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Master thesis

Estimating ungulate carrion biomass and possible ecological effects on red fox (*Vulpes vulpes*) in central Norway

Master in Applied Ecology

2014

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Abstract

Ungulates constitute the bulk of carrion in many terrestrial ecosystems. Knowledge of carrion availability is paramount to understand its ecological effects and I aimed to estimate carrion availability in Nord-Trøndelag county in central Norway. I also discuss possible ecological effects of carrion availability on a key stone predator in Scandinavia, the red fox (*Vulpes vulpes*).

I used literature to estimate average monthly carrion availability from wild ungulates (moose *Alces alces* and roe deer *Capreolus capreolus*) and livestock (domestic sheep *Ovis aries* and semi-domestic reindeer *Rangifer tarandus tarandus*). I estimated monthly carrion supply from four carrion sources; i) predation remains, ii) harvest remains, iii) traffic collisions and iv) other causes of death (OCD). Spatio-temporal carrion availability was divided in forest/agricultural areas and mountain areas during the cold and the warm season, respectively.

I found that domestic sheep contributed to maintain the annual stability of carrion supply in both areas by providing carrion only in the warm season. Estimated average annual carrion supply was by far most prominent in forest/agricultural areas (70 kg/km^2). The supply peaked in the end of the warm season due to remains from the autumn harvest (25 kg/km^2) from which discarded internal organs from moose constituted 20 kg/km^2 . Estimated carrion supply from harvest and OCD was of same magnitude and both resources are available over large areas. I suggest that harvest remains appear as more clumped distribution in lower altitudes near farmland due to moose and roe deer habitat preferences. I also suggest a similar distribution of OCD carcasses during the cold season due to migratory effects. Furthermore, winter severity most likely skews this availability towards late winter and spring.

Based on the findings, I expect increased red fox survival when the availability of voles is low. This is mainly due to the combined effect of estimated amounts of harvest remains in the face of winter and the amount of carrion supply during the cold season. Future research should focus on the importance of carrion availability on red fox distribution, density and reproduction.

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1. Introduction

Carrion is exploited by a wide range of scavengers, from bacteria to large carnivores (e.g. Cortés-Avizanda 2010). Examples are available for almost every world biome, from beached whales to carcasses from a variety of organisms such as ungulates or aquatic vertebrates (Valverde 1967; Houston 1978, 1979; Wilmers *et al.* 2003b; Selva 2004; Wikenros *et al.* 2013). The fact that nearly all vertebrate predators are scavengers to some extent (DeVault, Rhodes Jr. & Shivik 2003), underlines why carrion plays an important role in understanding animal communities and ecological processes in terrestrial ecosystems (e.g. DeVault, Rhodes Jr. & Shivik 2003; Melis *et al.* 2004; Selva & Fortuna 2007; Cortés-Avizanda *et al.* 2009). Wilson & Wolkowitch (2011) argued that more energy is generally transferred per link in food webs via scavenging than predation.

Ungulate carrion, which constitutes the bulk of carrion in many terrestrial ecosystems, is variable in spatial distribution (clumped versus dispersed) and temporal availability (constant versus pulsed) (Selva & Fortuna 2007). Large predators provides carrion that is consistent over time, dispersed in space and relatively predictable (Wilmers *et al.* 2003b; Selva 2004; Selva *et al.* 2005). In contrast, natural deaths caused by disease, cold or starvation appears to be more unpredictable, relatively random distributed in space and often highly aggregated in late winter (Selva & Fortuna 2007). In addition, humans may unintentionally provide food for scavengers through hunting and wildlife-vehicle collisions (Wikenros *et al.* 2013).

Scandinavia has experienced re-colonization of several species of large carnivores during the last decades, including brown bear (*Ursus arctos*), wolf (*Canis lupus*), wolverine (*Gulo gulo*), lynx (*Lynx spp.*) and golden eagle (*Aquila chrysaetos*) (Andersen *et al.* 2003). However, predator kills are often consumed to a large extent by the predator itself (Houston 1979), forcing scavengers to rely more on animals dying from other causes of death (DeVault, Rhodes Jr. & Shivik 2003). Besides the effect of carrion provision, large carnivores also represent risks for scavengers due to intra-guild predation (Palomares & Caro 1999). In areas with low population sizes of large carnivores, reduced top-down effects may lead to mesopredator release (mesopredator release hypothesis, see e.g. Crooks & Soulé 1999). However, mesopredator numbers are not only affected by presence or absence of apex predators, but also by the food resources (bottom-up mechanisms) (Elmhagen & Rushton 2007).

In northern latitudes, moose (*Alces alces*) and semi-domestic reindeer (*Rangifer tarandus tarandus*) carcasses during winter are shown to be important for scavengers when other food availability is generally low (Killengren *et al.* 2011; Needham *et al.* 2014). The interaction between amount, exploitation and climate should affect the time carrion resources are available. In the cold climate of high-latitude regions, large carcasses can last for long periods (Selva *et al.* 2003) and may represent an essential food resource for the community of predator- scavengers (Houston 1978; Wilmers *et al.* 2003b; Selva 2004; Selva *et al.* 2005; Wikenros *et al.* 2013).

Very few studies on scavenging have been conducted in cold regions (Selva 2004). However, use of camera-traps in recent years in Scandinavia have provided knowledge of some facultative scavengers that frequently visits carrion in winter, such as red fox, common raven (*Corvus corax*) and pine marten (*Martes martes*, Wikenros *et al.* 2013), wolverine (Mattisson *et al.* 2013) and eagles (golden eagle and white-tailed eagle *Haliaeetus albicilla*, Pálsdóttir 2012). Species generally considered being predominantly predacious, such as great-horned owls (*Bubo virginianus*) and red foxes are facultative scavengers and there is a growing recognition of their carrion use having far-reaching consequences on ecological communities (DeVault *et al.* 2011). Cortés-Avizanda *et al.* (2009) found that the availability of carcasses induces the aggregation of large numbers of facultative scavengers, increasing both the risk of predation on, and the avoidance of, other vertebrates that live around these areas.

The red fox is the most widely distributed carnivore in the world, being extremely adaptable and able to feed on a large variety of food sources (Jedrzejewski & Jedrzejewska 1992). The ecological role of the red fox was revealed during a period of natural reduction by sarcoptic mange (*Sarcoptes scabiei*) in the late 1970s and throughout the 1980s. At this time, the red fox decline was followed by an increase in some small game species and pine marten, thus underlining the role of the red fox as a key stone predator in Scandinavia (Lindström *et al.* 1994).

There has been an increase of ungulates in Scandinavia during the 20th century, followed by increased harvest (Lavsund, Nygrèn & Solberg 2003) and traffic collisions (Storaas *et al.* 2005). Increased carcass availability have been suggested to have had compensating effects on the red fox diet in years with low vole abundances, and that it may have caused a substantial increase in their abundance (Selås & Vik 2006). In the low arctic tundra in

northern Norway, Killengren *et al.* (2011) showed that red foxes primarily subsisted on semi-domestic reindeer carrion during winter when rodents were scarce. Furthermore, utilization of moose remains was shown to be a main foraging activity for red foxes during winter and spring in southern Norway (Needham *et al.* 2014). Moreover, Bino *et al.* (2010) showed abrupt spatial and numerical responses of red foxes to a reduction in anthropogenic resources. Hence, especially estimations of human-induced food subsidies should be useful if mitigation strategies to reduce carrion availability for scavengers should be incorporated.

