Inter-specific patterns of depredation on domestic sheep and semi-domestic reindeer in Norway, by a large predator guild.

Variasjoner i predasjons mønster på sau og tamrein i Norge av store rovdyr.

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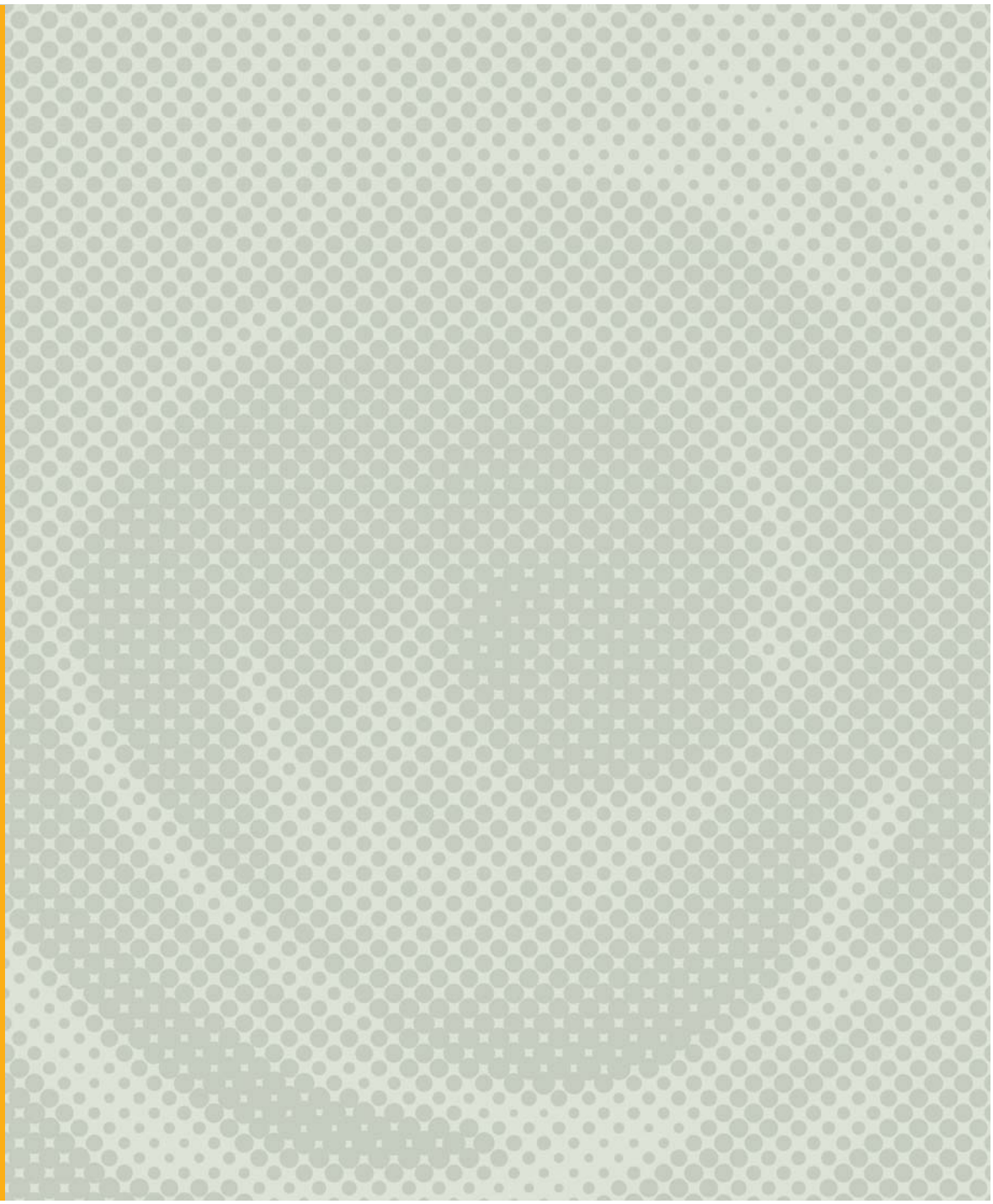

Preface

This master thesis completes my five years as a student in the master's program Natural resource management, at the Norwegian University of Life Sciences (UMB).

First, I would like to thank my supervisors Leif Egil Loe at UMB and John Linnell at the Norwegian Institute for Nature Research (NINA) for all the help and guidance regarding my master thesis. I would also like to thank Jenny Mattisson at NINA for a memorable fieldwork in Snåsa, and for here helpful comments regarding my thesis. The Norwegian Reindeer Authority and Annette Bye at Statistics Norway (SSB) also deserve thanks for the help with retrieving data on the standing stock of domestic sheep and semi-domestic reindeer.

I would also like to thank Department of Ecology and Natural Resource Management (INA) at UMB and especially Samfunnet i Ås for five fantastic years as a student. Thanks to Sangkoret Lærken for being a much needed (and sometimes too much) distraction when writing my master thesis, and to my roommates who have helped me keep my spirits up. Last but not least I would like to thank Kaffeklubben for the long coffee breaks and entertainment in the reading room.

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Abstract

Livestock depredation by large predators is the main cause of human-wildlife conflicts in Norway. The depredation on free-ranging semi-domestic reindeer (*Rangifer tarandus*) and domestic sheep (*Ovis aries*) can have severe economic impact on individual livestock owners. The losses are as a result fully compensated by the Norwegian government. Using data on documented losses livestock collected from a national database (Rovbase 3.0) in the period 2003 to 2011, I compared the depredation patters of the different predator species in northern Norway: lynx (*Lynx lynx*), wolverines (*Gulo gulo*), brown bears (*Ursus arctos*), wolves (*Canis lupus*) and golden eagles (*Aquila chrysaetos*). I investigated if there were any preferences by the multiple predators for age class (young or adult) and sex class (female or male) in the two livestock species, and if there was a relationship between a mean body weight of each predator species and the proportion of young and adult prey killed. I also investigated if there was a seasonal difference in the depredation of the five predator species. The standing population of reindeer and sheep was estimated using data from the Norwegian Reindeer Authority and Statistics Norway. The reindeer material was divided in a summer and a winter population, and the summer dataset was compared with the sheep dataset.

I found that juvenile livestock were preferred as prey by the majority of predator species, and only when brown bears depredated on sheep, a predator species showed a significant preference for adults. I also found that age selection within the sheep population correlated with the mean body weight of each predator species, meaning that the proportion of ewes killed increased with the body weight of the predator. My thesis provides an insight in the ecology of livestock depredation in a multiple predator system. One can see some clear trends in predation. Still, some kills are probably more underrepresented than other, depending on the age class of the kill and the difference in predator behavior. Estimating total kills based on documented kills are thus uncertain. Instead of using resources to locate and document individual kills, more effort should be put in place to estimate the population size of both predators and prey and to investigate the actual predation rate and preference of age and sex of each predator species. A compensation system based on such estimates could be preferred both from the management and the husbandry

Key words: livestock depredation, semi-domestic reindeer, domestic sheep, large predators, selection, seasonal variance

Sammendrag

Store rovdyrs predasjon på husdyr og tamrein er en av de vanligste årsakene til konflikter mellom mennesker og vilt. Predasjon på frittbeitende tamrein (*Rangifer tarandus*) og sau (*Ovis aries*) kan gi alvorlige økonomiske innvirkninger på individuelle bønder og reineiere. Som følge av dette erstattes all tap av husdyr og tamrein av staten. Jeg har samlet inn data på dokumenterte tap av sau og rein mellom 2003 og 2011 fra den nasjonale databasen Rovbase 3.0. Videre har jeg undersøkt predasjons mønster fra de fem store rovdyrene i Norge: gaupe (*Lynx lynx*), jerv (*Gulo gulo*), brunbjørn (*Ursus arctos*), ulv (*Canis lupus*) og kongeørn (*Aquila chrysaetos*), for å se om de viser noen preferanser for alder (juvenil eller voksen) og kjønn (han eller hun) når de dreper et byttedyr. Jeg har også undersøkt om det er noen sammenheng mellom rovviltets gjennomsnittelige kroppsvekt og andelen juvenile og voksne drept, og om det er noen sesongmessige variasjoner in predasjon på husdyr og tamrein. Den stående populasjonen av sau og rein ble estimert ved hjelp av data fra Reindriftsforvaltningen og Norges Statistiske Sentralbyrå. Tamreinpopulasjonen ble delt inn i en sommer- og en vinterpopulasjon.

Det ble vist at majoriteten av rovvilt artene prefererte juvenile over voksne, og bare når brunbjørnen drepte sau, viste en predator signifikant seleksjon for voksne. Aldersseleksjon på sau korrelerte med gjennomsnitts kroppsvekt til hver rovvilt art, der andelen drepte søyer økte med kroppsvekten til rovdyrene. Denne masteroppgaven gir en forståelse for økologien til predasjon av husdyr i et flere-predator system og man kan se en del klare trender i predasjon basert på dokumenterte tap. Likevel er drap av noen rovdyrarter mer underrepresenter enn andre, hovedsakelig på grunn av sannsynligheten for å oppdage et drap. Her spiller både alderen på byttet og adferden til rovviltet inn. Å estimere det totale tapet av husdyr og tamrein basert på et datasett på dokumenterte tap er derfor en usikker metode. I stedet for å bruke ressurser på å lokalisere og dokumentere drap, bør man heller fokusere på å estimere den faktiske drapsraten og seleksjonen på byttedyr, av de fem store rovdyrene i Norge. Et erstatningssystem basert på et slikt grunnlag er muligens mer foretrukket av både forvaltningen og primærnæringen.

Nøkkelord: husdyr predasjon, tamrein, sau, store rovdyr, seleksjon, sesong

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1. Introduction

Livestock depredation by large predators has been a problem since the first herbivores were domesticated, and is one of the most common causes of human-wildlife conflict worldwide (Cozza et al. 1996; Kaczensky 1996; Mazzolli et al. 2002; Thirgood et al. 2005). The socio-economic impact can be significant for individual farmers and herders, both due to the loss of livestock and due to the cost of measures to reduce the rate of predation (Swenson & Andrèn 2005; Thirgood et al. 2005). The rate of predation can be unevenly distributed both spatially and temporally, and between livestock species.

