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Master thesis

Scavenger community on wolf-killed ungulates in the boreal forest in south-east Norway

Master in Applied Ecology

6EV399

2022

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Abstract

Scavenging is one of multiple foraging strategies to utilize food resources and an important ecological process in the circle of life. It is common in periods of environmental stress such as lack of prey species, and as an alternative food resource. In a wolf (*Canis lupus*) territory there will always be available carcasses depending on the wolves kill rate.

In this study, I investigated the use of wolf-killed ungulates in south-eastern of Norway. Remote camera traps were used on 33 carcasses to monitor carcass utilization by scavengers. I investigated the activity patterns of six avian and four mammal species in the scavenger community.

All kill sites were visited by scavengers. The main visitors in terms of number time-lapse pictures were the corvid species (*Corvidae*), golden eagle (*Aquila chrysaetos*), red fox (*Vulpes vulpes*), and wolverine (*Gulo gulo*). Further analyses of the activity based on time-lapse pictures were done to show the activity pattern for each species through the day, and for the first 21 carcass days after camera placement. The results show a high degree of overlap in the activity pattern for all pairs of avian species, high/moderate for mammals, and moderate/low for the combination between mammal and avian species. Furthermore, the probability of presence for the mammal species at the carcass is highest at night, between 20:00 – 06:00, and for avian species from 04:30 – 20:30 in the daytime. Furthermore, the probability of presence was highest the first day after camera placement for most of the species except crow (*Corvus cornix*), raven (*Corvus corax*) and golden eagle, which also had probability of presence outside of this time window. I found that avian species would linger longer at each carcass compared to mammals.

Sammendrag

Åtselspising er en av flere fôringsstrategier for å utnytte matressurser, og en viktig økologisk prosess i nedbrytingen. Bruk av åter er vanlig i perioder med miljøstress, for eksempel ved mangel på byttedyrarter, og som en alternativ matressurs. I et ulverevir vil det alltid være tilgjengelige kadaver avhengig av ulvenes drapstakt.

I denne studien har jeg undersøkt bruken av ulvedrepte klauvdyr i Sørøst-Norge. Viltkameraer ble satt opp på 33 kadaver for å overvåke aktiviteten til åtselartene. Totalt undersøkte jeg aktivitetsmønsteret til 6 fugler og 4 pattedyr i åtseldyrsamfunnet.

Samtlige kadaver hadde besøk av åtseldyr. De mest tallrike besøkende ut ifra time-lapse bilder var kråkefamilien (*Corvidae*), kongeørn (*Aquila chrysaetos*), rødrev (*Vulpes vulpes*) og jerv (*Gulo gulo*). Analyser av aktiviteten basert på time-lapse bilder ble gjort for å vise aktivitetsmønsteret til hver art. Jeg skilte mellom aktivitet gjennom døgnet, og for de første 21 dagene etter kameraovervåking startet. Resultatene viser en høy grad av overlapp i aktivitetsmønsteret for alle kombinasjoner av fugler, høy til moderat for pattedyr, og moderat til lavt for kombinasjoner mellom pattedyr og fugler. Videre var sannsynligheten for pattedyrarter på kadaveret høyest mellom 20:00 – 06:00 om natten, og for fugler fra 04:30 – 20:30 på dagtid. Flertallet av arter hadde størst sannsynlighet for forekomst første dagen etter kamera ble satt opp med unntak av fuglesamfunnet som også hadde sannsynlighet utenom dette.

1. Introduction

The primary production is fundamental for all further biological processes in the sea and on land. This production is depending on a large amount of sunlight. At high latitudes, the highest production happens spring and summer. This is when the sun is highest in the sky. From the autumn and throughout the wintertime, the production is reduced to a minimum (Føyn et al., 2002). On the mainland, primary production is largest in the boreal forest, compared to low production mountain areas at higher elevation (M. Gough, 2011). Every process speeds up under the right conditions and reversed when conditions are not optimal (Gates, 1965). Plants and animals use the seasons to their benefit, to get enough energy when it is available (DeVault et al., 2003; Loureiro et al., 2009). Resource availability often vary throughout the year, and thus promote other various behavioral shifts (Loureiro et al., 2009; Nelson et al., 2012). At higher trophic levels, as such for carnivores, adapting to temporal and spatial changes in resource availability at lower trophic levels are crucial. The extent of predation and its rate may therefore vary versus utilizing scavenging as a strategy to optimally forage according to seasonal energetic needs (Linnell et al., 1995; Pereira et al., 2014; Schmidt, 2008).

Scavenging is a common foraging strategy among almost all predators at some level (Wikenros et al., 2013). The use of carcasses can be because of poor food supply, stressful environmental situations, or other factors such as damage. There are two types of scavenger strategies. One, living exclusively from dead animals that are killed by other predators or died of other natural causes (obligate scavenger). Second strategy is to utilize carcasses throughout different time of the seasons/year (facultative scavenger) (DeVault et al., 2003). Most vultures are obligate scavengers (Parks, 2020). The golden eagle is a good example of a more obligate scavenger (Blázquez et al., 2009; Nordli & Rogstad, 2016). Seasonal scavenging by birds and mammals in the European temperate zone is common under winter conditions (Selva et al., 2003). Different species have different strategies, and the same strategies may also be adapted by different individuals within the same species (Hertel et al., 2020). There is a risk in seeking out available food from other predators. Scavengers may be exposed to increased inter- and intra-predation risk on or around the carcasses, or may create interference competition (Selva et al., 2005; Selva & Fortuna, 2007).

When an animal dies, life lives on as organisms from all trophic levels will to some extent utilize the remains and circle energy back into the food chain. The most important factor that determines speed of this process is ambient temperature. The carcass will disappear at different

rate depending on the season, habitat type, predators, and micro-climatic conditions. (Beekers & Rewilding Europe, 2017; Jarmusz & Bajerlein, 2019; Wikenros et al., 2013). Winters with low temperatures will work as a freezer on carcasses. Due to freezing temperatures it will take longer time for the carcasses to decompose as opposed to the warmer climate (Feddern et al., 2019; Jarmusz & Bajerlein, 2019; WJHG, 2018). During the colder periods of the year, it is mostly the avian and mammal scavengers who are going for the available carcasses. Furthermore, is scavenging more common in biomes characterized by cold climate, in Norway's boreal forests, than in warmer habitat, since higher temperatures reduce the quality of a carcass (Beekers & Rewilding Europe, 2017; Mattisson et al., 2016; Nordli & Rogstad, 2016). Insects of different types are especially present under warmer conditions. The decomposers and detritivores are the last stage, that complete the process by consuming the remains left by the scavengers. Dependent on the temperature, the carcasses can return back to the nature thanks to the decomposition process (Beekers & Rewilding Europe, 2017; Jarmusz & Bajerlein, 2019).

Species have varying influences on other species and the environment relative to their density and abundance, often expressed as amensalism, facilitation, mutualism, competition or predation (Encyclopedia of Ecology, 2008). Keystone species for instance have an important ecological role relative to their numerical number in the ecosystem and can cause varying influences on a wide range of species. Apex predators, such as the wolf is often determined as a key stone species as they have the ability to cause trophic changes (Ripple & Beschta, 2012), and make food-surplus available to other species trough predation (Biodiversity, 2022). Especially in the winter, the availability of carcasses is important for many species, such as the wolverine which also has offspring during this time (Van Dijk et al., 2008; van Dijk et al., 2008).

After a period of absence, the wolfs returned to the southern part of Scandinavia through natural immigration from the Finnish-Russian population at the end of the 1970s (Wabakken et al., 2001). Population of wolves in Scandinavia by the winters of 2014-2015, was estimated to be about 460 individuals (Svensson et al., 2015). In this area is moose the main prey for the wolves, especially moose of the youngest cohort, i.e., calves and juveniles. Throughout the season the biomass (kg) of the moose calves will increase (Cederlund et al., 1991; Sand et al., 2008) in the winter period, the wolf-kill rate is lower than in the summer due to larger biomass in each calf. A higher kill rate is needed in the summertime when the calves have less biomass. At this time of the year, there will be more carcasses in wolf territory. Moose resources are

therefore widespread for the scavengers in a wolf territory but highly seasonal dependent (Nordli & Rogstad, 2016; Sand et al., 2008; Zimmermann et al., 2015).