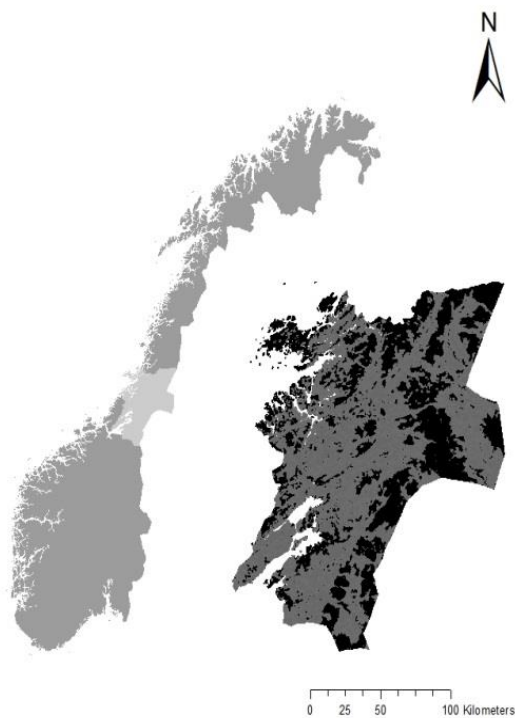
Earlier studies in boreal forests (Houston 1978; Gese, Ruff & Crabtree 1996; Wilmers *et al.* 2003a), African savannah (Houston 1974, 1979) and Neotropical forest (Houston 1986) have all provided some rough estimates of ungulate carrion supply in these ecosystems. In European boreal forests, monthly estimates of carrion supply from moose have been conducted in south-central Sweden (Wikenros *et al.* 2013) and bimonthly for all ungulates in a temperate forest (Białowieża Primeval Forest) in Poland (Selva 2004). However, to my knowledge, there are no estimates of monthly carrion biomass (human and non-human provided) from boreal forests in Scandinavia that includes both wild and domestic ungulate species, such as free-ranging sheep (*Ovis aries*) and semi-domesticated reindeer. DeVault *et al.* (2011) pointed out that, although our understanding of scavenging ecology has grown over the past decade, most research in this area has been conducted in predominantly undisturbed habitats. Knowledge of carrion availability is paramount to understand its ecological effects (DeVault, Rhodes Jr. & Shivik 2003) and obviously availability can vary in different landscapes with different impact of human disturbance.

It seems to have been a growing recognition of the importance to estimate carrion availability for predator-scavengers in Norway, especially to better understand ecological effects behind the observed long-term decline of small game densities (e.g. Pedersen & Pedersen 2012). The main goals of this thesis are therefore to (i) estimate monthly carrion biomass and (ii) discuss ecological effects this might have on red fox survival and reproduction. With the estimations of spatio-temporal carrion availability, this study aims at an increased understanding of the predator-scavenger community.

2. Methods

2.1 Study area

Nord-Trøndelag county (62°25'N12°48'E) is located in central Norway (Figure 1). The total land area is 20 881 km² (Statistics Norway 2012). Nord-Trøndelag is situated in the boreal zone with a mountain range in the east, bordering Sweden, and a coastline with fjords and islands in the west. The climate is sub oceanic and weakly continental. The human population density is highest in the west, which is a mosaic of forest and agricultural land. Agriculture in the eastern parts is more spread and characterized by large valleys with



Figur 1. Map of the study area (Nord-Trøndelag county) in central Norway. Grey is mostly forested areas and black is large open areas showing mainly the eastern and northern mountain areas.

livestock husbandry, mainly cattle and sheep. Most of the forests are commercially managed and are dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) (Elgersma & Asheim 1998). Central Norway has an average of 1000 mm of precipitation annually, mostly in autumn and early winter. Winter temperatures are ranging from just below zero near the coast and down to –35 °C in the inland (Store Norske Leksikon 2013). Norway is divided into 8 large carnivore regions and central Norway (region 6) comprises 3 counties, among those Nord-Trøndelag county (e.g. Odden *et al.* 2014).

2.2 Overview of methods

I estimated available carrion biomass from two ungulate categories; livestock (sheep and reindeer) and wild ungulates (moose and roe deer *Capreolus capreolus*). Domestic sheep are kept in barns during winter and the majority is left unguarded on summer pastures in forests

and mountains. Semi-domestic reindeer husbandry covers almost the entire study area and the animals are usually free-ranging all year round (Reindeer Husbandry Management 2013). Moose and roe deer are the most abundant wild ungulates in the study area. Red deer (*Cervus elaphus*) occur at relatively low numbers and are therefore not considered (see 2.4.1).

I used the following parameters to estimate carrion availability for scavengers:

- i) Predator densities
- ii) Ungulate densities
- iii) Number of dead ungulates from:
 - Predation
 - Harvest
 - Traffic collisions
 - Other causes of death (disease, starvation, accidents)
- iv) Ungulate weights
- v) Consumption by predators
- vi) Proportion of harvest remains
- vii) Proportion of animals removed after collisions

I averaged the number of dead ungulates from harvest, collisions and other causes of death for a period of five years (2008-2012). I used large carnivore densities in 2011/2012 to estimate carrion biomass from kill rates (see 2.5.1.1).

I used temporal distribution of dead ungulates and their respective available biomass to estimate seasonal carrion density within two different habitat types (Forest/agricultural areas and mountain areas).

2.3 Predator densities

The National monitoring program for large carnivores (lynx, brown bear, wolverine, wolf and golden eagle) was established in 2002 to standardize and ensure similar use of methods (Rovviltportalen 2014). Methods to monitor and estimate population sizes of mammals are mainly based on snow-tracking, counts of known reproductions and DNA-analysis.

Lynx population size was estimated from the number of family groups (adult female with dependent kittens) in the study area (Brøseth & Tovmo 2012). To obtain an estimate of total

population size, the number of family groups was multiplied with the overall extrapolation factor for lynx in Scandinavia (5.9 ± 0.64) (Andr en *et al.* 2002).

Wolverine population size was based on estimates of adult wolverine numbers in large carnivore region 6. I calculated number of wolverines in the study area based on the relative number of known breedings in my study area compared to the other counties in the region 6 (Br seth, Tovmo & Andersen 2012).

Brown bear is monitored by DNA-analysis of fecal matter and hair collected by hunters, farmers, and SNO (Norwegian Nature Inspectorate). Estimated population size in the study area was derived from Aarnes *et al.* (2013).

Golden eagle population size is mainly monitored by surveys in different zones in the study area. Fieldworkers are responsible for each zone and helicopter is used to count eagles at expected nesting sites in difficult terrain and in remote areas (Nyg rd &  ster s 2014).

Wolf establishment in carnivore region 6 is according to national policy unwanted, but “floaters” have been observed every year over the past years (Large Carnivore Board in region 6 2013). However, they reported only a few occasions of killed livestock and I estimated no remains from wolf-kills.

2.4 Ungulate densities

2.4.1 Livestock

Sheep population size and age distribution was derived from Forest and Landscape Institute (2014). *Goat* (*Capra aegagrus*) population size was very small and only nine were reported lost in 2012 (Sheep and Goat in Nord-Tr ndelag county 2012). I estimated no carrion biomass from goats. *Semi-domestic reindeer* population size in and age and sex distribution was derived from Reindeer Husbandry Management (2013).

2.4.2 Wild ungulates

The National monitoring program for wild cervids (moose, red deer and wild reindeer) is based on 21 years of monitoring population density, condition and structure (Solberg *et al.* 2012). They reported that no direct counts to estimate population size have been conducted

and reports from hunters (“Seen moose” and “seen red deer”) and culled numbers is mainly used as a population index for these two species.

Moose winter population size in the study area has been estimated in a previous study (May, Stokke & Sakshaug 2007). I assumed the population size to be the same subsequent to this study because numbers culled (Statistics Norway 2013a) and observed moose per day (Hedegart *et al.* 2012) was quite stable the last decade. In Norwegian moose populations, the majority of animals is reported to be adults (≥ 1 year old, Solberg *et al.* 2005). The combination of proportion observed adults and calves during the hunt and proportion culled in these age classes (The Cervid Register 2013) gave an estimate of 70 % adults in the winter population.

