Kill or Scavenge - The use of alternative food sources in Scandinavian wolves

Maike Demski

Abstract

Scavenging in wolves is a behaviour that has not been studied well. Many studies have looked at kill rate and the relationship between wolves (*Canis lupus*) and their ungulate prey but have not examined the aspect of scavenging. The significance of scavenging could be important for creating accurate management plans. The aim of this study was to determine to what extent adult wolves rely on scavenging as a food source and how this may differ between packs. The data used comes from GPS collard wolves from Norway and Sweden in winters 2001 to 2014. From a total of 24 wolf territories (combined 1393 study days) 604 carcasses were examined and classified according to cause of death. The results in this thesis show that there were significant variations in the amount of non-wolf killed carcasses found between territories. It was also found that a lower kill rate was correlated to a higher use of scavenged carcasses. A higher use of scavenged carcasses was also correlated with a lower body condition (below average body weight) of the studied wolves. The same was true for the kill rate and body condition. These results show that scavenging occurs more often when kill rate and the body condition of wolves is low. This indicates that scavenging may represent an important survival trait for wolves during parts of their lifetime.

Introduction

In Scandinavia wolves (*Canis lupus*) are at the top of the food chain. This apex predators' ability to kill large prey is matched only by brown bears (*Ursus arctos*). Wolves importantly contribute to a well functioning and complete ecosystem (Smith et al., 2003, Ripple et al., 2011, Beschta and Ripple, 2009). However, they are not just part of the predator-prey relationship but also providers of carrion to a large range of scavenging species (Vucetich et al., 2004, Wikenros et al., 2013). Wilmers et al. (2003) found that wolves, in their study, are important for providing a steady supply of carrion throughout the winter, reducing the carrion peak pulse at the end of the season. Additionally, wolves have been suggested to facilitate the re-colonisation of other predators such as the wolverine (*Gulo gulo*) (Van Dijk et al., 2008), through provision of carrion. For example, wolves in Białowieża are reportedly the only species able to open frozen bison carcasses, thus allowing other scavengers to feed on them (Selva et al., 2003).

1

It is not well known how important scavenging is as a food source for many predatory species (DeVault et al., 2003), however, most predators will take the opportunity to scavenge as they encounter a carcass (DeVault et al., 2003, Selva et al., 2005, Wilson and Wolkovich, 2011). Scavenging has also frequently been reported in African lions (*Panthera leo*) (Kruuk, 1972) and Spotted hyenas (*Crocuta crocuta)* (Cooper, 1991) as an important food source. Creel and Creel (1995) even reported observations of scavenging in African wild dogs (*Lycaon pictus)*, although these occasions are rare. Generally, predators switch to scavenging during times when killing live prey becomes increasingly more difficult, such as when calves grow sufficiently large to evade predation (Pereira et al., 2014), or at low prey densities (Messier and Crête, 1985).

There are several studies that report occurrences of wolves scavenging (Huggard, 1993, Śmietana and Klimek, 1993, Selva et al., 2003, Valdmann et al., 2005, Mateo-Tomás et al., 2015). Wolves often feed on carrion such as road or railway kills as well as remains from hunter harvest and may even steal kills from other predators, i.e. cleptoparasitism. In one study, wolves have been identified as one of the more common species observed visiting carcasses (Selva et al., 2003).

Wolf preying on ungulates has been studied extensively (Hayes et al., 2000a, Sand et al., 2012, Jędrzejewski et al., 2002) and much is known about kill rate, prey selection and estimates of biomass consumed. For example, it is known that there are differences in kill and consumption rate between prey species, and that pack size and geographical location can affect these (Hayes et al., 2000, Jędrzejewski et al., 2002, Vucetich et al., 2002, Sand et al., 2012). However, with the addition of scavenging the dynamics of feeding behaviour, both between and within packs, become much more complex and less well studied.

Pereira et al. (2014) provide a good summary of scavenging occurring in predators due to seasonal variation in prey availability and vulnerability. Nevertheless, the importance, and especially the frequency, of scavenging in wolves particularly has not been the focus in any study to date. Data about the composition of different types of food sources may therefore be an important tool for evaluating the impact and variation among large carnivores on the ecosystem. The importance of scavenging in

food webs is believed to be severely underestimated (Wilson and Wolkovich, 2011). Therefore there is a need to better understand what importance different food sources play in wolf diet, especially from a management perspective. A better understanding of how and what wolves feed on could be useful in understanding the problems resulting from human – wolf conflicts. It is not known how the availability of other food sources, such as carrion, affects the kill rate of a wolf pack. Additionally, the pack size itself may be important for the utilization of carcasses where some pack members (pups of the year) may rely more than adults on scavenging to provide additional biomass.

Within this thesis I quantify to what extent adult wolves may rely on sources other than wild prey species, i.e. carcass remains resulting from other causes than wolf predation and how this differs between wolf packs. I examine the following three research questions:

Question 1: Does the use of wolf-killed wild prey and other types of food sources differ between wolf packs?

Question 2: Does kill rate on wild prey correlate with age and body condition of wolves (weight), pack size and/or prey densities?

Question 3: Do wolf kill rates of wild prey correlate with the use of other food resources so that a higher use of other carcasses links to lower kill rates of wild prey?

Study area

Wolves became extinct in Sweden in the 1960's (Haglund, 1968) returning in the early 1980s through natural re-colonisation (Wabakken *et al.,* 2001). The first wolf reproduction was documented in 1983 and throughout the 1990's the population expanded rapidly (29% annually; Wabakken et al., 2001). The study area is located in south-central Sweden (Figure 1) and consists mainly of a mosaic of boreal forest resulting from clear-cutting and regeneration of different age class stands. Available prey species include moose (*Alces alces*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), and various small mammal and bird species.
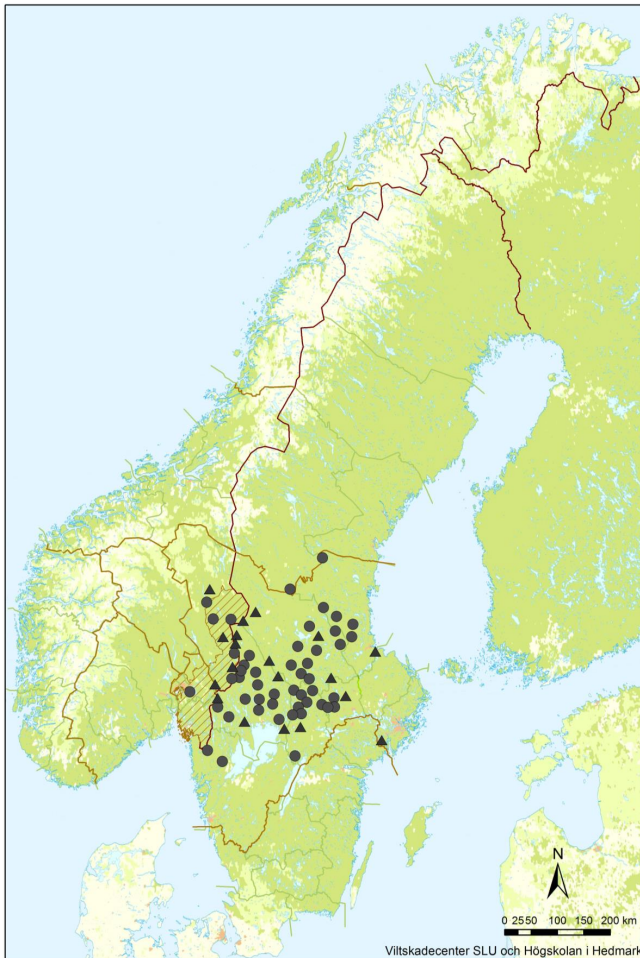
Figure 1: *Locations of wolf pack territories (circles) and territory marking pairs (triangles) in Scandinavia in the winter 2014-2015. Map from Anon. (2015).*

Methods

The definition of scavenging often includes wolves revisiting old kills as well as feeding on kills made by other members of the same pack (although in separate killing events) (Zimmermann et al., 2014, Palacios and Mech, 2011, Stahler et al., 2006). This is a very loose definition and results in difficulty when comparing field data among studies. There is a need to define the categories more clearly and in this study I therefore split carcasses into the following four categories:

Wolf killed wild prey is defined as wolf-kills of wild ungulates, moose or roe deer, as well as non-ungulate prey during the study periods. Carcasses that were previously determined to be wolf killed or probable wolf killed, during field surveys, are included in this category (see Sand et al., 2005 for criteria for classification).

