

# **Prey Choice of Scandinavian Wolves in Winter**

*Effects of prey density and composition on patterns of prey  
switching and optimal foraging*

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## **ABSTRACT**

Predators are able to influence the dynamics of their prey populations and may therefore be in conflict with man for game. In this study, I have evaluated the prey choice of wolves in a two-prey system, including moose (*Alces alces*) and roe deer (*Capreolus capreolus*), using data on a total of 353 wolf-killed ungulates in 14 Scandinavian wolf territories where wolves were fitted with GPS-collars. Using the Manly's alpha index as well as Jacob's and Murdoch's indices of preference, I detected a selection for roe deer (Fisher's exact test;  $p < 0.01$  and  $p < 0.001$ ) in two of the Scandinavian wolf territories with among the highest absolute roe deer population densities. The ratio of roe deer to moose did not seem to explain this preference.

A Generalized Linear Mixed Model with a binomial Bernoulli distribution reveals a significant ( $p = 0.001$ ) effect of the local roe deer population density on the prey choice of wolves. Around a threshold population density of 35 roe deer/10km<sup>2</sup>, roe deer become the more likely prey choice of wolves whereas at lower roe deer population densities, moose are the most likely prey. Including pack size as a variable improved the model slightly, although its effect was not statistically significant. I found no statistically significant effect of moose population density, snow depth, winter progress or the time since the previous kill on the wolves' choice to kill moose or roe deer. My results show that the availability of one prey species can have effects on the wolf predation pressure of another, suggesting that game management plans may favourably be made on an ecosystem level.

## 1. INTRODUCTION

### 1.1 *Returning wolves in Scandinavia*

Large carnivores are making a comeback in large parts of Europe. Subsequent to their temporary absence from Scandinavia, the wolf (*Canis lupus*) has now returned to reclaim its place as top predator in the native fauna (Sand et al. 2010). The return of the wolf has been a controversial issue with mixed opinions and political concern. One of the conflicts surrounding the returning wolf population is the competition with man for game animals (Ericsson et al. 2004, Sjölander-Lindqvist 2006, Bisi et al. 2010). Previous studies have shown that moose (*Alces alces*) and, in only a few areas, roe deer (*Capreolus capreolus*) are the main prey of Scandinavian wolves (Olsson et al. 1997; Sand et al. 2010). Moose and roe deer are also the most common game species for humans in Sweden and are subject to a substantial annual harvest (Swedish Hunters Association 2011). The deer hunt is an annual highlight to most of Sweden's 260,000 hunters (Risberg 2011), and most members of the public eat venison and are favourable toward hunting (Ljung 2011).

Since their re-establishment, the Scandinavian wolf population has mainly been distributed in areas where the relative moose density is high compared to that of other ungulate species, which likely influences the wolves' prey choice (Sand et al. 2010). But as the wolf population grows, it is expected to expand its range and wolves are already beginning to establish territories further south in Sweden (Sand et al. 2010). If the establishment continues south, wolves will soon be found in habitats with a different prey composition, with increased densities of roe deer, and eventually wild boar (*Sus scrofa*), red deer (*Cervus elaphus*), and fallow deer (*Dama dama*).

Although the Scandinavian wolf population and their predation on wild game have been thoroughly studied in moose rich areas (e.g. Zimmermann et al. 2007; Sand et al. 2010; Sand et al. 2012a), we have little knowledge of how the presence of multiple prey species will affect their prey choice. The objective of this study is to make a first investigation into the prey choice of Scandinavian wolves in a two-prey system with moose and roe deer. The results are important for the effective management of large carnivores and game in Scandinavia but also for the design of future research on wolf ecology. Although providing full answers on sustainable harvest of ungulates in wolf

territories is beyond the scope of this study, our aim is to improve our knowledge on the complexity of wolf predation in a two-prey wolf system.

### *1.2 Theory of prey switching and optimal foraging*

Food choice and efficient foraging are important factors affecting an animal's survival and reproduction and is therefore a strong force in the evolution of animals (e.g. Gregg & Crawford 2007, Whitehead et al. 2012). Wolves are highly adaptable predators that feed opportunistically and have a good ability to locate their food (Peterson & Cuicci 2003). Thus, wolves are likely able to adjust their diet and prey choice in order to forage efficiently and selectively in response to variation in prey availability and environmental conditions (Dale et al. 1995).

The effects of prey population density and proportional abundance of prey on the prey choice of predators have been described by two major theoretical concepts. Prey switching describes a change in the predator preference for a certain prey species (Murdoch 1969; Murdoch et al. 1975) where the proportion of a certain prey in the diet is disproportionately small at low relative prey densities and disproportionately large at high relative prey densities (Garrott et al. 2007, Bissett et al. 2012). Thus, the theory of prey switching describes a deviance from a proportional predation (1:1) dependent on the abundance of all prey in the system (Murdoch 1969). The theory of optimal foraging, on the other hand, assumes that the predator should ignore less profitable prey regardless of the total prey densities so long as the most profitable prey occurs at a sufficient density (Krebs et al. 1977). Hence, the predation pressure on a secondary prey species may vary depending on the density of a primary prey, with effects on the game availability to other carnivores and hunters.

### *1.3 Choosing profitable prey and effects of prey population density*

The basis of efficient and profitable prey acquisition is for the predator to maintain a positive energy budget, generally by maximizing the income of prey biomass to the costs of search and killing (MacArthur & Pianka 1966). Whereas all prey items available to the predators provide food and energy (Krebs 1978), the benefit of a specific prey animal depends largely on the size of the animal, i.e. the mass of food that it provides. A large prey animal is thus more beneficial than a small prey and should generally be

considered the preferred prey within the predator's size range (Kunkel et al. 2004, Shultz & Finlayson 2010). The cost of food acquisition will be affected by the energy that the predator spends to locate, chase, subdue and kill the prey. This effort will change with prey population density, as the likelihood of an encounter between predator and prey should increase with increasing numbers of prey (Giralderau 2008). Thus, the profitability of equally sized prey may be very different depending on their abundance, potentially inducing a shift in the predator's diet (Messier 1995).