Roe deer winter population size cannot be calculated in the same way as for moose because there are no reports of “seen roe deer” from hunters. However, annual reports of culled numbers are available (Statistics Norway 2013c) and rough estimates have been conducted based on culled numbers (population size = culled numbers * 4, Grøtan *et al.* 2005). In lack of data to estimate the age distribution, I used a study from southern Norway (Mysterud & Østbye 2006) assuming similar harvest rate in the different age classes.

Red deer abundance appeared to be very low. Based on harvested numbers, moose exceeds red deer population size (469 harvested, Statistics Norway 2013c) by 10-fold and adult natural death rate was shown to be only 7 % in a previous study from central Norway (Langvatn & Loison 1999). Very little carrion from red deer was therefore assumed to be available and no estimates were conducted.

2.5 Number of dead ungulates

Mortality was divided into 4 different causes (see 2.2). I defined other causes of death (OCD) as mortality not caused by human harvest, traffic collisions or depredation.

2.5.1 Livestock

2.5.1.1 Depredation and other causes of death

Every year, sheep farmers and sàmi-herders lose a certain number of animals. Large carnivores inflicts the losses, but “unknown causes” have been reported to be the most used

label on carcasses of lost animals in reindeer husbandry (Nybakk *et al.* 2002). Only a small proportion of the animals assumed to be killed by large carnivores have been subjected to autopsy by SNO. The remaining losses claimed to be caused by depredation are evaluated using subjective criteria by wildlife managers at the county level and emerge as compensated loss in Large Carnivore Database 3.0 (Directory for Environment 2013). However, total loss is higher, reflecting the number of animals that must have died from other causes. I derived total lost reindeer numbers in different age classes from the Large Carnivore Database 3.0 and total sheep losses from the Forest and Landscape Institute (2013).

Due to the uncertainty concerning livestock losses to large carnivores (e.g. Tveraa *et al.* 2013; Odden *et al.* 2014), I used two methods to estimate numbers killed by large carnivores:

- A) Losses compensated by the authorities.

- B) Kill rates and predator abundances (kill rate * predator abundance = numbers killed).
Kill rates was either i) directly derived from literature or ii) indirectly calculated as:
Kill rate/predator/year = proportion specific predator-loss of losses in the study area in year t / estimated specific predator population size in the study area in year t.

I assumed the gap between predator-killed numbers and total loss to be OCD numbers in both methods.

Sheep

Lynx kill rates on sheep (mostly lambs) was estimated from a study in southern Norway and based on predicted monthly kill rates for males and females (June – September) under different roe deer and lamb densities (Odden, Nilsen & Linnell 2014).

Brown bear kill rate on sheep was indirectly calculated from proportion losses in a study from the northwestern part of the study area (Knarrum *et al.* 2006).

Golden eagle kill rate on sheep was also indirectly estimated based on reported loss of lambs from a study in northern Norway (Nilsen, Hansen & Bjørn 2002).

Wolverine kill rate on sheep was not available and I assumed killed numbers from kill rates to be equal to compensated numbers (method A) in the calculations.

Reindeer

Lynx kill rate on reindeer was obtained from a previous study in the north-western part of the study area (Sunde *et al.* 2000). Minimum kill rates by lynx family groups during winter were shown to be 2.5 times higher on roe deer compared to reindeer. On average one of these ungulates were reported to be killed every 5 days (and thus the kill rate on roe deer was obtained as well). I used Nybakk *et al.* (2002) to obtain age-specific vulnerability from lynx depredation on reindeer.

Brown bear kill rate on adult reindeer is shown to be very low but considerably higher on calves (Støen 2012). However, calf consumption is shown to be 87 % (Støen 2012) and therefore no carrion estimates were conducted.

Wolverine and lynx kill rate on reindeer are related, because wolverine can scavenge on lynx-killed carcasses (Andrén *et al.* 2011; Mattisson *et al.* 2011b). I assumed no scavenging due to a low estimated kill rate by lynx and obtained kill rates by wolverine on reindeer from a model provided by Andrén *et al.* (2011). I obtained age-specific distribution of the kills from estimated increased number of killed adults and calves per breeding of wolverine (Tveraa *et al.* 2013).

Golden eagle kill rates on reindeer in different age classes were calculated from a study in the northwestern part of the study area (Nybakk, Kjelvik & Kvam 1999).

Monthly distribution of carcasses from livestock

I derived monthly numbers of carcasses autopsied by SNO from the Large Carnivore Database 3.0. I distributed killed livestock numbers according to documented and assumed killed by each predator in each month, assuming the number of autopsied carcasses to represent this distribution. I distributed OCD numbers from sheep equally each month during the grazing period (June – September) and reindeer OCD numbers were monthly distributed according to Nybakk *et al.* (2002).

2.5.1.2 Traffic collisions

In contrast to wild ungulates, there are no records of domestic ungulates killed on roads. However, very few collisions seem to occur on roads and animal owners retrieve dead animals (P. Malmo, wildlife ranger and search patrol, personal communication). I obtained

monthly numbers of reported railway-killed livestock in different age and sex from the Norwegian Railway Company (data from senior engineer J.B. Almåsbro).

2.5.2 Wild ungulates

2.5.2.1 Predation

Moose

Based on the combined effect of low brown bear population size (see 2.3.), a low kill rate on adult moose (0.4/year/bear, Swenson, Dahle & Sandegren 2001), a high consumption on calves (87 %, Støen 2012) and practically no wolves in the study area, no estimates of carrion biomass from predator-killed moose was conducted.

Roe deer

Estimated kill rates by lynx on roe deer is previously shown in 2.5.1.1. I used lynx predation patterns in Scandinavia (Gervasi *et al.* 2012) to calculate age-specific kill rates. I distributed killed numbers equally in each month of the year.

2.5.2.2 Other causes of death

Moose

Outside wolf territories and brown bear areas, average natural death rate in Scandinavian moose populations are reported to be 5 % for adult moose and slightly higher and more variable for calves (Solberg *et al.* 2005). However, this natural death rate included traffic collisions and these numbers were subtracted (estimated separately, see 2.5.2.4). The adult natural mortality rate was supported by a recent study in central Norway (Rolandsen *et al.* 2010). OCD in moose are shown to mainly occur during winter (Rönnegård *et al.* 2008; Rolandsen *et al.* 2010). I distributed OCD numbers equally in each month during November – April, assuming no such deaths during summer.

Roe deer

I derived roe deer OCD numbers in different age classes from a study in southeastern Norway (Melis *et al.* 2013) and I used a study from south central Sweden (Arbieu 2012) to obtain the monthly distribution.

2.5.2.3 Harvest

Moose and roe deer

I derived harvested moose and roe deer numbers from Statistics Norway (2013a,b). In contrast to moose, there are no records on harvested roe deer numbers in different age and sex classes in the study area. I assumed this distribution to be same as shown in study from southern Norway (Nilsen 2007). The moose hunting lasts from 25th September to 1th November and I assumed an equal harvest rate during the whole season. Roe deer hunting regulations allows males to be harvested from 10th August and all age- and sex classes can be harvested between 25th September and 23th December. I assumed that half of all males were culled in august and the second half during the rest of the hunting season.

2.5.2.4 Traffic collisions

During the last 40 years there has been a steady increase in the number of wild ungulate-vehicle collisions in Norway (Solberg *et al.* 2009). Based on rough population estimates, they reported that about 2.1 % of the moose population and 3.2 % of the roe deer population were killed in collisions on roads and railway lines.

Roads

I derived monthly numbers of reported road-collisions in different age and sex classes from The Cervid Register (2013). However, not all collisions are reported. To adjust for this bias, I followed Wikenros *et al.* (2013) by using 10 % mortality on 30 % non-reported moose collisions. I assumed all carcasses from non-reported vehicular mortality on roads to be available for scavengers.

