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Master thesis

A seasonal feast: the use of moose slaughter remains by the boreal forest scavenger community in south-eastern Norway



Master in Applied Ecology

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Abstract

Scavenging by vertebrates is one of multiple foraging strategies to utilize food resources and a key ecological process in food web dynamics. It is used in periods of environmental stress such as shortage of prey, and as an alternative food resource. Anthropogenic resources like hunting remains can provide scavengers with large amounts of temporally and spatially predictable nutrient rich food. However, the role and impacts of these food subsidies on the scavenger community, are still poorly understood.

In this study, I investigated the use of human provided carrion from the annual moose hunt in south-eastern Norway. Remote camera traps were used to monitor scavenger utilization at 17 sites with hunting remains. I examined whether the use of these remains was affected by the amount and type of biomass, if the visit frequency of scavengers changed over time, and I quantified the total amount of biomass from the shot moose in the study area available to scavengers.

All sites were visited by scavengers. The main visitors were corvid species (*Corvidae*), pine marten (*Martes martes*), and red fox (*Vulpes vulpes*). Every site was encountered within 24 hours after camera placement, with avian species arriving first. Sites with organs present were encountered faster, as were the sites with moose remains shot later in the hunting season. Positive correlation was found between start weight of the remains and visit frequency of mammals and large corvids. Avian species showed to be diurnal visitors, while mammals were more nocturnal. Also, the older the remains, the lower was the probability of avian scavengers to visit them. The decrease of biomass was higher for remains with organs present and was positively correlated to the scavenger biomass visiting the site. Average available biomass was estimated to 8.61 kg \pm 0.03 SE per km2.

I conclude that moose hunting remains are an important food source for a wide range of scavenger species in the Norwegian boreal forest. Especially in the first period of the moose hunting season this food source is very abundant, providing scavengers with an easy accessible and highly nutritious resource. This study helps to get a better understanding about the functioning of the scavenger guild.

Keywords: Alces alces, avian, biomass, camera traps, carrion, hunting, moose, scavenger.

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1. Introduction

Scavenging by vertebrates is one of multiple foraging strategies to utilize food resources and a key ecological process in food web dynamics (Lafferty, Loman, White, Morzillo & Belant, 2015; Kroftel, 2011). Scavenging behaviour is common in many avian and terrestrial species, as almost all predators are scavengers to some extent (Wikenros, Sand, Ahlqvist & Liberg, 2013). This strategy is a relevant contribution in energy transfer and plays an important role in ecosystem services, such as nutrient recycling. Also, preventing diseases from spreading can be seen as an important contribution (Mateo-Tomás et al., 2015). Since hunting can be energetically costly and dangerous (Mattisson et al., 2016), facultative scavenging is an alternative way to get access to high quality food, while circumventing certain costs (Lafferty et al., 2015). Amongst the activities related to scavenging, finding carrion is the most energetically demanding. Avian scavengers mainly rely on their sense of sight, they can travel long distances in a short time period, and share roosting spots and information (Cortés-Avizanda, Selva, Carette & Donázar, 2009; Huff, 2016). Especially, compared to terrestrial scavengers, avian species have a large foraging radius, the distance or area within which an animal can locate a food source in a given time period (Wilmers, Stahler, Crabtree, Smith & Getz, 2003). Terrestrial scavengers are more bound to their olfactory sense and how fast and far they can travel, as prey are often hidden from their sight (Krofel, 2011). For this reason, scavenging is more common in avian species (DeVault, Rhodes & Shivik, 2003; Krofel, 2011). In periods of environmental stress such as shortage of prey, and as an alternative food resource, scavenging behaviour can have an impact on scavenging communities and the distribution of animals. The use of carcasses takes mainly place during cold seasons when it is more difficult to utilize other food resources (Wikenros et al., 2013). Scavenging is more common in biomes characterized by cold climate, like Norway's boreal forests, than in warmer environments, since higher temperatures reduce the quality of a carcass, and alternative food sources are more difficult to find (Mattisson et al., 2016).

Carrion available to scavengers, from natural mortality, such as predation or starvation, is nowadays relatively widely studied. However, the role and impacts of anthropogenic food resources, on the scavenger community in the boreal forest, remains poorly understood (Mateo-Tomás et al., 2015). Especially, hunting can be an important source of carrion to scavengers (Moleón, Sánchez-Zapata, Selva, Donazár & Owen-Smith, 2014). Due to an increase in the number of ungulates through regulated harvest, in combination with low numbers of large carnivores in Fennoscandia caused by strict population management, the availability of carrion to scavengers from especially moose (Alces alces) has increased over the years (Dijk, Van, 2008; Gomo, Mattisson, Hagen, Fossland & Willebrand, 2017; Mateo-Tomás et al., 2015). During the first weeks of the annual moose hunt in end of September and beginning of October in Norway, hunters harvest on average about 35.000 moose nationally (Gomo et al., 2017. In comparison around 5.000 in the 1950's (Needham, Odden, Lunstadveen & Wegge, 2014), which causes nowadays a large flow of nutrient rich resources in the ecosystem. The offal mainly consisting of intestines, rumen and partially organs, is considered as waste and often left in situ at the kill site (Huff, 2016; Gomo et a., 2017). Carrion provided by hunters is, in comparison to carrion provided by many other sources, temporally and spatially highly clumped. The ungulate hunt takes place in a narrow time period, mainly during autumn and early winter in predefined areas, whereas for example wolf kills are more spatially spread and occur the whole year round (Wilmers et al., 2003). The food resources created by hunters are predictable and therefore easier to access compared to natural food resources. Hence, benefits like decreased foraging time can increase fitness of the scavengers. The amount of resources available for offspring is an important predictor for the reproductive success of scavengers (Oro, Genovart, Tavecchia, Fowler & Martínez-Abraín, 2013; Persson, 2005).

Since carrion and therefore also gut piles from harvested moose are available to many facultative scavengers, scavenger species have evolved different strategies to compete for these resources. The potential for scavenging itself also depends on the quality, amount and the temporal and spatial availability of the carrion (Moléon, Sánchez-Zapata, Sebastián-Gonzáles & Owen-Smith, 2015). To avoid competition, behavioural adaptations such as being nocturnal or diurnal have been observed in various mammalian carnivores and avian scavengers (Inger, Cox, Per, Norton & Gaston, 2016). This leads to temporal segregation possibly favouring inter-specific coexistence. Facilitation takes place when for example larger carnivores open carcasses and make them accessible to smaller species (Moleón et al., 2014). Big body size or social grouping can help outcompeting possible competitors (Kane, Healy, Guillerme, Ruxton & Jackson, 2016; Moleón et al., 2014).

In the boreal forest of south-east Norway, all Scandinavian large carnivores occur; the wolverine (*Gulo gulo*), the wolf (*Canis lupus*), the brown bear (*Ursus arctos*), and the lynx (*Lynx lynx*) (Walker, Vilà, Landa, Lindén & Ellegren, 2000). In addition there is the most abundant terrestrial species worldwide (Needham et al., 2014), the red fox (*Vulpes vulpes*).

Likewise, there are pine martens (*Martes martes*), badgers (*Meles meles*), stoats (*Mustela erminea*) and weasels (*Mustela nivalis*), and a variety of avian scavengers can be found. According to Wilmers et al. (2003) and DeVault et al. (2003), resource subsidies can lead to an increase in the scavenger activity and scavenger densities while the resource is available. Also, the available amount of remains can influence the abundance of a prey (DeVault, Zachary, Beasley & Rhodos, 2011). Cortés-Avizanda et al. (2008) have found that for example the abundance of red fox, and common ravens (*Corvus corax*) increased close to a carcass, while the abundance of their common prey decreased. Food resources provided by humans can influence feeding strategies, because they are a predictable and highly energetic source, especially when provided in autumn, a critical period to secure winter survival for many animals (Gomo et al., 2017; Persson, 2005). Because of this predictability and the availability of hunting remains, certain species can rely mainly on these remains. Since in almost all cases, carnivores are also facultative scavengers, and their distribution can be influenced by resource subsidies, the dynamics and structure of a community can be affected by scavenging on hunting remains (Huff, 2016; Wilson, Woolkovich, 2011).

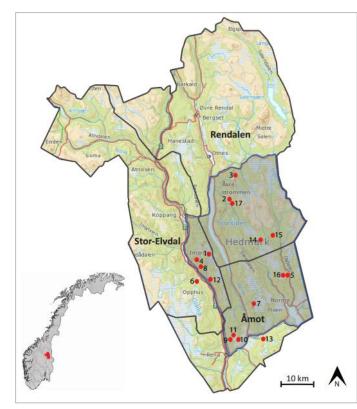
The possible consequences and long-term effects of this seasonally very abundant food source are still poorly understood. Predator occurrence has the potential to clash with human interests and also can negatively affect other animals, due to for example depredation on domestic sheep or predation on nesting birds (Dijk, Van 2008; Gomo et al., 2017; Moleón et al., 2014). Another factor directly relevant to the implementation of management and conservation measures, is the way scavengers utilize slaughter remains, as this for example has the potential to affect the spread of Chronic Wasting Disease (CWD), a contagious prion disease in cervid species (VKM, 2016).

The aim of this study was therefore to investigate the use of human provided carrion from the annual moose hunt in south-eastern Norway, and to get an overview of the total available biomass. Remote camera traps were used to monitor scavenger utilization of the remains. In this study I had three main objectives: Firstly, to determine whether the use of slaughter remains is affected by the amount and type of biomass. I predicted that scavengers are more often present at sites with a large volume of available biomass, and prefer sites with nutrient rich parts. Secondly, to determine if the visit frequency of scavengers is changing over time. I predicted avian species to be the first to arrive, and that the use of slaughter remains will decreases with the time since the moose was shot. Hence, avian and mammalian species would show a different temporal pattern during their visits, with the former being diurnal and the latter more nocturnal. Thirdly, to make an estimate of the total quantity of biomass from the shot moose, available to scavengers in the study area.