#### *1.4 Predictions and research questions*

Environmental factors may also affect the cost of prey acquisition. Snow depth may affect the effort involved for wolves to chase the prey animal or the efficiency by which the prey animal moves around (Mech & Peterson 2003; Nowak et al. 2005; Hegel et al. 2010). Likewise, snow depth and quality will change as the winter proceeds, and so will the condition of over-wintering animals (Mech & Peterson 2003; Nicholson et al. 2008; Keech et al. 2011). Additionally, the wolves' motivation to kill may change, depending on hunger (Sandre et al. 2010). Hence, we would expect that variables like pack size and the time since the previous meal could affect the prey choice. We would like to control for these factors. Because environmental factors may vary with locality, their effects on prey choice are likely of consequence for the effects of wolves on game populations.

In this study we use data from a number of geographically discrete Scandinavian wolf territories, to evaluate the effects of moose and roe deer population density as well as the effects of environmental factors on wolf prey preference and foraging response during winter. This is the first study that attempts to evaluate the prey choice in terms of moose and roe deer in Scandinavia, as wolves have only recently begun establishing in roe deer rich territories.

The specific research questions are:

1. Do Scandinavian wolves show a preference for one ungulate species over another?
2. Do wolves in Scandinavia change their predation focus from a primary to a secondary prey as a function of relative or absolute density of this prey in the environment?

3. How do prey characteristics, such as prey population density, and environmental conditions like snow depth and quality affect the prey choice in Scandinavian wolves in winter?
4. Using analyses of preference, can we find evidence of prey switching in the Scandinavian wolves in response to changing prey densities?

## **2. MATERIALS AND METHODS**

### *2.1 Study area*

The 14 wolf territories that are included in this study are located in the South Central parts of the Scandinavian Peninsula (GCS RT 1990: N°6533326-6879041, E°1247004-1657661), with one wolf territory on the Norwegian side of the border and the remaining territories located in Sweden. The area, and the territories therein, encompass forested areas with bogs and lakes, as well as cultivated agricultural land and human settlements. The main areas occupied by the wolves are in cultivated forest, mainly consisting of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), but with some intermixing of birch (*Betula pentula* and *Betula pubescens*), aspen (*Populus tremula*) and alder (*Alnus incana* and *Alnus glutinosa*) (Mattisson et al. 2012).

### *2.2 Kill location and identification*

In order to find kill sites and identify all the prey taken by wolves during the study periods we have used Global Positioning System (GPS) collars for wolves. The wolves were darted from helicopters and collars were fitted according to the methods of Sand et al. (2006). The collars were programmed so that at least one of the marked wolves in each territory sent positions at 30 or 60 minutes intervals. This positioning schedule provided us with an almost complete overview of the wolves' movement pattern during the study period. Using the geographical software ArcView GIS®, ArcGIS® and ArcMap™ by ESRI (2009) we plotted the coordinates on a map for viewing. Coordinates were then transferred to a hand held GPS and used as a basis for field visits of a selected sample (>90%) of all positions.

Because the wolves are assumed to spend some time at the carcass of a killed prey animal in order to handle, consume and digest the prey, we expect to get multiple positions from the collars at kill sites. All positions within 200 meters from one another

were visited in the field in search for prey carcasses. To identify such locations we created a buffer around each point in ArcView® or ArcMap™, with a radius of 100 meters (Sand et al. 2005, Zimmermann et al. 2007). Clusters of positions generated from overlaying buffers were all visited in the field, and as many single positions as possible were also located and searched for prey remains and traces of the wolves. Using this method we assume that the majority of larger prey items were detected.

For all kills found, field staff identified the species of the killed prey. A search was done for hunting tracks and signs of pipe bleeding at the kill site. Additionally, field staff also made an estimation of the proportion of the carcass consumed and the time of death of the animal for comparison with the wolves' first position at the site. Together, these observations were used to determine if wolves were responsible for the killing of the prey, or merely scavenged on an already dead animal. The study period in each territory was limited to the winter season, starting no earlier than December 11<sup>th</sup> and finishing no later than May 9<sup>th</sup>. Winter climate in the study area is generally cold with the maximum snow depth during this study measured to 76 centimetres.

### *2.3 Prey population density surveys*

Estimations of ungulate prey densities within the studied wolf territories were calculated based on pellet group counts in the field according to the methods by Neff (1968) and used by Sand et al. (2012a). Pellet group counts were performed during the spring at the end of the first winter study period in each territory, with the exception of two wolf territories where pellet counts were undertaken at the end of the second of two consecutive winter studies.

Pellet group counts were undertaken in 40 sample plots distributed along the sides of 1000m x 1000m squares that were systematically distributed throughout the area utilised by the wolves during the study period. The sample plots, 100m<sup>2</sup> (moose) and 10m<sup>2</sup> (roe deer), were located at 100m intervals along the sides of these predetermined squares. The only exception was the Stadra territory where sample plots were placed at 100m intervals along four parallel 1000m long lines 250m apart within the square, and where all sample plots had an area of 10m<sup>2</sup>, for moose and roe deer. The maximum number of sample plots per square was 40. However, plots located in water, on roads, or



in other habitat inaccessible to moose and roe deer were excluded from the survey. Surveying the correct area was easily done by attaching a rope of 5.64 meters (for plots of 100m<sup>2</sup>) or 1.78 metres (for plots of 10m<sup>2</sup>) to vegetation at the central point that was located using a hand held GPS, and walk around it in a circle, meanwhile taking record of pellets that occurred within the area.