In Norway, most of the terrestrial animals live in the boreal forest, both mammals and birds. All the big carnivores are also represented in a smaller part of this forest system. The raven is one of the common species in this area. It mainly consumes carcasses all the year, with occasional plants, insects, and eggs (Hogstad & Husby, 2021b). In the animal community, the raven is often the symbol of dead animals and food. The excellent vision is the perfect tool to follow dying animals or find carcasses, for example follow wolf packs from above. Other birds, such as the golden eagle, may often use the raven as a signal of safety before flying into the carcass and start consuming (Larsen, 2015; Stahler et al., 2002). Both the mammal and the avian community are present at carcasses, but the overlap between species is varying (Kronenberg, 2018; Nordli & Rogstad, 2016).

What happens to a wolf-killed ungulate after the wolves abandon the carcass? Many species are dependent on dead animals killed by others or natural death. In this study, I will look at the different activity patterns of the animal community on wolf-killed ungulates, in a wolf territory in the boreal forest of south-eastern Norway. Based on the animal community, I expect this:

I believed that scavengers will segregate their temporal niche to different times of the day to forage at carcasses, and thus could be categorized into a day-time community and a night-time community. Because most mammals are primarily nocturnal and supposedly avian species diurnal (Handler et al., 2021; Wikenros et al., 2022), I predict that **1**) mammals will primarily be present at carcasses during night-time and avian species would primarily be present at carcasses during daytime. Furthermore, I predict **2**) that biologically similar species in size and morphology will have a higher overlap of circadian activity than species that are more different. Therefore, I also predict **3**) that overlap of activity will be higher among the daytime community than the night-time community. Moreover, I predict **4**) that over the course of carcass decomposition as biomass decrease mammal species will be more at carcasses in the beginning and decrease their utilization of carcasses faster than avian species, and that avian species would linger longer at each carcass compared to mammals.

2. Methods

2.1 Study area

This study was conducted in the wolf territory Julussa located in Innlandet county, in southeastern Norway (Figure 1). During the years 2014 and 2015, the wolf territory covered 904 km² (100% MCP) (QGIS, 2020) (Nordli & Rogstad, 2016). The area is characterized by two valleys Østerdalen and Rendalen. The elevation ranges from 215 to about 1000 meters above sea level with the tree line on around 800-900 meters. The boreal forest dominates the area with mainly the species pine (*Pinus sylvestris*) and spruce (*Picea abies*), with elements of deciduous trees such as birch (*Betula spp.*), rowan (*Sorbus aucuparia*), willow (*Salix caprea*) and aspen (*Populus tremula*) (Thorsnæs et al., 2022). The area has a dry and cold continental climate, usually with cold, snowy winters. The territory is covered with snow from around October to the end of April (Yr, 2022). Human settlement is spread throughout the area, mostly along the valley bottoms (Norgeskart, n.d.).

Wolf-killed carcasses monitored with camera traps

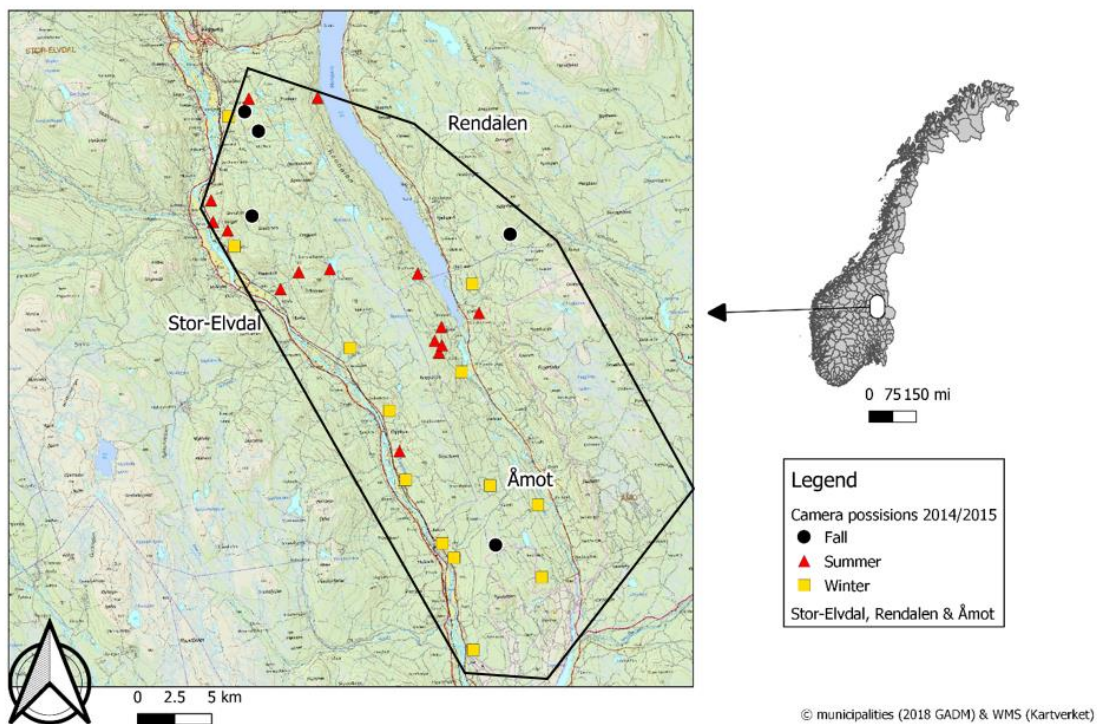


Figure 1. Distribution of monitored carcasses ($n = 33$) in the Julussa wolf territory (2014-2015) located in the municipalities Stor-Elvdal, Rendalen and Åmot. The different symbols represent the time of the year when the ungulates were killed. Black solid line indicates home range size (100% MCP) for the wolf territory.

In the study area, the moose is the main prey animal for the wolves throughout the year, with a relatively high density (1.2 per km² during the winter 2002-03) (Nordli & Rogstad, 2016; Zimmermann et al., 2007). In the wintertime, a majority of the moose population migrates from higher areas (600 – 850 m.a.s.l.) down to the areas around the valley bottoms (250 – 400 m.a.s.l.) (Eriksen et al., 2011). The timing of the migration depends on snow depth and temperature, but it usually begins around November/December and again April/May back to the summer area when the snow is melting (Eriksen et al., 2011). Other potential prey animals in the area are red deer and roe deer, both with low densities (0.01 per km²) (Gundersen, 2003; Zimmermann et al., 2007). All the large carnivores brown bear (*Ursus arctos*), lynx (*Lynx lynx*), wolverine and golden eagle are also present in the area (“Forvaltningsområder for Rovdyr,” 2015; Nordli & Rogstad, 2016).

2.2 Data collection

The data were collected in the winter and fall of 2014 and the winter and summer of 2015. Camera traps (n = 33) were set up after confirmed wolf-killed ungulates (Matten, 2016; Nordli & Rogstad, 2016) (*Tabel 1*). To sample data from wolf-killed ungulates, the Scandinavian wolf research project (SKANDULV) GPS-marked following wolves in February/March 2014: The scent-marking female (M1409) and the scent-marking male (M1410), with three of their nine-month-old pups (male M1406, male M1408, and female M1407). All the marked wolves were equipped with GPS neck collars with GSM download link (GPS plus, Vectronics Aerospace, Germany). The collars were programmed to give six GPS positions every 24 hours (UTC+1 00:00 - 04:00 - 08:00 - 12:00 - 16:00 - 20:00) (Nordli & Rogstad, 2016). The following winter, the project re-collared the alpha pair. Furthermore, they did only use GPS-data from the marked wolves within the wolf territory, mostly from the alpha couple and some from the pups prior to natal dispersal (Nordli & Rogstad, 2016; Svensson et al., 2015). The wolf positions made it possible to locate wolf-killed ungulates and mount remote-camera traps on the carcasses a short time after death. Time between death date and camera placed at the carcasses, was skewed by 2.5 (0 – 6 min-max) days on average.

During four intensive study periods, the project did follow at least two wolves regularly, when they were sending positions (Nordli & Rogstad, 2016). All received GPS coordinates were plotted into ArcGIS (ArcGIS 2014) continuously and buffered with 100 meters. “clusters”

were defined as positions within radius of 200 meters of each other (Zimmermann et al., 2007). Positions over 200 meters from each other were termed as “single positions”. The field crew checked the prioritized clusters and single positions based on the wolf’s movement pattern, time use, and daylight making sure not to disturb the wolves at carcasses. Positions closer than 1 km were not visited in the summer period. Wolf positions closer than 1 km to clusters or single points were delayed one to several days (Nordli & Rogstad, 2016).

