Inland Norway
University of
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Faculty of Applied Ecology, Agricultural Sciences and Biotechnology

Gjermund Gomo

The Vertebrate Scavenger Community Along a Boreal Forest-Alpine Gradient:

The Importance of Ungulate Management, Small Rodent Cycles and Winter Climate

PhD Dissertations in Applied Ecology and Biotechnology
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Author's address:

Gjermund Gomo

Inland Norway University of Applied Sciences

P.O. Box 400

NO-2418 Elverum, Norway

E-mail: gjermg@gmail.com

Main supervisors:

Morten Odden	Inland Norway University of Applied Sciences (INN), Faculty of Applied Ecology, Agricultural Sciences and Biotechnology, Dept. of Forestry and Wildlife Management, 2480 Koppang, Norway
Tomas Willebrand	Inland Norway University of Applied Sciences (INN), P.O. 400, Elverum, 2418, Norway

Co-supervisors:

Jenny Mattisson	Norwegian Institute for Nature Research (NINA), P.O. Box 5685 Torgarden, NO-7485 Trondheim, Norway
Nina E. Eide	Norwegian Institute for Nature Research (NINA), P.O. Box 5685 Torgarden, NO-7485 Trondheim, Norway
Pål F. Moa	Nord University, 8049 Bodø, Norway

Abstract

While the importance of carrion and scavenging is increasingly acknowledged, there are relatively few empirical studies of the scavenging community in Fennoscandia. There is limited knowledge on how habitat and potentially important drivers like winter climate, productivity, human subsidies or small rodent cycles affects the scavenger guild.

The objectives of my thesis were to investigate 1) the structure of the winter scavenger community across a forest-alpine gradient in central Scandinavia and the effects of temperature and snow depth; 2) effects of large quantities of gut piles left behind during the moose (*Alces alces*) harvest on scavenging communities and the influence of energy content and gut pile density on scavenging patterns; 3) how fluctuating small rodent abundance, landscape productivity and snow depth affected red fox scavenging during autumn and winter in forest and alpine habitat. To meet these objectives camera traps were set up on gut piles from moose harvest in autumn and on baits consisting of frozen blocks of discarded reindeer (*Rangifer tarandus*) meat, fat and connective tissue in winter.

Spatial variation in snow depth along the forest-alpine gradient interact with habitat to shape the structure of the scavenger community, while the impact of snow depth and temperature on species richness were weak in both forest and alpine habitats. When examining species separately diverse effects were observed, and most variation in individual species occurrence at baits was also explained by snow depth and habitat. Increasing snow depth only had negative effect on occurrence at baits for the species with stronghold in forest. The habitat generalists, and the alpine species showed no effect from climatic conditions at baits in alpine areas, but occurrence at baits in forest declined with decreasing snow depth and increasing temperature for red fox (*Vulpes Vulpes*), common raven (*Corvus corax*) and wolverine (*Gulo gulo*). Besides from the forest species Eurasian jay (*Garrulus glandarius*) which had a high probability of occurrence in forest, the habitat generalists red fox, common raven and golden eagle (*Aquila chrysaetos*) dominated in both habitats.

Depletion of gut piles was dependent on the different quality of gut pile parts, the energy rich parts were depleted first, and several times faster than the parts with lower energy content. This resulted in large differences in the magnitude and the duration between the parts with high and low energy content, where the latter accumulated to higher densities

and was present a long time after the end of the moose hunting season. Corvids arrived early at gut piles and their presence at gut piles decreased with gut pile age, probably reflecting depletion of gut pile parts with high energy content. Mammal presence at gut piles peaked at intermediate gut pile densities and I propose that lower mammal presence at high gut pile densities is due to resource saturation during this period.

I found contrasting patterns of red fox scavenging between forest and alpine habitat. I suggest that variation in red fox presence at alpine baits between the different phases of the small rodent cycle mostly reflects variation in red fox abundance. High red fox presence at alpine baits in the winter after the peak in rodent abundance is probably a numerical response, reflecting high red fox reproduction the preceding summer. In forest I found scavenging patterns probably reflecting a functional response. Red fox scavenging increased with low small rodent availability, when the snow was deep during winters of low small rodent abundance. Red fox scavenging on gut piles in autumn was not affected by small rodent phase, which may imply that gut piles is not a secondary choice for foxes.

Sammendrag

Mens viktigheten av åtsler og åtselspising får økende annerkjennelse, er det relativt få empiriske studier av åtseletersamfunnet i Fennoskandia. Det er begrenset kunnskap om hvordan habitat og potensielt viktige drivere som vinterklima, produktivitet, menneskelige subsidier eller smågnagersykluser påvirker åtseletersamfunnet.

Målsetningene med denne avhandlingen var å undersøke 1) strukturen til åtseletersamfunnet langs en skog-fjell gradient i sentrale deler av Skandinavia, og effekten av temperatur og snødybde om vinteren; 2) hvilken effekten de store mengder slakteavfall etter elgjakten har på åtseletersamfunnet, og hvilken effekt slakteavfallets energiinnhold og mengde har på utnyttelsen av slakteavfallet; 3) hvordan varierende tetthet av smågnagere, produktivitet og snødybde påvirker rødrevens bruk av åtsler om høsten og vinteren, både i skog og fjell. For å nå målsettingene ble det satt opp viltkamera på slakteavfall fra elgjakta om høsten og på åter bestående av frosne blokker med avskjær fra tamreinslakting bestående av kjøtt, fett og bindevev, om vinteren.

En interaksjon mellom variasjon i snødybde langs skog-fjell gradienten og habitat forklarte best strukturen i åtseletersamfunnet, mens effekten av snødybde og temperatur på artsrikdommen var svak både i skog- og fjellhabitat. Analysene av enkeltarters tilstedeværelse på åter viste varierende effekter, men storparten av variasjonen forklares med snødybde og habitat. Økende snødybde viste negative effekter, men bare for arter med tyngdepunkt i skogshabitat. Habitatgeneralistene og fjellartene viste ingen effekt av klimatiske forhold i fjellet, men tilstedeværelsen til rødrev, ravn og jerv ble redusert på åter i skogen med minkende snødybde og økende temperatur. Ved siden av skogsarten nøtteskrike som hadde stor sannsynlighet for tilstedeværelse på åter i skogen, dominerte habitatgeneralistene rødrev, ravn og kongeørn i begge habitater.

Kvaliteten på forskjellige deler av slakteavfallet hadde betydning for hvor fort de ble fjernet av åtseleterne. De mest energirike delene ble fjernet først, og mye raskere en delene med lavt energiinnhold. Dette resulterte i store forskjeller på mengden og varigheten for deler med høyt og lavt energiinnhold, hvor sistnevnte ble akkumulert til større mengder og var tilgjengelig lenge etter slutten på elgjaktsesongen. Kråkefugler fant slakteavfallet tidlig og deres tilstedeværelse minket med økende alder på slakteavfallet, noe som trolig reflekterer

at eldre slakteavfall i mindre grad har deler med høyt energiinnhold. Tilstedeværelse av pattedyr var størst ved middels tetthet av slakteavfall og jeg foreslår at lavere tilstedeværelse av pattedyr når antallet tilgjengelig slakteavfall er størst skyldes ressursmetning i denne perioden.

Jeg fant ulike mønstre I rødrevens åtselbruk mellom skog og fjell. Jeg foreslår at variasjonen i rødrevens tilstedeværelse på åter i fjellet mellom forskjellige faser i smågnagersyklusen først og fremst reflekterer variasjon i antall rødrever. Høy tilstedeværelse av rødrev på åter i fjellet om vinteren etter smågnagertopper er sannsynligvis en numerisk respons, som reflekterer høy reproduksjon hos rødreven sommeren før. I skog reflekterer sannsynligvis bruken av åter en funksjonell respons. Rødrevens bruk av åtene økte når tilgjengeligheten til smågnagere var lav, dvs. når snøen var dyp under bunnåret i smågnagersyklusen. Rødrevens bruk av slakteavfall om høsten var ikke påvirket av smågnagersyklusen, noe som kan bety at slakteavfall ikke er at andrevalg for rødreven.

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I. **Gomo, G.**, Rød-Eriksen, L., Andreassen, H. P., Mattisson, J., Odden, M., Devineau, O., & Eide, N. E. Scavenger community structure along an environmental gradient from boreal forest to alpine tundra in Scandinavia. Submitted.

II. **Gomo, G.**, Mattisson, J., Hagen, B. R., Moa, P. F., & Willebrand, T. Scavenging on a pulsed resource: quality matters for corvids but density for mammals. *BMC ecology* 17(1): 22

III. **Gomo, G.**, Mattisson, J., Rød-Eriksen, L., Eide, N. E., & Odden, M. Spatiotemporal patterns of red fox scavenging in forest and tundra: the influence of prey fluctuations and winter conditions. Submitted.

1. Introduction

Using camera-traps mounted on gut piles from moose harvest in autumn (**Papers II & III**) and on baits consisting of frozen blocks of discarded reindeer meat, fat and connective tissue in winter (**Papers I & III**), this thesis investigate the vertebrate scavenger community along a boreal forest-alpine gradient. The main focus is on how ungulate management, through provision of gut piles from the moose harvest, winter climate and small rodent cycles influence scavenging patterns. In the latter, the focus is on the red fox, an important species in the food web of northern Europe (Boonstra, Andreassen et al. 2016).

1.1 Scavenging

Scavenging is the consumption of carrion (dead animal tissue) by invertebrates and vertebrates (Olea, Mateo-Tomás et al. 2019). Scavenging includes consumption of carrion left by other predators or animals killed by other causes than predation but not predators consumption of its own kills (Olea, Mateo-Tomás et al. 2019). There are many natural sources of carrion, and in addition to predation, pathogens and diseases are important causes of mortality among ungulates (Pereira, Owen-Smith et al. 2014). Scavenging is common within many taxa, including both vertebrates and invertebrates (Mateo-Tomás, Olea et al. 2015, Anderson, Barton et al. 2019). Among terrestrial vertebrates there are few species which have evolved into obligate scavengers, i.e. mostly reliant on carrion, all of them being vultures (Ruxton and Houston 2004). There are also an unknown number of vertebrates which will scavenge opportunistically, called facultative scavengers. Among these species are skilled predators like the Eurasian lynx (*Lynx lynx*), that only scavenge occasionally (Selva, Jędrzejewska et al. 2005), and species more adapted towards scavenging, like Common raven (Stahler, Heinrich et al. 2002) and wolverine (Mattisson, Rauset et al. 2016). In addition to scavenging, carrion is also decomposed by microorganisms like bacteria, and fungi (Barton and Bump 2019).

Scavengers provide important ecosystem services, such as nutrient cycling (Wilson and Wolkovich 2011) and limit the spread of pathogens (Houston and Cooper 1975). Scavenging creates extra links in food webs, and may thus stabilize ecosystem (Wilson and Wolkovich 2011, Moleón, Sánchez-Zapata et al. 2014, Mateo-Tomás, Olea et al. 2017). Since a majority of scavengers also are predators, which may have a strong impact on co-existing prey and predator species through both direct and indirect interactions, effects from scavenging may be intricate and diverse (Moleón, Sánchez-Zapata et al. 2014, Pereira, Owen-Smith et al. 2014).

1.2 Ecological effects of carrion on facultative scavengers

Carrion can have both positive and negative effects on scavenger populations. For instance, some scavenger populations have experienced negative effects from poisoning, and thereby population declines, due to veterinary drugs in livestock carrion (Green, Newton et al. 2004) or lead poisoning from bullet fragments in carrion from game species (Pain, Fisher et al. 2009). Positive effects from carrion include range expansions (Sokolov, Sokolova et al. 2016), increased reproduction (Angerbjörn, Arvidson et al. 1991, Watson, Rae et al. 1992) and survival (Bino, Dolev et al. 2010). For instance, carrion and anthropogenic resources are important for range expansion into arctic and alpine tundra habitat by several scavenging species, like the red fox and the hooded crow (*Corvus cornix*) (Henden, Stien et al. 2014, Sokolov, Sokolova et al. 2016, Gallant, Lecomte et al. 2019). Carrion might also act as a direct subsidy, increasing scavenger carrying capacity and abundance (Bino, Dolev et al. 2010, Jahren, Odden et al. 2020). When carrion act as a substitute in periods when main prey is less abundant, available or vulnerable, carrion might increase scavenger survival and hence also stabilize scavenger populations (Jahren, Odden et al. 2020). In northern areas, carrion may be an important substitute during the low phases of the small rodent cycles or when small rodents are less available due to snow cover (Jędrzejewski and Jędrzejewska 1992, Lindström and Hörnfeldt 1994, Selas and Vik 2006, Gallant, Lecomte et al. 2019). Autumn is also a critical period for many carnivores and scavengers, especially for young individuals (Holyoak 1971, Kenward, Marcström et al. 1999). When the hunting skills of juvenile predators are not fully developed and their prey are increasingly difficult to catch, juveniles might suffer from starvation and high mortality (McIntyre, Collopy et al. 2006). Carrion might therefore be especially important for juvenile survival during this critical period.

1.3 Interspecific interactions

Predators do not actively search for live prey while scavenging. Hence, scavenging might reduce predation pressure (Mattisson, Andrén et al. 2011). However, this effect may be temporary, and higher survival and increased carrying capacity among predators that scavenge might lead to subsequently higher predation pressure (Moleón, Sánchez-Zapata et al. 2014, Coates, O'Neil et al. 2020). The effects from scavenging on predator prey interactions are therefore complex (Moleón, Sánchez-Zapata et al. 2014, Pereira, Owen-Smith et al. 2014). The timing of carrion resource pulses may be essential for food web effects. For instance, red fox winter abundance may increase in areas with high moose harvest due to the high amount of gut piles available for scavengers (Jahren, Odden et al. 2020). However, if this results in higher red fox abundance the proceeding spring, forest grouse may experience higher nest predation rates and delayed negative effects from carrion (Jahren, Storaas et al. 2016). Provision of carrion in spring has on the other hand resulted in higher reproductive success in forest grouse (Finne, Kristiansen et al. 2019). However, another study found local negative effects from "vulture restaurants" on ground-nesting birds (Cortés-Avizanda, Carrete et al. 2009). Carrion might also indirectly affect scavenger population as it might change levels of interspecific competition or intraguild predation within the scavenger guild (Moleón, Sánchez-Zapata et al. 2014). For instance, when red foxes expand into tundra habitat due to increased carrion resources, the smaller arctic fox seems to abandon historical breeding grounds (Elmhagen, Berteaux et al. 2017). If hooded crows expand their breeding range in response to increased carrion abundance (Sokolov, Sokolova et al. 2016), this might have negative effects on common ravens through restricted area use (Bodey, McDonald et al. 2009). Even though large predators can provide substantial amounts of carrion to smaller species (Wilmers, Crabtree et al. 2003, Wikenros, Sand et al. 2013), increased risk of intraguild killings at carrion can lead to population declines for smaller scavenging species (Prugh and Sivy 2020).

1.4 Temporal and spatial distribution of carrion

Carrion biomass from wild ungulates and livestock can range from few to several hundreds of kilo per km^2 (Barton, Evans et al. 2019). There are large temporal variation in carrion supply, both between and within years, especially in seasonal environments, due to effects of climatic conditions, predation and harvest (Wilmers, Crabtree et al. 2003). Ungulates often die of starvation or disease at the end of harsh seasons, e.g. in winters in northern areas or during the dry season in African savannahs (Pereira, Owen-Smith et al. 2014). The presence of apex predators provide a more temporally predictable carrion supply, however, often spatially unpredictable, as they leave some of their kills uneaten (Wilmers, Stahler et al. 2003). Hunting remains, on the other hand, create pulses of carrion during restricted hunting seasons (Wikenros, Sand et al. 2013). These pulses might be predictable in both space and time, and thus important for behavioural adaptations among scavengers utilizing such resources (Oro, Genovart et al. 2013). Resource pulse magnitude and duration are important determinants of competitive interactions among consumer species, and are thus key parameters for scavenger community responses to food pulses (Yang, Edwards et al. 2010).

1.5 Factors affecting scavenging patterns

When using camera-traps to investigate scavenging, we document presence of scavengers at carrion. Still, even if present in a given area, there are multiple and complex explanations to whether scavengers are present or not at a certain carrion. Firstly, mammals and birds have different abilities to discover carrion, as birds often find carrion using their vision, while mammals use their sense of smell. Secondly, energy expenditure while travelling long distances is lower in birds than in mammals (Schmidt-Nielsen 1972), which is important when searching for carrion (Houston 1979, Prior and Weatherhead 1991). These abilities are in turn affected differently by environmental factors such as habitat structure, snow cover or temperature (DeVault and Rhodes 2002, DeVault, Brisbin et al. 2004, Ruzicka and Conover 2012). The structure of the scavenger guild might also be important, as scavenger species often use cues from conspecifics or other species to locate carrion (Kruuk 1967, Knight and Knight 1983, Kane, Jackson et al. 2014). The distribution of carrion in space and time is also of importance. Predator kills might be scattered in space, while some seasonal pulses of carrion are both temporally and spatially predictable (Wilmers, Stahler et al. 2003). Predictability affects whether a species can locate carrion resources effectively or not, and in turn the scavenger species composition and patterns of interspecific competition. For instance, the predictable spawning migration of pacific salmon species is utilized by a range of predators and scavengers every year (Levi, Wheat et al. 2015).

Once located, carrion might not be accessible for all scavengers. Competition from superior species might hinder inferior species, or at least reduce their time spent feeding (Allen, Elbroch et al. 2015). Such competition might also arise from invertebrates (Ray, Seibold et al. 2014), or microorganisms which produce toxic chemicals preventing many vertebrates from feeding (Blandford, Katouli et al. 2019). Carrion from larger ungulates have thick hides, which can hinder smaller species from scavenging until the carcass is opened by larger species (Selva, Jedrzejewska et al. 2003, Orr, Nelson et al. 2019). Larger species might also impose a direct risk to smaller species through predation, affecting scavenger composition at carrion (Prugh and Sivy 2020). Gut piles from ungulate harvest is an example of highly nutritious carrion that is immediately accessible for all species (Gomo, Mattisson et al. 2017). Low temperatures result in deep frozen carcasses that are difficult to utilize by smaller species. Heavy snowfall or snowdrift might cover carrion within few hours, making then temporarily unavailable, especially for birds.

For many species, scavenging is a secondary strategy, where the decision to scavenge is dependent on the quality and abundance of carrion compared to other food sources (Jędrzejewski and Jędrzejewska 1992, Mattisson, Rauset et al. 2016, Peers, Konkolics et al. 2020).

1.6 Human impact

Human-induced climate change is one of the main drivers for ecosystem change worldwide (Nelson, Bennett et al. 2006). In temperate regions, altered weather patterns typically prolong the growing season (Christiansen, Markstrom et al. 2011) and increase primary productivity, while winter conditions become milder. This can lead to direct effects on the distribution range of species limited by harsh winter climate (Bevanger and Lindstrom 1995, Elmhagen, Kindberg et al. 2015, Tape, Jones et al. 2018). Such climate driven range expansion is documented for scavenging species, but other human-induced changes, such as land use change, apex predator regulation or provision of anthropogenic subsidies, may also play important roles (Pasanen-Mortensen, Pyykonen et al. 2013, Pasanen-Mortensen, Elmhagen et al. 2017).

Climate change can also affect prey populations (Melin, Mehtätalo et al. 2020) or abundance of other important food sources (Boulanger-Lapointe, Järvinen et al. 2017). Climate driven changes in the abundance and availability of important food sources may thus affect the importance of carrion for facultative scavengers. In addition, climate change affects carrion abundance through changes in ungulate abundance, distribution and mortality (Wilmers, Crabtree et al. 2003, Sokolov, Sokolova et al. 2016).