Railways

I obtained monthly numbers of reported railway-killed wild ungulates in different age and sex classes from Norwegian Railway Company (data from senior engineer J.B. Almåsbro).

2.6 Ungulate weights

I derived slaughter weights in different age and sex classes for moose, reindeer and roe deer from Hedegart *et al.* (2013); Reindeer Husbandry Management (2013) and Nilsen (2007),

respectively. Live weights in moose is approximately twice as high as the slaughter weights (Wallin, Cederlund & Pehrson 1996), and this relationship has also been shown in roe deer (Mysterud & Østbye 2006) and reindeer (Mattisson *et al.* 2011b). I calculated summer weight gain in calves assuming linear growth (Mattisson *et al.* 2011b; Wikenros *et al.* 2013), starting with average weights at birth (c. 1th June) (Gaillard, Delorme & Julien 1993; Andersen & Sæther 1996; Tveraa, Fauchald & Henaug 2003) and ending with live weights in October. Linear summer weight gain for yearlings was then based on calf weights in October because live weights were set to be constant throughout winter (see Ryg 1983; Cederlund, Sand & Pehrson 1991). Adult (> 1.5 years) live weights were set to be the same all year round. Lamb weights was calculated assuming linear growth during summer (as for cervid juveniles) based on average weights at birth in late April and average live weights in October (Animalia 2012). I used live weight in four year old ewes as average adult live weights (Boman 2010). Estimated monthly ungulate live weights in different age and sex classes are shown in Appendix.

2.7 Available carrion biomass from dead ungulates

To finally be able to calculate available carrion biomass, I estimated the remains from predation, harvest and traffic collisions.

2.7.1 Consumption by predators

Brown bear

Estimation of prey remains from brown bear was only conducted for sheep (see 2.5.2.1). When the supply of prey is high, brown bear is shown to have a lower consumption of ewes compared to lambs due to high preferences for chest fat and udder only (Knarrum *et al.* 2006). I estimated average consumption according to described consumption patterns in Knarrum *et al.* (2006).

Wolverine

I obtained the edible biomass of reindeer killed by wolverines from Mattisson *et al.* (2011b) and used the same on wolverine-killed sheep in lack of available data.

Lynx

I estimated average consumption on sheep killed by lynx based on relative consumption rates provided by Odden *et al.* (2002); 8 % completely consumed (>75 % of all edible tissue), 56 % partially consumed (75 % > 0 %), and 36 % were not eaten at all. Øvrum (2000) reported a utilization of ≥ 75 % on 94 % of lynx-killed cervids (roe deer, reindeer, red deer) based on slaughter weights in an area of low prey densities (roe deer; 0.3 /km²). This is quite similar as observed lynx consumption on ungulates in Polen (93 %, Okarma *et al.* 1997) and in Switzerland (90 %, Jobin *et al.* 2000). In areas where semi-domestic reindeer was the only ungulate prey, Pedersen *et al.* (1999) reported a meat consumption of 61 % (± 27 (SD), range; 5-90 %) which is in line with Andr en *et al.* (2011) who reported 41 % consumption of slaughter weights.

Golden eagle

Based on published data, Brown & Watson (1964) showed the proportion of wastage by golden eagles after consuming sheep and red deer. The proportion of wastage on red deer was used on reindeer in lack of data.

2.7.2 Proportion of harvest remains

Internal organs

When an animal is culled, hunters leave carrion biomass from internal organs behind (lungs, spleen, stomachs, intestines, sexual organs, and often also liver, kidney and heart) (Wikenros *et al.* 2013). I estimated the proportion of discarded internal organs (rumen excluded) from harvested moose numbers in different age and sex classes following Wikenros *et al.* (2013). I conducted the same calculations on harvested roe deer.

Shot-wounded loss

Unfortunately, hunters do not always find animals that are shot at and they may die from the injuries (shot-wounded loss). The proportion of shot-wounded loss on moose has been shown to range from 2 - 4 % (Paus 1965, 1966 in Stokke *et al.* 2012) and I used 3 % on both moose and roe deer. This is in line with reported shot-wounded loss from Poland on roe deer (Okarma *et al.* 1995) and on other ungulates (Selva 2004).

2.7.3 Proportion removed from traffic collisions

Roads

A check by search patrols from Steinkjer and Stjørdal municipalities (covers over 60 % of all road collisions in the study area), revealed that approximately 3 – 5 % of all reported moose and roe deer collisions on roads end up with an available carcass to scavengers (P. Malmo and A. Friberg, wildlife rangers and search patrols, personal communication). They also reported that no internal organs were left behind whether the animals are retrieved for human consumption or not.

Railways

The majority of railway collisions are lethal to the ungulates and practically none are retrieved for human consumption (Wikenros *et al.* 2013). However, railway-kills are supposed to be removed within a couple of days in human-dense areas and within a week in more rural areas according to policy in the Norwegian Railway Company (J.B. Almåsbro, personal communication). I estimated carrion biomass from railways regardless of removal, because I assumed a small proportion to be removed.

2.8 Spatio-temporal distribution

In order to estimate spatial and seasonal carrion availability, I first defined two main habitat types; forest/agricultural areas (mostly in the west) and mountain areas (mostly in the east). Forest/agricultural areas constitute about 10 250 km² and mountain areas 10 560 km² (Statistics Norway 2014). I divided seasonal distribution of carrion availability into two seasons. The cold season was defined as the approximate period of permanent snow cover in forest/agricultural areas (November – April) whereas the warm season was defined as the rest of the year. I used estimated monthly biomass in each of the four carrion sources to calculate the seasonal distribution. Spatial distribution of carrion followed main habitat use by carnivores (kill-remains) and ungulates (OCD, harvest remains, traffic collisions).

3. RESULTS

3.1 Ungulate and large carnivore densities

Seasonal variation in moose, roe deer and reindeer densities reflects the autumn harvest (Table 1). Average harvested moose and roe deer numbers during the last five years was 5000 and 2800, respectively. According to the estimated winter population sizes, the warm season should then comprise about 20000 moose and 11000 roe deer. Reindeer winter population size is about 13800 animals, increasing with approximately 8000 calves during spring.

Approximately 65 lynxes and 50 wolverines were estimated to be present in the study area (Table 1). These numbers were calculated from winter surveys and thus represent the number of individuals that most likely are capable of killing ungulate prey (no density estimates was conducted for the warm season). Both species are subjected to culling, however, but the annual hunt takes place in late winter and thus reduces the densities only in the end of the cold season. In addition, the number of killed large carnivores is low. Golden eagles are not hunted, but the reproduction was shown to be very low and the density estimates were conducted for adults only (49 pairs).

Table 1: Estimated densities of large carnivores (n/100 km²) and ungulates (n/km²) in the study area, divided by seasons and habitat types. Warm season = May – October. Cold season = November – April.

Species	Forest/Agricultural areas		Mountain areas		References
	Warm season	Cold season	Warm season	Cold season	
Brown bear	0.3	-	-	-	Aarnes <i>et al.</i> 2013
Lynx	0.6	0.6	-	-	Brøseth & Tovmo 2012, Andrén <i>et al.</i> 2002
Wolverine	-	-	0.5	0.5	Brøseth, Tovmo & Andersen 2012
G.eagle	0.4	0.4	0.4	0.4	Nygård & Østerås 2014
Moose	2.0	1.5	-	-	Solberg <i>et al.</i> 2006, May <i>et al.</i> 2007
Roe deer	1.1	0.8	-	-	Statistics Norway 2013, Grøtan <i>et al.</i> 2005
S.d.reindeer	-	0.7*	2.0	0.7*	Reindeer Husbandry Management 2013
D. sheep	3.3*	-	3.3*	-	Forestry and Landscape 2013

*Based on general descriptions of habitat use.

