# Comparing behavior and species diversity of scavengers between two areas with different density of brown bears

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Research report about the differences in diversity and behavior of scavengers at carcasses in wolf territories with high and low density of brown bears *(Ursus arctos)* in south-central Sweden.

University of Applied Sciences hasdenbosch

SKANDULV

GRIMSÖ WILDLIFE RESEARCH STATION

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# Foreword

This report is a research about the difference in diversity and behavior of scavengers between two areas with different density of brown bears in Sweden. This study is an internship by Janneke Scholten, student in Applied Biology at HAS Den Bosch University in the Netherlands. This report is accomplished under the authority and guidance of SKANDULV, which research is focused on wolf conservation and management in Sweden and Norway, at Grimsö Wildlife Research Station, Swedish University of Agricultural Sciences.

First a would like to thank Håkan Sand, my supervisor at the Grimsö Wildlife Research Station, for helping me when I had a problem with the project and for giving valuable comments on my report. Also, I thank Camilla Wikenros, my co-supervisor, for letting me use her data and help me understand these data and also for giving useful comments on my report. Lotte Bakermans was my supervisor from the HAS Den Bosch. I thank her also for the valuable comments on my report. Furthermore, I would like to thank Osama Almalik, statistic teacher at the HAS Den Bosch, for helping me with the statistical part of the project. Finally, I thank the students from HAS Den Bosch and the Grimsö Wildlife Research Station whom I could discuss my problems with and those who gave useful comments on parts of my report.

## Abstract

Scavengers are an important part of the food web. Red foxes (*Vulpus vulpus)* and common ravens (*Covus corax*) are both known to be frequent scavengers. In Sweden, grey wolves *(Canis lupus)* provide carcasses mostly from moose *(Alces alces)* for scavengers. Wikenros (2011) studied scavenging species at carcasses of wolf-killed moose. This research was done in wolf territories with a low density of brown bears *(Ursus arctos)* during several years. Studies about the effect of a high density of brown bears on the behavior of other scavenging species are nowhere to be found. Therefore, this study aimed to investigate if the behavior and species diversity of scavengers on wolf-killed moose in Sweden differed between two areas having different density of brown bears, another important scavenger on wolf-killed prey remains.

In the spring of 2011, movement trigger cameras were placed at carcasses of wolf-killed moose in a territory with a high density of brown bears. Thereafter, number of species, the proportion of detected carcasses, the scavenging frequency and the arrival time of the scavenging species were calculated. Finally, these results were compared to only the spring data of Wikenros (2011).

Red foxes, common ravens, brown bears, grey wolves and hooded crows (*Corvus corone cornix)* detected carcasses in both areas. In the high density area, also the scavenging species wolverine *(Gulo gulo)* and great-spotted woodpecker *(Dendrocopos minor)* detected carcasses. In the low density area, the species Eurasian jay *(Garrulus glandarius)*, white-tailed eagle *(Haliaeetus albicilla)*, European pine marten *(Martes martes)*, golden eagle *(Aquila chryaetos)*, Eurasian magpie *(Pica pica)* and Eurasian lynx *(Lynx lynx)* also detected carcasses. There was no significant difference in species richness at carcasses or carcass detection between the two areas.

Red foxes, common ravens and brown bears had the highest scavenging frequency. Scavenging frequency of ravens and red foxes was lower in the high density area. The presence of brown bears could have made it harder for the ravens and red foxes to scavenge, causing the lower scavenging frequency. However, ravens were seen together with brown bears at a carcass and red foxes were seen at the carcass between two feeding moments of brown bears, suggesting that the risk is low for these species when feeding near brown bears. Therefore, it seems more likely to suggest that there is a difference in density of ravens and red foxes between the areas, with a lower density in the high density bear area.

Ravens and red foxes arrived later while brown bears arrived earlier in the high density area. However, at the carcasses that were visited by red foxes, ravens and brown bears, brown bears discovered most of the carcass the latest. Furthermore, brown bears never arrived earlier than ravens. This makes it unlikely that red foxes and ravens arrived much later in the high density areas. A difference in density of red foxes and ravens could explain the difference in arrival time between the areas.

Brown bears are active from March to November. Data from the high density area were only from March to July. Therefore only a part of the data of Wikenros (2011) could be used. To improve this study more data must be obtained from the high density area from March to November.

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## 1. Introduction

Scavenging by vertebrates is known to be a part of a complex food web around a carcass. Partly consumed or unconsumed carcasses attract not only vertebrate scavengers but also *Nicrophorus* beetles and insect larvae (Houston 1978; Scott 1998; Wikenros 2011). These insects can serve as food for other animals, such as bears or birds (Houston 1978). A carcass also influences the vegetation, Towne (2000) found that one year after death the vegetation around a carcasses was more diverse compared to an area without a carcass. Therefore, a carcass can provide a niche for more species and even for species that are normally not present (DeVault et al. 2003; Melis et al. 2004). Furthermore, carcass availably may also increase reproductive success, increase survival rate and ensure a stable population of scavenging animals (Angerbjörn et al. 1991; Tannerfeldt et al. 1994; Carbone et al. 1997). Selva and Fortuna (2007) found that the community of facultative scavengers is not randomly assembled but highly nested.

Carcasses are an important food source for vertebrate scavengers and these animals are mostly found at carcasses in their own foraging habitat (DeVault et al. 2003; Selva et al. 2005). Scavengers can discover carcasses visually, by smell or by following the predator (Paquet 1991; Shivik & Clark 1997; DeVault & Rhodes 2002; Stahler et al. 2002). Common ravens *(Corvus corax)* are also attracted to vocalization from other scavengers that are present at a carcass (Heinrich 1988). Rare or sporadically scavenging species tend to associate with common scavenging species and are rarely seen on species-poor carcasses (Selva & Fortuna 2007). Snow depth and increasing temperature have also an influence on the presence of most of the scavenging species at a carcass (Huggard 1993; Gese et al. 1996; DeVault et al. 2004; Selva et al. 2005). Gese et al. (1996) found that coyotes stayed longer at a carcass, feeding and resting, with increasing snow depth and decreasing temperature. Huggard (1993) found that grey wolves (*Canis lupis)* scavenged a higher proportion in winters with deep snow than during other winters. Red foxes *(Vulpes vulpes)* increase their scavenging activity at lower temperatures, while ravens scavenge the most at a temperature of $0^{o}$C. In deep snow ravens scavenge less frequently (Selva et al. 2005). A carcass will attract the most scavengers when it still retains enough biomass and has a strong smell so that it can be detected from a distance (DeVault and Rhodes 2002).

The way scavenging species choose and use carcasses depends on their capacity to break into them, their visual and olfactory abilities, and their foraging behavior (Selva et al. 2005). For instance, ravens are unable to break into frozen, intact carcasses (Heinrich 1988; Selva et al. 2003). Furthermore, they are more often found at carcasses located in glades than in the forest, and at wolf-killed ungulates rather than at carcasses of ungulates caused by diseases or starvation (Selva et al. 2003; Selva et al. 2005). In general, mammal scavenging species consume more from a carcass in dense forests and during the night than avian scavenging species, probably because birds are limited in their ability to visually detect the carcasses in a dense forest and are more inactive during the night (Prior & Weatherhead 1991; DeVault & Rhodes 2002).