Rodent cyclicity is an important component of northern ecosystems, where many mammalian predators and birds of prey are adapted to respond quickly to high rodent abundances (Ims and Fuglei 2005, Gilg, Kovacs et al. 2017). Since the reproductive success of many of these species are closely dependent on small rodent abundance, dampening of multiannual rodent population cycles due to climate change has been a matter of concern during the last decades (Kausrud, Mysterud et al. 2008, Henden, Ims et al. 2009, Schmidt, Ims et al. 2012). Elevated winter temperatures alter snow conditions and can lead to a collapse of subnivean space, which in turn entails higher winter mortality in small rodents (Kausrud, Mysterud et al. 2008). Changes in snow conditions can also affect the availability of small rodents for predators (Jędrzejewski and Jędrzejewska 1992, Lindström and Hörnfeldt 1994). Climate driven changes in small rodent abundance and availability may thus affect survival and carrying capacity of predator populations and possibly the importance of carrion and anthropogenic food resources in their diet.

In the resource-limited arctic habitats of Scandinavia, changes in carrion abundance due to changes in management practices of semi-domestic reindeer is important for community-wide scavenger area occupancy (Henden, Stien et al. 2014). High abundances of ungulates in many areas are often consequences of synergetic effects. Management practices targeted to increase or sustain ungulate populations and indirect effects from other management practices like forestry and large carnivore regulation, can add to the effects of climate change (Selas and Vik 2006, Melis, Basille et al. 2010). Regulation of apex predator populations might also affect the scavenger guild more directly. This includes mesopredator or mesoscavenger release, where reduced suppression by apex predators can lead to trophic cascades possibly changing whole predator and prey communities (Ritchie, Elmhagen et al. 2012, O'Bryan, Holden et al. 2019). Apex predators such as wolves and bears can act as dominant scavengers that consume large amounts of carrion (Allen, Elbroch et al. 2015). In their absence, more carrion biomass may be available for smaller scavengers. Low abundance of apex predators can lead to changes in ungulate mortality patterns, where pulses of carrion more often arise in harsh winters due to starvation. However, this can be counteracted by climate change, if milder winters with less snow reduce ungulate winter mortality (Wilmers, Crabtree et al. 2003). However, the largest human impact on ungulate mortality is often harvest, and during the yearly harvest seasons, tonnes of gut piles are left in the field (Wilmers, Stahler et al. 2003, Wikenros, Sand et al. 2013, Hagen 2014). The magnitude, predictability and timing of this resource makes it potentially important for a range of scavenging species.

1.1 Study system

The study system includes boreal forest and alpine areas with both an altitudinal and a longitudinal climatic gradient, with variation in precipitation and temperature. This variation in habitat and climatic conditions possibly affect the distribution of scavenging species, as well as small rodent dynamics and ungulate area use. The latter potentially affect regional patterns in ungulate carrion biomass. The abundance of the most numerous ungulates, moose and semi-domesticated reindeer, are high because of management regulations, including historical and present regulation of apex carnivore populations. Harvest of moose in the autumn creates a large pulse of carrion, as gut piles are left in the field by hunters.

1.2 Study area

This study was conducted in the county of Trøndelag in central Norway (Fig. 1), and the study area covers an elevational gradient ranging from 90 to 850 m.a.s.l., with the forest line at approximately 560 m.a.s.l. Alpine tundra habitats are dominated by dwarf birch (*Betula nana*) and shrubs of willow (*Salix sp.*), whereas forested habitats are dominated by pine (*Pinus sylvestris*), spruce (*Picea abies*) and mountain birch (*Betula pubescens*) interspersed with bogs (Moen 1998). At elevations below 165 m the geology is dominated by marine deposits, mostly agricultural land interspersed with commercially managed forest, mainly Norway spruce. Semi-domesticated reindeer have perennial pastures within the region, including calving areas within or bordering our study area. Wild ungulates are mainly moose and roe deer (*Capreolus capreolus*). The autumn study on gut piles was restricted to an area of 65 km^2 90–485 m.a.sl.

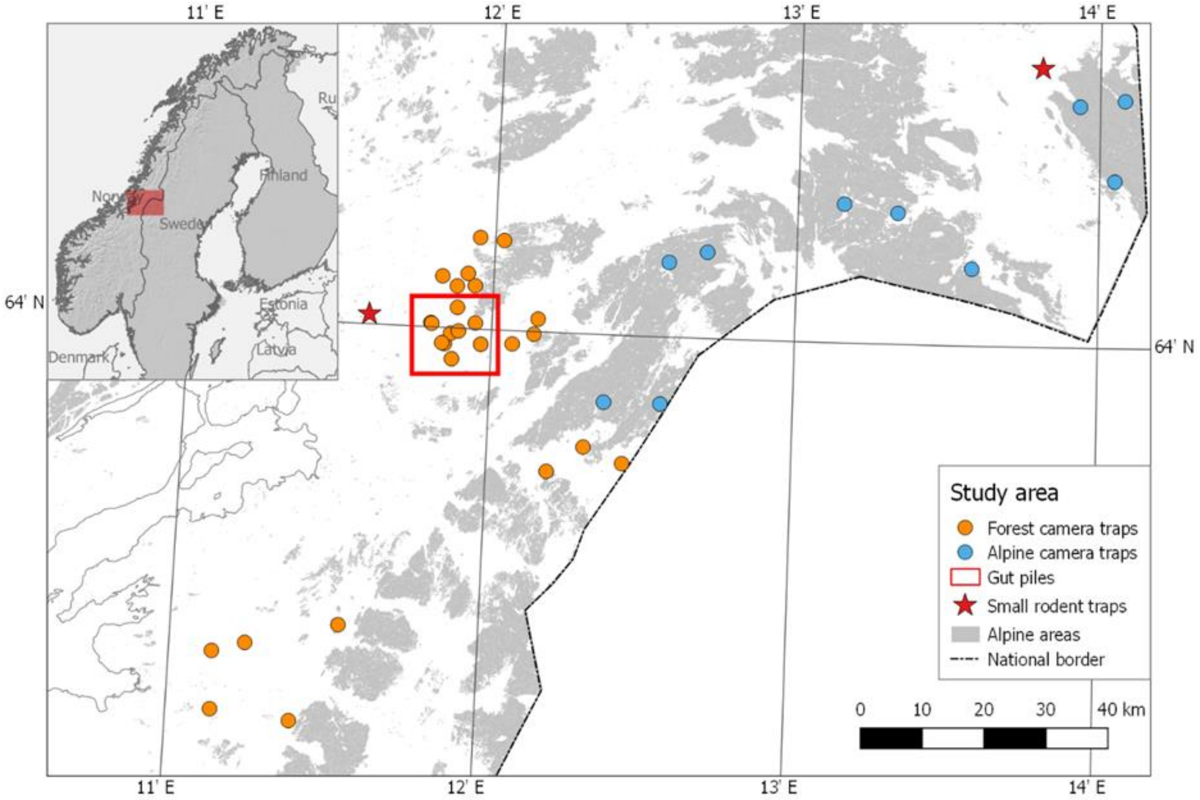

***Figure 1**. Spatial distribution of bait study sites in central Norway. Circles show the placement of camera traps in boreal habitats (orange) and alpine habitats (blue) in winter. Grey areas represent alpine habitat. The red square shows the area of the gut pile study in autumn, whereas red stars represent small rodent trapping locations.*

1.3 Climate

Average monthly temperature during the gut pile study (**Papers II & III**) in autumn varied between 3 to 5, 1 to 3 and −5 to 0 °C in October, November and December, respectively. Monthly precipitation in autumn ranged from 30 to 148 mm and snow covered the ground periodically, but snow depth >25 cm was restricted to a few days. Mean winter temperature (± 2SE) over all study sites and years was -0.46 °C (± 0.72) at forested and -4.02°C (± 1.37) at alpine tundra sites, whereas mean snow depth was 32 cm (± 9.9) at forested and 107.7 cm (± 9.9) at alpine tundra sites (**Paper I & III**). Snow depth also varied between years (Fig. 2).

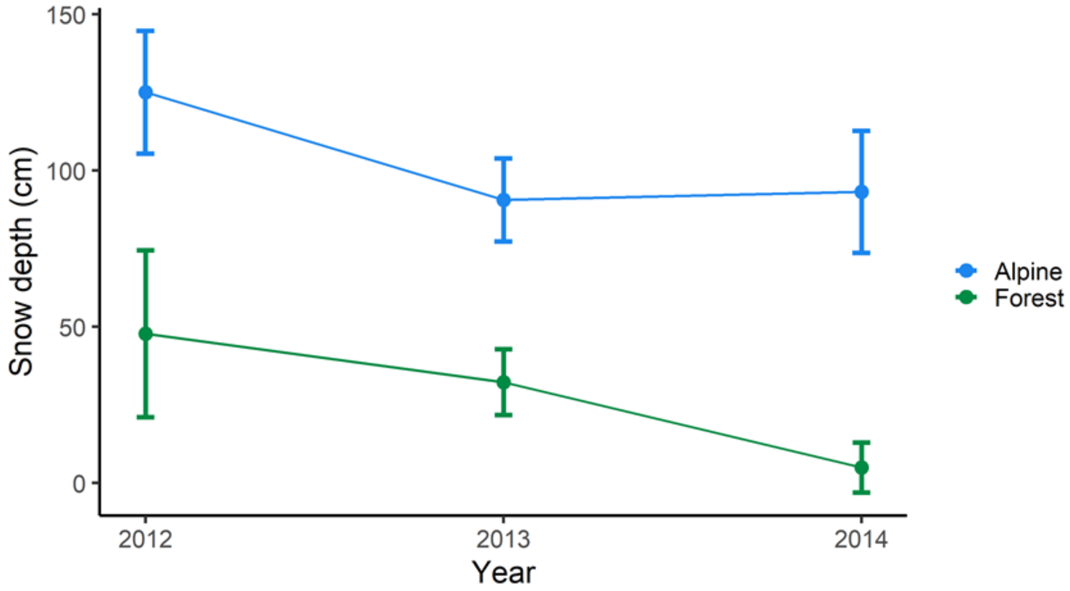

Figure 2. *Mean snow depth in centimetres (± SD) for bait stations per year within forest and alpine habitats.*

1.4 Small rodents

Small rodent abundance, based on autumn snap-trapping indices (Sørensen 2019, Sørensen 2020), varied between years and area (Fig. 3). While indices were similar in both areas during the low rodent phase in 2012, small rodent indices were higher in the eastern location representing the alpine area during the small rodent peaks in 2011 and 2014. The small rodent indices were slightly higher in the alpine area during the small rodent increase phase in 2013.

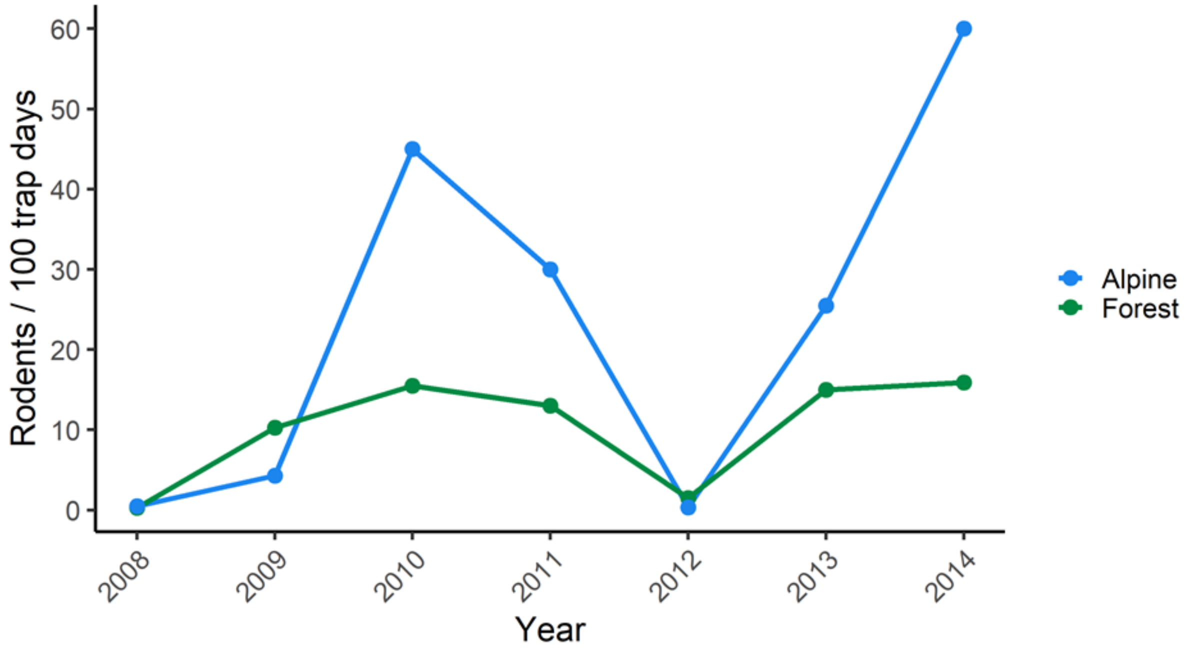

Figure 3*. Autumn snap-trapping indices for small rodents in forest (the westernmost trapping location of Ogndal; green line) and alpine (the easternmost trapping location of Lierne; blue line) habitats. During our winter study period, a post-peak rodent phase occurred in winter 2011/12, a low rodent phase in winter 2012/13, and a pre-peak rodent phase in winter 2013/14.*

1.5 Carrion resources

Natural carrion resources within our study area are dominated by domestic sheep during summer and cervid species during autumn and winter. Moose and semi-domesticated reindeer are the most important species, followed by roe deer. During the autumn period there is a pulse of carrion in the forest habitat due to moose and roe deer harvest. Gut piles left in the field and shot-wounded individuals not recovered by hunters were estimated to result in an average carrion biomass of 25.3 kg/km^2 within the forested part of the region. We estimated the amount of moose gut piles within our autumn study area to 33 kg/km^2 (roe deer and shot-wounded moose excluded). Carrion from ungulates provided an estimated average biomass of 29.1 kg/km^2 in boreal forest and 3.6 kg/km^2 in alpine tundra areas within our study region during the cold season (November to April) (Hagen 2014). Gut piles are an easily accessible and energy rich food source. Still, gut piles are heterogenous in quality, potentially affecting scavenging species differently. The lowest energy content in gut piles is in the stomach tissue with ~0.5 kcal/g, about half of what is found in muscle and liver.

Lungs have an intermediate energy content of ~0.85 kcal/g. The highest energy content is found in fat (~9 kcal/g dry weight). However, the energy content of fat tissue is lower, dependent on water content.

1.6 Scavenger guild

In the boreal forest and alpine tundra habitat of Scandinavia, the vertebrate scavenger guild consists of opportunistic facultative scavengers ranging from small sized terrestrial mammals and birds to large carnivores and raptors (Killengreen, Strømseng et al. 2012, Henden, Stien et al. 2014, Gomo, Mattisson et al. 2017). Corvid species and raptors are regular scavengers in northern areas, including the habitat generalist common raven which often specialise on scavenging during winter. Other known scavengers among the corvids are hooded crow, Eurasian magpie *(Pica pica)* and Eurasian jay, which are mainly found in or close to forest. There are several species of raptors in the area, among them known scavengers like the golden eagle, the white-tailed eagle (*Haliaeetus albicilla*), the northern goshawk (*Accipiter gentilis*) and the rough-legged buzzard (*Buteo lagopus*). The mammal scavengers are mainly canids and mustelids. Among these, the wolverine is found in both habitats with specialized adaptations towards scavenging. Other mustelids include European badger *(Meles meles),* Pine marten *(Martes martes),* stoat (*Mustela erminea*) and least weasel (*Mustela nivalis nivalis*). The two former are forest species, and the latter are habitat generalists. Among canids, the red fox is common, while there are a few breeding pairs of the threatened arctic fox (*Vulpes lagopus*) within the study area. Wolves (*Canis lupus*) visit the area occasionally. Bears are important scavengers outside the hibernation period in northern areas, but the brown bear *(Ursus arctos)* is only occasionally observed within our autumn study area. Several scavenging species of birds exhibit seasonal migrations and often gather at predictable food sources.

1.7 Red fox

The red fox is a generalist predator adapted to, and found in, a wide range of ecosystems around the globe (Schipper, Chanson et al. 2008). Increasing and expanding populations of red fox raise concern, as they negatively affect both populations of endangered species and important game species (Fletcher, Aebischer et al. 2010, Jahren, Storaas et al. 2016, Elmhagen, Berteaux et al. 2017, Marolla, Aarvak et al. 2019). Red foxes are facultative scavengers, and ungulate carrion are often an important part of their diet, especially during winter (Jędrzejewski and Jędrzejewska 1992, Killengreen, Lecomte et al. 2011, Needham, Odden et al. 2014) when the availability of live prey is lower (Cagnacci, Lovari et al. 2003). Hence, increasing densities of ungulate populations, and thereby carrion, have been linked to increased winter survival and elevated carrying capacity of red foxes in Fennoscandia during the last century (Selas and Vik 2006). More recent data from the arctic tundra in Scandinavia also links higher abundance of carrion from semi-domesticated reindeer to higher occupancy and range expansion of scavenging species including red fox, corvids, and eagles (Henden, Stien et al. 2014, Sokolov, Sokolova et al. 2016). Remains from hunting of ungulates is another source of food that can subsidise red foxes (Jahren, Odden et al. 2020).

2. Objectives

While the importance of carrion and scavenging is increasingly acknowledged, there are relatively few empirical studies of scavenging in Fennoscandia. There is limited knowledge on how habitat and potentially important drivers like winter climate, productivity, human subsidies or small rodent cycles affects the scavenger guild. In this thesis the focus is on these aims:

The aim of **Paper I** was to investigate the structure of the winter scavenger community across a forest-alpine gradient in central Scandinavia, with a special focus on the underlying drivers of the occurrence at baits by different scavenging species and species richness, with respect to climatic conditions and habitat types.

The aim of **Paper II** was to investigate scavenging patterns on the large quantities of gut piles from the moose harvest. Firstly, we measured how the different species in the scavenger community utilize the resource by comparing the arrival time and group size of different species at gut piles. Secondly, we quantified the rate of gut pile depletion and the temporal change in gut pile density. Thirdly, we evaluated how temporal variation in gut pile density and energy content influenced the foraging patterns of different functional groups of scavengers.

The aim of **Paper III** was to investigate how fluctuating small rodent abundance and environmental factors affected red fox scavenging during autumn and winter in forest and alpine habitat. We wanted to investigate if scavenging patterns could be explained by a functional response, with a shift to more scavenging when small rodent abundance was low or small rodents were less accessible due to increasing snow depth. Alternatively, if the scavenging patterns could be explained by numerical responses, where scavenging increases as a result of higher red fox abundance due to high red fox reproduction in small rodent peak years.

3. Methods

3.1 Field sampling

Camera traps were set up on gut piles from moose harvest in autumn (**Papers II & III**) and on baits consisting of frozen blocks of discarded reindeer meat, fat and connective tissue in winter (**Papers I & III**). We used the same setup in both seasons and all three years (2012-2014). Camera traps where placed 4–6 m away from the gut pile or bait, 1−1.5 m above ground, and the cameras were programmed to take a picture every 10 min. Camera traps were set up at 50 gut piles, totalling 1043 monitoring days in autumn, and at 65 baits totalling 1253 monitoring days in winter. Winter camera traps were set up at 29 forest locations and 9 alpine locations, for a total of 42 and 23 bait sessions in forest and alpine tundra habitat respectively. The average duration of a bait session was 19 ± 4 days (mean ± 2SE) in forest- and 20 ± 5 days in alpine tundra habitats, ranging from 4 – 62 days. Baits in alpine tundra habitat were monitored at the same sites all three years while the location of baits in the forest changed between the years, thus increasing the number of locations in this habitat type. All pictures were examined, and the number of individuals present of each species in each picture was registered. Images were aggregated to daily detections/non-detections of all individual scavenging species.

