Wolf inter-territorial variation in prey use and selection in a multi-ungulate system

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Abstract

Grey wolves (*Canis lupus*), as generalists and opportunistic predators, are highly adaptable and have shown to thrive on a wide variety of prey species. The wolf population in Scandinavia has recently been expanding from prey systems dominated by moose (*Alces alces*) and roe deer (*Capreolus capreolus*) in central Scandinavia to more southern areas in Sweden where multiple ungulate species are potential prey. This study investigated the inter-territorial variation in feeding behaviour of wolves in pairs and packs across Sweden, using a new DNA-method for prey detection on 1564 wolf scat samples. Based on the frequency of occurrence of prey species in the scats, the diet of wolves was mainly dominated by large ungulates with moose as the main prey in central Sweden, and roe deer followed by moose in southern Sweden. Wolves expanded their diet by including a higher proportion of alternative ungulate species where their abundance increased towards the south. Comparing prey selection across wolf territories showed that moose was overall selected, roe deer was consumed proportional to its abundance and red deer (*Cervus elaphus*), fallow deer (*Dama dama*) and wild boar (*Sus scrofa*) were in general avoided, but with a large variation among territories. Wolves' selection for moose was negatively influenced by high abundances of fallow deer, suggesting dietary shifts due to the presence of alternative prey species. These findings have management and conservation implications by showing how the presence of alternative ungulate species lowered the consumption and selection of the main prey, moose.

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1. Introduction

Understanding animals' feeding behaviour and diet is crucial for both their management and conservation (Thirgood et al. 2000; Jordan 2005; Margalida et al. 2009; Castle et al. 2020). Measuring the way animals use their niche is essential to gain insights not only into how they use resources, but also into the way they interact with other species in the environment (Whittaker et al. 1973; Wilson 1975; Fischer & B. Lindenmayer 2006; Wanniarachchi et al. 2022). As top predators, large carnivores have the potential to affect the whole community and the food web in different ways (Ritchie & Johnson 2009; Ripple et al. 2014). For example, top predators can cause trophic cascades and thus affect other trophic levels in the ecosystem with their presence (Estes et al. 2011; Ritchie et al. 2012; Ripple et al. 2014). The diet of large carnivores has been studied extensively as they often influence many species in their environment by direct predation, through altering the behaviour of their prey, or through competition with other predators (Ritchie & Johnson 2009; Ripple et al. 2014). These interactions tend to become more complex in increasingly anthropogenic environments (Dorresteijn et al. 2015; Ausilio et al. 2021).

In Europe, large carnivores faced a drastic decline during the nineteenth and early to mid-twentieth century (Boitani & Linnell 2015) when habitat loss and fragmentation as well as human persecution extirpated their presence or severely reduced their numbers in many areas (Chapron et al. 2014; Ripple et al. 2014). However, Eurasian lynx (*Lynx lynx*), brown bears (*Ursus arctos*), grey wolves (*Canis lupus*), and wolverines (*Gulo gulo*) all showed increased populations during the last century and are now more widespread across Europe than in the past (Chapron et al. 2014). Since the 1970s, restoration of wild ungulate populations and forest communities also contributed to the expansion of predators through natural dispersal or reintroductions (Linnell et al. 2010). Especially in Europe, where large carnivores and humans often share the landscape and resources, an increased understanding of their feeding ecology can be an important tool for conservation and management of both predators and their prey (Kuijper et al. 2016).

Wolves are generalists and opportunistic predators with a widespread distribution across various ecosystems (Peterson & Ciucci 2003). Their diet primarily consists of wild ungulate species, but because of their high degree of behavioural and dietary plasticity, they may also survive on a broader variety of prey, such as smaller species, domestic animals or fish (Mech & Peterson 2003; Peterson & Ciucci 2003). Nowadays, wolves and their interactions with prey are the world's most studied large carnivore (Ripple et al. 2014; Zimmermann 2014). Perhaps one of the most iconic and intensively studied predator-prey system is the reintroduction of wolves into Yellowstone National Park (e.g. Smith et al., 2003; Ripple & Beschta, 2012). These studies provided insights into trophic interactions and cascades (Ripple & Beschta 2012; Kuijper et al. 2016; Beschta et al. 2018). Research on wolf diet also offers valuable insights into other aspects of wolf ecology, including human-wildlife conflicts. One prevalent conflict involving wolves is their depredation on livestock, a widespread issue, particularly in Europe (Pereira & Navarro 2015). Here, studies have shown how predation on livestock increases when abundances of wild ungulates are reduced (Meriggi et al. 2011; Newsome et al. 2016), which underscores the complex interplay between predator behavior and prey availability.

Diet and feeding behaviour of predators can be characterized in different ways. Prey use is the proportional consumption of a prey species within the diet, whereas prey preference or selection occurs when a specific prey species is consumed disproportionally more than its availability in the environment (Hayward & Kerley 2005; Elbroch & Wittmer 2013). Avoidance of a certain prey species, on the other hand, can be defined as killing proportionally fewer prey than expected based on their availability in the environment (Hayward & Kerley 2005). Prey switching occurs when the preference for a prey species changes with the density of that species in the environment (Murdoch 1969; Murdoch & Oaten 1975). Generalist predators, often generate stability in their prey populations by “switching” between prey species when their relative abundances fluctuate (Murdoch 1969; Murdoch & Oaten 1975). Wolves in Yellowstone preferred the more vulnerable elk (*Cervus elaphus*), but are hypothesised to shift their diet to consuming more bison (*Bison bison*) when elk becomes rare relative to bison (Garrott et al. 2007). However, in that system wolves maintained a strong preference towards elk even when bison became nearly twice as abundant as the elk was considered the more vulnerable and therefore safer prey (Tallian et al. 2017). In a Mediterranean region in Italy, fallow deer (*Dama dama*) was selected by wolves, whereas roe deer (*Capreolus capreolus*) was avoided and wild boar (*Sus scrofa*) was used according to their availability (Ferretti et al. 2019). While the feeding behaviour in two-prey systems may be simpler to study, multi-prey systems add complexity given the different prey species available to wolves. There is a relatively small body of literature on the feeding behavior of wolves in multi-prey systems (Jędrzejewski et al. 2000; Nowak et al. 2011; Jędrzejewski et al. 2012; Ferretti et al. 2019; Guimarães et al. 2022), and the results are often context-dependent, which underscores the necessity for further research in multi-prey systems.

Wolf diet has been investigated with a variety of techniques. Kill site investigation of VHF- or GPS-collared wolves is an established method but likely underestimates the use of smaller prey species (Zimmermann et al., 2007; Sand et al., 2008; Webb et al., 2008). In some cases, stomach content of dead predators has been used to assess diet but differences in digestibility and the absence of stomach content in dead retrieved animals can bias the data. Non-invasive methods include traditional scat analysis which has been widely used by the macroscopic analysis of hard remains of consumed food items within predator scats (e.g. Ciucci et al., 1996, 2004). Stable isotope analyses on stomach content or scats is another method to study diet (DeNiro & Epstein 1981; Dalerum & Angerbjörn 2005) but has limitations when looking at taxonomic resolution and distinguishing species (Codron et al. 2012). More recently, new approaches based on the molecular analysis of predator scats have been developed to identify prey DNA by means of diagnostic PCR or metabarcoding (Rennstam Rubbmark et al. 2019; Massey et al. 2021; Roffler et al. 2021, 2023). Traditional macroscopic scat analyses have benefits, for instance allowing to calculate volume or biomass of prey. Molecular analyses of predator scats, on the other hand, detect more prey species which can be overlooked or cannot be distinguished at the species level with macroscopic analysis (Mumma et al. 2016). Further, a newly developed and validated molecular method using diagnostic PCR with multiple species-specific markers is available, where the processing of bioinformatic data is limited and costs per sample reduced (Di Bernardi et al., 2021, 2023). This method takes advantage of the Nanofluidic array technology (Fluidigm Inc.), which is already employed for species determination or individual identification in multiple species (Nichols & Spong 2017; Blåhed et al. 2018).

After their recolonization in the early 1980's, wolves in central Scandinavia have mainly been distributed in areas where moose (*Alces alces*) is the main prey (Sand et al. 2005, 2008; Zimmermann 2014). However, in areas with higher densities of roe deer, wolves' predation patterns were affected by the density of this smaller alternative ungulate prey (Sand et al. 2016). More recently, the wolf population has expanded further south into areas in Sweden where alternative wild ungulate species (i.e., red deer, fallow deer, and wild boar) are available at higher densities in addition to moose and roe deer (Rodríguez-Recio et al. 2022). A recent study using a DNA-method on wolf scats in Sweden gave first insights on how the use of moose and roe deer by wolves was affected by the abundance of red deer, fallow deer and wild boar in the environment, highlighting the important role of alternative ungulates on the use of their main prey species in this system (Di Bernardi 2022).

When wolves have access to a wider range of potential prey, the dynamics between wolves and ungulates may change, which is likely to have an impact on the management and conservation of predator and prey (Sand et al. 2016; Rodríguez-Recio et al. 2022).

This research aims to gain new insights into prey use and selection of wolves, particularly in the southern parts of Sweden where multiple ungulate species occur. Specifically, we investigated the variation in the diet among wolf pairs and packs in central and south Sweden. A DNA-based analysis for prey detection was used on 1564 wolf scats collected during 2012-2022 within the genetic monitoring of the Scandinavian wolf population. The objectives of the study were to: i) compare prey use among different wolf territories and consider how this use was influenced by the local abundance of wild ungulate species (moose, roe deer, red deer, fallow deer and wild boar), ii) investigate prey selection of wild ungulates species among different wolf territories, and iii) examine how the selection of moose and roe deer was affected by the local abundance of wild ungulate species. We predicted a broader diet in the south where more alternative ungulate species are available (P1). Also, we predicted a higher overall selection of moose (P2), and a higher use of alternative ungulate species along with their increased abundance (P3).