Ravens and red foxes are known to be common scavengers at carcasses (Jędrzejewski & Jędrzejewska 1992; Stahler et al. 2002; Kaczensky et al. 2005; Selva et al. 2005; Wikenros 2011). These two scavenging species depend especially on carcasses in the winter and associate with wolves to find the carcasses (Newton et al. 1982; Jędrzejewski & Jędrezejewska 1992; Stahler et al. 2002). Wolverines *(Gulo gulo*) and brown bears *(Ursus arctos)* are also known to be scavenging on ungulates wolf-kills (Clevenger et al. 1992; Mech et al. 2001; Ballard et al. 2003; Dijk et al. 2008; Wikenros 2011). Wolves often come back to their old prey (Huggard 1993).

In Sweden, throughout the whole year wolves provide carcasses of dead ungulates, mostly moose *(Alces alces)*, for scavengers (Sand et al. 2008; Wikenros 2011). Sand et al. (2008) discovered that, in Scandinavia, there is no relation between the pack size and the proportion of killed moose calves, their most important prey. This results in more food for wolves in small packs than for wolves in larger packs (≥7 wolves). Therefore there is more left over to scavengers from a carcass in small wolf packs compared to larger wolf packs.

Not only wolves provide carcasses for scavengers, also brown bears kill moose, mostly calves, in Sweden. Swenson et al. (2007) estimated a predation rate on moose calves by brown bears of 26%. Boertje et al. (1988) hypothesized that scavenging by brown bears would be more common than predation when the density of ungulates is high. Mattson (1997) found that predation was less frequent in areas with a high density of ungulates compared to areas with a low density of ungulates. These studies were done in Alaska and Yellowstone National Park, there is no currently study done on the scavenging activity of brown bears in Sweden. Studies on interactions between brown bears and other scavenging species are scarce. Some studies focused on the interactions between brown bears and wolves and about the kill rate or change in behavior of wolves when brown bears are present (Ballard et al., 2003, Metz et al. 2011). Other studies focused on the influence of two top predators or a dominant scavenger on other scavengers, by only comparing areas with and without these animals (Berger 1999; Berger et al. 2001; Olson et al. 2012).

This study was done to provide more information about the difference in diversity and behavior of scavengers at wolf-killed moose carcasses between a high and low density area of brown bears in Sweden. Pictures taken by camera traps during spring at carcasses of wolf-killed moose in a high density area of brown bears were compared with the data from the study of Wikenros (2011). Accordingly, the aims of this study were: (i) to investigate the diversity of scavenging species at carcasses of wolf-killed moose; (ii) to calculate the scavenging frequency of the most common scavenging species; (iii) to investigate the arrival time at a carcass of the most common scavenging species; (iv) to compare these results with the spring data of Wikenros (2011); and (v) evaluate any possible differences between the high and low density bear area in terms of scavenging behavior of scavenging species and species diversity.

The prediction was that the number of scavenging species and the scavenging frequency should be lower in areas with a high density of brown bears. Brown bears are larger than most of the scavenging species and larger species are usually dominant toward smaller species (Palomares & Caro 1999; Ballard et al. 2003). Ballard et al. (2003) found that brown bears won all of the encounters from wolves at feeding sites. This suggests that brown bears can probably claim large parts of the carcasses for themselves. This makes it harder for other scavenging species to scavenge and they will be seen less frequently at carcasses in the area with high brown bear density. The arrival time will probably not differ for ravens. Ravens are often found at a carcass or bait the first few days after the time of death or placement, while the arrival time of brown bears can differ from 2 to 34 days (Green et al. 1997; Heinrich 1998; Stahler et al. 2002; Kaczensky et al. 2005). On the other hand, Wikenros (2011) found that red foxes become more frequent visitors with increasing time after death of the moose. In a high density area, red foxes might come earlier to the carcass to scavenge before the brown bears claim it for themselves and leave nothing to eat behind.

# 2. Material and methods

## 2.1 Study area

The study was performed in six wolf territories in south-central Sweden, five wolf territories with a low density of brown bears and one wolf territory with a high density of brown bears (hereafter referred to low and high density areas) (fig.2.1). The pictures of carcasses of wolf-killed moose in the high density area were taken in the wolf territory Tenskog. This territory is located in the Dalarna and Gävleborg counties (61°N, 15°E) and within one of three reproduction areas of brown bears in Sweden. The density of brown bears in this area is high, approximate 30 brown bears per 1000 $km^2$ (Solberg et al. 2006). The size of the southern area of bear reproduction is 13000 $km^2$ and the wolf territory Tenskog has a surface of 1364 $km^2$. Lakes and bogs are common in these areas, but most of the area consist of coniferous forest, dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) (Friebe et al. 2001; Dahle & Swenson 2003; Bellemain et al. 2005; Solberg et al. 2006; Nelleman et al. 2007). The ground vegetation includes a variety of species of mosses, lichens, grass, heather and berries (Friebe et al. 2003). Various deciduous trees, such as downy birch (*Betula pubescens*), European white birch (*Betula pendula*), European aspen (*Populus tremula*) also occurs in the forests (Solberg 2006). The wolf territories in the low density area, used from the study of Wikenros (2011), were Ulriksberg, Gräsmark, Nyskoga, Uttersberg and Kloten. These wolf territories have a similar habitat as the wolf territory Tenskog but a more southern distribution.

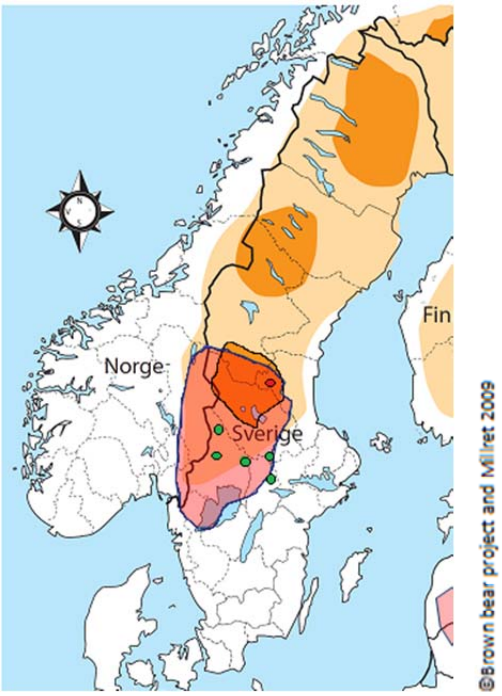


*Figure 2.1: Map of the brown bear and wolf areas in Sweden. The southern reproduction area of brown bears is marked with black lines. The area with reproducing wolves in 2009 is marked with a blue line. The red point is the wolf territory Tenskog, the green points are the wolf territories of Wikenros (2011) used in this study.*

Scavenging species in these wolf territories are red fox, common raven, Eurasian jay (*Garrulus glandarius*), European pine marten (*Martes martes)*, golden eagle (*Aquila chrysaetos*), hooded crow (*Corvus corone*), Eurasian magpie (*Pica pica)*, wild boar (*Sus scrofa*), northern goshawk *(Accipiter fasciatus*), white-tailed eagle (*Haliaeetus albicilla*), black woodpecker (*Dryocopus martius*), European badger (*Meles meles)*, common buzzard (*Buteo buteo*), great-spotted woodpecker (*Dendrocopos minor*) and Eurasian lynx (*Lynx lynx)* (Wikenros 2011).