3.2 Structure of the winter scavenger community

Paper I. We explored the relationship between the climatic factors and species occurrence using a canonical correspondence analysis (CCA; Ter Braak & Verdonschot, 1995). We decided to pool all data, totalling 61 site/years, since the data set was unbalanced. We included presence / absence data for 13 species, aggregated for each bait session (i.e. site-years). Hence, values for each species could range from zero (not present during the bait session) to one (present at all days during the bait session).

Due to our unbalanced study design and lack of repeated measures on all study sites, we utilized a joint species distribution model (JSDM) within the hierarchical modeling of species communities framework (Ovaskainen, Tikhonov et al. 2017) to model average site-level species richness and species-specific distribution along environmental gradients. The framework was utilized in a basic capacity form as a multivariate linear mixed model with a binomial (presence/absence) distribution. Hence, values for each species was zero (not present during the bait session) or one (present during the bait session).

3.3 Depletion of gut piles from moose harvest

Paper II. To estimate daily energetic quality of the remains of the gut pile, we visually examined the first picture of each day. Gut piles were then categorized into two classes: (1) high energy content (parts with high energy density like fat, liver and lungs still present) and (2) low energy content (only stomach and/or intestines present, including rumen content). To estimate how fast gut piles were depleted, we used Kaplan–Meier curves. To evaluate if depletion varied between years or hunting periods, we compared the depletion rates by using Cox proportional hazard models. We tested for the difference in depletion rate between class 1 and 2 in different years. There were no significant differences between years for either class, and data were therefore pooled among all years. Secondly, we calculated gut pile density throughout the hunting season (all years pooled). Separate estimates were calculated for the parts with high (class 1) and low (class 2) energy content. The change in density of the two classes was calculated by reducing the accumulated gut piles from harvest with the Kaplan–Meier depletion estimates for each day of the hunting season.

3.4 Scavengers response to gut pile quality and gut pile density

Paper II. To analyse if daily presence of scavengers responded primarily to days since the moose was killed or to density of gut piles we used binomial generalised linear mixed-effects models. We analysed the daily probability (N = 1043) for each scavenging species to visit gut piles (0 or 1, where 1 is defined as ≥1 pictures including the species). We pooled scavenging species into three functional groups: (1) mammals, (2) large corvids [magpie, hooded crow and common raven] and (3) small corvids [Eurasian jay and Siberian jay (*Perisoreus infaustus*)] for separate analyses. Raptors were not included in this analysis due to small sample sizes.

3.5 Spatiotemporal patterns of red fox scavenging

Paper III. To investigate the influence of small rodent phases, snow depth or primary productivity on carrion use by red foxes, we used binomial generalized linear mixed-effects models. We ran separate analyses for gut piles, forest baits and alpine baits as sample size was too small to support three-way interactions. We included productivity, rodent population phase, snow depth and an interaction between rodent phase and snow depth as explanatory variables in the bait models. The gut pile models included only productivity and rodent phase as snow cover was limited to a few days during the autumn study period. In addition, we included an estimate of local gut pile density, as this parameter was shown to affect mammal scavenging in this study area (**Paper II**).

4. Results

4.1 Structure of the winter scavenger community

Paper I. Along the forest-alpine gradient (Fig. 4), the structure of the winter scavenger community was best explained by snow depth and habitat, while we found no effect from temperature. Besides from the forest species Eurasian jay which had a high probability of occurrence in forest, the habitat generalists red fox, common raven and golden eagle (*Aquila chrysaetos*) dominated in both habitats, with a tendency to occur more often at alpine baits. The three smallest corvid species, pine marten and badger were only present at baits in forest, while hooded crow and white-tailed eagle occurred at baits in both habitats, but to a higher degree in forest. Arctic fox occurred only at alpine baits, while wolverine occurred at baits in both habitats, however only at higher altitudes in forest.

The impacts of snow depth and temperature on species richness were weak in both forest and alpine habitats. When examining species separately diverse effects were observed, and most variation in species occurrence at baits was explained by snow depth and habitat. Increasing snow depth only had negative effect on occurrence at baits for the five forest species, hooded crow and white-tailed eagle. For the latter two, this was only apparent in alpine habitat, where decreasing temperature also had a negative impact on occurrence at baits. The three common habitat generalists and the alpine species showed no effect from climatic conditions at baits in alpine areas, but occurrence at baits in forest declined with decreasing snow depth and increasing temperature for red fox, common raven and wolverine.

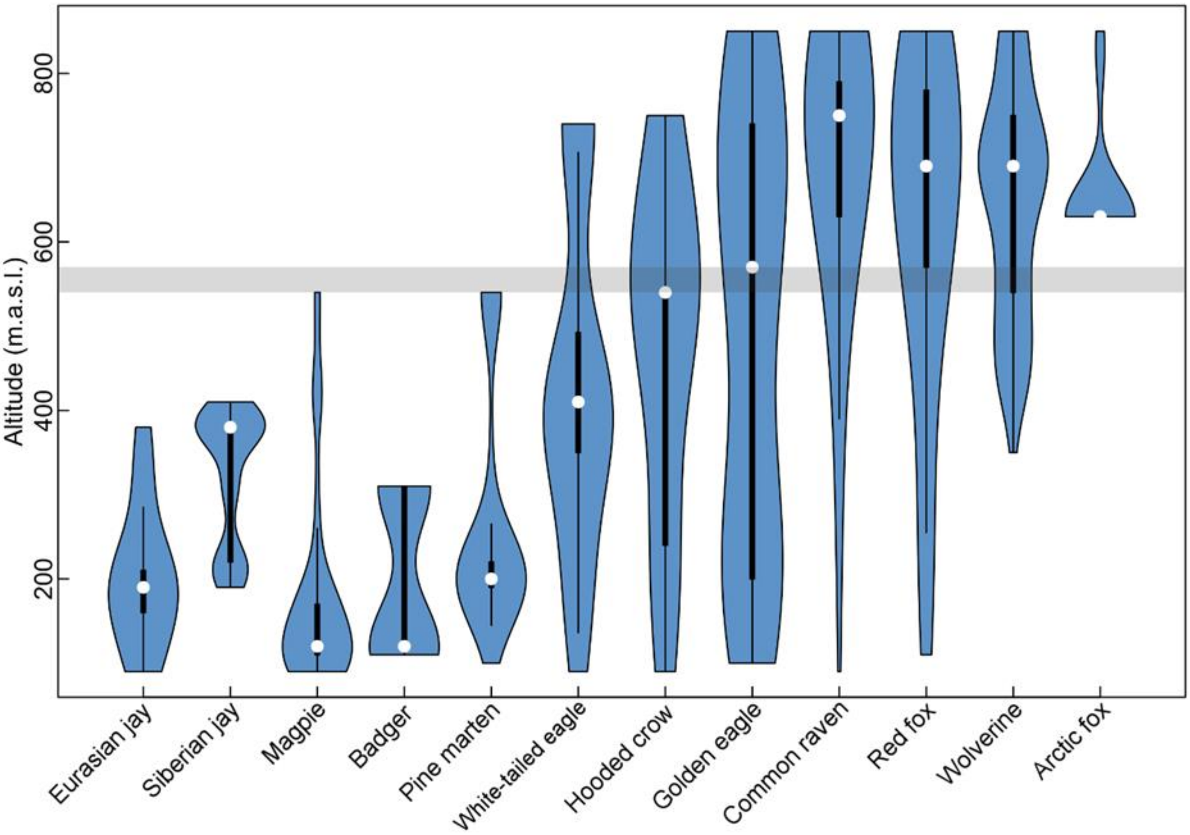

Figure 4. *The distribution of observed scavenger species along an altitudinal gradient, based on the number of photos of each species. Thickness of vertical columns indicate frequency of observations (thicker = more observations). White dots represent the median number of observations. Bold vertical lines indicate variability within the lower and upper quartile, whereas thin vertical lines indicate variability between minimum and maximum values. The shaded grey area represents the gap between forested (90 – 540 m.a.s.l.) and alpine tundra (570 – 850 m.a.s.l.) habitat classifications. Small mustelids, goshawk and rough-legged buzzard are not included in the plot due to too few site observations.*

4.2 Depletion of gut piles from moose harvest

Paper II. Depletion rate for gut pile parts depended on energy content, and while the parts with high energy content was depleted relatively fast, the parts with lower energy content accumulated to higher densities during the hunting season. Density of gut piles with high energy content parts was highest during the first hunting period, whereas low energy parts lasted longer and at higher density (Fig. 5).

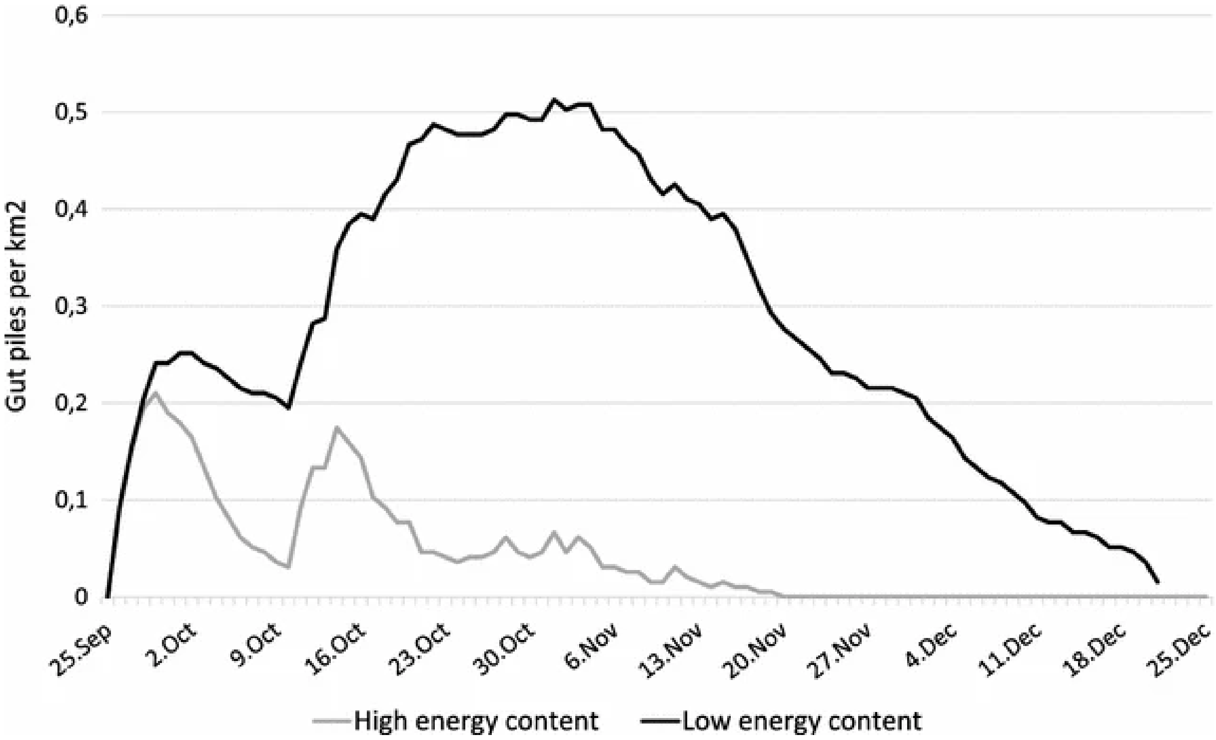

Figure 5. *Temporal development of the availability of gut pile parts with high and low energy content. Years are pooled.*

4.3 Scavengers response to gut pile quality and gut pile density

Paper II. Gut pile parts with high energy content were mainly consumed by corvids, that were present at all gut piles shortly after the remains were left at the kill site. Corvid presence declined with days since harvest, reflecting reduction in gut pile quality over time.

Mammals arrived 7–8 days later at the gut piles than corvids, and their presence depended only on gut pile density with a peak at intermediate densities (Fig. 6). The decline at high gut pile densities suggest a saturation effect, which could explain accumulation of gut pile parts with low energy content.

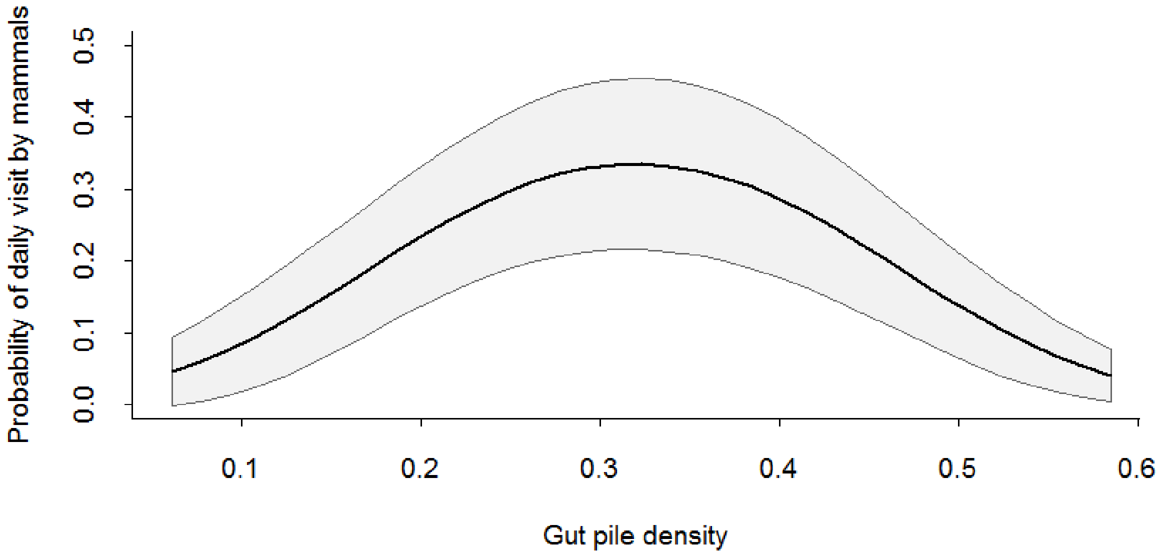

Figure 6. *Probability of scavenging mammals to visit gut piles in relation to gut pile density (Gut piles per km^2). Gut piles remaining after field dressing of hunted moose in Central Norway in 2012–2014*

4.4 Spatiotemporal patterns of red fox scavenging

Paper III. Red fox presence at carrion was higher in alpine habitat than in forest habitat, while there was no difference between gut piles in autumn and forest baits in winter. During winter, an interaction between small rodent phase and snow depth affected red fox scavenging in both habitats, but we found contrasting patterns between forest and alpine habitat. In alpine habitat scavenging increased when rodent abundance was high and snow cover was low. This was most evident during the post-peak small rodent phase, when the abundance of small rodents was at the highest levels the preceding summer. In forest, I observed an opposite influence of small rodents and snow, i.e. scavenging increased when small rodent abundance was low and snow cover was high (Fig. 7). In other words, the effect of snow cover was only evident during the low rodent phase in forest, while this was the only rodent phase without effects from snow depth in alpine habitat. Primary productivity did not affect red fox presence at baits in winter nor at gut piles in autumn. Red fox scavenging on gut piles in autumn was not influence by small rodent phase, but was best explained by density of gut piles. However, the best model had low explanatory value.

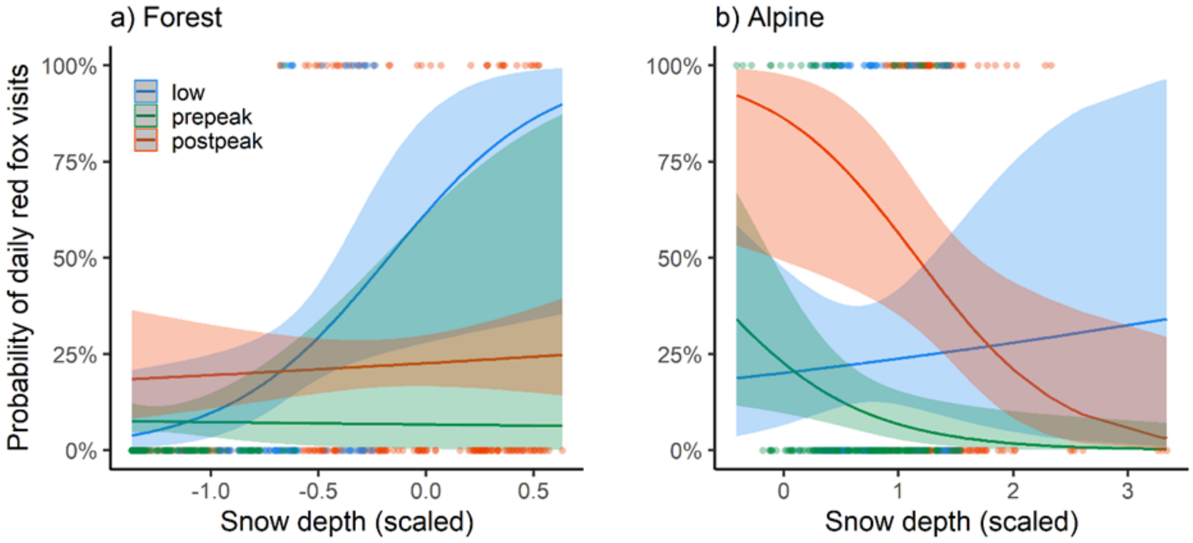

Figure 7. *Predicted probabilities of red fox daily use of bait stations in forest (a) and alpine (b) habitats. The predictions are based on the model including the interaction between small rodent phases (low, pre-peak, post-peak) and snow depth (top ranked model for alpine and second-ranked model for forest following AIC; Table 1). Dots are daily non-detections (bottom) and detections (top) from the raw data, color-coded for each rodent phase.*

5. Discussion

6.1 Structure of the winter scavenger community

Winter is a bottleneck for many species. Harsher environmental conditions may lead to thermal stress and increased energy demands (Careau, Morand-Ferron et al. 2007). Important prey may have migrated (Holyoak 1971, Solonen, Lokki et al. 2019), while other prey species become less vulnerable as increasing amounts of snow covers the ground (Halpin and Bissonette 1988). Food resources are also depleted throughout the winter season, potentially increasing the required time and energy spent searching for food. Ungulate carrion is potentially utilized by many species and is added to the food web throughout winter (Selva, Jędrzejewska et al. 2005). We found many species utilizing carrion along the forest-alpine gradient, supporting the view that carrion may be an important part of food webs. The structure of the winter scavenger community was best explained by snow depth and habitat, while we found no effect of temperature.

Habitat generalists dominated in both habitats. In fact, common ravens, golden eagles and red foxes are true habitat generalist found from desert to arctic tundra. Opportunism, including scavenging, may be an important adaptation to inhabit such a wide range of environmental conditions. The occurrence at baits by these species was not limited by environmental conditions in the harsher alpine habitat, and thus, available food, including prey and carrion, may be particulary important drivers for their area use (Carricondo-Sanchez, Samelius et al. 2016, Stoessel, Elmhagen et al. 2019) and occupancy of alpine habitat (Henden, Stien et al. 2014). Still, harsh environmental conditions can influence area use and food preferences in shorter time-scales than investigated in this study (**Paper III**) (Peebles and Conover 2017).