At every carcass, the body weight and biomass were registered based on categorized age classes: Newborn calf (0-1-month-old), calf (>2 months old), yearling (12-23 months old), and adult (>2 years old). Size, tooth wear, or tooth development defined the different classes in the field. Further categorization was made upon genitalia, antlers or rosary to define sex. Pictures of the carcasses were used to determine the consumption stage. Available biomass at carcass was defined by: 1) Assumption of linear growth for newborn calves of $y = 1.123x + 13$, where y is the estimated weight (kg) at day x , assuming a birth weight of 13 kg the 1 June (Sand et al., 2008). 2) For the other categories, an average constant weight was used depending on the time of the year for both sexes (Zimmermann et al., 2015). Time of death was defined by; 1) the first wolf’s position inside a buffer of 100 meters from the carcass and 2) earliest to the latest probable date by looking at blood coagulation, consumption, and decomposition. If estimated date in the field matched the wolf’s position inside the buffer (100 m), it became the time of death (Matten, 2016; Nordli & Rogstad, 2016).

2.2.1 Cameraspesification and programming

The cameras used, were of the type Reconyx Hyperfire HC 600. It takes 3.1 MP color images at daylight and monochrome at night. The cameras were used with 12 AA Lithium batteries and equipped with a 32 GB SDHC memory card for maximum storage to take around 30 000 – 40 000 pictures with this battery capacity. Pictures were saved as .JPEG files on the memory card. Cameras were set up with the correct date and time, and programmed with an advanced setup as follows: 1) Single pictures with a permanent time interval (time-lapse) of 5 minutes, 2) motion trigger with high sensitivity, with a series of three pictures with one-second intervals between a quiet period of one minute between each break, and 3) maximum picture quality. The cameras were mounted on nearby trees, with the carcass in the middle point of the frame. This process was done with a standardized procedure of 40 degree of field view and 30-meter

detection range (Reconyx, 2010). All cameras were tested before data collection, and at different detection distances at the carcasses. The cameras were placed 12 meters or less from carcass, to successfully determine pictures by night and day, with a mean distance of 5.1 meters in length from carcass (1-12 m) and a mean height of 1.2 meters (0.6 – 2.6 m) from ground (Matten, 2016).

During the first study period (1 Winter) there were more carcasses detected than there were available cameras (Table 1). Hence, cameras were placed randomly regardless of factors such as biomass and positions. During the last study period (4 Summer) single positions were also checked in the field in the addition to clusters (overlapping positions) with a dog on a leash, to detect smaller prey/or carcass remains (Nordli & Rogstad, 2016; Sand et al., 2008) (Table 1).

2.2.2 Reviewing camera data

Reconyx Mapview Professional was used to review all the camera pictures (n = 377 220) (Table 1) (Reconyx, 2014). Each picture was manually registered with the number of animals per species for mammals and birds. The following factors were also registered; illumination, snow, mists, carcass displaced, camera displaced, and disturbance of people or dogs in the picture. This metadata was also automatically registered with the manual registrations; time, date, year, temperature, moon phase, trigger type time-lapse (TP), and motion (MP) (Nordli & Rogstad, 2016). After the review of all the pictures, the download function transferred all the registrations to a Microsoft Excel file (Microsoft Office, 2021; Reconyx, 2014). For overview of the data in a map, I used QGIS 3.10.14 to plot all the positions distributed by season in the study area (QGIS, 2020).

Table 1. Number of monitored carcasses for each study period, with start/end date, number of camera days, and the number of time-lapse/ motion pictures.

Season	Year	Months (start - end)	Carcasses	Camera days	Time-lapse	Motion trigger
1 Winter	2014	27. March - 7. May	5	149	40 423	2 052
2 Fall	2014	28. August - 5. November	5	287	85 698	919
3 Winter	2015	20. March - 21. May	8	371	105 601	17 877
4 Summer	2015	1. June - 12. July	15	403	10 921	13 728
Total			33	1210	342 643	34 577

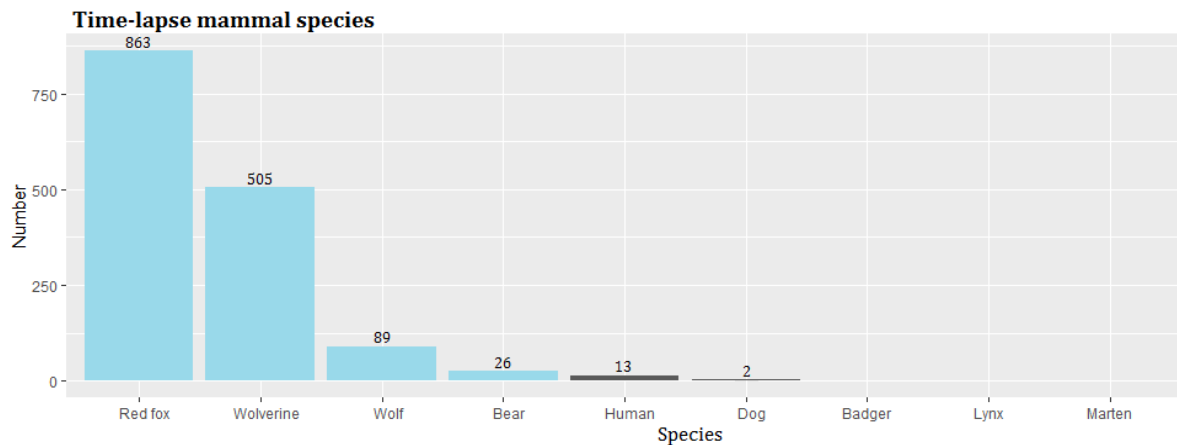
All statistical analyses were done in RStudio 4.1.2 (*RStudio Team*, 2020) in combination with Microsoft Excel 2021 (*Microsoft Office*, 2021) for data preparation. I explored the data with the “ggplot2” (Wickham et al., 2016) function in the R-package. All the cameras were operating during 14 – 67 days after placement. I used only time-lapse pictures from the first 21 days in further analysis, to extract a standardized sample of each carcasses over temporal gradient of time of day, as well as number of carcass days monitored. Furthermore, I picked the species with >25 pictures at the carcasses to this data. Of this species, I used only those who consumed the carcasses, and were registered at more than one camera for comparative purposes across carcasses. For data management I used the R-packages “Tidyverse” (Wickham, 2009) and “Lubridate” (Spinu et al., 2011). For my data analysis on the probability of presence at carcass, I used the R-packages “mgcv” (Wood, 2011), while for estimating the activity pattern as well as the pairwise overlap between species compositions on the time of day, I used the package “Overlap” (Meredith & Ridout, 2009). The overlap coefficient (Δ_2) were estimated by area under the curve that overlaps between the two species, and goes from 0 to 1, where 1 means that the curves completely overlap. Furthermore, I used “ggeffects” (Lüdtke, 2022) to extract predictions and “ggplot2” to visualization. To generate the averages and 95% confidence intervals, I used the R-package “boot” (Canty, 1997) to bootstrap 1,000 replications for each species combination. I sorted different overlap categories into 3 different classes: Low (0 – 0.33), moderate (0.33 – 0.66), High (0.66 – 1).

To investigate the probability of presence over the time of day and over carcass days, I used a Generalized Additive Mixed Model, with Y Species present with a logit link function alongside with the predictor variables X^i Time of day, and X^{ii} for carcass days, with a smooth-term S fitted to each predictor. I performed an initial test on the random structure using Carcass_ID by employing an AIC selection on the most fitting random structure. I retained the random structure including a random intercept for Carcass_ID for the best model fit across all species. After determining my final model structure, I checked for autocorrelation, although only sparse autocorrelation could be detected for a few species. Since the autocorrelation was considered small $<.2$ rho at the second time-lag, I decided to fit my all models without autocorrelation structures in order to retain all species compositions comparable across time of day, and carcass days. To perform model validations, I conducted diagnostic plots in the R-packages “itsadug” (Rij et al., n.d.) (Rij et al., n.d.) and “mgcv” (Wood, 2011).