2. Methods

2.1 Study system

This study was conducted in central and southern parts of Sweden, between 56°N and 64°N (Figure 1). Due to extensive hunting, the wolf was reduced to very low numbers in Scandinavia (Laikre et al. 2013) and considered functionally extinct in the late 1960s (Wabakken et al. 2001). After their natural immigration and expansion, wolves have now recolonised parts of Scandinavia and are likely expanding further in the future (Recio et al. 2018; Rodríguez-Recio et al. 2022). The Scandinavian population is mostly concentrated in south-central Sweden and south-east Norway with lower occurrences in southern and northern Sweden. The last monitoring counted 510 wolf individuals in Scandinavia, 450 of which in Sweden during the winter of 2022/2023 (Svensson et al. 2023). This geographical distribution is not caused by habitat suitability but mainly due to anthropogenic decisions. Indeed, as a highly adaptable species, wolves could potentially occupy most parts of Scandinavia but are restricted by the high probability of human-caused mortality (Recio et al. 2018). In the reindeer husbandry area where wolf settlement is not tolerated due to political decisions, wolf individuals immigrating from Finland and Russia seldom settle and reproduce (Wabakken et al. 2001; Karlsson et al. 2007; Åkesson et al. 2016; Recio et al. 2018; Rodríguez-Recio et al. 2022).

Central Sweden is dominated by boreal forest with mainly coniferous tree species consisting of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) and some deciduous tree species, like birch (*Betula* spp.) (Christiansen 2014). Tree compositions change following a latitudinal gradient with more and more broad-leaved species in the south, especially the far south of Sweden, which is part of the nemoral zone, characterized by mainly broad-leaved species. The most common broad-leaved tree species increasing towards the south are aspen (*Populus tremula*), alder (*Alnus glutinosa*), beech (*Fagus sylvatica*) and oak (*Quercus robur*). Forests in Sweden are managed with a cycle of clear-cutting and regeneration, resulting in a patchy landscape with variable forest growth (Christiansen 2014). The ecosystem includes a variety of large mammalian prey species, the five main ungulate species being moose, roe deer, red deer, fallow deer and wild boar. Mouflon (*Ovis aries musimon*) occurs in low numbers in very confined areas in the counties of Södermanland and Västra Götaland. Smaller prey species include for example hares (*Lepus europeus* and *Lepus timidus*) and forest birds such as Western capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*). In addition to wolves, the study area hosts other large predators, including lynx in various parts and both brown bears and wolverines exclusively in the northern region. Smaller predator species include European badger (*Meles meles*) and red fox (*Vulpes vulpes*) (Sand et al., 2008; Chapron et al., 2014, www.jagareforbundet.se, www.artfakta.se). The area also holds livestock species such as sheep (*Ovis aries*) and cattle (*Bos taurus*), which increase in their density towards the south and are not kept free ranging in Sweden (Linkowski et al. 2017; Dalerum et al. 2020).

2.2 Wolf scat collection and selection

Scat samples were collected in Sweden as part of the genetic monitoring of the Scandinavian wolf population. All samples were collected during monitoring seasons which run from 1st October until 31st March (Åkesson et al. 2022). This study includes scats collected in wolf territories from central and southern Sweden during the monitoring seasons of 2012/2013 until 2022/2023, hereafter referred to by the first year only, e.g. 2022 for 2022/2023 (Figure 1). An additional collection effort was made during 2022 to increase the number of scats collected per territory in multi-ungulate areas in southern Sweden, where wolves have been establishing in the recent years. Scat collection in the field was conducted by car or on foot depending on the terrain. The collector gathered all collectable scats which were believed to be from wolves while walking or slowly driving along small roads or paths. A small piece, around 1cm^3, was cut off, and stored in a 50 ml tube filled with silica grains, which was sent in for genetic analyses.

After scats were analysed for wolf identity within the monitoring, we selected samples that were: a) assigned to wolf individuals; b) from members of pairs or packs and c) located within the minimal convex polygons of their territory, plus a 3 km buffer. This selection was applied in order to exclude solitary wolves, as prey use and selection in this study focuses on pair or pack members. The information on pair and pack composition was obtained from the annual Scandinavian wolf monitoring (Svensson et al. 2023; Åkesson et al. 2023). A temporal separation of 7 days between scats of the same individual was also applied to minimize the risk of multiple scat sampling from the same kill, considering an average kill rate of 4.5 days per moose for adult wolves in Scandinavia and including a buffer to be conservative (Sand et al. 2005).

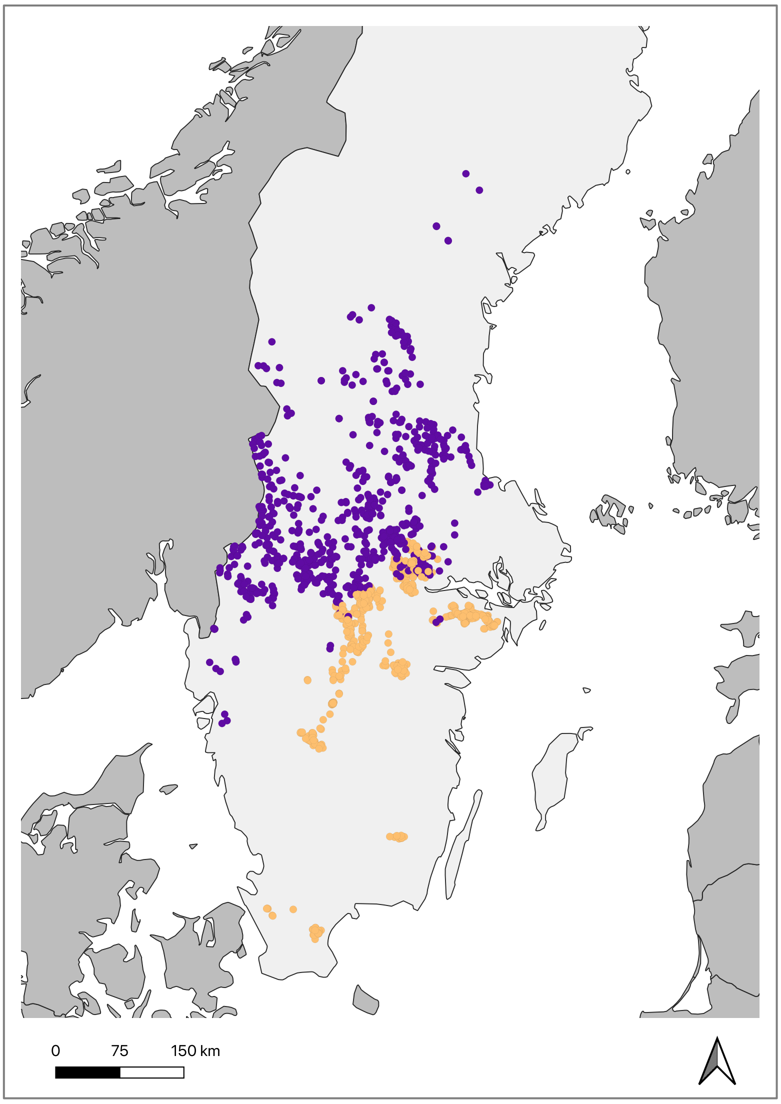

Figure 1. The study area and distribution of the wolf scat samples used for the prey use analysis. All samples were collected in Sweden during the monitoring seasons in winter (October-March) 2012/2013 until 2022/2023. Samples coloured in purple are from central Sweden (n = 750) and in orange from southern Sweden (n = 814).

2.3 DNA extraction and genotyping wolf individuals

Within the monitoring effort, DNA from wolf scats samples was extracted using the Quick-DNA™ Fecal/Soil Microbe DNA Miniprep Kit (Zymo Research) following the manufacturer's instructions, and subsequently stored in tubes in -80°C freezers. The extracted DNA was examined to determine the species and wolf individual identity using 96 Single-Nucleotide Polymorphism (SNP) markers. When using SNP markers, the DNA was amplified using a PCR method developed by Fluidigm Inc. (San Francisco, USA) and visualised with fluorescence (Fluidigm

Inc.). Each run enabled the PCR amplification of 96 markers on 96 samples simultaneously. In each run 47 scat samples were analysed, which were replicated and complemented with both a negative (distilled water) and a positive control (reference tissue from previously identified wolf). This technique is applied to differentiate between dog (*Canis lupus familiaris*), wolf, and red fox. A reference database with a genetic profile of up to 96 SNP markers was utilised to identify the wolf individual, of which 88 are autosomal markers and the remaining ones used to distinguish between genders. There is a single base pair difference between the marker alleles. For details regarding the methods, see Åkesson & Svensson (2022) and Åkesson et al. (2023).

2.4 DNA analysis for prey detection

Detection of prey DNA from wolf scat samples was carried out with a recently developed method using a high-throughput Nanofluidic array technology (Fluidigm Inc.) with species-specific molecular markers (Di Bernardi et al., 2021, 2023). The list of target species included in the prey detection analysis was based on known prey species and on allopatric medium-sized and large carnivore species to wolves in northern Europe (Gade-Jørgensen & Stagegaard 2000; Sand et al. 2008; Nowak et al. 2011; Chapron et al. 2014). The markers, located on the cytochrome b (*cyt b*), target the following species: moose, roe deer, red deer, fallow deer, wild boar, reindeer (*Rangifer rangifer*), sheep, cattle, European hare, mountain hare, European badger, red fox, Eurasian beaver (*Castor fiber*), Western capercaillie, black grouse, brown bear, Eurasian lynx and wolverine. As hybridization occurs between European and mountain hare, these two species were not always distinctly separated and were therefore merged as hares, summing up to a total of 17 target prey detectable. The analysed samples in each PCR run were 75 scat samples, 19 reference tissue samples from the target species, one wolf tissue sample, and one negative control (distilled water). To get a binary detection for prey species in each scat sample, the protocol described in Di Bernardi et al. (2021) was followed. Tissue samples were used as negative controls to establish non-arbitrary cut-offs for each marker in every PCR run. Finally, from a set of four or five markers per species, the amplification of at least two markers per species was applied as a threshold to get a detection, as suggested by Di Bernardi et al. (2023). In this study, scats with a detection of more than 4 species per scat were excluded, as they were seen as outliers based on the distribution curve of the number of prey species found per scat (Appendix 3). This decision was determined based on comparative studies done with macro analysis of scats where the mean number of items per scat was determined to be 1.05 items per scat for Mexican wolves in America (Reed et al. 2006), or 1.09 ± 0.38 items per wolf scat done in Italy (Ciucci et al. 2004). Since molecular methods can detect more species than macro analysis (Massey et al.