Snow depth explained most of the variation in scavenger occurrence at baits. It may be reasonable to expect that species searching for or caching food on the ground will be strongly affected by changes in snow depth. Range expansions within the boreal forest is documented for the Eurasian jay and badger, and it has been linked to climate change (Elmhagen, Kindberg et al. 2015). Restricted access to earthworms are proposed to be de determinant factor of badger winter activity (Kowalczyk, Jędrzejewska et al. 2003). Both jay species in the study area are considered as corvid species which have evolved to specialize on caching (De Kort and Clayton 2006). While Siberian jays cache food in the tree canopy (Sklepkovych 1997), Eurasian jays cache food on ground (Chettleburgh 1952). Interestingly, Eurasian jay was the scavenger showing the most atrong negative effect of increasing snow depth in our study.

Habitat and snow depth were the two major factors explaining the structure of the scavenger community along the forest-alpine gradient. As the climate becomes warmer, arctic and alpine areas can shift to forest. However, this process is quite slow (Kullman 2001), and can be counteracted by ungulate herbivory (Speed, Austrheim et al. 2010) and rapid invertebrate range expansions (Vindstad, Jepsen et al. 2019). Hence, temperature may have diverse ecosystem effects at the forest-alpine ecotone. Still, the most drastic ecological change in temperature is at zero degrees Celsius, when water changes between liquid and solid states (Berteaux, Gauthier et al. 2016). Climate, including snow conditions, are suggested to be important for large scale differences between ecosystems in western parts of northern America and Europe (Boonstra, Andreassen et al. 2016), and a growing body of studies show that a range of species in both boreal forest, alpine and arctic habitat is affected by changes in snow or ice conditions. Effects are found on many taxa and among different-sized animals, from the largest land-living carnivore, the polar bear (Hamilton, Kovacs et al. 2017), to the smallest, the least weasel (Ylönen, Haapakoski et al. 2019). Snow conditions can affect small rodent population dynamics (Kausrud, Mysterud et al. 2008), while shorter winters may increase hare and grouse mortality (Pedersen, Odden et al. 2017, Melin, Mehtätalo et al. 2020) and lead to range expansions in beavers (Tape, Jones et al. 2018). Snow conditions also affect winter range (Rivrud, Meisingset et al. 2019) and mortality patterns among ungulates, directly affecting scavenging species (Wilmers, Crabtree et al. 2003, Sokolov, Sokolova et al. 2016). Since snow conditions may have impact on all trophic levels and within multiple taxa, predicting ecosystem change may be difficult. Adding additional complexity is the fact that changes in snowfall patterns also show large regional differences (Brown and Mote 2009). This study provides novel insight into how snow depth may affect the structure of the scavenger community along the forest-alpine gradient and is thus a contribution into understanding possible effects from climate change on boreal ecosystems.

6.2 Depletion of gut piles from moose harvest

Depletion of gut piles depended on the quality of gut pile parts. The stomach and intestines are rich in collagen and have a low energy content compared to liver, kidney, lungs, and especially fat. Not surprisingly, the energy rich parts were depleted first, and several times faster than the parts with lower energy content. How fast different species arrive will therefore be important for their potential energy gain from the gut piles (Lafferty, Loman et al. 2016). First to arrive, first to get served, is not necessary the case for other carrion resources. Smaller species might not be able to break through the thick skin of whole carcasses and will have to wait for larger species to join the buffet (Selva, Jedrzejewska et al. 2003, Orr, Nelson et al. 2019). Humans are probably the only predator leaving the most nutritious parts of their prey behind, making gut piles a special carrion resource. Differences in depletion rates between gut pile parts resulted in large differences in the magnitude and the duration between the parts with low and high energy content (Fig. 5). Such basic knowledge is important, as these parameters determine the magnitude, the lag and the duration of consumer responses to resource pulses (Yang, Edwards et al. 2010).

6.3 Scavengers response to gut pile quality and gut pile density

Corvids arrived early at gut piles and their presence at gut piles decreased with gut pile age. It is likely that this reflects a rapid depletion of energy rich parts of the gut piles. Searching for new gut piles when the energy rich parts are utilized might be a better foraging strategy than feeding on remains of poorer quality (Darimont, Reimchen et al. 2003, Knarrum, Sørensen et al. 2006). Gut pile parts with low energy content accumulate to high densities during the hunting season. Mammal presence at gut piles peaked at intermediate densities and we propose that lower mammal presence at high gut pile densities is due to resource saturation during this period. This should reduce both intra- and interspecific competition allowing less competitive species or individuals to utilize this resource. Juveniles often suffer from high mortality in autumn, and starvation is for instance reported as an important cause of mortality for corvids and raptors (Holyoak 1971, Kenward, Marcström et al. 1999, McIntyre, Collopy et al. 2006). Scavenging mammals might also experience increased juvenile mortality in autumn due to food shortage (Helldin 1999, Johnson, Fryxell et al. 2009). Gut piles may thus be especially important for juvenile survival (Oro, Margalida et al. 2008). Still, the long duration of the gut piles resource pulse may also result in long-lasting effects on scavenger populations (Yang, Edwards et al. 2010). Many scavengers in northern area have adaptations for utilizing yearly seasonal resource pulses (Holt 2008). Body fat reserves are important for winter survival (Kowalczyk, Jędrzejewska et al. 2003), and several of the species utilizing gut piles cache food that may be eaten during winter (Fjeld and Sonerud 1988, Sklepkovych and Montevecchi 1996, Heinrich and Pepper 1998, Helldin 2000, Legg and Clayton 2014).

6.4 Spatiotemporal patterns of red fox scavenging

We found contrasting patterns of red fox scavenging between forest and alpine habitat, which may be explained by several factors. Average snow depth was much higher in alpine habitat, thus limiting access to small rodents (Lindström and Hörnfeldt 1994, Willebrand, Willebrand et al. 2017). The climatic differences between the habitats result in different abundances of small rodents, i.e. small rodent abundances in the alpine habitat were much higher during rodent peaks (Fig. 3) (Hansson and Henttonen 1985, Andreassen, Johnsen et al. 2020). In contrast, carrion biomass was previously estimated to be eightfold higher in the forest than the alpine region during winter (Hagen 2014). Still, red fox presence at carrion was higher in the alpine habitat. In this harsh environment, red foxes may have to utilize all available resources. Higher red fox presence at alpine baits may thus be a result of food limitation (Killengreen, Lecomte et al. 2011, Henden, Stien et al. 2014).

We suggest that variation in red fox presence at alpine baits mainly reflects variation in red fox abundance (Stoessel, Elmhagen et al. 2019). Accordingly, high red fox presence at alpine baits in the post-peak rodent phase is probably a numerical response, reflecting high red fox reproduction the preceding summer (Englund 1970). Red fox presence at forest baits showed less variation through the small rodent phases. Lower amplitudes of small rodent cycles and more food in forest habitat, including carrion, may lead to more stable red fox populations (Selas and Vik 2006, Jahren, Odden et al. 2020). The increased bait use with increasing snow depth during the low small rodent phase in forest habitat is likely a functional response to less available prey (Jędrzejewski and Jędrzejewska 1992, Lindström and Hörnfeldt 1994, Cagnacci, Meriggi et al. 2004).

Red fox scavenging in alpine habitat increased during the post-peak small rodent phase, but only where snow depth was low. This may reflect adjustment of area use towards higher small rodent accessibility when small rodent abundance is above some threshold (Carricondo-Sanchez, Samelius et al. 2016, Stoessel, Elmhagen et al. 2019). During the low rodent phase, snow depth did not affect red fox presence at alpine baits. Red fox home ranges in Fennoscandia are shown to increase in resource-limited areas (Walton, Samelius et al. 2017), and may be an important adaptation to locate carrion. Overall, our results imply that large habitat differences in snow depth may be a key factor modifying the effects of small rodents on red fox scavenging.

6.5 Management implications

Management decisions regarding human infrastructure, ungulate management practices and human subsidies can interact with effects from climate change, with both indirect and direct effects on scavenger populations (Henden, Stien et al. 2014, Gallant, Lecomte et al. 2019, Bargmann, Wheatcroft et al. 2020, Fisher, Burton et al. 2020). For instance, changes of ungulate harvest quotas or seasons could possibly lead to changes in resource pulse magnitude and duration. Such changes may in turn cause different responses among functional groups of scavengers (**Paper II**). The timing of resource pulses can alone affect the scavenger community (Levi, Wheat et al. 2015), and snow depth may play a key role if harvest seasons are stretched into winter (**Paper I**). Local or national legislation banning the practice of leaving gut piles in the field may reduce carrying capacity for the red fox (**Paper III**) (Bino, Dolev et al. 2010, Jahren, Odden et al. 2020), but may also have positive (Legagneux, Suffice et al. 2014) or negative (Margalida, Donazar et al. 2010) effects on species of conservation interest. Hence, an ecosystem approach to ungulate management, including the role of carrion subsidies, should be encouraged.

Changes in snow patterns may affect all trophic levels in northern ecosystems (Berteaux, Gauthier et al. 2016, Boonstra, Andreassen et al. 2016). As discussed earlier, snow depth may affect carrion use and winter range for many of the scavenging species in different ways (**Paper I & III**). Hence, making good predictions about the outcome of climate change and management decisions may be complex. Changes in snow cover are also expected to vary greatly between regions and can be highly affected by altitude (Brown and Mote 2009). Hence, creating good tools for predicting regional changes in snow conditions, and implementing these tools into research and management may be crucial in northern ecosystems (Boelman, Liston et al. 2019).

Increased human populations, human area use and subsidies, including carrion, are important for red fox populations worldwide (Main, Davis et al. 2020), in boreal forest (Walton, Samelius et al. 2017, Jahren, Odden et al. 2020) and alpine/arctic habitat (Elmhagen, Berteaux et al. 2017, Gallant, Lecomte et al. 2019). Red fox range expansion and high abundance is of management concern, due to negative impact on endangered species, as well as important game species (Fletcher, Aebischer et al. 2010, Jahren, Storaas et al. 2016, Aarvak, Øien et al. 2017, Elmhagen, Berteaux et al. 2017). We found habitat differences in the combined effects from small rodent abundance and snow depth on red fox scavenging patterns (**Paper III**). The effects of higher red fox abundance on prey or competitors are often negative and influenced by small rodent dynamics (Jahren, Storaas et al. 2016, Ims, Killengreen et al. 2017, Marolla, Aarvak et al. 2018). Our results indicate that habitat differences in snow conditions are important for the effects of small rodent abundance on red fox scavenging in winter. This may add important knowledge on temporal variation of ecosystem functioning in boreal areas, and hence improve management decisions.

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Paper I

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Gjermund Gomo
Inland Norway University of Applied Sciences
P.O. Box 400
NO-2418 Elverum, Norway
+47 97 07 17 12
gjermg@gmail.com

Scavenger community structure along an environmental gradient from boreal forest to alpine tundra in Scandinavia

GJERMUND GOMO[1], *Inland Norway University of Applied Sciences (HINN), Faculty of Applied Ecology, Agricultural Sciences and Biotechnology (Fac. Appl. Ecol.), NO-2480 Evenstad, Norway*

LARS RØD-ERIKSEN, *Norwegian Institute for Nature Research (NINA), P.O. Box 5685 Torgard, NO-7485 Trondheim, Norway; Centre for Biodiversity Dynamics (CBD), Dept. of Biology, Norwegian University of Science and Technology (NTNU), NO-7491 Trondheim, Norway*

†HARRY P. ANDREASSEN, *HINN, Fac. Appl. Ecol., NO-2480 Evenstad, Norway*

JENNY MATTISSON, *NINA, P.O. Box 5685 Torgard, NO-7485 Trondheim, Norway*

MORTEN ODDEN, *HINN, Fac. Appl. Ecol., NO-2480 Evenstad, Norway*

OLIVIER DEVINEAU, *HINN, Fac. Appl. Ecol., NO-2480 Evenstad, Norway*

NINA E. EIDE, *NINA, P.O. Box 5685 Torgard, NO-7485 Trondheim, Norway*

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[1] Corresponding author: gjermg@gmail.com
†Deceased 21 May 2019

ABSTRACT

Scavengers can have strong impacts on food webs, and awareness of their role in ecosystems have increased during the last decades. In our study, we used baited camera traps to quantify the structure of the winter scavenger community in central Scandinavia across a forest-alpine continuum and assess how climatic conditions affected spatial patterns of species occurrences at baits. Canonical correspondence analysis revealed that the main habitat type (forest or alpine tundra) and snow depth were main determinants of the community structure. According to a joint species distribution model within the HMSC framework, species richness tended to be higher in forest than in alpine tundra habitat but was only weakly associated with temperature and snow depth. However, we observed stronger and more diverse impacts of these covariates on individual species. Occurrence at baits by habitat generalists (red fox, golden eagle and common raven) typically increased at low temperatures and high snow depth, probably due to increased energetic demands and lower abundance of natural prey in harsh winter conditions. On the contrary, occurrence at baits by forest specialists (e.g. Eurasian jay) tended to decrease in deep snow, which is possibly a consequence of reduced bait detectability and accessibility. In general, the influence of environmental covariates on species richness and occurrence at baits was lower in alpine tundra than in forests, and habitat generalists dominated the scavenger communities in both forest and alpine tundra. Following forecasted climate change, altered environmental conditions is likely to cause range expansion of boreal species and range contraction of typical alpine species such as the arctic fox. Our results suggest that altered snow conditions will possibly be a main driver of changes in species community structure.

KEY WORDS scavengers, community, bait, alpine tundra, boreal forest, camera traps

1 INTRODUCTION

Scavengers are an important component of ecosystems due to their effect on nutrient cycling, stabilizing food webs, and disease transmission (Mateo-Tomás, Olea et al. 2017). Interest in scavenging has increased during the last decade, and recent studies have highlighted that scavengers may impact food webs in more intricate ways than only consumption of carrion (Wilson and Wolkovich 2011). The traditional focus on obligate scavengers and bottom-up processes have been broadened to include facultative scavengers that potentially have a strong impact on co-existing prey and predator species through both direct and indirect interactions (Wilson and Wolkovich 2011, Pereira, Owen-Smith et al. 2014)

Large scale patterns in scavenger guild structure are driven by species' physiological capability, landscape productivity, climatic constraints, as well as inter- and intraspecific competition (Moleón, Sánchez-Zapata et al. 2014, Elmhagen, Kindberg et al. 2015, Mateo-Tomás, Olea et al. 2015). As a consequence, different large scale habitats (e.g. forest, tundra, grassland) likely host rather different scavenger guilds, despite some scavengers occurring across various habitats (Arrondo, Morales-Reyes et al. 2019, Pardo-Barquín, Mateo-Tomás et al. 2019). A recent review of global patterns in vertebrate scavenger distribution concluded that the degree of human impact was a main predictor of richness in the scavenging guild (Sebastián-González, Barbosa et al. 2019). Along a human footprint index overall species richness was lowest at high index values and highest at medium values. Scavenger richness was highest at carrion of medium size and in the winter season, while average temperature and rainfall had no effect on scavenger richness.

In the boreal forest and alpine tundra habitat of Scandinavia, the vertebrate scavenger guild consists of opportunistic facultative scavengers ranging from small sized terrestrial mammals and birds to large carnivores and raptors (Killengreen, Strømseng et al. 2012, Henden, Stien et al. 2014, Gomo, Mattisson et al. 2017). Harsh winter conditions in the alpine tundra habitats may function as a barrier for boreal forest species. However, climate change affects both temperature and precipitation, and hence overall primary productivity, which opens the possibility for northwards expansion for species limited by these factors (Elmhagen, Kindberg et al. 2015, Gomo, Mattisson et al. 2017). Climate change at northern latitudes also impacts the cover, depth and structure of snow, which e.g. is likely to influence the predators' access to rodents and other food sources (Halpin and Bissonette 1988, Willebrand, Willebrand et al. 2017). Deep snow can also restrict locomotion and area use in mammals (Pozzanghera, Sivy et al. 2016).

Many scavengers utilize carrion resources in northern areas during winter, thus potentially strengthening food web interactions between species that otherwise have weak connections in these ecosystems (Moleón, Sánchez-Zapata et al. 2014). For instance, carrion consumption by red fox (*Vulpes vulpes*), an important generalist predator, increase during periods of low natural prey availability (Jędrzejewski and Jędrzejewska 1992, Killengreen, Lecomte et al. 2011, Needham, Odden et al. 2014). The documented increase in ungulate populations during the last century have generated a large amount of ungulate carrion available for scavenging species, including gut piles left in the field by hunters (Selas and Vik 2006, Wikenros, Sand et al. 2013, Hagen 2014). The expansion of boreal associated species into alpine and arctic tundra habitats can be facilitated by access to carrion (Killengreen, Strømseng et al. 2012, Sokolov, Sokolova et al. 2016). For example, high abundance of carrion from semi-domesticated reindeer (*Rangiferus tarandus*) has been linked to high occupancy of scavenging species including corvids, eagles and red fox on the arctic tundra in northern Scandinavian (Henden, Stien et al. 2014).

This study aims to quantify the structure of the winter scavenger community across a forest-alpine gradient in central Scandinavia, with a special focus on the underlying drivers of the occurrence at baits by different scavenging species with respect to climatic conditions and habitat types. We did this by placing baited camera traps along the forest-alpine gradient. In general, species richness at baits is expected to be higher in forest than in alpine tundra habitats, but snow depth and temperatures can influence species-specific occurrence at baits within and between habitat types, resulting in complex structures of the scavenger guild.

Some scavenging species are likely very restricted to their preferred habitats, while generalists are typically not so selective. We predict that the scavenger guild structure in large will be clustered into habitat specialists and habitat generalists. Scavenger species could also be restricted by climatic conditions. We predict that both temperature and snow depth are important factors structuring the scavenger guild by limiting their distribution and affecting their activity patterns when present. Snow can also restrict species utilization of food resources such as e.g. carrion. We predict that snow depth will have the greatest impact on species utilizing food sources or prey which might be covered in snow, for example small rodents or plants. Since birds mostly locate food by eyesight, and have limited ability to dig through deep snow, we predict that snow depth might affect bird scavenging more than mammal scavenging.

2 MATERIALS AND METHODS

STUDY AREA

Our study was conducted between January and April in the areas of Lierne, Blåfjella and Skjækerfjella in central Norway from 2012 to 2014 (Fig. 1a). The area covers an elevational gradient ranging from 90 to 850 m.a.s.l., with the forest line at approximately 560 m.a.s.l. (Fig 1b). Alpine tundra habitats are dominated by dwarf birch (*Betula nana*) and shrubs of willow (*Salix sp.*), whereas forested habitats are dominated by pine (*Pinus sylvestris*), spruce (*Picea abies*) and mountain birch (*Betula pubescens*) (Moen 1998). Semi-domesticated reindeer have perennial pastures within the region, including calving areas within or bordering our study area. Wild ungulates are mainly moose and roe deer. Carrion from ungulates provide an estimated biomass of 29.1 kg/km^2 in boreal forest and 3.6 kg/km^2 in alpine tundra areas during the cold season (November to April) (Hagen 2014).