The multi-use landscape of Norway is an important component of Norwegian cultural heritage and has been subject to a variety of uses over time, like forestry, livestock grazing, hunting and recreation. In conflict with these uses the interests of wildlife have often been sacrificed. Between the 17th and 18th century a wide range of local and state bounties were set in action, to persecute large predators in Norway (Linnell et al. 2010; Linnell et al. 2009). The goal was to exterminate all predator species that constituted a threat to livestock and game. By the mid 20th century large mammalian carnivores were nearly exterminated, and the population of birds of prey was at its lowest (Basille et al. 2009; Hjeljord 2008; Rovdata 2012a). By the 1960's there was a major shift in policy, and the large predators went from being persecuted to being protected by law (Landa et al. 1999; Linnell et al. 2010). Through protection and regulated harvest the large predator populations increased, creating significant conflicts between the conservation of large predators and other interests in the rural communities of Norway.

In Norway, livestock depredation is the main source of economic conflict between wildlife and humans. Two domestic species, reindeer (*Rangifer tarandus*) and sheep (*Ovis aries*), are subject to extensive rates of depredation by the five large predators: lynx (*Lynx lynx*), wolverine (*Gulo gulo*), wolf (*Canis lupus*), brown bear (*Ursus arctos*), and the golden eagle (*Aquila chrysaetos*) (Aanes et al. 1996; Bjärvall et al. 1990; Mattisson et al. 2011a; Mattisson et al. 2011b; Nybakk et al. 2002). There is a strong seasonal difference in the availability of semi-domestic reindeer and domestic sheep as prey. A total of 2 million domestic sheep graze on forest and alpine tundra pastures only in summer. The sheep are released in early June, and are herded back to the farm during September (Nielsen et al. 2013). The extermination of predators during the 19th and 20th century resulted in a practice where sheep were left to graze

freely in the forest and alpine habitat, unguarded and only intermittently supervised. The lack of protection and the generally low anti-predator behavior in domestic sheep makes them an easy prey for large predators (Kaczensky 1996; Squires 1975). While the practice of sheep husbandry occurs only in summer in all parts of Norway, reindeer husbandry is practiced outdoors year-around, covering the northernmost 40 % of Norway's land area. The reindeer husbandry is almost entirely practiced by indigenous people, the Sami, and is an important component of the Sami cultural heritage. Approximately 250,000 semi-domestic reindeer are herded between seasonal pastures in different reindeer husbandry districts in Norway. Throughout large parts of the reindeer husbandry area, semi-domestic reindeer are the only suitable-sized ungulate prey for lynx, wolverines and golden eagles (Mattisson et al. 2011a; Nybakk et al. 2002). Reindeer also compose a smaller part of the diet of wolves and brown bears.

In order to decrease the economic impact of livestock depredation, the Norwegian government fully compensates the loss livestock. Total loss of livestock is estimated based on the presence of documented losses and on estimated losses. Substantial resources are used to locate and examine carcasses in the field. Despite this effort, documented losses are only a small part of the total number of livestock compensated each year (2- 3 percent; Rovbase 3.0, 2013). Kaczensky (1999) found that Norway had among the highest rates of livestock depredation in Europe, based on the number of livestock compensated. When considering the relative low population size of predator species in Norway, the difference is even greater. In 2011, approximately 30,400 domestic sheep and 19,500 semi-domestic reindeer were compensated because of depredation by the five large predator species, costing the Norwegian state roughly 137 million NOK (23 million US$).

The detection rate of killed livestock in Norway is low due to a widely distributed predator population and a free-ranging livestock population (detection rate is roughly 9 % in winter and 2 % in summer; Mattisson et al. (2011b)). Only a low proportion of the missing animals have a verified cause of death. Thus, the present compensation system is considered uncertain and costly, and the information retrieved on kill rates is limited (Mattisson et al. 2011b). Despite this, the compensation system seem to have a conflict-reducing effect on a larger scale, and protects livestock owners from severe economic loss (Swenson & Andrèn 2005). There is a need to better understand the ecology of livestock depredation, to better design a system that is affordable, fair and that focuses on the impact of depredation on production, rather than simply the number of livestock killed.

In ecosystems with minimal human intervention, predation is in many cases the primary cause of mortality, and can have a large demographic impact on ungulate populations under certain conditions (Gervasi et al. 2012; Jędrzejewski et al. 2002; Latham et al. 2011; Linnell et al. 1995; McLaren & Peterson 1994; Messier 1991). Large predators can select for age or sex within a prey species (Knarrum et al. 2006; Knopff et al. 2010; Norberg et al. 2006; Pierce et al. 2000), or for individuals in relatively poor condition (small, weak, sick, or injured) (Fitzgibbon & Fanshawe 1989; Temple 1987). Juveniles are often more vulnerable to predation than larger adults in good condition (Linnell et al. 1995; Nybakk et al. 1999; Stahl et al. 2001), and within the adult population, females are probable more preferable as prey than males, due to the sexual dimorphism (males are bigger than females) in ungulates (Miquelle et al. 1992; Vernon et al. 1997).

Selection of prey can often be explained by the predator-prey body size ratio, implying that large predators tend to kill larger prey (Cohen et al. 1993; Nakazawa et al. 2013; Vézina 1985; Warren & Lawton 1987). Studies have shown that stalking predators with a body size similar to their prey do not need to select for smaller sized individuals (Andersen et al. 2007; Fitzgibbon & Fanshawe 1989; Gervasi et al. 2012; Mejlgaard et al. 2013; Pierce et al. 2000). Predators with a high predation rate on adult reproductive females, such as the lynx, will have a much higher demographic impact than predators preying primarily on juveniles (Andersen et al. 2007; Atwood et al. 2007; Gaillard et al. 2000; Gervasi et al. 2012; Sinclair et al. 2003).

Rates of predation often vary throughout the season. Factors that contribute to the variation can be due to both external environmental conditions and intrinsic life history strategies, of both predator and prey. Winter predation rates on ungulates are often a function of the depth of snow cover (Jędrzejewski et al. 2002; Nilsen et al. 2009; Wikenros et al. 2009). While large and medium-sized ungulates step through the snow cover, medium-sized carnivores can run on top of the snow and easier pursue their prey (Jędrzejewski et al. 2002; Pedersen et al. 1999). Considering the reduction in food availability during winter ungulate species tend to move less to save energy. Nilsen et al. (2009) found that that the uniform distribution of roe deer in summer, changed to a clumped and more predictable distribution during winter, making it easier for lynx to find prey. The natural mortality of ungulates is high during some winters, and yearlings and older animals surviving harsh winters are often in bad condition and can be subject to a higher rate of predation during spring (Persson et al. 2001). Many predator species show a preference for juvenile ungulates simply because they are easier to kill (Linnell et al. 1995). The kill rates during spring and summer can consequently be much

higher than the rest of the year due to the body development of juvenile prey (Knopff et al. 2010; Norberg et al. 2006; Sand et al. 2008).

The overall impact of predation on ungulate populations is not necessarily only determined by kill rates, but rather the age and sex composition of killed individuals (Gervasi et al. 2012). The selection of individuals within a prey species is thus important to take into account when managing a predator-prey system, especially when the wild prey to a high extent is replaced with livestock. To better understand the ecology of livestock depredation, in an ecosystem with two livestock species and multiple predators, I here examine the data on documented livestock kills available in a national database in Norway (Rovbase 3.0; Direktoratet for naturforvaltning (2013)). The aim of the thesis is to compare the depredation patterns of the different predator species in Norway, with respect to any different preferences by the multiple predators for age class (young or adult) and sex class (female or male) in the two livestock species. I will also investigate the seasonal patterns within livestock depredation.

Based on ecological insights from the studies outlined above I predict that (i) juveniles are selected over adults and that (ii) the proportion of killed juveniles' increases with the decreasing body weight of the predator species. Within adult depredation I predict that (iii) females are selected over males. I also predict that (iiii) the smaller predator species show a pronounced peak in predation during birth season of reindeer, and timing of release of domestic sheep on summer pastures. Larger predators would thus kill a higher proportion of adults and they would not show a distinct peak in predation during the neonatal period.

2. Method

2.1. Study site

I restricted the study area to the six northernmost counties in Norway (Finnmark, Troms, Nordland, Nord-Trøndelag, Sør-Trøndelag and Hedmark) in order to focus on areas where all five predator species were present, and where sheep reindeer are broadly sympatric. Within the reindeer husbandry, I only focused on Sami reindeer husbandry (Figure 1). While the Sami reindeer husbandry area ends at Engerdal, in north-eastern Hedmark, the summer pastures of sheep covers most of Hedmark County. The data used in estimating the numbers of sheep on summer pastures was restricted to the county level. I could not restrict the number of sheep killed to just the municipalities that were part of the Sami reindeer husbandry, but had to account for sheep killed throughout Hedmark.

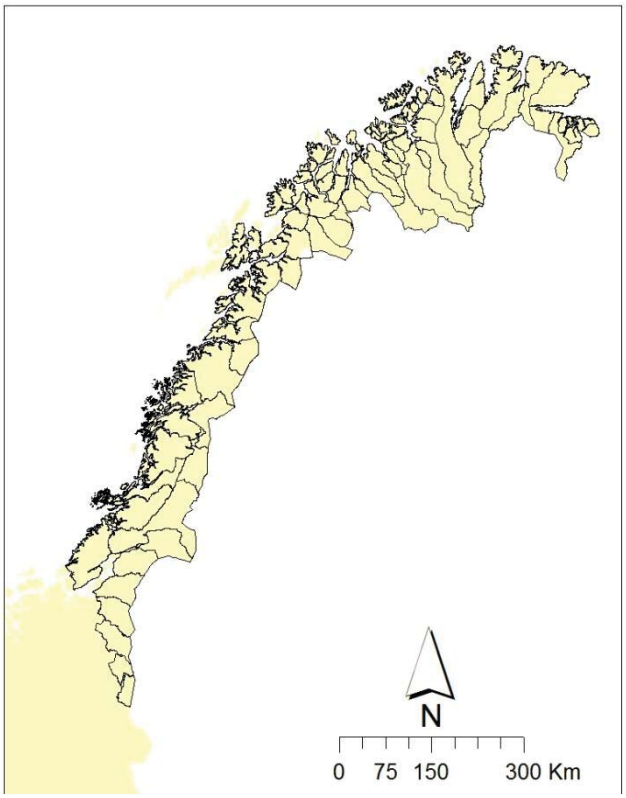

Figure 1. The reindeer husbandry area in Norway marked in black. The area covers almost 40 % of Norway (Reindriftsforvaltningen [The Norwegian Reindeer Authority] 2013).