2. Materials and methods

2.1 Study area

The study area (± 1950 km²) is located in Southeast Norway, Hedmark county, and consists of sites in the municipalities Åmot, Rendalen and Stor-Elvdal (Figure 1, 61°N, 011°E). Hedmark county is dominated by boreal forests with Norway spruce (*Picea abies*), Scotch pine (*Pinus sylvestris*) and mountain birch (*Betula pendula*) as main tree species (Torgersen, 2008). The county is characterized by a continental inland climate, including long winters and short summers. Because the topography is varying, there is also a variation in the amount of precipitation and temperature. The mean annual temperature is 3.1°C with on average 670 mm of precipitation (Norsk Kilmaservicesenter, 2017). The winters are cold and dry with a snow cover from approximately mid-October until the end of April. The tree line is situated between 800 - 900 meters above sea level (Meteorologisk institutt, 2016; Nordli



& Rogstad, 2016). The main valley is formed by the longest river of Norway, the Glomma. The elevation of the sites in the study area varies from 258 to 779 meter above sea level (Kartverket, 2017). Main large carnivores in the study area are brown bear. lynx, wolf. and wolverine (Rovdata, 2017c). The most common ungulate in the study area is moose (Alces alces), with about 1.2 individuals per km², estimated in the winter of 2002-2003 (Zimmermann, Wabakken, Sand,

Figure 1. Overview of the study area, illustrated by the grey area (with blue border line). Located in the municipalities Åmot, Rendalen and Stor-Elvdal (represented by the grey border lines). The locations with the gut piles (n = 17) are represented by the red dots (nr. 1-17).

Pedersen & Liberg, 2007). Red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and reindeer (*Rangifer tarandus*) occur at low densities (Odden, Linnell & Andersen, 2006).

The study area is located on the east side of the river Glomma within the Julussa wolf territory, except for location 6 which is located on the west side and outside of the wolf zone and location 13 south of the study area but within the wolf zone. In 2016-2017 the Norwegian wolf population was estimated at 80 individuals, with 9.17 pairs and packs in Hedmark county (Svensson, Wabakken, Maartmann, Åkesson & Flagstad, 2017). The lynx population was estimated at 329 individuals national during the 2016-2017 winter, respectively 9.5 family groups in Hedmark county (Zetterberg & Tovmo, 2017). The brown bear population consisted in 2016 out of 125 individuals in Norway and 46 in Hedmark county (Aarnes et al., 2017). The wolverine population was estimated at 324 individuals in total, and 33 individuals in Hedmark county (Tovmo, Mattisson & Brøseth, 2017).

The moose hunt is organized at different spatial levels: Hunting teams led by the hunting leader operate in hunting fields ("jaktfelt"). Several hunting fields together make up hunting management areas, organized by landowner associations. On this level, landowners agree on the distribution of moose quotas in the different hunting fields. The hunting management areas cover parts of the municipalities and can stretch across municipality borders. The municipality is responsible for reporting hunting statistics to national authorities.

2.2 Hunter-killed moose

During the moose hunting season (September - December), from the 25th of September 2016 until the 14th of November 2016, I mapped the number, age, and sex of the shot moose in the study area in cooperation with municipalities, hunters and landowners. With this information, I quantified the hunting related biomass available to scavengers, and identified the utilization of the remains.

In cooperation with the three municipalities, hunting leaders were asked to report shot moose as soon as possible by providing the GPS-coordinates of the sites. Landowners were asked for permission of placing camera traps at the sites situated on their property. In total, I received the GPS-coordinates of 17 sites reported with moose slaughter remains where I was able to set up camera traps.

At the study sites I estimated the biomass which was left in situ by the hunters. This was done by weighing the slaughter remains in a tarp, attached to a hanging scale used by

wildlife veterinarians (Alfa Laval Agri 100kg, accuracy 500gr). I took the start weight of the remains at the date of placing the camera and the end weight after 21 days when I removed the cameras, except for two locations (Appendix 1) where I was not able to examine the start weight. I also reported the type of remains, which were divided into sites where organs were present (n = 10), and sites were no organs were present (n = 5). Habitat type was divided into open habitat (clear-cuts; n = 6), and closed habitat types (boreal forest; n = 11). The shot date of the moose was divided into two periods. Because most moose are shot within the first weeks of the moose hunting season (Hagen, 2014; Gomo et al., 2017), period one represents the first week of the moose hunt (n = 7), and period two (n = 8) the rest of the moose hunting season (12 weeks).

2.3 Camera use and picture registration

To collect information on the scavenging behaviour of animals, I placed 11 camera traps of the type 'Reconyx HC 600 (US)', and 6 camera traps of the type 'WingCam II TL', both supported with IR diodes, which I located at moose slaughter remains. The cameras (n = 17) were set on the correct time and date, and were programmed on time lapse (TL) with a one minute interval. In addition, I activated the movement sensor, set on high sensitivity, for the Reconyx cameras with series of 3 pictures (one per second) and a subsequent break of one minute. I did not use the movement sensor of the WingCam-cameras due to limited storage space on the SD memory cards. Movement-triggered data was later not used in the analysis due to small number of cameras and poor detection probability.

Cameras were mounted on nearby trees, and the slaughter remains were situated in the centre of the camera detection angle and range. The distance, height, and angle of the camera varied due to the different placement availabilities at the sites. The mean distance was 4.77 meter (2.89 - 7.33 meter), with a mean height of 0.99 meter (0.52 - 1.41 meter) above the ground. All the positions of the slaughter remains and cameras were recorded with GPS-coordinates. The camera locations were determined by the reporting time of the hunters. To have as less as possible missed visits at the remains, I decided to only put cameras on sites where the moose was shot the same day or latest one day after the kill. The cameras were removed after approximately 21 days, however the operation time was different per camera at the different study sites caused by the life time of the batteries. I truncated the data by discarding the last day of data if it covered less than 45% of the 24-hour period.

For analysing the pictures I used the MapView Professional software from Reconyx.

All the obtained pictures were manually checked and registered. Animals which were visually detected close to or at the slaughter remains were identified and counted. The metadata time, date, year, temperature (for Reconyx only), moon phase, trigger type (time lapse TP or motion picture MP) were together with the manually registered data transferred into the program Microsoft Excel 2013. I categorized every picture into dawn, day, dusk or night, by using the day specific times of sunrise, sunset and civil twilight (Astronomical Applications Department, 2016). For further analysis, species were pooled into two main groups: 1) Mammalian scavengers (bear, badger, fox, marten, wolverine) and 2) avian scavengers (Eurasian jay, golden eagle, hooded crow, magpie, raven, Siberian jay). To focus on sub-groups, species were additionally pooled into 3) the most abundant mammalian scavengers (fox, marten, wolverine), 4) large corvids (hooded crow, magpie, raven), 5) small corvids (Eurasian jay, Siberian jay), and 6) raptors (golden eagle).

2.4 Data analyses

Overview and hunting remain visitors

For the statistical analyses I used the program RStudio 3.2.2 (R Development Core Team, 2017) in combination with Microsoft Excel 2013 for data preparation. Data was explored using the R package 'ggplot2' (Wickham & Chang, 2016).

Collinearity between explanatory variables was evaluated with Pearson correlation coefficient with a correlation threshold of > 0.5 (Dornmann et al., 2013). Model selection was performed with the use of Akaike's Information Criterion (package 'AICmodavg', (Mazerolle, 2017)), using AICc to correct for small sample sizes (Zuur, Ieno, Walker & Saveliev, 2009). The candidate models were generated with the function 'dredge' from the package 'MuMIn' (Bartón, 2018) and based on ecological thinking. Models with an AICc value better than the null model and a difference < 2 AICc from the top model, were considered to be equally supported by the data (Burnham, & Anderson, 2004). Final models were selected for interpretation according to the AICc and AIC ω , hence the best explanative model. When it was not possible to select one model only, I applied model averaging including the models within 2 Δ AICc from the top model and better than the null model.

Normality was evaluated visually with Q-Q plot (quantile-quantile plot), and with Shapiro-Wilk test, as well as residual plots to assure that homogeneity of variance and normality assumptions were met to assess goodness of fit (Ghasemi & Zahediasl, 2012).

Frequency of scavenger visits

To analyse possible influences from the type and weight of the remains, the habitat type, and date the moose was shot on the animal presence at the remain sites, I performed negative binomial regression models to account for over-dispersion with logit link, using package 'MASS' (Riply et al., 2018). The number of pictures with the sum of animal presence (animal minutes) per location (n = 15) were used as response variable, and start weight, type of remains, habitat type, and shot date of the moose as predictor variables. An offset with the log of the total amount of pictures taken per location was added to account for different length of camera days per location.

Species richness

The possible influence of moose biomass on species richness (the total number of species visiting) was evaluated with a generalized linear model (GLM) with Poisson distribution and log link, performed with package 'lme4' (Bates et al., 2017). Species richness per location (n = 15) was used as response variable, and start weight, type of remains, habitat and shot date of the moose as predictor variables. An offset with the total amount of pictures taken per location was added. Due to a small sample size, species were pooled into groups (Gomo et al., 2017): all species grouped together, and the groups 'avian scavengers' and as representation of the mammalian scavengers 'fox, marten, wolverine' (see paragraph 2.3.1).

Time to first arrival

A negative binomial regression with log link was used to determine if time of first arrival at remains per scavenger species (n = 10) was influenced by habitat type, type of hunting remains, differences in start weight, or the shot date of the moose.

To discover possible differences between the first arrival of species per location (n = 15), and differences in first arrival with varying type of remains, habitat type, weight of the remains, and shot date of the moose, I performed generalized linear mixed models (GLMM) with negative binomial distribution ('glmmADMB', (Skaug, Fournier, Nielsen, Magnusson & Bolker, 2018). The models were run using the default link, although if that caused convergence problems, I switched to either the identity or logit link instead. Location was included as random effect in the model to account for different length of camera days per location. Due to a small sample size, species were pooled into groups. For the first analysis I only looked at the two main groups, 'mammals' and 'avian'. In further analysis I split the main groups into sub-groups: 'fmw' representing the most present mammals, and the avian subgroups 'large corvids', 'small corvids', and 'raptors'. The day of first arrival per species

group per location was used as response variable. Habitat type, type of hunting remains, start weight, and the shot date of the moose were the predictor variables.

Temporal activity pattern

For analysing possible differences in probability of being present per species group (mammals, large corvids, small corvids, raptors) over the days after the moose was shot, I used a logistic regression with the presence or absence of the species per days after the moose were shot per location as response variable. I conducted a GLMM including location as random effect to account for spatial autocorrelation and different length of camera days per location, with logit link. Predictor variables were the days after kill, and the species sub-groups tested as additive effect and as interaction.

The species diversity (H') was calculated with the library 'Vegan' (Oksanen et al., 2018), using the proportion of species visits per location per day, following the Shannon Wiener diversity index. Where Pi is the proportion of the total sample represented by species *i*. The number of individuals of species *i* was divided by the total number of samples (Spellerberg & Fedo, 2003). With a H' of 0 for a community with a single species and therefore low species diversity, and for example a H' of 5 for a very diverse community. The data did not meet the assumption for normality, even after transformation attempts, and was therefore analysed with a Kruskal-Wallis rank sum test, followed by the post hoc analyses 'Dunn's Test of Multiple Comparisons'.

$$H' = -\sum_{i=1}^{S} Pi(\ln(Pi))$$

To determine if there were differences present in the temporal activity pattern (dawn, day, dusk, and night) of the species main groups, the presence or absence of the species over the different locations and the day after kill was used as response variable with a GLMM with location number as random effect. Predictor variables were time of the day and species groups tested as additive effect and as interaction.