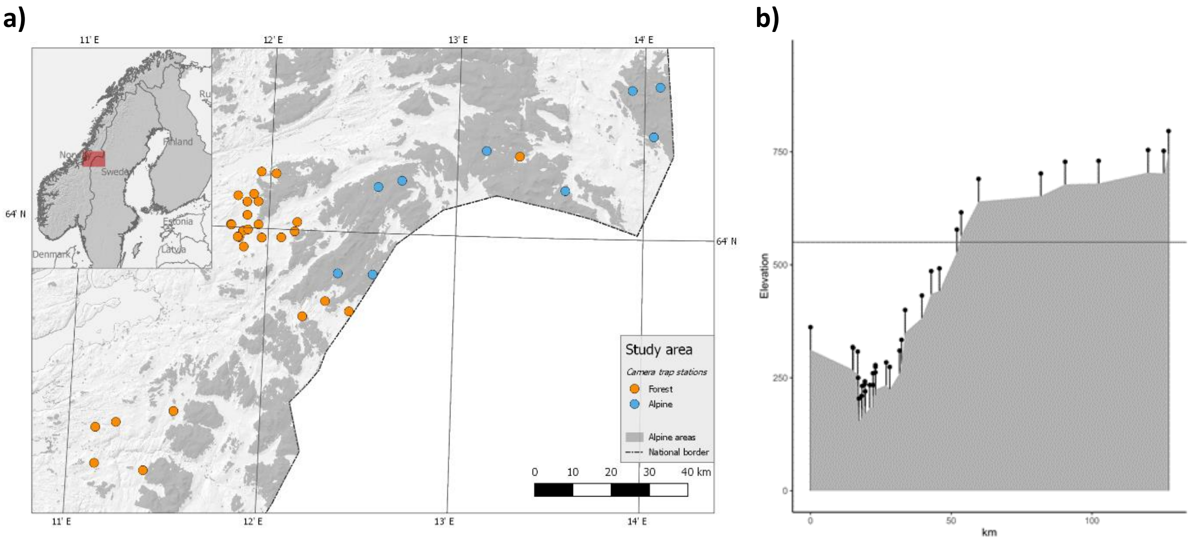

Figure 1. a) Spatial distribution of study sites in central Norway. Circles show the placement of camera traps in boreal forest habitats (orange) and alpine tundra habitats (blue). Grey areas represent alpine areas. **b)** Distribution of camera trap sites (pinned dots) along an elevational gradient on a longitudinal axis from west to east. The horizontal line illustrates the forest line.

STUDY DESIGN AND FIELD SAMPLING

Camera traps (Reconyx Hyperfire Professional PC 800 and PC 900, Reconyx Inc., Wisconsin, USA) were set up at 38 locations (29 in forest and 9 in alpine tundra habitat) for a total of 65 (42 in forest and 23 in alpine tundra habitat) bait sessions, i.e. camera site per year, and 1253 monitoring days between January and April from 2012 – 2014. Baits in alpine tundra habitat was monitored at the same site all three years (but 4 bait sessions were excluded due to failure to observe any species) while the location of baits in the forest changed between the years creating the high number of locations. Bait sessions started when bait was deployment and ended when bait was depleted. The average duration of a bait session was 19 ± 4 days (mean ± 2SE) in forest- and 20 ± 5 days in alpine tundra habitats, ranging from 4 – 62 days. Bait consisted of frozen blocks of discarded reindeer meat, fat and connective tissue weighing between 10 and 20 kg and measuring approximately 60 x 40 x 15 cm. To ensure that the bait was not removed immediately by large scavengers, and to keep the bait frozen, the bait was buried in the snow in a vertical position such that only 5 cm of the top was visible. Cameras were placed 4–6 m from the baits at approximately 1−1.5 m above the ground and tilted slightly downwards towards the bait. Camera traps were programmed to take a picture every 10 minutes to increase capture probability of elusive species (c.f. Hamel, Killengreen et al. 2013). All pictures were examined and the number of individuals of each species in each picture was recorded. To reduce sampling bias, only images where the bait was present (i.e. not consumed) and thus acting as an attractant to animals were included in the analyses (Figures S7a-c). The time from baits was placed out to the first picture of any scavenger was similar between forest ($\bar{x}$ = 5.7 days ± 2.10 SE) and alpine tundra ($\bar{x}$ = 7.0 days ± 3.87 SE) habitats.

STATISTICAL ANALYSES

We used canonical correspondence analysis (CCA) (Ter Braak 1986) to structure the species community in relation to environmental variables. We included presence / absence data for 13 species, aggregated per camera site within each year, resulting in a total of 61 bait sessions (i.e. site-years), where four sites with no observations had been removed to reduce noise in the models. Small mustelids (*M. erminea, M. nivalis*), goshawk (*Accipiter gentilis*) and rough-legged buzzard (*Buteo lagopus*) were excluded from the CCA analysis due to too few site observations. Habitat, i.e. alpine tundra (above forest line) or forested (below forest line), was included as a categorical variable. Daily means of temperature and snow depth were extracted from interpolated maps (NMI, 2019) with a spatial resolution of 1 km pixels, and calculated as an average within a 1.5 km buffer (~7 km^2) around each camera site for each bait session. The size of the buffer was selected to average over multiple pixels encompassing a camera trap site, as a site could potentially be located at the fringes of a singular 1x1 km pixel which might not be representable for the overall snow depth or temperature at the site. Mean site temperature (± 2SE) over all study sites and years was -0.46 °C (± 0.72) at forested and -4.02°C (± 1.37) at alpine tundra sites, whereas mean snow depth was 32 cm (± 9.9) at forested and 107.7 cm (± 9.9) at alpine tundra sites.

We mostly followed the procedure of CCA modeling described in Ter Braak and Verdonschot (1995) to explore the effects of the included environmental variables on the scavenger community structure, and created a set of candidate models from the three environmental variables. The models were compared through an analysis of variance (ANOVA). CCA models were constructed and visualized using the package ‘vegan’ in R version 3.6.1 (Oksanen, Blanchet et al. 2019, R-Core-Team 2019).

We utilized a joint species distribution model (JSDM) within the hierarchical modeling of species communities framework (Ovaskainen, Tikhonov et al. 2017) using the package ‘Hmsc’ (Tikhonov, Ovaskainen et al. 2019) in R to model average site-level species richness and species-specific distribution along environmental gradients. This framework was preferred over occupancy models due to an unbalanced study design where most camera trap sites within forest habitats were active in only one or two years, thus reducing the number of repeated measures over years and revealing spurious occupancy estimates. Furthermore, occupancy models have been found to overestimate the probability of area use for rare and highly mobile species captured by camera traps (e.g. (Neilson, Avgar et al. 2018)), i.e. > 50% of the species identified in our study. Although we recognize that the Hmsc framework currently does not account for imperfect detection, we considered this framework more robust when dealing with unbalanced species occurrence data.

The Hmsc framework was utilized in a basic capacity form as a multivariate linear mixed model with a binomial (presence/absence) distribution with a probit link function. The basic model was defined as:

$$y_{ij} = \alpha_j + \beta_{1j}x_{1i} + \beta_{2j}x_{2i} + \beta_{3j}x_{3i} + \varepsilon_{ij}^{S}$$

where y is a matrix of presence/absence (1/0) data corresponding to site/years (bait session *i*) and species (*j*), α and β are the true intercept and slope parameters for covariates, and *x* the three main covariates included (habitat, snow depth and temperature). The ε parameter represents here the random effect at the site level (*S*; Camera trap ID) to account for temporal autocorrelation between sites with repeated measures (i.e. > 1 year of sampling). We included all observed species to estimate species richness, retaining the 61 bait sessions used in the CCA analysis. We used the same environmental variables as in the CCA analysis; habitat (forested/alpine tundra), snow depth and temperature, as predictors of species richness and occurrence at baits. The interaction between habitat and each environmental variable was included in the models to assess species-specific responses to environmental gradients within each habitat. The posterior distribution was sampled using MCMC with 7500 samples over 2 chains, a thinning of 5 and burn-in of 2500 samples. MCMC convergence was evaluated using trace-plots of β parameters, by comparing effective sample sizes of each parameter to the total number of samples, and by potential scale reduction factors (Gelman and Rubin 1992, Plummer, Best et al. 2006). The trace plots revealed similar patterns for both chains and no sign of autocorrelation. Most potential scale reduction factors were centered around 1.00 (i.e. the number of chains gave consistent results), however, the effective sample size was generally lower than the maximum posterior samples drawn (2000), which is not uncommon with non-normally distributed data (Tikhonov, Ovaskainen et al. 2019) (Fig. S1). The explanatory power of the model for each species was validated using Tjur's D (coefficient of discrimination; Tjur 2009) which showed quite low explanatory power of the model on species probability of occurrence at baits ($D < 0.2$; Fig. S2a). However, the predictive power of the model, evaluated from a 5-fold cross validation, was equivalent to the explanatory power, indicating relatively good model fit (Fig. S2b).

3 RESULTS

We included 217 951 photos in the analysis, from which we observed 15 scavenging species at the bait stations during the study period, including nine bird species and seven mammalian species (Table 1). Seven species were found only in forest, 2 only in alpine tundra habitat whereas 6 species were found in both habitats.

SCAVENGER COMMUNITY STRUCTURE

The structure of the scavenger guild along environmental gradients, as determined from the exploratory CCA analysis, was largely explained by habitat and mean snow depth (Fig. 2; Table S2). Axis 1 (CCA1) explained 91.1% (eigenvalue = 0.27) of the constrained variance, with relatively strong effects of habitat and snow depth. Axis 2 (CCA2) explained 6.0% (eigenvalue = 0.02) of the constrained inertia and was not statistically significant (Table S1). Overall, the included variables explained 18.4% of the variance in the model. The three smallest corvid species (Eurasian jay (*Garrulus glandarius*), Siberian jay (*Perisoreus infaustus*), magpie (*Pica pica*)), badger (*Meles meles*) and pine marten (*Martes martes*) occurred at the far left on axis 1 of the CCA (Fig. 2) and were only present at baits in forest (Fig. 3; Table 1). Hooded crow (*Corvus cornix*) and white-tailed eagle (*Haliaeetus albicilla*) occurred at baits in both habitats, but to a higher degree in forest. Red fox, common raven (*Corvus corax*) and golden eagle (*Aquila chrysaetos*) were clustered close to the midpoint of axis 1 (Fig .2) and occurred at bait stations in both habitats (Fig. 3; Table 1). Arctic fox (*Vulpes lagopus*) and wolverine (*Gulo gulo*), the two most cold adapted species, were positioned well into the alpine tundra habitat (Fig. 2 and 3). Arctic foxes occurred only at baits in the alpine tundra, while wolverine occurred at baits in both, however only at higher altitudes in forest (Fig. 2 and 3).

The species community model showed a tendency for higher richness of scavenging species in forest than in alpine tundra habitats, with species-specific associations to different habitats, similar to the CCA-analysis (Fig. 4a; Fig. 3; Fig. S4). Species richness was independent of snow depth in forested habitats (Fig. 4b), whereas it declined with increasing snow depth in alpine tundra habitats (Fig. 4c). Species richness decreased slightly with increasing temperature in forested habitats (Fig. 4d) but increased slightly with warmer temperatures within alpine tundra habitats (Fig. 4e). The impact of snow depth and temperature differed among species. Among corvids occurring at baits solely in forests (Table 1), only the Eurasian jay exhibited marked effects of these factors, i.e. occurrence at baits was negatively affected by increasing snow depth and positively affected by increasing temperature (Fig. 5). Most of the species occurring at baits in both habitats exhibited similar impacts of snow and temperature (common raven, golden eagle, red fox, wolverine). In general, neither of the two factors affected species occurrence at baits in alpine areas, but occurrence at baits in forest increased with increasing snow depth and declined with increasing temperature (Fig. 5). We observed a different pattern in the occurrence at baits by hooded crow, which was negatively associated with snow depth and positively related to temperature at baits in alpine tundra. Weaker, but somewhat similar impacts of snow and temperature, were observed at baits in forest for this species (Fig. S5a, b; Fig. S6a, b).

Table 1. Identified scavenging species from baited camera traps and their daily visiting rate as a percentage of total camera trap days within forested and alpine tundra habitats (*Trap days*). *Sites* refers to the pooled number of active sites over all study years with observations of the species. *Photos* are the total number of images recorded of the species over all camera sites and years.

		Trap days (%)			**Sites (n = 61)**		
Species	**Linnaeus, 1758**	**Forest**	**Alpine**	**All**	**Forest**	**Alpine**	**Photos**
Eurasian jay (*ej*)	*Garrulus glandarius*	25.1	0	15.7	23	0	2523
Siberian jay (*sj*)	*Perisoreus infaustus*	5.9	0	3.7	7	0	270
Magpie (*mp*)	*Pica pica*	2.9	0	1.8	12	0	377
Goshawk (*gh*)	*Accipiter gentilis*	1.3	0	0.8	2	0	133
Small mustelids (*mus*)	*M. erminea, M. nivalis*	0.3	0	0.2	2	0	4
Badger (*bg*)	*Meles meles*	1.9	0	1.2	3	0	28
Pine marten (*pm*)	*Martes martes*	7.8	0	4.9	11	0	162
White-tailed eagle (*wte*)	*Haliaeetus albicilla*	0.9	0.2	0.6	7	1	52
Hooded crow (*hc*)	*Corvus cornix*	9.2	2.1	6.5	21	4	4357
Golden eagle (*ge*)	*Aquila chrysaetos*	8.9	9.0	8.9	23	17	1285
Common raven (*cr*)	*Corvus corax*	12.5	25.8	17.5	27	18	5903
Red fox (*rf*)	*Vulpes vulpes*	17.1	22.6	19.2	31	19	1897
Wolverine (*wo*)	*Gulo gulo*	1.3	3.2	2.0	4	7	133
Rough-legged buzzard (*rlb*)	*Buteo lagopus*	0	0.2	0.1	0	1	1
Arctic fox (*af*)	*Vulpes lagopus*	0	0.9	0.3	0	3	16

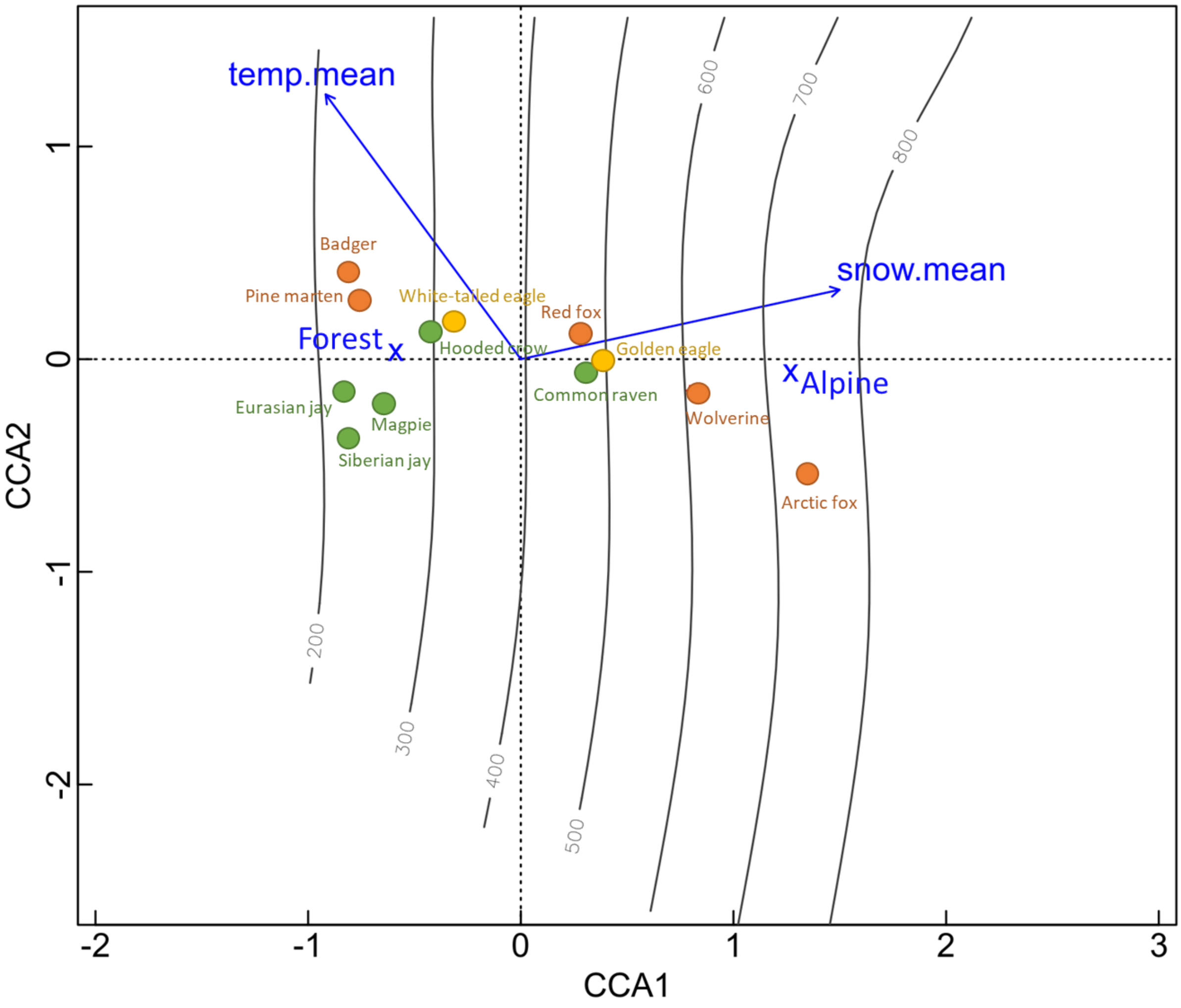

Figure 2. Results from a canonical correspondence analysis (CCA) showing habitat preference of the species structured along environmental gradients, additionally illustrated by altitudinal isoclines (100-meter intervals). Blue arrows, crosses and text represents the environmental gradients, where arrows show the direction of continuous environmental variables (temperature and snow depth). Species distribution within the environmental space is illustrated by coloured circles, where green circles = corvids, yellow = raptors, and red = mammals.

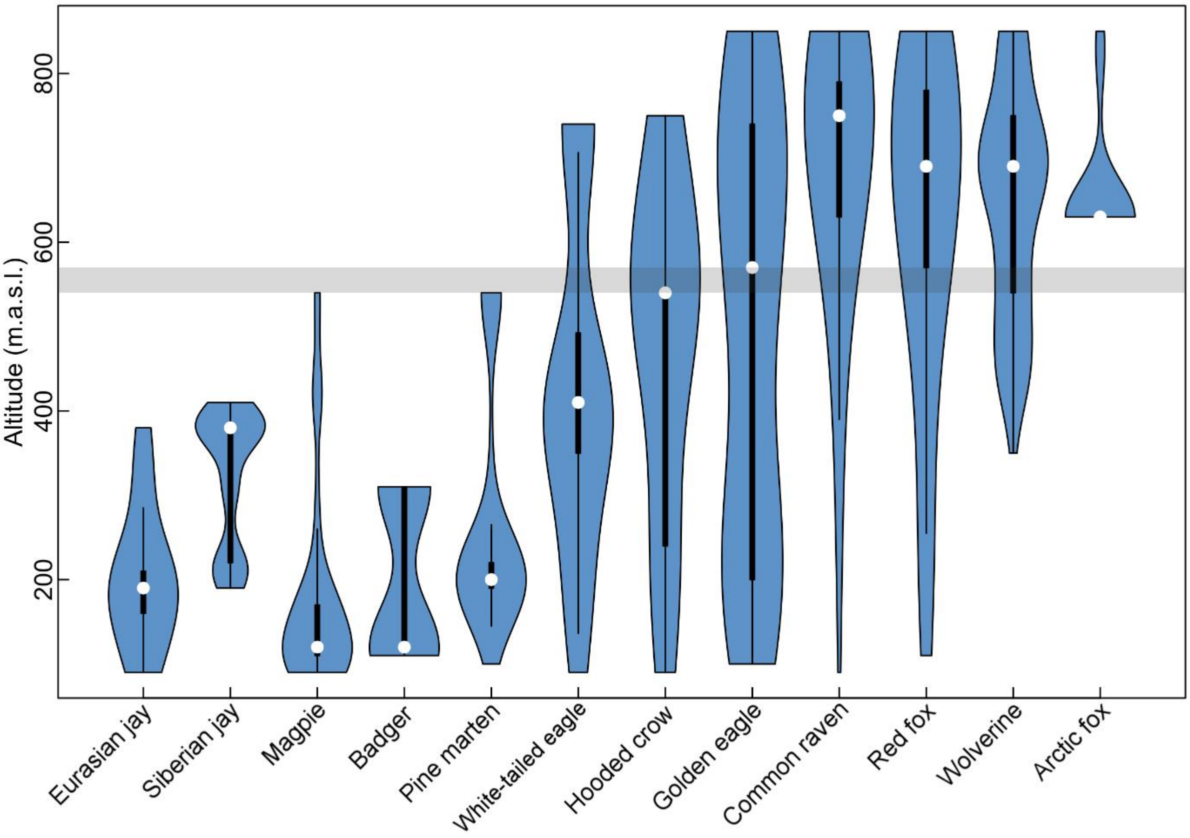

Figure 3. The distribution of observed scavenger species along an altitudinal gradient, based on the number of photos of each species. Thickness of vertical columns indicate frequency of observations (thicker = more observations). White dots represent the median number of observations. Bold vertical lines indicate variability within the lower and upper quartile, whereas thin vertical lines indicate variability between minimum and maximum values. The shaded grey area represents the gap between forested (90 – 540 m.a.s.l.) and alpine tundra (570 – 850 m.a.s.l.) habitat classifications. Small mustelids, goshawk and rough-legged buzzard are not included in the plot due to too few site observations.