2.2. Data collection

2.2.1. Population of semi-domestic reindeer

The Norwegian Reindeer Authority reports the annual population of semi-domestic reindeer, number of calves and adult slaughtered, and the estimated loss of reindeer. The reports are published each year and are available to the general public (Reindriftsforvaltningen 2003-2012). The numbers are based on the reindeer herders' annual counts and are often corrected by the authorities subsequently. The quality of the data varies between districts and year and some random errors are expected. Thus, the calculated population of semi-domestic reindeer should be considered as estimates and not exact numbers (Fauchald et al. 2004b; Herfindal et al. 2011).

The estimation on the standing stock of reindeer was based on the reports published by the Norwegian Reindeer authorities between 2003 and 2011. I divided between age and sex within the population. From 2003 and onwards, the reports had the exact same format, and separated between adult females, adult males and calves. The reports before year 2003 did not have the same structure. To standardize the data material and avoid any errors in the age and sex composition I chose to not use reports from earlier years. The population size given in the reports reflects the population of reindeer at the end of a 'reindeer year', which is in early spring the following year (31.March), before calving and after slaughtering.

The age and sex composition can vary greatly before and after slaughtering and the standing stock of reindeer was thus calculated separately to represent both a winter- and a summer population. The winter population was estimated based on the number of reindeer at the end of a 'reindeer year' (Table 1). At this time the population size is at the lowest due to predation and natural mortality throughout the year, and slaughtering in the autumn. The summer population was estimated by adding the proportion of slaughtered calves, adult females and males to the winter estimates (Table 1). The mortality of calves is especially high in the first months after calving (Fauchald et al. 2004b; Tveraa et al. 2003) and is not accounted for in these estimates. The proportion of calves in the population is as a consequence underestimated, and in the cases where selection of calves is reported the results are considered conservative results.

Table 1. The mean age and sex distribution in the standing population of semi-domestic reindeer and domestic sheep in the study period. The reindeer population is divided in a summer and winter population. No sheep rams older than one year are free-grazing on pastures in Norway.

	Adult		
	Male	Female	Juvenile
Sheep	Ca 0 %	39 %	61 %
Reindeer summer	8 %	64 %	28 %
Reindeer winter	8 %	70 %	22 %

2.2.2. Sheep on grazing pastures

Husbandries with sheep free-grazing on summer pastures are subsidized by the Norwegian state, and can apply for financial support if certain requirements are met. This subsidy provides an overview over lambs and adult sheep grazing on pastures in Norway and is used by the Statistics Norway (SSB) and the Norwegian Agricultural Authority (pers.com. Bye

2013). However, there has been a slight change over time concerning the requirements for the subsidies. Between 2000 and 2008 the requirement for applying was that the grazing period was for a minimum of eight weeks, but from year 2008 the requirements were changed to a minimum of five weeks. Therefore, the number of sheep after 2008 might be slightly different in my estimates than the actual number of grazing sheep.

To estimate the number of sheep grazing on summer pastures, I based my calculations on the number of grazing sheep subsidized in Norway between 2003 and 2011. The data was obtained from Statistics Norway (Bye 2013). The data collected from Statistics Norway contained the proportion of ewes and lambs on summer pastures (Table 1), and did not contain any information on sex composition within lambs. Rams are not allowed to freely graze on pastures according to Norwegian law and are typically kept fenced on small grass patches close to the farm. The purpose is to prevent unwanted breeding among free-grazing sheep. When calculating the age ratio, we used two categories, lambs and adult ewes, and when calculating the sex ratio we assumed that newborn lambs had a sex ratio 50:50. Although the quality of the data probably varies locally, regional estimates on sheep numbers are considered quite robust.

2.2.3. Documented losses of reindeer and sheep

The data on documented losses of semi-domestic reindeer and domestic sheep were collected from Rovbase 3.0 (Direktoratet for naturforvaltning 2013). Rovbase 3.0 is a national database, which includes information on all registered carcasses of sheep and reindeer killed by the "five large predator species", and all documented predator mortalities. It also contains registered tracks, feces and hair samples collected in the field. The information is supervised by the county governor's office in the different counties, the Norwegian Nature Inspectorate (in Norwegian: Statens Naturoppsyn; SNO) and the Norwegian Institute for Nature Research (NINA). Rovbase 3.0 is an important tool in the monitoring of the five Norwegian predator species, and is the basis for management when considering compensation for damage to livestock or measures to prevent livestock depredation (Statens naturoppsyn 2010). Livestock suspected of being killed or injured by predators are reported to SNO. SNO is then obligated to send a trained warden to examine the carcass and determine the cause of death based on field autopsy, and state whether the cause can be classified as 'documented', 'assumed' or 'uncertain'. The examination is conducted with the use of established guidelines for

evaluation of carcasses, and the SNO staff are well trained to use standardized evaluation procedures (Skåtan & Lorentzen 2011). The category 'documented killed' is used when the cause of death is inconclusive, and cannot be confused with other causes of death (Statens naturoppsyn 2010). For most analyses I have confined myself in documented kills. However, when estimating the brown bear-killed reindeer I also used data classified 'assumed kills', due to the small sample size in documented brown bear-kills.

The dataset collected from Rovbase 3.0 includes documented kills of domestic sheep and semi-domestic reindeer between the year 2003 and 2011 (Table 2). SNO was established in 1997, and routines and standardization were more or less incorporated by the end of the 1990's corresponding to the development of SNO and the Norwegian Predator Monitoring Program (Braa et al. 2000-2001). To avoid a bias in the proportion of documented carcasses because of the initial phase of standardization, I chose to start at year 2003.

Table 2. Number of semi-domestic reindeer and domestic sheep killed in the study period, and the responsible predator species. The data is collected from Rovbase 3.0, and is restricted to the six northernmost counties in Norway.

	2003	2004	2005	2006	2007	2008	2009	2010	2011	
					Semi-domestic reindeer					**Total**
Brown bear	1	5	10	3	8	6	7	4	1	45
Lynx	65	120	137	162	199	289	324	405	243	1944
Wolverine	84	89	202	178	192	125	97	173	185	1325
Golden eagle	83	47	110	102	110	114	142	105	103	916
Wolf	2	0	10	15	0	4	17	17	4	69
					Domestic sheep					
Brown bear	379	333	410	590	562	392	642	444	332	4084
Lynx	104	150	146	138	138	189	149	97	66	1177
Wolverine	346	425	457	501	264	191	147	149	150	2630
Golden eagle	21	47	32	32	51	50	89	64	60	446
Wolf	37	337	188	15	346	63	230	93	161	1470
Total	1122	1553	1702	1736	1870	1423	1844	1551	1305	**14106**

The data on reindeer was divided in summer- and winter-kills as for the estimated standing reindeer population. Kills between May and September were classified as summer-kills and kills between October and April as winter-kills. All kills of sheep was classified as summer-kills and were only compared with the summer-kill data on reindeer.

2.2.4. Data material

Between 2003 and 2011, 4299 reindeer and 9807 sheep was documented as killed by a known or assumed predator species in our study area. The number of documented reindeer-kills in winter (3567) was much higher than in summer (373), probably due to a lower rate of detection in summer (pers.com. J. Mattisson).

Lynx were the primary predator of reindeer and brown bears the primary predator of sheep, in the data collected (Table 2). Wolverines were the secondary most important predator on both livestock species (Table 2).

2.3. Statistical analysis

2.3.1. Statistical analysis

Statistical analyses were performed using the statistical software R (R Development Core Team 2013). The data on domestic sheep and semi-domestic reindeer were analyzed separately. I examined the age and sex selection of the different predator species, and the seasonal difference in the livestock depredation. Chi square tests (Eq. 1) were used to test if observed frequencies deviated from the frequencies expected from the null hypothesis (McDonald 2009). I investigated if proportion of kills was a function of mean body weight of predators and prey. Simple regression and correlation analysis was used to test if there was a significant correlation between two variables. The results of all statistical tests were regarded as being significant with a p-value ≤ 0.05. In addition to statistical tests I also visualized the results in figures with proportions together with their Clopper-Pearson confidence interval.

$$X^2 = \sum_{i=1}^{n} \frac{(O_i - E_i)^2}{E_1}$$

Equation 1. The chi-squared (χ^2) formula.

X^2 = Chi-squared value

O_i = Observed frequencies

E_i = Expected frequencies

2.3.2. Seasonal patterns of predation

The proportion of killed livestock per month and per predator species was calculated to test if livestock depredation was constant over the year, or if the depredation varied significantly throughout the year, Chi square tests were used for the analysis. Reindeer are exposed to predation throughout the year, while sheep are exposed to predation only in the summer months. When testing if there was a significant seasonal variation in depredation of sheep, I thus used the months where sheep were definitely on grazing pastures (June-September). When testing for seasonal difference in reindeer-kills I tested for the whole year.

2.3.3. Age selection

I calculated the proportion of killed semi-domestic reindeer and domestic sheep in per class (juvenile and adult), and compared the results with the standing population of the two livestock species. Chi square tests were used to find if there was a significant selection for an age class. I also used chi square tests to investigate if there was a significant difference in age selection between all pairs of predators. In these pairwise tests the frequencies of juvenile and adult prey for predator 1 (observed) was tested against the same frequencies for predator 2 (expected).

2.3.4. Sex selection

The proportion of killed males and females within the two livestock species was calculated. Chi square tests were used to find if there was a significant sex selection within the population of adult reindeer and within the lamb population of sheep. I did not have any information on the sex ratio of lambs but assumed that when newborn, they had a sex ratio at 50:50. I did not test for significant sex selection in the reindeer calf population.

2.3.5. Body weight ratio models

I investigated if there was a correlation between the mean body weight of each predator species and the proportion of juveniles killed by calculating the Pearson's product-moment correlation. The body weight of each predator species was based on an average body weight obtained from Rovdata (2012b) (Table 4). I did the same for proportion of adults killed, only I used a body weight ratio of both predator and prey (the mean body weight of each predator

and the mean body weight of ewes and reindeer cows). Mean ewe body weight was set to 80 kg (Mysterud et al. 2002; Mysterud & Austrheim 2008) and mean reindeer cow body weight to 60 kg (Fauchald et al. 2004a; Kojola & Eloranta 1989; Reimers 2010; Weladji et al. 2002). Both models were expected to show the same trend.