Natural causes of death include carcasses of wild prey that were known to have died from natural causes (such as starvation, accidents, disease), or that have been killed by another predator species.

4

Anthropogenic causes include carcasses of wild and domestic prey that were not killed by wolves but where the cause of death could be linked to human activity. These are road and railway kills, hunter harvest remains and dumped domestic carcasses.

Unknown causes are carcasses found during study periods, which were not possible to be classified into the other three categories. The majority of these carcasses were old, i.e. died before the start of the study periods, and therefore no specific cause of death could be assigned to them due to lack of information. However, many of these carcasses are likely to be old wolf-kills re-visited during study periods.

I used data from 24 field studies, of 15 different wolf territories, that had previously been carried out during 13 winters (2001-2014) by the Scandinavian Wolf Research Project (SKANDULV). Usually two wolf territories were studied per year and seven territories were studied for more than one winter. All data was collected during winter and the start and end date for each study ranged between 6th November and 29th April. The 30th April was considered the last day of winter due to the imminent birth of pups. Data used from these 24 studies resulted in a total of 1393 study days (mean study length = 58 days +/- 4 days, range = 33-132, Table 1). Each winter study is henceforth referred to as a "territory" with the name and year as identification. This distinction between territories is important because adult reproducing wolves and territory boundaries, as well as pack size and body condition, may change between years.

One or two adult wolves from each territory were collared with GPS (SimplexTM of Followit AB, or GSP PLUS of Vectronic). Animals were first snow tracked until their approximate location could be determined, after which they were located and darted (anesthetised) from helicopter. Licensed and trained personnel carried out the darting and anaesthesia and wolves were fitted with GPS collar before release. More details on animal capture and handling techniques are described in Sand et al. (2006). All captures were carried out in accordance with ethical requirements approved by the Swedish Animal Welfare Agency and the Norwegian Experimental Animal Ethics Committee.

In each territory the collars were programmed to transmit hourly GPS locations during study periods, whereas some studies used 30 minute positions. In these cases

the data was reduced to hourly locations for equal comparison across studies. Cluster analysis was carried out during each field study (for method on cluster analysis see Sand et al., 2005). Locations that were within 200 m of each other form a "cluster". Clusters were generally visited within 3-5 days, but not before the collard wolves left the area. Each position within the cluster and the surrounding area was searched for prey remains. For each carcass found, data on species, age, gender, cause of death, time of death and the percentage biomass consumed was recorded. All carcasses found were compiled and sorted into the 4 categories described above, with a total of 609 carcasses across all studies (wolf killed prey = 450, natural death = 17, anthropogenic causes = 34, unknown = 108, Table 1).

Table 1: *List of wolf winter predation studies conducted in Norway and Sweden from 2001 until 2014, including territory name and year, number of days each study lasted, and the number of carcasses found within the territory according to four different classes.*

Territory	Study days	Wolf-killed Wild Prey	Natural Causes	Anthropogenic causes	Unknown Causes
Bograngen03	63	29	0	1	3
Djurskog04	56	28	0	0	1
Gråfjell01	69	19	0	2	0
Gråfjell02	132	40	2	2	1
Gråfjell03	63	37	0	0	1
Hasselfors03	63	52	3	1	30
Jangen04	60	17	0	0	5
Kloten08	50	15	0	0	14
Kloten10	50	10	1	3	2
Kukumaki13	63	4	0	2	5
Kukumaki14	53	5	0	4	3
Nyskoga04	33	12	0	0	0
Riala10	42	39	4	1	8
Stadra03	50	20	2	5	11
Tandsjön12	71	15	1	0	2
Tandsjön14	37	6	0	0	0
Tenskog10	57	10	1	2	2
Tenskog11	48	11	0	0	0
Tyngsjö02	84	26	0	0	1
Ulriksberg06	57	20	0	0	2
Ulriksberg07	54	20	1	0	2
Uttersberg06	35	4	0	4	12
Uttersberg05/06	61	7	1	4	2
UttersbergDec06	42	4	1	3	1
Total	**1393**	**450**	**17**	**34**	**108**

Data on age, weight, and sex of wolf was recorded during each collaring event. For most studies (21 studies out of 24) wolves were collared directly before the start of the study period. Three with multiple study periods (but within the same year) only have a single collaring event. A body condition index was estimated, for each territory, using the number of kg above or below the average body weight of all wolves used in this study (Table 2). This number was then averaged between the male and the female in territories that had both adult male and female collared. The index eliminates the weight differences between males and females. Similarly, the average age of the alpha pair was used in the analysis, when both animals were available (15 studies with alpha pair, 9 studies with only the male or the female).

Pack size was estimated for each territory using snow tracking and in later years combined with DNA analysis (Table 2, for further details see Wabakken et al. [2001, 2003, 2004a, 2004b, 2005, 2006, 2007, 2008, 2009, 20010, 2011] and Svensson et al. [2012, 2013, 2014]).

To estimate the time spent by wolves at different types of carcasses the number of GPS locations that were within 200 m of the carcass were calculated. Each location was assumed to represent one hour spent at the carcass site. A radius of 200 m from the carcass was previously determined to represent wolves feeding at the carcass (Sand et al., 2005, Colombo, 2013). Selection of GPS locations within 200 m of each carcass was carried out in R (R Core Team, 2015).

Per capita kill rate (estimated as kg biomass consumed) was calculated using the average weight, according to species, age and sex, of each carcass found (Zimmermann, 2014). If the age or gender was unknown a median weight was used. First, the biomass for each prey species was calculated to edible biomass (amount of tissue and bone that is consumable by wolves), which was set to 65% for moose of any age and 75% for all other species (Zimmermann, 2014). This edible biomass, available from killed prey, was used to further calculate how much kg biomass was consumed by wolves from each carcass (estimated when the carcass was found). The total biomass consumed, for each territory, was then divided by the number of study days and the number of wolves to obtain an average estimate of the amount of biomass consumed per day per wolf (Table 2).

The age of carcass (time since death) was determined based on the physical condition and decomposition of the carcass in combination with recent weather conditions during fieldwork. Carcasses were then classified into: less than 1 week old (1), 1 - 2 weeks old (2), 2 - 3 weeks old (3), 3 - 4 weeks old (4) and older than 4 weeks (5).

Prey densities for moose and roe deer were estimated for each territory using a grid system of square kilometres. Squares were evenly distributed throughout each territory and on each side of the square 10 sample plots were placed (100 m apart). Moose pellets were counted within 100 m^2 and roe deer pellets within 10 m^2 from the centre of the sample plot. From this prey density in km^2 was calculated for moose and roe deer for each territory (Table 2).

The proportion of wolf-killed carcasses, in each territory, was calculated from the total number of carcasses found (Table 2). The majority of carcasses of unknown cause were estimated to be killed before the start of the study period and may therefore represent possible revisits to old kill sites (77 out of 107 unknown carcasses).