2021), the maximum number of items found per scat was set at four. Additionally, scats identified as outliers with regards to the signal of the passive reference dye ROX were invalidated by following the detection protocol (see Di Bernardi et al., 2021). The bioinformatic processing of the prey DNA data was conducted in R (R Core Team, 2023).

2.5 Local abundance of wild ungulate species

The yearly hunting bag records (individuals harvested/1000 ha) were used as an index for the abundance of the five wild ungulate species in the study area: moose, roe deer, red deer, fallow deer, and wild boar. Hunting statistics on roe deer in Scandinavia are highly correlated to the relative species abundance (Mattisson et al. 2013) and were therefore assumed to be the most accurate available measure. For moose, data on hunting statistics was available at the moose management unit level from 2012 onward and was provided by the County Administrative Boards (www.algdata.se). Hunting statistics on roe deer, red deer, fallow deer and wild boar were provided by the Swedish Association for Hunting and Wildlife Management (www.jagareforbundet.se) and recorded in smaller units called "kretsar" (hunting districts). For red deer, data on bag statistics was available until 2020, while for roe deer, fallow deer and wild boar until 2021. For 2022, an approximation from the year 2020 was therefore used for all species, for red deer this value was additionally used for the year 2021. The index of wild ungulate abundance was then calculated for each wolf territory by using the territory centroid and applying a buffer according to the estimated size of the territory. Estimated territory size was taken from Rodríguez-Recio et al. (2022) where the authors suggested larger territories in the central and smaller territories in the south of Scandinavia. Four different buffer sizes (r = 19975 m, 18129 m, 16072 m, 13710 m, 10845 m), were applied on territory centroids across Sweden with a radius corresponding to the mean size of the territories in the corresponding region. The wild ungulate abundance was then calculated as a weighted average, proportional to the overlap of each hunting unit with the buffer of the territory. This gave an estimate of ungulate abundance for each territory per monitoring season by utilising spatial data on territories for each year of their presence. If a territory occurred for multiple years, an average of ungulate abundance in the period was calculated.

2.6 Prey use

Prey use was calculated as the proportional occurrence (%) of DNA of a given target prey i, obtained as the number of its occurrences N_i on the total number of DNA occurrences N. The proportional occurrence for each of the 17 target prey was measured on the total number of occurrences instead of the total number of scats, since multiple species could be detected in the same scat. Samples were grouped based on local prey compositions in Sweden and it was differentiated between scats collected in more moose / roe deer dominated systems (central) and multi-ungulate prey systems (south) to detect possible differences among these regions (Figure 1). Scats from central Sweden were collected between 2012 and 2019 (n = 893), while scats from southern Sweden were collected between 2019 and 2022 (n = 671). The southern sample size was supplemented by the samples collected inside southern territories that existed already prior to 2019, resulting in different sample sizes for central (n = 750) and southern (n = 814) areas for the analysis. Overall, samples from 152 territories were included in the prey use analysis, of which 118 were located in central and 34 in southern Sweden. Out of these, all territories across Sweden which had a sample size of at least 20 scats were a formed unit and were included in the subsequent analyses, resulting a total sample size of 805 scats collected in 19 territories during the monitoring season 2012 until 2022. For these territories, the relative prey use of the five wild ungulates was related to their relative local abundance. The relative use of a given ungulate species was measured as the number of its DNA occurrences on the total number of DNA occurrences of wild ungulates per territory. The same was applied for the relative local abundance of the wild ungulate species. The relationship was investigated using the 'ggplot2' package in R, along with the additional features provided by the 'ggpmisc' extension package. A regression model was applied to calculate the regression equation, R-squared value, confidence interval, and p-value as part of the analysis.

2.7 Prey selection

Prey selection was estimated for the five ungulate species (moose, roe deer, red deer, fallow deer and wild boar) across wolf territories, and scat samples were included from territories in southern and central Sweden. The Jacob’s Index of Food Selection (Jacobs 1974) was applied for each territory as one unit and calculated as follows for each of the five wild ungulate species separately. The used formula was:

$$D = (r - p) / (r + p - 2rp)$$

where r is the proportion of DNA detections of a species on the total DNA detections for all ungulate species together and p is the proportion of local abundance for the same ungulate species on the total abundance of all ungulate species together. The calculated selection index ranges from -1 to 1, where negative values are considered avoidance and positive values selection towards the prey species, while values around 0 are considered consumption in relation to their abundance.

Further, the influence of the local abundance of the other ungulate species on the selection index of moose and roe deer was investigated separately. For that, a generalized linear model (GLM) with a beta regression (‘betareg’ package R 4.2.3) was used, which included the selection index for the main prey species (moose or roe deer) as response variable and the local ungulate abundances for moose, roe deer, red deer, fallow deer and wild boar as explanatory variables. A previously calculated selection index (D) was available for moose and roe deer in 19 of the territories. As beta regressions for GLM require a response variable ranging from 0 to 1, the selection index was transformed to positive values by adding 1 and dividing by 2. One territory in the south of Sweden (Linderödsåsen) had a transformed selection index for moose of 0, as the originally calculated selection index was -1. This index is considered as a total avoidance of the species, as there was no moose found in the diet but recorded in the bag statistics. This data point was excluded from the GLM analysis for moose. Several models (univariate, multivariate) were tested for both prey species, and the best model was selected based on the AICc with a backward selection. For a summary of all models tested see Appendix 8.

3. Results

3.1 Prey use

The total number of analysed scats for prey detection was 2721 from all Sweden. The following number of target prey were detected per scat: no target prey (29%, n = 804), 1 target prey (56%, n = 1512), 2 target prey (10%, n = 268), 3 target prey (2%, n = 58), 4 target prey (1%, n = 30), or >4 target prey (2%, n = 49) (see Appendix 3). For further analyses on prey use and selection only scats collected with a temporal separation of seven days and with an identification of one to four prey species per scat were included (n = 1564). The average number of target prey detected per scat was 1.23 (range 1 – 4).

The sample size for central Sweden consisted of 750 scats with a total number of 888 detections of prey species. Prey use of wolf pairs and packs in central Sweden was dominated by moose (58%), followed by roe deer (25%) (Figure 2A). Together with red deer (1%), fallow deer (2%) and wild boar (2%), wild ungulates made up the dominating proportion of wolves' diet (88%). Medium to small prey contributed with 5% of their diet and domestic ungulates with 4%. In 3% of the species detections other carnivores were found, including red fox, brown bear, and wolverine.

Diet composition in southern Sweden was analysed from 814 scat samples which had a total number of 1029 prey detections. Prey composition in southern Sweden was dominated by roe deer (28%), closely followed by moose (27%) (Figure 2B). Also in this area wild ungulates made up the largest proportion of the wolves' diet (85%), consisting of moose, roe deer, red deer (4%), fallow deer (9%) and wild boar (17%). Medium to small prey contributed to 7% of the diet. Domestic ungulates made up 4% of the prey use and other carnivores 4%. Overall, the summed proportion of the five wild ungulates together were similar for both regions, with moose being more frequent in scats from central Sweden whereas alternative ungulate species (red deer, fallow deer and wild boar) were more often found in scat samples from southern Sweden.

