact that males are often solitary with no group-shared vigilance (Taylor 1984), and thus more vulnerable to predation.

In summary, wolves showed very low selection towards different age and sex categories. This selection pattern tended to be proportional to prey category availability in the population and could illustrate the opportunistic behavior of wolves (Okarma *et al*. 1995).First, in Scandinavia moose is the major prey for wolves (Wabakken 1992; Olson 1997; Muller 2006), but where roe deer are present at high densities wolves appears to be diverse and opportunistic and they will locally prey on roe deer intensively (Appendix II), which is common according to Okarma (1995). In this case wolves will show a lower selection and prey upon all age categories available. Moreover, unlike moose which are big and relatively dangerous prey, roe deer are smaller and do not represent a threat for wolves (see above).

In order to identify which factors influence the prey choice among roe deer categories two models were constructed. First, for age categories, it appeared that roe deer density within wolf territories influenced the prey choice. Indeed, when roe deer density is higher, wolves tend to kill more adult individuals, whereas when the density is lower they prey upon younger ones. Kjellander *et al*. (2004) observed for high roe deer densities, that competition for food or territory defense increase among adult individuals, leading to less awareness of predation risk, or poorer body condition, possibly making them more vulnerable to predation. Wolf pack structure was also identified as a significant factor influencing prey choice among sex categories. Results showed a significant preference towards male individuals when the pack is large (family group, *i.e*. alpha pair with pups). Cooperative hunting among wolves could allow them to select stronger animals, such as males (Pierce *et al*. 2000, Sand *et al.* 2005).

Body condition comparison of wolf and hunter-killed roe deer

Results from this study show that both wolves and hunters predated on roe deer in fair body conditions (62.5 and 80%, respectively). Hunters killed higher proportion individuals in fair body condition, possibly because recreational hunting is associated to trophy hunting hence, providing an honest signal of male phenotypic quality (Vanpé *et al.* 2007).

Unlike hunters, who would be able to judge body condition of a prey, I expected that wolves select a random sample of animals within each body condition group. Here, the prey selection pattern for wolves failed to support the hypothesis that coursing predators show stronger selection for prey in poor body condition. This pattern of killing prey in good body condition was also observed for other canids such as coyotes (Poulle *et al.* 1993). This phenomenon can be explained by the fact that individuals in poor body condition were under represented in the population, although it was not confirmed.

Age and sex selection among roe deer population by wolves, lynx and recreational hunters

Concerning *age* categories, two types of selection patterns can be distinguished; wolves and hunters on the one hand, and lynx on the other hand (Fig. 9.a). This is according to what I expected and suggested by other authors (Okarma *et al*. 1997; Molinari-Jobin *et al*. 2002). Wolves and hunter exhibited a greater tendency to select fawns and adult individuals, than did lynx (Fig. 10). The first explanation could be that hunters may hunt upon adults for trophies, and upon fawns, for meat quality. By contrary, lynx tend to fed also upon yearlings (Fig. 5), therefore, resulting in a broader trophic niche (Fig. 8).

Regarding *sex* categories, again two distinct prey selection patterns emerged when comparing prey attributes for the three predator species (Fig. 9.b), with on the one hand lynx and wolves together, and on the other hand hunters. Thus hunters had a higher proportion of males in comparison to wolf and lynx, whereas the proportion is lower for females in relation to the other predators. This can be related to the priority for trophy hunting exerted by hunters, while females are still represented in higher proportion for all predator species (Fig. 6).

Finally, even if selection patterns among age/sex categories are likely to differ between wolves and hunters, as expected, the results showed more similarities. I expected that wolf predation would be largely compensatory to human harvesting, however, both wolves and recreational hunters selected animals in good physical condition and prime age adults. This indicates that their effect on roe deer mortality is likely to be mostly additive, thus increasing their impact on the population. While most populations can sustain quite high predation rates on yearlings, a rapid growth rate decline occurs when prime-age animals, especially females, are affected by increased mortality (*e.g*., Kinley & Apps 2001; McLoughlin & Owen-Smith 2003). This is what happened in this study and might undermine roe deer population in south-central Sweden.

