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Tesi di Laurea

SCAVENGING DYNAMICS AT WOLF KILLS AND REMAINS AFTER HUNTER HARVEST

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Abstract

Some predator species are fundamental component of the ecosystem due their ability to shift their feeding strategy, from predation to scavenging to adapt to changes in resources availability. Resource availability is probably the most important factor for carrion use, and it depends on several factors. Large predators often provide a stable food source to scavengers year-round. Also, humans' activities could increase carrion amount as well as scavenging behaviour due to the supply of anthropogenic food sources such as remains after hunter harvest of large ungulates. However, one disadvantage of the scavenging strategy is competition within the scavenger guild, and the predation risk if encountering a dominant predator when utilizing carrion. Consequently, if the best feeding habitat also is the riskiest animals could lose both time and energy to vigilant behaviour, which would reduce time assigned to feeding behaviour. In this study I used camera data from wolf-killed ungulates and slaughter remains after hunter harvested of moose to compare carrion use, as well as vigilance and feeding behaviour of brown bear (*Ursus arctos*), wolf (*Canis lupus*), wolverines (*Gulo gulo*), red fox (*Vulpes vulpes*) and pine marten (*Martes martes*) in south-central Scandinavia. Red fox was the species which showed the higher probability of visit at slaughter after hunter harvest remains, but pine marten was the species which did the highest number of visits. This result was likely due to that, although red fox visited most carrion, pine marten made a very high number of visits at three sites. The average duration of visit was longer for wolverines at slaughter after hunter harvest remains and for both red foxes and pine martens at wolf-killed carcasses. Pine marten and wolverine did not show any proportion of vigilant behaviour at wolf-killed carcasses. In addition, wolverine was the only species which did not show any proportion of feeding behaviour at wolf-killed carcasses. From a comparative perspective, between wolf-kills and human-hunter-harvest remains, my results should be interpreted with care, because of smaller sample size at wolf-killed carrion, limiting a rigorous comparison on intra-guilds interactions on carrion with different type of origin. My findings demonstrate that factors such as the carrion origin and the risk-level to be predated by dominant predators influence the use of carrion and the behaviours displayed at different types of sites.

KEYWORDS: *camera trapping, carrion use, interspecific competition, risk allocation, scavenging*

Introduction

Scavenging is an alternative foraging strategy which animals may utilize to satisfy their physiological needs during hard periods, such as: times of prey shortage and stressful environmental conditions (Nordli & Rogstad, 2016; Schmitz et al., 2008; Wikenros et al., 2013). Many mammalian generalist species opportunistically make use of carrion when available and when they are not, they keep up themselves with other resources (Schmitz et al., 2008), such as rodents or berries. In fact, carrion unreliability has impeded the evolution of strict or obligate scavenging behaviour in most of the mammalian species (Schmitz et al., 2008) probably for two reasons: because their limited foraging radii does not allow them to travel rapidly as birds (to arrive on time at the carrion to consume its highest nutritional quality) and, because the costs associated with scavenging do not outweigh the benefits of carrion use (DeVault et al., 2003).

Some predator species are fundamental component of the ecosystem because of their ability to shift their feeding strategy, from predation to scavenging, to adapt to changes in resources availability, allowing them to access food resources without need to kill prey (Wilson & Wolkovich, 2011). Notwithstanding these benefits, the main disadvantage brought by this feeding strategy is competition within the scavenger guild, and the predation risk if encountering a dominant predator when utilizing a carrion (Selva et al., 2005a; Selva & Fortuna, 2007). Therefore, the scavenger's choice to shift their feeding strategy is influenced by the resource availability and the balance between risks and benefits. For example, wolverines (*Gulo gulo*), as most other scavenger, are facultative: they opportunistically shift between scavenging and predation depending on available resources (Dalerum et al., 2009; van Dijk et al., 2008)

Resource availability is probably the most important factor for carrion use, and as suggested by previous research, it depends on several factors, e.g., the cause of animal mortality, the accessibility of carrion (the location where the animal died) and the habitat composition. If a carrion is more available due the habitat composition (e.g., open spaces) it would be easier to be found and consumed by scavengers (Gese & Crabtree, 1996; Jędrzejewski et al., 1992; Selva et al., 2005b). However, it could also be a larger danger for scavengers because they would be more exposed to predators (Elbroch et al., 2015; Krofel et al., 2012). According to Houston (1979), scavengers consume few carrion from predators kills, which usually consume entire animals or guard their prey. Moreover, top predators may be more motivated to maintain primacy on the carrion after the kill to increase the benefits in relation to the energetic costs while hunting (energy spent to catch and kill the prey) (Caro

& Laurenson, 1994; Gorman et al., 1998). Consequently, if the best feeding habitat also is the riskiest (Lima & Dill, 1990) animals could lose both time and energy to vigilant behaviour, which would reduce time assigned to feeding behaviour (Lima & Bednekoff, 1999).

Carrion use, particularly in prey shortage periods, may fundamentally influence behaviour of the predator (DeVault et al., 2003): predators, hunting during all the year, provide a stable number of carrion which could influence the spatial composition of scavenging species in an area and change their seasonal behaviour (Schmitz et al., 2008). Moreover, scavengers may influence top predators' dynamics forcing them to hunt more frequently (Schmitz et al., 2008) also thus potentially altering predators kill-rate.

Also, humans' activities could increase carrion amount as well as the prevalence of scavenging behaviour (Wilson & Wolkovich, 2011) due to anthropogenic food sources such as remains after hunter harvest, which could influence predators' behaviour at different trophic levels (Wikenros et al., 2013; Wilmers et al., 2003). For example, the presence of predictable food resources, which increase the seasonality amount of carrion, seem to increase the scavenging behaviour for wolverines, which feed at carrion with no preferences for if they were created by humans or by top predators, and as result it may decrease their predation (i.e., killing less prey of their own) (Mattisson et al., 2016). Nevertheless, carrion from anthropogenic activities could also reduce carrion availability and scavenging opportunities because they may simplify the food-webs (i.e., systems based exclusively on anthropogenic food sources, such as slaughter remains after hunter harvest) which are less stable and may provide fewer food resources (Möllmann et al., 2009). In fact, hunter harvesting may remove high-quality biomass and nutrients from the system and decrease the natural carrion quality (Wilson & Wolkovich, 2011).

In Scandinavia, due the intense persecution in the 1900s, the wolverine population was severely reduced and confined to northern alpine areas in the north (Flagstad et al., 2004). In northern Scandinavia the wolverine distribution overlaps with the reindeer husbandry area, thus semi-domestic reindeer (*Rangifer tarandus*) are the main prey for wolverines (Mattisson et al., 2011). To avoid predation damages and economic losses for the native Sámi reindeer-herding community (Thompson Hobbs et al., 2012), the Swedish national management plan aims to increase wolverine distribution south of the reindeer husbandry area while maintaining a stable population of wolverines (Aronsson & Persson, 2017; Landa & Kojola, 2000). Today the Swedish wolverine population has expanded into the boreal forest landscape east and south of the alpine area, in areas which do not overlap with

the reindeer husbandry area, (Aronsson & Persson, 2016). Probably this expansion is the result of an excessive increase of wolverine population in alpine area following legal protection (Persson et al., 2015) resulting in an increased number of dispersers who settled in the boreal forest landscape. Moreover, the increasing of Scandinavian wolf (*Canis lupus*) population (Milleret et al., 2021; Svensson et al., 2021; Wabakken et al., 2001) that are now overlapping with the southern periphery of the wolverine distribution are probably increasing the opportunities for wolverines to scavenge on wolf-killed carrion (van Dijk et al., 2008). In addition, wolves provide scavenging opportunities also to other species such as brown bear (*Ursus arctos*), red fox (*Vulpes vulpes*) and pine marten (*Martes martes*) (Wikenros et al., 2013).