Biomass consumption

Possible influence on the difference between start and end weight of the remains was evaluated with a multiple linear regression (where *e* is normal) with Δ weight as response variable. Habitat type, type of remains, species richness, shot date, the proportion of the total amount of visits of all scavenger species (animal minutes) transferred to biomass minutes,

proportion of animals minutes, and the proportion of presence pictures, were used as predictor variables. Biomass minutes were calculated by taking the mass exponent (3/4) of the animal minutes per species, following the 'Brody-Kleiber law' (White & Seymour, 2003). Biomass minutes were used since minute presence of different species differ in impact. The metabolic rate of an animal is proportional to the mass^{0.75}, using mass^{0.75} gives a weight to the different species minutes depending on their size (Appendix 4). I divided biomass minutes with the number of minute pictures taken per camera, ending up as the mean scavenger biomass per minute "metabolic scavenger biomass". Scavenger biomass and proportion of presence pictures were not combined in candidate models due to multicollinearity (r = 0.80).

Total quantity of biomass

An estimation of the total amount of available biomass from hunter-killed moose during the moose hunting season of 2016 in the study area, was calculated from the reported kills by the three municipalities Åmot, Rendalen and Stor-Elvdal. These reports included shot date, location (hunting area), slaughter weights, sex- and age classes. Calculation was based on comparing average remain weight per age class between my gathered samples (n = 15), and the calculations of remain weight per age class performed by Sundli (1993). The recorded animals minutes of the sites with moose slaughter remains, were translated to theoretically possible animal minutes for the total available biomass within the whole study area, using daily average visits over the 21 monitored days.

3. Results

3.1 Overview and hunting remain visitors

In total 17 locations with moose slaughter remains from 11 males, 3 females, and 3 calves were monitored. At these sites the slaughter remains consisted of intestines and rumen, and in 12 cases, there were also some of the organs left (heart, lungs, liver, kidneys). The start weight of the remains did not differ significantly between remains with and without organs (Welch t-test, $t_{7.53} = -1.45$, p = 0.19), despite of the seemingly heavier weights of remains with organs (mean \pm SE = 57.3 kg \pm 5.09 kg, n = 10) than without organs (43.8 \pm 7.79 kg, n = 5). The small sample size did not allow to apply multiple regression models, and so I was not able to correct for sex and age of the shot moose. Correspondingly, end weight after 21 days did not differ between remain type (Welch t-test, $t_{10.92} = 0.77$, p = 0.46), with 19.3 \pm 7.42 kg and 25.0 \pm 5.34 kg for remains with and without organs, respectively.

The operation time of the cameras varied between 7.3 and 22.1 days (Appendix 1). After truncating to days with at least 10.8 hours of monitoring (45% of the 24-hour day length), I was left with a total of 292 camera days. Erroneous pictures due to sunlight or other environmental influences made up 0.03% of all pictures, and after removing those, I ended up with 392 472 valid TL pictures taken at 1-minute intervals at 17 hunting remains.

3.2 Frequency of scavenger visits

All 17 remain sites were visited by scavengers. Among the mammalian species, red fox, pine marten and wolverine were most often detected at the remains, with 64.7%, 41.2% and 29.4% of all remain sites, respectively (Table 1). Among the avian species, Eurasian jay and common raven were present at all but one site (94.1%), and the hooded crow was present at 70.6% of all sites. Multiple species such as the common raven, jays and magpies were observed foraging at the remains simultaneously.

Overall, avian scavengers (magpie, hooded crow, common raven, Siberian jay, Eurasian jay, golden eagle) were present during 241 operation days (82.5%) out of the 292 operation days. Present at most days was the Eurasian jay, at 206 days (70.5%), followed by the Siberian jay (100 days; 34.2%), magpie (99 days; 33.9%), hooded crow (83 days; 28.4%), common raven (76 days; 26.1%), and the golden eagle (12 days; 4.1%). Mammalian scavengers (badger, bear, red fox, marten, wolverine) were present on 104 days (35.6%) out

of the 292 operation days. The red fox was most present, at 55 days (18.8%), followed by the pine marten (41 days; 14.1%), wolverine (14 days; 4.8%), badger (3 days; 1.0%), and bear (2 days; 0.7%).

Table 1. Species documented at 17 moose slaughter remains in south-eastern Norway, monitored with wildlife cameras that made pictures at 1-minute intervals. Summary statistics for the maximum and mean $(\pm SE)$ number of individuals per species present at the same picture (*present at 7 out of 17 locations but 2 removed from analysis (see paragraph 2.3), ** removed from analyses because it was only present on one picture).

Species		Presenc	e at sites	Inc	lividuals j	present at	one time
Common name	Scientific name	nr. of sites	% of sites	% of TL	max.	mean	± SE
Eurasian jay	Garrulus glandarius	16	94 %	5.70 %	5	1.17	< 0.01
Magpie	Pica pica	9	53 %	2.88 %	14	1.77	0.01
Hooded crow	Corvus cornix	12	71 %	2.31 %	19	2.04	0.02
Common raven	Corvus corax	16	94 %	1.65 %	23	2.88	0.03
Siberian jay	Perisoreus infaustus	12	71 %	1.63 %	6	1.44	0.01
Golden eagle	Aquila chrysaetos	6	35 %	0.14 %	2	1.02	< 0.01
Other birds	-	15	88 %	0.14 %	3	1.10	0.01
Owl	Strigiformes sp.	2	12 %	< 0.01 %	1	1	-
Marten	Martes sp.	7	41 %	0.19 %	1	1	-
Red fox	Vulpes vulpes	11	65 %	0.17 %	2	1	< 0.01
Wolverine*	Gulo gulo	5	29 %	0.07 %	1	1	-
Badger	Meles meles	1	6 %	0.03 %	1	1	-
Brown bear	Ursus arctos	1	6 %	0.02 %	1	1	-
Lynx**	Lynx lynx	1	6 %	<0.01 %	1	1	-
Human	Homo sapiens	3	18 %	<0.01 %	1	1	-
Rodent	Rodentia sp.	8	47 %	0.04 %	1	1	-
Hunting dog	Canis domesticus	9	53 %	0.02 %	2	1.02	0.08
Moose	Alces alces	4	24 %	<0.01 %	2	1.10	0.01
Red deer	Cervus elaphus	1	6 %	<0.01 %	2	1.06	0.06
Total		17	100%	14.99%	23	1.24	0.02

TL-pictures with visitors made up 15.0 % (n = 58 836) of all valid TL-pictures (Table 1). Nine mammalian species were recorded on a total of 2044 pictures (0.5%), and seven avian species on 56 683 pictures (14.5%). The most frequently observed species was the Eurasian jay with 5.7% of all TL pictures. Among the mammalian scavengers, pine marten was most common with 0.2% of all TL pictures. The highest amount of animal minutes (1-minute presence) for avian scavengers was represented by the Eurasian jay (26 176). Among mammalian scavengers, marten (755) had the highest amount of animal minutes (Figure 2).

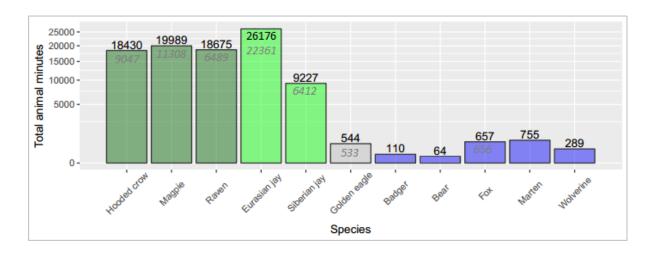


Figure 2. Animal minutes (sum of animals present per picture, black numbers), and number of presence pictures (grey numbers, when different) per species recorded with 1-minute time lapse pictures of cameras located at 17 offal sites from the moose hunt 2016 in south-eastern Norway. The y-axis is visualized on logarithmic scale. Species grouped as large corvids (dark green), small corvids (green), raptors (grey), and mammals (blue).

The model explaining the total time spent per species (animal minutes per picture per site) retained only the predictor start weight (Appendix 2, Table 2). The model estimates animal presence on average to be double as high on remains of 60 kg start weight compared to those with 40 kg start weight (Fig. 3a). This relationship was similar for the mammalian scavenger sub-group fox, marten and wolverine (Fig. 3b), avian scavengers in general (Fig. 3c) and large corvids in particular (Fig. 3d) (Appendix 2, Table 2). Remain type, habitat and the shot date did not influence the presence frequency of these species groups. For small corvids however, the shot date was the only variable retained in the best model (Appendix 2, Table 2). The mean of the minutes by small corvids was on average 2872 (\pm 0.35 SE) at remains of moose shot during the first hunting week, and 937 (\pm 0.32 SE) on remains of moose shot later (Fig. 4). The null model was within $\Delta AICc < 2$ of the best model explaining presence frequency of the mammalian scavengers and small corvids (Appendix 2), and therefore the model results should be treated with caution for these species groups. The model explaining raptor presence frequency did not converge, due to small sample size.

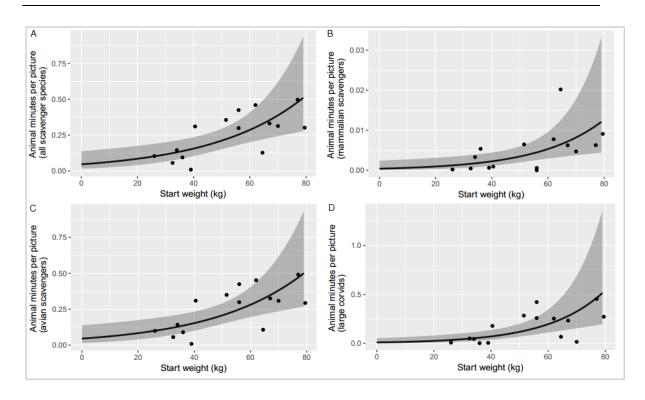


Figure 3. Proportion of animal minutes per picture in relation to different start weight of the moose hunting remains for, A: all species grouped together, B: the mammalian sub-group (fox, marten, wolverine), C: all avian species grouped together (Eurasian jay, Siberian jay, magpie, hooded crow, raven, and golden eagle), D: the sub-group large corvids (common raven, hooded crow, and magpie), located at 15 offal sites from the moose hunting season of 2016.