Lynx exerted the less prey selectivity. The lack of selectivity in lynx pattern can be attributed to the fact that lynx is a stalking predator, thus selecting the prey most easily approached. Lynx's predation pattern in this study is similar to those from the Jura Mountains in Switzerland (Molinari-Jobin et al. 2002) and from Białowieza in Poland (Okarma et al. 1997). All adult lynx can safely kill any roe deer category due to their hunting strategy (*e.g.* stalking predation). Another plausible explanation is that stalking lynx select its prey based on the actual position of the animal, thus do not need to select a vulnerable animal like coursing predators (Fuller 1989).

2. Data sampling: limitations and recommendations

Even if some trends were identified among the different predators' patterns, we have to be aware of some limitations. The analyses were based on data from different time and spatial scale. Wolf predation studies were carried out in fifteen different territories among South-Central Sweden, but data from hunting or lynx killed roe deer were only gathered at GWRA, and Koberg area in a lesser extent. These two territories are characterized by very high densities of roe deer (1.2 and 10 roe deer/km², respectively). Moreover, wolf predation studies within the different wolf territories occurred mainly during late winter (February to May), whereas general roe deer hunting season occurs from the 1st of October to the 31st of January. In addition, the fact that there was no geographical nor time overlap between wolves, hunters, and lynx should be taken into consideration. For an accurate comparison, wolf predation study and hunting season has to be matched in time and space.

Using pellet count as proxy for roe deer density did not allow for estimating the population structure within wolf territories, forcing the use to ideal population structure data. Moreover, the ideal roe deer population used as a control cannot be representative of all wolves' territories. The ideal population was monitored at GWRA, which is not describing the general environmental characteristics of all wolf territories (snow depth, habitats). Indeed, GWRA is characterized by a relatively higher density of roe deer, and by less harsh winter conditions than in some other areas (SMHI 2012, www.smhi.se).

Finally, few data on bone marrow fat content for wolf killed and hunted roe deer were available. The performed analyses were insufficient. With a larger data set it could be interesting to compare body condition among different age and/or sex categories. Moreover, body condition analyses across temporal scale could also be very instructive in order to investigate prey choice with variable body condition. It would be also interesting to carry out predation studies throughout the year in order to get different seasonal predation data, corresponding to the whole hunting season.

V. Conclusions and implications for prey population management

The long-term monitoring of this study suggests that re-colonizing predators play an important role in regulating roe deer population. In summary, the five main results of our study are as follows: (*i*) I did not find the expected wolf predation pattern. Wolves tend to prey upon adults, fawns, senescent and yearlings. Moreover, (*ii*) wolves and hunters select mainly upon individual in fair body condition. Also, (*iii*) analyses do not really reveal a selection toward roe deer males: females seem to be more selected. But I can't really assess

that a sex category is preferred than another: predation is equi-distributed among the two sexes. As I expected (i*v*) lynx are following the pattern: a weaker selected among prey and a selection mainly equi-distributed. Finally, (*v*) wolf predation seems to be largely additive to human-related mortalities.

I can't really predict the influence of wolf predation on roe deer population. In order to calculate real impact, kill rates data would also be necessary. Moreover, the observed disparity between predators in terms of specific prey selection patterns highlights the importance of other factors associated with the predator-prey interaction, such as predator capture success. But if trends have identified are representative of reality, I can predict that: wolf predation risks could be largely additive to human-related mortality causes, which could increase total mortality (Gasaway *et al.* 1992). From an adaptive management point of view, if a management plan tries to control population with the ambition to stabilize a desired level and with specific prey composition, the additive effect of predation has to be taking into account in order to avoid over-predation on one prey type and avoid decreasing population growth-rate. Thus, a hunting management plan could be done in order to compensate wolf-predation, by reducing quotas of adults, especially females.

VI. Acknowledgments

References

Andersen, R., and J. D. C. Linnell. (1997). Variation in maternal investment in a small cervid: the effects of cohort, sex, litter size and time of birth in roe deer (*Capreolus capreolus*) fawns. *Oecologia.* **109**:74-79.

Andersen, R., Karlsen, J., Austmo, L.B., Odden, J., Linnell, J. & Gaillard, J.M. (2007) Selectivity of Eurasian lynx Lynx lynx and recreational hunters for age, sex and body condition in roe deer Capreolus capreolus. *Wildlife Biology.* **13:** 467–474.