In this study, within the ongoing cross-border (Sweden and Norway) collaboration project "Grensevilt" (Wildlife Across Borders) (https://grensevilt.weebly.com/), I will use camera data from wolf-killed ungulate carcasses and slaughter remains after hunter harvested moose to compare carrion use, as well as vigilance and feeding behaviour of brown bears, wolves, wolverines, red foxes and pine martens in south-central Scandinavia. Carrion use will be estimated as probability of visits, number of visits and duration of visits. The results from this thesis will provide a better understanding of how predator guilds compete for and benefit from carrion with different origin (i.e., killed by top predator's or provided by humans as remains after hunter harvest).

Materials and methods

Study area and study species

The study was conducted in an area consisting mainly of boreal forest, in south-central Sweden and in the adjacent eastern part of Norway (hereafter Scandinavia). The managing of most of the forests consists of clear-cutting regeneration resulting in forests stands of different age classes (mainly Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*)). A continental climate characterizes the area (Vedin et al. 1995) which is usually snow-covered between November and April (Dahlström et al. 1995).

In Scandinavia, the wolf population decline started during the 19th century and at the beginning of the 20th century the distribution was confined to the northern areas (Haglund, 1968). The wolf was already functionally extinct at the time when it was protected (1966 in Sweden and 1972 in Norway). Wolves returned to the study area through natural recolonization and the first reproduction was registered in 1983 (Wabakken et al., 2001). This was the start of an increase in wolf numbers and distribution, and during the winter 2020/2021 the estimated number of wolves in Scandinavia was 480 (95% CI = 379 - 624), of which 395 (95% CI = 312 - 513) within Sweden (Svensson et al., 2021).

In Scandinavia, due the intense persecution in the 1900s, the wolverine population was reduced in nearly all Scandinavia and confined to northern alpine areas (Flagstad et al., 2004). Today the Swedish wolverine population is expanding into the boreal forest landscape east and south of the alpine area. Based on the number of wolverine reproductions (a total of 160 during the 2021 census) the Scandinavian population size is today estimated to 1,023 adults (95% CI = 871 – 1,273), of which 386 wolverines (95% CI = 324 - 493) are in Norway and 637 wolverines (95% CI = 518 - 826) are in Sweden (Hedmark et al., 2021).

In the 1980s the pine marten population increased (Storch et al., 1990) and during the same period, the density of red fox population decreased due to an outbreak of the epizootic disease sarcoptic mange (caused by the mite *Sarcoptes scabei*) (Lindström et al., 1995). In Sweden the present red fox population includes about 150,000 individuals and the pine marten population about 100,000 individuals (Swedish Association for Hunting and Wildlife Management 2021).

The Scandinavian moose (*Alces alces*) population increased in the 1960s and was the most productive and harvested population in the world, with about 100,000 individuals harvested annually at the beginning of 21st century. The winter regional density varied from <0.2 to about 2 moose/km^2 in 2003 and later increased to between 0.6 and 2.5 moose/km^2 in 2012 (Lavsund et al., 2003; Sand et al., 2006, 2012).

Camera trap and registration of photos

Sixty-four cameras (one camera per site) have been put up in the field: 49 near moose remains after hunter harvest sites and 15 near wolf-killed ungulate carrion sites (11 moose, 3 red deer (*Cervus elaphus*) and 1 wild boar (*Sus scrofa*)). First, I excluded from the analysis all the cameras which did not record any of my study species or were wrongly placed, so from a total of 64 cameras I included 56. Then, to standardize the camera periods, I considered the first 28 days of cameras recording period only. Doing that, 2 more cameras were excluded since they did not record visits by my study species within 28 days. Consequently, I included 54 cameras in the analysis (42 from remains after hunter harvest sites and 12 from wolf-killed carrion sites) (Table 1).

Table 1. Number of monitored sites per kind of sites, with start and end date, number of camera days, and the number of time lapse photos and motion pictures.

	Start date	End date	N. sites	Camera days	Time lapse photo	Motion photo
Slaughter remains	16.10.2019	23.12.2019	42	1,974	887,698	22,727
Wolf-killed carrion[1]	22.03.2018	11.05.2019	12	261	173,549	14,486
Total			**54**	**2,235**	**1,061,247**	**37,213**

[1] No metadata (i.e., illumination, moon phase, label, contrast, brightness, sharpness, date, and time) from camera Kadaver 7_Rihöjden

Cameras were located to have the carrion, or the slaughter remains after hunter harvest, well visible in the centre of the image. The carrion and the remains after hunter harvest were in different kind of environments: forests and open spaces.

Cameras of different brands were used (Table 2) and programmed to use both motion triggered and time-triggered photos (also called time-lapse). For all cameras, motion triggered photos were taken as series of three photos with one second interval, followed by a one-minute quiet period before the next motion triggered photo burst. The time-triggered photos were either taken at every 1 minute (5 cameras) or 5 minutes (49 cameras), independent of movement.

Table 2. Different brands of camera used to record scavenging behaviour at remains after hunter harvest sites (n = 42) and wolf-killed carrion sites (n = 12) in south central Scandinavia, 2018-2020.

Camera type	Number of cameras	
	Slaughter remains	**Wolf-killed carrion**
HF2 PRO COVERT	18	4
HC600 HYPERFIRE	12	5
PC800 PROFESSIONAL	12	3

I compiled all the data for 10 cameras while data from 54 cameras were previously compiled. Then all the data from the cameras were examined, and the metadata of each photo were obtained using RECONYX Map View Professional software (Reconyx 3.7.2.2). All the data were compiled using Excel from Microsoft Office 360 suite.

Each photo recorded information (metadata) such as illumination, moon phase, label, contrast, brightness, sharpness, date, and time. Each photo was analysed manually to compile information on the presence of animals, separated by species for mammals (e.g., pine marten, fox, bear, lynx (*Lynx lynx*), wolf, wolverine) and birds (e.g., Eurasian jay (*Garrulus glandarius*), magpie (*Pica pica*), hooded crow (*Corvus cornix*), raven (*Corvus corax*), golden eagle (*Aquila chrysaetos*), and northern goshawk (*Accipiter gentilis*)). Furthermore, the number of individuals per species detected in the same photo were recorded. In case of no species in the photo it was recorded as "empty photo" and in case nothing could be seen due to e.g., snow or fog, the photo was recorded as "failed photo" (Fig. 1). Other manually data to compile were camera name, camera location, consumption stage of the carrion or slaughter remains after hunter harvest and snow cover at the site. I used the data from all cameras and compiled the final dataset containing all photos of my study species.
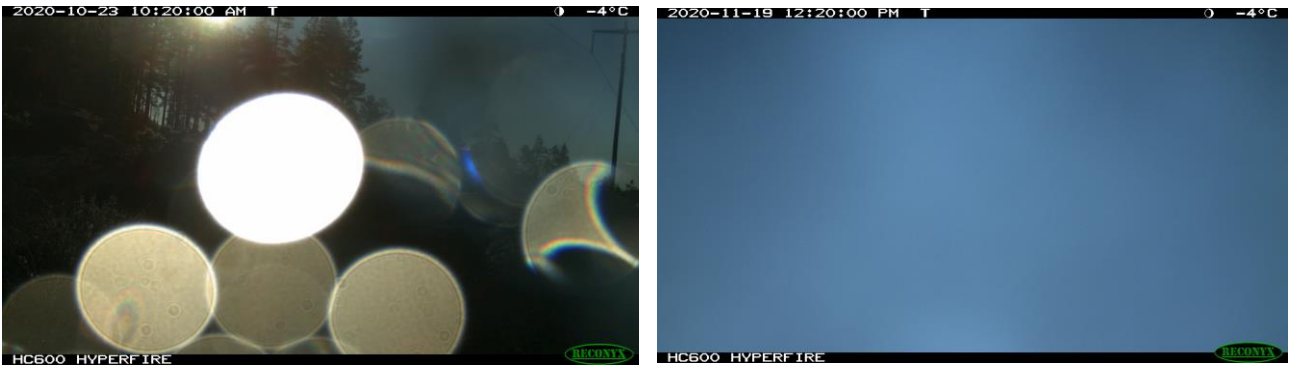
Fig 1. Examples of photos compiled as "failed photo".