Table 3. Mean body weight of the five predator species in kilogram

Body weight in kilogram				
Lynx	Wolverine	Golden eagle	Wolf	Brown bear
20	12	5	40	160

3. Results

3.1. Seasonal patterns in predation

3.1.1. Seasonal patterns in reindeer predation

All five predators showed a seasonal variation in the predation pattern on semi-domestic reindeer, during the year (brown bear: $\chi^2 = 55.5$, df = 11, $p < 0.001$; lynx: $\chi^2 = 1462.3$, df = 11, $p < 0.001$; wolverine: $\chi^2 = 1101.4$, df = 11, $p < 0.001$; golden eagle: $\chi^2 = 471.5$, df = 11, $p < 0.001$; wolf: $\chi^2 = 59.5$, df = 11, $p < 0.001$; Figure 2), although the sample size of brown bear and wolf-kills was quite small (brown bear = 45; wolf = 69). The monthly proportion of brown bear-killed reindeer peaked in May and wolf-killed reindeer peaked in October (Figure 2). The proportion of kills found from lynx and wolverines was highest between January and May and then decreased. The proportion of golden eagle-kills was highest in May during calving, but there was also a high proportion of kills between January and April (Figure 2).

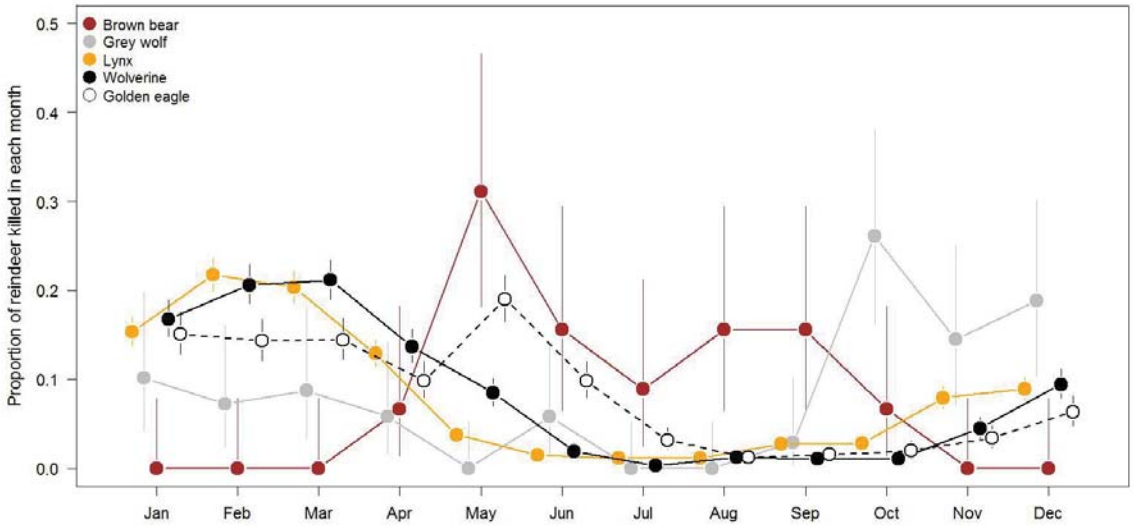

Figure 2. The proportion of killed reindeer per month and per predator species. Error bars are 95 % Clopper-Pearson confidence limits.

3.1.2. Seasonal patterns in sheep predation

There was a significant seasonal variation in predation of sheep between June and September for all predators (brown bear: $\chi^2 = 619.6$, df = 3, $p < 0.001$; lynx: $\chi^2 = 53.7$, df = 3, $p < 0.001$; wolverine: $\chi^2 = 1243.2$, df = 3, $p < 0.001$; golden eagle: $\chi^2 = 105.1$, $p < 0.001$; wolf: $\chi^2 = 564.9$, df = 3, $p < 0.001$; Figure 3). Brown bears and wolverines seemed to have the highest

proportion of kills late in the grazing season, between August and September (Figure 3). The highest proportions of sheep killed by lynx, golden eagles and wolves were found earlier, between May and July (Figure 3).

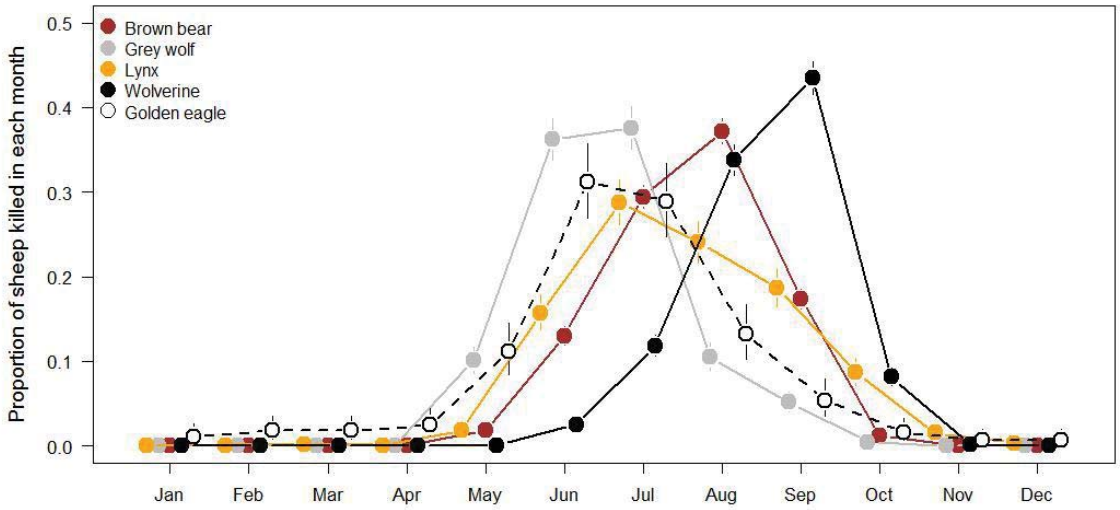

Figure 3. The proportion of killed sheep per month and per predator species. Error bars are 95 % Clopper-Pearson confidence limits. Due to the late season kills of wolverine all twelve months are given in the figure.

3.2. Age selection in predation

3.2.1. Age selection in summer

Brown bears, lynx and golden eagles selected calves over adults, in summer (brown bear: χ^2 = 24.9, df = 1, p < 0.001; lynx: χ^2 = 18.3, df = 1, p < 0.001; golden eagle: χ^2 = 686.2, df = 1, p < 0.001; Figure 4). Wolverines and wolves (note the very low sample size in wolf kills; n = 6) did not show a significant selection for juvenile or adult reindeer (χ^2 = 0.7, df = 1, p = 0.39; χ^2 = 1.9, df = 1, p = 0.16; Figure 4) When preying on sheep, all five predator species had a significant selection for a given age class. Brown bears selected adult females over lambs (χ^2 = 3689.7, df = 1, p < 0.001; Figure 4), and the remaining four predator species significantly selected lambs (lynx: χ^2 = 313.5, df = 1, p < 0.001; wolverine: χ^2 = 827.2, df = 1, p < 0.001; golden eagle: χ^2 = 149.8, df = 1, p < 0.001; wolf: χ^2 = 101.1, df = 1, p < 0.001; Figure 4).

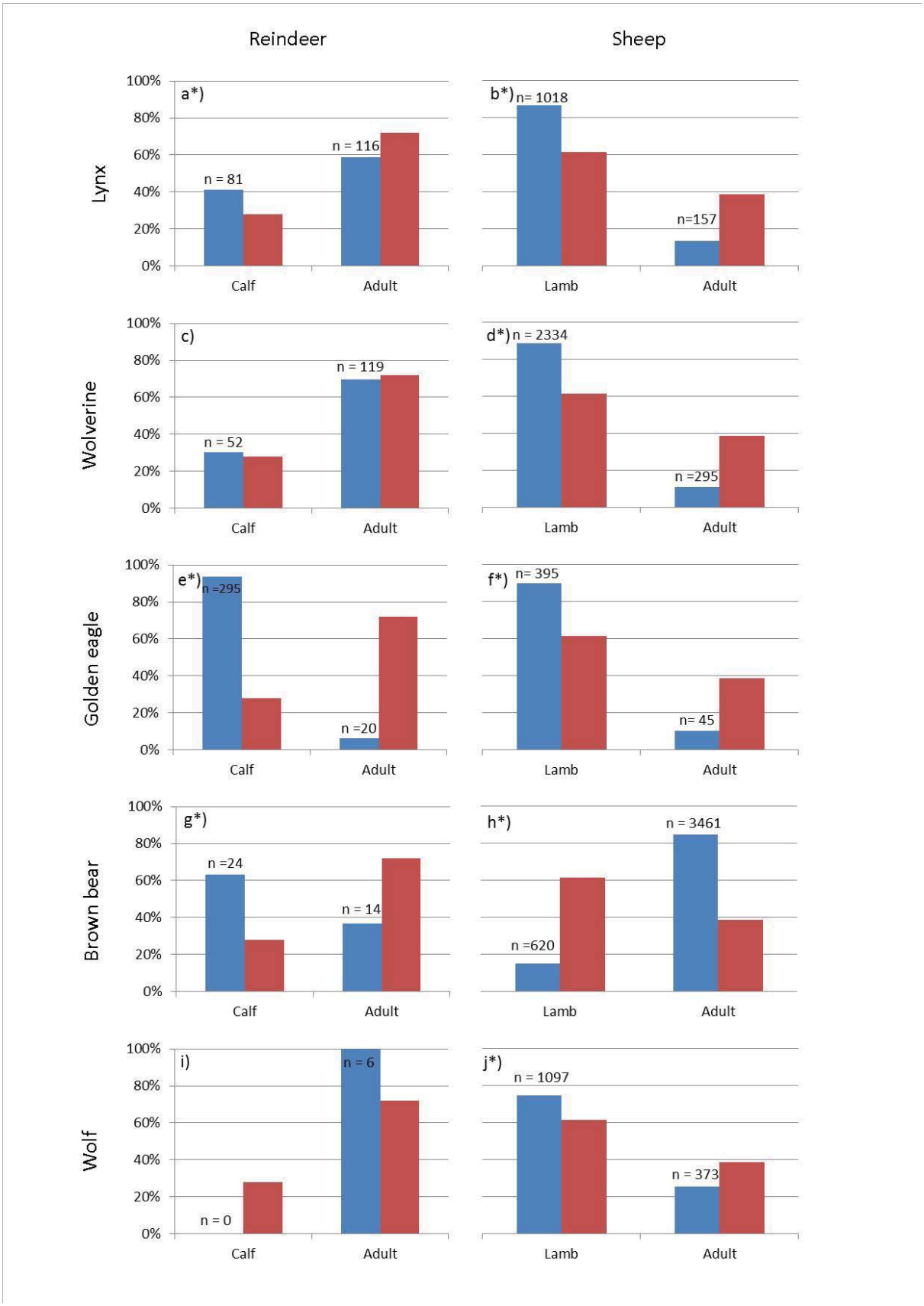

Figure 4. The summer-availability of each age class of livestock represented in the red bars, compared with the proportion of summer-kills (blue bars) of lynx (a, b), wolverine c, d), golden eagle (e, f), brown bear (g, h) and wolf (I, j). Figures on the left hand side represent semi-domestic reindeer and figures on right hand side represent domestic sheep. Predators with a significant selection are marked with a star (*).