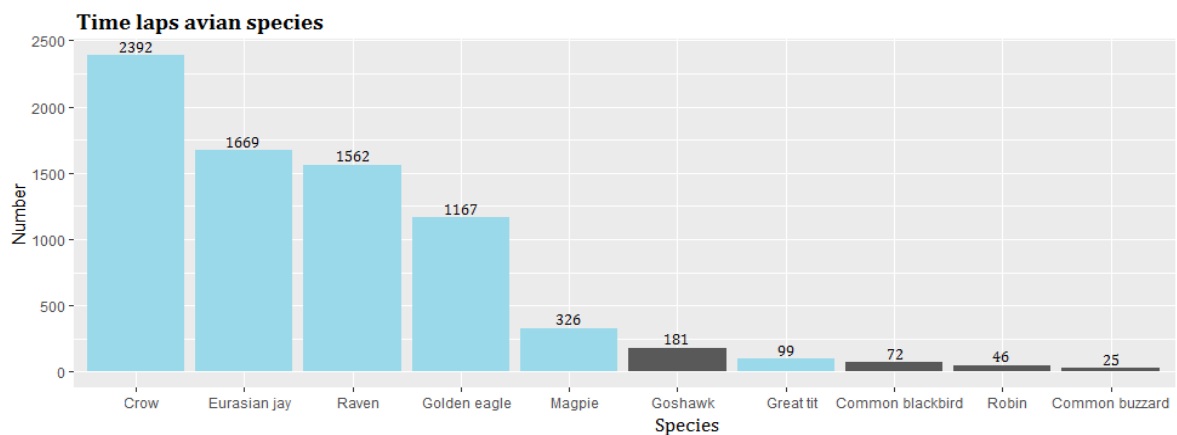
3. Results

A total of 33 cameras were placed out at wolf-killed ungulates, 32 moose and 1 red deer. 45 % were newborn calves ($n = 15$), 45 % calves ($n = 15$), 3% adult ($n = 1$) and 3% adult red deer ($n = 1$). The estimated average edible biomass at the carcasses varied significantly between seasons, with 15.6 kg in the fall, 1.6 kg in summer, and 36.9 kg in winter (*Figure 6A*, $F(2,30) = 6.5$, $p = 0.004$). Furthermore, the average elevation (m a. s. l.) also differed between seasons, with 610 m in the fall, 449 m in summer, and 325 m in winter (*Figure 6B*, $F(2,30) = 14.3$, $p < 0.001$). All 33 carcass sites were visited by different scavengers. I selected four mammals and six avian species out of a total of 31 for further comparisons. There were more time-lapse pictures of avian than for mammalian scavengers (*Figure 2A-B*).

A)



B)



*Figure 2. Distribution of species at wolf-killed carcasses estimated by 5-minute time-lapse pictures for A) all mammals; red fox, wolverine, wolf, brown bear, human (*Homo sapiens*), dog (*Canis lupus familiaris*), badger (*Meles meles*), lynx and marten (*Martes martes*). B) top 10 of 25 avian species; crow, eurasian jay (*Garrulus glandarius*), raven, golden eagle, magpie (*Pica pica*), goshawk (*Accipiter gentilis*), great tit (*Parus major*), common blackbird*

(*Turdus merula*), robin (*Erithacus rubecula*), common buzzard (*Buteo buteo*). The rest of the avian had <25 time-lapse pictures. The blue bars indicate the selected species.

The circadian overlap between species varied from moderate to high for the six avian species and the four mammals (Table 2-3). In the mammal community, the highest overlap in circadian activity curves ($\lambda = 0.81$) was for wolverines and wolves (Table 2). In contrast, bears and wolves had smaller circadian overlap ($\lambda = 0.57$) (Table 2, figure 3A). The raven and the hooded crow had the highest overlap in activity curves ($\lambda = 0.96$) in the avian community (Table 3, figure 3B). The smallest circadian overlap in the avian community was for great tit and magpie ($\lambda = 0.76$) (Table 3). Furthermore, overlap between pairs of species from the avian and mammalian community was highest for Eurasian jay and bear ($\lambda = 0.40$), and lowest for magpie and wolf ($\lambda = 0.21$) (Table 4, figure 3C).

Table 2. Circadian activity pattern with overlap coefficient, 95% confidence interval (CI) and the degree of overlap for all paired combinations of the **mammal species**; wolverine, wolf, brown bear and red fox at wolf-killed carcasses.

Species combination	Overlap coefficient $\Delta 2$	95% CI	Degree of overlap
Wolf - Wolverine	0.81	0.80 - 0.86	High
Red fox - Wolverine	0.78	0.77 - 0.81	High
Red fox - Bear	0.70	0.66 - 0.78	High
Bear - Wolverine	0.67	0.62 - 0.78	High
Red fox - Wolf	0.66	0.64 - 0.72	Moderate
Bear - Wolf	0.59	0.54 - 0.72	Moderate

Table 3. Circadian activity pattern with overlap, coefficient, 95% confidence interval (CI) and the degree of overlap for all paired combinations of the **avian species**; raven, crow, eurasian jay, golden eagle, great tit and magpie at wolf-killed carcasses.

Species combination	Overlap coefficient $\Delta 2$	95% CI	Degree of overlap
Crow - Raven	0.96	0.95 - 0.97	High
Eurasian jay - Crow	0.92	0.91 - 0.94	High
Eurasian jay - Raven	0.91	0.90 - 0.93	High
Great tit - Eurasian jay	0.89	0.83 - 0.94	High
Great tit - Raven	0.87	0.80 - 0.92	High
Golden eagle - Crow	0.87	0.86 - 0.89	High
Great tit - Crow	0.86	0.81 - 0.91	High
Golden eagle - Raven	0.86	0.86 - 0.89	High
Golden eagle - Eurasian jay	0.84	0.83 - 0.88	High
Magpie - Raven	0.83	0.82 - 0.86	High
Magpie - Golden eagle	0.83	0.82 - 0.86	High
Great tit - Golden eagle	0.83	0.77 - 0.90	High

Magpie - Crow	0.82	0.81 - 0.86	High
Magpie - Eurasian jay	0.79	0.78 - 0.84	High
Magpie - Great tit	0.76	0.69 - 0.82	High

Table 4. Circadian activity pattern with overlap, coefficient, 95% confidence interval (CI) and the degree of overlap for all paired combinations between avian- and mammal- species at wolf-killed carcasses.

Species combination	Overlap coefficient $\Delta 2$	95% CI	Degree of overlap
Eurasian jay - Bear	0.40	0.34 - 0.49	Moderate
Great tit - Red fox	0.40	0.38 - 0.47	Moderate
Eurasian jay - Red fox	0.38	0.38 - 0.41	Moderate
Crow - Bear	0.37	0.31 - 0.46	Moderate
Golden eagle - Red fox	0.37	0.37 - 0.40	Moderate
Great tit - Bear	0.37	0.34 - 0.48	Moderate
Raven - Bear	0.36	0.31 - 0.45	Moderate
Great tit - Wolverine	0.36	0.34 - 0.43	Moderate
Golden eagle - Wolverine	0.35	0.35 - 0.39	Moderate
Eurasian jay - Wolverine	0.34	0.34 - 0.38	Moderate
Crow - Red fox	0.34	0.33 - 0.36	Moderate
Raven - Red fox	0.33	0.33 - 0.36	Moderate
Magpie - Bear	0.32	0.31 - 0.41	Low
Golden eagle - Bear	0.31	0.32 - 0.42	Low
Great tit - Wolf	0.31	0.28 - 0.38	Low
Magpie - Red fox	0.30	0.30 - 0.33	Low
Golden eagle - Wolf	0.30	0.28 - 0.34	Low
Crow - Wolverine	0.30	0.29 - 0.33	Low
Raven - Wolverine	0.29	0.29 - 0.32	Low
Eurasian jay - Wolf	0.29	0.27 - 0.34	Low
Magpie - Wolverine	0.26	0.26 - 0.30	Low
Crow - Wolf	0.24	0.23 - 0.29	Low
Raven - Wolf	0.24	0.23 - 0.28	Low
Magpie - Wolf	0.21	0.20 - 0.25	Low