Behaviour when vigilant and feeding

For each photo I classified the behaviour of every individual (for mammal species only) in three behaviour categories: "feeding", "vigilant", or "other". I defined "feeding" as having food in the mouth or being positioned with the head down; "vigilant" as being positioned with the head up, the ears erect and the gaze directed outward (following Atwood & Gese, 2008), and "other" as including moving around the area, climbing trees (for pine martens only), interacting with conspecifics, or undetermined behaviours and positions (following Klauder et al., 2021; Wikenros et al., 2014) (Fig. 2).

Fig 2. Examples of photos in which the behaviour was compiled as "vigilant" (upper left image – red fox) and "feeding" (upper right image – red fox) and "other" (lower centre image – brown bear).

Visits at sites

I defined a visit at a site as a sequence of presence photos for a species within 30 minutes. If a sequence was interrupted by the presence of another species or the same species returned at the site more than 30 minutes from the last presence, it was considered as a new visit (Lamichhane et al., 2018; Nordli & Rogstad, 2016). Moreover, from the start and end time of each visit, I calculated the total time spent per visit.

Failure rate

To determine the failure rate (%), I have made a proportion between the number of "failed photos" and the number of total photos. As result the percent of failure in sites set up at slaughter remains after hunter harvest sites was higher than at wolf-killed carrion sites (Table 3).

Table 3. Percent of failures (%) at both slaughter remains after hunter harvest sites (n = 42) and wolf-killed carcasses (n = 12) south-central Sweden. Data collected 2019-2020.

	N. sites	Motion photos (MP)	Time lapse photos (TP)	Failed photos	Total photos	Failure rate (%)
Slaughter remains	44	22,727	887,698	29,763	940,188	3.2
Wolf-killed carrion	12	14,486	173,549	162	188,197	0.01
Total	**54**	**37,213**	**1,061,247**	**29,925**	**1,128,385**	**3.21**

Data analysis

Following Klauder et al, (2021), I divided the concept of carrion use into 5 measurable variables, all calculated per species:

1) Number of visits,
2) Duration (minutes) of visits,
3) Probability of visit,
4) Proportion of vigilant behaviour, and
5) Proportion of feeding behaviour.

To get the proportion of individual behaviours per visit I have followed Klauder's (2021) method, according to which "the vigilance and feeding behaviours have been measured as the proportion of time an animal exhibited a certain behaviour while on camera, with each photo representing a second of time". In fact, always following Klauder's (2021) definition, the unit which I considered was not photos but individuals. In case of multiple animals in the photo, behaviour proportions were divided between the number of animals. For example, a photo with three animals in which two were feeding and one was vigilant, the total was divided on the following way: 0.66 for feeding and 0.33 for vigilant behaviours.

For each variable I calculated the mean per species per site, to account for that every site has different characteristic, such as: environment, weather conditions or eventual camera traps malfunctions, and because of that one sites is considered as an independent from others (i.e., photos from the same site are not independent), thus my final sample size were number of cameras per food source (i.e., remains after hunter harvest sites (n = 42) and from wolf-killed carrion (n 0 12)). Using this information, I then calculated the mean, standard deviation, standard error, and 95% confidence intervals for my five variables described above for all cameras, separated by type of site (slaughter remains after hunter harvest sites or wolf-killed carrion).

All the variables (except for probability of visit) were represented in box plot graphs because, due the consideration of each site as an isolate case from others, I wanted give indication of how the values in the data are spread out. Using this type of representation, I could show if my data were symmetrical, how tightly my data were grouped and if and how my data were skewed. In addition, I could also show both mean and median.

Results

Carrion use

Number of photos

Cameras worked for a total of 2,235 days (1,974 days at slaughter remains after hunter harvest sites and 261 days at wolf-killed carrion) and produced a total of 1,098,455 photos, of which 1,088,135 (99%) were of other species, empty or failed photos and 10,320 (1%) photos were of my study species (brown bear, wolf, wolverine, red fox, pine marten). A total of 7,956 (77%) photos were taken at slaughter remains after hunter harvest sites (n = 42) and 2,364 (23%) photos were taken at wolf-killed carrion sites (n = 12) (Fig.3).

Other species photographed (not in order of occurrence) were moose, red deer, roe deer (*Capreolus capreolus*), wild boar, badger (*Meles meles*), hare (*Lepus europaeus*), squirrel (*Sciurus vulgaris*), rodents, capercaillie (*Tetrao urogallus*), black grouse (*Lyrurus tetrix*), crane (*Gruidae Vigors*), seagull, wood pigeon (*Columba palumbus*), golden eagle (*Aquila chrysaetos*), northern goshawk (*Accipiter gentilis*), common buzzard (*Buteo buteo*), raven (*Corvus corax*), grey headed woodpecker (*Picus canus*), black woodpecker (*Dryocopus martius*), hooded crow (*Corvus cornix*), magpie (*Pica pica*), eurasian jay (*Garrulus glandarius*), siberian jay (*Perisoreus infaustus*), mistle thrush (*Turdus viscivorus*), song thrush (*Turdus philomelos*), eurasian green finch (*Chloris chloris*), great tit (*Parus major*), sandpiper, unidentified mammal, unidentified bird, dog (*Canis lupus familiaris*) and humans.
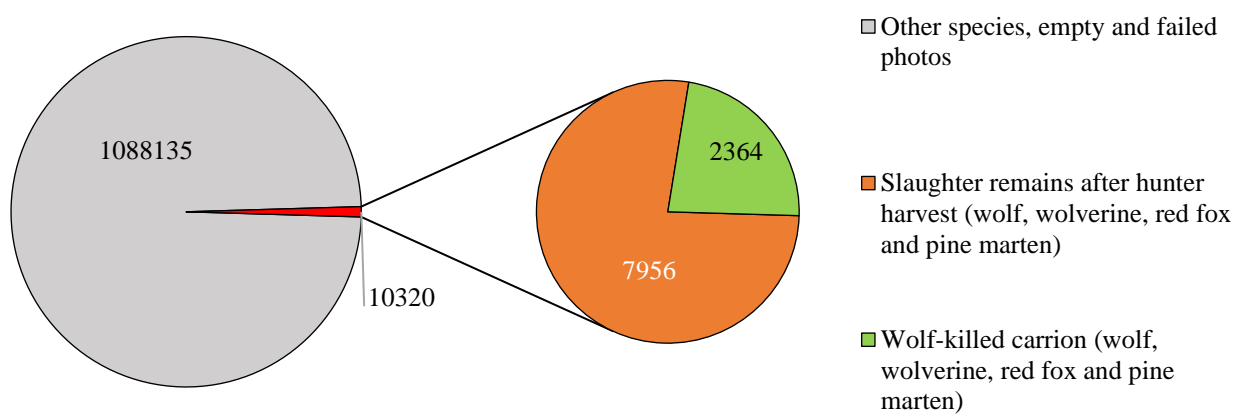
Fig 3. Number of other species, empty and failed photos (grey); number of photos of my study species (red). Photos produced at slaughter remains after hunter harvest sites (n = 42) (orange) and at wolf-killed carrion sites (n = 12) (green) in south-central Scandinavia. Data collected 2018-2020.