Arnemo, J., Ahlqvist, P., Segerström, P. (2004). Biomedical protocol for free-ranging gray wolves (*Canis lupus*) in Scandinavia. *Norwegian School of Veterinary Science*, Tromsø, Norway. Unpublished report.

Aronson, Å., Wabakken, P., Sand, H., Steinset, O.K. & Kojola, I. (2003). Varg i Skandinavien. Statusrapport för vintern 2001/2002. Högskolan i Hedmark, Viltskadecenter, Grimsö forskningsstation, Vilt- och fiskeriforskningen, Oulu. Høgskolen i Hedmark Oppdragsrapport.

Bakker,R . T. (1983).T he deerf lees,t he wolf pursues:in congruities in predator-prey coevolution. In Futuyama,D . J. and Slatkin, M. (eds), Coevolution. Sinauer, p. 350-382.

Ballard, W.B., R. O., Stephenson, And T. H. Spraker. (198l). Nelchina Basin wolf studies. *Alaska Dep. Fish and Game Fed. Aid in Wildl. Restoration Final Prog. Rep. Proj*. W-17-8 through W-17-11. 201p.

Ballard, W.B., Whitman, J.S., Gardner, C.L. (1987). Ecology of an exploited wolf population in South-Central Alaska. *Wildlife Monographs*, 98:1-54.

Bartmann, R.M., White, G.C., and Carpenter, L.H. (1992). Compensatory mortality in a Colorado mule deer population. *Wildlife Monographs*. **121**: 3–39.

Caro,T . M. and Fitzgibbon,C . D. (1992). Large carnivores and their prey: the quick and the dead. In: Crawley, M.J. (eds.), Natural enemies. *Blackwell Scientific Publications*. p. 117-142.

Caughley, G. (1977). Sampling in aerial survey. Journal of Wildlife Management. **41**:605-615.

Caughley, G., and Sinclair, A.R.E. (1994). Wildlife ecology and management. *Blackwell Scientific Publications*, Cambridge, Mass

Cederlund, G. and Liberg, O. (1995). Rådjuret. *Viltet, ekologin och jakten. Almqvist & Wiksell Tryckeri*, Uppsala.

Charnov, E. L. (1976). Optimal foraging: the marginal value theorem. *Theor. Pop-ul. Biol*. **9**:129-36 29.

Cheatum, R.L. (1949). Bone marrow as an index of malnutrition in deer. *N.Y. State Conservation*. **3**: 19–22.

Curio, E. (1976). The ethology of predation. Springer-Verlag, Berlin.

Dauphine, T.C. (1971). Physical variables as an index to condition in barren-ground caribou. *Northeast Fish Wildlife Conference*. **28**: 91– 108.

Errington , P.L. (1946).Predation and vertebrate populations. *The Quarterly Review of Biology*. **21**: 221-245.

Estes, R. D. and Goddard, J. (1967). Prey selection and hunting behavior of the African wild dog. *Journal of Wildlife Management*. **31**: 52-70.

Ewer, R.F. (1973). The carnivores. Cornell University press.

Fitzgibbon. ,D .(1990). The anti-predator behavior of Thomson's gazelle. *Animal Behaviour*, **40**:846-855

Fong, D.W. (1981). Seasonal variation of marrow fat content from Newfoundland moose. *Journal of Wildlife Management*. **45**: 545–548.

Franzmann, A.W., Arneson, P.D. (1976). Marrow fat in Alaskan moose femurs in relation to mortality factors. *Journal of Wildlife Management*. **40**(2): 336–339.

Franzmann, A.W., and Schwartz, C.C. (1998). Ecology and management of the North American moose. *Smithsonian Institution Press*, Washington, D.C.

Fritts S.H. & Mech L.D. (1981). Dynamics, movements and feeding ecology of a newly-protected wolf population in north-western Minnesota. *Wildlife Monographs*. No. 80.

Fuller, T. K., Keith, L.B. (1980). Wolf population dynamics and prey relationships in northeastern Alberta. *Journal of Wildlife Management*. **44**:583-602.