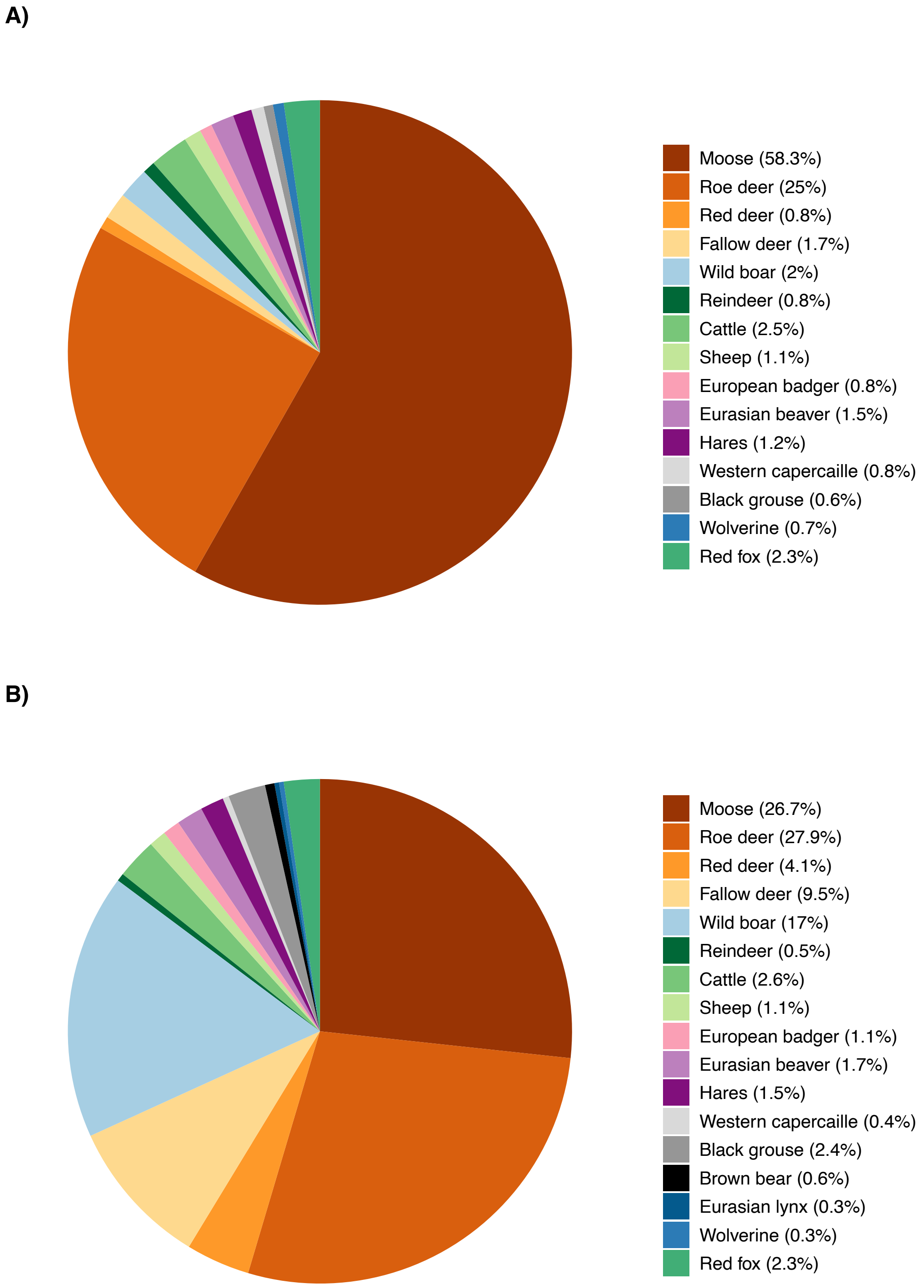

Figure 2. Frequency of occurrence (%) for each of the 17 targeted prey in wolf scats from territorial pairs or packs from A) central Sweden (n = 750) and B) southern Sweden (n = 814), collected during monitoring season 2012 - 2022. Prey use was calculated as the proportional occurrence (%) of a given target prey *i* as the number of its occurrences N_i on the total number of occurrences N.

3.2 Local abundance of wild ungulate species

The abundance of the five wild ungulate species for each wolf territory was based on harvest statistics (n^o individuals shot per 1000 ha) (Appendix 7). Moose and roe deer were the only two ungulate species present in all territories throughout the study area. The harvest data of moose showed that this species was the most evenly distributed with a mean harvest of 2.3 ind. / 1000 ha (range 0.1 – 4.7), while roe deer increased towards the south with an average of 2.1 ind. / 1000 ha (range 0.02 – 13.3) (Appendix 7). Red deer was present only in certain territories with an overall average harvest of 0.2 ind. / 1000 ha (range 0 – 5.2), as was fallow deer with a mean harvest of 0.8 ind. / 1000 ha (range 0 – 27.6). Wild boar also increased towards the south with an overall average harvest of 2.2 ind. / 1000 ha (range 0 – 39.7).

3.3 Prey use in relation to local abundance

The relative frequency of occurrence (FO) for each ungulate species in the diet of 19 analysed wolf territories across Sweden was plotted in relation to their relative abundance (Figure 3). The relative FO was calculated as the proportional occurrence of DNA of a given ungulate species on the total occurrences of all ungulates in the diet. The relative ungulate local abundance was calculated as the proportional abundance of a given ungulate species on the total abundance of all ungulates. The dotted line in the plots represents a 1:1 relationship where FO is proportional to the local abundance of the species in the environment. Overall, moose were consumed to a higher relative frequency in relation to their relative local abundance in the environment as most of the territories in the graph are on the left of the dotted line. For roe deer, there was a larger variation among territories, as some territories showed that more roe deer was consumed than was available in the environment, and vice versa. Red deer tended to be consumed according to its local abundance although data was only available at low densities. Fallow deer showed no clear trend at lower densities, but seemed to be strongly selected only when local abundances became high. Wild boar was generally avoided by wolves in Sweden, as consumption was lower than local abundance in many areas. However, in 16 out of the 19 targeted territories wolves did have wild boar in their diet.

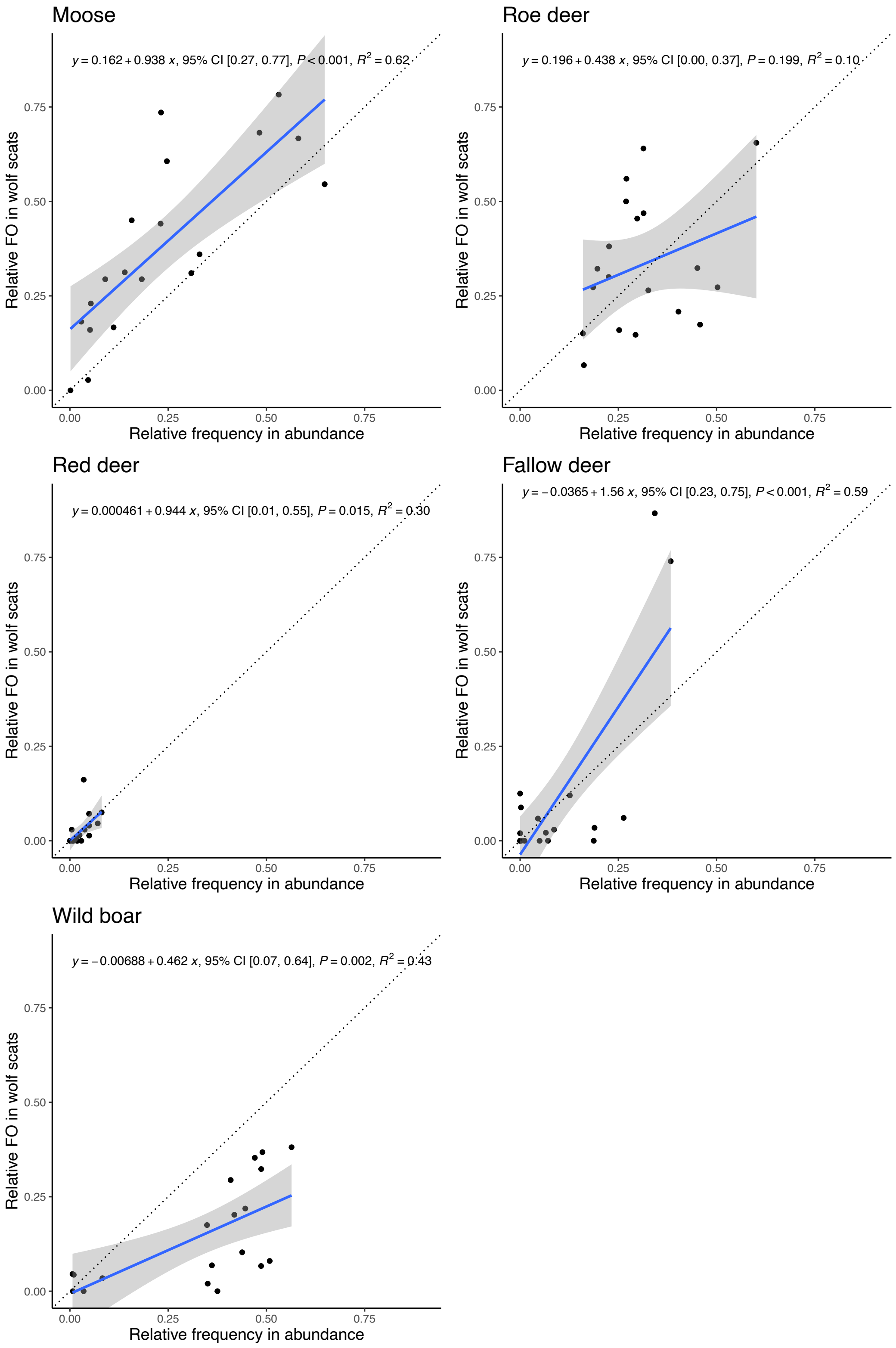

Figure 3. The relationship between the relative frequency of occurrence (FO) in wolf diet and the relative local abundance for each of the five ungulate species. The regression model with the equation, confidence interval, p-value and R-squared value are shown. The analysis was

done on 19 territorial wolf pairs or packs across Sweden, sampled during monitoring season 2012 until 2022. Each dot represents a wolf territory.

3.4 Prey selection

The Jacob's Index of Selection (D) showed a large variation across territories and ungulate species (Figure 4). Preference for moose was indicated, being the most selected prey species across the 19 territories, with positive selection indexes in 16 out of 19 territories and with a median selection index of 0.45. However, one territory had a selection score of -1, where moose was harvested but was absent from their diet. Roe deer, with a median of 0.12, was selected less compared to moose. The median selection index for all alternative ungulate species (red deer, fallow deer, wild boar) was negative, indicating an overall avoidance with values of -0.42, -0.52, and -0.48, respectively. However, the selection index for the three alternative ungulates showed a high variation, ranging from -1.00 (25th percentile) to -0.11 (75th percentile) for red deer and from -0.85 to -0.29 for wild boar. Fallow deer showed the widest range from -1.00 to 0.69 between the 25th and 75th percentile.