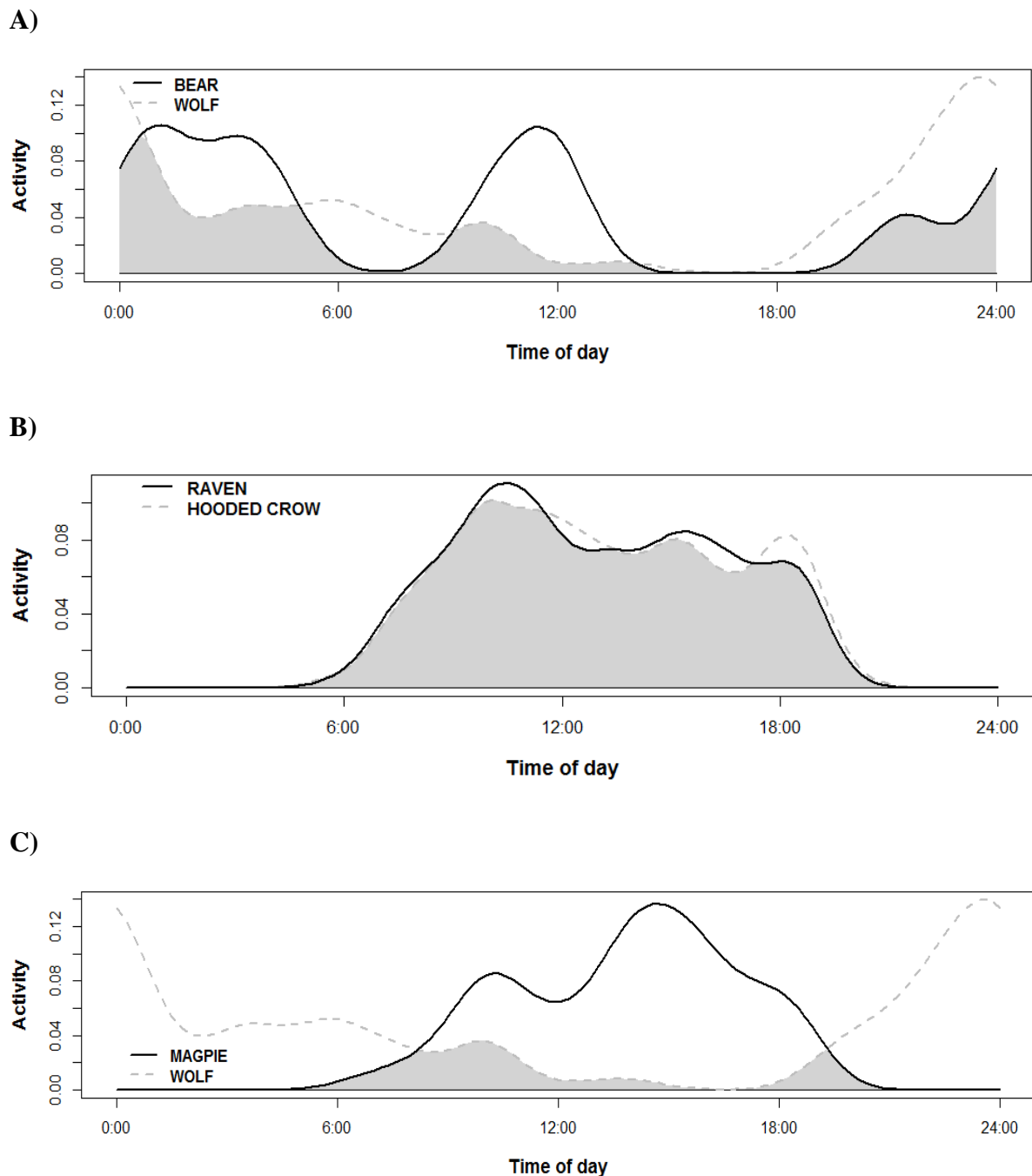


Figure 3. Overlap plots of the combined activity curves of pairs of bird and mammal species at wolf-killed ungulate carcasses. The gray colored area indicates the overlap between the species during average 24 hours. λ is the overlap estimate between 0-1, **A)** bear and wolf ($\lambda = 0.59$) (lowest mammal species combination), **B)** raven and hooded crow ($\lambda = 0.96$) (highest avian species combination), and **C)** magpie and wolf ($\lambda = 0.21$) (lowest avian and mammal species combination).

The avian and the mammalian community had different circadian activity pattern during time of day. The mammal community had highest activity in the time between 20:00 – 06:00, but also during daytime (*Figure 4A*). The red fox had the highest probability of presence the four species. The brown bear had the lowest probability, with a minimum flat level. In the avian community, all the activity was during daytime, from around 04:30 – 20:30 (*Figure 4*). The crow and the raven had the highest probability of presence, while great tit and magpie had the lowest.

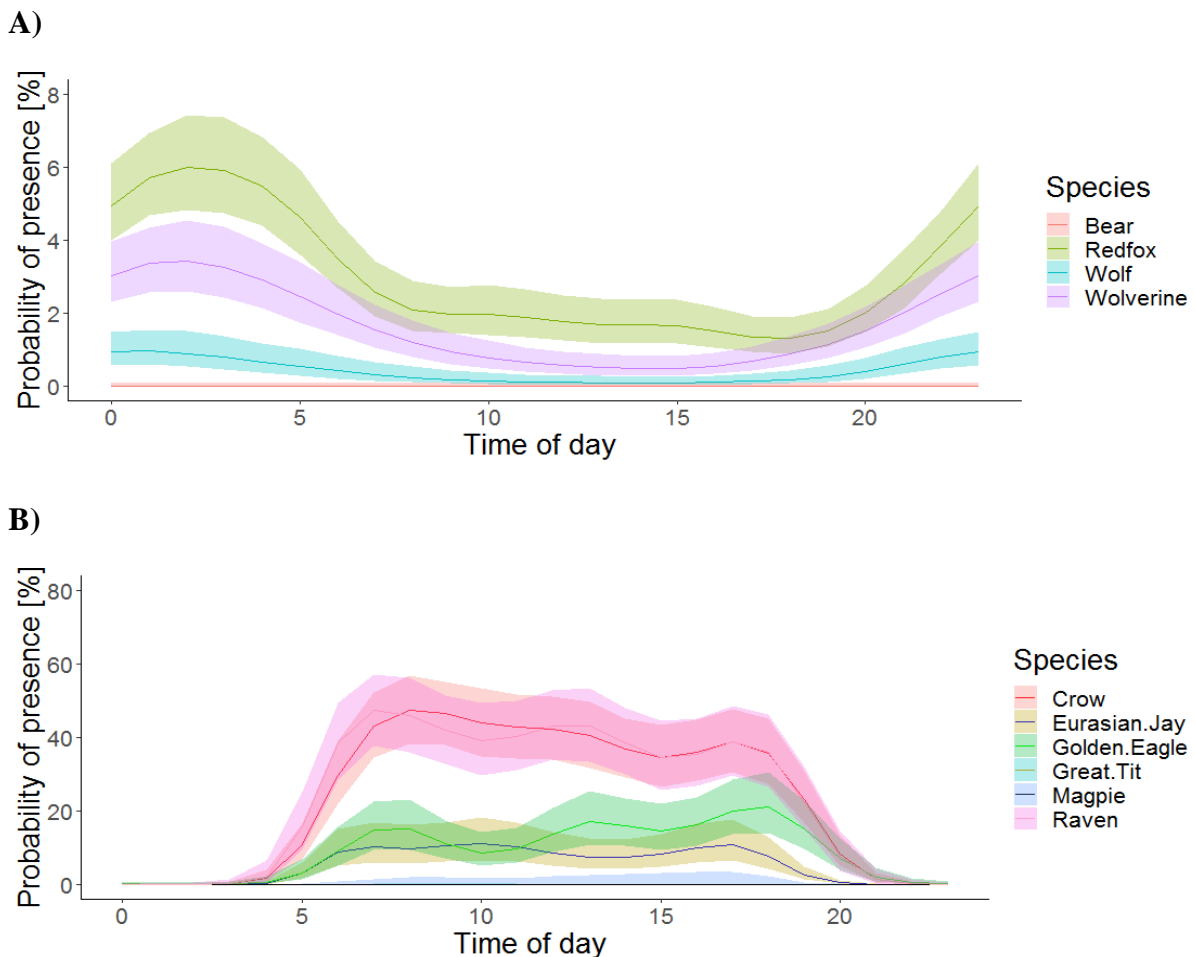


Figure 4. Predicted circadian activity patterns from GAMM models for individual species present at wolf-killed carcasses, divided in A) mammals and B) avian species. Solid lines show the predicted mean and colored ribbons indicate confidence intervals (95% - CI). Probability of presence (y-axis) for mammals ranges from 0-8 and avian species from 0-80. See supplementary; model summary for each species (Table 5-14).

For both the mammalian and the avian community, the highest probability of presence was primarily the first days after camera placement (*Figure 5A-B*). The species crow, raven, and golden eagle had a different probability pattern from the other species. Crow had a high probability day one, with a top around day 14 before decreasing. Raven had a stable probability the first days before decreasing, and golden eagle had a stable probability to day 15 before decreasing (*Figure 5B*).