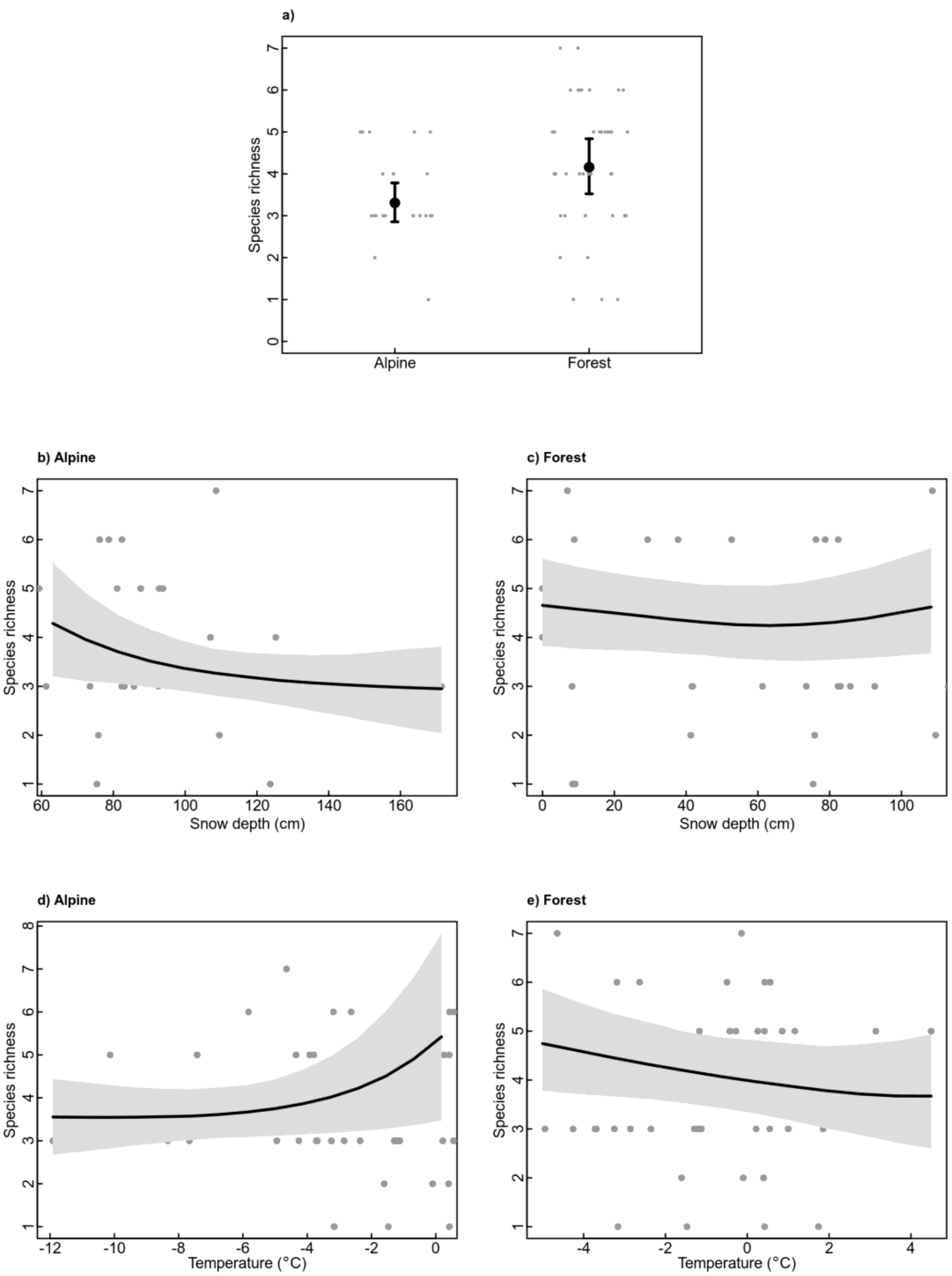

Figure 4. Results from the species community model, showing model predictions of species richness along environmental gradients. Shaded areas represent 95% credible intervals from the predicted posterior distributions, whereas points are observations at camera sites (bait sessions). **a)** Habitat effect on species richness; **b-c)** Effect of mean site snow depth on species richness in forested and alpine tundra habitats. **d-e)** Effect of mean site temperature on species richness

in forested and alpine habitats. Snow depth and temperature were constrained to their minimum / maximum values within each habitat type.

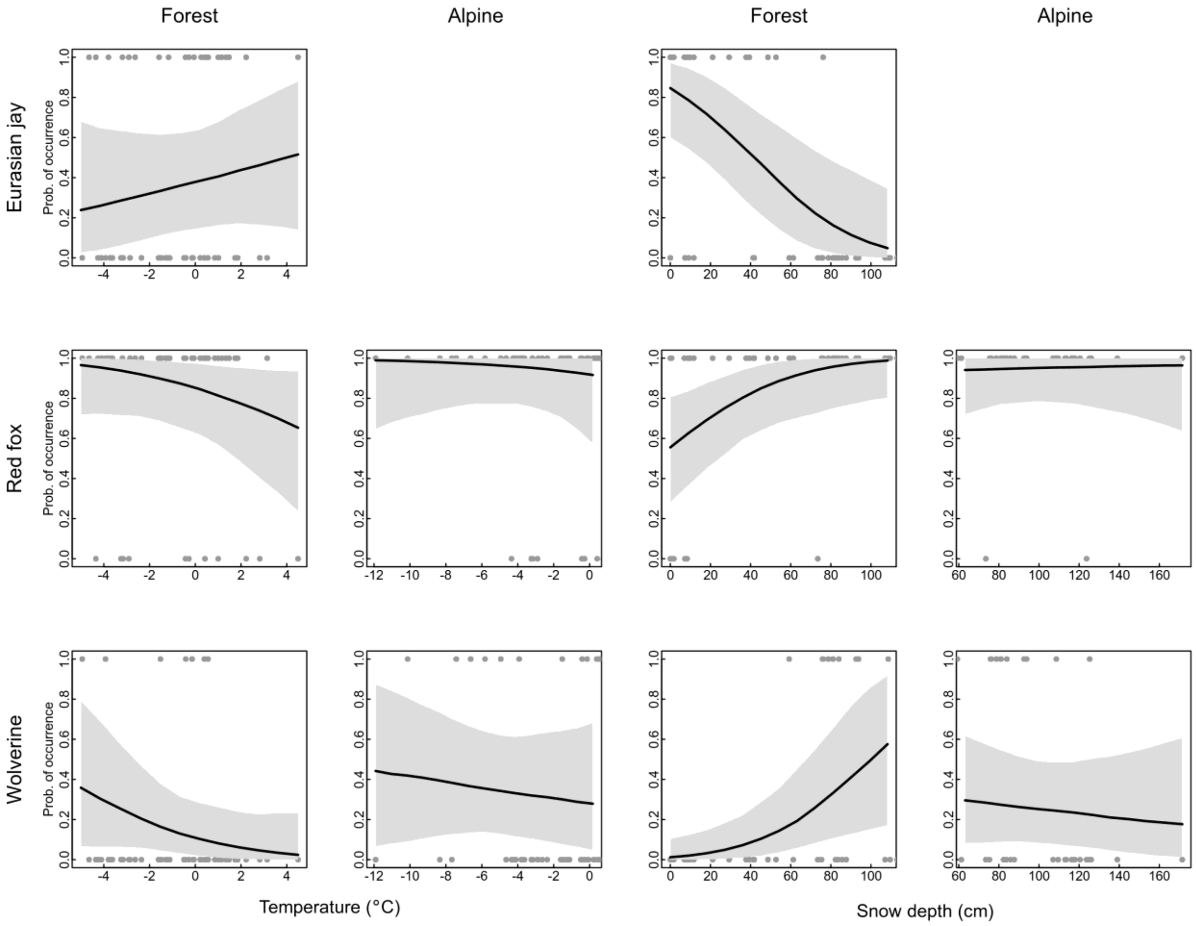

Figure 5. The probability of occurrence at baits in response to temperature and snow depth for selected species associated with either forest (Eurasian jay) or alpine tundra (wolverine), or habitat generalists (red fox). Solid lines are predicted posterior probability of occurrence at baits from the species community model, whereas shaded grey areas represent 95% credible intervals. Grey points represent the bait sessions. Snow depth and temperature were constrained to their minimum / maximum values within each habitat type.

4. DISCUSSION

Although the occurrence at baits by different species changed along the forest-alpine gradient, we found a surprisingly small difference in species richness between forest and alpine tundra habitats. This relates to the fact that species richness, which we expressed as the number of different species visiting bait stations, is inherently a product of the probabilities of occurrence at baits by each of the different species present in each of the habitats. These probabilities are influenced by multiple factors, that we will discuss below. However, the main reason behind the small difference in species richness between habitats likely relates to the high dominance of generalist species, such as common raven, golden eagle and red fox that occur at baits along the whole gradient, and the low occurrence of several habitat specialists at baits.

The impacts of snow depth and temperature on species richness were weak in both forest and alpine habitats, but diverse effects were observed when examining species separately. Temperature and snow depth had a negligible effect on the occurrence at baits by species common in alpine tundra habitats, and consequently, species richness remained almost unaffected by the climatic variables in alpine tundra habitats. On the contrary, the impacts of temperature and snow depth on species were both stronger and more diverse in forest habitats. Opposite effects among different species in the forest likely evened out differences and resulted in relatively stable species richness along the environmental gradients of temperature and snow depth.

The contrasting effects of the environmental covariates on species occurrence at baits was evident when comparing the group of habitat generalists to the group of forest dwelling species. These patterns may be driven by several factors. Snow depth and temperature might affect factors typically associated with carrion use, such as the likelihood to find and access the bait , and the availability of alternative food sources (Killengreen, Lecomte et al. 2011, Pardo-Barquín, Mateo-Tomás et al. 2019). However, snow depth and temperature might also restrict species winter range, area use and activity patterns (Kowalczyk, Jędrzejewska et al. 2003, Pozzanghera, Sivy et al. 2016, Rivrud, Meisingset et al. 2019).

Species only found in forest were most common at baits when temperature was high and snow depth low. This group were dominated by smaller species potentially more affected by cold stress and less adapted to scavenge frozen meat than larger species. However, snow depth was the factor explaining most of the variation in occurrence of these species (Fig. S3). This pattern was evident for all the smaller corvid species, despite that these species have different adaptations to harsh winter conditions. It is therefore likely that their access to baits was restricted by increasing snow depth. The low impact from temperature might indicate that the distribution of these species is not limited by temperature within our study area. It is also important to acknowledge that the impact from temperature might be higher at natural carcasses, as these might be harder to handle for smaller species compared to baits The scavenging probability of the pine marten was also negatively affected by snow depth. Pine martens are adapted to locate and dig for food beneath snow. However, their efficiency in capturing voles, one of their main prey, is reduced with increasing snow depth (Willebrand, Willebrand et al. 2017). We hence suggest that the pine marten might adapt to increased snow depths by adjusting area use towards areas with less snow where there is a sufficient gradient in elevation, and hence snow depth, within their home range. On the contrary, occurrence at baits by the larger habitat generalists in forests was highest at deep snow and low temperature. Under such conditions, accessibility to important subnivean prey like small rodents is typically reduced, while energetic demands may increase. Accordingly, high occurrence at baits might simply be explained by increased importance of carrion when snow depth increases. The importance of carrion may also explain the contrasting responses to temperature and snow depth comparing occurrence at baits for the same group of generalists in alpine tundra vs. forest habitat. In alpine tundra habitat, snow depth and temperature had little impact on these species' occurrence at baits. However, with our study design we could not detect more short term responses to snow conditions (Richard, Wilmshurst et al. 2014). The relationship between increased carrion use, under periods of low availability of live prey and harshness of winter has been demonstrated for the most important mammalian habitat generalist, the red fox (Jędrzejewski and Jędrzejewska 1992, Killengreen, Lecomte et al. 2011, Needham, Odden et al. 2014).

Following forecasted climate changes, a release in climatic constraints could be expected with shorter winters (fewer days with permanents snow cover), and higher winter temperatures (Räisänen and Eklund 2012). This will likely result in range expansion of boreal scavengers. For instance, Eurasian jays and badgers have expanded their range in Scandinavian boreal forests since the 20th century, possibly driven by climate warming ((Elmhagen, Kindberg et al. 2015). Our results suggest that within forest habitats, changes in snow conditions will have higher impact on scavengers than changes in temperature. This might be important for predicting the scavenging community responses to future climate change. Winter temperatures are expected to rise, even more at higher latitudes. Snowfall patterns might on the other hand show regional patterns, and snowfall is expected to decline more at lower altitudes (Räisänen and Eklund 2012), affecting winter ranges for species limited by snow cover (Rivrud, Meisingset et al. 2019).

As several recent studies have pointed out, resource subsidies, including carrion, could facilitate generalist scavenger establishment and increased abundance in alpine ecosystems (Henden, Stien et al. 2014, Sokolov, Sokolova et al. 2016, Gallant, Lecomte et al. 2019). Our results add support to earlier studies pointing to carrion as an important subsidy for generalist scavengers during harsh winter conditions (Temple 1974, Jędrzejewski and Jędrzejewska 1992, Pulliainen and Ollinmäki 1996). It might, on the other hand, be reasonable to infer from our results that carrion is of less importance for habitat generalists when snow is shallow. Taking into account that ungulate carrion biomass during winter is estimated to be eight times higher in forest compared to alpine tundra areas in this region (Hagen 2014), and the fact that ungulates often concentrate in areas with less snow, low occurrence at baits under such conditions might be related to carrion saturation (Gomo, Mattisson et al. 2017).

Our study provides a temporal and spatial snapshot of the scavenger guild along a forest – alpine gradient in Fennoscandia during winter. Many scavengers have significant ecosystem impacts, acting as important predators (Pereira, Owen-Smith et al. 2014, Jahren, Storaas et al. 2016) or superior competitors (Bodey, McDonald et al. 2009, Elmhagen, Berteaux et al. 2017). Climate change might have direct impact on some species, while others might be more affected by changes in carrion availability. Carrion availability is of wild and domestic ungulates is to great extent affected by management practices (Selas and Vik 2006, Henden, Stien et al. 2014), possibly strengthening ecosystem disturbance caused by changes in climatic conditions (Ims, Henden et al. 2019). Management should take both factors into account, and we encourage further studies of the underlying mechanisms driving observed patterns of scavenger occurrence at baits, as these might be important to understand and predict ongoing ecosystem changes.

AUTHORS' CONTRIBUTION

GG and NEE conceived the idea of this study. GG, NEE, LRE collected and compiled the data; LRE & GG performed statistical analyses under supervision from JM and OD. HPA contributed with conceptualization and methodology. GG, LRE, MO, OD, JM & NEE all contributed in the writing of the manuscript. All authors, except HPA, read and approved the final manuscript.

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DATA AVAILABILITY STATEMENT

The analysed data are available in the Dryad digital repository:

https://doi.org/10.5061/dryad.gxd2547h3

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Supporting information

Table S2. Results from the CCA model (ANOVA: $F_{3,57} = 4.071$; $p < 0.001$) including habitat (factorial, forested and alpine), temperature and snow depth (continuous). Continuous variables consist of yearly (i.e. within study period) means for each site. The left table shows statistics of included terms, whereas the right table shows statistics by CCA axis, from an ANOVA analysis.

Parameter	*df*	*X^2*	*F-statistic*	*p-value*
habitat	1	0.179	7.460	< 0.001
temperature	1	0.036	1.479	0.141
snow depth	1	0.079	3.273	< 0.001
Residual	57	1.367		

Axis	*df*	*X^2*	*F-statistic*	*p-value*
CCA1	1	0.265	11.041	< 0.001
CCA2	1	0.019	0.781	0.935
CCA3	1	0.010	0.390	0.967
Residual	57	1.367		

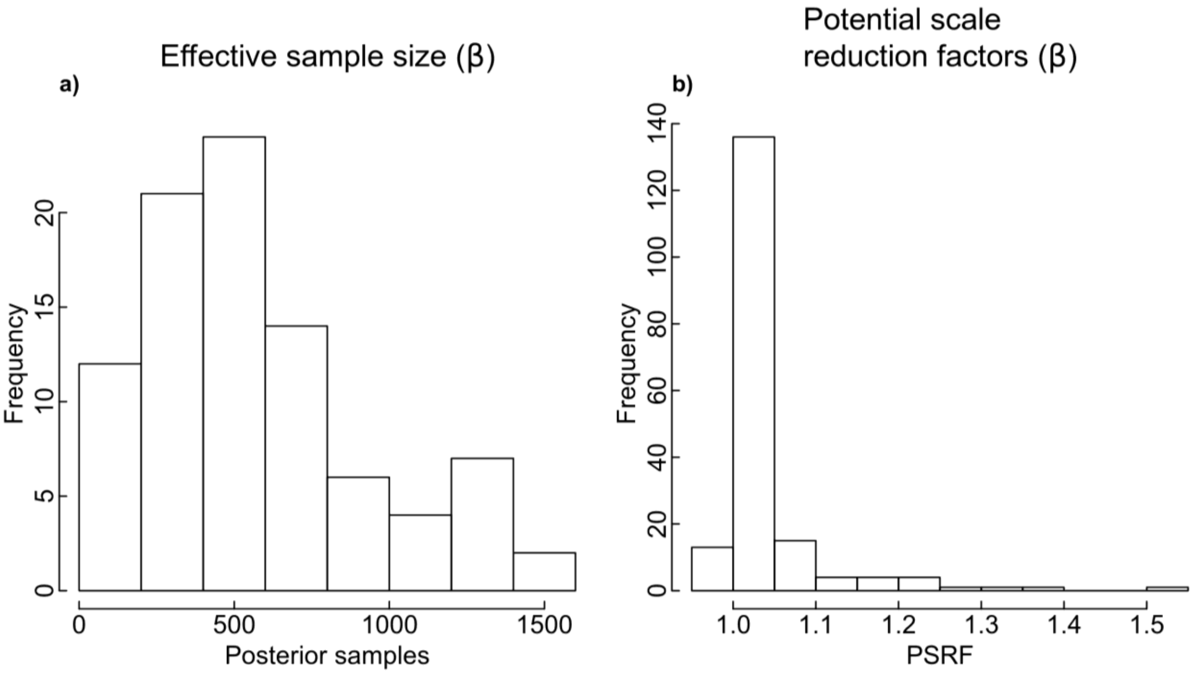

Figure S1. Assessment of convergence of the species community model. **a**) the distribution of the effective posterior sample size of βparameters (optimal = 2000). **b**) the distribution of the potential scale reduction factors of β parameters (optimal = 1.00).