3.2 Number of dead ungulates

The number of carcasses and gut-piles (internal organs) that were used to estimate carrion biomass is shown in table 2. In general, the number of carcasses from depredated livestock was higher in method A (derived from compensated loss) than in method B (calculated from carnivore densities and kill-rates). The discrepancy between the two methods was shown to be largest for sheep and especially lynx-killed sheep. The only exception was for lynx-killed adult reindeer where the number of carcasses was estimated to be higher in method B. Livestock OCD numbers reflects the discrepancy between the two methods because these numbers was estimated as inversely correlated with those killed by large carnivores and total loss.

Table 2. Estimated annual average number of available carcasses from the different carrion sources in ungulate age classes (J = juveniles (< 1 year) and A = adults). Predator-killed livestock numbers are based on compensated loss in Large Carnivore Database 3.0 and estimated kill-rates (in parenthesis). Livestock dying from other natural causes of death (OCD) are calculated as the gap between compensated loss and kill rates (in parenthesis) and reported total loss from animal owners.

Carrion sources		Carrion category							
		Moose		Roe deer		D. sheep		S.d.reindeer	
		J	A	J	A	J	A	J	A
Depredation	Lynx			576	2730	1156 (585)	179 (23)	1025 (783)	307 (583)
	Wolverine					707 (NA)	91 (NA)	906 (630)	276 (90)
	Brown Bear					337 (204)	663 (600)		
	Golden Eagle					193 (110)		255 (233)	
OCD*		135	316	671	1333	2516 (3230)	471 (719)	1752 (2297)	688 (635)
Harvest	Gut-piles**	2020	2950	672	2138				
	Wounded	62	89	15	59				
Traffic	Railway	11	138	1	19	10	29	3	61
	Road	4	22	5	29				

* OCD = Other causes of death (disease, starvation and accidents)

** Discarded internal organs

3.3 Available biomass from predation

When corrected for consumption, I calculated total available biomass (kg/km²) from killed livestock (kill rates vs. compensated loss) for the whole area (Table 3), because livestock were present in both area types (Table 1). I calculated available biomass from carnivore-killed roe deer from the size of forest/agricultural areas. In total, the different estimated

carrion biomass from kill-remains in method A vs. method B, summed up to 2.0 kg/km² (Table 3). As expected from the number of kills among carnivores (Table 2), I found lynx to be the main provider of kill-remains from livestock. However, in terms of biomass, lynx increased its provision of leftovers from livestock compared to other carnivores due to a rather low consumption rate. The biomass from lynx-killed reindeer between the two methods showed to be quite similar (Table 3). Golden eagle was quit abundant (Table 1), but kill mostly juveniles (Table 2) at a rather low rate and thus provide small amounts of leftovers for scavengers.

Table 3: Average available biomass from large carnivores (kg/km²) based on estimated kill rates and consumption in ungulate age classes (A=adults, Y=yearlings, J = juveniles). Biomass from killed livestock based on compensated loss (method A, see methods) is shown in parenthesis.

Carnivores	Prey	Age classes	Kill rate/month	Con- sumption (%)	Available biomass (kg/km ²) in method B (and A)
Lynx	Sheep	J	2.2	24	0.9 (2.1)
		A	0.7	61	2.3 (2.0)
	Reindeer	J	1.0	61	
		A	2.8	75	
		Y J	0.7	75	4.0 *
Wolverine	Sheep	A J	-	75	(NA) 0.4
		A	1.4	75	0.4 (0.8)
	J	0.2	75		
Brown bear	Sheep	A	5.0	37	1.7 (1.9)
		J	1.7	74	
Golden eagle	Sheep	J	0.3	50	0.06 (0.1)
	Reindeer	J	0.2	60	0.1 (0.1)

* Calculated from the size of forest/agricultural areas

3.4 Available biomass from other causes of death

I estimated wild ungulate OCD biomass from the size of forest/agricultural areas. By contrast, livestock used both areas, and thus the density of OCD carcasses was lower (Figure 2). I estimated OCD biomass from livestock from the relationship of total loss and different numbers killed in method A and B, respectively (Table 2). The different estimated amount of

OCD biomass from livestock in the two methods was 4.8 kg/km², and it was higher for reindeer (2.9 kg/km²) than for sheep (1.9).

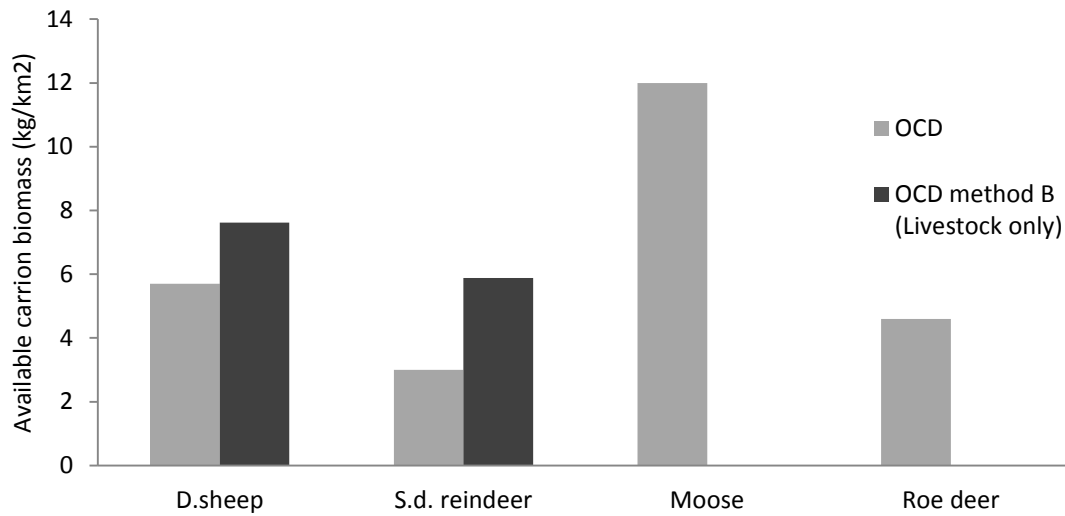


Figure 2. Estimated average annual carrion biomass (kg/km²) from other causes of death (OCD) from livestock and wild ungulates. Differences in livestock OCD biomass is calculated as the gap between compensated loss (method A), losses based on kill rates (method B) and total loss.

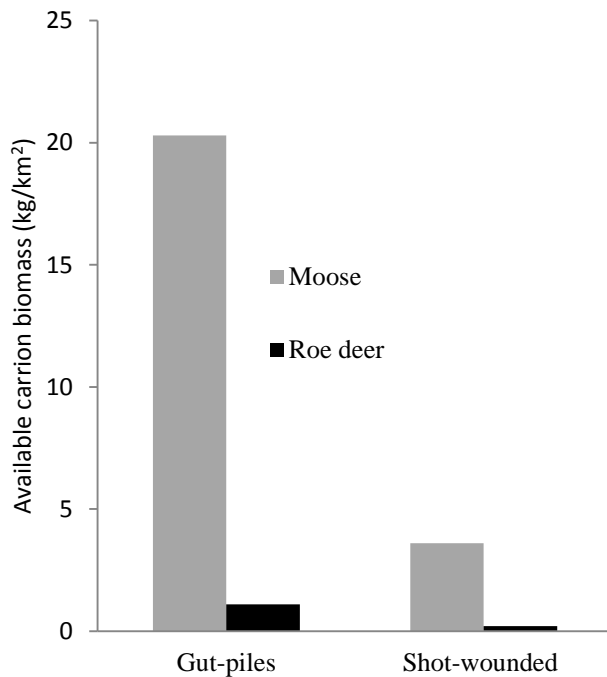


Figure 3. Estimated average annual carrion biomass (kg/km²) from harvested ungulates. Gut-piles = discarded internal organs, shot-wounded loss = died from shot injuries.