Fuller, T., Coy P. & Peterson W. (1986). Marrow fat relationships among leg bones of white tailed deer. *Wildlife Society Bulletin*. **14**: 73–75.

Fuller, T.K. (1989): Population dynamics of wolves in north-central Minnesota. *Wildlife Monograph.* **105**:1-41.

Gaillard, J.-M., Delorme, D., Boutin, J.-M., Van Laere, G., Boisaubert, B., & Pradel, R. (1993b). Roe Deer Survival Patterns: AComparative Analysis of Contrasting Populations. *The Journal of Animal Ecology*. **62**(4):778.

Gasaway,W., R . O. Stephensoln, D.J.A. Vips,.E . K. Shephearndi, O . E. Burris. (1983). Interrelationships of wolves, prey, and man in interior Alaska. *Wildlife Monographs.* No. 84.

GasawayW. C., Boertje, R. D, Grangaard, D. V.,Kelleyhouse, D.G., Stephenson RO. (1992). The role of predation in limitingmoose at low densities in Alaska and Yukonand implications for conservation. *Wildl.Monogr*. **120**:1-59

Gazzola, A., ferroglio, E., avanzinelli, E., rosso, M., kurschinski, F., apollonio, M. (2007). The physical condition of roe and red deer killed by wolves in a region of the western Alps, Italy. *Folia Zoologica*, **56**(4): 349–353.

Griffen, B. D., & Byers, J. E. (2006). Intraguild predation reduces redundancy of predator species in multiple predatorassemblage. *Journal of Animal Ecology*. **75:** 959-966.

Griffin, K.A., Hebblewhite, M., Robinson, H. S., Zager, P., Barber-Meyer, S. M., Christianson, D., Creel, S., Harris, N.C., Hurley,M.A., Jackson, D.H., Johnson, B. K., Myers, W.L., Raithel, J. D., Schlegel, M., Smith, B.L., White, C., & White, P.J.(2011). Neonatal mortality of elk driven by climate, predator phenology and predator community composition. *The journalof animal ecology*. **80:** 1246-57.

Gustine, D. D., Parker, K. L., Lay, R. J., Gillingham, M. P., & Heard, D. C. (2006). Calf Survival of Woodland Caribou in aMulti-Predator Ecosystem. *Wildlife Monographs.* **165:** 1-32.

Huggard, D. J. (1993). Prey selectivity of wolves in Banff National Park. II. Age, sex and condition of elk. *Canadian Journal of Zoology*. **71**: 140-147.

Husseman, J.S., Murray, D.L., Power, G., Mack, C., Wenger, C.R., Quiley, H. (2003). Assessing differential prey selection patterns between two sympatric large carnivores. *Oikos* **101**: 591 601.

Jacobs, J. (1974). Quantitative measurements of foodselection; a modification of the forage ratio and Ivlev's electivity index. *Oecologia* (Berlin). **14**:413-417.

Jedrzejewski, W., Schmidt, K., Milkowski, L., Jedrzejewska, B., & Okarma, H. (1993). Foraging by lynx and its role in ungulate mortality: The local (Bialowieza Forest) and the palaearctic viewpoints. *Acta Theriologica*. **38**(4): 385-403.

Karanth, K. U. & Sunquist, M. E. (1995). Prey selection by tiger, leopard and dhole in tropical forests. J. Anim. Ecol. **64**:439-450.

Kinley, T.A. & Apps, C.D. (2001). Mortality patterns ina subpopulation of endangered mountain caribou. *Wildlife Society Bulletin.* **29**: 158-164.

Kjellander, P., Gaillard, J.-M., Hewison, M., & Liberg, O. (2004). Predation risk and longevity influence variation in fitness of female roe deer (Capreolus capreolus L.). *Proceedings of the Royal Society the Royal Society, London B (suppl.).* **271:** 338-340.

Kleiman, D. G. and Eisenberg, J. F. (1973). Comparisons of *canid* and *felid* social systems from an evolutionary perspective. *Animal Behavior*. **21**: 637-659.

Krebs, J.R. (1973). Perspectives in ethology, **1973** - *Plenum Press*, New York

Krebs, C.J. (1998). Ecological Methodology, HarperCollins, New York, USA (1998)

Kruuk, H. (1972**).** The Spotted Hyena. A Study of Predation and Social Behaviors. *University of Chicago Press,* Chicago.