In total, 4,172 photos (40%) were of pine martens, 4,084 photos (40%) were of red foxes, 1,683 photos (16%) were of wolverines, 309 photos (3%) were of wolves and 71 photos (1%) were of brown bears (Fig. 4). Brown bears only appeared at 2 slaughter remains after hunter harvest sites in the late fall 2020 and were not active during most camera deployments, consequently they were excluded from further analysis.
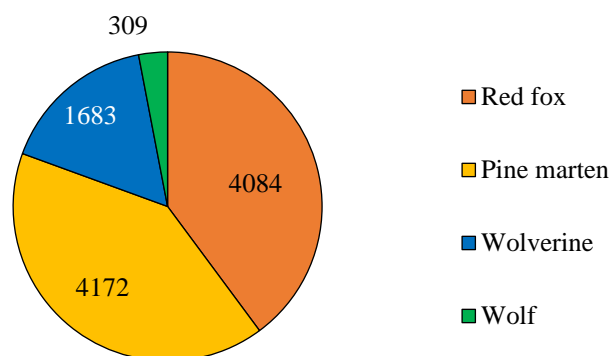
Fig 4. Number of photos taken per species at both slaughter remains after hunter harvest sites (n = 42) and wolf-killed carrion sites (n = 12) in south-central Scandinavia. Data collected 2018-2020.

From both types of sites there were photos in which >1 individual of the same species was present. At slaughter remains after hunter harvest sites there were 35 photos (3 visits, 2 sites) of multiple wolves and 4 photos (2 visits, 2 sites) of multiple red foxes. At wolf-killed carrion there were 8 photos (3 visits, 3 sites) of multiple wolves and 68 photos (5 visits, 1 site) of multiple red foxes.

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Visits at sites

I collected data from a total of 789 visits, of which 677 (86%) were at remains after hunter harvest sites and 112 (14%) were at wolf-killed carrion sites (one camera per site). In total, I documented 366 visits by red foxes, 334 visits by pine martens, 56 visits by wolverines and 33 visits by wolves.

The most visited site detected a total of 65 visits, 54 visits by pine martens, 7 visits by wolverines and 4 visits by red foxes. Four sites had only 1 visit, of these 3 were visited by foxes and 1 by pine martens. The other sites detected from 2 to 56 visits. Two sites were visited by all 4 different species, while 20 sites were visited by one species only. The other thirty-two sites were visited by 2-3 different species. Red fox was the species which visited most sites, while wolverines and wolves visited nearly the same number of sites in total (14-15, Table 4).

Table 4. The relative occurrence of four species of scavengers at slaughter remains after hunter harvest and wolf-killed carrion sites in south-central Scandinavia, expressed as the number of visited sites. Data collected 2018-2020.

Species	Slaughter remains (n = 42)	Wolf-killed carrion (n = 12)	Total (n = 54)
Red Fox	36	10	**46**
Wolf	7	7	**14**
Pine marten	23	3	**26**
Wolverine	14	1	**15**

Slaughter remains after hunter harvest sites

Number of photos

A total of 7,884 photos of my study species were taken at remains after hunter harvest sites, of which 4,156 (53%) were of pine martens, 1,952 (25%) of red foxes, 1,671 (21%) of wolverines and 105 (1%) of wolves (Fig. 5).
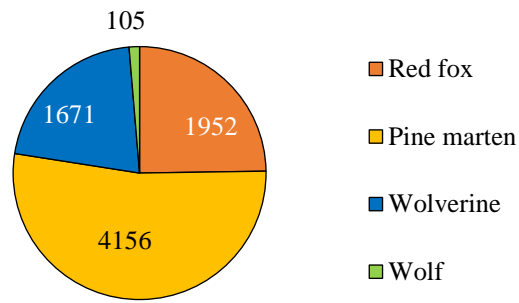
Figure 5. Number of photos taken per species at slaughter remains after hunter harvest sites (n = 42) in south-central Scandinavia. Data collected 2019-2020.

Visits at sites

I collected data from a total of 679 visits at remains after hunter harvest sites, of which the highest number of visits was made by pine martens (329 visits) and red foxes (278 visits) followed by wolverines (55 visits) and wolves (13 visits). The most visited site detected a total of 65 visits, 54 visits by pine martens, 7 visits by wolverines and 4 visits by red foxes. The three least visited sites had 1 visit only, all by wolverines. The other sites detected from 2 to 56 visits per camera. One site was visited by 4 different species, while 15 ones were visited by one species only. Other sites (n = 26) were visited from 2-3 different species. Red fox was the species which visited most sites (n = 36), while wolf was the species which visited less sites (n = 7).

About the probability of visit, red fox was the species which showed the highest probability of visit (μ = 0.86 ± 0.06 SE), followed by pine marten (μ = 0.55 ± 0.08 SE) and wolverine (μ = 0.33 ± 0.07 SE), while wolf was the species which showed the lowest probability of visit (μ = 0.17 ± 0.06 SE) (Table 5).

Table 5. Number of presence (sites visited by the species), number of absence (sites not visited by the species) and estimates of probability of visit across four species of scavengers at slaughter remains after hunter harvest sites (n = 42) in south-central Scandinavia. Data collected 2019-2020.

Species	N. Presence (1)	N. Absence (0)	Mean (μ)	Standard Deviation (σ)	Standard Error (SE)	Confidence Interval (95%)
Red fox	36	6	0.83	0.35	0.06	0.71 - 0.95
Pine marten	23	19	0.55	0.50	0.08	0.39 – 0.71
Wolf	7	35	0.17	0.38	0.06	0.05 – 0.29
Wolverine	14	28	0.33	0.48	0.07	0.19 – 0.47
Total	**80**	**88**	**0.48**	**0.50**	**0.04**	**0.40 - 0.56**