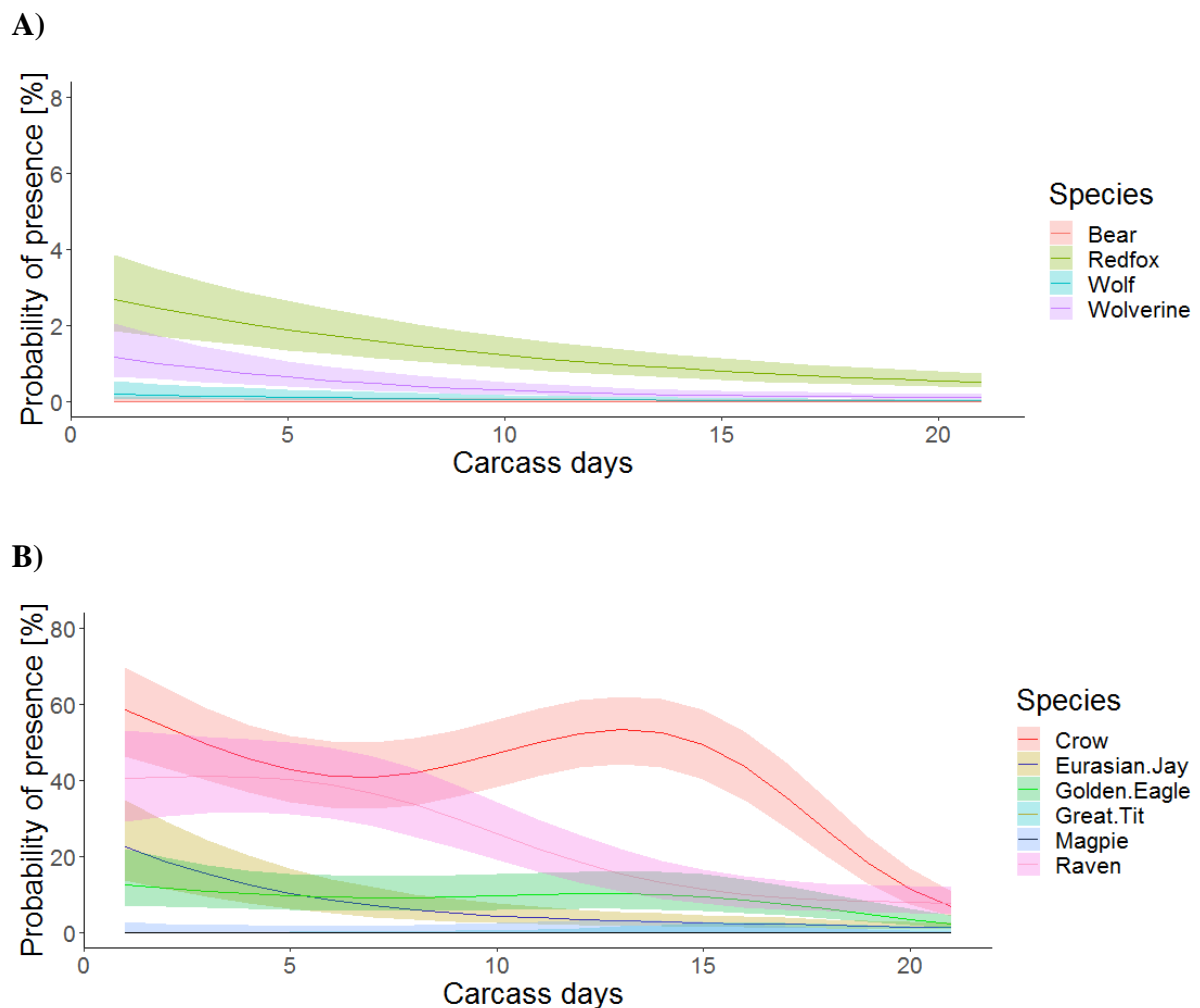


Figure 5. Predicted circadian activity patterns from GAMM models for individual species present at wolf-killed carcasses, divided in A) mammals and B) avian species. Solid lines show the predicted mean and colored ribbons indicate confidence intervals (95% - CI). Probability of presence (y-axis) for mammals ranges from 0-8 and avian species from 0-80. See supplementary; model summary for each species (Table 5-14).

4. Discussion

It is known that carcasses are important for scavengers in a landscape with limited resources. A carcass leads to increased survival and reproduction for many of the species (Houston, 1978; Needham et al., 2014; Wikenros et al., 2022; Wilmers et al., 2003). This study also shows the importance of dead animals for the scavenger community. In this context, I look at different activity patterns among the scavengers.

In total, 31 species were registered at the carcasses. I am looking more closely at six avian species and four mammal species through fall, summer and winter. Consistent with my first prediction, species are distributed into one day-time and one night-time community, with the highest overlap in the circadian pattern within the two communities. The avian community had the highest activity at daytime and the mammal community the main activity concentration at night (*Figure 4A-B*). In accordance with prediction 2), the overlap in the avian community was classified as high ($\lambda = 0.96 - 0.76$). The Corvidae family had the highest overlap on ($\lambda = 0.96$) for raven and crow (*Figure 4B*), and the smallest overlap for crow and magpie ($\lambda = 0.82$) (*Table 3*). The mammal community had the highest overlap ($\lambda = 0.81$) for wolverine and wolf, and smallest for wolf and brown bear ($\lambda = 0.59$) (*Table 2, figure 3A*). Overlap combinations for pairs of birds and mammals was highest ($\lambda = 0.40$) for Eurasian jay and brown bear, and lowest ($\lambda = 0.21$) for magpie and wolf (*Table 4, figure 3C*). My prediction 3) about overlap in the daytime community was supported. The average overlap in the daytime community was 86% and 70% in the nighttime community (*Table 2-3*). To answer my prediction 4) about the time spent on carcasses between avian and mammal species, I found that avian species would linger longer at each carcass compared to mammals. The avian community had more variation seen in carcass days (*Figure 4*).

Both large predators and smaller birds were registered at the carcasses (*Figure 2*). None of these species are obligate scavengers, but essential for the decomposing system. My findings in this study are consistent with earlier studies on activity on carcasses. Many of the same species were registered at the carcasses. The mammals had around the same circadian activity as I found (Parks, 2020; Wikenros et al., 2013, 2022). I tested all the paired combinations of overlap between the species. The avian community had a high overlap (*Table 3*), mammals had high to moderate overlap (*Table 2*), and the combinations between birds/mammals was moderate to low (*Table 4*). These findings agree with other studies such as the avian scavengers in Kenya consisting of vultures and stork. All the different vultures and stork are

not closely related to each other, as many other avian communities in Norway. In accordance with my study, also this avian community had a high degree of overlap around daytime. As opposed to my study, these scavengers had an activity peak around 12:00 (Handler et al., 2021). For this study, the probability had not any marked peaks around 12:00. Further, interspecific social information can play a key role in finding carcasses in the wild. Mammals are often using birds to find available food. The carcasses will attract more noise after a given number of days. This will increase the probability of finding carcass for other animals in the area (Kane & Kendall, 2017). This seems not to affect the probability of presence for mammals in this study. A reason could be the time between moose death and camera placement. When the available biomass on the carcass is small, can scavengers consume fast and reduce the chance of more visitors. This can happen between moose kill and camera placement. Overall, corvids were dominating the time-laps pictures, which is probably due to higher population density than the mammals (*Figure 2*) (Lafferty et al., 2016; Roen & Yahner, 2005; Wikenros et al., 2013).

Further, pairs of species from the avian and mammalian communities had an overlap between 04:30 to 20:30. The average overlap between this communities were low ($\lambda = 0.32$) at the carcasses (*Table 4*). The mammals were mainly night active with less activity at daytime. The avian community were active in the day, with a low probability of presence around midnight. Jays, eagles and tits are dependent of light to hunt or search for food, and will therefore use the daylight (Elnan, 2020; *Fugler, Universitetsmuseet i Bergen, 2022*; Handler et al., 2021). Mammals such as red foxes, wolverines, wolves and brown bears are primarily nocturnal or crepuscular, and will therefore mostly use the night with less activity in the daytime to consume food (Wikenros et al., 2022) (*Figure 4A*). Earlier studies have also shown a similar activity pattern for wolves (Eriksen et al., 2011) and wolverines with GPS data (Mattisson et al., 2013). Furthermore, the probability of presence at the carcass was highest the first day after camera placement for red fox, wolverine and wolf, before decreasing. Bear had the same low probability all 21 days (*Figure 5A*). There was more biomass available in the winter when bears were still in the den-hibernation (*Figure 6A*). The avian community also had a low probability of presence all 21 days for magpie and great tit. Probability of presence for raven was high the first five days before decreasing, and golden eagle the first 15 days before decreasing. Eurasian jay had a high probability the first day before decreasing (*Figure 5B*).