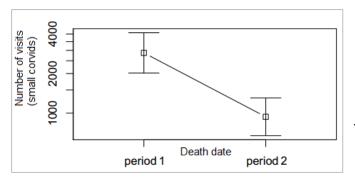


Figure 4. Number of animal minutes from the sub-group small corvids (Eurasian jay and Siberian jay), per shot date of the moose (n = 15). Period 1 representing the first week of the moose hunting season of 2016, and period 2 the rest of the hunting season (13 weeks).

Table 2. Summary statistics with parameter estimates (β) and respective confidence interval (95% *CI*) for the negative binomial regression models of the total amount of animal minutes per species group, looking at the start weight of the moose hunting remains (n = 15).

Response	Model	Parameter	Estimate	95% CI
Visit count (all species)	start weight + offset	Intercept	-3.07	-4.19 / -1.84
		Start weight	0.03	<0.01 / 0.05
Visit count (fmw)	start weight + offset	Intercept	-7.84	-9.67 / -5.75
		Start weight	0.04	<0.01 / 0.08
Visit count (avian)	start weight + offset	Intercept	-3.09	-4.25 / -1.82
		Start weight	0.03	<0.01 / 0.05
Visit count (large corvids)	start weight + offset	Intercept	-4.68	-6.73 / -2.41
		Start weight	0.05	0.01 / 0.09
Visit count (small corvids)	shot date + offset	Intercept ⁽¹⁾	-2.09	-2.71 / -1.31
		Shot date (period2)	-1.12	-2.09 / -0.17

⁽¹⁾Intercept included Shot date (period1)

3.3 Species richness

A maximum number of 7 scavenger species at one site (species richness; total amount of species visiting per location) was recorded over the 17 sites. The minimum species richness per site was 3 species, resulting in a mean of 5.6 (\pm 0.28 SE) species. Species richness for mammalian scavengers had a mean of 1.5 (\pm 0.19 SE; min = 0, max = 3), and for avian scavengers the mean was 4.2 (\pm 0.25 SE; min = 2, max = 6).

The species richness (15 sites) grouped as total of the scavenger species, and subgroups mammalian-and avian scavengers did not vary with start weight of the remains, remain type, habitat type, or shot date (Appendix 3).

3.4 Time to first arrival

Every site (n = 17), except for one location, had been visited within 24 hours after camera set up. Avian scavengers arrived for the first time on average 1.12 days (SE \pm 0.12) after the moose was shot. Mammalian scavengers visited a site for the first time on average 4.6 (SE \pm 0.91) days after the moose had been shot (Figure 5). The combined group fox, marten, and wolverine arrived for the first time after 4.7 days (SE \pm 0.94).

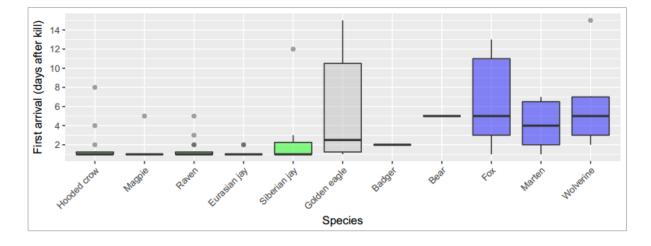


Figure 5. First arrival (days after the moose was shot) of main scavenger species, with median of 17 offal sites from the moose hunt 2016 in south-eastern Norway. Species grouped as large corvids (dark green), small corvids (green), raptors (grey), and mammals (blue).

Time to first arrival at a remain (n = 15) independent of species did not differ with habitat type, type of hunting remains, differences in start weight, or the shot date of the moose (Appendix 4). However, time of first arrival differed between mammals and avian scavenger species in general. The best model included species (avian or mammal) and habitat type, and predicted that avian scavengers arrived first (1.16 days SE \pm 1.34), followed by mammals (5.45 days SE \pm 1.80), and with shorter arrival times in open habitat (Table 3, Figure 6). Three more models were within Δ AICc < 2 from the most parsimonious model (Appendix 4), and they all contained the species and two of them the habitat type and one additional variable.

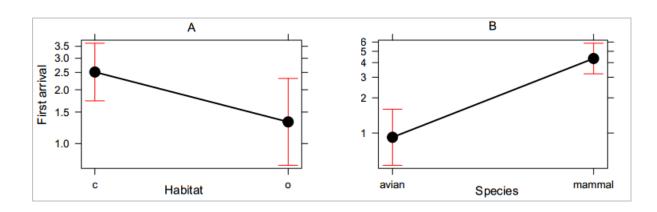


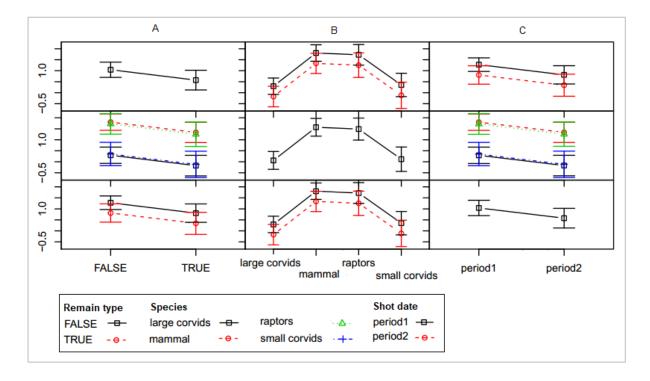
Figure 6. Effect plot for GLMM result; A: looking at habitat type (o = open and c = closed) per species group (avian and mammal), B: looking at the influence on the first arrival for the scavenger groups mammals, and avian, located at 15 remain sites from the moose hunt 2016 in south-eastern Norway. The y-axis is visualized on logarithmic scale.

Table 3. Summary statistics with parameter estimates (β) and respective confidence interval (95% *CI*) for the negative binomial regression models analysing the first arrival per species groups (mammal and avian, and mammals and avian sub-groups), looking at the shot date, habitat type, and type of remains of the moose hunting remains (n = 15).