At visited sites, red fox and pine marten were the species which made the highest number of visits (μ = 6.62 ± 1.25 SE and μ = 7.88 ± 2.22 SE, respectively), while wolf (μ = 0.31 ± 0.14 SE) and wolverine (μ = 1.31 ± 0.37 SE) made the lowest number (μ = 0.31 ± 0.14 SE and μ = 1.31 ± 0.37 SE, respectively) (Fig. 6). The external points represent a very high number of visits; e.g., at 5 different sites I recorded from 28 to 55 visits by pine marten. Duration of visits were longest for wolverines (μ = 11.08 ± 2.14 SE) while for pine martens (μ = 8.71 ± 1,77 SE), red foxes (μ = 8.52 ± 1.83 SE), and wolves (μ = 8.00 ± 3.78 SE) the visit length was nearly the same (Fig. 6).
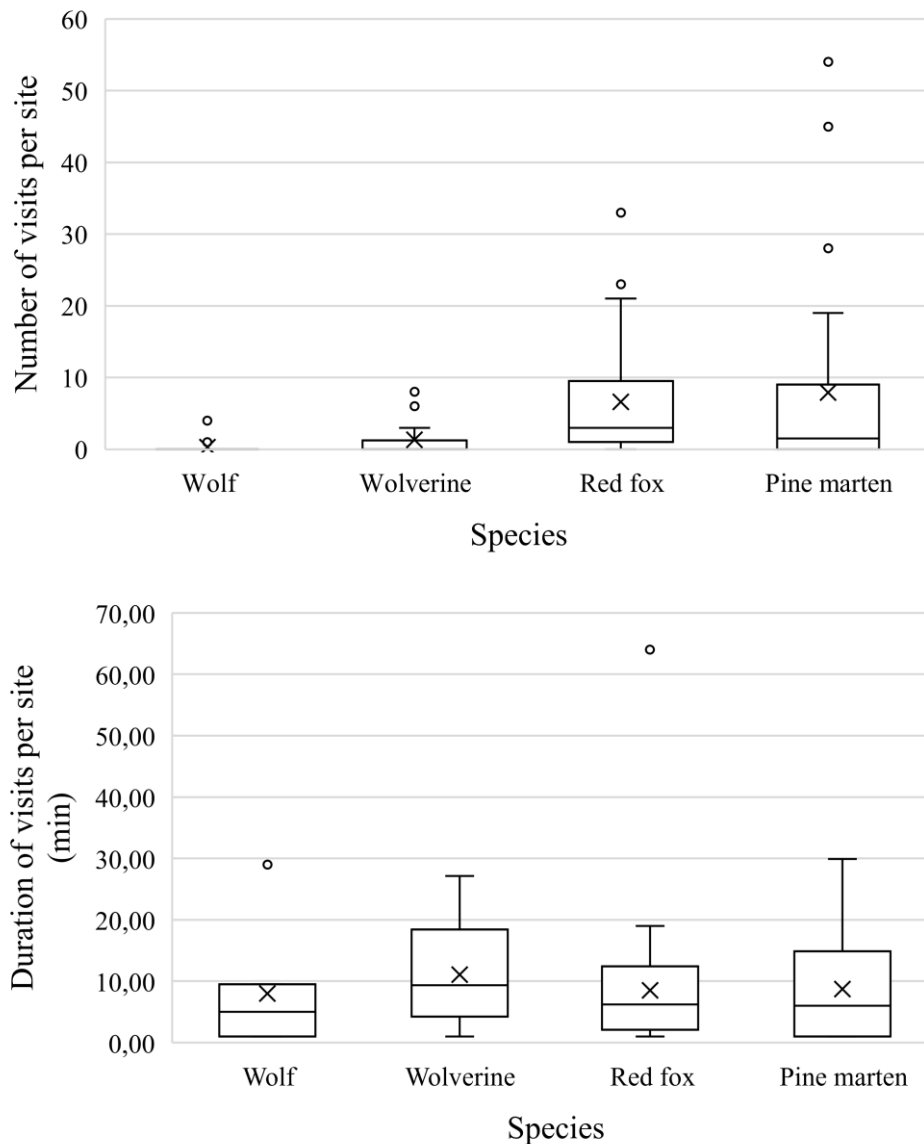
Fig 6. Boxplots of number of visits per site (upper panel) and duration of visits per site in minutes (lower panel) across four species of scavengers at slaughter remains after hunter harvest sites (n = 42) in south-central Scandinavia. In addition, the "x" shows the mean and the line shows the median. Data collected 2019-2020.

Proportion of vigilant and feeding behaviours

At slaughter remains after hunter harvest sites both proportions of vigilant and feeding behaviours varied between species. Red foxes displayed the highest proportion of vigilance behaviour ($\mu = 0.51 \pm 0.06$ SE) while pine martens ($\mu = 0.29 \pm 0.07$ SE), wolverines ($\mu = 0.28 \pm 0.06$ SE) and wolves ($\mu = 0.26 \pm 0.14$ SE) spent a similar proportion of time to vigilant behaviour (Fig. 7). Differently, pine martens displayed the highest proportion of feeding behaviour ($\mu = 0.56 \pm 0.07$ SE), followed by wolverines ($\mu = 0.49 \pm 0.08$ SE), while for wolves ($\mu = 0.21 \pm 0.09$ SE) and red foxes ($\mu = 0.22 \pm 0.04$ SE) it was similar proportions (Fig. 7).

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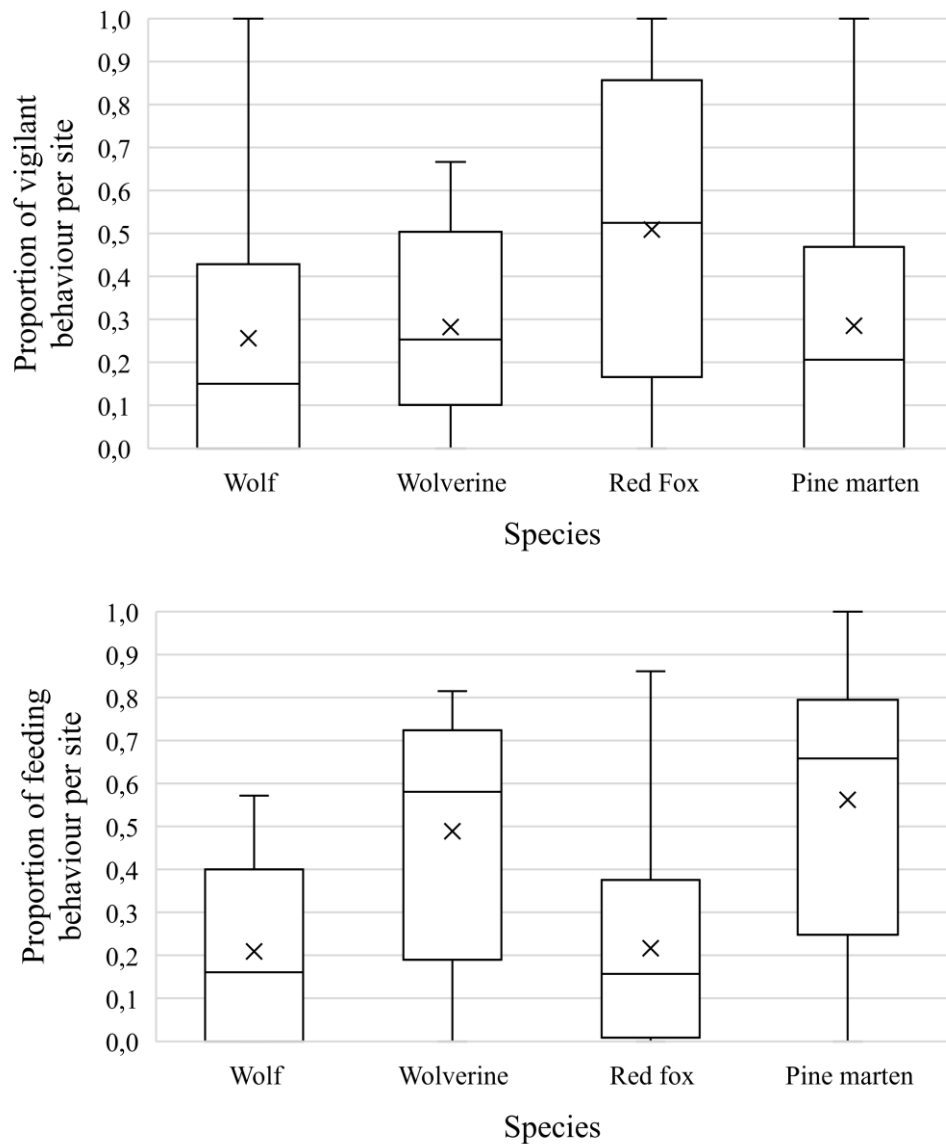
Fig 7. Boxplots of proportion of vigilant behaviour per site (upper panel) and proportion of feeding behaviour per site (lower panel) across four species of scavengers at slaughter remains after hunter harvest sites (n = 42) in south-central Scandinavia. In addition, the "x" shows the mean and the line shows the median. Data collected 2019-2020.