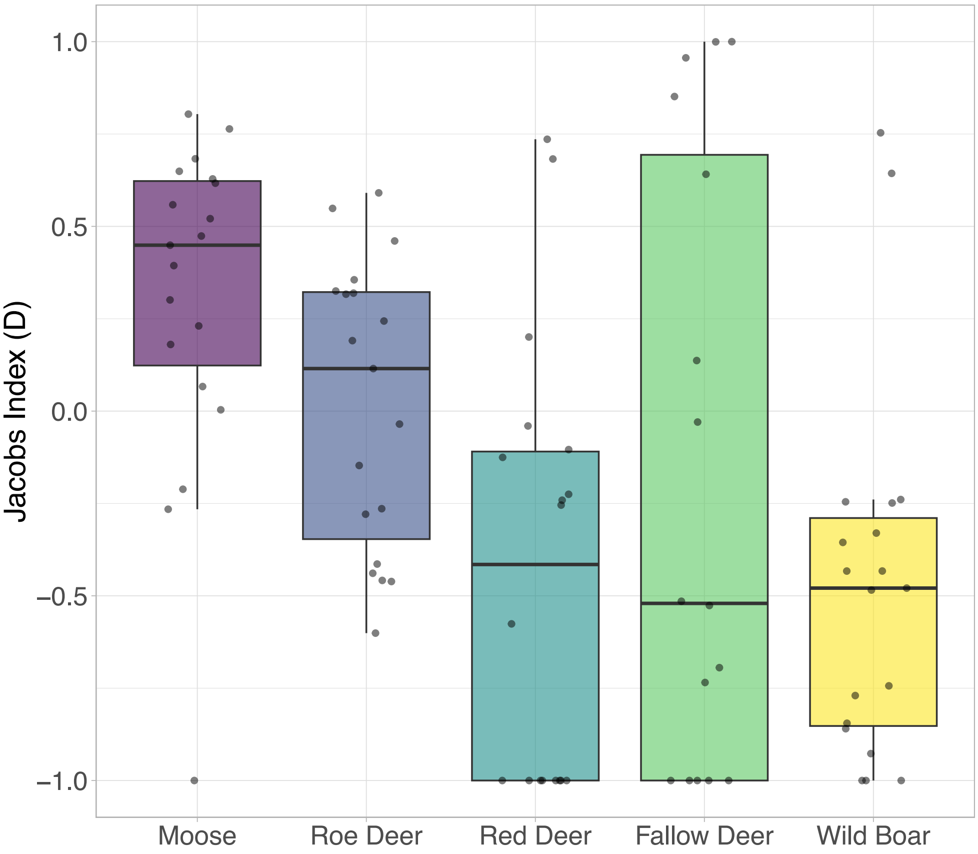

Figure 4. Jacob's Index of Selection (D) calculated for five ungulate species across wolf pairs and packs. The selection index was calculated using the relative occurrence of the ungulate species in wolves' diet and the relative local abundance of the ungulate species. Analyses were done on 19 territorial wolf pairs or packs across Sweden, sampled during monitoring season 2012 until 2022. Each dot represents a territory.

Model results showed that the main prey of wolves in Sweden, moose and roe deer, are influenced by the abundance of other ungulate species in the environment. The best-fitting model explaining the selection index of moose (D_{Moose}, Table 1) showed a negative influence of the local abundance of fallow deer on the selection of moose, whereas the abundance of wild boar had a positive impact (Table 2). For roe deer selection (D_{Roe}, Table 1), the null model was the best-fitting model, followed by a model (Delta AICc = 1.7) where the selection of roe deer was negatively influenced by the abundance of fallow deer and moose, while positively influenced by the abundance of red deer (Table 2).

Table 1. Generalized linear models (GLM, beta regression) of the selection index of moose (D_{Moose}) and the selection index of roe deer (D_{Roe}) as a function of local moose abundance (Moose), local roe deer abundance (Roe deer), local red deer abundance (Red deer) and local wild boar abundance (Wild boar). For both D_{Moose} and D_{Roe} the best-fitting model, the full model and the null model are presented. The AIC is corrected for small sample sizes (AICc) and the differences between the models (ΔAICc) and the R^2 are also shown in the table.

Model	**AICc**	**ΔAICc**	**R^2**
Moose (D_{Moose})			
Fallow deer + Wild boar	- 15.79	0.0	0.333
Null (intercept only)	- 14.12	1.7	-
Moose + Roe deer + Red deer + Fallow deer + Wild boar	- 1.97	13.8	0.331
Roe deer (D_{Roe})			
Null (intercept only)	- 6.88	0.0	-
Moose + Red deer + Fallow deer	- 5.20	1.7	0.353
Roe deer + Moose + Red deer + Fallow deer + Wild boar	- 3.93	10.8	0.366

Table 2. The parameter estimates for the best-fitting models for the selection index of Moose (D_{Moose}) and the selection index of Roe deer (D_{Roe}), in addition to the null model. The selection towards moose or roe deer respectively is in relation to the different wild ungulate local abundances. Significant levels: p-value < 0.001 ***, < 0.01 **, < 0.05 *.

Parameter	**Estimate**	**Std. Error**	**Z value**	**Pr (>|z|)**
Moose (D_{Moose})				
(Intercept)	0.440	0.193	2.286	0.022 *
Fallow deer	- 0.157	0.052	- 3.006	0.003 **
Wild boar	0.126	0.039	3.205	0.001 **
Roe deer (D_{Roe})				
(Intercept)	1.632	0.744	2.195	0.028 *
Moose	- 0.808	0.339	- 2.379	0.017 *
Red deer	0.696	0.266	2.613	0.009 **
Fallow deer	- 0.109	0.039	- 2.816	0.005 **

4. Discussion

Analysis of wolf scat contents in both central and southern territories unveiled wild ungulates as the predominant prey species, accounting for 88% and 85% of the wolves' dietary composition, respectively. Roe deer and moose were the two main prey species in southern territories, whereas moose was the main prey species in central territories. Moose was consumed to a larger extent compared to its relative local abundance, indicating a preference toward the species. Consumption of roe deer on the other hand showed a larger inter-territorial variation, where wolves in some areas consumed more roe deer than was proportionally available, and vice versa. In general, there was neither preference nor avoidance towards roe deer. Alternative ungulate species (red deer, fallow deer, wild boar) showed a high variation in terms of selection or avoidance across different wolf territories, with wild boar being overall avoided. However, the local abundance of fallow deer influenced the selection of their main prey species (both moose and roe deer) negatively, whereas wild boar abundance had a positive influence on the selection of moose as did red deer abundance on the selection for roe deer.

4.1 Prey use and local abundance of ungulates

Prey use of wolves in central and southern Sweden reflected the available prey, with some exceptions. The first prediction of wolf pairs and packs having a broader diet in the south (P1) was confirmed, and indicated by a higher proportion of alternative ungulates in their diet. Moose was consumed to a much higher proportion in central than in southern Sweden whereas roe deer was consumed to almost the same extend in both areas. Considering the even distribution of moose across the study area, the observed difference in consumption of moose was likely due to the presence of other ungulate prey species in the environment. The increased abundance of these other three ungulate species (red deer, fallow deer, wild boar) also explained the lack of increase in roe deer consumption, even though this species was more abundant towards the south. This result stands in contrast to previous studies investigating the switch to roe deer when their availability increased (Sand et al. 2016). However, it may not be the change in roe deer abundance that matters but instead its proportion within the ungulate community, as other ungulate species may also form a substitution for moose. Other prey species such as livestock and smaller prey did not show large differences in their frequency of occurrence between the two areas. Thus, it appears that the lower consumption of moose in southern Sweden was compensated by the higher proportion of alternative wild ungulate species in the diet. In particular, the presence of alternative ungulate species in the diet of wolves was found to be more common in regions where these species were more abundant, i.e. southern Sweden.

4.2 Prey selection

The second prediction of an overall higher selection for moose (P2) was confirmed, as the median of the selection index was highest for moose. The relative consumption of moose increased with their relative local abundance and was consumed disproportionally more than their relative abundance in the environment. The large use of moose by wolves in Scandinavia has been largely reported by other studies (Sand et al. 2008; Zimmermann et al. 2015; Åkesson et al. 2016), but formed a different pattern compared to studies from wolf populations in other regions of Europe. In Poland, red deer was considered wolves' main prey (Jędrzejewski et al. 2000, 2012), although moose also occured in low densities in this system, but the density of red deer in Poland was almost seven times higher compared to Sweden.

The third prediction, that alternative wild ungulate species will be used more when their local abundance becomes higher (P3), was supported for all three alternative ungulate species (red deer, fallow deer and wild boar). Results showed the linear relationship between relative frequency of occurrence and relative local abundance to be significant for all three species. The frequency of occurrence in consumption of fallow deer did likely not follow a linear trend but rather an exponential curve or a flatter regression line with two outliers where wolves consumed exceptionally high numbers of fallow deer compared to other ungulate species. Local prey abundance therefore explained only a part of the inter-territorial variability in wolves' feeding behaviour, a finding supported by other studies highlighting the role of local prey abundance (Fuller & Keith 1980; Meriggi et al. 2011; Gable et al. 2017). However, the large variation in selection index for alternative ungulate species suggested that other factors related to the wolf pairs or packs may also be of importance. A possible mechanism under the high selection index values towards certain alternative ungulates in some territories could be driven by specialisation of certain wolf pairs or packs on specific prey species, in line with what Gable et al. (2017) hypothesised in their study.

In multi-prey systems in Europe where moose was absent or available at very low densities, the ungulate community was generally composed by only two deer species and wild boar. One study from Slovakia found that, while red deer was the most frequently detected species in wolves' scats, wild boar was selected and both red deer and roe deer were instead avoided (Guimarães et al. 2022). Nowak et al. (2011)'s results from Poland showed the opposite: a selection towards red deer and avoidance for wild boar. In Italy, wolves selected fallow deer, whereas roe deer was used less than its availability (Ferretti et al. 2019). This seemingly highly context-dependent feeding behaviour of wolves underlines that the selection of certain ungulate species might depend more on the composition of these multi-prey systems rather than the mere abundance of one specific species. This may also explain why wolves showed such a large variability in selection indexes for the wild ungulate species occurring in Sweden.

4.3 Influence of other ungulate species on the selection for moose and roe deer

The selection of moose decreased with increasing local abundance of fallow deer. Further, the relative consumption versus abundance of fallow deer had two outliers, one of them was the Linderödsåsen pack, where the relative consumption of the species was exceptionally high. These territories had the highest relative abundance of fallow deer, suggesting that wolves may potentially switch from moose to fallow deer when fallow deer abundance becomes especially high. Also, the Linderödsåsen pack in the south was not included in the model for moose selection as there was no moose consumption detected in this territory. There, fallow deer made up around 50% of the prey use (Appendix 5) which would support that wolves may have switched from moose to fallow deer in this territory or just preferred fallow deer over moose from the start.