The survey was done during a short period of time after the snowmelt but before the leaves of the undergrowth had sprung out to increase detectability of pellet groups. Only new pellet groups, i.e. those that had been added during the previous winter, were used for density estimation. These were identified as pellets that lay on top of last year's vegetation/moss and which had not yet begun withering. Those otherwise were counted as old pellets. Only pellet groups within the radius of the circle were counted. In cases where a pellet group occurred on the circle border, at least 20 of the pellets for moose, and 10 for roe deer, had to be within the circle for the pellet group to be included in the count.

To convert the number of pellet piles into prey population density per 10km<sup>2</sup>, we assumed that moose defecate 14 times (Rönnegård et al. 2008) and roe deer 22 times per day (Pehrson 2004). The mean date for leaf fall was set to the 10<sup>th</sup> of October. Moose population density (number of moose per 10 km<sup>2</sup>) was then calculated for each square from the formula:

$$Density_{prey/10km^2} = \frac{(N_{piles} \times 100,000)}{(N_{plots} \times D_{day} \times T_{days})}$$

Where  $N_{piles}$  is the counted number of new pellet piles within each square,  $N_{plots}$  is the number of sample plots within each square,  $D$  is the defecation rate for the prey species per day, and  $T$  is the time since leaf fall in days. For roe deer (and moose in the Stadra territory) the number of piles was multiplied by 1,000,000 to reach a density unit for 10 km<sup>2</sup> as the sample plot was only one tenth the size of the moose sample plot.

#### 2.4 Inter-territorial differences in prey preference

To evaluate the preference of a certain prey over another in the Scandinavian two-prey-wolf system I will apply three selection indices. This analysis is done on an inter-

territorial level with each territory as the statistical unit. Prey availability in the environment is the average prey population density as estimated from the pellet count, for the entire area of the wolf territory. In one territory (Tenskog), the roe deer population density was estimated to 0 roe deer/km<sup>2</sup>. A preference analysis cannot be performed on this territory, as the wolves are unable to choose prey items that are non-existent regardless of preference, and the territory was thus excluded from the analysis. All other territories were included in the preference analysis. The occurrence of a certain prey in the diet is based on the total number of killed moose and roe deer in the territory during the study period.

The Murdoch (1969) preference index  $c$  identifies the deviance from a linear relationship ( $c = 1$ ) between the ratio of a certain prey in the diet to its ratio in the environment.

$$c = \frac{P_1/P_2}{N_1/N_2}$$

where  $P_1/P_2$  is the ratio of the two species in the diet and  $N_1/N_2$  is the ratio available in the environment (Murdoch 1969). Where no selection occurs,  $c = 1$  (Murdoch 1969). However, the Murdoch index suffers from a skewed scale, with a  $c$ -value for avoidance ranging between 0 and 1, and a  $c$ -value for preference ranging from 1 to infinity (Krebs 1999).

The Manly's Alpha Index  $\alpha$  (Manly 1974) is commonly used in ecology studies (e.g. Rohner & Krebs 1996, Kunkel et al. 1999, Edenius et al. 2002) and has a limited scale ranging between 0 and 1, hence making it easier to overview. The Manly's Alpha Index ( $\alpha$ ) is calculated as:

$$\alpha_i = (r_i/n_i) \left[ \frac{1}{\sum(r_j/n_j)} \right]$$

where  $r$  is the proportion of the prey  $i$  in the diet and  $n$  is the proportion of prey  $i$  in the environment. A preference occurs when  $\alpha_i$  is greater than  $1/m$  where  $m$  is the number of prey types that are available to the predator in the environment (Olson et al. 2003).

The Manly's Alpha index does, however, only determine whether or not there is a preference, it does not reveal the strength of the preference or avoidance. Therefore, I

will additionally apply the Jacobs (1974) Index of Food Selection ( $D$ ) to the data set. The Jacobs' Index ( $D$ ) is calculated as:

$$D = \frac{(r - p)}{(r + p - 2rp)}$$

Where  $r$  is the proportion of kills from the total in the study area and  $p$  is the proportional availability of prey. This index provides a symmetrical scale from -1 to 0 for avoidance and from 0 to 1 for preference. Values around zero show a neutral prey selection and I will consider values from -0.5 to 0.5 as neutral (Cromhout 2006).

To add further strength to the analysis of preference, a Fisher's exact test was used to compare the observed number of kills within each territory and study season, to the expected number of kills based on the prey's proportional abundance and the total number of ungulate kills. Using the three indices gives an overview of if and how the prey preference of Scandinavian wolves changes with changing relative prey density.

### *2.5 Modelling prey selection*

Although the preference indices can give us an indication of the wolves' preference for a certain prey species and show inter-territorial differences in prey preference, it does not reveal what factors affect the prey choice. The fitting of a Generalised Linear Mixed Model (GLMM) targets this question whilst allowing the inclusion of multiple predictor variables that may affect the prey choice of wolves. Because I have two alternative prey species (i.e. moose and roe deer), the response variable has a Bernoulli distribution and I chose to fit a GLMM with a binomial distribution and logit function. This is achieved by using the `lmer` function of the `lme4` package in R 2.15.0 (R Foundation for Statistical Computing 2012).