3.2.2. Age selection in winter

Both lynx and golden eagles had a significant selection for reindeer calves within the winter population ($\chi^2 = 326.8$, df = 1, $p < 0.01$; $\chi^2 = 1145.5$, df = 1, $p < 0.001$; Figure 5). Brown bears (low sample size; n = 6), wolverines and wolves did not show a significant selection for age (brown bear: $\chi^2 = 1.4$, df = 1, p = 0.23; wolverine: $\chi^2 = 0.08$, df = 1, p = 0.78; wolf: $\chi^2 = 0.08$, df = 1, p = 0.77; Figure 5).

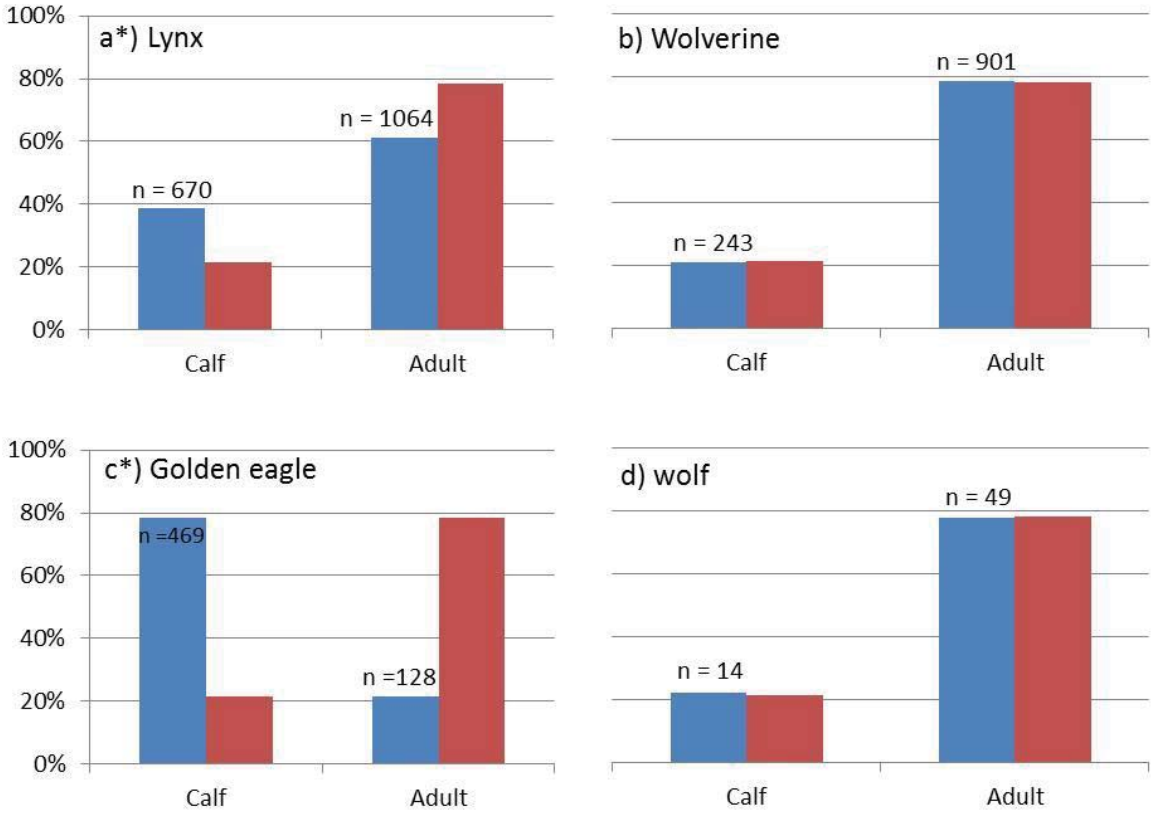

Figure 5. The winter-availability of each age class of the reindeer population (red bars) compared with the proportion of winter-killed reindeer (blue bars) by lynx (a), wolverine (b), golden eagle (c) and wolf (d). Predators with a significant selection are marked with a star (*). Brown bear is not represented due to low sample size (n = 6).

3.2.3. Age selection between all pairs of predators.

Golden eagles had a significant difference in age selection for reindeer in summer and winter compared with the four other predator species (Table 4). Golden eagles almost exclusively selected calves over adults, compared to the other predator species which included more adults, as shown in figure 4 and 5. Lynx and wolverines also showed a significant difference in selection of reindeer age class (Table 4). While lynx selected for calves, wolverines showed no selection for age (Figure 4 and 5). Brown bears had a significant difference in age

selection of reindeer, only in summer, when compared with the four other predator species (Table 4). The summer p-value in brown bear selection is probably influenced by a low sample size.

Table 4. Age selection of reindeer for all pairs of predators represented with χ^2 value and p-values (degrees of freedom = 1). Cells in the upper diagonal represent the winter age selection, and cells in the lower diagonal represent the age selection in summer. The p-values ≤ 0.05 are regarded significant. The values marked in **Bold** are significant and the squares not marked are not significant. Significant p-values report that there is a difference in age selection between pairs of predator species, not significant p-values report no difference in age selection between pairs.

Winter age selection					
	Lynx	**Wolverine**	**Brown bear**	**Wolf**	**Golden eagle**
Lynx		**χ2 = 95.52, p < 0.001**	χ2 = 2.31, p = 0.13	**χ2 = 6.27, p = 0.01**	**χ2 = 281.65, p < 0.001**
Wolverine	**χ2 = 4.09, p = 0.04**		χ2 = 0.59, p = 0.44	χ2 = 7e-04, p = 0.98	**χ2 = 530.83, p < 0.001**
Brown bear	**χ2 = 5.40, p = 0.02**	**χ2 = 13.03, p < 0.001**		χ2 = 0.58, p = 0.45	**χ2 = 16.91, p < 0.001**
Wolf	χ2 = 2.57, p = 0.10	χ2 = 1.33, p = 0.25	**χ2 = 5.98, p = 0.01**		**χ2 = 89.31, p < 0.001**
Golden eagle	**χ2 = 170.44, p < 0.001**	**χ2 = 215.91, p < 0.001**	**χ2 = 33.23, p < 0.001**	**χ2 = 57.94, p < 0.001**	
Summer age selection					

Both brown bears and wolves showed a strongly significant difference in age selection of domestic sheep, compared with the other predator species (Table 5). While brown bears selected a higher proportion of ewes than lambs, the four other predator species selected for lambs (Figure 4).

Table 5. Sheep age selection for all pairs of predators represented with χ^2 value and p-values (degrees of freedom = 1). The p-values ≤ 0.05 are regarded significant. The values marked in **Bold** are strongly significant, and the values not marked are not significant. Significant p-values report that there is a difference in age selection between pairs of predator species, not significant p-values report no difference in age selection between pairs.

	Wolverine	**Brown bear**	**Wolf**	**Golden eagle**
Lynx	χ^2 = 3.35, p =0.07	**χ^2 = 2167.53, p < 0.001**	**χ^2 = 58.07, p < 0.001**	χ^2 = 2.69, p = 0.10
Wolverine		**χ^2 = 3510.53, p < 0.001**	**χ^2 = 137.41, p < 0.001**	χ^2 = 0.32, p =0.57
Brown bear			**χ2 = 1784.10, p < 0.001**	**χ2 = 1270, p < 0.001**
Wolf				**χ^2 = 45.03, p < 0.001**

3.3. Sex selection in predation

When comparing the assumed 50:50 sex ratio of domestic lambs, I did not find that the five predator species showed any significant preference for sex (brown bear: χ^2 = 0.01, df = 1, p = 0.9; lynx: χ^2 = 2e-04, df = 1, p = 0.99; wolverine: χ^2 = 0.01, df = 1, p = 0.91; golden eagle: χ^2 = 4e-04, df = 1, p = 0.98; wolf: χ^2 = 9e-04, df = 1, p = 0.98). The proportion of killed male and female lambs varied within an interval from 0.44-0.56.

Within the estimated adult summer-population of reindeer, lynx showed a significant selection for males over females (χ^2 = 13.5, df = 1, p < 0.001; Figure 6). Brown bears, wolverines, golden eagles and wolves did not show any significant selection for sex within the adult population in summer (brown bear: χ^2 = 1.01, df = 1, p = 0.31; wolverine: χ^2 = 1.4, df = 1, p = 0.24; golden eagle: χ^2 = 0.9, df = 1, p = 0.35; wolf: χ^2 = 0.5, df = 1, p = 0.47; Figure 6). Lynx, wolverines and golden eagles selected a significantly higher proportion of male reindeer within the estimated winter-population of adult reindeer (lynx: χ^2 = 79.1, df = 1, p < 0.001; wolverine: χ^2 = 31.4, df = 1, p < 0.001; golden eagle: χ^2 = 15.8, df = 1, p < 0.001; figure 6). Brown bears and wolves did not show any significant selection for a sex classes in winter (χ^2 = 0.5, df = 1, p = 0.47; χ^2 = 0.3, df = 1, p = 0.59; figure 6).