Roe deer was selected to a lower extent when moose and fallow deer became more locally abundant. Further did wolves seem to substitute moose with one or more other available ungulate species (red deer, fallow deer, wild boar) rather than with roe deer. However, as the model describing the influence of other ungulates species on the selection of roe deer was 1.7 Delta AICc below the top-ranked null model, results should be interpreted with caution. Nevertheless, the impact of fallow deer on both the selection of moose and roe deer can also be explained by their strong herding behaviour resulting in spatially clumped distribution and thereby being present either at very high or low numbers (range 0 – 27.6 ind. / 1000 ha). Red deer, however, was either absent or occurred at low abundances and their positive influence on the selection towards roe deer is therefore hard to interpret. Additionally, the use of fallow deer and red deer should be considered as a minimum estimate as the sensitivity of the method in detecting these two species is lower compared to the other ungulates (Di Bernardi et al. 2023). It is therefore likely that these two species were underestimated in prey use and might have a bigger influence on the selection of moose and roe deer.

4.4 Implications for ungulate abundance

Rodríguez-Recio et al. (2022) predicted that wolf recolonization would have a minor impact on population densities of alternative ungulate species in southern Sweden but may cause a significant reduction in human harvest of moose and roe deer. The results of Sand et al. (2016) showed that the functional response of wolves in Scandinavia was closely linked to roe deer density in a two-prey system. Territory size of wolves was further linked to local roe deer density but not to moose density (Mattisson et al. 2013), probably due to the fact that moose abundance is more evenly distributed than roe deer abundance. However, based on our findings on prey selection, it is suggested that not only roe deer but other alternative prey species influence wolves' predation on moose and potentially also their territory size. These results have implications for management as the predation rate on moose is likely to be lower in multi-prey systems. However, human harvest should be considered, given its anticipated stronger effect on the ungulate community in Sweden compared to large carnivores. Indeed, both ungulate and predator densities here are primarily regulated by hunting (Dorresteijn et al. 2015; Ausilio et al. 2021).

4.5 Strengths and limitations of the study

The sample size and geographical distribution of the samples used in this study is considered to be a strength. Estimations of prey use and selection consequently become more accurate when sampling across different prey communities. This study further benefited from scat samples collected during previous years of monitoring the Scandinavian wolf population. This however formed a temporal limitation, as only winter diet is represented. Winter diet has often been used for analyses on wolf feeding behaviour (Peterson & Ciucci 2003) but results should be complemented with samples collected during other months (Roffler et al. 2023). Kill rates, for example, may often be an underestimation when only data on winter predation is considered (Sand et al. 2008). Also, foraging behaviour differs when wolves have pups, as they are more stationary and their relative diet niche changes (Roffler et al. 2023). As this study did not only include scat samples from marking individuals but also from other pack members, samples from pups may cause a bias if they make their own kills. While other research presumes that wolf adults and pups have the same diet, certain studies have identified differences (Gable et al. 2017). On the other hand, the time frame targeted in this study is later on in the year when pups are around six months old and move together with the adult individuals in the pack. Furthermore, winter diet likely underestimated the contribution of livestock to wolf diet as many livestock owners keep their animals inside during winter in Sweden. Domestic species were found to a high extent in wolf diet in Europe (Newsome et al. 2016) and predation might also shift based on availability of ungulates versus livestock (Meriggi et al. 2011).

The analyses on frequency of occurrence of prey species in wolves' diet gave new insights into predator-prey relationships but should be complemented with analyses of kg biomass or number of individuals consumed. Traditional prey selection studies often use either data from collared wolves (e.g. Sand et al., 2016) which compare the numbers of individuals consumed with the numbers of individuals available, or calculations on biomass from traditional scat analyses in relation to available prey biomass in the environment (e.g. Nowak et al., 2011). The approach used in this study likely underestimated the use of smaller species as larger prey may be present in a greater number of scats per kill, leading to their more frequent detection. It should be complemented by calculations on biomass, which are a better approximation to true diet (Klare et al. 2011) or by numbers of killed prey individuals which could provide better interpretable data for stakeholders or management. This is particularly relevant in Scandinavia where hunters conduct an adaptive management by adjusting their harvest in response to wolf presence (Wikenros et al. 2015).

Prey selection analysis in this study should not be biased by scavenging as wolf pairs and packs in Scandinavia obtain the majority of their food from killing prey and not from scavenging (Wikenros et al. 2023). Still, the estimated prey selection for different species should be compared with caution to findings of other studies using different methods and preferably be used as a comparison between sampled pairs and packs across Sweden.

The use of hunting statistics as an index of ungulate local abundance could potentially be another limitation. Even though bag statistics are considered to be a reliable estimate of abundance (Jędrzejewski et al. 2012; Guimarães et al. 2022), hunters' preference for certain ungulate species may cause a higher hunting pressure on these, which in turn can create biases among species in how well the bag records mirror population sizes. Ungulate density based on pellet counts would represent a more reliable option but was not available for all five ungulate species within the broad area of this study. The methodology used in this study was therefore the best one available.

Questions on how future expansions of large carnivores will influence prey populations are important and the consequences of the return of apex predators and their impact on ecosystems and social aspects are often yet unknown (Garrott et al. 2007). This study is highly relevant for the management of wolves and their prey species, as it provided more knowledge on how wolves used and selected different ungulate species in a multi-ungulate system in Scandinavia. The significant use of alternative ungulate species (red deer, fallow deer, wild boar) by wolf pairs and packs in southern Sweden has not been described before, as their distribution into these areas is relatively recent. How consumption and selection of moose shifted in multi-ungulate areas was another relevant result as wolves' expansion will likely continue and lead to more challenges in the future (Recio et al. 2018; Rodríguez-Recio et al. 2022).

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Popular science summary

All of Europe's large carnivore species have shown population increases during the past century. Their more widespread occurrence is a positive sign for some and a new challenge for others. In Europe, large carnivores and humans often share landscapes and resources, which can cause conflicts between different interest groups. Understanding a predators' feeding behaviour can therefore give valuable insights for management.

Since its functional extinction in the 1960s, the Scandinavian wolf population has grown and counts around 510 individuals in 2023. The wolf population have recently been expanding from areas that were dominated by moose and roe deer in central Scandinavia to more southern areas in Sweden where multiple ungulate species are also available to wolves. Previous studies on moose / roe deer systems found moose to be wolves' main prey species but wolves tend to consume more roe deer when they became more abundant. In ecosystems with a variety of prey species, the question arises: which species will wolves eat and to what extent?

This study investigated which prey species were consumed by wolves in both central and southern parts of Sweden, and to what extent. To investigate this, a new DNA-method using scats was applied to examine potential differences in diet between pairs and packs across Sweden. Analysis on scats offers the benefit of being non-invasive, ensuring minimal disruption to the target species and the ecosystem in general.

The 1564 examined scats revealed that wolves' diet in Sweden was largely dominated by wild ungulates. However, their menu differed between territories from central and more southern parts. While moose was the most commonly found species in central Sweden, both roe deer and moose were considered their main prey species in scats from southern Sweden. Further, a higher proportion of red deer, fallow deer and wild boar was found in wolf scats where their abundance increased towards the south. These species were substituted for moose, as moose was consumed to a smaller proportion in the southern territories. When comparing the consumption of an ungulate species to its local abundance, some species were selected and some avoided. If a species is consumed proportionally more than its abundance in the environment, this indicates a selection or preference, the opposite would be considered avoidance. Our results showed that moose was overall selected, roe deer was consumed proportional to its abundance and red deer, fallow deer and wild boar were generally avoided but with a large variation between wolf territories.

Lastly, we found that when fallow deer was abundant, wolves were less likely to select for moose, suggesting that the abundance of different ungulate species affected what wolves chose to eat. These findings have implications for the management and conservation of both wolves and their ungulate prey species. In multi-ungulate systems, consumption of moose tend to be lower, emphasizing the importance of considering the presence of different ungulate species in management efforts.

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Appendix 1

Table A1. Sample size used for the analyses in this study. Only territories which had ≥ 20 scats, across monitoring years 2012-2022 and from both southern and central Sweden were included. For analyses, the southern sample size was supplemented by the samples from Di Bernardi (2022) collected inside southern territories that already existed prior to 2019.

	Number of Scats
Total analysed south	1532
South[a]	975
South (7-day separation)	671
Central (7-day separation, data from Di Bernardi, (2022))	893
Prey selection[b]	805

[a] Scats from total analysed samples which had positive calls for prey species (1-4) and no ROX outliers.

[b] Scats used for the prey selection analysis.