Table 2: *List of winter studies, with territory name and year, included in the study. The per capita kill rate (kg biomass) and variables used: pack size, wolf age, body condition index, moose density and roe deer density (per km^2) as well as proportion of wolf killed carcasses out of all carcasses found in territory used in the GLM analysis.*

Territory	Kill Rate	Pack Size	Wolf Age	Body Condition Index	Moose Density	Roe Deer Density	Proportion Wolf Kill
Bograngen03	15.63	3	9	2.37	3.44	0.06	0.88
Djurskog04	10.26	5	2.5	0.98	1.68	0.30	0.97
Gråfjell01	12.52	2	3.5	5.24	1.74	0.05	0.90
Gråfjell02	7.58	3	4.5	5.24	1.74	0.05	0.89
Gråfjell03	7.22	6	5.5	2.24	1.74	0.05	0.97
Hasselfors03	7.59	5	5	1.37	1.19	3.28	0.60
Jangen04	14.74	2	2.5	1.99	0.80	0.40	0.77
Kloten08	10.12	2	3	-4.05	1.27	0.56	0.52
Kloten10	2.26	7	5	-2.62	1.27	0.56	0.63
Kukumaki13	1.16	2	3	-6.52	1.64	0.07	0.36
Kukumaki14	6.24	3	2.5	-0.77	1.64	0.07	0.42
Nyskoga04	11.41	4	7	2.37	1.37	0.07	1.00
Riala10	6.65	2	2	-1.05	1.46	4.02	0.75
Stadra03	5.43	2	1	-4.27	3.23	0.90	0.53
Tandsjön12	6.22	5	4	1.24	0.52	0.04	0.83

Tandsjön14	3.11	8	6.5	-0.27	0.52	0.04	1.00
Tenskog10	7.37	2	1.5	-5.27	0.87	0.00	0.67
Tenskog11	9.58	2	2.5	-5.77	0.87	0.00	1.00
Tyngsjö02	5.17	6	4	1.95	1.38	0.09	0.96
Ulriksberg06	8.04	2	5	-0.77	0.98	0.28	0.91
Ulriksberg07	3.23	7	6	-0.77	0.98	0.28	0.87
Uttersberg06	1.18	9	6	-4.55	0.86	1.49	0.20
Uttersberg05/06	1.26	9	3	-1.13	0.86	1.49	0.50
UttersbergDec06	2.32	5	6	-4.55	0.86	1.49	0.44

Analysis

Question 1: Does the use of different food sources differ between wolf packs?

To examine if there are differences of carcass use between territories I used a chi square analysis. This was done for both the number of different carcasses in each territory as well as the time spent at the different carcass types. I then also combined the data for all 24 territories to calculate the average number of carcasses used and the average time spent at each type of carcass by wolves. Further, I examined the composition of wolf killed wild prey. This category was divided into: adult moose (n = 92), moose calf (n = 200), moose of unknown age (n = 38), roe deer (n = 111) and small game species (grouse [9], beaver [7], hare [6], red fox [2], badger [1], raven [1], and squirrel [1]).

I used a Generalised Linear Mixed Model (GLMM) to investigate how pack size (2-9 wolves), age of carcass (5 categories) and carcass type (4 categories) affected the time (hours) spent at carcass sites by wolves. The territory ID was used as a random effect. In this analysis each carcass was used as a separate observation and carcasses with any missing data were removed resulting in a total sample size of 540 (total data set n = 604, missing values n = 64).

Question 2: Does kill rate on wild prey correlate with age, body condition (weight), pack size and prey densities?

A Generalised Linear Model (GLM) was used to test if pack size, wolf age, body condition index and prey densities of moose and roe deer affect per capita kill rate. In this analysis each territory was used as a single data point (Table 2). A GLM

including the same three variables (pack size, wolf age and body condition index) was used to test for effects on the proportion of wolf-killed carcasses found in a territory.

Question 3: Does a higher kill rate result in a lower use of other carcasses?
I used a linear regression to test if kill rate was dependent on the proportion of wolf-killed carcasses found in each territory.

All statistical tests were done in R. R package MuMIn was used for model selections (Barton, 2015). Models were selected based on Akaike's information criterion for small sample size (AICc) with the smallest value considered to be the best model (Burnham and Anderson, 2002). Models with a Δ AICc value of less than two were considered of equal importance.

Results

Question 1: The use of food sources differs between wolf packs.
The types of carcasses used by wolves differed between territories in terms of both the proportion of each type of carcass (x^2 = 224, df= 69, p< 0.001), as well as proportion of time spent at each type (x^2 = 2990, df= 69, p< 0.001, Figure 2). Wolf-killed wild prey was the dominant type. However, the proportion of this prey type varied between the territories from 20% to 90% (percentage from the total number of carcasses in each territory). Within three territories wolves fed exclusively on their own kills of wild prey (Nyskoga04, Tandsjön14 and Tenskog11, Figure 2A). Non-wolf kills (both of natural and anthropogenic causes of death) made up the second most important type of carcass but varied between territories (from 2% to 35%).

There was also variation in the time spent on each type of carcass in different territories (Figure 2B). Out of the total time spent feeding at carcasses the majority of time was spent at wolf killed wild prey (which is in line with the finding that the majority of carcasses were wolf killed wild prey). In none of the 24 studies did wolves kill domestic prey.
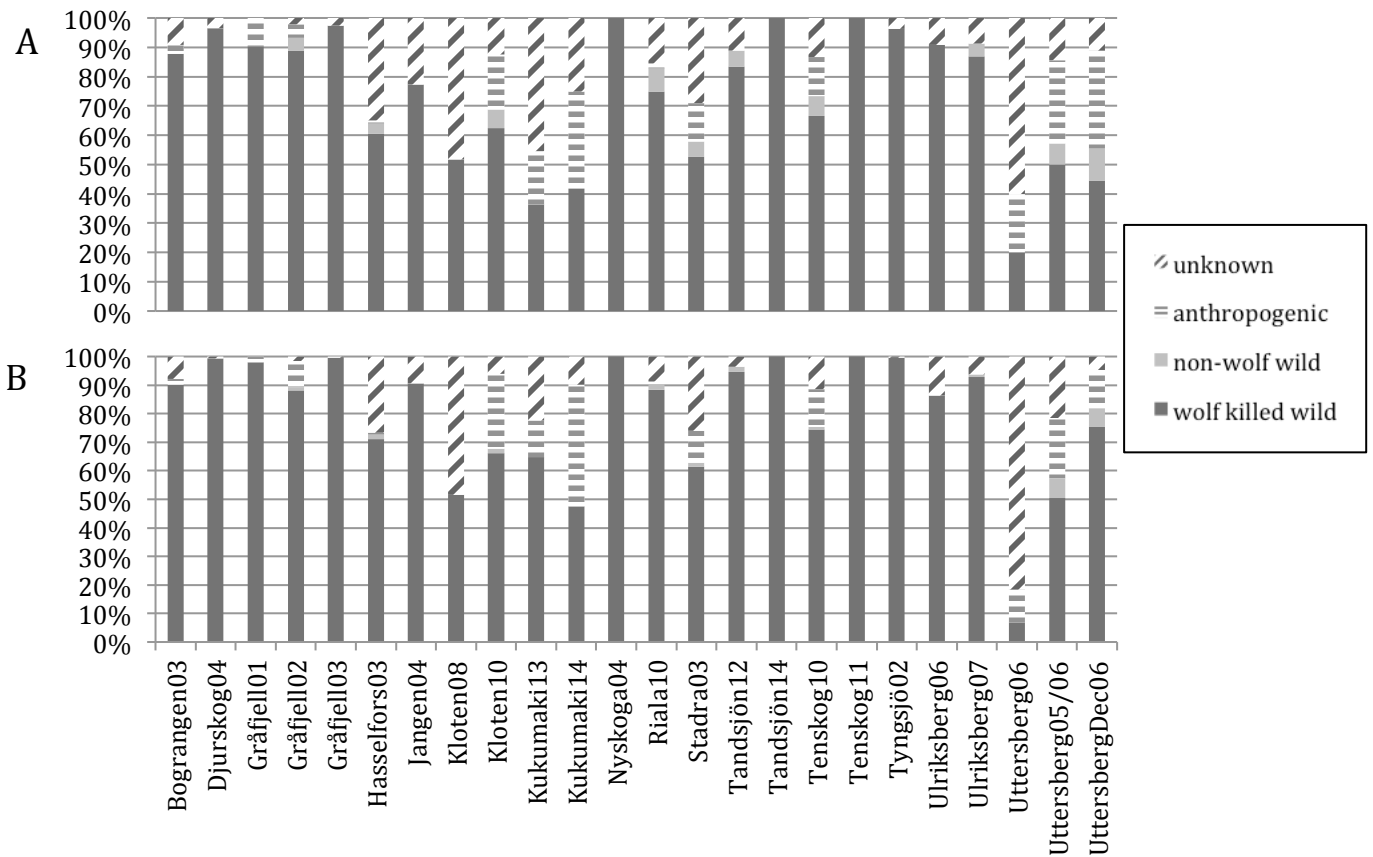
Figure 2: *The proportion of different carcass types visited by wolves (A) and the proportion of time spent at each type of carcass (B) in 24 wolf territories in Scandinavia during winter (2001-2014).*