Response	Model	Parameter	Estimate	95 % CI
First arrival (avian & mammal)	species + habitat + random effect	Intercept ⁽¹⁾	0.146	-0.43 / 0.72
`````		Habitat (o)	-0.64	-1.25 / - 0.03
		Species (mammal)	1.55	-0.97 / 2.13
First arrival (avian sub -groups & mammal)	species + remain type + shot date + random effect	Intercept ⁽²⁾	0.53	-0.13 / 1.19
		Remain type (organs)	-0.47	-0.92 / -0.02
		Species (mammal)	1.51	0.88 / 2.14
		Species (raptors)	1.43	0.63 / 2.23
		Species (small corvids)	0.06	-0.71 / 0.82
		Shot date (period2)	-0.46	-0.91 / -0.01

⁽¹⁾Intercept included Habitat (c), Species (avian), and intercept ⁽²⁾ Remain type (no organs), Species (large corvids), Shot date (period1).

I also run models where I split up the avian species into three sub-groups (large corvids, small corvids, and raptors). The model outcome from the most parsimonious model showed that large corvids and small corvids arrived as first species at a carcass, on average after 1.70 days (SE  $\pm$  1.40), followed by mammalian (7.69 SE  $\pm$  1.93) species and raptors



(7.07 SE  $\pm$  2.10). Arrival times tended to be shorter if organs were present at the remains, and when the moose was killed later in the hunting season (Table 3, Figure 7, Appendix 4).

**Figure 7.** Mean interaction plot for GLMM result, looking at the influence of remain type and habitat on the first arrival for the scavenger groups mammals (fox, marten, wolverine), small corvids, large corvids, and raptors, at 15 remain sites from the moose hunt. A: effect of remain type (FALSE = no organs present, TRUE = organs present) on the first arrival, B: first arrival of the different species groups, C: effect of shot date of the moose on the first arrival (period1 = first week of moose hunting season, period2 = rest of the period).

#### 3.5 Temporal activity pattern at carcass

#### 3.5.1 Presence over time

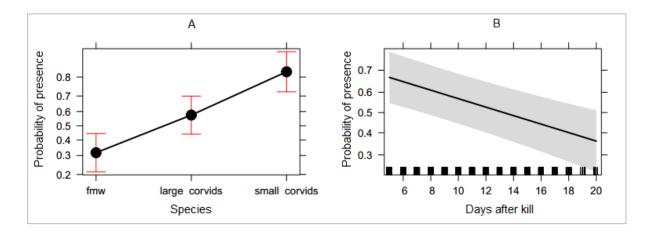
The probability of avian scavengers to visit the remains differed over the days after the moose had been shot (Appendix 5). The most parsimonious model showed a decreasing pattern in bird presence over time (Table 4, Figure 8 and 9). Contrary, mammalian species (fox, marten and wolverine), did not show such a decreasing pattern (Table 4, Figure 10). A model including raptor presence over the days after the moose had been shot did not converge, presumably due to small sample size. Hence, due to convergence problems, interactions between days after kill and species were not possible to model.

**Table 4.** Summary statistics with parameter estimates ( $\beta$ ) and respective confidence interval (95% *CI*) for the GLMM analysing the decrease in the probability of presence per day after the moose was shot per species groups (sub-group; fox, marten, wolverine, and large corvids, small corvids, and raptors).

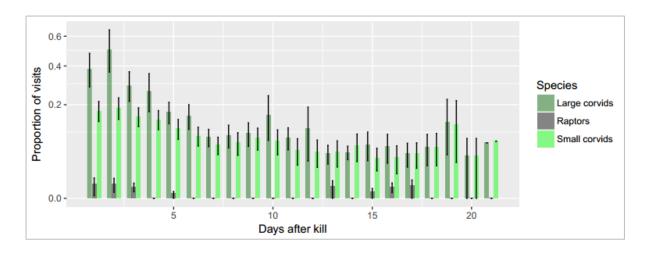
Response	Model	Parameter	Estimate	95% CI
Presence	days after kill + species + random effect	Intercept ⁽¹⁾	< 0.01	-0.62 / 0.63
		Species (large corvids)	1.07	0.69 / 1.46
		Species (small corvids	2.30	1.87 / 2.75
		Days after kill	-0.09	-0.12 / -0.05

⁽¹⁾Intercept included Species (fmw)

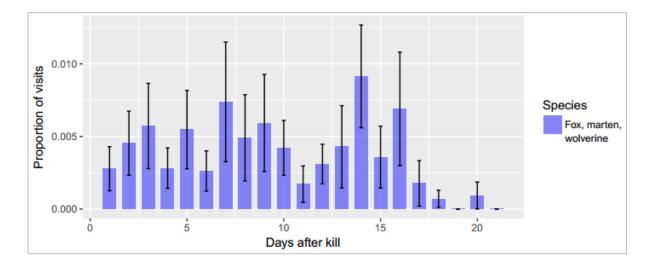
Scavenger presence was highest for small corvids, followed by large corvids and finally the mammalian scavengers fox, marten and wolverine (Figure 8A, Table 4). For avian scavengers, there was a strong decrease in presence over time (Figure 8B, Table 4).



**Figure 8.** Effect plot of GLMM looking at possible differences in visit frequency of the different species groups (fox, marten, wolverine, and large corvids and small corvids) over the days after the moose was shot, at the 17 offal sites from the moose hunting season of 2016. A: probability of being present per species group, B: probability of being present over the days after kill for the avian scavengers.



*Figure 9.* Average proportion of visits per days after kill for the avian scavenger sub-groups small corvids, large corvids, and raptors at 17 locations with moose hunting remains. The y-axis visualized on logarithmic scale.

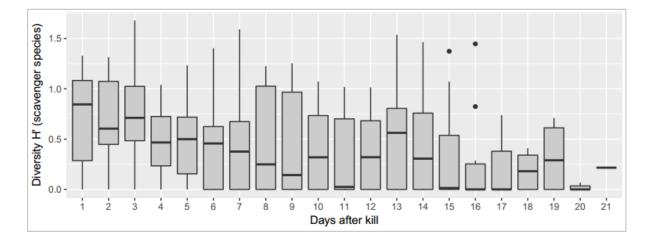


*Figure 10.* Average proportion of visits per days after kill for mammalian scavengers pooled together (fox, martens, and wolverine), at 17 locations with moose hunting remains. The y-axis visualized on logarithmic scale.

#### 3.5.2 Species composition over time

The species diversity (H'), similar to the species richness but taking abundance into account, had over the 21 days after the moose were shot, a minimum value of 0, and a highest value of 1.67. For scavenger species the mean was 0.45 ( $\pm$  0.03 SE), and for all species present at the carcasses a mean of 0.51 ( $\pm$  0.03 SE).

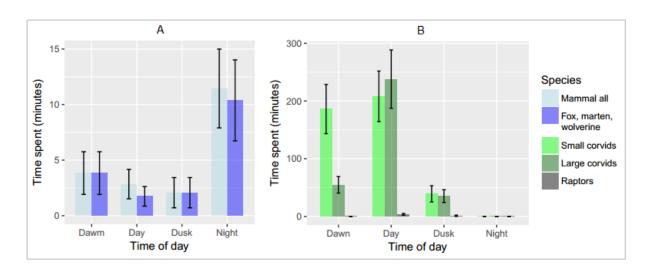
Species diversity and the days after kill had no linear relationship (Figure 11). However a significant test result was found implying differences in the spreading of the mean ranks of species diversity over the different days after kill (Appendix 6), for scavenger species (Kruskal-Wallis H= 37.66, df= 20, p= 0.009), and for all species present at the carcasses (Kruskal-Wallis H= 34.40, df= 20, p= 0.023).



*Figure 11.* Boxplot showing the Shannon Wiener Diversity index (H') for the scavenger species over the 21 days after the moose were shot, from 17 sites with moose slaughter remains from the moose hunt 2016 in south-eastern Norway.

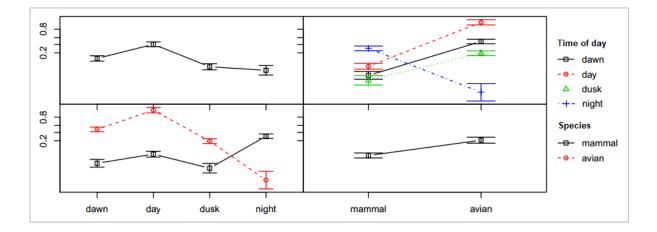
#### 3.5.3 Presence at different times of the day

The activity pattern of scavengers varied during the time of the day. The Eurasian jay had with 49.1 % the largest proportion of visits during daytime, followed by 43.1 % during dawn. Golden eagle was mostly present during the day (75.5%) and during dusk (24.5%), hooded crow during day (67.0 %), followed by dusk (18.4 %), magpie at day (80.8%) and dawn (17.2%), common raven at day (68.9 %) and dawn (18.8 %), and the Siberian jay was most frequently observed during day (44.8 %), respectively during dawn (40.8 %). Among the mammalian scavengers, the red fox was observed most during night (91.1 %), marten at night (37.1 %) and dawn (33.0 %), and the largest proportion of visits for wolverine was found at night (66.3 %) and dusk (20.0 %). Likewise, figure 12 shows a separation between mammals being more nocturnal and avian scavengers more diurnal.



*Figure 12.* Average time spent per period of the day over the 17 sites with moose slaughter remains. *A: mammalian scavengers pooled together and the sub-group; fox, martens, and wolverine; B: sub-groups of avian scavenger small corvids, large corvids, and raptors.* 

Avian species (common raven, Eurasian jay, golden eagle, hooded crow, Siberian jay) showed a significant increase in the probability of being present from dawn to day, and a decreasing pattern from dawn to night. Mammalian species (fox, marten, wolverine) probability of presence was highest during night, and increased from dawn to day and night (Figure 13, Table 5, Appendix 7). I focussed only on the main groups mammals and avian scavengers due to model convergence problems for some avian sub-groups, caused by small sample size.



*Figure 13.* Mean interaction plot for GLMM result, looking at the probability of being present over the period of the day (dawn, day, dusk, night) for the scavenger groups mammals and avian, at the 17 moose hunting remains.

**Table 5.** Summary statistics with parameter estimates ( $\beta$ ) and respective confidence interval (95% *CI*) for the GLMM looking at the presence of mammalian and avian scavengers during the time of the day, over the 17 sites with moose remains.

Response	Model	Parameter	Estimate	95% CI
Presence	time of day * species +	Intercept ⁽¹⁾	-4.03	-5.01 / -3.20
	random effect			
		Time of day (day)	1.07	0.22 / 2.03
		Time of day (dusk)	-0.58	-1.93 / 0.65
		Time of day (night)	3.17	2.44 / 4.07
		Species (avian)	3.98	3.24 / 4.87
		Time of day (day) : Species (avian)	1.18	0.12 / 2.18
		Time of day (dusk) : Species (avian)	-0.80	-2.08 / 0.64
		Time of day (night) : Species (avian)	-9.13	-12.09 / -7.38

⁽¹⁾Intercept included Time of day (dawn), Species (mammal), Time of day (dawn) : Species (avian)

# 3.6 Biomass consumption

Of the 15 remain sites where  $\Delta$  weight could be calculated, 2 (13%) were consumed < 25% after 21 days, 3 (20%) between 25-50%, 8 (53%) between 50-90%, and 2 (13.3%) more than 90%. In general, I observed mainly stomach content to be left over at the sites.

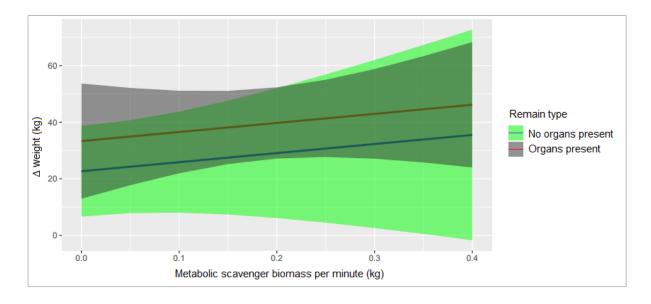
**Table 6.** Summary statistics with parameter estimates ( $\beta$ ) and respective confidence interval (95% *CI*) for the model averaged linear model analysing the decrease in available biomass, looking at the metabolic scavenger biomass per minute, shot date, species richness, and remain type at the moose hunting remains from 15 remain sites from the moose hunt of 2016.

Response	Model	Parameter	Estimate	95% CI
$\Delta$ weight	Scavenger biomass + shot	Intercept ⁽¹⁾	9.18	-43.35 / 61.72
(all species)	date + species richness +			
	remain type			
		<b>Biomass minutes</b>	75.32	-0.81 / 151.46
		Shot date (period2)	-15.76	-32.28 / 0.76
		Species richness	6.06	-0.69 / 12.81
		Remain type	18.56	0.94 / 36.17
		(organs)		

⁽¹⁾Intercept included Shot date (period1), Remain type (no organs)

The decrease in weight ( $\Delta$  weight) was according to the model averaging best explained by a model including the metabolic scavenger biomass, shot date, species richness,

and remain type (Table 6, Appendix 8). Habitat, proportion of presence pictures or proportion of animal minutes were not retained in the model. The slope term in the model says that for every 1 kg increase in metabolic scavenger biomass per minute, the  $\Delta$  weight increased with 75.32 kg (SE ± 35.08), and the  $\Delta$  weight was smaller when organs were present compared to no organs present (Figure 14). However, the results should be treated with caution because of the small sample size. Nevertheless, the  $\Delta$  weight differed between remain type (Welch t-test, t_{9.65} = -2.38, p = 0.03, and was greater for remains with organs (38 SE ± 7.39 kg) than those without organs (18.8 SE ± 6.14 kg). In addition, collinearity was found between start weight and  $\Delta$  weight (r = 0.63).

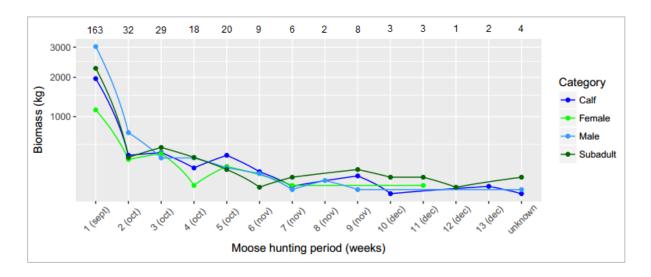