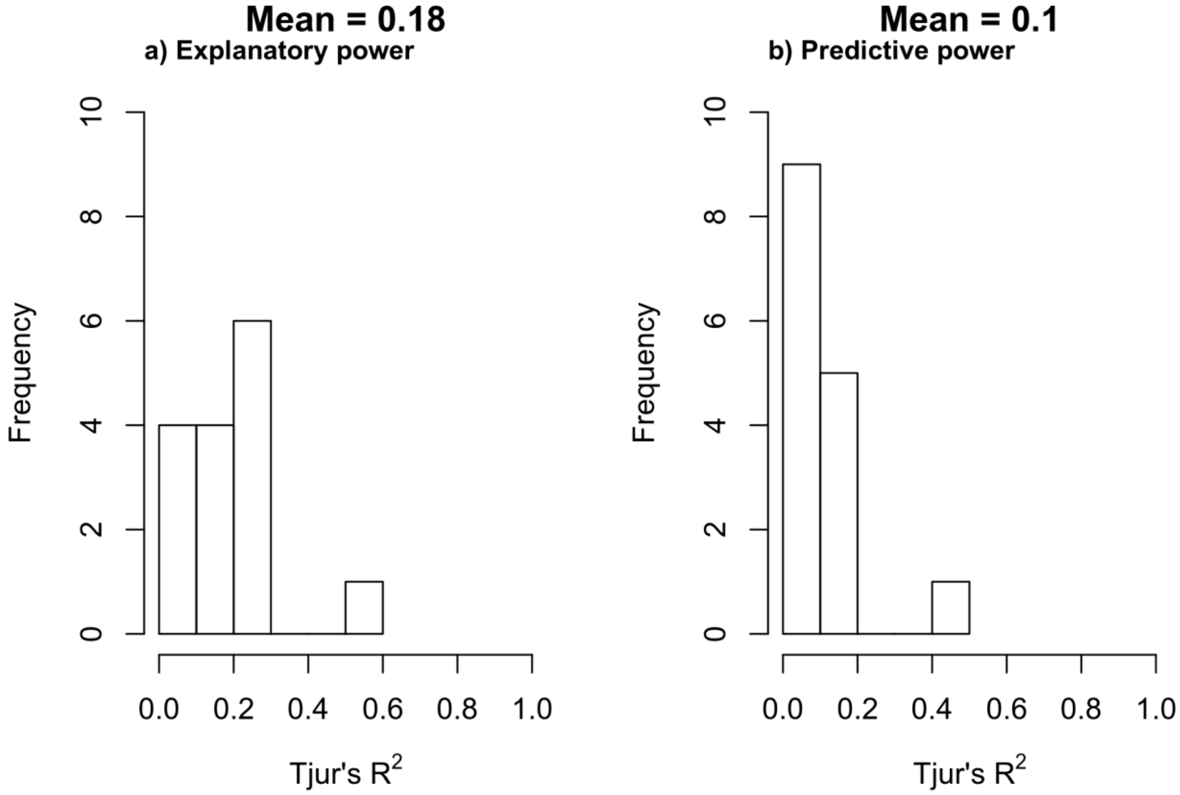

Figure S2. Model validation using Tjur's coefficient of discrimination (R^2) for logistic models. **a**) the proportion of variance explained by the model for each species. **b**) the predictive power of the model for each species, obtained from a 5-fold cross validation.

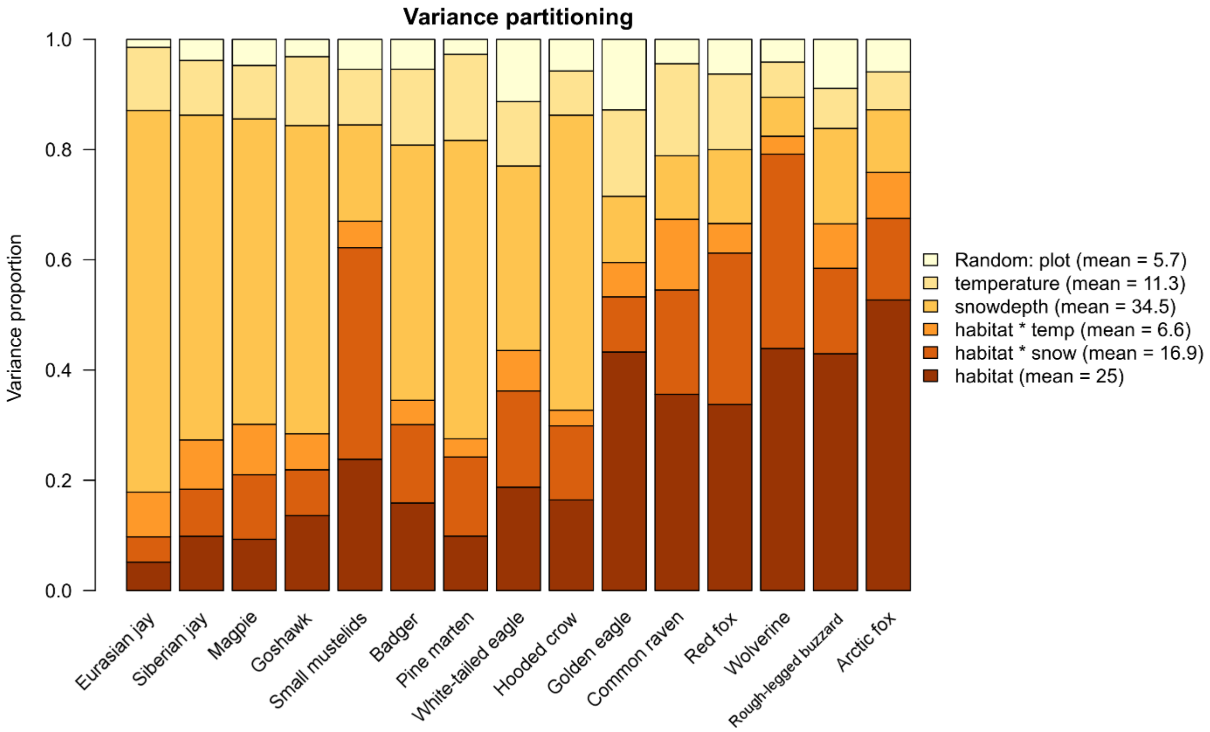

Figure S3. Variance partitioning of the species community model, showing to which degree occurrence at baits by each species is explained by explanatory variables. Random indicates leftover unexplained variance for each species relative to the other species.

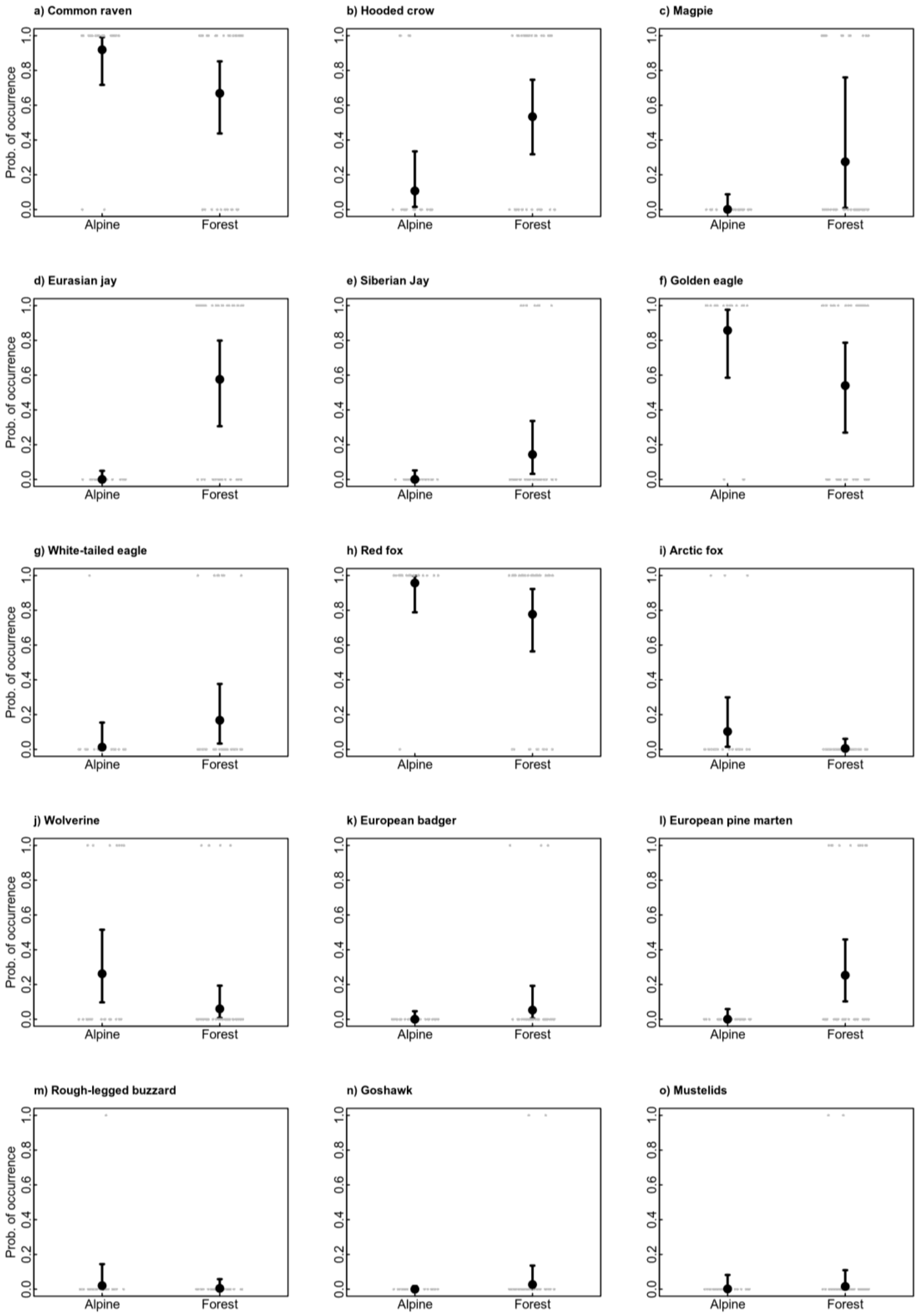

Figure S4. Habitat effects on the probability of species occurrences at baits, predicted from the species community model. Black points are the predicted probability of occurrence at baits, whereas vertical bars represent 95% credible intervals. Grey points are the camera stations (bait sessions).

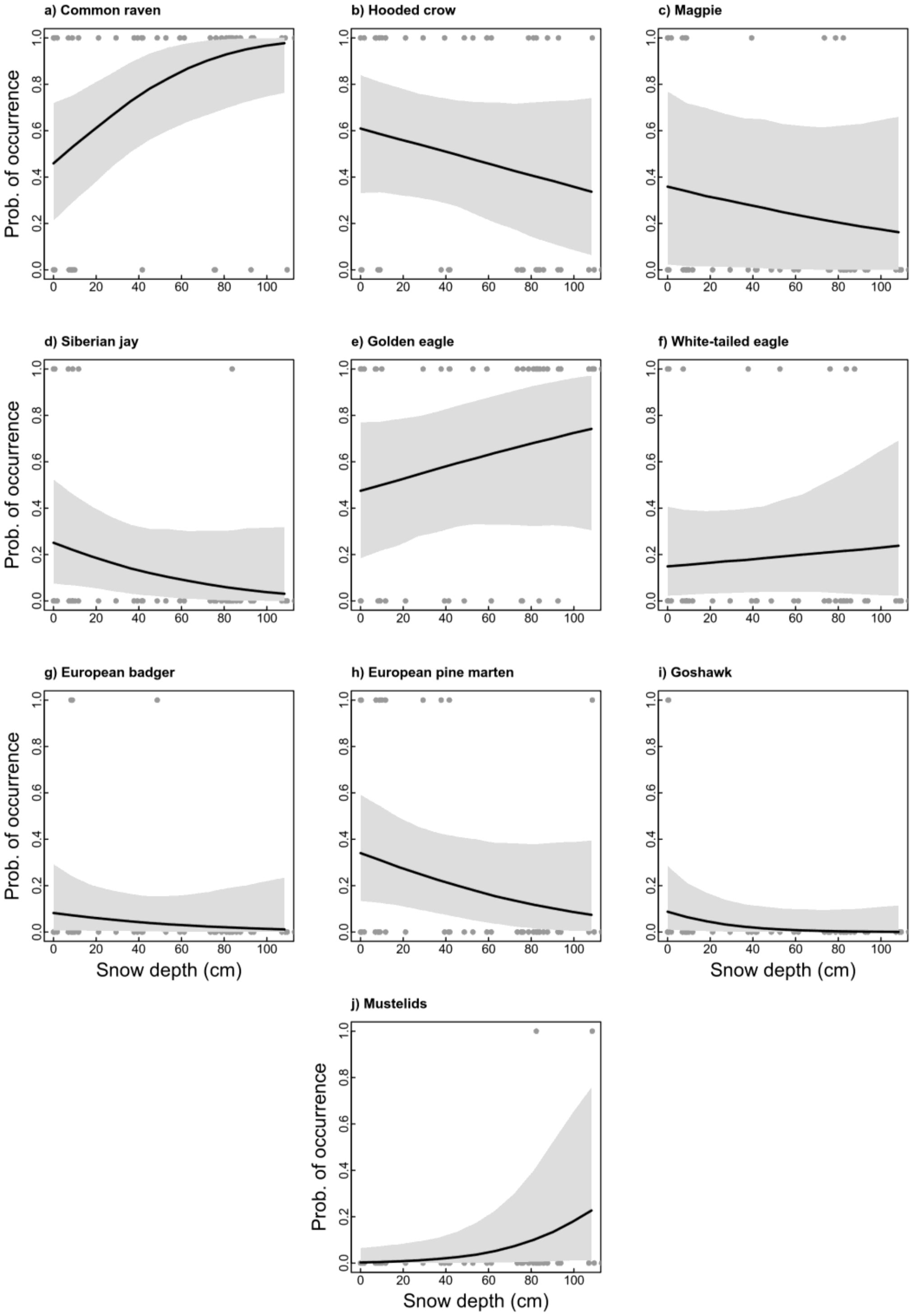

Figure S5a. Effects of snow depth (cm) on the probability of species occurrences at baits within forest habitats, predicted from the species community model. Shaded areas represent 95% credible intervals, whereas grey points are the camera stations (bait sessions). Plotted effects are constrained to the minimum/maximum value of snow depth within forested habitats. Only species occurring at baits within forested habitats are presented.

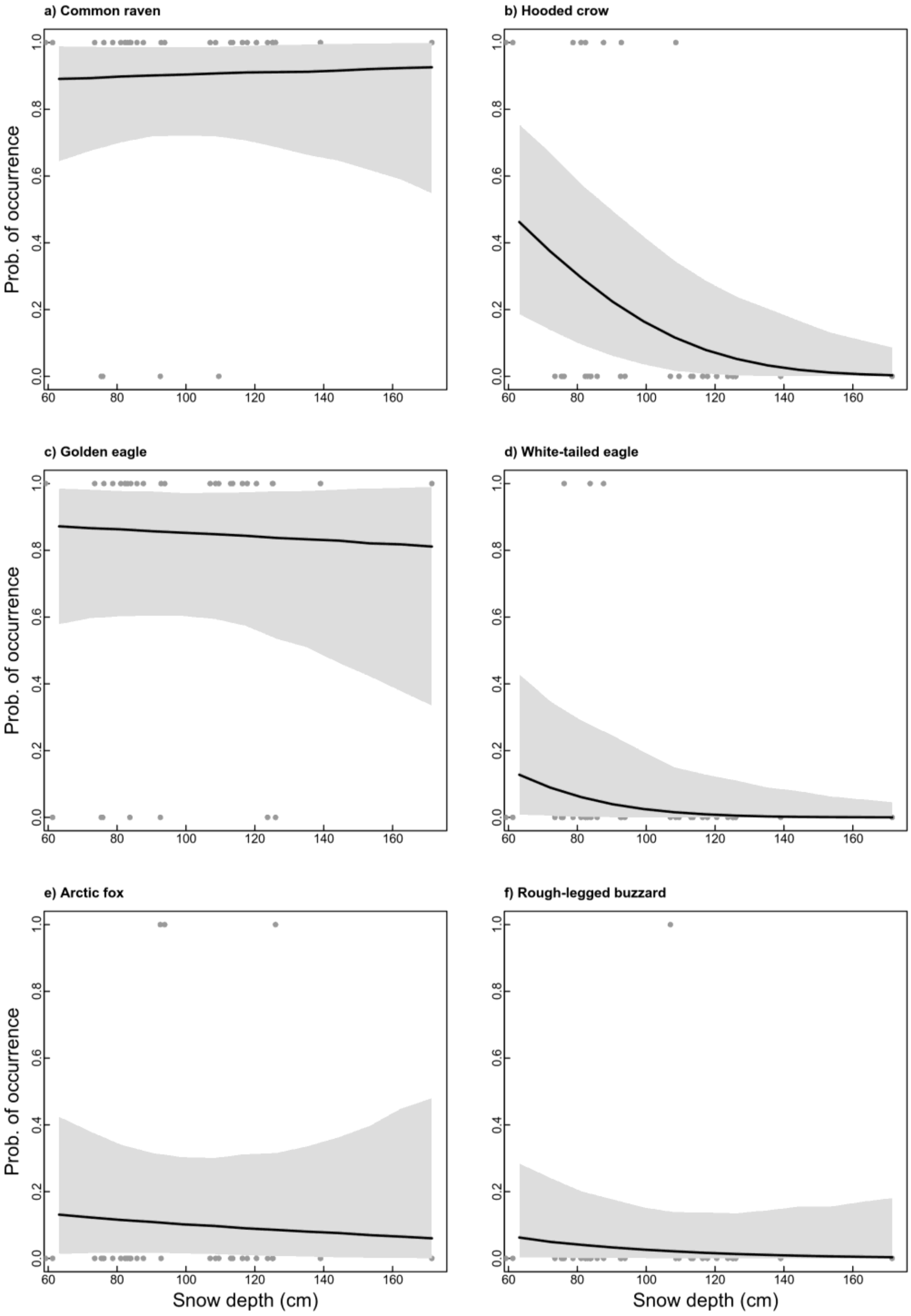

Figure S5b. Effects of snow depth (cm) on the probability of species occurrences at baits within alpine habitats, predicted from the species community model. Shaded areas represent 95% credible intervals, whereas grey points are the camera stations (bait sessions). Plotted effects are constrained to the minimum/maximum value of snow depth within alpine habitats. Only species occurring at baits within alpine tundra habitats are presented.