All the species at the carcass are biologically different, but to different degrees. Crows and ravens are closely related but showed a surprisingly different probability of presence after the

camera placement (Figure 5B). One reason can be the different preferred diets. The crow is an omnivore, and prefers different types of insects (Hogstad & Husby, 2021). The raven is a more common scavenger on dead animals (Hogstad & Husby, 2021). An older carcass will attract more insects, and therefore become a better choice for species that have this niche. Especially during cold periods in the nesting season, insectivorous birds will use this niche. This illustrates the complexity and importance of the food web relationship for many animals (Houston, 1978).

Furthermore, the avian species are consuming the carcass with a bill. Pecking on a big animal takes longer than using teeth. Especially when its frozen. The right time of day when the sun is warming can be an optimal time to consume the carcasses in the cold season. Avian species also find it difficult to move carcasses compared to mammals (Vander Wall & Smith, 1987). Predators like the wolf will use shorter time to consume a large mammalian prey. Also factors such as strength and less competition from other predators is important for the time use. Different environmental adaptations among species leads to varied time use at the carcass (Aarnes, 2006). Avian scavengers such as ravens and crows are social and often in groups, therefore consuming big amounts of the most nutrient-rich parts and use more time at the carcass than mammals (*Figure 2*) (Moreno-Opo et al., 2016). Other birds, such as the Eurasian jay and golden eagle are operating alone or in couples, probably to avoid interspecific competition (Kendall, 2014; Ruxton & Houston, 2004). The low numbers of mammals at the carcasses could be because of the sound from the camera traps (Lafferty et al., 2016). Other studies have seen reactions from the mammals at the carcasses, possibly because of the cameras. Furthermore, the low number of mammals could also be because of other sources of food in or outside the wolf territory (Kronenberg, 2018) (Nordli & Rogstad, 2016).

The carcasses in this study corresponded to earlier predation studies of the wolf population in Europe, with the same killed age distribution of moose by season (Sand et al., 2008; Zimmermann et al., 2015). In the summer, the wolves preferred to take the small newborn calves and further into the season they also preferred calves. Through fall and summer, the calves were growing, and the biomass of the carcasses increased. During the winter there was more biomass left from the wolves at the carcasses than during the summer (Figure 6A). The wolf can also kill adult moose, especially in winter (Zimmermann et al., 2015), as we also saw in this study.

As the available biomass was increasing in the winter, there was also a different pattern in the elevation of the carcass sites during seasons. The kill sites had a higher elevation in the early season compared to the later winter season (*Figure 6B*). This reflects the migration pattern of the moose, from higher areas in the fall and down to lower areas in the winter. Because of the snow, is the moose move to the valley bottoms during winter (Eriksen et al., 2011). Supplementary food in the valley bottom is also a factor possibly contributing to larger accumulations of mammals in the wintertime (Andreassen et al., 1997). Furthermore, the moose exploit the late growing plants at higher elevation during summer (Bischof et al., 2012).

The wolf-killed carcasses aren't the only available food in the area. Also, naturally dead animals are available to different degree in the area. Predators like the lynx, bear and the golden eagle are also killing animals to different degrees (Knutsen & Andersen, 2011). Another big source of carcasses is the traffic in the wally bottom in Østerdalen. Just in Stor-Elvdal municipality, there were 300 collisions of ungulates hit by motor vehicle and 223 by train in the period 2017 – 2021. Specially in the wintertime this number is high (*Fallvilt*, 2021; “Viltpåkjørsler,” n.d.). Some of these dead animals are picked up and destroyed or sold, but some will always be available as a resource for scavengers.

In the hunting season, hunting remains are also an important food source for many scavengers in the boreal forest. Earlier studies have shown this by looking at the scavenger community at hunting remains from the shot moose. This biomass is especially available around two months after the moose hunt for the scavengers (Kronenberg, 2018). This mean that it is more available food in the boreal forest than the wolf-killed ungulates. Animals can often select the best food source. A brown bear can for example be at a carcass for more than a week (Wikan & Günther, 2002). With a better estimate of available biomass, I could use it as an explanatory variable including also seasons.

Use of camera traps is a cheap method compared to other methods such as GPS marking. Through camera monitoring you can sample data in selected locations without disturbing the animals. This method and the same type of cameras (Reconyx) are also used in the management and research by different institution, including the Norwegian Nature Inspectorate (SNO). Also, other projects use it due to the camera's reliability. The combination of lithium batteries and the 32 GB SD card didn't set any limitation for the data sampling. Another factor is punctual pictures with regular identical intervals that are easy to categories,

plus the time-lapse. The picture review in the Reconyx MapView is also a good solution to extract well organized data (Nordli & Rogstad, 2016; *Reconyx*, 2014).

More cameras available during the data collection could increase the amount of data, especially in the first winter period when there were more carcasses than cameras. This could have increased the data on species such as brown bear with a higher sample size in fall and summer. One we could sample more data the next season. More data on brown bear could potentially said more about the probability in time of day and carcass days. But more important, to sample a better estimate of all the available carcasses in or around the wolf territory. This can potentially be a source for less time-lapse pictures on the carcasses we had in the field. Further is it important to remember the time before we mounted cameras. This space of time can underestimate the scavengers on the carcasses.

4.1 Conclusion and management

And along with that, carcasses are an important food source, that probably changes and alter facultative scavengers/predators functional responses –hence their numerical responses over time. In a human dominated landscape, a surplus of carcasses/scavenger food is often propagated with human presence and influence, and this is likely to give an additive effect on the local, but also potentially on the landscape level. If some species are subsidized more than others, the other species may be prone to a larger degree of interactions, such as predation or competition. This in turn may have implications on a variety of trophic levels and should be of both of conservation and management interest. Total, 31 different species were registered at the carcasses. There is a complex temporal activity pattern between the scavengers and an important role in the nutrient cycling (Handler et al., 2021).

The probability of presence for wolverines and red foxes at carcass sites decreased after the first day. For golden eagle, the probability was almost the same until day 15 before decreasing. A manager or photographer will therefore have the highest probability of seeing these mammals the first days, and golden eagles the first 15 days. To detect wolverine DNA at a carcass, I would recommend waiting one week until the probability of activity is low.

I will further recommend doing a similar study where the activity at individual carcasses is monitored closely, to see the real overlap in time between the species at the same place. Further, more data sampling on the available biomass in seasons, to use it as an estimate on other sources of available food in the area.

Acknowledgement

First and foremost, I am grateful to SKANDULV and my supervisors Kristoffer Nordli, Petter Wabakken, Ane Eriksen and Barbara Zimmermann for letting my use, and write on this carcass data. Thanks for your help and motivation. Also, thanks to Damaris Matten for the data on avian species at the carcasses.

I will further give Kristoffer, Petter and Erling Maartmann a special thanks for all the field work experience with big carnivores. I have not collected the data to this thesis by my selves, but other data on the same topic. Thanks for letting my work with big carnivore research and management at Evenstad in different projects.

Also, a thanks to all my friends who have been helping and motivating!

Evenstad 27. Mai 2022

Rune Ebran

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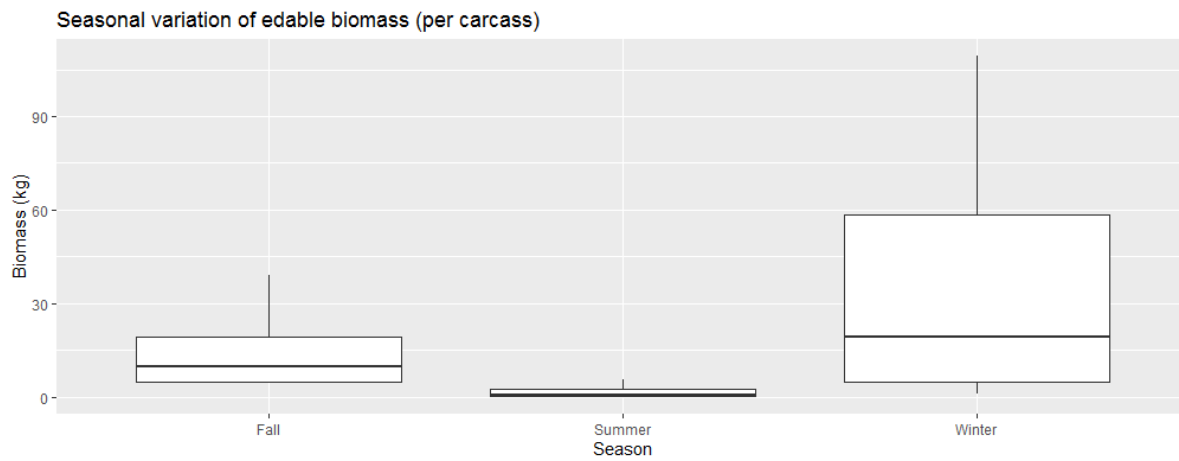
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SUPPLEMENTARY