Each wolf pack was responsible for multiple kills in the study, which leads to pseudo-replication unless this is corrected for. The Scandinavian wolf packs and territories may well differ from one another in several ways, e.g. there are latitudinal and altitudinal differences, differences in forest habitat and human disturbance as well as individual effects from relatedness between wolves in the same packs. Therefore, each pack may have a different starting point for the intensity of their prey choice. Using a mixed model that includes the territory id as a random factor allows an analysis of prey choice whilst

allowing the intercept of the model to vary between territories, yet assuming that the other factors have the same effect on the prey choice in all wolf packs (Koper & Manseau 2012). I chose the model of best fit by using the *drop1* function in R on the full model and by stepwise removing variables, ultimately selecting the model with the lowest AIC value, but recognising all models with a  $\Delta AIC < 2$  as equally supported (Burnham & Anderson 2004). For increased understanding of the model results, I add interactions between predictor variables one by one to the most parsimonious model selected through stepwise backward selection of the main variables.

### *2.5.1 Local prey population density*

The estimates of local prey population densities were derived from an Inverse Distance Weighting interpolation of the pellet count survey squares, using the Spatial Analyst Tools in ArcGIS® 9 and ArcMap™ 9.3.1 by ESRI (2009). The prey density estimates included in the model correspond to each kill site. In some cases no values could be estimated as the kill sites were outside of the pellet count survey area. These data points were excluded from further analysis. In territories where the roe deer population densities were estimated to zero during pellet count but where the wolves still managed to kill roe deer, we could only assume that roe deer were present in the area but at a very low density. Therefore, I added a standard value of 0.0001/10km<sup>2</sup> to the roe deer density in these cases.

A pair-wise comparison of predictor variables reveals a strong correlation ( $r = 0.89$ ) between the roe deer population density and the proportion of roe deer out of the total density of moose and roe deer in the data set. To avoid collinearity only the total prey population densities, and no prey proportions, were included as predictors in the model.

### *2.5.2 Snow depth*

The snow depth measures for Swedish and border territories were obtained from the Swedish Meteorological and Hydrological Institute (SMHI 2012), measured at meteorological stations within or no longer than 5000m away from the area utilised by the wolves in each territory during the study period. I established which meteorological station to use for each territory by calculating the Minimum Convex Polygon for the wolf positions, using Hawth Tools in ArcMap™ version 9.3.1 (ESRI 2009). For the Norwegian

wolf territory Gråfjell, the snow depth measures were obtained from the Norwegian Meteorological Institute web portal eKlima (NMI 2012), using measures taken at the weather station Rena-Haugedalen.

The data on snow depth included in the model correspond to the measured snow depth for the date of each kill. However, snow depth was not measured on a daily basis at all stations, and no data was registered when the snow cover was lacking. For kill dates where no snow depth data was available I calculated the mean of the last measure before the kill and the first measure after, to represent the snow depth of the day of the kill. Where no more snow measures occurred after the kill date, I assumed that there was no snow cover on the days that the kills had occurred.

#### *2.5.3 Number of days since New Years*

The “No. of days since New Years” was included in the model to correct for any potential effects of the proceeding winter other than snow depth. The “No. of days since New Years” corresponds to the day number since the first of January, easily obtained by subtracting the date by January 1<sup>st</sup>.

#### *2.5.4 Time since last kill*

Assuming that the wolves’ hunger would increase as time passes from the previous meal I include the time lapse between kills as a variable in my model. The time elapsed between kills was calculated for this purpose and is based on the time between the wolves’ first position at one verified kill site and the first position at the subsequent kill.

#### *2.5.5 Pack size*

The pack size of Scandinavian wolf packs is documented each winter season. In Sweden the field staff at the County Administration Boards and the Wildlife Damage Centre makes the documentation of wolf packs. In Norway, it is the staff and students at Hedmark University College that are in charge of the wolf tracking and documentation, and the researchers at Hedmark University College are also in charge of writing the annual status report of Scandinavian wolves. The number of wolves in each wolf pack that I have included in my model is taken from these annual reports.

### 3. RESULTS

The Scandinavian wolf project Skandulv has provided data on wolf predation during 11 winters (2001-2011) and from 14 different wolf territories, three of which were studied for two, or in one case for three, subsequent years. The duration of the study periods varied between territories, ranging from 19 days (Fulufjället 2010) to 127 days (Gråfjell 2002), all starting and ending with a recorded kill made by the wolves. The full dataset, on which the analyses of this study are based, includes a total of 353 wolf-killed moose ( $n = 243$ ) and roe deer ( $n = 110$ ).

#### *3.1 Preference analysis*

An inter-territorial comparison of prey selection using data from 13 territories (see methods), with both moose and roe deer presence, shows that wolves in two territories selected roe deer over moose. This result is consistent for all three selection-indices used (Table 1). A Fisher's exact test revealed a significant difference in the observed to expected number of killed roe deer and moose in the same two territories (Table 1). The Jacob's index additionally suggests a preference ( $D > 0.5$ ) for roe deer over moose in the Bograngen territory, whereas roe deer are avoided in 7 territories ( $D < -0.5$ ) as shown in Table 1. There is, however, no statistically significant difference in the observed to expected number of killed roe deer and moose in these territories (Table 1).

The two territories where wolves show a preference for roe deer have the highest and the third to highest absolute roe deer population densities (Riala: 40.2 roe/10km<sup>2</sup>, Stadra: 9.0 roe/10km<sup>2</sup>) of all territories surveyed (Figure 1A). In the remaining territories, predation on roe deer and moose occurred at levels close to what would be expected based on their relative abundance and the total number of kills in the territory. The two territories do, however, not have the highest ratio of roe deer to moose in the environment. In Riala, the ratio of roe deer to moose in the environment is high at a ratio of approximately 3:1, but in Stadra the ratio is near the opposite at 1:4 (Figure 1B).

Table 1. The results of the three preference analyses with the selection for roe deer over moose as prey in 13 Scandinavian wolf packs or pairs, and the results of Fisher's exact test of statistical significance in prey choice.