3.5 Available biomass from harvest and collisions

Harvest and collisions can be defined as the most prominent human-induced carrion providers and they occur in forest/agricultural areas. I used the size of this area to estimate the corresponding biomass (Figure 3 and 4). Total estimated carrion biomass from harvest was 25.3 kg/km² from which gut-piles during moose and roe deer hunting season comprised 20.3 and 1.1 kg/km², respectively. Whole carcasses from moose that die from shot injuries summed up to 3.6 kg/km².

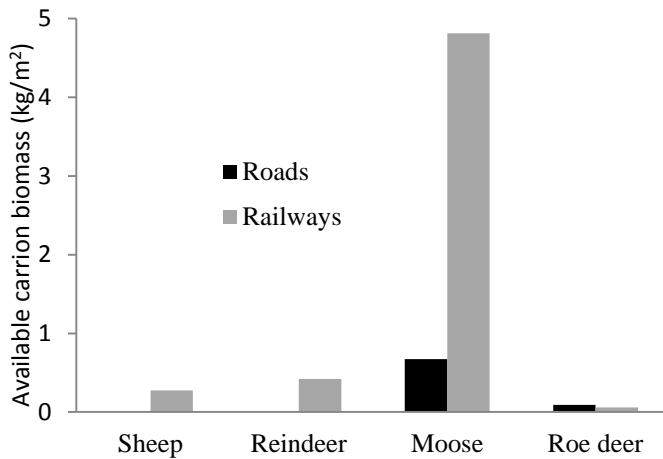


Figure 4. Estimated average annual ungulate carrion biomass (kg/km^2) from traffic collisions.

Total estimated carrion biomass from traffic was $6.3 \text{ kg}/\text{km}^2$ (Figure 4). Moose was also the main provider of carrion from collisions as from harvest. Railway-killed moose dominated the carrion provision from traffic (79 %) and only $0.7 \text{ kg}/\text{km}^2$ was available from roads due to removal of road-kills.

3.6 Monthly biomass supply

In total, the discrepancy in estimated biomass from method A and B summed up to $2.8 \text{ kg}/\text{km}^2$ in favor of method B (Table 3 and figure 2). Because of the uncertainty concerning livestock losses to large carnivores and thus the corresponding estimates of livestock OCD biomass, a minimum estimate was used to show estimated monthly carrion supply from livestock (i.e. method A). The minimum total estimated average annual carrion biomass was then $39 \text{ kg}/\text{km}^2$ (equivalent to 816 tons) when total biomass is divided by total area size. OCD (35 %) and harvest remains (33 %) was the main providers of carrion for scavengers, followed by depredation remains (24 %) and traffic collisions (8 %). Monthly carrion supply peaked in October due to the autumn harvest. Winter supply was highest in January but decreased each month towards spring. The lowest estimated carrion biomass was in May, followed by an increase as summer progressed (Figure 5 and 6).

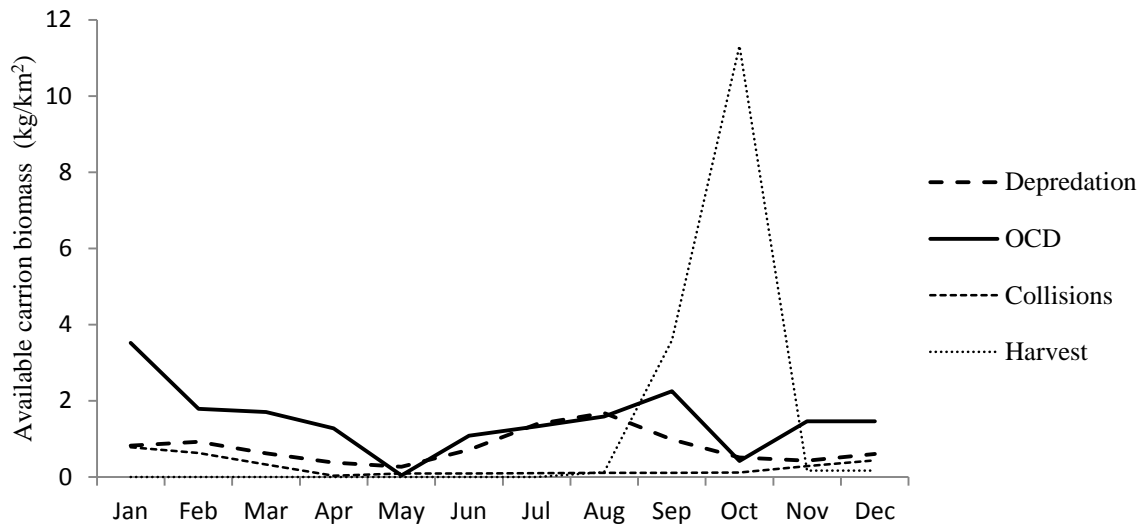


Figure 5. Monthly distribution of carrion biomass (kg/km^2) from the different sources used to estimate carrion biomass. (OCD = Other causes of death; mainly disease, starvation and accidents).

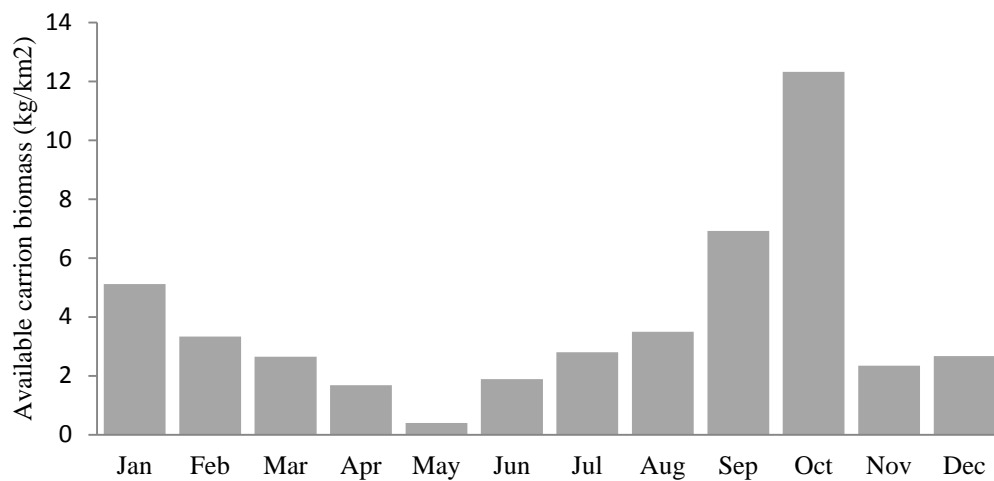


Figure 6. Estimated monthly average carrion biomass (kg/km^2) in the study area.

3.7 Spatial and seasonal biomass supply

I also used the minimum biomass estimates from method A to estimate spatio-temporal distribution of carrion biomass from livestock. The sizes of forest/agricultural areas and mountain areas were close to 50/50 and had very little impact on the amount of ungulate carrion per km^2 between the areas. Estimated average annual carrion biomass was considerable higher in forest/agricultural areas compared to mountain areas (Table 4). This

was mainly explained by a higher presence of both carnivores (kill-remains) and ungulates in forest/agricultural areas. Carrion from moose, especially from harvest and OCD, contributed greatly to the supply of carrion in these areas.

Carrion availability was slightly higher in the warm season (58 %) than in the cold season (Table 4). My estimates also shows that the warm season in forest/agricultural was dominated by carrion from the autumn harvest (61 %) and OCD was the main carrion provider to scavengers in the cold season (60 %) in these areas. Based on the estimated standing crop of ungulate biomass in forest/agricultural areas in the cold season (429 kg/km²), about 7 % of it was available for scavengers. In the mountains, OCD from sheep and reindeer was the main carrion provider in the warm and cold season, respectively.