On average, wolf-killed wild prey made up 73% of the carcasses used by wolves, natural deaths 3%, anthropogenic causes 5% and unknown 19% (Figure 3A). On average, 81% of the time spent close (proximity within 200 m) to a carcass was on wolf-killed wild prey (Figure 3B). Wolves spent 7% of the time at carcasses that were scavenged and 12% of the time on carcasses with unknown causes of death. Of these scavenged carcasses, 14% of the time (1% of total) was spent at carcasses with a natural cause of death and the remainder of the time was spent at carcasses provided from hunter harvest, traffic accidents and slaughter pits (6% of the total time).
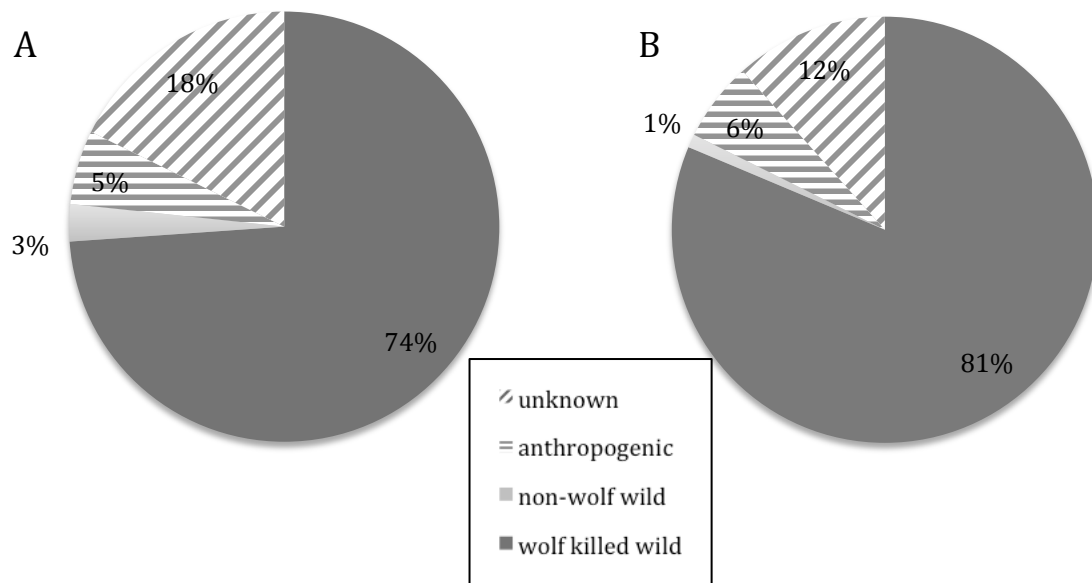
Figure 3: *The average proportion of carcasses of each type (A) and the average proportion of time spent at each type of carcass (B) across wolf territories. Data derived from 24 winter studies of Scandinavian wolf territories from 2001-2014.*

I further investigated the composition of wolf killed wild prey (Figure 4). Wolves preyed on moose calves most often, making up 43% of all killed wild prey (n = 200). Second and third most common were roe deer (24%, n =111) and adult moose (20%, n = 92). Only a small portion was made up of small game species (5%, n = 25) and the remaining 8% (n= 38) was moose of unknown age. Also the composition of wolf-killed prey varied between territories. Wolves in three of the 24 territories preyed almost exclusively on roe deer, while all others preyed mainly on moose calves.
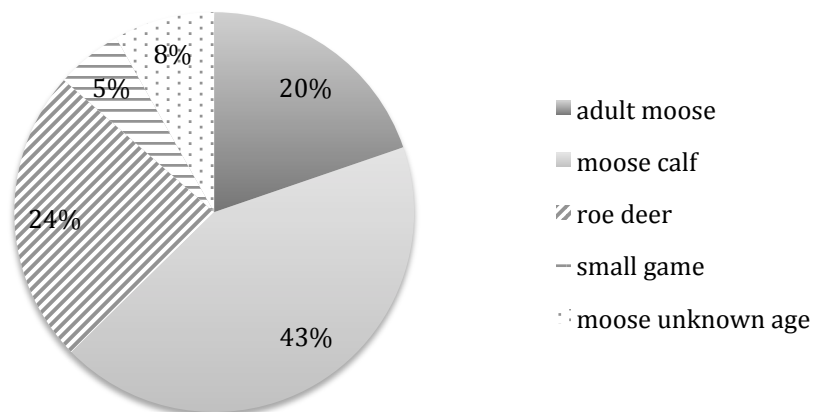

Figure 4: *Composition of 466 wolf killed wild prey carcasses compiled from 24 winter studies of Scandinavian wolf territories form 2001 to 2014.*

Which factors affect time spent at carcass?

The carcass type and the age of carcass were the two most important variables influencing the time spent at a carcass. The carcass type was also the most important explanatory variable according to AICc weight (Table 3).

Table 3: *Model selection, based on Akaike's information criterion for small sample size (AICc), for variables affecting the time spent by wolves at carcasses (wolf-killed prey, natural deaths, anthropogenic causes, unknown causes) in Scandinavia.*

	Carcass Type	Pack Size	Age of Carcass	AIC	delta	weight
Model1	x		x	3618.30	0.00	0.42
Model2	x			3619.67	1.36	0.21
Model3	x	x	x	3620.30	2.00	0.15
Model4			x	3621.25	2.95	0.10
Model5	x	x		3621.66	3.36	0.08
Model6		x	x	3623.25	4.95	0.04
Model7				3632.19	13.88	0.00
Model8		x		3634.12	15.82	0.00
Importance	0.87	0.27	0.71			

Question 2: Does kill rate on wild prey correlate with age, body condition (weight), pack size and prey densities?

Two models were selected, the first containing only wolf body condition and pack size and the second also including wolf age (Table 4) as significant predictors of per capita kill rate. Pack size was most important for explaining variation in the per capita kill rate. Model 1, however, had 43% probability of being the best model compared to only 16% of Model 2. I therefore considered wolf body condition and pack size to be the variables that best explained variation in the per capita kill rate between wolf territories (F = 3.74, df = 7.99, p= 0.002). To achieve the average per capita kill rate (study average of 6.93 kg biomass/wolf/day) the two adult wolves of a pack needed to have a body weight approximately 5 kg higher than a pair of wolves (Figure 5). The analysis showed that kill rate was not dependent on densities of neither moose nor roe dear.