Pack <sup>1</sup>	Manly's Alpha <sup>2</sup>	Murdoch's Index <sup>3</sup>	Jacob's Index <sup>4</sup>	Fisher's p-value (df=1) <sup>5</sup>
Stadra	0.59	1.43	0.87	< 0.001
Riala	0.59	1.41	0.87	< 0.01
Bograngen	0.25	0.33	0.54	1.00
Ulriksberg	0.19	0.23	0.40	0.43
Tyngsjö	0.17	0.21	0.35	1.00
Gråfjell -01	0.13	0.15	0.21	1.00
Gråfjell -02	0.10	0.11	0.04	1.00
Djurskog	0.08	0.09	-0.04	1.00
Hasselfors	0.08	0.09	-0.07	1.00
Jangen	0.03	0.03	-0.53	0.39
Kloten	0.02	0.02	-0.70	0.33
Fulufjell-09	0.00	0.00	-1.00	1.00
Fulufjell-10	0.00	0.00	-1.00	1.00
Gråfjell -03	0.00	0.00	-1.00	1.00
Nyskoga	0.00	0.00	-1.00	1.00
Gräsmark	0.00	0.00	-1.00	0.49

<sup>1</sup>Pack ID, <sup>2</sup>Manly's preference index for roe deer (preference  $\alpha > 0.5$ , avoidance  $\alpha < 0.5$ ), <sup>3</sup>Murdoch's preference index for roe deer (preference  $c > 1$ , avoidance  $c < 1$ ), <sup>4</sup>Jacob's index for roe deer (preference  $D > 0.5$ , neutral  $D = -0.5 > 0.5$ , avoidance  $D < -0.5$ ), <sup>5</sup>P-value of Fisher's exact test with one degree of freedom.

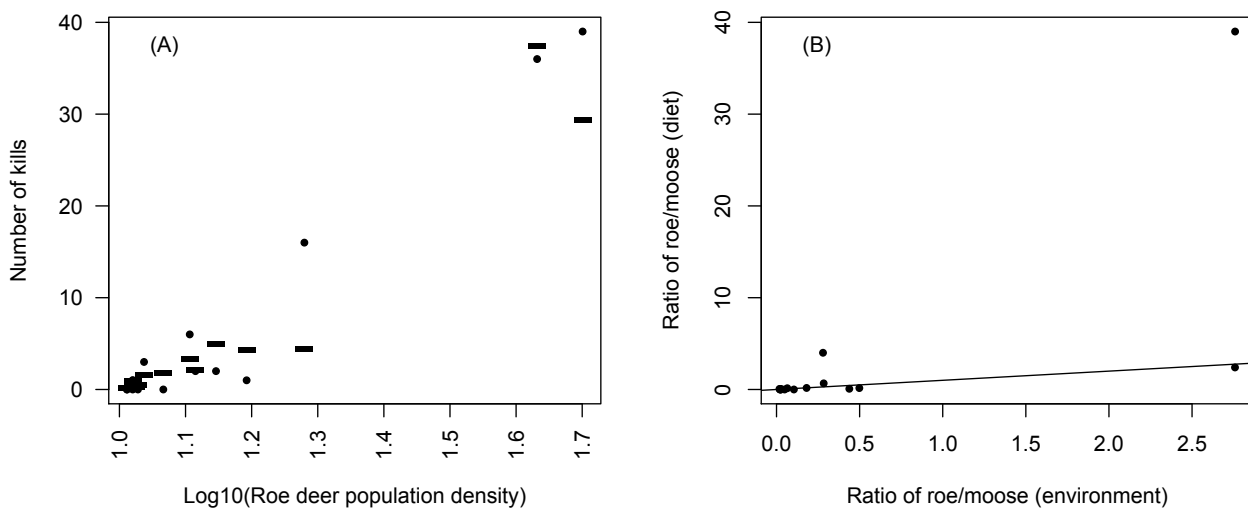


Figure 1A. Expected (lines) and observed (black dots) numbers of roe deer kills in 13 Scandinavian wolf territories in relation to the average roe deer population density in the territory, presented as the logarithm of roe deer population density +10 to get a better overview of values at low density. Expected values are based on the proportional abundance of roe deer to moose and the total number of killed ungulates during the study.

Figure 1B. The relationship between the ratio of roe deer to moose in the environment, and the ratio of roe deer to moose in the wolf diet. The line represents equal ratio in the environment as in the wolf diet, indicating no selection for either prey species,  $c=1$  (Murdoch 1969). The two wolf territories with selection for roe deer over moose appear clearly above the line.

### 3.2 Model of prey choice

A Generalized Linear Mixed Model (GLMM) with binomial distribution and a logit function reveal that roe deer population density is an important factor affecting prey choice of wolves during winter in the Scandinavian two-prey system (Table 2, Table 3). In a subsample I used data from a total of 271 kills ( $n_{\text{moose}}= 173$ ,  $n_{\text{roe}}= 98$ ) from 12 territories, for which I could obtain estimates of local prey densities, data on the contemporary snow depth, and the time lapse since the previous kill.

Ultimately, model selection was made from the full model:  $Prey\ choice_{\text{moose}} = f(\text{Pack size}, \text{Time since last kill}, \text{Snow depth}, \text{No. of days since new years}, \text{Roe deer population density}, \text{Moose population density}, \text{Territory}_{\text{random factor}})$ . The variables were ranked according to the sum of AIC weights in table 3. The only variable with a statistically significant effect on the prey choice of wolves in all models is *Roe deer population density* (Table 2). The most parsimonious model M1 (figure 2A and 2B) suggests that the model is improved slightly by inclusion of the predictor *Pack size* although the effect of this variable is not statistically significant (Figure 2B).