**Figure 14.** Linear regression form model averaging estimates, showing increase of  $\Delta$  weight with confidence interval per remain type (no organs present; blue line, organs present; red line) with increasing proportion of biomass minutes of the moose remains (n = 15), for all the species grouped together.

### 3.7 Total quantity of biomass

In the hunting season of 2016 there were in total 5047 moose shot in Hedmark county (Statistisk sentralbyrå; Statistics Norway, 2016). In the three municipalities (Åmot, Rendalen, Stor-Elvdal), 1108 moose were shot (Hjortevilt registered, 2017). Within my study area (Figure 15) a total of 300 moose were shot in total. Estimated average weight of the slaughter remains (rumen, longs, liver, intestines), used for biomass calculations, was 35 kg for calves, for sub-adults 65 kg (Sundli, 1993), for adult males 53 kg, and for adult females 75 kg. The 300 shot moose represented in total over 15 000 kg of biomass available

to scavengers. 163 moose (8.401 kg) were shot in the first week (period 1), and 133 moose (6.833kg) spread over the rest of the hunting season (period 2). For 4 moose (218 kg) it remained unknown at which date they were shot.

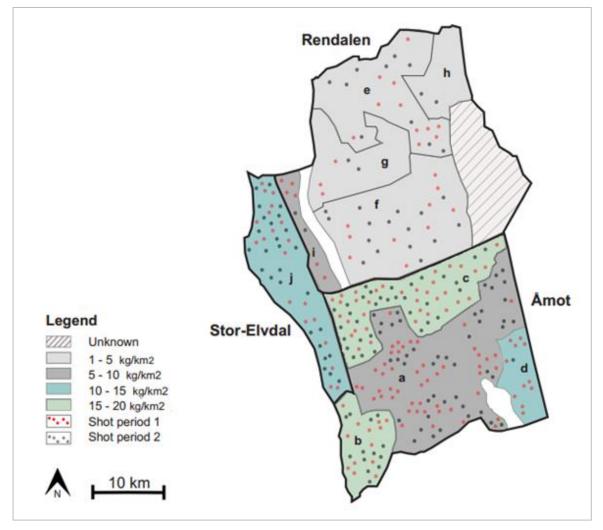


**Figure 15.** Total amount of available biomass per age category from the shot moose during the hunting season of 2016 ( $25^{th}$  September –  $31^{st}$  December) in the study area in south-eastern Norway, spread over the 13 hunting weeks. Number on top of the graph represents the total number of moose shot per week, y-axes on logarithmic scale.

**Table 7.** Total number of moose shot, and available biomass during the moose hunting season of 2016 ( $25^{th}$  September –  $31^{st}$  December) in the study area in south-eastern Norway, calculated per hunting area (surface areas obtained with ArcGIS).

Hunting area	Area km ²	nr. shot moose	Biomass (kg)	Mean of shot moose /km ²	Mean biomass /km ²
Åmot	785 km ²	192	9764	$0.24\pm0.02~SE$	$12.44\pm0.08~\text{SE}$
Deset-Osen Viltlag	42 895 ha	86	4136		
Amot Grunneierlag	9185 ha	26	1492		
Løset Utmarkslag	20 570 ha	68	3468		
Osen Grunneierlag	5850 ha	12	668		
Rendalen	805 km ²	61	3277	$0.08 \pm < 0.01 \text{ SE}$	$4.07\pm0.11~\text{SE}$
Østsida viltstellområde	23 295 ha	21	1145		
Jaktfelt Sjølie	28 645 ha	11	1364		
Andra viltlag	14 755 ha	5	205		
Grøndalen	6305 ha	2	110		
Storsjølia	7500 ha	7	453		
Stor-Elvdal	205 km ²	47	2411	$0.23~\text{SE}\pm0.00$	$11.76~\text{SE}\pm0.00$
Stor-Elvdal	20 500 ha	47	2411		
grunneierlag					
Total	1795 km ²	300	15 452 kg	$0.17/ \text{ km}^2 \pm 0.02 \text{ SE}$	8.61/ km ² ± 0.03 SE

In the 3 municipalities within the study area, there were 80 hunting fields where shot moose were reported. These hunting fields are organized in 10 hunting areas (Figure 16), for which I calculated the mean number of shot moose per km² and the mean of available biomass in kg/km². Over the whole hunting season of 2016, there were on average 0.17 ( $\pm$  0.02 SE) moose shot per km², and 8.61 kg ( $\pm$  0.03 SE) of biomass available per km² (Table 7). As 55 % of the moose were shot within the first week of the hunting season (period 1), most biomass was available in this period. The more than 15 ton of biomass would represent a minimum of 1 297 499 scavenger minutes or 901 scavenger days within the 21 days when the eatable parts of the remains seem to be totally removed.



**Figure 16.** Map showing total amount of available biomass from the shot moose (300) during the hunting season of 2016 (25th September – 31st December) in the study area (Rendalen, Stor-Elvdal, Åmot) in south-eastern Norway, on hunting area level (a: Deset-Osen Viltlag, b: Amot Grunneierlag, c: Løset Utmarkslag, d: Osen Grunneierlag, e: Østsida viltstellområde, f: Jaktfelt Sjølie, g: Andra viltlag, h: Grøndalen, i: Storsjølia, j: Stor-Elvdal grunneierlag).

# 4. Discussion

#### 4.1 Overview and hunting remain visitors

In this study I found that moose hunting remains are an important food source for a wide range of scavenger species in the Norwegian boreal forest. Especially in the first period of the moose hunting season this food source is very abundant, providing animals with an easy accessible and highly nutritious resource. On the longer term hunting remains can be important by being cached and utilized later (Persson, 2005), possibly giving an advantage for winter survival (Needham et al., 2014). Moose hunting remains are probably the most abundant food source during autumn, within and outside of wolf territories. Within wolf territories, the abundance of moose slaughter remains is about double as high as remains from wolf kills (Needham et al., 2014; Wikenros et al., 2013).

Overall, corvids were dominating the scavenger guild, which is probably partially due to higher population densities compared to mammalian scavengers (Lafferty et al. 2014, Roen & Yahner, 2005; Wikenros et al., 2013). Also, avian scavengers like ravens, and crows have a different social structure, coming often in large groups, consuming big amounts of the most nutrient rich parts, and therefore leaving less behind for later arriving mammalian species (Cortés-Avizanda et al., 2009; Moreno-Opo, Trujillano & Margalida, 2016). However, mammalian species can use other species to find a carcass (Kane & Kendall, 2017). In contrast with other bird species, Eurasian jay occurred most of the times alone or in pairs at the remains, probably avoiding interspecific competition (Kendall, 2014). Likewise, the golden eagle almost always foraged alone at the remains, being able to monopolize the carcass (Ruxton & Houston, 2004). The pine marten was the dominating species of the mammalian scavengers, followed by the red fox, a generalist with high abundance (Mateo-Tomás et al., 2015), and wolverine. Another reason for the relative low visit frequency of mammalian species and maybe not returning to a site, could be the sound of the camera traps (Lafferty et al., 2016). The sound and light flashes might be avoided by cautious species (Schipper, 2007; Wegge, Pokheral & Jnawali, 2004). I observed especially mammalian species looking right into the camera, likely perceiving the camera trap. Despite mammalian species having lower visit frequencies, they were observed to take away larger amounts of the remains, probably to cache (Vander Wall & Smith, 1987), while avian species mainly ate directly at the carcass. Because the sites with hunting remains were situated within a wolf territory, the presence of wolf kills nearby could be another reason for the low visit frequency at the moose hunting remains. Nordli & Rogstad (2016) recorded for example wolverines present at all of the monitored wolf kills within their study area during winter.

Even though the study area was situated within the wolf zone and therefore within a wolf territory, wolves were absent on my pictures. Likewise, Wikenros et al. (2013) also did not register any wolf visits at remains from hunter harvest. This may be explained by own kills being more important than relatively small carrion piles of hunting remains. Also avoidance of human presence in forested areas has been found in other wolf populations (Lafferty et al., 2014; Theuerkauf, Jędrzejewski, Schmidt & Gula 2003,). Another reason could be the age of the pups in autumn, not dispersing yet and mainly feeding on the kills of their parents. Pups from the previous year have already dispersed (Kojola et al., 2006).

#### 4.2 Utilization of the hunting remains

As predicted, my results suggest that the start weight of the remains is the most important factor for species visit frequency for large corvids, and for fox, marten and wolverine. This is in line with DeVault et al. (2004) and Moleón et al. (2015), saying that the size of a carcass is the driving factor behind the functioning and structure of the scavenger network in this context. However, small corvids visit frequency was also driven by the period the moose were shot, with a higher visit frequency in the first period of the moose hunt. This is in contrast to other studies who found an increase in visits with for example increasing snow cover (Selva, , Jędrzejewska, Jędrzejewski & Wajrak, 2005). Apart from the size of a carcass, the type of remains could also play a role in the removal of remains (DeVault et al. 2003; Gomo et al., 2017; Olsson, Beasley & Rhodes, 2016). This is not supported by my results, a preference for start weight for more nutrient rich parts was not found, and therefore in contrast with my prediction. Perhaps caused by my small sample size (n = 17), decreasing the ability to detect a smaller effect which on the other hand increases the probability of a Type II error (Ellis, 2010). However, remains with organs present showed a significantly higher decrease in biomass weight than those without organs. Although start weight and the type of remains showed neither correlation or significance, these results could suggest that the presence of organs does have an effect on the difference in start weight, especially thinking about the large proportion of not eatable rumen (up to 60%) from the slaughter remains (Sundli, 1993). The positive relation of the start weight and all species and avian species grouped together, is most likely due to the larger significant sub-groups.

Species richness per location did not differ with the start weight of the remains, type of the remains, habitat type, or shot date. This is in contrast with the findings of Moleón et al. (2015), who found strong evidence that carcass weight is a major factor also driving scavenger assemblages, therefore species richness increases with increasing carcass weight. Besides, Wilmers et al. (2003), found species richness to be higher at wolf kills compared to hunting remains. In my study however, the weight of the hunting remains may not have differed enough to find differences in scavenger assemblages.

Time of fist arrival was as predicted shorter for avian than for mammalian scavengers. The time to find the carcass was also shorter in an open habitat type (clear cut) compared to a more closed habitat (forest). Avian scavengers use mainly their eyesight to find food sources, and this is easier in an open habitat. Mammals however rely more on their olfactory sense. Additionally, avian species have the capability of searching large areas in a relatively short time (Krofel, 2011; Wilmers et al., 2003). Focusing more on the different sub-groups, corvid species were the first to arrive, followed by mammals and raptors. The arrival times were shorter when organs were present at the sites. One reason for this could be a possible difference in smell since also some avian scavengers can use sense of smell (Harriman & Berger, 1986; Krofel, 2011). Arrival times were also shorter later in the hunting season, probably due to a decrease in the amount of shot moose (Gomo et al., 2017; Hagen, 2014), making individual carcasses more valuable. The difference in arrival times between main groups and sub-groups (depending on habitat preference for main groups, and remain type and shot date for sub-groups), might be caused by the distinction between large and small corvids. The corvid group was dominated by visits of large corvids, who prefer open habitat types (Manzer & Hannon, 2005; Roen & Yahner, 2005).