Wolf-killed carrion sites

Number of photos

A total of 2,548 photos of my study species were taken at wolf-killed carrion sites, of which 2,144 (84%) were of red foxes, 376 (15%) of wolves, 16 (0,6%) of pine martens and 12 (0,5%) of wolverines (Fig. 8).
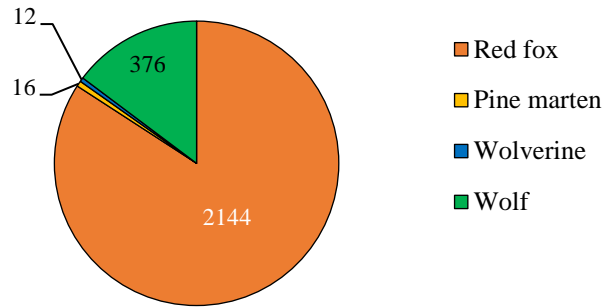
Fig 8. Number of photos taken per species at wolf-killed carrion sites (n = 12) in south-central Sweden. Data collected 2018-2019.

Visits at sites

A total of 112 visits were detected at wolf-killed carrion sites, of which the highest number was made by red foxes (88 visits) and wolves (20 visits) followed by pine martens (3 visits) and wolverines (1 visit). The most visited site detected a total of 46 visits; 44 visits by red foxes, 1 visit by wolves and 1 visit by pine martens. The least visited site had 1 visit only, by wolverines. The other 10 sites detected from 2 to 15 visits. No sites were visited by all the 4 different species, while 5 sites were visited by one species only. The other 7 sites were visited by 2-3 different species. Red fox was the species which visited most sites (n = 10), while wolverine was the species which visited less sites (n = 1).

About the probability of visit, red fox was the species which showed the higher probability of visit (μ = 0.83 ± 0.11 SE), followed by wolf (μ = 0.58 ± 0.15 SE) and pine marten (μ = 0.25 ± 0.13 SE), while wolverine was the species which showed the lower probability of visit (μ = 0.08 ± 0.08 SE) (Table 6).

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Table 6. Number of presence (sites visited by the species), number of absence (sites not visited by the species) and estimates of probability of visit across four species of scavengers at wolf-killed carrion sites (n = 12) in south-central Sweden. Data collected 2018-2019.

Species	N. Presence (1)	N. Absence (0)	Mean (μ)	Standard Deviation (σ)	Standard Error (SE)	Confidence Interval (95%)
Red fox	10	2	0.83	0.39	0.11	0.61 – 1.05
Pine marten	3	9	0.25	0.45	0.13	-0.01 – 0.51
Wolf	7	5	0.58	0.52	0.15	0.28 – 0.88
Wolverine	1	11	0.08	0.29	0.08	-0.08 – 0.24
Total	**21**	27	0.44	0.50	0.07	**0.30 – 0.58**

At visited carrion red fox was the species which made the highest number of visits, followed by wolf and pine marten ($\mu = 7.33 \pm 3.55$ SE, $\mu = 1.67 \pm 0.68$ SE and $\mu = 0.25 \pm 0.13$ SE, respectively) while wolverine made only one visit at one wolf-killed carrion site ($\mu = 0.08 \pm 0.08$ SE). The external points represent a very high number of visits; e.g., at 1 site I recorded 44 visits by red fox (Fig.9). Duration of visits were longest for red foxes ($\mu = 14.53 \pm 5.83$ SE); for pine martes and wolves the visits length was nearly the same ($\mu = 10 \pm 7.55$ SE and $\mu = 9.26 \pm 5.12$ SE, respectively) (Fig. 9). The wolverine made only one visit at one wolf-killed carrion site, so this mean ($\mu = 3$) coincides with the length of the visit (3 minutes). For this reason, the raw data, mean, and median are the same for number of visits by wolverines.
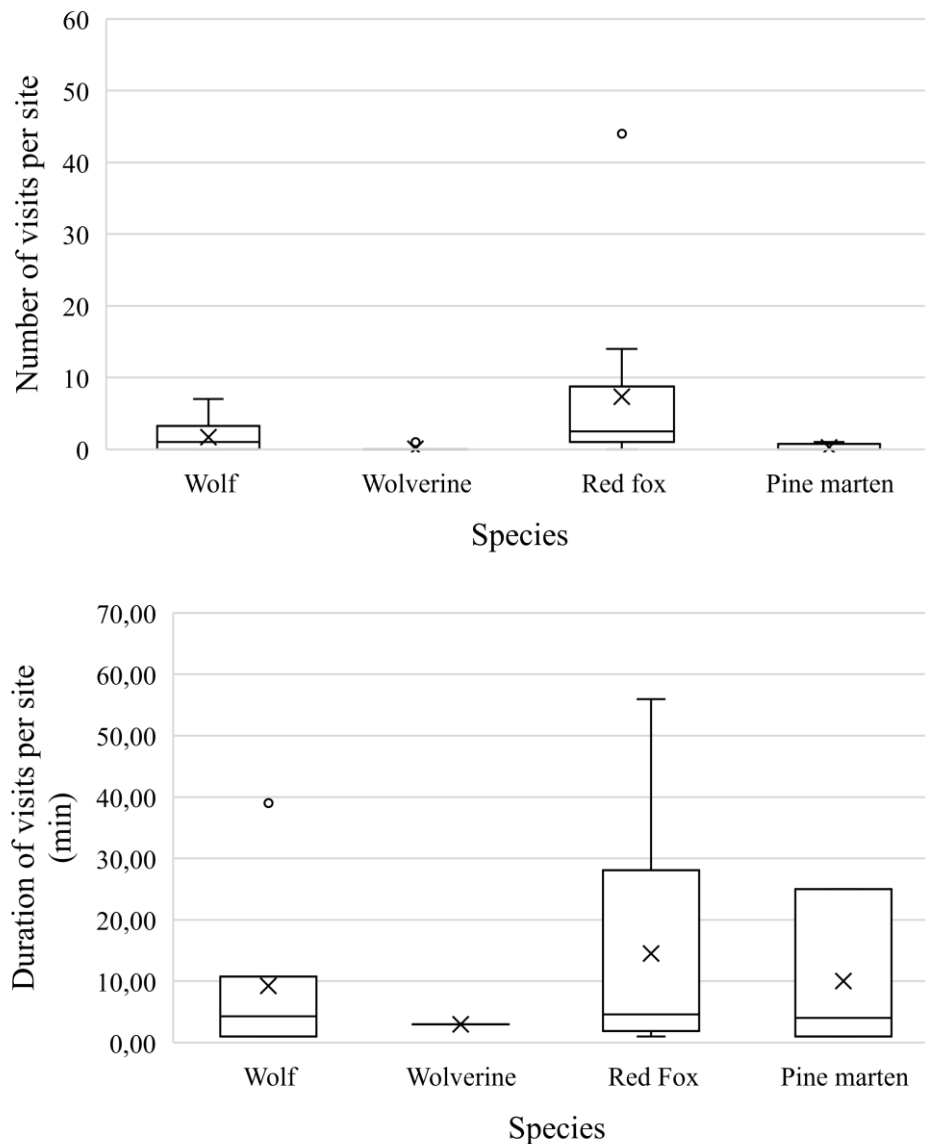
Fig 9. Boxplots of number of visits per site (upper panel) and duration of visits per site in minutes (lower panel) across four species of scavengers at wolf-killed carrion sites (n = 12) in south-central Sweden. In addition, the "x" shows the mean and the line shows the median. Data collected 2018-2019.