## 2.2 The brown bear

Female brown bears emerge from the den around the 20th of April (Friebe et al. 2001). Male brown bears emerge from the dens 17 days earlier than females (Manchi & Swenson 2005). During the research of Manchi and Swenson (2005), the first male bear emerged from the den on the 6th of March. Around this time of the year and late in the winter, carcasses are an important food source for brown bears (Clevenger et al. 1992; Persson et al. 2001). Berries, insects, forbs and vegetation are also a part of the brown bears' diet (Clevenger et al. 1992; Dahle et al. 1998; Persson et al. 2001). The presence of wolves provides more dead ungulates (carcasses), thus a high protein food source for brown bears (Servheen & Knight 1993). Brown bears leave the skin of an intact carcass mostly undamaged but penetrate the abdomen. In a later phase they break the bones and tear the skin apart (Elgmork & Tjørve 1995). The first visit of a brown bear at a carcass usually occurs from two days up to 34 days after time of death (Green et al. 1997). Green et al. (1997) found that if a grizzly bear (*Ursus arctos horribilis*) finds the carcass within three days after the animals' death it probably will eat high proportions. However, the probability that they find edible biomass on a carcass decrease with increasing time after death of the animal. Mattson (1997) found that, in Yellowstone National Park, predation contributed by 30% of all ungulate biomass that the grizzly brown bears consumed. However, in April to May this contributed only 9% of the total biomass that grizzlies consumed.

## 2.3 Camera monitoring

In the spring (March to July) of 2011, movement-triggered cameras (Keep guard; STC-DVIR-HD; Scout Guard and Stealth Cam; STC-WD2-1R) were placed at carcasses of wolf-killed moose in the high density area. When a carcass was found, the time of death and the age were estimated by a field researcher. The cameras were set up the same way as Wikenros (2011) described, approximately 0.5 above ground and two to six meters away from the carcasses. The cameras took three to six pictures each minute when triggered by movement.

## 2.4. Analyzing pictures

Pictures used by Wikenros (2011) were selected by date of death of the moose and only pictures of carcasses found in March to July were used in this study. Statistical analyses were performed using SPSS v.20 for Windows (SPSS Inc., USA).

### 2.4.1. Scavenging species

The scavenging species, number of species and number of individuals was noted for each picture. Pictures without animals were classified as empty or failed pictures. Also the place and time of death of the moose, picture ID, date and time when the picture was taken, time after death and if there was more than one picture per minute was noted. An example of this table is shown in Appendix I. For all scavenging species it was noted if they discovered the carcass or not. A species was considered scavenging on a carcass when it was on the picture and known to be a scavenging species, also wolves counted as a scavenging species.

To test if certain species have a higher chance to discover a carcass than the scavenging species that discovered the fewest carcasses, a logistic regression was used. The response variable in this case is a binary variable, i.e. 0/1 variable, 0 if they did not detect the carcass and 1 if they did. The model is used to estimate the probability whether a carcass was detected or not. The following formula was used to test the probability of detecting a carcass for a specific species:

$$P_i = \frac{1}{1+e^{-(\beta_0+\beta_1 * species)}}$$

$P_i$ is the probability that a species detect more carcasses than the species that discovered the least carcasses, $\beta_0$ is the constant of the model and $\beta_1$ is the coefficient belonging to the scavenging species.

### 2.4.2. Scavenging frequency

The pictures of the carcasses were reduced to one picture per minute and empty and failed pictures were excluded. After that, the scavenging frequency was calculated. This was calculated as the number of pictures taken of a certain scavenging species at a carcass divided by the total number of pictures of animals of that carcass. For example, if a red foxes discovered five carcasses it also had five scavenging frequencies. The mean scavenging frequency was calculated by calculating the mean of all the scavenging frequencies of that species. To test for a difference in scavenging frequency between the scavenging species a one-way ANOVA was used. If there was a significant difference between the species a LSD test was used to see between which species this difference was. The test was only performed for the scavenging species that discovered more than two carcasses.

### 2.4.3. Arrival time

The arrival time of the scavenging species was noted at each carcass. The variable for the arrival time is the time after the estimated time of death of the moose when the species was first seen at the carcass. A mean arrival time is only calculated from species that discovered more than two carcasses. The same tests used for scavenging frequency was used to find a difference in arrival time between the scavenging species.

### 2.4.4. Comparing the two areas

For comparison of the proportion carcasses of detected by each of the scavenging species between the high density area and the low density area, a logistic regression was used. The following formula is used to test the probability of detecting a carcass for a specific species in a specific area:

$$P_i = \frac{1}{1+e^{-(\beta_0+\beta_1*species+\beta_2*area)}}$$

$P_i$ is the probability that a species detect more carcasses that the species that discovered the least carcasses, $\beta_0$ is the constant of the model, $\beta_1$ is the coefficient belonging to the scavenging species, and $\beta_2$ is the coefficient belonging to the area.

An unpaired t-test was used to detect a difference in species richness at carcasses. Linear mixed model was used to detect a difference in scavenging frequency and in arrival time of the corresponding scavenging species between the two areas with carcass ID as random factor. The tests were only performed for species that discovered more than two carcasses in both areas.

# 3. Results

In the high density area, nine carcasses of wolf-killed moose were monitored with movement trigger cameras (Appendix II). A total of 5147 pictures were taken of which 3116 were empty or failed pictures. When reduced to one picture per minute, 403 pictures were taken of scavenging species.

In the low density area, pictures of 16 carcasses of wolf-killed moose were used, distributed on five different wolf territories (Appendix II). A total of 22737 pictures were used of which 4365 were empty or failed pictures and when reduced to one picture per minute, 6254 pictures of scavenging species remained.

## 3.1 Scavenging species

Seven scavenging species were registered at carcasses in the high density area. The most common species were brown bear (detected 89% of the carcasses), red fox (44%) and common raven (67%). Also the wolves, wolverines, hooded crows and the great-spotted woodpecker were seen at carcasses. These scavenging species detected less than 23% of the carcasses. In the low density area, 11 scavenging species were registered at the carcasses. Here, the most common scavenging species were red fox (detected 75% of the carcasses) and common raven (62%). Eurasian jays detected 37% of all the carcasses and hooded crows detected 31%. The species brown bear, grey wolf, white-tailed eagle, European pine marten, golden eagle, Eurasian magpie and Eurasian lynx detected less than 19% of all the carcasses (Appendix III).

In general, red foxes and ravens detected the most carcasses (64% of the carcasses), followed by brown bears (44%) (Appendix III). Red foxes and ravens had a significantly higher chance to detect a carcass than the scavenging species that detected the fewest carcasses, white-tailed eagle, great spotted woodpecker and Eurasian lynx (Logistic regression, likelihood ratio test, $X^2$=81.51, p<0.001). Red foxes and ravens were 11.6 times more likely to detect a carcass than the species that discovered the fewest carcasses (p=0.001), brown bears were 7.2 times more likely to detect a carcass (p=0.007) and jays and crows were 4 times more likely to detect a carcass than the species that discovered the fewest carcasses (p=0.05) (Appendix IV). Red foxes, ravens, brown bears, wolves and crows were present in both of the areas (fig. 3.1).