Table 4: *Model selection, based on Akaike's information criterion for small sample size (AICc), for variables affecting per capita kill rate of Scandinavian wolves. Showing the top five models out of 32 tested ones.*

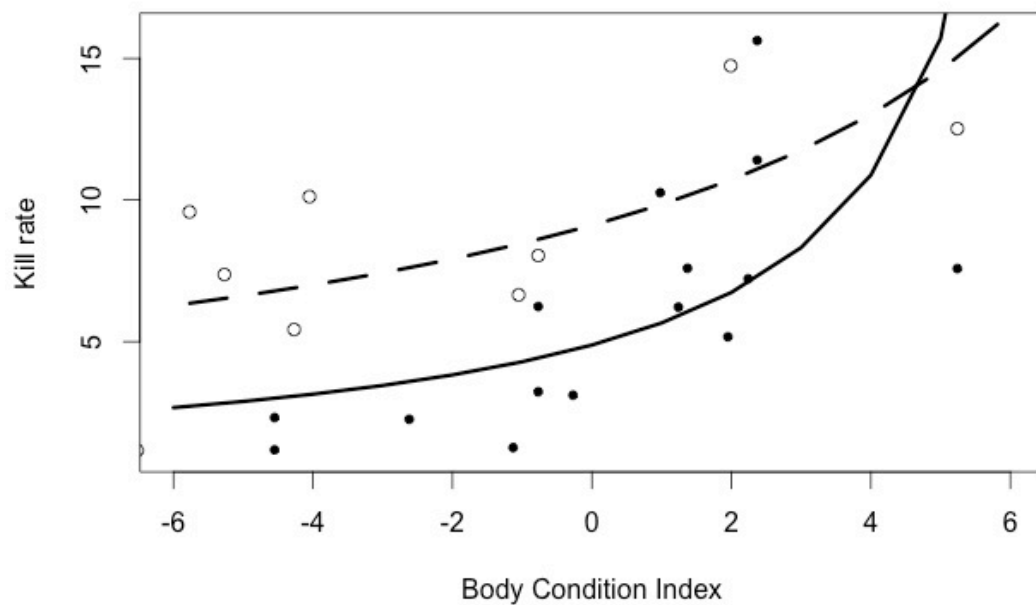| Model	Body Condition Index	Pack Size	Wolf Age	Moose Density	Roe deer Density	AICc	delta	weight
Model 1	x	x				126.27	0.00	0.43
Model 2	x	x	x			128.24	1.98	0.16
Model 3	x	x			x	129.24	2.97	0.10
Model 4	x	x		x		129.31	3.05	0.09
Model 5		x	x			130.64	4.37	0.05
Importance	0.86	0.99	0.29	0.17	0.18			

Figure 5: *Model estimates of the kill rate in relation to body condition for packs (of >2 wolves, solid line) and pairs (dashed line). Points represent real data of packs (solid points) and pairs (circles). Data derived from 24 winter studies conducted in Scandinavia from 2001 to 2014.*

Factors affecting the proportion of wild prey and other carcasses in a territory

Next I investigated the effect of three variables (wolf body condition index, pack size and wolf age) on the proportion of wolf killed wild prey in each territory. Model selection showed that only one model, containing body condition index, was of best quality (Table 5). Neither of the other two variables, pack size nor wolf age, appeared to have a strong effect on the proportion of wolf killed prey.

Table 5: *Model selection, based on Akaike's information criterion for small sample size (AICc), for variables affecting proportion of wolf killed carcasses in territories of Scandinavian wolves.*

	Body Condition	Pack Size	Wolf Age	df	AICc	delta	weight
Model1	x			3	-5.51	0.00	0.60
Model2	x	x		4	-3.26	2.24	0.19
Model3	x		x	4	-2.63	2.87	0.14
Model4	x	x	x	5	-0.41	5.10	0.05
Model5				2	2.58	8.09	0.01
Model6			x	3	4.04	9.55	0.01
Model7		x		3	4.92	10.43	0.00
Model8		x	x	4	5.61	11.12	0.00
Importance	0.98	0.25	0.2				

Wolves with above average body weight appeared to have a higher proportion of wolf-killed prey in their territory than those with below average body weight (Figure 6, F= 8.18, df= 3.22, p= 0.001). Conversely, this means wolves in poorer condition (those with body weight below the study average) fed on a higher proportion of non-wolf killed carcasses as compared to wolf-killed prey.
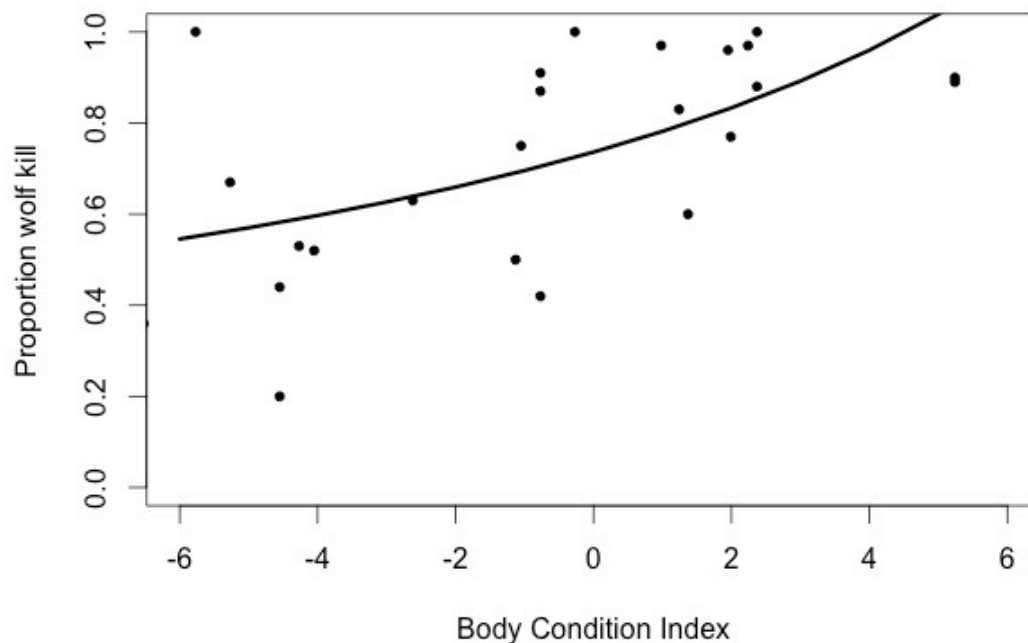

Figure 6: *Model estimates of the proportion of wolf-killed wild prey in relation to body condition in Scandinavian wolves (points representing real data). Data derived from 24 winter studies from 2001 to 2014.*

Question 3: Does a higher kill rate result in a lower use of other carcasses?