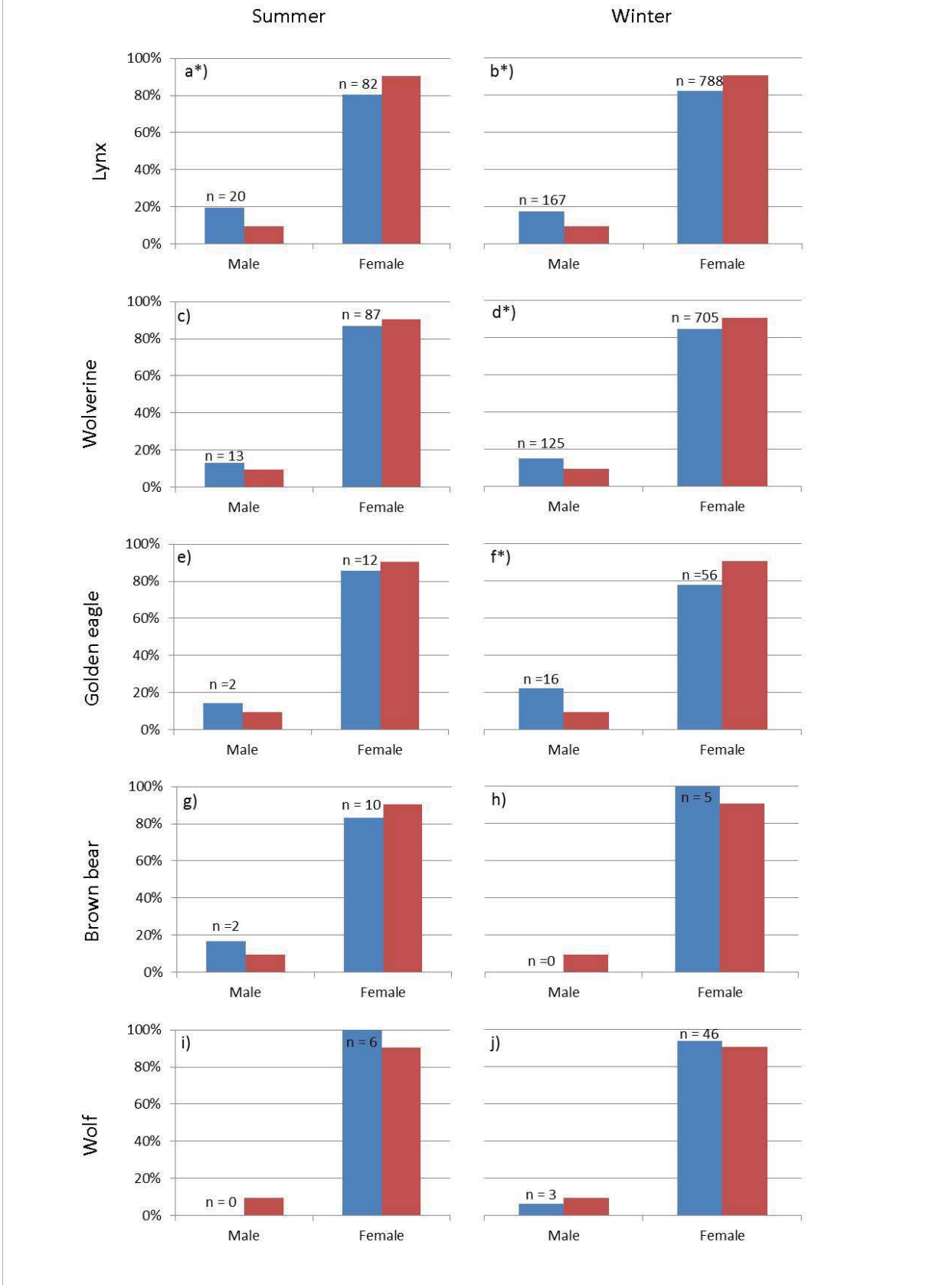

Figure 6. The availability of adult males and females within the population of semi domestic reindeer (red bars) compared with the proportion of killed reindeer (blue bars) by lynx (a, b), wolverine (c, d), golden eagle (e, f), brown bear (g, h) and wolf (i, j). The summer availability and kills to the left and winter availability and kills on the right. Predators with a significant selection are marked with a star (*).

3.4. Age selection as a function of predator body weight

3.4.1. Predator-reindeer body weight ratio

There was no correlation between body weight of the predator species and the proportion of killed reindeer calves ($r^2 = 0.08$, $p = 0.89$; Figure 7) and cows.

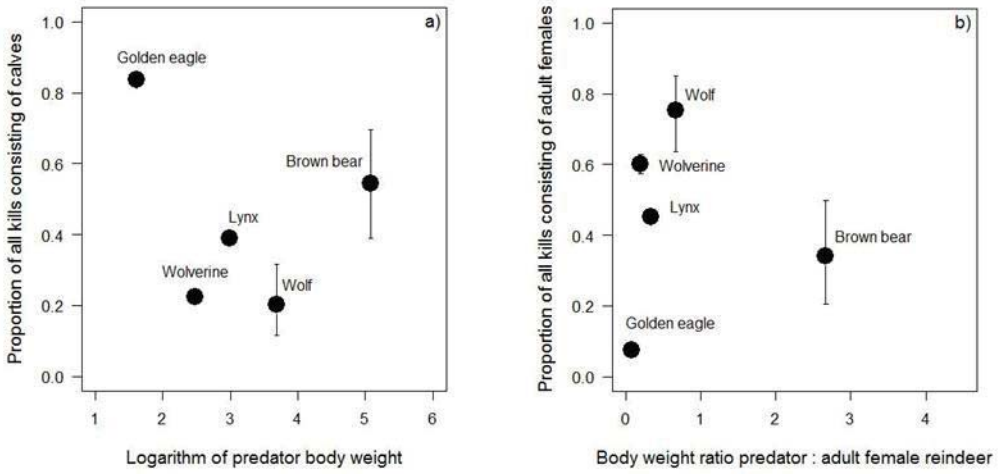

Figure 7. Scatterplot of the proportion of killed reindeer calves on the y-axis and (a) the mean body weight of each predator species on the x-axis; (b) the body weight ratio of the five predator species and reindeer cows on the x-axis No correlation was found between the variables x and y (a) $r^2 = 0.08$, $p = 0.89$).

3.4.2. Predator-sheep body weight ratio

There was a significant correlation between body weight of the predator species and the proportion of killed lambs ($r^2 = -0.89$, $p = 0.04$; Figure 8) and ewes. The smallest predator, the golden eagle, had the highest proportion of lamb kills and the biggest predator, the brown bear, had the highest proportion of adult ewes killed.

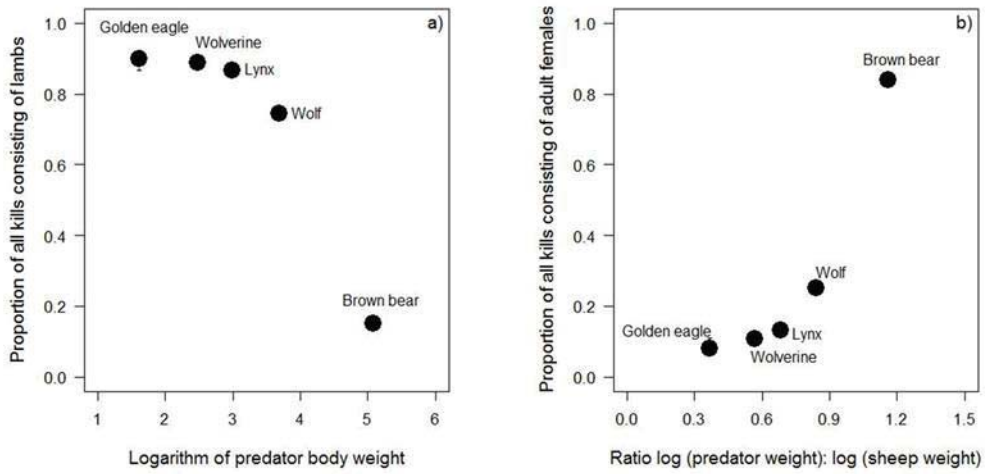

Figure 8. Scatterplot of the proportion of killed lambs on the y-axis and (a) the mean body weight of each predator species on the x-axis; (b) the body weight ratio between the five predator species and ewes on the x-axis. There was a correlation between the two variables (a) $r^2 = -0.89$, $p = 0.04$).

4. Discussion

In my thesis I report that there was a significant selection for juveniles in seven out of ten predator-prey cases (five predator- and two livestock species), partially supporting my prediction . Only when brown bears depredated on sheep, did the predator species select a significantly higher proportion of adults than juveniles. The correlation between predator body weight and proportion of juveniles killed was only significant in the sheep depredation analysis, indicating that lambs are highly preferred over ewes, especially by smaller predators. Only in lynx depredation of reindeer did I find a clear selection for sex in the adult population, but it was not for females as predicted. Golden eagles peaked in predation of both livestock species in spring, but so did the brown bear predation of reindeer, rejecting prediction (iiii).

4.1. Predator-prey body weight ratio

Prey selection is often a function of predator-prey body weight ratio, where solitary, smaller sized predator species often are more constrained in choice of prey than larger predators (Cohen et al. 1993; Sinclair et al. 2003; Vézina 1985). Larger predators on the other hand do not necessary specialize on larger prey, but rather exploit a wider range of prey sizes, depending on what's available (Hayward & Kerley 2005; Radloff & Toit 2004). When assessing age selection of prey, juveniles should thus be more prone to predation than adults, since a wider range of predator species are able to kill them. Several studies have reported that neonatal mortality is high in ungulate population, and that predation is the main cause of mortality in systems where predators are present (Adams et al. 1995; Kjelvik et al. 2000; Linnell et al. 1995).

My results indicate that a higher proportion if juveniles were selected, by the majority of predator species. I predicted that the proportion of killed juveniles would increase with decreasing predator body weight, and to some extent this prediction was verified. There was a correlation between the two variables predator body weight and the proportion of juvenile sheep killed (Fig. 7), where the smallest predator, the golden eagle, killed a much higher proportion of lambs than the largest predator. I did not find a correlation between the body weight of the five predator species and the proportion of calves among the reindeer killed. Mainly due to the fact that brown bears selected calves over adults (Figure 8) despite their very large body size.

4.2. Golden eagle predation on juveniles

Golden eagles are reported to depredate on both young and adult ungulates (Bergo 1987; Norberg et al. 2006; Nybakk et al. 1999; Watson 2010). I found that golden eagles selected a high proportion of juvenile prey of both livestock species, at a much higher proportion than the four other predator species (Figure 4 and 5). The peak in predation corresponded with the period of reindeer calving and with the timing of releasing sheep onto summer pastures, but the predation was also high during winter (Figure 2). Other studies have also emphasized the importance of ungulate juveniles in golden eagle diet, especially during the breeding season (Johnsen et al. 2007; Norberg et al. 2006; Tjernberg 1981; Warren et al. 2001). Norberg et al. (2006) found that the golden eagle was the dominant predator on reindeer calves in northern Finland, and in one study area the eagles accounted for at least 40% of the total reindeer mortality.

The proportion of livestock killed by golden eagles decreased as the summer progressed, as shown in figure 2 and 3. Golden eagles are opportunistic predator, scavenging on carrion when it is available (Bergo 1987; Tjernberg 1981). Warren et al. (2001) did not report any golden eagle kills of domestic sheep late in the grazing season and suggested that the increased rate of sheep depredation by wolverines provided the golden eagles with abundant carrion and thereby reduced their need to kill sheep. One might see the same trend for sheep depredation in figure 3, where predation by golden eagles decreased as the predation by the wolverines increased. Relating the predation back to predator-prey body ratio, an obvious reason for the seasonal difference in predation of juveniles, would be that the juveniles grow bigger and thus are harder to kill later in the season. Golden eagles may thus select a higher proportion of carrion later in the season simple because of the body development of juveniles.