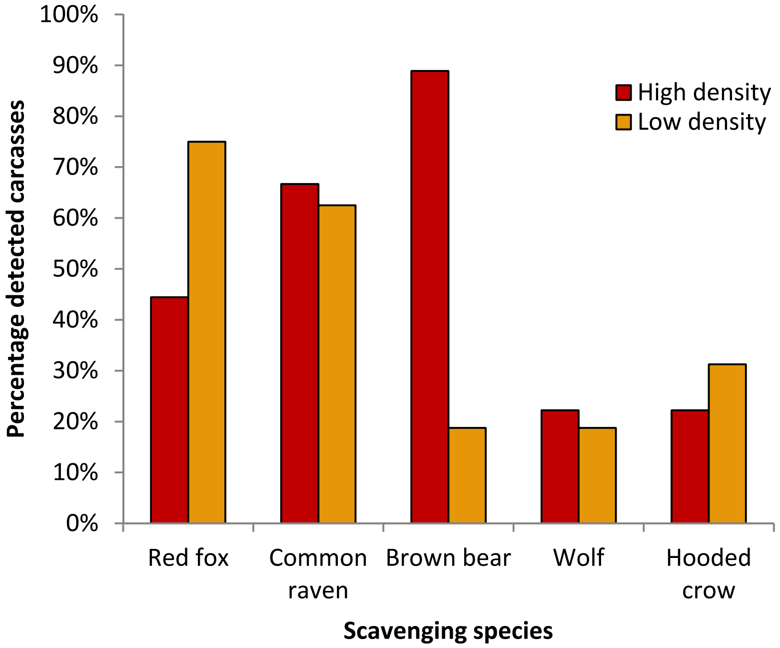


*Figure 3.1: The proportion of detected carcasses for the corresponding species in two areas with different densities of brown bears.*

There was no significant difference in species richness at the carcasses between the two areas (T-test, t=3.3538, df=23, p=0.07). It appears that there was also no significant difference in carcass detection between the two areas (Logistic regression, likelihood ratio test, $X^2$=4.30, p=0.231) (Appendix IV).

### 3.2 Scavenging frequency

In general, ravens had the highest scavenging frequency (0.46), followed by red foxes and brown bears with frequencies of 0.41 and 0.38 respectively (Appendix III). There was a significant difference in scavenging frequency between the scavenging species (ANOVA, $F_{5,56}=3.374$, $p=0.01$). Red foxes scavenged significantly more often than jays ($p=0.03$), wolves ($p=0.04$) and crows ($p=0.02$). Ravens also scavenged significantly more often than jays ($p=0.01$), wolves ($p=0.02$) and crows ($p=0.05$). Brown bears scavenged significantly more often than crows ($p=0.04$) (Appendix VI).

In the high density area, brown bears had the highest mean scavenging frequency of 0.50. Ravens and red foxes had a mean scavenging frequency of 0.31 and 0.28 relatively. In the low density area, ravens had the highest mean scavenging frequency of 0.58, followed by red foxes with a scavenging frequency of 0.46 (fig. 3.2). The scavenging frequency of jays, crows, wolves and brown bears was lower than 0.15 (Appendix III).

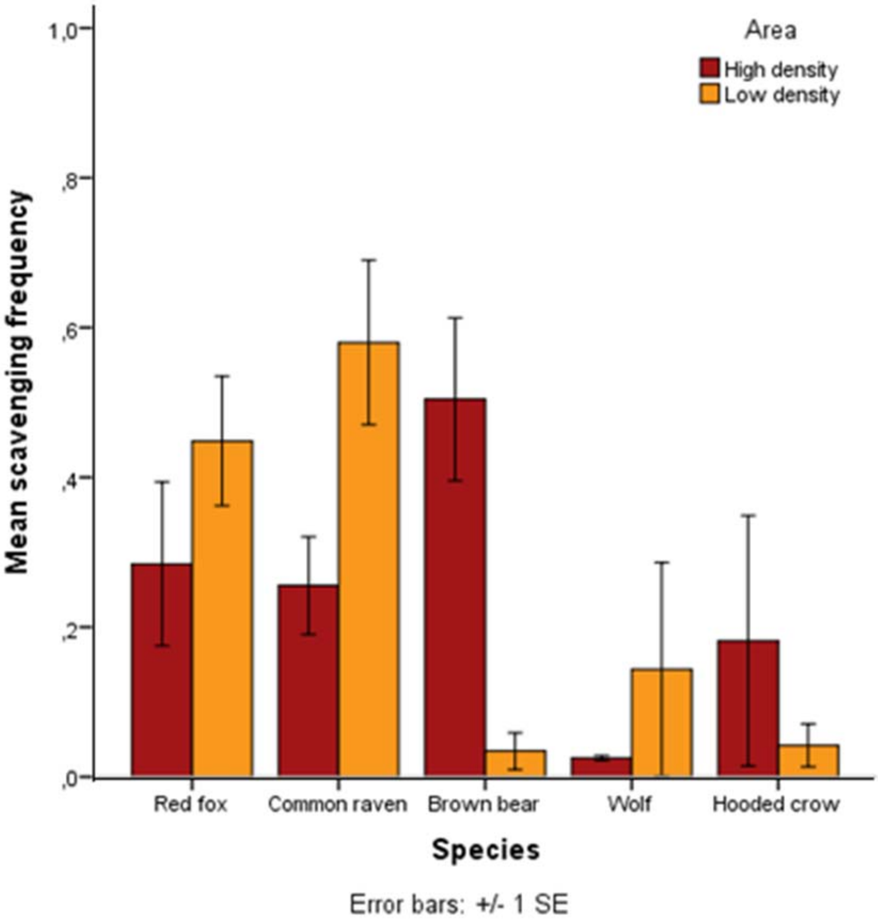


*Figure 3.2: Scavenging frequency of the corresponding species in two areas with different densities of brown bears.*

The scavenging frequency was influenced by the type of area with a lower scavenging frequency of red foxes ($p=0.01$) and ravens ($p=0.002$) and a higher scavenging frequency of brown bears ($p=0.002$) in the high density area ($F_{2,37}=6.114$, $p=0.005$) (Appendix V).

### 3.3 Arrival time

In general, wolves arrived the latest (27 days after time of death of the moose) and magpie arrived the earliest (8 days). However, there was no significant difference in arrival time between the scavenging species (ANOVA, $F_{5,56}$=0.777, p=0.6).

In the high density area, the mean arrival time of red foxes was the latest and they arrived 45 days after time of death of the moose. In the low density area, the mean arrival time of brown bears was the latest, they arrived 49 days after time of death of the moose (fig. 3.3) (Appendix III).