There was a tendency for wolf packs with a high proportional use of wolf-killed prey to also have a high kill rate (Figure 7, F= 5.18, df= 3.22, p= 0.032). This result may also be interpreted as that a high kill rate results in a lower use of non-wolf killed carcasses.
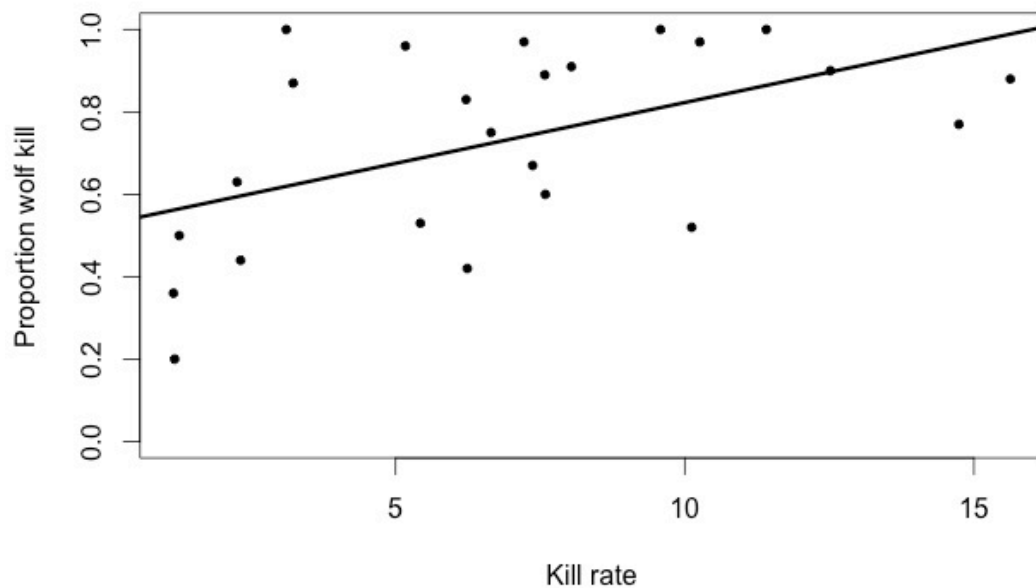

Figure 7: *Linear regression of the proportion of wolf killed wild prey in relation to kill rate in Scandinavian wolves (points representing real data). Data from 24 winter studies from 2001 to 2014.*

Discussion

Question 1: The use of different food sources differs between wolf packs

I showed that the number of carcasses of different types varied between wolf territories. It is possible that the frequency of encountering different types of carcasses determines the number utilised by wolves in a territory. Therefore, a territory with no carcasses classified into either of the non-wolf-killed categories (natural death and anthropogenic causes) may just reflect a very low abundance of these carcass types. Re-colonising wolves in parts of Poland were found to consume prey species in a similar proportion to the abundance (Nowak et al., 2011), although that study also found that some selection towards certain prey species does occur according to pack

size. A similar logic may then be applied to the abundance and use of carcass types in this study. It has often been found that wolves will scavenge when given the opportunity (Smithet al., 2000, Jędrzejewski et al., 2002, Selva et al., 2003, Jung, 2011). Therefore differences found in this study might to some extent reflect variation in availability. A territory with a relatively low density of roads and railways may have much less carcasses resulting from this cause of death. The intensity of human activity was not used in this study but may show promise for future studies investigating the role scavenging plays in the diet of wolves.

Composition of wolf killed prey

The composition of prey species found in this study confirm what has been found in other studies (Śmietana and Klimek, 1993, Gade-Jorgensen and Stagegaard, 2000, Sand et al., 2005, 2012). Usually one ungulate species is the main prey type, and in Scandinavian wolves this prey type is moose (Olsson et al., 1997, Sand et al., 2005, 2008). However, since I used carcasses found during field surveys it is likely that small species are underrepresented due to less biomass left to be found (Sand et al., 2008, Webb et al., 2008). Studies using DNA from faeces has shown that small prey make up a larger proportion in the diet than what is commonly found during field surveys (Jędrzejewski et al., 2002, Marucco et al., 2008) and can be as much as 2.5 times higher (Sand et al., 2008).

Time at carcass

I found that the time spent at carcasses was most influenced by the carcass type and the age of the carcass (the time since death). Wolves spend around 4 times more time (proportionally) feeding on wolf-killed prey compared to on non-wolf killed carcasses. A likely explanation for this finding may be that the majority of non-wolf killed carcasses contain less edible biomass (for example hunter remains). This may also be the reason why the age of a carcass was significantly negatively related to the time spent at the carcass by wolves. The older the carcass the more likely it was killed before the start of the study period. The majority of the available biomass of a carcass is consumed immediately after the kill is made (Jędrzejewski et al., 2000, Wikenros et al., 2013). Thus, for old carcasses very little, or even no, biomass may be available thus resulting in less time spent at carcass.

Question 2: Does kill rate on wild prey correlate with factors such as age, body condition (weight), pack size and prey densities?

I found that the per capita kill rate in this study (1.18-15.63 kg/wolf/day, mean = 6.93) was in accordance with, and at the upper end of, kill rates found elsewhere in the literature (Table 6). Body condition index and pack size was positively correlated with per capita kill rate and whereas wolf age and prey densities had no effect.

Table 6: *List of kill rate (kg/wolf/day) found in the literature compared to kill rate found in this study.*

kg/wolf/day	Study
5.6	(Jędrzejewski et al., 2002)
4.4 - 6.3	(Mech, 1967)
0.5 - 7.0	(Fritts and Mech, 1981)
1.6 - 2.8	(Messier and Crête, 1985)
4.5 - 14.9	(Ballard et al., 1987)
2.0	(Fuller, 1989)
4.4 - 7.8	(Thurber and Peterson, 1993)
4.1 - 6.4	(Hayes et al., 2000)
1.18 - 15.63	This study

Body condition index

I found that a low body condition (below average body weight) correlated with a lower kill rate and a lower proportion of wolf-killed carcasses. It is possible that some wolves are forced to scavenge more due to an inability to hunt successfully from injury, disease or because of lower hunting skills. An example of this was observed in the alpha pair of the Uttersberg pack. Both wolves appeared to be in poor condition, with leg and jaw deformities, and were found to survive mainly on carcasses from train accidents and hunter remains (only 8 out of 29 carcasses were wolf kills). The use of a body condition index as a variable was used to represent this relationship. Though one should be mindful that a correlation does not necessarily equal causation, it is thus difficult to determine if a good body condition is the cause of a high kill rate. It could also be that a high kill rate actually results in a good body condition. This suggests that wolves might prefer to make fresh kills to using other carcasses, but when this fails scavenging becomes an important survival trait.

Body condition index and pack size

Previous studies have found a relationship between pack size and kill rate (Thurber and Peterson, 1993, Creel 1990, Hayes et al., 2000, Vucetich et al., 2004). When I examined both variables together (pack size and body condition index, Figure 5) packs had a lower per capita kill rate than pairs. The reason is likely due to the sharing of food among pack members. This is supported by results showing that per capita kill rate decreases with increasing pack size, meaning larger packs have less biomass available per wolf than a pack of only two (Schmidt and Mech, 1997, Hayes et al., 2000, Zimmermann et al., 2014). However, per pack kill rate during summer in Scandinavian wolves has been found to be more or less equal across all pack sizes (Sand et al., 2008) and group size did not affect hunting success in wolves during winter (Sand et al., 2006). This is likely due to the hunting being carried out by the alpha pair (Zimmermann et al., 2014) as other pack members are most often the offspring of the same year (Wabakken et al., 2001).

Prey density and kill rate

Messier (1994) and Hayes et al. (2000) found that at low moose density (0.2-2.5 moose/km^2) kill rates were density dependent but this was not the case at medium to high densities. All densities used in this study are well within this range (only one territory was above this density with 3.44 moose/km^2), yet no density dependent per capita kill rate of kg biomass was found in Scandinavian wolves. It is difficult to compare such results as most studies use a number of prey/day/wolf and not biomass/day/wolf. Yet there are still other possible reasons this effect was not found in this study. Moose densities used begin at 0.5 moose/km^2, which is at the upper end of the range used in Messier (1994). Therefore, it may be necessary to have data with densities lower than 0.5 moose/km^2 to be able to detect a density dependent kill rate. Other reasons may also be tied to the differences in pack dynamics observed between North American and European wolves. North American wolves often hunt in larger packs, including offspring of several years and even unrelated individuals (Olson, 1938, Fuller, 1989, Smith, 2005), whereas most European wolf packs are made up of the alpha pair and offspring of the same year (Wabakken et al., 2001). The reason a density dependent kill rate is not observed in the Scandinavian population may be that the alpha pair is already hunting at its maximum capacity, regardless of prey density.