Proportion of vigilant and feeding behaviours

At wolf-killed carrion sites both proportions of vigilant and feeding behaviours varied between species. Red foxes and wolves displayed a very similar proportion of vigilant behaviour ($\mu = 0.29 \pm 0.11$ SE and $\mu = 0.28 \pm 0.14$ SE, respectively), while pine marten did not display any vigilant behaviour (Fig. 10). Differently, pine martens displayed the highest proportion of feeding behaviour ($\mu = 0.67 \pm 0.33$ SE), followed by red foxes ($\mu = 0.30 \pm 0.09$ SE) and wolves ($\mu = 0.29 \pm 0.14$ SE). Wolverines did not display neither vigilant nor feeding behaviour (Fig. 10).
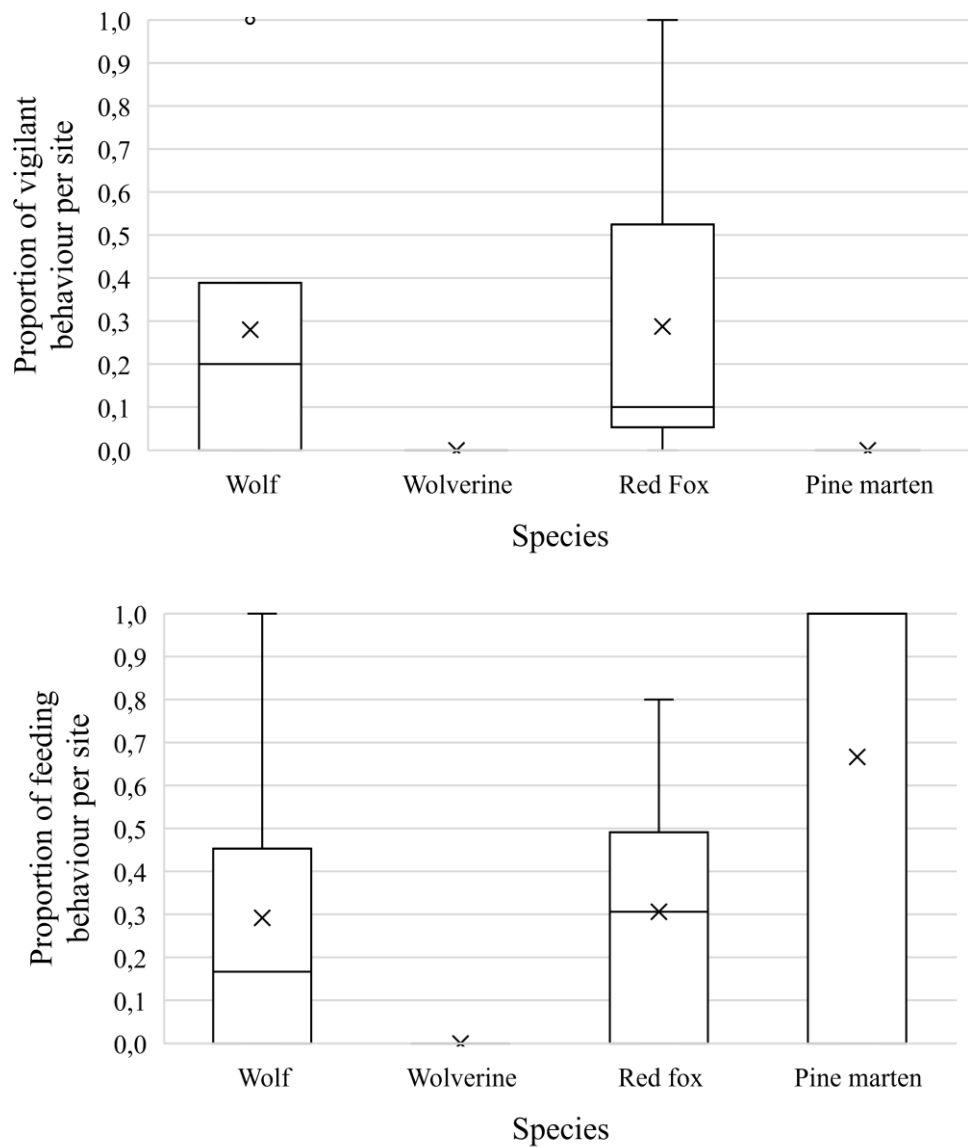
Fig 10. Estimates of proportion of vigilant behaviour per site (upper panel) and proportion of feeding behaviour per site (lower panel) across four species of scavengers at wolf-killed carrion sites (n = 12) in south-central Sweden. In addition, the "x" shows the mean and the line shows the median. Data collected 2018-2019.

Discussion

My findings reveal that my study species show different use and display different behaviours in relation to the origin of the carrion utilized (i.e., killed by top predator's or provided by humans as remains after hunter harvest). Red fox was the species which showed the higher probability of visit at slaughter remains after hunter harvest, but pine marten was the species which made the highest number of visits. This result was obtained because, although red fox dominates regarding visiting most sites, pine marten made a very high number of visits at 3 sites (potentially due the carrion location in woody habitat, the habitat preferred by martens). Both the number of visits and duration of visit was higher for wolverine at slaughter remains after hunter harvest compared to wolf-killed carrion. While both red foxes and pine martens spent a longer duration of time at wolf-killed carrion compared to slaughter remains after hunter harvest. Red fox displayed the higher proportion of vigilant behaviour at both types of sites, while both pine marten and wolverine did not show any proportion of vigilant behaviour at wolf-killed carrion. In addition, wolverine was the only species which did not show any proportion of feeding behaviour at wolf-killed carrion.

Carrion use

For scavenger species the foraging process is characterized by a trade-off between the need to satisfy their food requirements and the necessity to keep themselves safe by potential predation by dominant predators (Krebs & Davies, 2016). Both abiotic, such as environmental characteristics and habitat composition, and biotic factors, such as the interference competitions between species and predation risk, influence both carrion availability and the probability of scavenger species to visit and use it (Kane et al., 2016; Krebs & Davies, 2016; Smith & Smith, 2013). In my study the cameras were set up in woody and open environments and recorded in both autumn, winter, and spring/summer seasons. The biomass availability from wolf-killed carrion differed between sites and seasons but was higher than the biomass available at hunter harvest remains. The carrion's origin (provided by predators or humans) influences both the predation risk-level and the amount of biomass available.