Table 2. The most parsimonious Generalised Linear Mixed Model (binomial logit), describing the wolves' choice of moose as prey over roe deer. The table includes all models with  $\Delta\text{AIC} < 2$ , and additionally the model of moose population density as a predictor for prey choice and the full model as a baseline.

Model	Variables	AIC	$\Delta\text{AIC}$	AIC weight
M1	RdD <sup>1**</sup> , T <sup>2</sup> , PS <sup>3</sup>	193.19	0	0.184
M2	RdD <sup>1**</sup> , T <sup>2</sup> , PS <sup>3</sup> , DNY <sup>4</sup> x RdD <sup>1</sup>	193.22	0.033	0.181
M3	RdD <sup>1**</sup> , T <sup>2***</sup>	193.72	0.539	0.141
M4	RdD <sup>1**</sup> , T <sup>2</sup> , PS <sup>3</sup> , DNY <sup>4</sup>	194.41	1.217	0.100
M5	RdD <sup>1***</sup> , T <sup>2</sup> , PS <sup>3</sup> , MD <sup>5</sup> x SnD <sup>6</sup>	194.75	1.564	0.084
M6	RdD <sup>1**</sup> , T <sup>2</sup> , PS <sup>3</sup> , PS <sup>3</sup> x TK <sup>7</sup>	195.16	1.973	0.069
FULL	RdD <sup>1**</sup> , T <sup>2</sup> , PS <sup>3</sup> , DNY <sup>4</sup> , MD <sup>5</sup> , SnD <sup>6</sup> , TK <sup>7</sup>	199.52	6.333	0.007
M7	T <sup>2</sup> , MD <sup>5</sup>	205.51	12.321	0.0004

<sup>1</sup>Roe deer population density, <sup>2</sup>Territory (included in the model as a random factor), <sup>3</sup>Pack size, <sup>4</sup>Day since new years (day number after 1<sup>st</sup> January), <sup>5</sup>Moose population density, <sup>6</sup>Snow depth, <sup>7</sup>Time since last kill, \*p < 0.05, \*\* p < 0.01, \*\*\* p < 0.001

Table 3. Factors included in the full model are ranked according to their importance to the prey choice of wolves in Scandinavia. The sum of AIC-weights is 1 for factors that are included in all models and descend with their decreasing importance to the model.

	RdD <sup>1</sup>	T <sup>2</sup>	PS <sup>3</sup>	DNY <sup>4</sup>	MD <sup>5</sup>	SnD <sup>6</sup>	TK <sup>7</sup>
Sum of AIC weight	1	1	0.72	0.35	0.15	0.06	0.02

<sup>1</sup>Roe deer population density, <sup>2</sup>Territory (included in the model as a random factor), <sup>3</sup>Pack size, <sup>4</sup>Day since new years (day number after 1<sup>st</sup> January), <sup>5</sup>Moose population density, <sup>6</sup>Snow depth, <sup>7</sup>Time since last kill



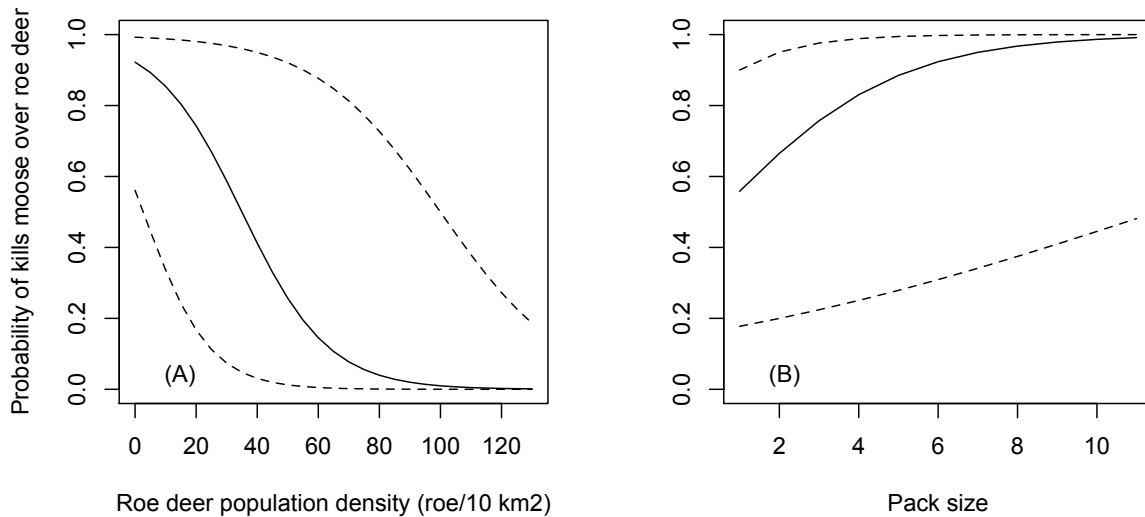


Figure 2. Response of prey choice as predicted by roe deer population density (figure 2A:  $p < 0.01$ ) and pack size (figure 2B:  $p = 0.14$ ) on the choice of moose over roe deer in the most parsimonious model M1:  $\text{logit}(\text{Prey Choice}_{\text{Moose}}) = 0.85 + 0.45 \cdot \text{Pack Size} - 0.07 \cdot \text{Roe deer Population Density}$ . Values included in the graphs are back-transformed from the original binomial model with logit function. The solid line represents the model for figure 2A the mean pack size ( $\bar{x}=3.59$ ) and in figure 2B roe deer population density ( $\bar{x}=15.14$ ), and the dashed lines shows the standard error of the mean. Because of the Bernoulli distribution of the data, the wolves' choice of roe deer over moose produces the opposite graph.