Kruuk, H. (1986). Cats of the world :Interactions between *felidae* and their prey species: a review.In: Miller, S. D. and Everett, D. D. (eds), *National Wildlife Federation*, Washington DC, p. 353-374.

Kunkel, K.E., and Pletscher, D.H. (1999). Species-specific population dynamics of cervids in a multipredator ecosystem. *Journal of Wildlife Management*. **63**: 1082–1093.

Lima, S.L., Dill, L.M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**: 619-640.

Litvak, M. K. and Leggett, W. C. (1992). Age and size-selective predation on larval fishes: the bigger-is-better hypothesis revisited. *Marine Ecology Progress*. **81**: 13-24.

Loison, A., Festa-Bianchet, M., Gaillard, J.-M., Jorgenson, J. T., & Jullien, J.-M. (1999). Age-Specific Survival in Five Populations of Ungulates: Evidence of Senescence. *Ecology*. **80**(8): 2539-2554.

MacArthur, R. H. Pianka, E. R. (1966). On optimal use of a patchyenvironment. *Am. Natur*. **100**:603-9114.

McCullough, D.R. (1979). The George Reserve deer herd: population ecology of a K-selected species. *University of Michigan Press*, Ann Arbor.

McLoughlin, C.A. & Owen-Smith, N. (2003). Viability of a diminishing roan antelope population: predation is the threat. *Animal Conservation*. **6**: 231-236.

Mech, L.D. (1970). The wolf: the ecology and behavior of an endangered species. *Doubleday/Natural History Press*, Garden City, N.Y.

Mech L.D., Meier T.J. Burch J.W. & Adams L.G. (1995). Patterns of prey selection by wolves in Denali National Park, Alaska. In: Carbin L.N., Fritts S.H. & Seip D.R. (eds), Ecology and conservation of wolves in a changing world. *Canadian Circumpolar Institute Occasional Publication*. **35**: 231–243.

Mech, L.D., and DelGiudice, G.D. (1985). Limitations of the marrow fat technique as an indicator of body condition. *Wildlife Society Bulletin*. **13**: 204–206.

Mech, L. D., Smith, D. W., Murphy, K. M. and MacNulty, D. R. (2001). Winter severity and wolf predation on a formerly wolf-free elk herd. – *Journal of Wildlife Management*. **65**: 998- 1003.

Molinari-Jobin A., Molinari, P., Breitenmoser-Würsten, C, Breitenmoser, U. (2002) Significance of lynx *Lynx lynx* predation for roe deer *Capreolus Capreolus* and chamois *Rupicapra rupicapra* mortality in the Swiss Jura Mountains. *Wildlife Biology*. **8**:109–115.

Müller, S. (2006). Diet composition of wolves (*Canis lupus*) on the Scandinavian peninsula determined by scat analysis. English summary of the diploma thesis, School of Forest Science and Resource Management, Technical University of München, Germany

Neiland, K.A. (1970). Weight of dried marrow as indicator of fat in caribou femurs. *Journal of Wildlife Management*. **34**(4): 904–907.

Nordström, J. (2010). Temporal and Spatial Variation in Predation on Roe Deer Fawns. *Acta Universitatis Agriculturae Suecia*.Doctoral thesis No. 2010:6.

Olsson, O., Wirtberg, J., Andsson, M., Wirtberg, I. (1997): Wolf *Canis lupus* predation on moose *Alces alces* and roe deer *Capreolus capreolus* in south-central Scandinavia. *Wildlife Biology*. **3**(1): 13-25.

Okarma H. (1984). The physical condition of red deer falling prey to the wolf and lynx and harvested in the Carpathian mountains. *ActaTheriologica*. **29** (11–25): 283–290.

Okarma H. (1991) Marrow fat content, sex and age of red deer killed by wolves in winter in the Carpathian mountains. Holarctic Ecology. 14: 169–172.

Okarma, H., B. Jedrzejewskaw, . Jedrzejewskzi,. A. Krasinski, And L. Milkowski. (1995). The roles of predation, snow cover, acorn crop, and man-related factors on ungulate mortality in Bialowieza Primeval Forest, Poland. *Acta Theriologica.* **40**:197-217.