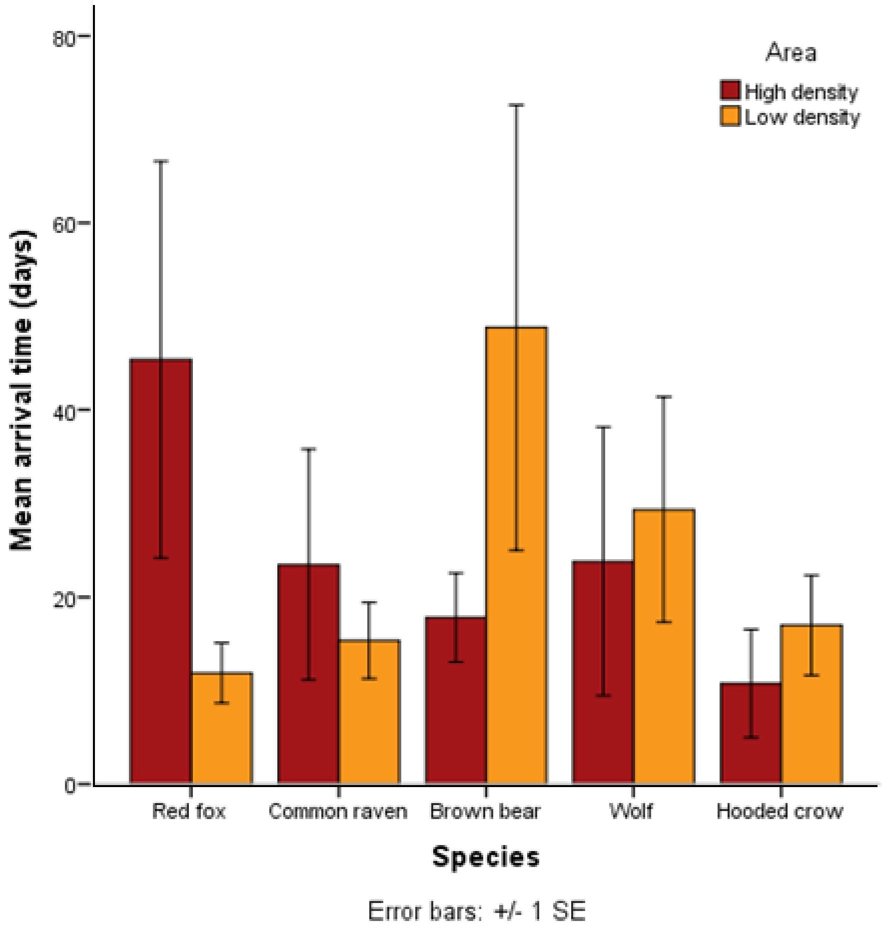


*Figure 3.2: Arrival time of the corresponding species in two areas with different densities of brown bears.*

The type of area influenced the arrival time with a later arrival time of red foxes (p=0.02) and ravens (p=0.04) in the high density area whereas the opposite pattern was evident for brown bears (p=0.04) ($F_{2,37}$=6.114, p=0.008) (Appendix VI).

## 4. Discussion

The result that in both areas ravens and red foxes had a higher chance of detecting a carcass is equivalent to the results of Selva et al. (2003; 2005). Furthermore, this study reconfirms the finding of Selva and Fortuna (2005) that ravens and red foxes were the ultimate scavengers.

As expected, ravens and red foxes scavenged less in the high density area. It could be caused by a difference in density of ravens and red foxes between the two areas. Unfortunately, it was not possible to differentiate the individuals for each species to get an index of the density of red foxes and ravens in any of the areas. Another explanation could be that brown bears make it harder for these species to scavenge. However, at one carcass a brown bear and several ravens were seen together, suggesting that the risk is low for ravens to feed near brown bears. Red foxes were seen before and after brown bears had eaten from the carcass. Even between two feeding moments of brown bears, red foxes were seen. This suggests that brown bears did not claim the carcasses for themselves and that the risk was also low for red foxes to feed at the carcasses while brown bears were still around. Finally, ravens scavenge less in deep snow and scavenged the most with a temperature of $0^{o}C$ (Selva et al. 2005). However, there was no snow at the carcasses in the high density area. The scavenging activity of red foxes increase with decreasing temperatures (Selva et al. 2005). It could be that the temperature was higher in the high density area causing a lower scavenging frequency for red foxes. On the other hand, this should cause a higher scavenging frequency for ravens.

The expectation that there would be no difference in arrival time for ravens and that red foxes arrived earlier in the high density area does not correspond with the results. However, one carcass was first discovered 79 days after time of death of the moose by a red fox. Three days later a raven was seen at the carcass. This could have affected the mean arrival time of red foxes and ravens in the high density area. On 67% of the carcasses scavenged by all the three species in the high density area, red foxes and ravens arrived earlier than brown bears at the carcasses. Furthermore, only at 33% of the carcasses in the high density area scavenged by brown bear and red foxes, brown bears arrived earlier than red foxes. Brown bears never arrived earlier than ravens in the high density areas. This makes it unlikely that ravens and red foxes arrived much later at a carcass in the high density areas while brown bears arrived earlier compared to the low density area. The same explanation given for the difference in scavenging frequency, that there could be a difference in densities of ravens and red foxes, could also have caused the difference in arrival time between the two areas. With a higher density it is more likely for a species to discover a carcass earlier. It could be that the density of red foxes and ravens is higher in the low density area causing the differences in arrival time.

Brown bears were seen at 19% of the carcasses in the low density area, while they were present at 89% of the carcasses in the high density area. In the high density area it is more likely that bears discover a carcass sooner than in the low density area due to the difference in density. However, the result of the arrival time of brown bears in the high density area is more reliable because of the higher number of data.

In both study areas wolves were not frequent visitors at carcasses after cameras were mounted though it is known that wolves come back to their old preys (Huggard 1993). Wikenros (2011) investigated if wolves, ravens and red foxes avoided the cameras. She found that red foxes and wolves were probably not affected by the cameras. However, at three carcasses they observed ravens at the time of camera set up but there were no ravens seen on the pictures of these carcasses, suggesting that raven may avoid the cameras. This may also apply to the other bird species like crows. Hooded crows are attracted to meadows, pastures and gardens around houses (Andrén 1992; Rollando & Laiolo 1994). Andrén (1992) found that they are even negatively correlated with young and old forests. This suggests that they are attracted to a more human environment. The human density is lower in the high density area than in the low density area (Sand personal communication). It could be that crows are more attracted to the low density area causing a lower density in the high density area. This could explain the fact that crows discovered five carcasses in the low density area and only two in the high density area.

The wolverine and the great-spotted woodpecker were both only present in the high density area during spring. These two species were also found by Wikenros et al. (2011) in the low density area, but in January and February. In this study they were seen at only one carcass. Van Dijk (2008) discovered that wolverines living inside wolf territories have a smaller diet and rely almost exclusively on wolf-killed moose whereas wolverines outside wolf territories relied on reindeer *(Rangifer tarandus)*, mountain hare *(Lepus timidus)*, birds and rodents. This suggests that wolverines should be frequent scavengers in wolf territories. The low number of visits by wolverines in this study could be explained by the low density of the wolverine in the study areas (Persson and Brøseth 2011). In the study of Selva and Fortuna (2007) the great-spotted woodpecker discovered the fewest number of carcasses, which is similar to the results of Wikenros (2011) and this study. This would suggest that this bird is a sporadically scavenging species.

The low number of visits of the white-tailed eagles could be caused by the low density of the white-tailed eagle in the study areas (listed as near threatened, Gärdenfors 2010). Selva and Fortuna (2007) found a low scavenging frequency for the lynx (1-10%) and Wikenros (2011) found that wolves had no influence on the lynx population. It is likely that the lynx is also a sporadically scavenging species, which explains the low proportion of detected carcasses by lynxes. Pine martens, golden eagles and magpies were seen at 13% of the carcasses. All these species prey upon small mammals (Tjernberg 1981; Storch et al. 1990; Helldin 2000; Soortenbank 2012). It could be that these species only scavenge in the winter when small rodents are rare due to the snow (Sonerund 1986). There was no snow during the research in the area with a high density of brown bears. During the study in the area with a low density of brown bears there were four carcasses with more than 20 cm snow, one carcass with 5 cm and one carcass with 2 cm snow. Magpies and pine martens were seen at one carcass with 35 cm snow and golden eagles were seen at one carcass with 25 cm of snow. It could be that pine martens, golden eagles and magpies did not have to scavenge in the area with a high density of brown bears because there were more rodents available due to the lack of snow. It is also known that pine martens and jays avoid clear cuts (Branerd and Rolstad 2002; Selva et al. 2005). However, from the nine carcasses, in the high density area, only three carcasses were in a more open area. Selva et al. (2005) found that with increasing snow depth the scavenging frequency of jays also increase. In this study, jays where recorded on seven carcasses of which three carcasses had more than 25cm of snow. The fact that there was no snow at the carcasses in the high density area could have caused the absence of jays, pine martens, golden eagles and magpies.