### 4.3 Temporal activity pattern at hunting remains

Presence of avian scavengers was highest in the first days after a moose was shot and decreased over time. For mammalian species I found no such temporal pattern of visit frequency. The decline in presence of corvids could be caused by reduced quality of the resource (Wikenros et al., 2014) which makes them go to another carcass nearby (Gomo et al., 2017). Because mammals arrive later than avian scavengers, the most nutritious parts are already gone, which makes it un-profitable to come back several times. Also, the density of carcasses is way higher in the first week of the hunting season, providing mammals with enough resources on a relatively small spatial scale (Hagen, 2014).

Parallel to avian visit frequency, I expected species diversity to decrease over time. However, there was no such linear relationship in my data. Species diversity decreased within the first 9 hunting days, followed by an increase until day 14. This result could be caused by the different arrival times of avian and mammalian species. Avian scavengers arrive first and show a decreasing pattern in visit frequency, the first 9 days. When mammalian species found the remains, the species richness was increasing again. Also, especially in the first period of the hunting season, avian scavengers can easily move between carcasses of higher quality and leaving less attractive carcasses behind (Gomo et al., 2017).

Overall, avian scavenger species showed to be diurnal, and mammalian species were more nocturnal, which is in line with my predictions. Competition and fear for humans is probably the driving force behind this temporal separation (Olsen et al., 2016,). Also, mammals monopolize the remains at night, in advantage of absence of avian species, avoiding competition (Kane et al., 2017).

## 4.4 Total quantity of biomass available from hunting remains

Not all remains were totally consumed after 21 days. However, at 11 of the sites (where  $\Delta$ weight was calculated, n = 15), over 40% of the weight of the remains was consumed. Assuming rumen representing around 60% of the weight of hunting remains in general (Sundli, 1993), scavengers consume most of the remains within 21 days and leave mainly rumen content behind. Nevertheless, for adult male moose this part could be lower at this time of the year, since they eat less due to the rutting season (Dale, 1990). Remain type, in combination with the metabolic scavenger biomass, shot date and species richness, seemed to be the most important factors of the differences in the decrease of the remains over the sites. However as mentioned, only remain type showed a clear pattern, most likely due to the small sample size. Metabolic scavenger biomass was included in the model, idicating that not the time spent at a carcass by scavengers, but the amount they can utilize is at a higher deggree responsible for the depletion of a carcass (Inger et al., 2016). Increase in species richness has also been shown in other studies to affect the depletion of a carcass (Moleón et al., 2015; Olson et al., 2015). Interestingly, the decrease in weight was less in the second period of the hunting season. I would expect a larger decrease since most moose (> 55%) were shot in the first week of the hunting season and food therefore is less abundant in the rest of the hunting season. According to Olsen et al. (2016), time to depletion of a carcass was found to be influenced by carcass type, habitat connectivity, and season. However, carcasses which were not totally depleted by scavengers, were only found in fall and winter when temperatures were low and activity of invertebrates at carcasses decreased. Possible explanations for a smaller decrease in biomass in the second period of the hunting season therefore may be colder temperatures resulting in lower depletion by invertebrates (Turner, Abernethy, Conner, Rhodes & Beasley, 2017).

In total 300 moose were shot in my study area (1795 km²) spread over 13 weeks of moose hunt, which made 15 ton of biomass available to scavengers. Sundli (1993) estimated an average of 53 kg of moose slaughter remains per moose, which is similar to my estimated average amount of available biomass (53 kg  $\pm$  4.44 SE). However, this is less than the peak of 11 kg of moose slaughter remains per km² between September and October estimated by Hagen (2014), respectively 12 kg estimated by Wikenros et al. (2013). Therefore, my calculation might be an underestimation of the average biomass available in the study area.

#### 4.5 Study methods

An important aspect to take into account for further research is density of the hunting remains. It has been shown that for mammals the density of gut piles plays an important role in their visit frequency (Gomo et al., 2017), and would therefore be an important variable to include. Besides, cameras placed at sites close to each other could show different mean results than locations where remains were further apart, since animals may spread more when less carcasses are available. Also, environmental conditions are more similar at places close to each other (Ancrenaz, Hearn, Ross, Sollman & Wilting, 2012; Koenig & Knops, 1998). For further research it would therefore be important to account for possible spatial autocorrelation.

Snow depth and temperature are two variables which were not included in my analysis. Especially later in the second hunting period, this could have played a role looking at visit frequency and encounter speed (Olsen et al., 2016).

Changing batteries of the camera traps in between the study period, could have been beneficial to collect more equal data per location and get obtain a bigger dataset (Lafferty et a., 2015). However, this is a trade-off considering disturbance caused by handling the camera could change animal behaviour (Caravaggi et al., 2017).

#### 4.6 Conclusion and management implications

The findings of this study have shown that a wide variety of avian scavengers are utilizers of moose slaughter remains, and mammalian scavengers are less frequent than I expected. The boreal forest scavenger guild plays an important role in decomposing the remains. Diseases may be hold from spreading by the quick utilization of the remains, however also a possible thread considering the CWD outbreak (VKM, 2016). In addition, food subsidies could cause an increased fitness resulting in higher winter survival, positive to endangered species (Huff, 2016), but may lead to a higher predation pressure and influencing population dynamics (DeVault et al., 2003; Mateo-Tomás et al., 2015). Also lead poisoning from the bullet fragments staying behind in the remains, is known to be a thread to especially avian species (Legagneux et al., 2014). These aspects are all important to keep in mind considering management implications. This study is therefore an important contribution to get a better understanding about how scavenger guilds function.

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# 7. Appendix

#### Appendix 1:

Number of monitored moose slaughter remain sites, with start and end date, number of operation days, amount of biomass (in kg at start date and at end date), sex of the moose; male (m), female (f), calf (c), the number of time lapse (TL) and movement pictures (M), type of habitat; closed for forest (C), open for clear cuts (O), and remain type; organs present (True), no organs present (False).

Site	Start date	End date	Operation	Start	End	Remain	Sex	TL	М	Habitat
			days	weight	weight	type				
1	25-09-2016	17-10-2016	22.12	70 kg	30 kg	False	f	30 412	1863	0
2	26-09-2016	12-10-2016	17.11	64.5 kg	0 kg	True	m	23 200	765	С
3	26-09-2016	16-10-2016	20.53	56 kg	12 kg	True	m	28 120	1194	С
4	27-09-2016	18-10-2016	21.19	36 kg	0 kg	True	m	29 079	246	0
5	27-09-2016	14-10-2016	17.87	40.5 kg	17 kg	True	m	24 296	1704	С
6	28-09-2016	16-10-2016	18.90	26 kg	4 kg	False	m	25 781	852	С
7	29-09-2016	14-10-2016	15.27	62 kg	13.5 kg	True	m	20 554	1083	С
8	03-10-2016	20-10-2016	17.83	67 kg	34 kg	True	m	23 672	0	0
9	07-10-2016	25-10-2016	19.02	51,5 kg	33 kg	False	m	25 910	0	С
10	07-10-2016	25-10-2016	19.03	34 kg	16 kg	True	с	25 912	0	0
11	08-10-2016	26-10-2016	18.21	77 kg	56 kg	True	f	24 762	0	С
12	09-10-2016	25-10-2016	17.17	32.5 kg	27 kg	False	с	23 266	0	С
13	13-10-2016	26-10-2016	13.53	79.5 kg	17 kg	True	f	18 048	906	С
14	11-10-2016	30-10-2016	19.62	?	43 kg	True	m	26 767	0	С
15	15-10-2016	22-10-2016	7.28	?	1 kg	True	m	9 038	438	С
16	16-10-2016	24-10-2016	8.92	56 kg	27 kg	True	m	11 407	9 995	0
17	28-10-2016	14-11-2016	18.27	39 kg	31 kg	False	с	24 864	90	0
	Total		291.54	791.5	317.5			395 088	19 136	

#### Appendix 2:

Table of model selection from negative binomial generalized linear models with an offset with the total amount of pictures taken per location, used to determine possible differences between the total amount of animal minutes (all species, mammals, avian sub-groups) per habitat type, shot date of the moose, start weight of the remains, and remain type. Only models with  $\leq \Delta AIC$  5 are displayed (final model in bold).

Model	df	AICc	ΔAICc	AICω
All species ~ start weight + offset	3	290.5	0.00	0.482
All species ~ start weight + type of remains + offset	4	293.3	2.85	0.116
All species $\sim 1 + offset$	2	293.6	3.07	0.104
All species ~ start weight + habitat + offset	4	293.9	3.45	0.086
All species ~ start weight + shot date + offset	4	294.1	3.62	0.079
All species ~ type of remains + offset	3	294.9	4.41	0.053
Avian species ~ start weight + offset	3	290.4	0.00	0.500
Avian species $\sim 1 + offset$	2	293.2	2.81	0.123
Avian species ~ start weight + type of remains + offset	4	293.3	2.88	0.118
Avian species ~ start weight + habitat + offset	4	293.9	3.48	0.088
Avian species ~ start weight + shot date + offset	4	294.1	3.65	0.080
Avian species ~ type of remains + offset	3	294.6	4.22	0.061
Large corvids ~ start weight + offset	3	279.9	0.00	0.354
Large corvids ~ $1 + offset$	2	282.3	2.37	0.108
Large corvids ~ type of remains + offset	3	282.8	2.88	0.084
Large corvids ~ habitat + shot date + type of remains +	5	282.9	3.03	0.078
offset				
Large corvids ~ start weight + type of remains + offset	4	283.0	3.08	0.076
Large corvids ~ start weight + habitat + offset	4	283.1	3.17	0.073