Model M3 alone includes only statistically significant predictor variables. These are *roe deer population density* and *territory id* (table 2). Figure 3A shows the effects of roe deer population density ( $p = 0.001$ ) on the choice of moose over roe deer in model M3:  $\text{logit}(\text{Prey Choice}_{\text{Moose}}) = 2.47 - 0.689 \cdot \text{Roe deer population density}$ . In contrast, moose population density had no statistically significant effect on the prey choice of wolves in any model (table 2). The relationship between *moose population density* ( $p = 0.42$ ) and prey choice of wolves is shown in figure 3B for the model M7:  $\text{logit}(\text{Prey Choice}_{\text{Moose}}) = 1.95 + 0.02 \cdot \text{Moose Population Density}$ .

The turning point in both model M1 and model M3 (table 2), i.e. when roe deer and moose are equally likely to be chosen as prey ( $Y=0.5$ ), occur at an absolute roe deer population density of approximately 35 roe deer/10 km<sup>2</sup> (Figure 2, Figure 3). The model predicts that at roe deer population densities higher than 35 roe deer/10 km<sup>2</sup>, wolves are more likely to choose roe deer whereas at densities lower than this threshold moose is the more likely kill.

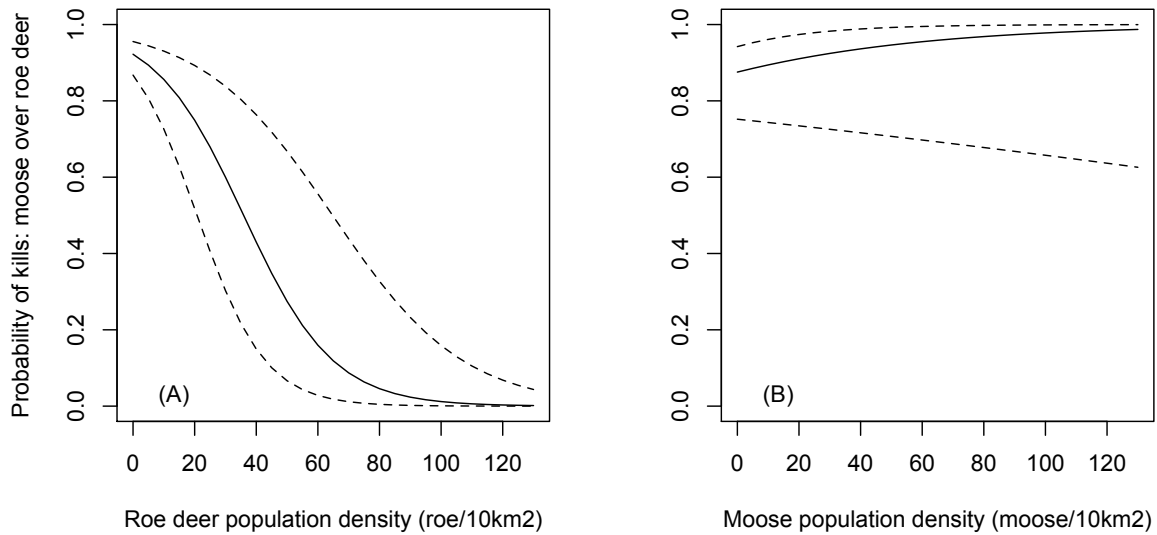


Figure 3A. Responding prey choice, moose over roe deer, as predicted by *Roe deer population density* ( $p = 0.001$ ) in model M3.

Figure 3B. Model M7 with *Moose population density* ( $p = 0.42$ ) as a predictor of the prey choice moose over roe deer. Values included in the graphs are back-transformed from the original binomial model with logit function and the dashed lines show the standard error. Due to the Bernoulli distribution of the response the choice of roe deer over moose produce the opposite curve.

## 4. DISCUSSION

### 4.1 Inter-territorial differences in prey preference of wolves for roe deer

I have been able to describe a preference for roe deer over moose as prey in two of the Scandinavian wolf territories (Riala and Stadra). These two territories where both have a high absolute roe deer population density compared to other wolf territories in Scandinavia. The results offer some support for the optimal foraging theory where prey other than roe deer are ignored when this prey occur at a sufficient density (Krebs 1977), in this case at a regional (inter-territorial) level. However, another wolf territory (Hasselfors) had high roe deer population density, yet no selection for any ungulate species was detected, increasing the ambiguity of the results. In order to draw reliable conclusions about the effect of roe deer density on prey preference, more data is needed from wolf territories in areas of intermediate and high roe deer population densities. Although in the remaining wolf territories roe deer appeared to be avoided according to the three preference indices, the Fisher's exact test showed that wolf predation was not significantly different from what would be expected from the proportional ungulate abundance. This may, in part, be a result of extremely small values for the expected number of killed roe deer.

Using the definition of prey switching by Murdoch (1969) there is at present no support for prey switching. For this type of switching we assume a lower than expected predation ratio when the prey occurs at a low ratio in the environment, and a higher than expected predation ratio at a high occurrence ratio in the environment (Garrott et al. 2007). This was not observed in our study. Out of the two territories where a preference was detected, the strongest selection for roe deer was found in a territory with a higher moose than roe deer population density. Our results are, however, generalising the effects of prey density throughout the different Scandinavian wolf territories, when it is possible that the threshold ratio at which a switch would occur could vary between territories. Theoretically, the switching threshold could for instance vary with local differences in prey vulnerability or body size (Garrott et al. 2007).