Common cranes (*Grus grus*), common blackbirds (*Turdus merula*) and western capercaillies (*Tetrao urogallus*) were also seen on the pictures. However, there is no literature found about these bird species scavenging at carcasses. The diet of common cranes consists of seeds, crops, insects, snails, worms but also vertebrate animals like snakes, lizard and rodents. Blackbirds eat berries, worms and insects, and the diet of western capercaillies consists of berries, shoots and stems (Soortenbank.nl 2012; RSPB 2012). Common cranes were seen at two carcasses on several pictures, it could be that the cranes were attracted to the carcass because of the number of insects, considering *Nicrophorus* beetles and insect larvae are attracted to carcasses (Scott 1998; Houston 1978; Wikenros 2011). Blackbirds and western capercaillies were only seen at three pictures, suggesting that they were probably just passing by.

In the area with a high density of brown bears, pictures were only taken from March to July. This resulted that only a part of the data of Wikenros (2011) could be used for this study. Therefore, this study provides only information about the spring, when the brown bears emerge from the den. Brown bears enter the den around the end of October (Friebe et al. 2001, Manchi & Swenson 2005).

The high scavenging frequency of brown bears is equivalent to the results of Mattson (1997). He found that, in spring, only 9% of the total biomass that grizzlies consumed was from predation, so the scavenging frequency was high during this period. On the other hand, Boertje et al. (1988) found a high predation rate of grizzly bears on moose in the spring. However, the prey availability in the study of Boertje et al. (1988) was low (11 moose per grizzly bear) while the ungulate density in the study of Mattson (1997) was high. The moose density in this study was 0.87 moose/km$^2$ in the high density area (Sand personal communication). Swenson et al. (2007) found that, in Sweden, brown bears had a relatively high predation rate of 26% on moose calves. In their study the moose density was 0.92 moose/km$^2$. Despite the high scavenging activity of brown bears in high density area, the predation rate on moose calves could still be high. Furthermore, moose calves are relatively small during their first summer and brown bears probably have consumed most of it when they leave the carcasses. Therefore, the food from the carcasses that they provide for other scavengers is probably low during this time period.

## 5. Conclusion

In this study the scavenging species red fox, common raven, brown bear, Eurasian jay, grey wolf, wolverine, hooded crow, great-spotted woodpecker, white-tailed eagle, European pine marten, golden eagle, Eurasian magpie and Eurasian lynx were seen at carcasses of wolf-killed moose in south-central Sweden.

Red foxes, ravens, brown bears, jays and crows had a significantly higher chance to detect a carcass than the scavenging species that detected the fewest carcasses, white-tailed eagle, great-spotted woodpecker and Eurasian lynx. Red foxes and ravens scavenged significantly more frequent than jays, wolves and crows. Brown bears scavenged significantly more frequent than crows. There was no difference in arrival time between the scavenging species.

Ravens, red foxes, brown bears, wolves and crows were seen in both areas. However, wolves and crows detected not enough carcasses to test for a difference in scavenging frequency or arrival time between the two areas. Table 5.3 shows a summary table of the conclusions of the tests used for ravens, red foxes and brown bears to compare the two areas.

*Table 5.3: Summary table comparing the carcass detection, scavenging frequency and arrival time of three corresponding species in the areas with a high density compared to the area with a low density of brown bears.*

| Scavenging species | Carcass detection | Scavenging frequency | Arrival time |
|---|---|---|---|
| Common raven | No sig. | Lower | Later |
| Red fox | No sig. | lower | Later |
| Brown bear | No sig. | Higher | Earlier |

Brown bears probably do not provide a lot of food to other scavengers, because they kill mostly moose calves and consume most of their prey. Despite of their high scavenging frequency on wolf killed carcasses, there was no difference in species richness or carcass detection between the different areas. However, there was a difference in scavenging frequency and arrival time of the two most common scavengers at carcasses of wolf-killed moose.

There were nine carcasses in only one wolf territory and from one year, while data from the low density area were from 16 carcasses in five wolf territories and from three years. This could have caused a less reliable result for the high density area. To improve this study pictures of more carcasses must be obtained from the high density area. More carcasses could be found by using more wolf territories. This would also improve the reliability. Furthermore, brown bears are active from March to November. The data used in this study is from March to July. To have cameras from March to November in wolf territories with a high density of brown bears would be desirable.

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## Appendix I

*Table I: An example of the table to fill in data from the pictures*

| Place | Time of death | Picture ID | Date and time (picture) | Time after death | Number of species | Number of individuals (per species) | Species/ Empty picture/ Failed picture | Doublets* (Yes/No) |
|---|---|---|---|---|---|---|---|---|
| **Lindsberg** | 2011-04-29 21:00 | PICT0001.JPG | 2011-05-01 12:15 | 1.64 | 1 | 1 | Raven | Yes |
| | | PICT0002.JPG | 2011-05-01 12:18 | 1.64 | 1 | 1 | Raven | Yes |
| | | PICT0003.JPG | 2011-05-01 15:43 | 1.78 | 1 | 1 | Raven | Yes |
| | | PICT0004.JPG | 2011-05-01 15:49 | 1.78 | 0 | 0 | Failed picture | Yes |
| | | PICT0005.JPG | 2011-06-01 10:05 | 2.55 | 1 | 1 | Raven | Yes |
| | | PICT0006.JPG | 2011-06-01 10:09 | 2.55 | 1 | 1 | Raven | Yes |
| | | PICT0007.JPG | 2011-06-01 11:00 | 2.58 | 1 | 1 | Raven | Yes |
| | | PICT0008.JPG | 2011-06-01 111:13 | 2.59 | 0 | 0 | Empty picture | Yes |
| | | PICT0009.JPG | 2011-06-01 11:14 | 2.59 | 0 | 0 | Empty picture | Yes |
| | | PICT0010.JPG | 2011-06-01 12:30 | 2.65 | 1 | 1 | Red fox | Yes |
| | | PICT0011.JPG | 2011-06-01 13:11 | 2.67 | 1 | 1 | Red fox | Yes |

*more than 1 picture per minute

## Appendix II

*Table II: Information about the nine different carcasses in the high density area*

| Place | Adult/ yearling /calf | Date/time estimated of the death | %consumed on the carcass at the start | %consumed on the carcass at the end | Date/Time of the start up | Date/Time of the End |
|---|---|---|---|---|---|---|
| Abborrtjärn | Calf | 14-4-2011 23:00 | 100% | 100% | 21-4-2011 12:00 | 28-6-2011 |
| Ehns | Calf | 2-5-2011 6:00 | 95% | 100% | 8-5-2011 17:00 | 31-5-2011 |
| Högsten | Calf | 9-5-2011 3:00 | 80% | 80% | 16-5-2011 18:00 | 28-6-2011 |
| Lindsberg* | Calf | 29-4-2011 21:00 | 90% | 95% | 1-5-2011 11:30 | 28-6-2011 |
| Risberget* | Yearling | 29-3-2011 2:00 | 98% | 100% | 18-4-2011 12:00 | 28-6-2011 |
| Rickonen | Calf | 18-4-2011 11:00 | 98% | 100% | 22-4-2011 15:00 | 28-6-2011 |
| S.Hedbäcken | Adult | 11-6-2011 | 70% | Unknown | 12-6-2011 2:30 | 28-6-2011 |
| S.Stensjön | yearling | 28-5-2011 | 65% | Unknown | 30-5-2011 14:30 | 28-6-2011 |
| Tenskog | Adult | 16-4-2011 | 95% | 95% | 21-4-2011 11:00 | 30-5-2011 |

*The moose carcasses from Lindsberg and Risberget are male. The gender of the other carcasses are unknown.