S1

A)



B)

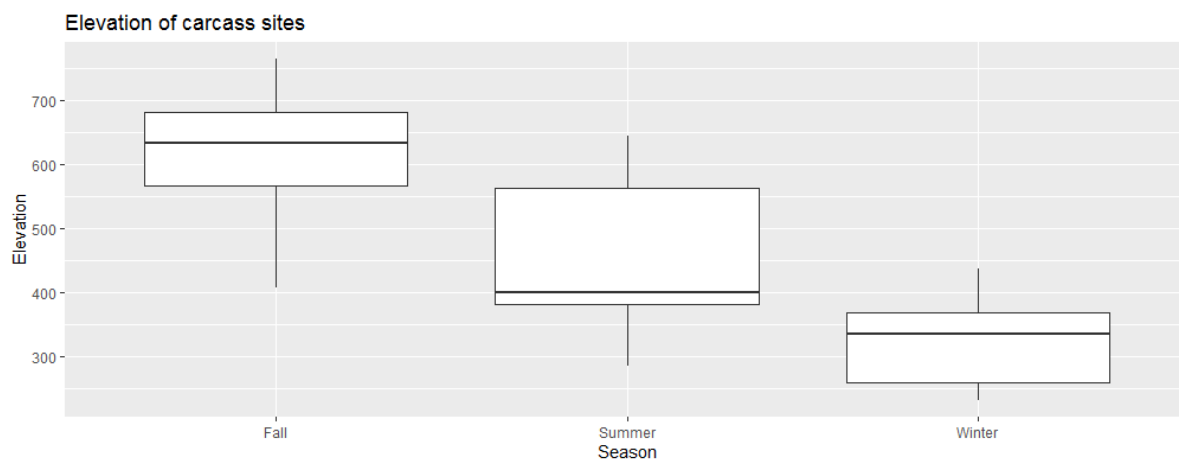


Figure 6. A) Season (fall, summer and winter) variation in biomass per carcass in kg with median and variation. B) Elevation of carcass sites by seasons (fall, summer and winter) with median and variation.

S2

Model summary for each species in GAMM (Table 5-14).

Table 5. Model summary from the ordered factor cohesion model (GAMM) on days, hour and camera nr. for *wolverine*.

A: Parametric coefficient	Estimate	Std.error	Z-value	Pr(> z)
Intercept	-5.672	0.275	-20.63	<2e-16
B: Approximate smooth terms	Edf	Ref.df	Chi.sq	P-value
s(Days)	2.6998	3.369	128.37	< 2e-16
s(Hour)	3.4403	8	55.85	5.34E-14
s(Cameranr)	0.9748	1	38.65	3.04E-10

R-sq.(adj) = 0.0144, deviance explained = 15.6%, fREML = 41624.

Table 6. Model summary from the ordered factor cohesion model (GAMM) on days, hour and camera nr. for *wolf*.

A: Parametric coefficient	Estimate	Std.error	Z-value	Pr(> z)
Intercept	-6.969	0.427	-16.32	<2e-16
B: Approximate smooth terms	Edf	Ref.df	Chi.sq	P-value
s(Days)	1.0006	1.001	30.75	3.01E-08
s(Hour)	2.7782	8	20.72	1.41E-05
s(Cameranr)	0.9461	1	17.57	1.64E-05

R-sq.(adj) = 0.00599, deviance explained = 16.3%, fREML = 34646.

Table 7. Model summary from the ordered factor cohesion model (GAMM) on days, hour and camera nr. for *brown bear*.

A: Parametric coefficient	Estimate	Std.error	Z-value	Pr(> z)
Intercept	-6.725	1.167	-5.764	8.23E-09
B: Approximate smooth terms	Edf	Ref.df	Chi.sq	P-value
s(Days)	1.68147	2.107	3.555	0.20233
s(Hour)	0.01617	8	0.016	0.375758
s(Cameranr)	0.90856	1	9.936	9.43E-04

R-sq.(adj) = 0.00169, deviance explained = 23%, fREML = 28273.

Table 8. Model summary from the ordered factor cohesion model (GAMM) on days, hour and camera nr. for *red fox*.

A: Parametric coefficient	Estimate	Std.error	Z-value	Pr(> z)
Intercept	-4.3315	0.1152	-37.59	<2e-16
B: Approximate smooth terms	Edf	Ref.df	Chi.sq	P-value

s(Days)	2.0636	2.606	196.79	< 2e-16
s(Hour)	5.0792	8	99.51	< 2e-16
s(Cameranr)	0.9828	1	57	2.61E-14

R-sq.(adj) = 0.0195, deviance explained = 10.4%, fREML = 42677.

Table 9. Model summary from the ordered factor cohesion model (GAMM) on days, hour and camera nr. for *raven*.

A: Parametric coefficient	Estimate	Std.error	Z-value	Pr(> z)
Intercept	-11.406	1.204	-9.474	<2e-16
B: Approximate smooth terms	Edf	Ref.df	Chi.sq	P-value
s(Days)	4.013	4.506	202.71	< 2e-16
s(Hour)	6.738	8	86.08	3.04E-16
s(camera)	22.773	32	369.77	< 2e-16

R-sq.(adj) = 0.238, deviance explained = 51%, fREML = 28564.

Table 10. Model summary from the ordered factor cohesion model (GAMM) on days, hour and camera nr. for *crow*.

A: Parametric coefficient	Estimate	Std.error	Z-value	Pr(> z)
Intercept	-11.2411	0.9053	-12.42	<2e-16
B: Approximate smooth terms	Edf	Ref.df	Chi.sq	P-value
s(Days)	5.4	6.001	209.1	<2e-16
s(Hour)	7.009	8	1296.6	<2e-16
s(camera)	21.616	32	424.3	<2e-16

R-sq.(adj) = 0.447, deviance explained = 65.8%, fREML = 28517.

Table 11. Model summary from the ordered factor cohesion model (GAMM) on days, hour and camera nr. for *eurasian jay*.

A: Parametric coefficient	Estimate	Std.error	Z-value	Pr(> z)
Intercept	-9.7852	0.6518	-15.01	<2e-16
B: Approximate smooth terms	Edf	Ref.df	Chi.sq	P-value
s(Days)	4.729	5.596	406.7	<2e-16
s(Hour)	6.906	8	153.7	<2e-16
s(camera)	24.833	32	545.5	<2e-16

R-sq.(adj) = 0.319, deviance explained = 54.6%, fREML = 30916.

Table 12. Model summary from the ordered factor cohesion model (GAMM) on days, hour and camera nr. for *golden eagle*.

A: Parametric coefficient	Estimate	Std.error	Z-value	Pr(> z)
Intercept	-12.847	1.923	-6.68	2.39E-11

B: Approximate smooth terms	Edf	Ref.df	Chi.sq	P-value
s(Days)	3.298	3.724	54.57	2.67E-07
s(Hour)	6.509	8	90.22	3.18E-16
s(camera)	18.651	32	239.39	< 2e-16

R-sq.(adj) = 0.178, deviance explained = 52.7%, fREML = 27727.

Table 13. Model summary from the ordered factor cohesion model (GAMM) on days, hour and camera nr. for *great tit*.

A: Parametric coefficient	Estimate	Std.error	Z-value	Pr(> z)
Intercept	-9.7123	0.5878	-16.52	<2e-16

B: Approximate smooth terms	Edf	Ref.df	Chi.sq	P-value
s(Days)	5.645	6.66	75.04	4.85E-13
s(Hour)	4.946	8	36.48	1.01E-07
s(camera)	14.378	32	204.76	< 2e-16

R-sq.(adj) = 0.228, deviance explained = 50.5%, fREML = 36948.

Table 14. Model summary from the ordered factor cohesion model (GAMM) on days, hour and camera nr. for *magpie*.

A: Parametric coefficient	Estimate	Std.error	Z-value	Pr(> z)
Intercept	-13.53	2.06	-6.571	5.01E-11

B: Approximate smooth terms	Edf	Ref.df	Chi.sq	P-value
s(Days)	3.916	4.432	41.33	3.93E-08
s(Hour)	5.444	8	60.02	9.55E-11
s(camera)	10.904	32	100.97	< 2e-16

R-sq.(adj) = 0.254, deviance explained = 62.6%, fREML = 26912.