Appendix 2

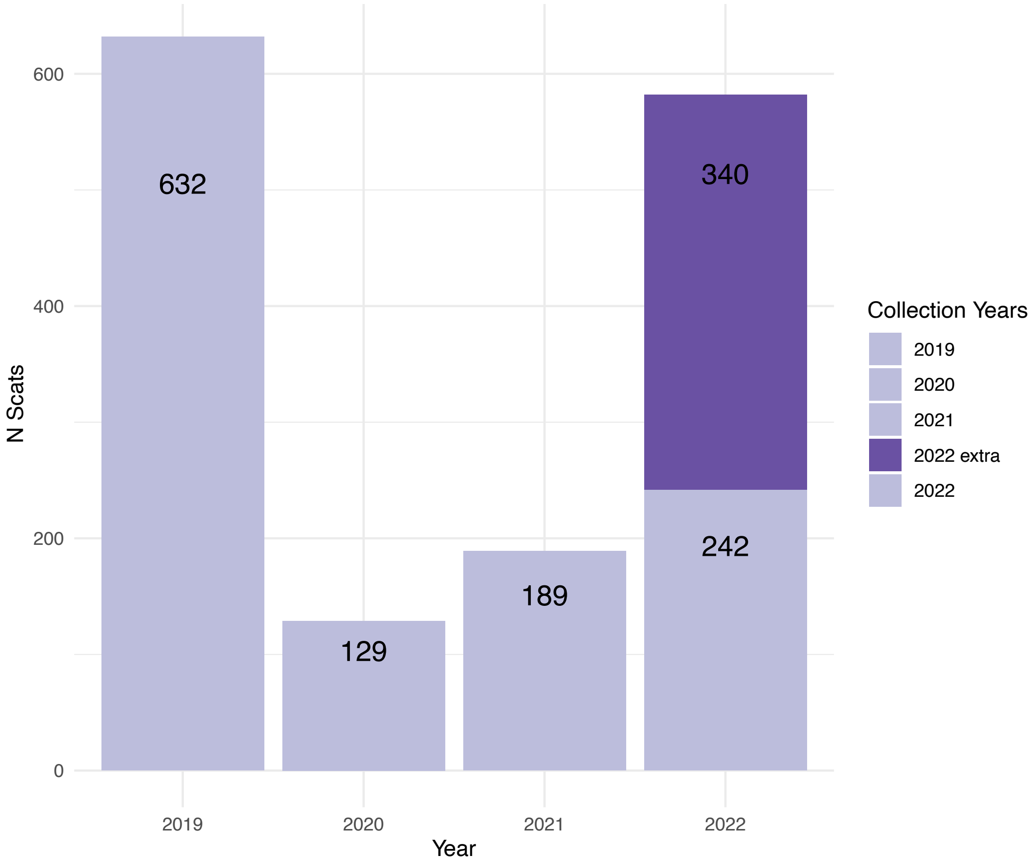


Figure A2. Number of scats collected in south Sweden between 2019 and 2022. During the 2019 monitoring season, additional scat collection was conducted as part of the monitoring. In the 2022 season, the additional scat collection was made for the current research project.

Appendix 3

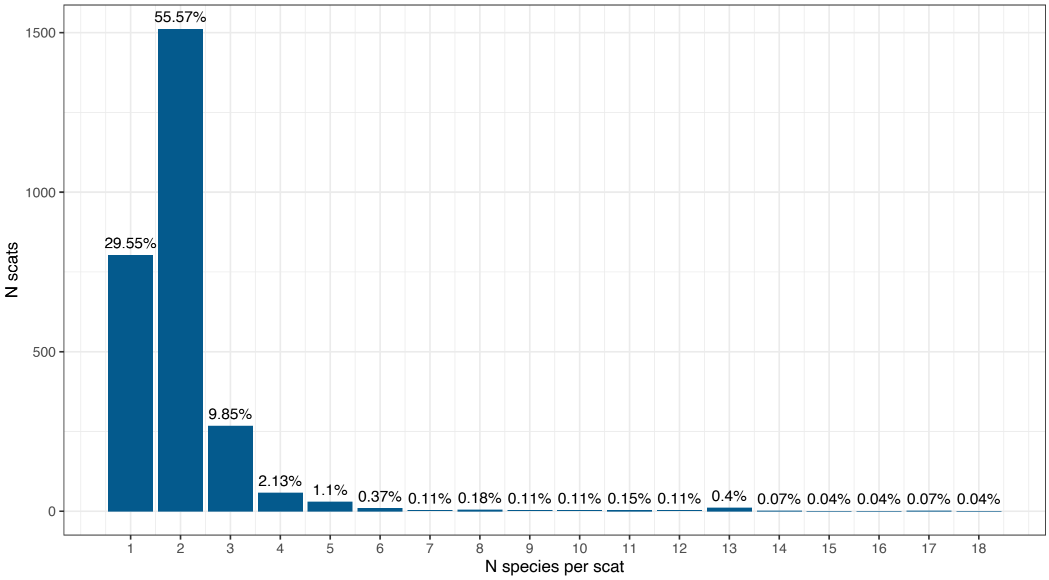


Figure A3. Number of detected species per scat for the total data set. Sample size was 2721, scats were from central Sweden (n = 1203) and southern Sweden (n = 1518) before selections were applied.

Appendix 4

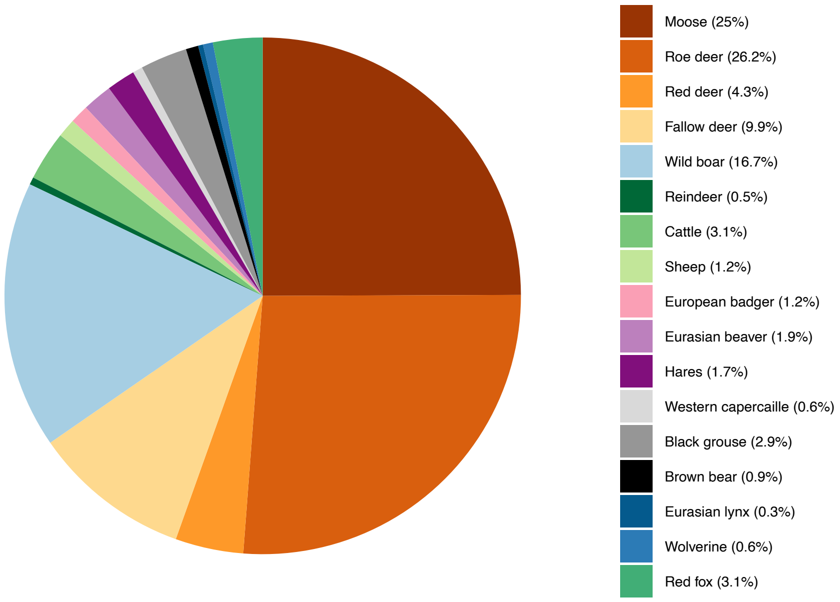


Figure A4. Frequency of occurrence (FO) of the 17 target species for all scats in the south without a temporal selection applied. N scats = 975, n detections = 1291.

Appendix 5

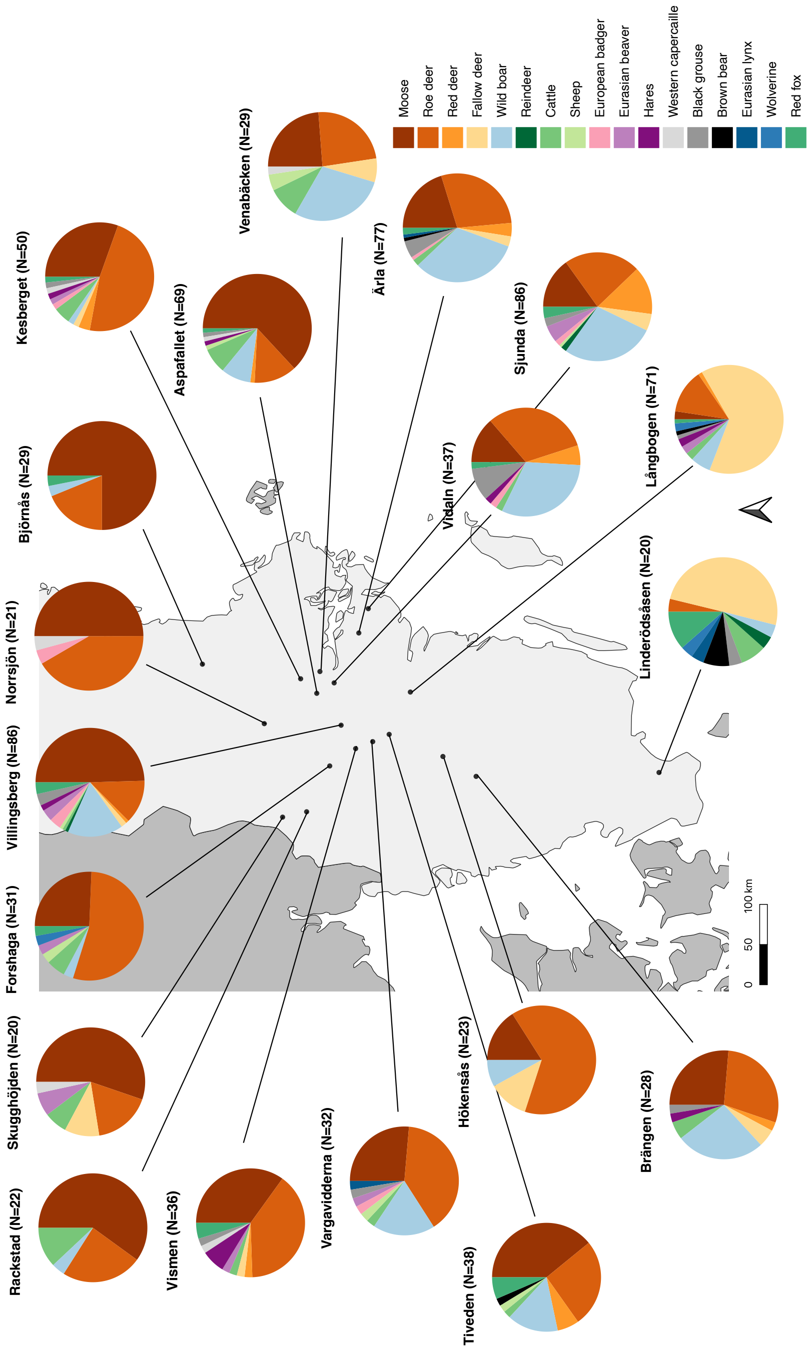


Figure A5. Frequency of occurrence (FO) of the target species per wolf territory across Sweden from 19 territories used in all analyses on territory level.