Pine marten showed a higher probability of visit at slaughter remains after hunter harvest compared to wolf-killed carrion. Similar to pine marten, wolverines also show a higher probability of visits at slaughter remains after hunter harvest than at wolf-killed carrion. Habitat selection for both wolverine and pine marten are influenced by habitat that can be perceived as safe; i.e,, wolverine prefer steep and rugged terrain while pine martens prefer spruce-dominated forest with tall trees (≥ 20 m) and

avoid clear-cuts and open habitats (Brainerd & Rolstad, 2002; Rauset et al., 2015). In line with this, they might also utilize the less risky carrion resources (slaughter remains) compared to wolf-killed carrion. In addition, pine marten might prefer to scavenge at slaughter after hunter harvest remains also because (due its small size) the risk to encounter all other large predators (wolf, red fox and wolverine) is lower than at wolf-killed carrion. In addition, pine martens and wolverines (both mustelids) are good climbers. Thus, they can in that way (climbing trees) evade a larger, apex predator to greater extent than the red fox can (than cannot climb trees).

Red fox was the species which showed the higher probability to visit both types of carrion resources. According to Wikenros et al. (2014), red foxes broad use of the habitat allows them to benefit of much more alternative food sources than more habitat specialized species, such as pine martens, which benefit from food sources found in restricted areas only. Furthermore, wolverine's home ranges are much larger than the home ranges for red fox and pine marten (i.e., $170 – 669$ km^2 for wolverine compared to $10 – 30$ km^2 for red fox; Persson et al., 2009; Goszczyński, 2002; $10 – 30$ km^2 for red fox compared to 7 km^2 for pine marten; Helldin, 2000), thus wolverines occur at much lower density in the landscape and roam over large areas in search of food sources. This could explain that the probability of wolverine visits at both carrion types are lower for wolverine compared to fox and marten.

In Scandinavia wolf is the dominant top predator, however several studies report scavenging occurrences of wolves at slaughter remains after hunter harvest sites (Demski, 2015; Huggard, 1993; Selva et al., 2003; Śmietana W & Klimek A, 1993; Valdmann et al., 2005). Also, wolves' habitat selection seems to be more influenced by prey's availability than by the density of other predators (Uboni, 2012). Furthermore, during the winter wolves' prey are more vulnerable and more available because of poor health conditions while, during summer, preys are more fit and can move across larger areas and thus, become less available to predators (Mao et al., 2005). Being a top-predator, wolves might not need to prioritize safety when selecting food resources. Therefore, if wolves do not have to care much about safety, they would maybe select scavenging on the carrion with the highest available biomass (choosing the wolf-killed carrion and not the slaughter after hunter harvest remains).

Also, the interference competitions between species with overlapping niches can influence the probability to visit the different carrion types, particularly in presence of larger predators (Smith & Smith, 2013). From the results, it was possible to determine that wolf-killed carrion were riskier than

slaughter after hunter harvest remains due the high probability of wolves to visit wolf-killed carrion compared to slaughter hunter harvest remains. Species such as pine martens and wolverines (which showed a higher probability of visit at slaughter remains after hunter harvest compared to wolf-killed carcasses) prefer to assume a safer behaviour. Slaughter after hunter harvest remains give less benefits (due the different available biomass) compared to wolf-killed carrion, thus both wolverines and pine martens should show a higher probability of visit at wolf-killed carrion than at slaughter after hunter remains. Thus, these two species showed a high probability of visit at slaughter after hunter harvest remains because the cost is too high at the wolf-killed carrion (the risk to be predated is higher than the gain from more available biomass). On the contrary, red fox (which showed nearly the same probability of visit at both types of sites) seems to have a riskier behaviour, which might indicate that its needs for food were higher than the carrion's risks and therefore they scavenge at both types of carrion.

However, based on the knowledge that wolverines have a pronounced food-caching strategy, my results that it was more probable to visit the slaughter remains was somewhat surprising. Food-caching is a storage strategy, adopted by several species, which is aimed to compensate for periods of food source shortage (van der Veen, 2017). It is an alternative strategy to storage resources as fat in its own body, which could be a disadvantage for animal needing to escape from a predator (Krebs & Davies, 2016). An earlier study (van der Veen et al., 2020) found that wolverine survival (through food-caching activity) and reproduction success are positively influenced by a food availability (Rauset et al., 2015) . Thus, wolverine use to cache 1-6 times per carrion (van der Veen, 2017). Consequently, number of visits per carrion would be affected by the available carrion biomass on the site and by the wolverine ability to take away as much meat as possible. In line with this, one would expect that the number of visits of wolverine should be higher at wolf-killed carrion (due to the highest biomass available) than at slaughter remains after hunter harvest (characterized by a lower amount of biomass available). However, the duration of the wolverine visit, at the slaughter remains were long, and one reason for this could be that they used the slaughter reminas as a direct food source, not to cache.

Behaviour

Depending on the situation, animals could display much more of one type of behaviour compared to others and it could be displayed with different intensity. The behaviour intensity could depend on the risk the animal is experiencing (Lima & Bednekoff, 1999). If an animal is subjected to a high level of risk of predation, it could have two possibilities; the first one would be to spend a high proportion of time to vigilance behaviour with the consequence to not have enough time for feeding, the second would be to spending a high proportion of time to feeding behaviour to be able to leave as soon as possible. Moreover, if a vigilant behaviour is displayed with high proportion, the quantity of energies spent would be higher.

In my study, red fox was the species that displayed the highest proportion of vigilant behaviour at both slaughter remains after hunter harvest and wolf-killed carrion. Consequently, the proportion of feeding behaviour was lower at both types of carrion. Wolves did not show any differences between the proportions of vigilant and feeding behaviour at both type of sites. This is probably due to that wolf do not risk being predated by other species (except by humans). Pine marten displayed a higher proportion of feeding behaviour than vigilance at slaughter remains after hunter harvest. For wolverine I had a similar result: they displayed a higher proportion of feeding behaviour than vigilance at slaughter remains after hunter harvest sites. Therefore, both pine martens and wolverines might spend more time feeding than being vigilance because they have already selected a less risky site (the slaughter remains after hunter harvest one).

Limitations with the study

- First, information which could influence the results were not possible to consider in my study, e.g., habitat characteristics, time of year, what other species that are utilizing the carrion, time of day and available biomass.

- Second, due the different number of cameras put up in the field per type of sites, the amount of data collected at wolf-killed carrion sites were only one third of the data collected at slaughter remains after hunter harvest sites. This result in an unequal comparison between the two types of sites.

- Third, the raw data were compiled by different operators, everyone characterized by personal interpretation (observer-bias) of the animal behaviour displayed so the behaviour observed could have been classified in different way.

- Fourth, due to weather conditions (e. g., snow or fog) some animals' identification were not so much accurate as in the photos where the weather conditions were better, so it is possible that some photos were compiled with a wrong behaviour.

Conclusions

My findings demonstrate that factors such as the carrion origin and the risk-level to be predated by dominant predators influence the use of carrion and the behaviours displayed at different types of sites. Slaughter after hunter harvest remains and wolf-killed carrion give benefits and disadvantages to scavenger species. Wolves often provide a stable food source to scavenger species year-round. Also, humans' activities increase carrion amount due to the supply of anthropogenic food sources (e.g., remains after hunter harvest of large ungulates) but slaughter remains after hunter harvest are limited to the hunting season in the autumn. In my study the low amount of data collected at wolf-killed carrion influenced the results, avoiding making a real comparison between the two types of sites. However, the data collected were enough to determine that slaughter after hunter harvest remains are safer than wolf-killed carrion, due the lower risk of encountering predators. In addition, the amount of available biomass at slaughter after hunter harvest remains is lower compared to wolf-killed carrion. Therefore, scavenging species such as wolverine and pine marten may prefer to scavenge at slaughter remains after hunter harvest because the lower risk of predation, while red fox may prefer to scavenge at wolf-killed carrion because the carrion benefits (higher amount of available biomass) are higher.

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