Okarma, H., W. Jedrzejewskik, . Schmidt, R. Ko- Walczyk, And B. Jedrzejewska. (1997). Predation of Eurasian lynx on roe deer and red deer in Bialowieza Primeval Forest, Poland. *Acta Theriologica.* **42**:203-224.

Pastorok, R. A. (1981). Prey vulnerability and size selection by *Chaoborus larvae*. *Ecology* **62**: 1311-1324.

Pianka, E. R. (1974). Niche overlap and diffuse competition. *Proceedings of the National Academy of Science*, USA. **71**:2141-2145.

Pehrson,A. (1997): Metoder för viltövervakning – erfarenheter fran forsok vid Grimsö . - Report no 4758, Naturvardsverket, Stockholm, 48 pp. (In Swedish).

Persson, J. and Sand, H. (1998). Vargen: viltet, ekologin ochmanniskan. Uppsala: *Svenska Jagareforbundet.*

Persson, J., Sand, H., Wabakken, P. (1999). Biologiska karaktärer hos varg viktiga för beräkningar av livskraftig populationsstorlek. Ebenhard, T. & Höggren, M. (reds). *Livskraftiga rovdjursstammar*. Uppsala. P. 55-67.

Peterson, R. O. (1977). Wolf ecology and prey relationships on Isle Royale. *U. S. National Park Service's Science Monographs*. Ser. No. 11.

Peterson R.O., Woolington J.D., Bailey T.N. (1984): Wolves of the Kenai Peninsula, Alaska. *Wildlife Monograms*. No 88.

Pierce, B.M., Bleich, V.C.&Bowyer, R.T. (2000). Selection of mule deer by mountain lions and coyotes; effects of hunting style, body size, and reproductive status. *Journal of Mammalogy*. **81**: 462-472.

Pimlott, D.H. (1967). Wolf predation and Ungulate populations. *American Zoologist*. **7**, No. 2, p. 267-278

Pole, A., Gordon, I.J., and Gorman, M.L. (2003). African wild dogs test the 'survival of the fittest' paradigm. Proceeding Royal Society of London -B Biology Sciences. 270(Suppl.1): S57.

Polechova, J., Storch, D. (2005). Ecological niche. In: Encyclopedia of Ecology.Elsevier, Amsterdam, The Netherlands.

Poulle, M.L., Crête, M., Huot, J., and Lemieux, R. (1993). Prédation excercée par le coyote, Canis latrans, sur le Cerf de Virginie, Odocoileus virginianus, dans un ravage en declin de l'Est de Québec. *Can. Field-Nat*. **107**: 177–185.

Ratcliffe P.R. (1980). Bone marrow fat as an indicator of condition in roe deer. *Acta Theriologica*. **25**: 333–340.

Rosenzweig, M. L. (1966). Community structure in sympatric carnivora. *Journal of Mammalogy*. **47**: 602-612.

Sand, H., Zimmermann, B., Wabakken, P., Andrèn, H., and Pedersen, H.C. (2005). Using GPS-technology and GIS-cluster analyses to estimate kill rates in wolf–ungulate ecosystems. *Wildlife Society Bulletin*. **33**(3): 914–925.

Sand, H., Wabakken, P., Zimmermann, B., Johansson, Ö., Pedersen, H.-C., and Liberg, O. (2008). Summer kill rates and predation pattern in a wolf-moose system: can we rely on winter estimates? *Oecologia*. **156**(1): 53-64.

Sand, H., Wikenros, C., Ahlqvist, P., Strømseth, T.H., Wabakken, P. (2012). Comparing body condition of moose (*Alces alces*) selected by wolves (*Canis lupus*) and human hunters: consequences for the extent of compensatory mortality. *Canadian Journal of Zoology*. **90**(3):403-412

Schaller, G. B. (1972). The Serengeti lion: a study of predator prey relationships. - *Univ. of Chicago Press.*

Sih, A. (1987). Predator and prey lifestyles: an evolutionary and ecological overview. In: Kerfoot WC, Sih A (eds) *Predation: direct and indirect impacts on aquatic communities*. University Press of New England, Hanover, p. 203-224

Sih, A. and Moore, R. D. (1990). Interacting effects of predator and prey in determining diets. In Hughes, R. N. (eds.). *Behavioural mechanisms of food selection*,Springer-Verlag, p. 771-796.