Recent studies found that the prey-to-predator ratio has been a stronger predictor of kill rate than prey density (Vucetich et al., 2002). Literature shows that a multitude of additional factors may affect kill rate (Schmidt and Mech, 1997, Jędrzejewski et al., 2002) including pack size (Creel, 1997, Vucetich et al., 2004), age structure of the prey population (Sand et al., 2012) and presence of other predator species (Gervasi et al., 2012). These are all factors that should be examined in relation to scavenging in wolves and may help to shed more light on its importance.

Age

My results showed that the age of the alpha pair appeared to have little effect on the kill rate, even though an age range of one to nine years was used. Interestingly, Sand et al. (2006) showed that male age was significantly positively related to hunting success of Scandinavian wolves, increasing after the age of 1.5-2.5 years. Such results were also found in spotted hyenas (Holekamp et al., 1997). Additionally, MacNulty et al. (2009) found that, in Yellowstone wolves, the ability to attack, select and kill decreased significantly after the age of three years. One of the reasons my results differ may be due to the fact that the kill rate was calculated from alpha pairs combined and not per individual. Thus effects of a very old or very inexperienced individual might be offset by the ability of its partner.

Question 3:Does a higher kill rate result in a lower use of other carcasses?

Many studies focus on factors influencing kill rate but not how this influences scavenging. Therefore, it is interesting that the current study found a high kill rate does correlate to a low use of scavenged carcasses. However, it is possible that levels of scavenging might also vary seasonally. Kill rate varies during summer and winter (Sand et al., 2005, 2008) and therefore the proportions of scavenging in a territory may also differ over time due to seasonal variation in availability of wild prey species and carcasses resulting from causes other than wolf predation. Additionally, scavenging may be a key source of food for a young wolf currently learning to kill successfully and whilst establishing a new territory.

Implications of the results

It is important to find ways to mitigate the conflict between wolves and humans. Regarding moose harvesting in Sweden, an increase in non-wolf killed carcasses

(such as supplemental feeding) would likely only result in a marginal reduction in kill rate. However, I found that in this study (a real situation without supplemental feeding) a lower kill rate is also correlated to a lower body condition. Thus, more data needs to be collected to understand what impact it would have to artificially increase non-wolf killed carcasses (Oro et al., 2013). Additionally, studies have found compelling evidence that an increase in the availability of carcasses would facilitate an increase in the survival and population size of wolves (summarised in Newsome et al., 2015) ultimately leading to an increase in the overall harvest of ungulates by wolves. Increasing supply of carrion has been shown to reduce kill rates in a facultative scavenger, wolverine (*Gulo gulo*) (Mattisson et al., 2011). Wolves, however, are generally thought to prefer hunting fresh kills over scavenging and thus seems unlikely a similar effect would be seen (Newsome et al., 2015). Nonetheless, fully understanding the complexity of the feeding behaviour of wolves is still a long way off. While I show that there are differences between wolves in terms of scavenging it is not clear what the drivers are behind this. The fact that both kill rate and proportion of wild kill correlate with the body condition index is an indicator that scavenging is important for supplementing the diet for some wolves. This is an important result, as scavenging is not considered in management plans for wolves or moose. Therefore, it may be beneficial to investigate at what intervals scavenging occurs and whether it falls into long periods between kills. More importantly, finding out how scavenging varies seasonally, especially during hunting seasons. With more data in these areas it would be possible to predict wolf kill rate more accurately by season, pack size and perhaps even the condition of the wolves.

None the less, I have found that there is a large variation between packs in their kill rate and that scavenging appears to fill the difference for wolves with relatively low kill rate of wild prey (see Messier and Crête, 1985 for similar findings). I have shown that the body condition may be able to act as an indicator for both the kill rate and the level of scavenging in wolves. Knowledge of additional factors such as body weight may be helpful in accurately predicting predator impact on prey populations.

References

Anon. (2015). Inventering av varg vintern 2014-2015. Inventeringsresultat för stora rovdjur i Skandinavien. Redaktion: Svensson L, Wabakken P, Maartmann E, Åkesson M, och Flagstad Ø. Viltskadecenter, SLU, Rapport nr. 1 – 2015. 52 s.

Ballard, W.B., Whitman, J.S., and Gardner, C.L. (1987). Ecology of an exploited wolf population in south-central Alaska. Wildl. Monogr. *98*, 1–54.

Barton, K. (2015). MuMIn: Multi-Model Inference. R package, version 1.13.4

Beschta, R.L., and Ripple, W.J. (2009). Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biol. Cons. *142*, 2301–2414.

Burnham, K.P., and Anderson, D.R. (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer, New York

Colombo, M. (2013). Determinants of winter kill rates of wolves in Scandinavia. Master´s Thesis Biology. Sveriges lantbruksuniversitet, 2013:16, 28 p.

Cooper, S. M. (1991). Optimal hunting group size: the need for lions to defend their kills against loss to spotted hyaenas. Afr. J. Ecol. *29*, 130–136.

Creel, S. (1997). Cooperative hunting and group size: assumptions and currencies. Anim. Behav. *54*, 1319–1324.

Creel, S. and Creel, N.M. (1995). Communal hunting and pack size in African wild dogs, Lycaon pictus. Anim. Behav. *50*, 1325–1339.

DeVault, T.L., Rhodes, Jr., O.E. and Shivik, J.A. (2003). Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. Oikos *102*, 225–234.

Van Dijk, J., Gustavsen, L., Mysterud, A., May, R., Flagstad, Ø., Brøseth, H., Andersen, R., Andersen, R., Steen, H. and Landa, A. (2008). Diet shift of a facultative scavenger, the wolverine, following recolonization of wolves. J. Anim. Ecol. *77*, 1183–1190.

Fritts, S.H., and Mech, L.D. (1981). Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. Wildl. Monogr. *80*, 3–79.

Fuller, T.K. (1989). Population dynamics of wolves in north-central Minnesota. Wildl. Monogr. *105*, 3–41.

Gade-Jorgensen, I., and Stagegaard, R. (2000). Diet composition of wolves Canis lupus in east-central Finland. Acta Theriol. (Warsz.) *45*, 537–547.

Gervasi, V., Nilsen, E.B., Sand, H., Panzacchi, M., Rauset, G.R., Pedersen, H.C., Kindberg, J., Wabakken, P., Zimmermann, B., Odden, J. (2012). Predicting the potential demographic impact of predators on their prey: a comparative analysis of two carnivore-ungulate systems in Scandinavia. J. Anim. Ecol. *81*, 443–454.

Hayes, R.D., Baer, A.M., Wotschikowsky, U., and Harestad, A.S. (2000). Kill rate by wolves on moose in the Yukon. Can. J. Zool. *78*, 49–59.

Holekamp, K.E., Smale, L., Berg, R., and Cooper, S.M. (1997). Hunting rates and hunting success in the spotted hyena (Crocuta crocuta). J. Zool. *242*, 1–15.

Hosseini-Zavarei, F., Farhadinia, M.S., Beheshti-Zavareh, M., and Abdoli, A. (2013). Predation by grey wolf on wild ungulates and livestock in central Iran. J. Zool. *290*, 127–134.

Huggard, D.J. (1993). Effect of snow depth on predation and scavenging by gray wolves. J. Wildl. Manag. *57*, 382–388.

Jędrzejewski, W., Schmidt, K., Theuerkauf, J., Jędrzejewska, B., Selva, N., Zub, K., and Szymura, L. (2002). Kill rates and predation by wolves on ungulate populations in białowieża primeval forest (poland). Ecology *83*, 1341–1356.

Jędrzejewski, Wl., Jędrzejewska, B., Okarma, H., Schmidt, K., Zub, K., and Musiani, M. (2000). Prey selection and predation by wolves in Bialowieża Primeval Forest, Poland. J. Mammal. *81*, 197–212.

Jung, T.S. (2011). Gray wolf (Canis lupus) predation and scavenging of reintroduced American bison (Bison bison) in Southwestern Yukon. Northwest. Nat. *92*, 126–130.