Large corvids ~ start weight + shot date + offset	4	283.3	3.46	0.063
Large corvids ~ shot date + type of remains + offset	4	283.4	3.54	0.060
Large corvids ~ shot date + offset	3	284.2	4.33	0.041
Large corvids ~ habitat + type of remains + offset	4	284.6	4.72	0.033
Large corvids ~ habitat + offset	3	284.8	4.87	0.031
Small corvids ~ shot date + offset	3	259.0	0.00	0.419
Small corvids $\sim 1 + offset$	2	260.4	1.46	0.202
Small corvids ~ habitat + shot date + offset	4	261.7	2.74	0.107
Small corvids ~ start weight + shot date + offset	4	262.5	3.52	0.072
Small corvids ~ shot date + type of remains + offset	4	262.8	3.82	0.062
Small corvids ~ habitat + offset	3	263.3	4.33	0.048
Small corvids ~ start weight + offset	3	263.4	4.38	0.047
Small corvids ~ remain type + offset	3	263.5	4.49	0.044
FMW ~ start weight + offset	3	173.3	0.00	0.399
$FMW \sim 1 + offset$	2	175.0	1.69	0.171
FMW ~ start weight + type of remains + offset	4	175.9	2.60	0.109

FMW ~ start weight + shot date + offset	4	176.5	3.21	0.080
FMW ~ type of remains + offset	3	176.6	3.30	0.077
FMW ~ start weight + habitat + offset	4	177.0	3.73	0.062
$FMW \sim habitat + offset$	3	177.5	4.20	0.049
$FMW \sim shot \ date + offset$	3	177.9	4.59	0.040

### Appendix 3:

Model selection table from generalized linear models used to determine possible differences between the species richness (all species, mammals, avian scavengers) per habitat type, shot date of the moose, start weight of the remains, and remain type. Only models with  $<\Delta AIC 5$ are displayed (final model in bold).

Model	df	AICc	ΔAICc	ΑΙϹω
All species ~ 1 + offset	1	60.7	0.00	0.459
All species ~ remain type + offset	2	62.4	1.65	0.201
All species ~ start weight + offset	2	62.7	1.96	0.173
All species $\sim$ habitat + offset	2	63.4	2.69	0.120
All species ~ start weight + remain type + offset	3	65.2	4.51	0.048
Mammal ~ 1 + offset	1	40.2	0.00	0.559
Mammal ~ start weight + offset	2	42.8	2.65	0.148
Mammal ~ remain type + offset	2	42.9	2.68	0.147
Mammal ~ habitat + offset	2	49.9	2.68	0.146
Avian ~ 1 + offset	1	58.2	0.00	0.398
Avian ~ remain type + offset	2	59.3	1.04	0.237
Avian $\sim$ start weight + offset	2	59.6	1.41	0.196
Avian $\sim$ habitat + offset	2	60.9	2.68	0.104
Avian ~ start weight + remain type + offset	3	61.8	3.62	0.065

#### Appendix 4:

Model selection table from generalized linear models with an offset with the total amount of pictures taken per location, used to determine possible differences between the first arrival per species in general with different habitat types, shot date of the moose, start weight of the remains, and remain type. Only models with  $<\Delta AIC$  5 are displayed (final model in bold).

Model	df	AICc	ΔAICc	ΑΙϹω
Arrival time ~ 1 + offset	2	68.5	0.00	0.306
Arrival time ~ habitat + offset	3	69.4	0.96	0.189
Arrival time ~ remain type + offset	3	70.2	1.70	0.131
Arrival time ~ shot date + offset	3	70.5	2.01	0.112
Arrival time ~ habitat + shot date + offset	4	70.9	2.39	0.093
Arrival time ~ start weight + offset	3	71.5	3.06	0.066
Arrival time ~ remain type + habitat + offset	4	72.7	4.20	0.038
Arrival time ~ shot date + remain type + offset	4	73.0	4.48	0.033
Arrival time ~ start weight + habitat + offset	4	73.0	4.49	0.032

Model selection table from generalized linear mixed models with location as random effect, used to determine possible differences between the first arrival per species groups mammals and avian per location with different habitat types, shot date of the moose, start weight of the remains, and remain type. Only models with  $<\Delta AIC$  5 are displayed (final model in bold).

	-			
Model	df	AICc	ΔAICc	ΑΙϹω
Arrival time ~ species + habitat + random effect	5	109.4	0.00	0.199
Arrival time ~ species + habitat + start weight + species +	6	109.7	0.32	0.170
random effect				
Arrival time ~ species + random effect	4	110.3	0.95	0.124
Arrival time ~ species + habitat + remain type + random effect	6	110.7	1.39	0.100
Arrival time ~ species + habitat + shot date + random effect	6	111.8	2.40	0.060
Arrival time ~ species + start weight + random effect	5	112.0	2.59	0.054
Arrival time ~ species + shot date + random effect	5	112.1	2.75	0.050
Arrival time ~ species + remain type + random effect	5	112.2	2.79	0.049
Arrival time ~ species + habitat + remain type + shot date +	7	112.3	2.92	0.046
random effect				
Arrival time ~ species + habitat + shot date + start weight +	7	112.5	3.15	0.041
random effect				
Arrival time ~ species + habitat + remain type + start weight +	7	112.8	3.45	0.035
random effect				
Arrival time ~ species + shot date + remain type + random	6	113.6	4.25	0.024
effect				
Arrival time ~ species + shot date + start weight + random	6	114.2	4.82	0.018
effect				

Arrival time ~ 1 + random effect	3	143.1	33.72	0.000
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Model selection table from generalized linear mixed models with location as random effect, used to determine possible differences between the first arrival per species groups mammals and the avian subgroups (large corvids, small corvids, raptors) per location with different habitat types, shot date of the moose, start weight of the remains, and remain type. Only models with  $<\Delta AIC$  5 are displayed (final model in bold).

Model	df	AICc	ΔAICc	AICω
Arrival time ~ species + shot date + remain type + random effect	8	172.9	0.00	0.167
Arrival time ~ species + random effect	6	173.4	0.46	0.132
Arrival time ~ species + remain type + random effect	7	173.8	0.86	0.108
Arrival time ~ species + shot date + random effect	7	173.8	0.86	0.108
Arrival time ~ species + shot date + remain type + habitat + random effect	9	174.1	1.17	0.093
Arrival time ~ species + habitat + remain type + random effect	8	174.8	1.88	0.065
Arrival time ~ species + habitat + random effect	7	174.8	1.89	0.065
Arrival time ~ species + start weight + shot date + remain type + random effect	9	175.0	2.05	0.060
Arrival time ~ species + shot date + habitat + random effect	8	175.8	2.82	0.041
Arrival time ~ species + species + random effect	7	176.2	3.23	0.033
Arrival time ~ species + shot date + remain type + habitat + start weight + random effect	10	176.3	3.39	0.031
Arrival time ~ species + start weight + remain type + random effect	8	176.4	3.42	0.030
Arrival time ~ species + shot date + start weight + random effect	8	176.7	3.72	0.026
Arrival time ~ species + shot date + random effect	8	176.7	3.72	0.026
Arrival time ~ species + habitat + start weight + random effect	8	177.7	4.78	0.015
Arrival time $\sim 1 + random  effect$	3	199.0	26.04	0.000

### Appendix 5:

Model selection table from generalized linear mixed models with location as random effect, used to determine possible differences in visit probability in days since the moose was shot. Tested models are displayed (final model in bold).

Model	df	AICc	ΔAICc	ΑΙϹω
Presence ~ days after kill + species + random effect	5	918.7	0.00	1
Presence ~ species + random effect	4	943.5	24.80	0
Presence ~ days after kill + random effect	3	1042.4	123.69	0
$Presence \sim 1 + random \ effect$	2	1062.9	144.22	0

# Appendix 6:

Sca	venger specie	S	All species				
Comparison	z value	p unadj.	Comparison (days)	z value	p unadj.		
(days)							
1-6	1.992	0.046	1-6	2.323618	0.020		
1 - 10	2.104	0.035	1 - 7	2.095386	0.036		
1 - 11	2.588	0.010	1 - 11	2.656165	0.008		
1 - 12	1.996	0.046	1 - 12	2.472502	0.013		
1 - 14	2.070	0.038	1 - 15	2.096699	0.036		
1 - 15	2.638	0.008	1 - 16	3.273786	0.001		
1 - 16	3.270	0.001	1 - 17	3.200288	0.00		
1 - 17	3.345	0.001	1 - 18	3.229215	0.001		
1 - 18	2.736	0.006	1 - 20	2.834303	0.005		
1 - 20	-2.053	0.040	2 - 11	-2.29838	0.022		
2 - 10	-2.537	0.011	2 - 12	-2.11472	0.034		
2 - 11	-2.019	0.043	2 - 16	-2.92978	0.003		
2 - 14	-2.590	0.010	2 - 17	-2.87274	0.004		
2 - 15	-3.221	0.001	2 - 18	-2.94699	0.003		
2 - 16	-3.298	0.001	2 - 20	2.631909	0.008		
2 - 17	-2.695	0.007	3 – 11	-2.06687	0.039		
2 - 18	2.531	0.011	3 - 16	-2.70719	0.007		
2 - 20	2.502	0.012	3 - 17	-2.6608	0.008		
3 – 11	-2.367	0.018	3 - 18	-2.76437	0.006		
3 – 15	-2.430	0.015	3 - 20	-2.50095	0.012		
3 – 16	-3.057	0.002					
3 – 17	-3.143	0.002					
3 – 18	-2.561	0.010					
3 - 20	-2.405	0.016					
4 – 16	-2.112	0.035					
4 - 17	-2.243	0.025					
5 – 16	-1.998	0.046					
5-17	-2.134	0.033					

Results from post-hoc test 'Dunn's Test of Multiple Comparisons', comparing the species diversity (H') over the days after the moose were shot. Only significant results are displayed.

### Appendix 7:

Model selection table from generalized linear mixed-effects models with location as random effect, used to determine possible differences in visit probability per species group per time of the day. Tested models are displayed (final model in bold).

Model	df	AICc	<b>AAICc</b>	ΑΙCω
Presence ~ species * time of day + random effect	9	1415.3	0.00	1
Presence ~ species + time of day + random effect	6	1991.1	575.75	0
$Presence \sim 1 + random \ effect$	2	2489.1	1073.81	0

#### Appendix 8:

References for calculation of the mass exponent (3/4) following the 'Brody-Kleiber law' per species using their average weight.

Species	Average weight (kg)	Reference
Badger – Meles meles	11.00	Store Norske Leksikon (2017a)
Brown bear – Ursus arctos	150.00	Rovdata (2017a)
Common raven – Corvus corax	1.15	Store Norske Leksikon (2017g)
Eurasian jay – Garrulus glandarius	0.17	Store Norske Leksikon (2017f)
Golden eagle – Aquila chrysaetos	4.50	Rovdata (2017b)
Hooded crow - Corvus cornix	0.50	Store Norske Leksikon (2017c)
Red fox – Vulpes vulpes	5.50	Store Norske Leksikon (2017h)
Marten – Martes sp.	1.45	Store Norske Leksikon (2017e)
Magpie – Pica pica	0.25	Store Norske Leksikon (2017i)
Siberian jay – Perisoreus infaustus	0.10	Store Norske Leksikon (2017d)
Wolverine – Gulo gulo	16.50	Store Norske Leksikon (2017b)

Model selection table from linear regression to determine possible influences from habitat type, shot date, remain type, proportion of present pictures, proportion of animal minutes, and scavenger biomass on the decrease of the remains ( $\Delta$  weight). Models from model averaging with AICc values within 2  $\Delta$ AICc of the top model and better than the null model are displayed.

Model	df	AICc	ΔAICc	AICω
Delta weight ~ scavenger biomass + shot date	4	130.7	0.00	0.102
Delta weight ~ species richness + remain type	4	130.8	0.06	0.099
Delta weight ~ remain type	3	131.2	0.54	0.078
Delta weight ~ remain type + shot date	4	131.4	0.67	0.073
Delta weight ~ biomass minutes + species richness	4	132.5	1.78	0.042
Delta weight ~ biomass minutes	3	132.5	1.80	0.042
Delta weight ~ shot date	3	132.8	2.09	0.036
Delta weight ~ species richness	3	132.8	2.09	0.036
Delta weight ~ 1	2	132.9	2.22	0.034