Śmietana, W. (2005). Selectivity of wolf predation on red deer in the Bieszczady Mountains, Poland. *Acta Theriologica*. **50**(2): 277-288.

Sunquist,M.E., Sunquist, F.C. (1989). Ecological constraints on predation by large *felids*. In: Gittleman, J.L. (eds.), *Carnivore Behavior, Ecology, and Evolution.* Cornell University Press, Ithaca, p. 283-301.

Taylor, R.J. (1984) Predation. - Chapman and Hall, London, 166 pp.

Temple, S. (1987). Do predators always capture sub-standard individuals disproportionately from prey populations? *Ecology*, **68**(3): 669–674.

The-Berge, J.B., Gauthier, D.A. (1985). Models of wolf-ungulate relationships: when is wolf controlled justified ? *Wildlife Society Bulletin*. **13**(4): 449-458

Vanpé, C., Gaillard, J.M., Kjellander, P., Mysterud, A., Magnien, P., Delorme, D., Van Laere, G., Klein, F., Liberg, O. & Hewison, A.J.M. (2007) Antler size provides an honest signal of male phenotypic quality in roe deer. *American Naturalist.* **169:** 481–493.

Wabakken, P., Sand, H., Liberg, O. & Bjärvall, A. (2001). The recovery, distribution and population dynamics of wolves on the Scandinavian Peninsula, 1978-98. *Canadian Journal of Zoology* **79**: 710-725.

Wabakken, P., Aronson, Å., Strømseth, T.H., Sand, H., Kojola, I. (2004). Ulv i Skandinavia. Statusrapport for vinteren 2003-2004. Høgskolen i Hedmark, Viltskadecenter, Grimsö forskningsstation, Rovdata, SKANDULV, Vilt- og fiskeriforskningen Oulu. Høgskolen i Hedmark Oppdragsrapport.

Wabakken, P., Aronson, Å., Strømseth, T.H., Sand, H., Maartmann, E.M., Svensson, L., Flagstad, Ø., Hedmark, E., Liberg, O. & Kojola, I. (2011). Ulv i Skandinavia. Statusrapport for vinteren 2010-2011. Høgskolen i Hedmark, Viltskadecenter, Grimsö forskningsstation, Rovdata, SKANDULV, Vilt- og fiskeriforskningen Oulu. Høgskolen i Hedmark Oppdragsrapport.

Wabakken, P., Sand, H., Liberg, O., & Bjärvall, A. (2011). The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978-1998. *Canadian Journal of Zoology.* **79:** 710-725.

Wikenros, C., Liberg, O., Sans, H., Àndren, H. (2010).Competition between recolonizing wolves and resident lynx in Sweden. *Canadian Journal of Zoology.* **88**(3): 271-279

Websites:

R Development Core Team (2011). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Skandulv website, visited on March 31st 2012,
http://skandulv.nina.no/.

Swedish Hunters Association's Wildlife Monitoring website, visited on April 27th 2012,
http://www.jagareforbundet.se/Hunting-in-Sweden/.

Swedish Meteorological and Hydrological Institute, visited on June 14th 2012, September 18th,
http://www.smhi.se/

APPENDIX I

Table 1: Number of roe deer killed by wolves, lynx and hunters during winter, for a) each age, b) sex, and c) body condition categories.

a)

	Fawns (n=277)	Yearlings (n=47)	Adults (n=328)	Senescents (n=28)
Wolves	26	4	32	3
Lynx	13	6	18	3
Hunt harvesting	238	37	278	22

b)

	Males (n=359)	Females (n=287)
Wolves	17	11
Lynx	25	15
Hunt harvesting	317	261

c)

	Extremely poor (n=6)	Poor (n=5)	Fair (n=27)	Good (n=1)
Wolves	4	4	16	1
Hunt harvesting	2	1	11	0

Table 2: Number of roe deer for age and sex category in the model population

age category			
Fawns	Yearlings	Adults	Senescents
606	524	751	118
Sex category			
Males	Females		
354	335		