Kruuk, H. (1972). The spotted hyena: a study of predation and social behavior. Chicago, IL. University of Chicago Press.

MacNulty, D.R., Smith, D.W., Vucetich, J.A., Mech, L.D., Stahler, D.R. and Packer, C. (2009). Predatory senescence in ageing wolves. Ecol. Lett. *12*, 1347–1356.

Marucco, F., Pletscher, D.H. and Boitani, L. (2008). Accuracy of Scat Sampling for Carnivore Diet Analysis: Wolves in the Alps as a Case Study. J. Mammal. *89*, 665–673.

Mateo-Tomás, P., Olea, P.P., Moleón, M., Vicente, J., Botella, F., Selva, N., Viñuela, J., and Sánchez-Zapata, J.A. (2015). From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. Divers. Distrib. *21*, 913-924

Mattisson, J., Andrén, H., Persson, J., and Segerström, P. (2011). Influence of intraguild interactions on resource use by wolverines and Eurasian lynx. J. Mammal. *92*, 1321–1330.

Mech, L.D. (1967). The Wolves of Isle Royale. The Sciences *7*, 6–9.

Messier, F. (1994). Ungulate Population Models with Predation: A Case Study with the North American Moose. Ecology *75*, 478–488.

Messier, F., and Crête, M. (1985). Moose-wolf dynamics and the natural regulation of moose populations. Oecologia *65*, 503–512.

Newsome, T.M., Dellinger, J.A., Pavey, C.R., Ripple, W.J., Shores, C.R., Wirsing, A.J. and Dickman, C.R. (2015). The ecological effects of providing resource subsidies to predators. Glob. Ecol. Biogeogr. *24*, 1–11.

Nowak, S., Mysłajek, R.W., Kłosińska, A., and Gabryś, G. (2011). Diet and prey selection of wolves (Canis lupus) recolonising Western and Central Poland. Mamm. Biol. - Z. Für Säugetierkd. *76*, 709–715.

Olson, S.F. (1938). Organization and range of the pack. Ecology *19*, 168–170.

Olsson, O., Wirtberg, J., Andersson, M., and Wirtberg, I. (1997). Wolf Canis lupus predation on moose Alces alces and roe deer Capreolus capreolus in south-central Scandinavia. Wildl. Biol. *3*, 13–25.

Oro, D., Genovart, M., Tavecchia, G., Fowler, M.S. and Martínez-Abraín, A. (2013). Ecological and evolutionary implications of food subsidies from humans. Ecol. Lett. *16*, 1501–1514.

Palacios, V. and Mech, L.D. (2011). Problems with studying wolf predation on small prey in summer via global positioning system collars. Eur. J. Wildl. Res. *57*, 149–156.

Pereira, L.M., Owen-Smith, N. and Moleon, M. (2014). Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons. Mammal Rev. *44*, 44–55.

R Core Team (2015). R: A language and environment for statistical computing. (Vienna, Austria: R Foundation for Statistical Computing).

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., et al. (2011). Status and Ecological Effects of the World's Largest Carnivores. Earth Sci. *333*, 301–306.

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. Wildl. Soc. Bull. *33*, 914–925.

Sand, H., Wikenros, C., Wabakken, P., and Liberg, O. (2006). Effects of hunting group size, snow depth and age on the success of wolves hunting moose. Anim. Behav. *72*, 781–789.

Sand, H., Wabakken, P., Zimmermann, B., Johansson, O., 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*, 53–64.

Sand, H., Vucetich, J.A., Zimmermann, B., Wabakken, P., Wikenros, C., Pedersen, H.C., Peterson, R.O. and Liberg, O. (2012). Assessing the influence of prey–predator ratio, prey age structure and packs size on wolf kill rates. Oikos *121*, 1454–1463.

Schmidt, P.A. and Mech, L.D. (1997). Wolf Pack Size And Food Acquisition. Am. Nat. *150*, 513–517.

Selva, N., Jedrzejewska, B., Jedrzejewski, W., and Wajrak, A. (2003). Scavenging on European bison carcasses in Bialowieza Primeval Forest (eastern Poland). Ecoscience *10*, 303–311.

Selva, N., Jedrzejewska, B., Jedrzejewski, W. and Wajrak, A. (2005). Factors affecting carcass use by a guild of scavengers in European temperate woodland. Can. J. Zool.-Rev. Can. Zool. *83*, 1590–1601.

Śmietana, W., and Klimek, A. (1993). Diet of wolves in the Bieszczady Mountains, Poland. Acta Theriol. (Warsz.) *38*, 245–251.

Smith, D.W. (2005). Ten years of Yellowstone wolves. Yellowstone Sci. *13*, 7–33.

Smith, D.W., Peterson, R.O., and Houston, D.B. (2003). Yellowstone after wolves. BioScience *53*, 330–340.

Stahler, D.R., Smith, D.W., and Guernsey, D.S. (2006). Foraging and feeding ecology of the gray wolf (Canis lupus): Lessons from Yellowstone National Park, Wyoming, USA. J. Nutr. *136*, 1923S – 1926S.

Svensson, L., Wabakken, P., Maartmann, E., Strømseth, T., Kojola, I., Åkesson, M., Flagstad, O. and Zetterberg, A. (2013). Varg i Skandinavien: Statusrapport för vintern 2012-2013 (Høgskolen i Hedmark).

Svensson, L., Wabakken, P., Maartmann, E., Kojola, I., Strømseth, T., Åkesson, M. and Flagstad, O. (2014). Varg i Skandinavien: Statusrapport för vintern 2013-2014 (Høgskolen i Hedmark).

Thurber, J.M. and Peterson, R.O. (1993). Effects of population density and pack size on the foraging ecology of gray wolves. J. Mammal. *74*, 879–889.

Valdmann, H., Andersone-Lilley, Z., Koppa, O., Ozolins, J., and Bagrade, G. (2005). Winter diets of wolfCanis lupus and lynxLynx lynx in Estonia and Latvia. Acta Theriol. (Warsz.) *50*, 521–527.

Vucetich, J.A., Peterson, R.O., and Schaefer, C.L. (2002). The effect of prey and predator densities on wolf predation. Ecology *83*, 3003–3013.

Vucetich, J.A., Peterson, R.O., and Waite, T.A. (2004). Raven scavenging favours group foraging in wolves. Anim. Behav. *67*, 1117–1126.

Wabakken, P., Sand, H., Steinset, O., Kojola, I., and Aronson, A. (2001a). Ulv i Skandinavia: Statusrapport for vinteren 2000-2001 (Høgskolen i Hedmark).

Wabakken, P., Sand, H. akan, Liberg, O., and Bjärvall, A. (2001b). The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978-1998. Can. J. Zool. *79*, 710–725.

Webb, N.F., Hebblewhite, M., and Merrill, E.H. (2008). Statistical Methods for Identifying Wolf Kill Sites Using Global Positioning System Locations. J. Wildl. Manag. *72*, 798–807.

Wikenros, C., Sand, H., Ahlqvist, P., and Liberg, O. (2013). Biomass Flow and Scavengers Use of Carcasses after Re-Colonization of an Apex Predator. Plos One *8*, e77373.

Wilmers, C.C., Stahler, D.R., Crabtree, R.L., Smith, D.W., and Getz, W.M. (2003). Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. Ecol. Lett. *6*, 996–1003.

Wilson, E.E., and Wolkovich, E.M. (2011). Scavenging: how carnivores and carrion structure communities. Trends Ecol. Evol. *26*, 129–135.

Zimmermann, B., Sand, H., Wabakken, P., Liberg, O., and Andreassen, H.P. (2014). Predator-dependent functional response in wolves: from food limitation to surplus killing. J. Anim. Ecol. *84*, 102-112