4.3. Brown bears preferred adult ewes but not reindeer cows

Brown bears selected a significantly higher proportion of ewes (Figure 4), consistent with the findings in other studies (Aanes et al. 1996; Dahle et al. 1998; Knarrum et al. 2006; Mysterud & Warren 1997). Knarrum et al. (2006) found that only the energy rich parts of the ewes, the fat from the udder and sternum regions, were eaten of 69 % of the ewes killed. They suggested that brown bears, according to the optimal foraging theory (Pyke et al. 1977), chose the prey that provided the greatest energy benefit for survival and reproduction. The sheep depredation by the brown bears was quite low at the start of the grazing season, and did

not peak until August (Figure 3), similar to brown bear depredation patterns found in a study by Aanes et al. (1996). Brown bears are opportunistic omnivores, with a diet mostly consisting of berries, ants, forbs and ungulate carrion (Dahle et al. 1998). They are in need of more high fat- and protein rich food just before the hibernating period. Although brown bears are able to build sufficient fat stores on a blue berry diet, domestic sheep can be an important contribution to the late summer diet, and increase the probability of survival during winter (Dahle et al. 1998; Mysterud & Warren 1997; Sagør et al. 1997).

Within the reindeer population, brown bears did not show selection for adult reindeer but rather for calves (Figure 4), with a peak in predation in spring (Figure 2). The behavioural and physological differences in reindeer and sheep are probably the main reasen for the different age preference. Reindeer are still bred for living outdoors throughout the year, making the anti-predator behaviour, and the abillity to escape much stronger in reindeer compared with the most common Norwegian breeds of sheep. Nieminen (2011) and Nieminen et al. (2011) found that brown bears were an important predator on semi-domestic reindeer calves in Finnish forest areas in spring, supporting my results. Also in northern Sweden, neonatal mortality in reindeer was reported to be influenced by brown bear predation (Karlsson et al. 2012). Karlsson et al. (2012) found that during the short breeding period when brown bears were in the area, mean brown bear kill rates on reindeer calves were 0.4 calves per day. Moose calves are born later than reindeer calves, and Kindberg et al. (2012) reported that brown bears in northern Sweden shifted from reindeer calves to moose calves as the spring progressed. The studies conducted by Karlsson et al. (2012) and Kindberg et al. (2012) suggest that reindeer could be an important prey in the neonatal period.

4.4. Late season sheep depredation by wolverines

Wolverines did not seem to exploit domestic sheep until late in the grazing season with a peak as late as September, when predation by other predator species almost ceased (Figure 3). Landa et al. (1999) reported that sheep grazing in alpine wolverine habitats and especially in cub-rearing areas, were exposed to higher rates of predation than sheep in other areas. Warren et al. (2001) discussed that the cause of death in sheep could be divided into two distinct periods, as a result of the change in foraging a-long a phenological gradient. They argued that sheep changed their grazing patterns from lower latitudes to higher alpine areas as the season

went by, and thus temporarily went through the preferred habitat of different species within the predator guild. The argument is probably more valid locally, and not that much on a larger scale due to the huge difference in topography and climate in Norway. Still, there are some similarities in my study, where especially the forest dwelling wolf and lynx are represented earlier in the season and the alpine living wolverine late in the season (Figure 3).

4.5. Wolf depredation

The Norwegian government declared in a policy white paper in 2003 that the wolf population in Norway should not be allowed to establish in the Sami reindeer husbandry area, thus the sample size of wolf-killed reindeer is relatively small (n = 69; The Norwegian Ministry of the Environment (2003)). The kills represented in our data are most likely made by solitary wolves immigrating from Russia or Finland into northern Norway (the northernmost county of Finnmark was where 61 out of 69 wolf-kills were found;Wabakken et al. (2001)). The sample size on sheep depredation by wolves was on the other hand quite large (n =1470). Out of the 1470 wolf kills in the study period, 1405 kills were found in Hedmark county. A large part of Hedmark county is a part of the Norwegian wolf zone, or borders to the wolf zone, making the area a hot-spot for wolf –human conflict. Wolves are opportunistic predators, and where wild ungulates are scarce and wolves and livestock coexist the impact of livestock depredation by wolves can be severe (Gula 2008; Kaartinen et al. 2009; Kojola et al. 2004; Meriggi & Lovari 1996).

4.6. Lynx and wolverine age selection of prey

Other studies suggest that both lynx and wolverines, as relatively small predators, should select juveniles over adults when depredating livestock (Landa et al. 1999; Mattisson et al. 2011a; Nybakk et al. 2002; Stahl et al. 2001; Warren et al. 2001). On the other hand, lynx are an efficient predator on medium-sized ungulates, and are known to not have any clear preferences within the overall age composition for roe deer which are their main wild prey (Andersen et al. 2007; Gervasi et al. 2012; Mejlgaard et al. 2013). I found that both predator species selected lambs over adult sheep (Figure 4), but only lynx significantly selected calves over adult reindeer (Figure 4 and 5). Wolverines are mainly regarded as scavengers in the Norwegian fauna (Landa et al. 1997; Myhre & Myrberget 1975), and are regarded as a less

skilled predator on ungulates, especially adults (Bjärvall et al. 1990; Haglund 1966; Mattisson et al. 2011a). Thus, the wolverine results regarding age selection were unexpected, which might suggest a bias in detection rates of kills, discussed closer in section 4.8.

The behavior of the predator is an important factor in influencing possibility of kill detection. While lynx do not disarticulate their kills, and in the case of ungulate kills do not always consume the entire prey (Falk 2009; Mattisson et al. 2011a; Pedersen et al. 1999), the wolverine tends to dismember the kill and hide larger parts of it in food caches (Vander Wall 1990). This could make it harder to find the kill and to assess what actually killed it, and would also imply that adult kills are easier to find than kills of juveniles. Semi-domestic reindeer are also more free-roaming, using larger areas than domestic sheep, making it harder to detect kills of reindeer. The selection for age of the overall age composition of reindeer may thus be more similar to the selection found in the population of domestic sheep.

4.7. Sex selection

Sexual dimorphism (males are larger than females) in ungulate species should make females more preferable as prey than males (Miquelle et al. 1992; Vernon et al. 1997). On the other hand, some studies have shown that males are subject to a greater risk of predation than females because of their reproductive activity (Fitzgibbon & Fanshawe 1989; Fitzgibbon 1990). During the rutting season, males spend less time feeding and instead use more energy and time on reproductive traits. If males are in a lower condition due to exhaustion and decreased energy uptake during rutting, they should be preferred as prey during and after this period (Knopff et al. 2010; Pole et al. 2004).

Within the adult reindeer population lynx selected for bulls in both winter and summer (Figure 6). Lynx selection for bulls within the adult population of reindeer was also shown by Mattisson et al. (2013, Submitted). They suggested that the observed selection for bulls was not caused by lynx actively selecting males, but rather due to an increased encounter rate with bulls. Sexual segregation during calving (Loe et al. 2006) where cows select higher ground in order to avoid forest dwelling predators (Mårell & Edenius 2006), and bulls gather below the tree line to select the best foraging areas, could increase the likelihood of lynx encountering more bulls than females (Mattisson et al. 2013, Submitted). Still, I found a selection in both winter and summer, suggesting that there is more to it than sexual segregation in spring.

Within the lamb population I did not find any selection for a sex class when assuming a lamb sex ratio of 50:50 at the time of release. May et al. (2008) suggested that male lambs were more exposed to wolverine predation than females, later in the season, due to sex-specific behavioral difference. Other studies have shown that increasing mother-juvenile distance, a higher level of locomotive behavior and more risk taking resulted in higher predator mortality among male juveniles compared to female juveniles (Aanes & Andersen 1996; Mathisen et al. 2003; Warren & Mysterud 1995). My results suggest that on a national level the sex of a juvenile prey does not matter when selecting prey.

4.8. Source of errors in documenting seasonal reindeer depredation

The proportion of documented killed reindeer was much lower in summer than in winter as seen in figure 2, especially for the two predators with the greatest depredation impact on semi-domestic reindeer, the lynx and wolverine (Andren et al. 2011; Mattisson et al. 2011a; Mattisson et al. 2011b; Pedersen et al. 1999; Sunde et al. 2000). The results do not necessarily suggest that the predation rate is lower in summer, but rather suggests a seasonal bias in the detection of kills. Still the comparison between the different predator species will be valid as the seasonal variation in delectability is likely to affect all predator kills equally.

Mattisson et al. (2011b) stated that the detection rate was lower in summer than winter (2 % in summer and 9 % in winter), something that could explain the low numbers of documented summer kills in my dataset. Kills in winter are easy to see and to document due to the snow; revealing blood from quite long distances, revealing tracks of the responsible predator species, and permitting reindeer herders to more easily patrol their pastures using snowmobiles. This, in addition to the effect of slaughtering on age composition, was my main motivation for splitting the analysis into winter and summer. While there might still be some bias due to detectability also within season, the main difference is accounted for.

Especially spring- and summer- killed calves are most likely underrepresented in my study. Calves killed by a predator in summer are often totally consumed, either by the predator responsible or by scavengers, and the chances of detecting the kill and document what killed it is thus low (Fauchald et al. 2004b). If calves are underrepresented in the data material retrieved from Rovbase 3.0, there is a possibility that the proportion of each age class killed is skewed over to a higher proportion of adult kills. Still, the analysis managed to find a significant selection for calves among three out of five predator species. The results are thus

considered conservative results, and more accurately reflecting relative differences between predator species than absolute estimates of actual proportions killed. In wolves and wolverines on the other hand, no significant preference for age was found. If the proportion of summer kills is underrepresented, the calf depredation by lynx and wolverine might be higher than what I found.

4.9. Management implications

Based on the result from my study I suggest that one should shortening the grazing period for sheep to reduce the predation by brown bears and wolverines. A large part of the predation done by the two predator species are late season kills seen in figure 3. I also suggest that by reducing the proportion of ewes on late season grazing pastures the impact of brown bear predation could be reduced. Golden eagles and brown bears showed a peak in predation during reindeer calving. By keeping reindeer in a more secure location during calving, one could reduce the predation by the two predator species.