*Table III: Information about the 16 different carcasses in the low density area*

| Place | Year | Age (years) | Date/time estimated of the death | %consumed on the carcass at the start | %consumed on the carcass at the end | Date/Time of the start up | Date/Time of the End |
|---|---|---|---|---|---|---|---|
| S. Siksjön* | 2006 | 1-2 | 23-3-2006 2:00 | 0-85% | 0-85% | 29-3-2006 11:16 | 10-4-2006 10:28 |
| Svartbergsfallet | 2006 | 0-1 | 5-4-2006 4:00 | 0-85% | 0-85% | 10-4-2006 21:00 | 30-4-2006 15:06 |
| Gällingsbergen* | 2007 | 0-1 | 5-3-2007 0:00 | 90-95% | 100% | 7-3-2007 20:13 | 25-4-2007 7:13 |
| Venberget** | 2007 | 1-2 | 21-3-2007 17:05 | 0-85% | 90-95% | 3-4-2007 17:57 | 27-6-2007 15:44 |
| Skallbytäppan** | 2007 | 0-1 | 29-3-2007 0:00 | 100% | 100% | 3-4-2007 20:22 | 11-6-2007 10:22 |
| Mengkroken* | 2007 | 2+ | 6-4-2007 2:06 | 0-85% | 90-95% | 25-4-2007 13:47 | 30-6-2007 9:50 |
| Hedströmmen** | 2007 | 1 | 13-5-2007 4:01 | 0-85% | 100% | 14-5-2007 14:40 | 29-6-2007 12:21 |
| Nyängen** | 2007 | 2 | 20-5-2007 4:00 | 0-85% | 100% | 21-5-2007 16:22 | 26-6-2007 13:52 |
| Oxtorp | 2008 | 0-1 | 8-3-2008 18:01 | 0-85% | 90-95% | 13-3-2008 9:40 | 14-5-2008 14:08 |
| Gräsberget** | 2008 | 1-2 | 16-3-2008 20:00 | 0-85% | 100% | 21-3-2008 17:02 | 30-6-2008 1:00 |
| Granhult | 2009 | 0-1 | 22-3-2009 22:00 | 90-95% | 100% | 25-3-2009 10:59 | 29-4-2009 14:00 |
| Sandsjöåsen* | 2009 | 2-1 | 25-3-2009 7:00 | 0-85% | 100% | 27-3-2009 10:51 | 2-6-2009 0:22 |
| Harfallsberget | | 0-1 | 15-4-2009 3:02 | 90-95% | 100% | 21-4-2009 10:03 | 13-5-2009 12:00 |
| Ölsjön | | 1 | 5-5-2009 0:00 | 90-95% | 100% | 13-5-2009 8:23 | 15-6-2009 15:11 |
| St Gäddtjärnen | | 1 | 12-5-2009 20:00 | 0-85% | 100% | 14-5-2009 8:46 | 17-6-2009 11:08 |
| Källtjärn | | 1 | 17-6-2009 23:00 | 0-85% | 0-85% | 21-6-2009 16:15 | 30-6-2009 18:58 |

Carcasses with * are female, carcasses with ** are male, the sex is unknown of the carcasses without star

## Appendix III

*Table IV: The proportion detected carcasses, the scavenging frequency and the arrival time of the scavenging species in both areas (n=25).*

| Scavenging species | Number detected carcasses | Proportion | Mean scavenging frequency | Mean arrival time (days) |
|---|---|---|---|---|
| Red fox | 16 | 0.64 | 40.75% | 20.26 |
| Common raven | 16 | 0.64 | 45.75% | 18.40 |
| Brown bear | 11 | 0.44 | 37.62% | 26.28 |
| Eurasian jay | 7 | 0.28 | 12.54% | 8.80 |
| Hooded crow | 7 | 0.28 | 8.19% | 15.22 |
| Wolf | 5 | 0.2 | 9.63% | 27.13 |
| Wolverine | 2 | 0.08 | - | - |
| Golden eagle | 2 | 0.08 | - | - |
| European pine marten | 2 | 0.08 | - | - |
| Eurasian magpie | 2 | 0.08 | - | - |
| White-tailed eagle | 1 | 0.04 | - | - |
| Eurasian lynx | 1 | 0.04 | - | - |
| Great-spotted woodpecker | 1 | 0.04 | - | - |

*Table V: The proportion detected carcasses. the scavenging frequency and the arrival time of the scavenging species in the high density area (n=9).*

| Scavenging species | Number detected carcasses | Proportion | Mean scavenging frequency | Mean arrival time |
|---|---|---|---|---|
| Brown bear | 8 | 0.889 | 50.43% | 17.82 |
| Common raven | 6 | 0.667 | 25.30% | 23.46 |
| Red fox | 4 | 0.444 | 28.43% | 45.39 |
| Wolf | 2 | 0.222 | - | - |
| Wolverine | 2 | 0.222 | - | - |
| Hooded crow | 2 | 0.222 | - | - |
| Great-spotted woodpecker | 1 | 0.111 | - | - |

*Table VI: The proportion detected carcasses, the scavenging frequency and the arrival time of the scavenging species the low density area (n=16).*

| Scavenging species | Number detected carcasses | Proportion | Mean scavenging frequency | Mean arrival time (days) |
|---|---|---|---|---|
| Red fox | 12 | 0.75 | 44.85% | 11.89 |
| Common raven | 10 | 0.625 | 58.01% | 15.36 |
| Eurasian jay | 7 | 0.375 | 12.54% | 8.80 |
| Hooded crow | 5 | 0.313 | 4.19% | 17.00 |
| Wolf | 3 | 0.188 | 14.37% | 29.30 |
| Brown bear | 3 | 0.188 | 3.45% | 48.82 |
| Golden eagle | 2 | 0.125 | - | - |
| European pine marten | 2 | 0.125 | - | - |
| Eurasian magpie | 2 | 0.125 | - | - |
| White-tailed eagle | 1 | 0.063 | - | - |
| Eurasian lynx | 1 | 0.063 | - | - |

## Appendix IV

*Table VII: Results of the logistic regression for the carcass detection in both areas (n=25)*

| Scavenging species | | Nagelkerke | Hosmer and Lemeshow | P |
|---|---|---|---|---|
| Red fox | Percentage correct: 81.8% | 0.338 | $X^2$=11.557 | P=0.001 |
| Common raven | | | sig.= 0.116 | p=0.001 |
| Brown bear | | | | p=0.007 |
| Eurasian jay | | | | p=0.045 |
| Wolf | | | | p=0.115 |
| Hooded crow | | | | p=0.045 |
| Eurasian magpie | | | | p=0.559 |
| Golden eagle | | | | p=0.559 |
| European pine marten | | | | p=0.559 |
| Wolverine | | | | p=0.559 |
| Eurasian lynx | | | | p=1 |
| White-tailed eagle | | | | p=1 |
| Great-spotted woodpecker | | | | - |