Table 4. Estimated annual average spatial and seasonal carrion availability (kg/km²) from ungulates in each of the four carrion sources used to estimate carrion biomass availability. Warm season = May – October. Cold season = November – April.

Sources	Ungulates	Forest/Agricultural areas		Mountain areas	
		Warm	Cold	Warm	Cold
Predation	Sheep	8.3		1.0	
	Reindeer		4.0	0.3	1.4
	Roe deer	2.0	2.0		
OCD*	Sheep	2.9		2.8	
	Reindeer		2.3	0.8	2.2
	Moose		12.0		
	Roe deer	1.5	3.1		
Collisions	Sheep	0.3			
	Reindeer	0.2	0.3		
	Moose	0.8	4.7		
	Roe deer		0.1		
Harvest	Moose	24.0			
	Roe deer	0.7	0.6		
TOTAL		40.6	29.1	4.9	3.6

*OCD = Other causes of death (disease, starvation, accidents)

4. DISCUSSION

The main goal in this thesis was to estimate carrion biomass in the study area. In all carrion biomass calculations, I added several parameters to obtain estimated carrion biomass in each of the four carrion sources (depredation remains, OCD, harvest remains and traffic collisions). These estimates contain no estimates of measurement error. Robustness in each parameter will affect the outcome of estimated biomass in each carrion source and eventually total estimated biomass. To give an overview of robustness in the estimates, I evaluated the different parameters by a subjective “quality score” (Table 5).

Table 5. Evaluation of estimated carrion biomass accuracy. Wild ungulates = Moose and roe deer. Domestic ungulates = Domestic sheep and semi-domestic reindeer. OCD = other causes of death (mainly disease, starvation and accidents).

Carrion source	Parameters	Parameter quality	Estimate evaluation	Comments
Harvest	Harvested numbers in age classes	Good	Good	Best on moose
	Gut-pile weights	Good		
	Proportion shot-wounded loss	Poor		
	Live weights	Good		
OCD Wild	Population size in age classes	Good	Good	Best on moose
	Death rate in age classes	Good		
	Live weights	Good		
Predation	Large carnivore population sizes	Satisfying	Satisfying	
	Kill rates in age classes	Satisfying		
	Proportion consumed /consumable	Poor		
	Weights	Good		
OCD Domestic	Killed numbers in age classes	Satisfying	Satisfying	
	Total loss in age classes	Good		
	Live weights	Good		
Collisions	Reported numbers in age classes	Good	Satisfying	Best on moose
	Proportion non-reported (roads)	Poor		
	Proportion available (roads)	Satisfying		
	Proportion available (railway)	Satisfying		
	Live weights	Good		

I found harvest remains and OCD to be the main carrion providers for scavengers in the study area. They constituted 68 % of total estimated biomass based on the minimum estimates of OCD from livestock. Estimated carrion biomass from harvest and OCD from wild ungulates (moose and roe deer) constituted 75 % of this biomass.

4.1 Harvest remains and other causes of death from wild ungulates

Moose was the main carrion provider in the study area. Estimated biomass from gut-piles and OCD from moose was in line with estimations from south central Scandinavia with similar densities and harvest rate (Wikenros *et al.* 2013). With the additional known culled numbers in different age and sex classes, and the support of adult natural death rate in moose from a recent study in the study area (Rolandsen *et al.* 2010), estimated amount of carrion from moose was considered robust. However, harvest remains might have been slightly underestimated due to discarded slaughter remains (heads, skin, left-over legs) that also may constitute an important food resource for red foxes (Needham *et al.* 2014). Nevertheless, it was difficult to estimate this type of carrion biomass due to different practices. In some hunting areas, such waste can be dumped in containers intended for such use (own observations) or in some other way prevented from being available for scavengers (for example used as food for hunting dogs).

4.2 Depredation remains and other causes of death from livestock

I estimated biomass from kill-remains to constitute as much as 25 % of total biomass. However, this was estimated from method A (compensated loss numbers) which gave a minimum estimate of biomass from the combined effect of carrion from kill-remains and OCD from livestock. In short; when large carnivores kill fewer livestock, more carrion is available, because the difference in available biomass is the difference from kill-remains and OCD when measured against total lost numbers. I have used the best available data on total losses and total biomass from livestock is probably more in line with the estimated biomass from method B. Odden *et al.* (2014) evaluated the compensated losses on sheep based on depredation from lynx in several large carnivore regions in Norway (region 6 not incorporated). Compensated sheep numbers assumed to be killed by lynx was found to be generally higher (on average from 2 to 4 times) than calculated from kill rates and lynx population sizes. On reindeer, Nybakk *et al.* (2002) showed an OCD loss of 16 % in a study

from the northwestern parts of the study area, which is in line with the estimated number of OCD losses in method B.

4.3 Spatial variation

Estimated spatial carrion availability was much more prominent in forest/agricultural areas than in the mountains. Wolverine was set to be the only mammalian apex predator that provided scavengers with carrion in the mountains. Lynx and brown bear were by contrast set to provide kill remains only in the forest. Even if large carnivores, with wide geographical ranges, can use different macro habitats (Gittleman & Harvey 1981), the overall spatial distribution of kill remains used here should be rather robust (see e.g. May *et al.* 2008).

Moose densities during harvest have been shown to vary a lot in the study area (0.2 – over 2 moose/km²) due to a more clumped distribution in areas with agricultural activity compared to less productive areas in higher altitudes (Solberg *et al.* 2006). Harvest remains are then distributed all over forest/agricultural areas, but appear as more clumped and fine-scaled distributed in lower altitudes near farmland. Roe deer also seem to prefer such habitats (Panzacchi *et al.* 2008), supporting the more fine-scaled distribution of harvest remains within forest/agricultural areas. I also suggest a similar fine-scaled carrion availability in the cold season in these areas. Migrating moose in central Norway have been showed to move towards lower altitudes in the major valleys in winter (Rolandsen *et al.* 2010). Roe deer also shows to confirm the common pattern among temperate cervids of migration to low elevations during winter (Myrsterud 1999) and semi-domestic reindeer also tend to use forested areas with little snow cover during winter (Suominen & Olofsson 2000). Moreover, carrion from traffic collisions appears in valleys and other parts of lower altitude where the human population is denser, giving further support to this more fine-scaled suggested carrion distribution.

4.4 Temporal variation

Unexpectedly, estimated temporal carrion availability was higher in the warm season than in the cold season when large ungulates like moose and reindeer die from starvation, disease and accidents. This could partly be explained by sheep only providing carrion during summer, but was mainly explained by the high pulse of estimated harvest remains from moose in autumn. Decomposers decrease carrion availability for vertebrate scavengers in the warm season, but this is also the time when the availability of prey such as rodents, birds, insectivores and amphibians is high.

The main importance of carrion lies in its timing in the cold season when other resources are unavailable or depleted (Selva 2004). The estimated decreasing carrion supply with the advance of winter (January - April) was similar as estimated for moose in absence of wolves in south central Scandinavia (Wikenros *et al.* 2013). However, large and intact ungulate carcasses last longer than more open ones (Selva 2004) and large frozen carcasses can indeed be long lasting (Selva *et al.* 2003). Some may even be available only when the snow has melted (Wikenros *et al.* 2013). This skewed supply towards spring (freezer-effect) is more likely to reflect the actual temporal carrion availability in this time of year, especially in severe winters. Furthermore, the surplus of more easy hand-able food from gut-piles in autumn may leave whole carcasses (i.e. shot-wounded) more untouched and skew carcass availability into the cold season. Moreover, estimated carrion biomass from moose OCD was equally distributed throughout winter, but there are most likely more moose carcasses as winter progresses.