Mattisson et al. (2011b) suggested moving into a new risk-based compensation system, where the government compensates for the impact on production rather than compensating the estimated total loss. The impact on production depends highly on the composition of age and sex class within the total loss. My results can be used in estimating the compensation by looking at the profile of killed juveniles and adults.

5. Conclusion

Juvenile sheep and reindeer are preferred as prey by the majority of predator species in Norway. My results demonstrated that the age selection of prey was a function of the body weight ratio of predator and prey for sheep, but not for reindeer. Predators selecting adult females would have the greatest impact on livestock populations (Gaillard et al. 2000; Gervasi et al. 2012). Thus, I suggest that brown bear predation on sheep would probably have the most severe economic impact on individual farmers. Where brown bear depredation occurs, farmers are impacted in two ways; by directly losing their most reproductive animals, and also by the decreased probability of survival for lambs left to care for them self (Aanes et al. 1996).

The depredation patterns on sheep and reindeer are different from each other. When investigated, it is important to separate the two livestock species, both because of the seasonal difference in availability as prey, and because predators differ in their age preference within

the two prey species. More effort should be put in place to estimate the population size of both predators and livestock and to investigate the preference of age and sex in livestock, instead of documenting each individual kill. A compensation system based on these estimates, rather than estimates on total loss based on documented kills, could be preferred both from the management and the husbandry (Herfindal et al. 2011; Mattisson et al. 2011b).

6. References

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Appendix

Appendix 1: Map of number of killed domestic sheep and semi-domestic reindeer in each municipality in the study area

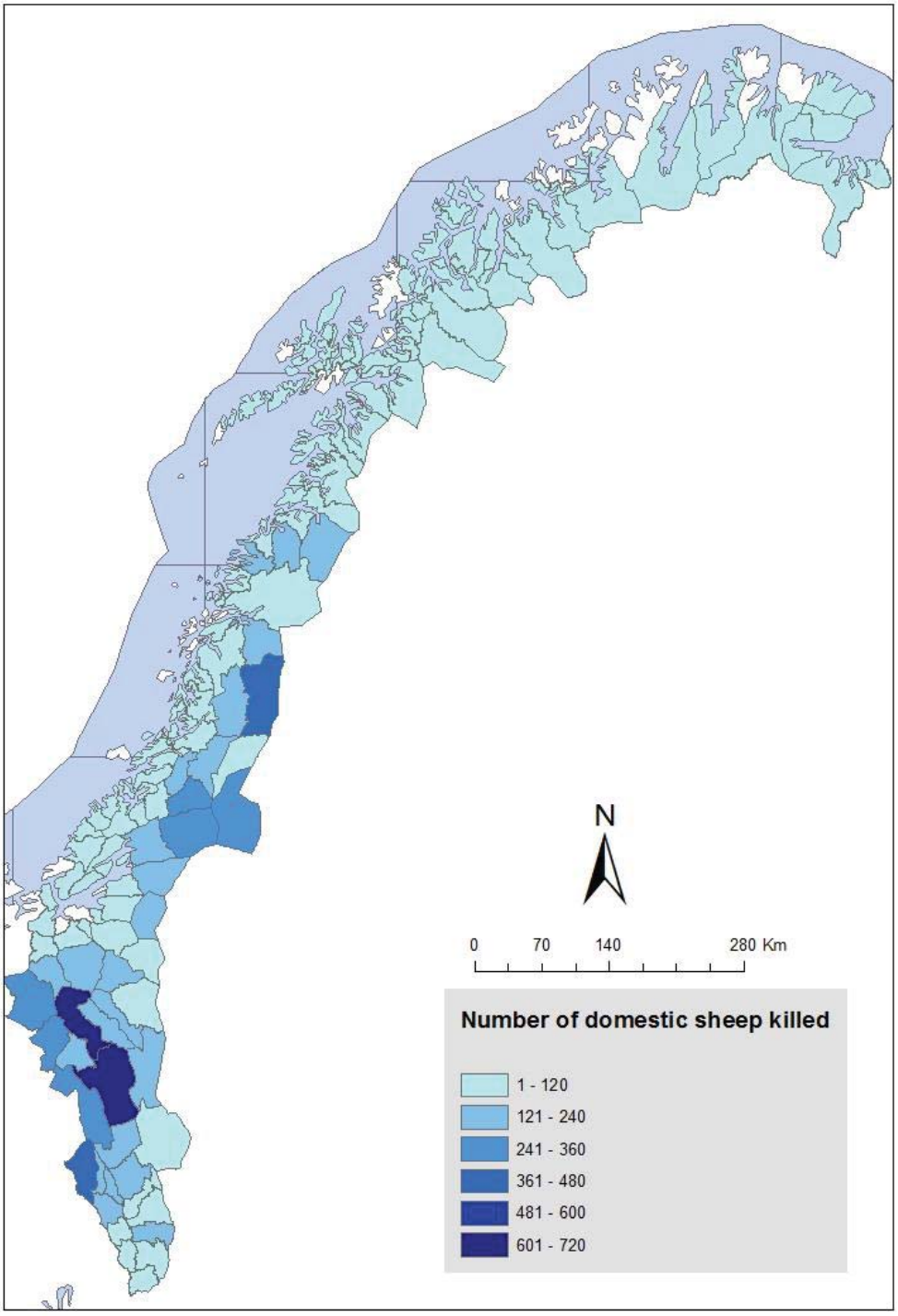

Figure 9. Number of domestic sheep killed in each municipality in the study period 2003 to 2011

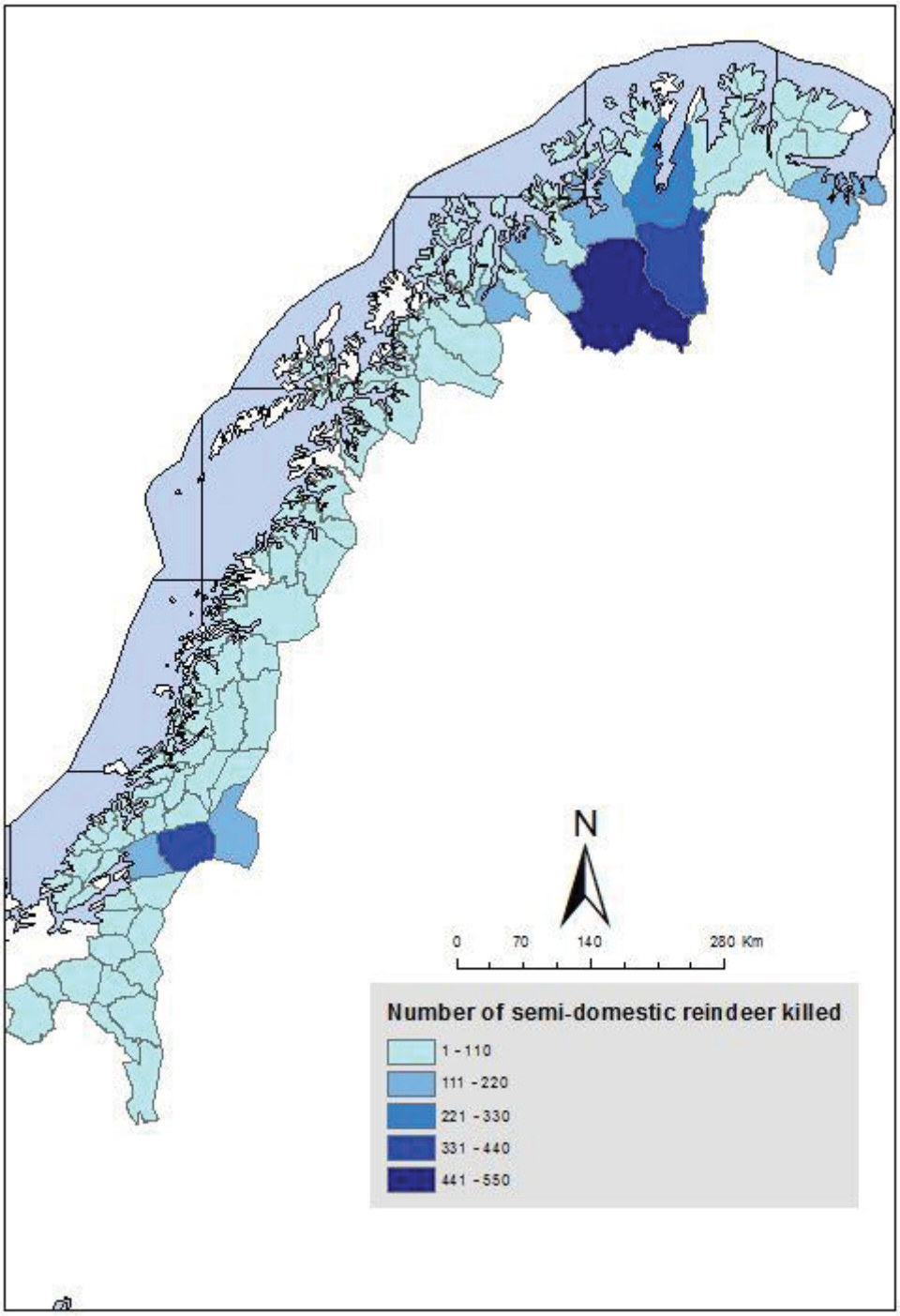

Figure 10. Number of semi-domestic reindeer killed in each municipality in the study period 2003 to 2011

Appendix 2: Documented losses of semi-domestic reindeer and domestic sheep in the study period, divided in responsible predator species and in number of kills in each county.

Table 6. Documented losses of semi-domestic reindeer in the six northernmost counties in Norway, between 2003 and 2011. The brown bear losses also contain assumed losses.

County	Brown bear	Lynx	Wolverine	Golden eagle	Wolf	Grand Total
Finnmark	10	582	491	617	61	1761
Hedmark	3	41	7	24	2	77
Nordland	8	313	232	58	0	611
Nord-Trøndelag	17	631	402	74	5	1129
Sør-Trøndelag	7	79	20	41	0	147
Troms	0	298	173	102	1	574
Grand Total	45	1944	1325	916	69	**4299**

Table 7. Documented losses of domestic sheep in the six northernmost counties in Norway, between 2003 and 2011.

County	Brown bear	Lynx	Wolverine	Golden eagle	Wolf	Grand Total
Finnmark	157	41	44	2	0	**244**
Hedmark	1669	172	957	102	1405	**4305**
Nordland	402	337	633	124	11	**1507**
Nord-Trøndelag	1232	455	327	105	46	**2165**
Sør-Trøndelag	520	72	420	45	8	**1065**
Troms	104	100	249	68	0	**521**
Grand Total	4084	1177	2630	446	1470	**9807**