*Table VIII: Results of the logistic regression for the difference in carcass detection between the two areas*

| Scavenging species | | Nagelkerke | Hosmer and Lemeshow | P |
|---|---|---|---|---|
| Red fox | Percentage correct: 70.7% | 0.075 | $X^2$< 0.001 | p= 1 |
| Common raven | | | sig.= 1 | p= 0.2 |
| Brown bear | | | | p= 0.3 |

## Appendix V

*Table IX: Results of the LSD for the scavenging frequency of all species who discovered more than two carcasses*

| (I) Species | (J) Species | Mean Difference (I-J) | Std. Error | Sig. | 95% Confidence Interval Lower Bound | Upper Bound |
|---|---|---|---|---|---|---|
| Red fox | Common raven | -,050896328 | ,100943601 | ,616 | -,25311066 | ,15131800 |
| | Brown bear | ,031329600 | ,111827685 | ,780 | -,19268817 | ,25534737 |
| | Eurasian jay | ,282038548* | ,129383440 | ,033 | ,02285237 | ,54122472 |
| | Wolf | ,311187892* | ,146281175 | ,038 | ,01815148 | ,60422430 |
| | Hooded crow | ,325554495* | ,129383440 | ,015 | ,06636832 | ,58474067 |
| Common raven | Red fox | ,050896328 | ,100943601 | ,616 | -,15131800 | ,25311066 |
| | Brown bear | ,082225929 | ,111827685 | ,465 | -,14179184 | ,30624370 |
| | Eurasian jay | ,332934876* | ,129383440 | ,013 | ,07374870 | ,59212105 |
| | Wolf | ,362084220* | ,146281175 | ,016 | ,06904781 | ,65512063 |
| | Hooded crow | ,376450823* | ,129383440 | ,005 | ,11726465 | ,63563700 |
| Brown bear | Red fox | -,031329600 | ,111827685 | ,780 | -,25534737 | ,19268817 |
| | Common raven | -,082225929 | ,111827685 | ,465 | -,30624370 | ,14179184 |
| | Eurasian jay | ,250708947 | ,138043092 | ,075 | -,02582459 | ,52724249 |
| | Wolf | ,279858291 | ,153993516 | ,075 | -,02862779 | ,58834437 |
| | Hooded crow | ,294224894* | ,138043092 | ,037 | ,01769135 | ,57075844 |
| Eurasian jay | Red fox | -,282038548* | ,129383440 | ,033 | -,54122472 | -,02285237 |
| | Common raven | -,332934876* | ,129383440 | ,013 | -,59212105 | -,07374870 |
| | Brown bear | -,250708947 | ,138043092 | ,075 | -,52724249 | ,02582459 |
| | Wolf | ,029149344 | ,167178486 | ,862 | -,30574941 | ,36404809 |
| | Hooded crow | ,043515947 | ,152612380 | ,777 | -,26220339 | ,34923528 |
| Wolf | Red fox | -,311187892* | ,146281175 | ,038 | -,60422430 | -,01815148 |
| | Common raven | -,362084220* | ,146281175 | ,016 | -,65512063 | -,06904781 |
| | Brown bear | -,279858291 | ,153993516 | ,075 | -,58834437 | ,02862779 |
| | Eurasian jay | -,029149344 | ,167178486 | ,862 | -,36404809 | ,30574941 |
| | Hooded crow | ,014366603 | ,167178486 | ,932 | -,32053215 | ,34926535 |
| Hooded crow | Red fox | -,325554495* | ,129383440 | ,015 | -,58474067 | -,06636832 |
| | Common raven | -,376450823* | ,129383440 | ,005 | -,63563700 | -,11726465 |
| | Brown bear | -,294224894* | ,138043092 | ,037 | -,57075844 | -,01769135 |
| | Eurasian jay | -,043515947 | ,152612380 | ,777 | -,34923528 | ,26220339 |
| | Wolf | -,014366603 | ,167178486 | ,932 | -,34926535 | ,32053215 |

**The mean difference is significant at the 0.05 level*

*Table X: Results of the linear mixed model for the scavenging frequency for red foxes, ravens and brown bears.*

| Model | Variables | Coefficient | SE | t | P |
|---|---|---|---|---|---|
| Compared to brown bear | Intercept | -0.152 | 0.192 | -0.788 | 0.436 |
| | High density | 0.296 | 0.212 | 1.297 | 0.171 |
| | Low density | 0* | | | |
| | Red fox | 0.458 | 0.179 | 2.555 | 0.015 |
| | Common raven | 0.556 | 0.181 | 3.072 | 0.004 |
| | Brown bear | 0* | | | |
| | High density*Red fox | -0.667 | 0.245 | -2.720 | 0.010 |
| | High density*Common raven | -0.793 | 0.234 | -3.393 | 0.002 |
| | High density*Brown bear | 0* | | | |
| | Low density*Red fox | 0* | | | |
| | Low density*Common raven | 0* | | | |
| | Low density*Brown bear | 0* | | | |
| Compared to common raven | Intercept | 0.404 | 0.135 | 2.994 | 0.005 |
| | High density | -0.297 | 0.174 | -2.855 | 0.007 |
| | Low density | 0* | | | |
| | Red fox | -0.098 | 0.119 | -0.821 | 0.417 |
| | Brown bear | -0.556 | 0.181 | -3.071 | 0.004 |
| | Common raven | 0* | | | |
| | High density*Red fox | 0.127 | 0.214 | 0.593 | 0.557 |
| | High density*Brown bear | 0.793 | 0.234 | 3.393 | 0.002 |
| | High density*Common raven | 0* | | | |
| | Low density*Red fox | 0* | | | |
| | Low density*Brown bear | 0* | | | |
| | Low density*Common raven | 0* | | | |

**This coefficient is set to zero because it is redundant*

## Appendix VI

*Table XI: Results of the linear mixed model for the arrival time of red foxes, ravens and brown bears*

| Model | Variables | Coefficient | SE | t | P |
|---|---|---|---|---|---|
| Compared to brown bear | Intercept | 48.819 | 12.544 | 3.892 | <0.001 |
| | High density | -30.997 | 14.709 | -2.107 | 0.042 |
| | Low density | 0* | | | |
| | Red fox | -36.934 | 14.025 | -2.633 | 0.012 |
| | Common raven | -33.457 | 14.303 | -2.339 | 0.025 |
| | Brown bear | 0* | | | |
| | High density*Red fox | 64.499 | 19.332 | 3.336 | 0.002 |
| | High density*Common raven | 39.098 | 18.500 | 2.113 | 0.041 |
| | High density*Brown bear | 0* | | | |
| | Low density*Red fox | 0* | | | |
| | Low density*Common raven | 0* | | | |
| | Low density*Brown bear | 0* | | | |
| Compared to common raven | Intercept | 15.362 | 6.871 | 2.236 | 0.031 |
| | High density | 8.100 | 11.220 | 0.722 | 0.475 |
| | Low density | 0* | | | |
| | Red fox | -3.477 | 9.303 | -0.374 | 0.711 |
| | Brown bear | 33.457 | 14.303 | 2.339 | 0.025 |
| | Common raven | 0* | | | |
| | High density*Red fox | 25.401 | 16.830 | 1.509 | 0.140 |
| | High density*Brown bear | -39.098 | 18.500 | -2.113 | 0.041 |
| | High density*Common raven | 0* | | | |
| | Low density*Red fox | 0* | | | |
| | Low density*Brown bear | 0* | | | |
| | Low density*Common raven | 0* | | | |

**This coefficient is set to zero because it is redundant*