Appendix 6

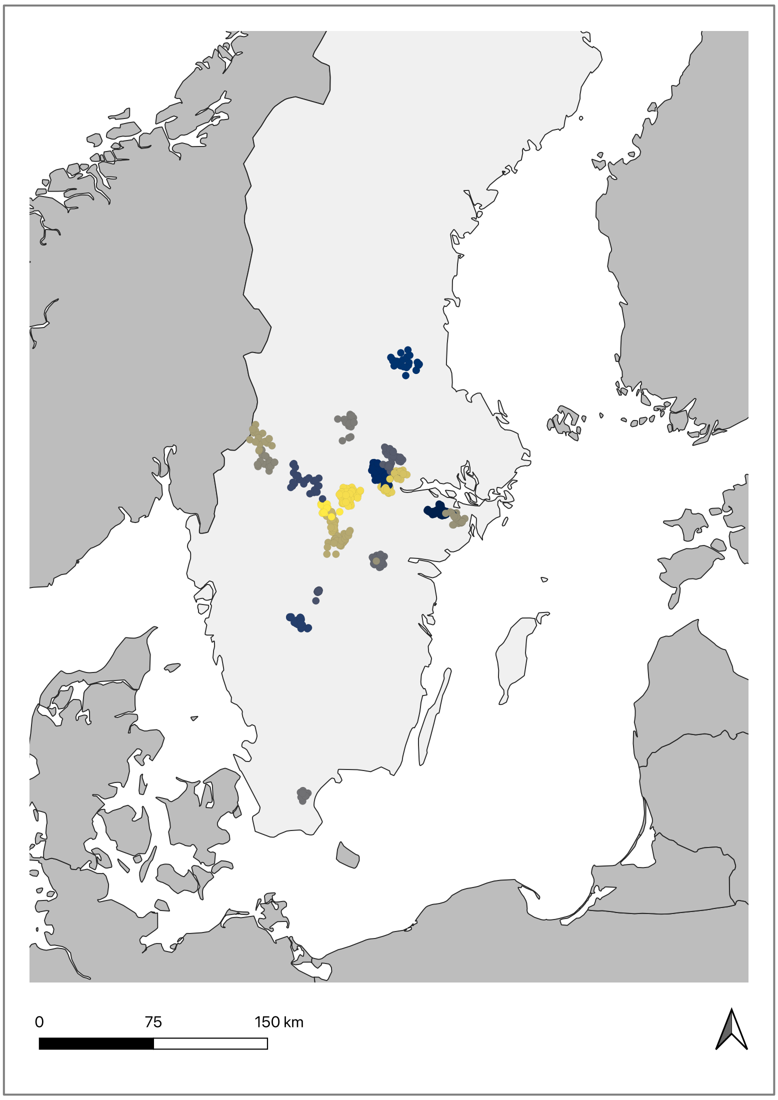
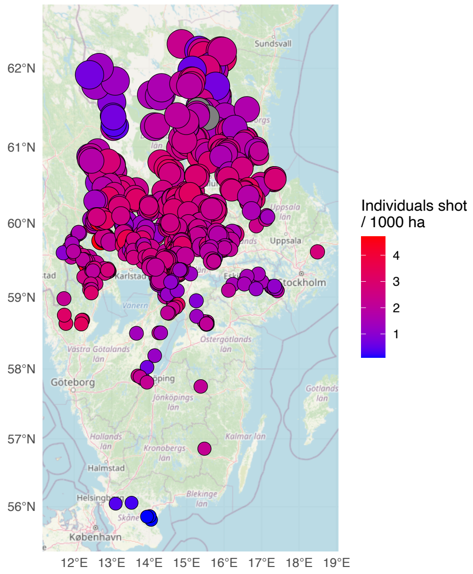
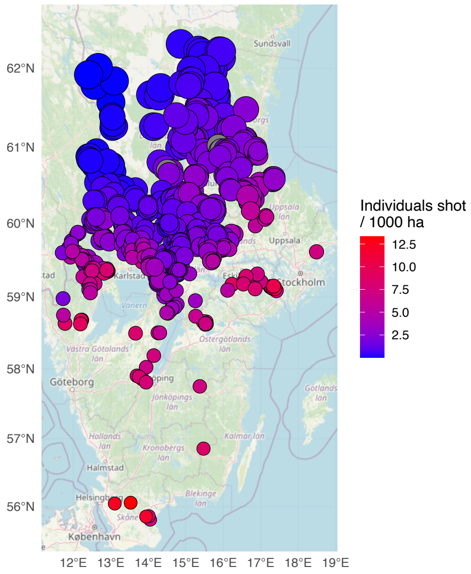
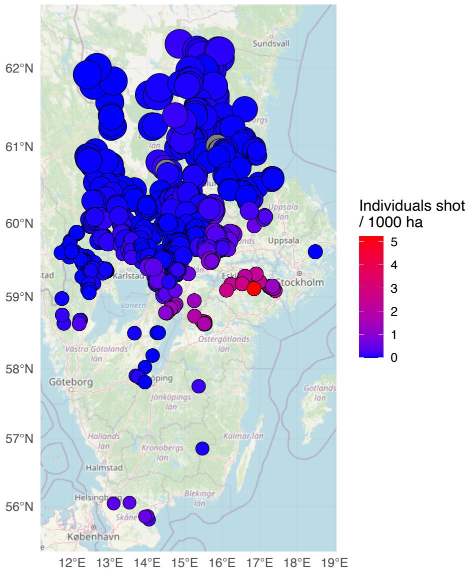


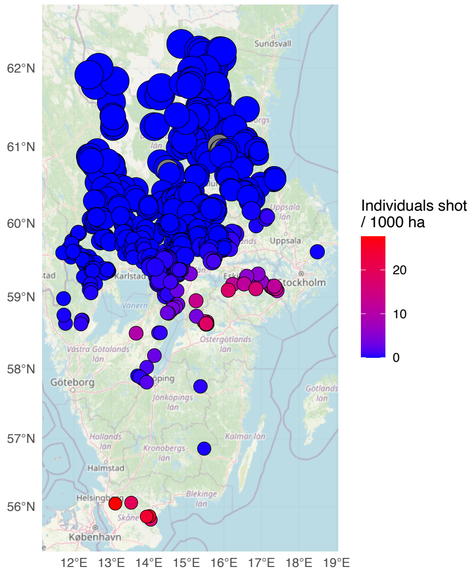
Figure A6. Samples and territories included in the scat analysis on territory unit (prey use in relation to prey abundance, prey selection) across Sweden. All scats with the same colour belong to the same pair or pack but could come from different monitoring years.

Appendix 7


Moose Abundance


Roe deer Abundance


Red deer Abundance


Fallow deer Abundance

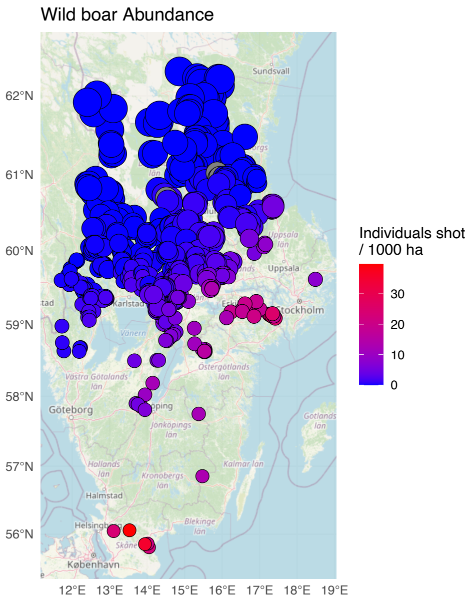


Figure A7. Average ungulate local abundance per territory for each separate year for moose, roe deer, red deer, fallow deer and wild boar in Sweden. Each circle represents a territory in one year with the centroid in the middle and a buffer according to the geographical location, with larger buffers in the northern part of the study area and smaller buffers in the southern parts. Ungulate local abundance is measured as the average number of individuals shot per 1000 ha within the territory buffer and has a different scale for each of the 5 ungulate species.

Appendix 8

Table 8. List of all generalized linear models **(**beta regression) run of the selection index of moose (D_{Moose}) and the selection index of roe deer (D_{Roe}) as a function of local moose abundance (Moose), local roe deer abundance (Roe deer), local red deer abundance (Red deer) and local wild boar abundance (Wild boar). For both D_{Moose} and D_{Roe}, 10 models plus the null model were tested to find the lowest AICc with a backward elimination.

Predictors	**AICc**	**ΔAICc**	**R^2**
Moose (D_{Moose})			
Fallow deer + Wild boar	- 15.79	0.0	0.333
Null (intercept only)	- 14.12	1.7	-
Roe deer + Fallow deer	- 10.89	4.9	0.148
Red deer + Wild boar	- 10.36	5.4	0.150
Roe deer + Wild boar	- 9.47	6.3	0.094
Roe deer + Red deer	- 9.15	6.6	0.077
Fallow deer + Red deer	- 8.52	7.3	0.042
Roe deer + Red deer + Fallow deer	- 8.33	7.5	0.210
Moose + Red deer + Fallow deer + Wild boar	- 7.53	8.3	0.331
Roe deer + Red deer + Fallow deer + Wild boar	- 7.32	8.5	0.333
Moose + Roe deer + Red deer + Fallow deer + Wild boar	- 1.97	13.8	0.331
Roe deer (D_{Roe})			
Null (intercept only)	- 6.88	0.0	-
Moose + Red deer + Fallow deer	- 5.20	1.7	0.353
Fallow deer + Red deer	- 3.97	2.9	0.162
Fallow deer + Wild boar	- 3.30	3.6	0.127
Moose + Fallow deer	- 3.03	3.6	0.115
Red deer + Wild boar	- 2.41	4.5	0.085
Moose + Red deer	- 2.20	4.7	0.075

Moose + Wild boar	- 1.68	5.2	0.049
Moose + Red deer + Fallow deer + Wild boar	- 0.97	5.9	0.358
Moose + Red deer + Fallow deer + Wild boar	- 0.97	5.9	0.358
Roe deer + Moose + Red deer + Fallow deer + Wild boar	3.93	10.8	0.366

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