4.5 Carrion supply and the red fox

One carcass with a body weight of >200 kg may sustain a red fox (daily food requirements c. 500 g, Sillero-Zubiri, Hoffmann & Macdonald 2004) for several months during the critical winter period (Selva *et al.* 2003). Red fox is a very effective scavenger (Sidorovich *et al.* 2000; Selva *et al.* 2005) and scavenging on ungulate carcasses has been shown to be a main foraging activity in the north temperate Białowieża Primeval Forest in Poland (Jędrzejewski

and Jędrzejewska 1992; Kidawa & Kowalczyk 2011), in the Italian Alps (Cagnacci, Lovari & Meriggi 2003), and on the arctic tundra of northern Norway (Killengren *et al.* 2011)

During winter, food resources of generalist predators become narrower (Sidorovich *et al.* 2000) and numerous studies shows that carrion from ungulates in winter can be an important food resource for red foxes (Jędrzejewski & Jędrzejewska 1992; Cagnacci, Lovari & Meriggi 2003; Selva 2004, 2005; Sidorovich, Sidorovich & Izotova 2006; Baltrūnaitė 2006; Killengren *et al.* 2011; Kidawa & Kowalczyk 2011; Wikenros *et al.* 2013; Needham *et al.* 2014). Furthermore, they are expected to starve if both carcass and small rodent availability is low (Jędrzejewski & Jędrzejewska 1992) and carrion can act as a survival bottleneck that directly influences scavengers` fitness (Marzluff & Heinrich 1991). The growth in red fox populations in Norway during the previous century are shown to be positively associated with the growth in cervid numbers (Selås & Vik 2006) and additional food during winter is shown to increase reproductive success (Lindström 1982). Although we lack quantitative data on how carrion availability may affect the demography of scavenging species, increased survival and reproduction are expected due to a higher observed utilization in late winter (Selva 2004) and spring (Wikenros *et al.* 2013).

Red foxes and ravens (*Corvus corax*) were shown to be the only habitat generalists when feeding on carrion in BPF (Selva 2004). Habitat generalists are likely to be less affected by habitat alteration and composition and thus be able to feed more efficient. Ravens have been reported to remove on average 14 kg daily from wolf-simulated kills in Canada (Promberger 1992) and thereby reduce carrion availability rather fast. However, red foxes may be able to feed more efficient on more intact and frozen carcasses than corvids, and thus experience less competition on this type of resource. This dominance by red foxes in the hierarchical scavenger community (see e.g. Selva 2004) is likely to be enforced by low wolverine densities and especially in lower altitudes in forested areas that wolverine seem to avoid (May *et al.* 2008). Furthermore, eagles were shown to be competitors to red foxes only during daylight on artificial carcasses (Strømseng 2007). Hence, temporal segregation of carcass utilization in forested areas might result in monopolization by red foxes when feeding during the long dark winter hours in northern latitudes.

I estimated moose to be the main ungulate carrion provider during winter. Needham *et al.* (2014) showed that remains from moose were the dominating food category during winter in red fox scats in southeastern Norway. The proportion of ungulate items in scats was still as high as 20 % in spring. They also observed scavenging by red foxes on average every 3 km of snow tracking, underlining the importance of ungulate carrion. These results were found in an area with similar moose density and harvest rate as in my study area.

Gut-piles (rumen excluded) have large nutrition value and a rather fast consumption by scavengers is observed (Sundli 1993; Selva 2004). However, a scavenger like the red fox which frequently visits gut-piles (Selva 2004; Wikenros *et al.* 2013) is commonly known for caching of surplus food (Macdonald 1976; Sillero-Zubiri, Hoffmann & Macdonald 2004). Even though caching is shown to be short-termed (e.g. Henry 1986), it protects food from competitors and increase the time available for foraging, probably having positive effects on survival (Macdonald 1976). When large amounts of harvest remains are available over large areas in the face of winter, they can contribute to early winter diet as cached food for many foxes when other food niches starts to decrease. Furthermore, harvest remains become available when red foxes disperse at the age of about 6 months in autumn (Pils & Martin 1978, Lloyd 1980; Lindström 1989; Dekker, Stein, & Heitkönig 2001). Dispersal has several costs, such as increased energy demands, difficulty of finding prey in unfamiliar habitat and competition with other foxes (O'Neal, Flinders & Clary 1987). Higher mortality during dispersal is highly expected if vole densities are low (Lindström 1989). Annual occurrence of large amounts of harvest remains over large areas may then contribute to increased survival in this time of the year.

4.6 Management implications

Needham *et al.* (2014) assumed higher predation pressure on small game species such as Tetraonidae in years when vole densities are low, because the supplementation of red fox diets with ungulate carrion could lead to more stable red fox densities. In addition, red foxes can be a threat to endangered species like the arctic fox (*Alopex lagopus*) due to predation and

competition (e.g. Elmhagen, Tannerfeldt & Angerbjörn 2002; Norén *et al.* 2009), highlighting the importance of carrion availability. Mountain areas in the study area are shown to be important “step-stone” areas to arctic foxes (Ulvund *et al.* 2012) and models by Henden *et al.* (2010) showed the biggest negative impact on arctic foxes when an area receives food subsidies and the dominant red fox monopolize the resource.

High densities of moose created high amounts of harvest remains in the face of winter. Removal of gut-piles and carcasses from moose has already been suggested because it was expected to have negative effect on predator-scavenger abundances (Smedshaug & Sonerud 1997). Removal of gut-piles seems to be even more important in the future because the moose hunting period is extended with up to a month from 2014 in several municipalities in the study area. This will most likely favor the scavenger community even further due to a prolonged temporal availability of an already existing large food resource. Reduced moose densities in most of the study area has also been recommended to prevent further increase of vehicular collisions and declining body condition (Hedegart *et al.* 2013). Hence, I suggest further focus on carrion supply to obtain more baseline data on food availability for predator-scavengers. It seems advantageous to especially address winter and spring carrion availability and try to reveal a more fine-scaled spatial carrion availability in this time of year. Secondly, future research should focus on the importance of carrion availability on red fox distribution, density and reproduction.

Acknowledgements

I want to thank my supervisor Morten Odden at Hedmark University College (HiHM) and Pål Fosslund Moa at Nord-Trøndelag University College (HiNT) for comments and support. I also want to thank Barbara Zimmermann (HiHM) for help during the last days of writing.

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Appendix

Estimated monthly ungulate live weights

Species	Age and sex	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Semi-domestic reindeer	Calves	40	40	40	40	6	12	17	23	29	35	40	40
	Yearling males	60	60	60	60	40	43	47	50	53	57	60	60
	Yearling females	56	56	56	56	40	43	45	48	50	53	56	56
	Adult males	80	80	80	80	80	80	80	80	80	80	80	80
	Adult females	68	68	68	68	68	68	68	68	68	68	68	68
Domestic sheep	Lambs	63	70	76	5	11	18	24	31	37	44	50	57
	Ewes	90	90	90	90	90	90	90	90	90	90	90	90
Moose	Calves	196	196	196	196	196	11	48	85	122	159	196	196
	Yearling males	293	293	293	293	196	212	228	244	260	276	292	293
	Yearling females	249	249	249	249	196	207	217	228	238	249	249	249
	Adult males	342	342*	342	342	342	342	342	342	342	342	342	342
	Adult females	348	348*	348	348	348	348	348	348	348	348	348	348
Roe deer	Fawns	20	20	20	20	2	5	8	11	14	17	20	20
	Yearling males	26	26	26	26	20	21	22	23	24	25	26	26
	Yearling females	26	26	26	26	20	21	22	23	24	25	26	26
	Adult males	30	30	30	30	30	30	30	30	30	30	30	30
	Adult females	30	30	30	30	30	30	30	30	30	30	30	30

*Heavier moose females than males reflects management regulations allowing few older (and heavy) bulls to be culled.