#### *4.2 Prey choice governed by roe deer density*

On a local level it is the roe deer population density that acts as the main predictor of the prey choice by wolves according to our model. Moose population density, on the contrary, had no effect on the prey choice. This further strengthens the hypothesis that when roe deer are available at sufficient densities, this is the preferred prey of wolves, and that the shift of wolf predation towards roe deer governs the predation pressure on other prey species, also on a local (intra-territory) level. Jędrzejewski et al. (2000) found a similar association between the wolf prey choice and red deer population density during their study in Poland. Interestingly, whereas red deer are relatively large, thus beneficial prey, roe deer provide at best 1/6 the body mass of a moose (Sand et al. 2005). Also, the chase distance for wolves to capture roe deer is on average longer than that to capture moose, although the success rate of the chase is no higher (Wikenros et al. 2009). Thus, the roe deer chase appears to be less profitable than a chase on moose.

One might speculate how roe deer, being small and difficult to catch, becomes the predictor of wolf prey choice despite appearing to be a less profitable prey than moose. Mattioli et al. (2011) found wolves to select the most vulnerable prey, given the option. Moose, being so much larger and stronger than roe deer, are known to pose a larger threat to an attacking wolf and are capable of causing severe injury or death to the wolf (Aronsson et al. 2002). Predators should, and do, evaluate the risk involved in foraging

(Berger-Tal et al. 2009) and it is likely that the risk of injury is a cost great enough for the wolves to avoid moose when the smaller roe deer are available.

However, in Scandinavia, local roe deer population densities must be relatively high (>30 roe deer/10km<sup>2</sup>) for wolves to make this shift in their prey choice. Thus we may assume that the roe deer profitability increases with roe deer population density. Due to their small size roe deer may simply not be profitable for wolves when energy must be spent searching for them. Thus, it is likely that wolves only prey on roe deer opportunistically when roe deer occur at low population densities (Gervasi et al. 2012a). A high population density can lead to behavioural effects of the roe deer, by increasing their tendency to aggregate in numbers (Vincent et al. 2009), potentially making their location more predictable to wolves. Previous studies have shown that wolves are able to adjust the utilisation of their home range in response to the location of predictable prey (Kunkel et al. 2004). One could hypothesise that wolves spend more time in areas with aggregated roe deer, thereby reducing their search distance and increasing the profitability of roe deer as prey (Giraldeau 2008). Theoretically, moose predation would then be further limited as wolves may rarely encounter moose in the roe deer habitat (Messier 1995, Murdoch 1975). However, this hypothesis is not supported in a first investigation of wolf movement in Scandinavia (Gervasi et al. 2012a).

Another hypothesis for how roe deer population density increases the profitability of the roe deer as prey is that there are indirect effects of roe deer population density on their vulnerability through intra-specific competition and limitation of resources (Rockwood 2006). Roe deer with reduced home range sizes (Kjellander et al. 2004), and subadults that are unable to establish permanent home ranges (Vincent et al. 2009) at high population densities could potentially become weak, thus become vulnerable to predation (Mattioli et al. 2011).

Furthermore, roe deer are sensitive to increasing snow depth (Danilkin 1995), as snow can severely hamper their chances of escape, and potentially make them vulnerable to predation (Nowak et al. 2005). However, counter our expectations we found no effect of snow depth on the prey choice in this study, results similar to the conclusions of Sand et al. (2005) and Dale et al. (1995). It is possible that the regional snow depth measure

did not accurately describe the local snow conditions at each kill site causing a type II error in the analysis, or snow depths may simply not have reached the extremes at which it becomes problematic for roe deer.

Previous to this study moose have generally been considered the most important prey species for Scandinavian wolves (Olsson et al. 1997; Sand et al. 2005, 2010) whereas in other parts of Europe, with a different prey composition, roe deer have been found as the main prey for wolves (Nowak et al. 2011; Wagner et al. 2012). This study, in agreement with other research (Jędrzejewski et al. 2000; Nowak et al. 2011; Wagner et al. 2012; Milanese et al. 2012), shows that the wolves adjust their diet according to prevailing prey densities. We would expect to observe several changes in wolf prey choice if establishment of territories occur throughout southern Scandinavia, in areas with different prey composition than in the wolf area hitherto. Thus, the collection of more data and the analysis thereof, is necessary throughout the Scandinavian Peninsula. This provides an interesting opportunity for wolf ecology research in the future, as the wolf population grows and colonise new areas.

## **5. MANAGEMENT IMPLICATIONS**

When wolves establish territory in an area their presence and numbers have the potential to cause great impact on their prey populations (Post et al. 2002, Ripple & Beschta 2011). Moose and roe deer are important game species in Sweden (Swedish Hunters Association 2011) and gaining knowledge of how the wolves' affect the game communities is important for management and the estimation of sustainable harvest quotas.

As the subject of a substantial annual human harvest, the moose is the most important game species in Scandinavia (Swedish Hunters Association 2011). Increased wolf predation has a negative effect on moose population growth rate (Gervasi et al. 2012b), as winter predation from wolves on moose is only in part compensatory to starvation, but is mainly additive (Sand et al. 2012b). Thus, a relief from wolf predation due to the wolves' choice of other prey should have positive effects on the moose population growth rate (Gervasi 2012b). With wolves shifting their prey choice from moose to roe deer at high roe deer population densities, it is possible that effects of wolf predation on

the moose population locally could be reduced if management actions are aimed to increase the roe deer population density (Hayward et al. 2007).

How the roe deer populations will cope with wolf predation depends largely on what other factors affect the survival, e.g. other predators, disease and hunting (Seip 1995). Supplementary feeding may provide a mean to increase survival (Rehbinder & Ciszuk 1985) and alterations in hunting pressure can greatly affect the population growth (Gervasi et al. 2012b). Gervasi et al. (2012b) also found lynx predation to have a great impact on roe deer population growth. Perhaps in the future, management plans should not focus on the effects of separate species, but the ecosystem rather be managed as a multi-species web.

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