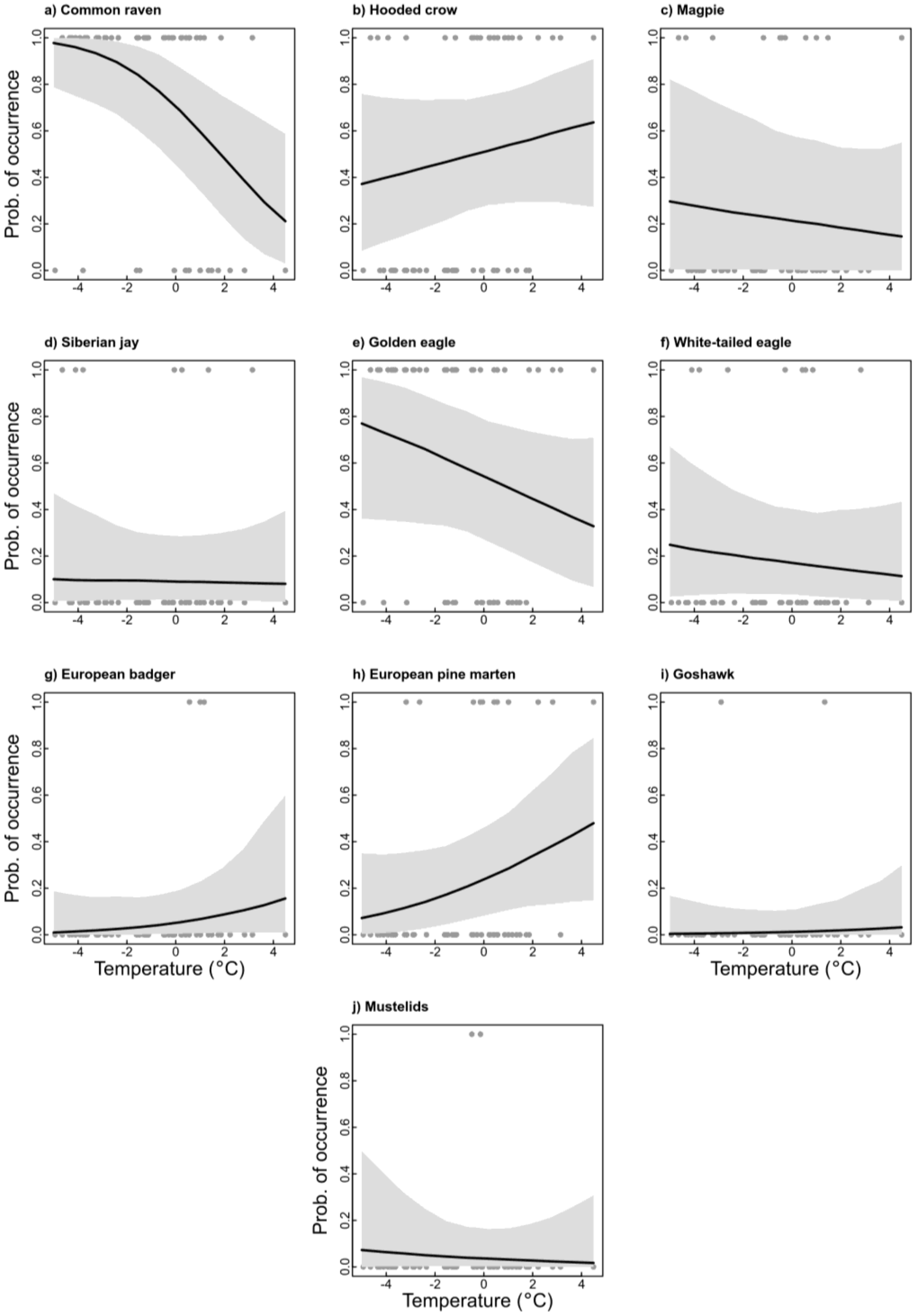

Figure S6a. Effects of temperature (°C) on the probability of species occurrences at baits within forested habitats, predicted from the species community model. Shaded areas represent 95% credible intervals, whereas points are the camera stations (bait sessions). Plotted effects are constrained to the minimum/maximum value of temperature within forested habitats. Only species occurring at baits within forested habitats are presented.

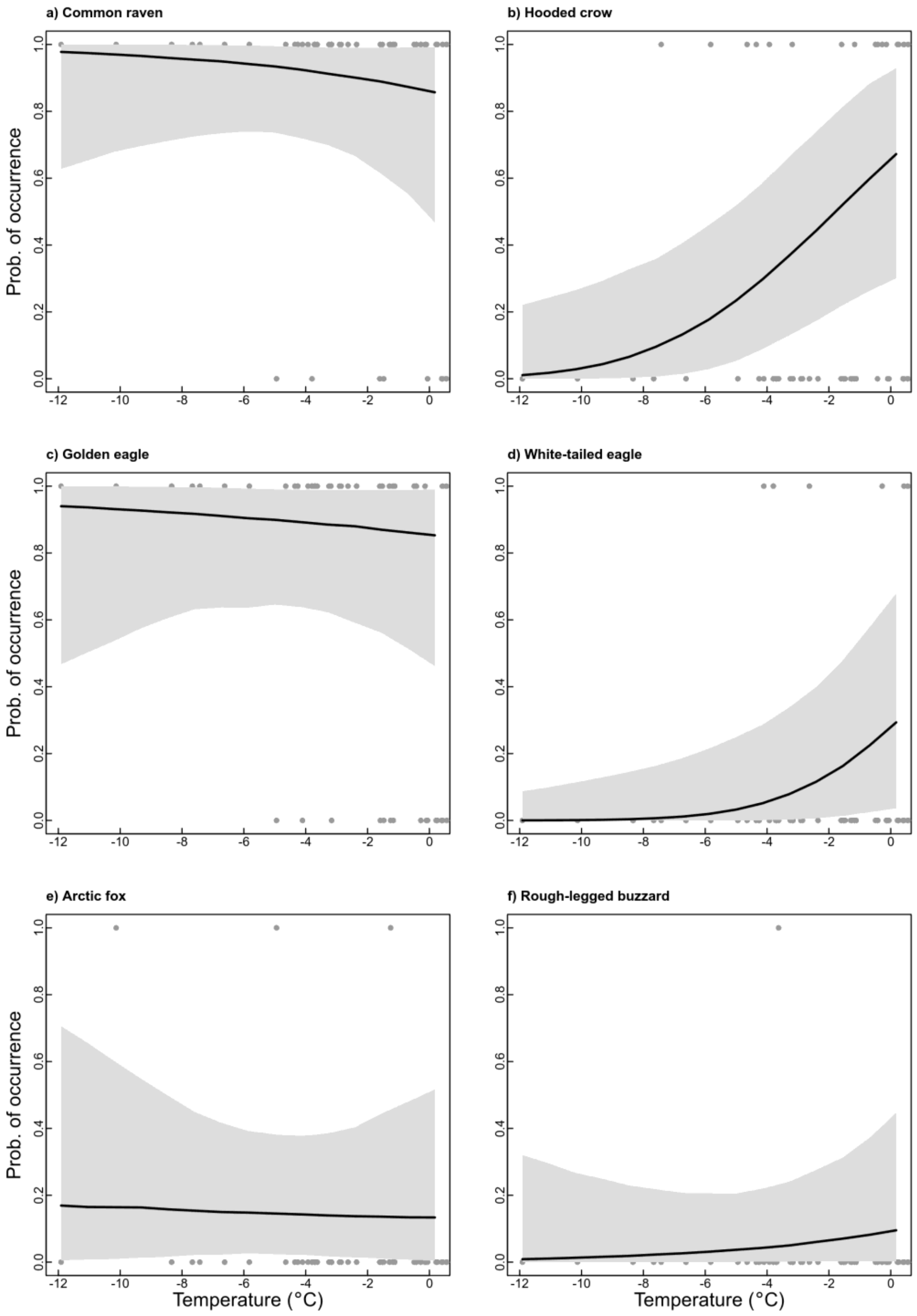

Figure S6b. Effects of temperature (°C) on the probability of species occurrences at baits within alpine habitats, predicted from the species community model. Shaded areas represent 95% credible intervals, whereas points are the camera stations (bait sessions). Plotted effects are constrained to the minimum/maximum value of temperature within alpine habitats. Only species occurring at baits within alpine tundra habitats are presented.

Figure S7a. Example of first image of bait after setup.

Figure S7b. Example of near depleted bait included in the analyses.

Figure S7c. Example of image of depleted bait, not included in the analyses.

Paper II

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BMC Ecology

RESEARCH ARTICLE

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Scavenging on a pulsed resource: quality matters for corvids but density for mammals

Gjermund Gomo[1*], Jenny Mattisson[2], Bjørn Roar Hagen[1], Pål Fossland Moa[1] and Tomas Willebrand[3]

Abstract

Background: Human food subsidies can provide predictable food sources in large quantities for wildlife species worldwide. In the boreal forest of Fennoscandia, gut piles from moose (*Alces alces*) harvest provide a potentially important food source for a range of opportunistically scavenging predators. Increased populations of predators can negatively affect threatened or important game species. As a response to this, restrictions on field dressing of moose are under consideration in parts of Norway. However, there is a lack of research to how this resource is utilized. In this study, we used camera-trap data from 50 gut piles during 1043 monitoring days. We estimated depletion of gut piles separately for parts with high and low energy content, and used these results to scale up gut pile density in the study area. We identified scavenger species and analyzed the influences of gut pile quality and density on scavenging behavior of mammals and corvids (family Corvidae).

Results: Main scavengers were corvids and red fox (*Vulpes vulpes*). Parts with high energy content were rapidly consumed, mainly by corvids that were present at all gut piles shortly after the remains were left at the kill site. Corvid presence declined with days since harvest, reflecting reduction in gut pile quality over time independent of gut pile density. Mammals arrived 7–8 days later at the gut piles than corvids, and their presence depended only on gut pile density with a peak at intermediate densities. The decline at high gut pile densities suggest a saturation effect, which could explain accumulation of gut pile parts with low energy content.

Conclusions: This study shows that remains from moose harvest can potentially be an important food resource for scavengers, as it was utilized to a high degree by many species. This study gives novel insight into how energy content and density of resources affect scavenging patterns among functional groups of scavengers.

Keywords: Carrion ecology, Scavenging, Human subsidies, Pulsed resources, Gut piles, Scavenger community

Background

Human subsidies such as food waste, crop residuals, feeding stations for game species and carcass remains from hunting, are abundant in large quantities worldwide. Predictable Anthropogenic Food Subsidies (PAFS) are resources offered intentionally, or unintentionally, to wild animals by humans and are predictable in time and/or space [1]. PAFS can increase body condition, fecundity and survival of scavengers [2–7], and in the end lead to multiple changes of processes in the ecosystem. For example, predator species can increase in abundance through buffered temporal variability in food [8, 9], leading to altered predator–prey dynamics potentially affecting whole communities [1]. PAFS could also be negative for certain species when artificially increased populations disrupts the social system [10].

In temperate ecosystem, scavenging on remains from ungulate harvest are potentially important as PAFS [11–14]. A regulated harvest of ungulates and historical low numbers of large carnivores in Fennoscandia have resulted in large populations of ungulates, especially the moose (*Alces alces*) have shown an unprecedented increase the last 75 years [15, 16]. About 35,000 moose are annually harvested during a few weeks in September and October in Norway. Internal organs including lungs, intestines, liver and sometimes the heart are removed at the kill site and these gut piles dominate the amount of available moose carrion in autumn [17, 18]. Gut piles from moose are a predictable and high

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*Correspondence: gjermund.gomo@nord.no
[1] Nord University, 8049 Bodø, Norway
Full list of author information is available at the end of the article

amplitude temporal resource pulse during a time when low temperatures reduce the proliferation of insects, bacteria and fungi on the remains [18–20]. Autumn is also a critical period for many carnivores and scavengers, especially for young individuals. Autumn mortality in juvenile corvids is high, [21], and starvation is an important mortality factor in juvenile raptors as goshawks (*Accipiter gentilis*) [22] and golden eagles (*Aquila chrysaetos*) [23]. Mortality in dispersing juvenile American martens (*Martes americana*) was related to body condition [24], and low food availability increase trapping vulnerability of the European pine marten (*Martes martes*) [25]. Hence, gut piles might increase juvenile survival of scavengers by increasing availability of food resources. In addition, adaptations by scavengers, e.g. storing of body fat or food caching may lead to prolonged effects of food pulses [26–30].

Gut piles from harvested moose at kill sites have recently become a conservation concern, and this artificial support of scavenging species can have negative impact on other species. For example, ground nesting birds may suffer increased nest predation as a consequence of increased densities of scavenging generalist predators [31–33]. In Scandinavia, the red fox (*Vulpes vulpes*) is of special concern, as it has been documented to reduce breeding success through nest and chick predation [32, 34] and as a threat to the arctic fox (*Vulpes lagopus*) through interference and resource competition [35]. An increasing number of landowners now enforces restrictions on field dressing of ungulates, but the potential effect of this management policy is unclear.

The aim of this study was to investigate scavenging patterns on the large quantities of gut piles from the moose harvest in Norway. We hypothesize that a wide range of facultative scavengers will use this human created resource, and that avian species will be the first to detect the remains. Firstly, we measured how the different species in the scavenger community utilize the resource by comparing the arrival time and group size of different species at gut piles. Secondly, we quantified the rate of gut pile depletion and the temporal change in gut pile density as an indication on the potential effects pulsed resource can have on the scavenging community [36, 37]. Thirdly, gut piles contains different tissues as fat, muscle and connective with varied energy content, which could be expected to influence foraging behavior [19, 38–41]. Therefore we evaluated how temporal variation in gut pile density and energy content influenced the foraging patterns of different functional groups of scavengers.

Methods

Study area

The study was conducted in an area of 65 km^2 90–485 m.a.sl. within the Ogndal valley in central Norway (63.95 N–64.03 N, 11.76 E–11.97 E). At elevations below 165 m the geology is dominated by marine deposits, mostly agriculture land interspersed with commercially managed forest, mainly Norway spruce (*Picea abies*). The area above the marine deposits is dominated by coniferous forest (Norway spruce and Scots pine *Pinus sylvestris*) interspersed with bogs. Potential scavenging species are red fox, European badger (*Meles meles*), pine marten, golden eagle, white-tailed eagle (*Haliaeetus albicilla*), northern goshawk and corvid species. There is no obligate scavengers in Scandinavia. Ungulate present includes moose, roe deer (*Capreolus capreolus*), and occasional red deer (*Cervus elaphus*). Free ranging semi-domesticated reindeer (*Rangifer tarandus*) are usually present in the area from October to May. Eurasian lynx (*Lynx lynx*) populations were relatively low during the study period [42] while wolverine (*Gulo gulo*) and brown bear (*Ursos arctos*) were only sporadically registered within the area. Average monthly temperature varied between 3–5, 1–3 and −5 to 0 °C in October, November and December, respectively. Monthly precipitation ranged from 30 to 148 mm. Snow covered the ground periodically each winter and snow layer >25 cm was restricted to a few days.

The number of moose harvested in the study area was 61 in 2012, 62 in 2013 and 60 in 2014, resulting a pooled average of 0.94 moose/km^2. Calves constituted 60% of the harvest. The hunting season was closed during 1 week at the peak rut to avoid disturbance. The first hunting period was starting at September 25th, and the second hunting period began October 10 and lasted to October 30 in 2012 and to November 14 in 2013 and 2014. Head, legs, hide and often the heart were brought out with the carcass, while gut piles, containing stomachs and intestines, including visceral fat, and other internal organs were usually left in the field. The lowest energy density of the gut piles is in the stomach tissue with ~0.5 kcal/g, about half of what is found in muscle and liver. Lungs have an intermediate energy density of ~0.85 kcal/g [43]. Highest energy density is found in fat (~9 kcal/g dry weight), however the energy density of fat tissue is lower, dependent on water content [44]. Estimated biomass of moose gut piles in our study area (rumen contents excluded; calculated as Wikenros et al. [18]) was higher (33 kg/km^2) compared to the surrounding region (20 kg/km^2 in the county of Nord-Trøndelag [17]).

Scavenging observations

Camera traps (Reconyx Hyperfire PC 900 in 2012 and Wingcam II TL in 2013/2014) were set up on 50 gut piles, totaling 1043 monitoring days, during the hunting season in 2012–2014 (Fig. 1). Cameras were set up by the hunters before they left the dressing site (1 camera per site) and were placed 4–6 m away from the gut pile and 1−1.5 m above ground. The cameras were programmed to take a picture every 10 min and also when triggered by the motion sensor, with a 2 min delay between triggers to maintain battery and memory card capacity. Cameras were removed when only the rumen contents remained and occasionally smaller pieces of the intestines. All pictures were examined and the number of individuals present of each species in each picture was registered. To estimate daily energetic quality of the remains of the gut pile, we visually evaluated the first picture of each day. Gut piles were then categorized into two classes: (1) high energy content (parts with high energy density like fat, liver and lungs still present), (2) low energy content (only stomach and/or intestines present, including rumen content).

Gut pile depletion curves and gut pile density

Kaplan–Meier curves were used to estimate gut pile depletion for class 1 and 2 separately due to different usage by different scavengers. Right censored events occurred when presence of high energy parts were uncertain due to snow cover or when the gut pile was moved so that only low energy parts were visible on pictures, this was included as a right-censored event in the Kaplan–Meier analyses for class 1. Class 2 was categorized as depleted when only rumen content was left.

To evaluate if depletion varied between years or hunting periods, we compared the depletion rates by using Cox proportional hazard models. We tested for the difference in depletion rate between class 1 and 2 in different years. There were no significant differences between years for either class (coxph class 1; year 2012 v 2013: $z = 1.083$, $p = 0.279$, year 2012 v 2014: $z = -0.843$, $p = 0.399$, coxph class 2; year 2012 v 2013: $z = -0.043$, $p = 0.966$, year 2012 v 2014: $z = -0.819$, $p = 0.413$), and data were pooled for all years. We further compared depletion rates between the early (Sep 25–Oct 1) and late (Oct 10–Nov 14) hunting period. All analyses were done in R [45] with the package

Fig. 1 Location of gut piles with camera-traps 2012–2014. Map showing the location of moose gut piles with camera-traps, N = 50 out of totally 183 moose killed within the study area. Locations of moose gut piles without camera-traps were not recorded. *Grey* show agricultural areas. *Lines* are roads

survival [46]. The function cox.zph was used to evaluate the assumptions of constant proportional hazard models.

Secondly, we calculated gut pile density throughout the hunting season (all years pooled). Separate estimates were calculated for the parts with high (class 1) and low (class 2) energy content. The change in density of the two classes was calculated by reducing the accumulated gut piles from harvest with the Kaplan–Meier depletion estimates for each day of the hunting season.

Scavenging patterns

For each scavenging species, we estimated the proportion of gut piles visited, the mean number of days with visits and the maximum number of individuals recorded at one time for each day. Maximum number of individuals was used to investigate variation in aggregation of individuals between species.

To analyze if daily presence of scavengers responded primarily to days since the moose was killed or to density of gut piles we used binomial generalised linear mixed-effects models (GLMM; in R-package lme4 [47]). We analysed the daily probability ($N = 1043$) for each scavenging species to visit gut piles (0 or 1, where 1 is defined as ≥ 1 pictures including the species). We pooled scavenging species into three functional groups: (1) mammals, (2) large corvids [magpie (*Pica pica*), hooded crow (*Corvus cornix*) and common raven (*Corvus corax*)] and (3) small corvids [Eurasian jay (*Garrulus glandarius*) and Siberian jay (*Perisoreus infaustus*)] for separate analyses. Raptors were not included in this analysis due to small sample sizes. We included gut pile ID ($N = 50$), nested under year ($N = 3$), as random intercept in the model to account for possible variation in scavenger densities between the years of the study and for repeated measures at the same gut pile within a single year. As gut pile densities were not independent of days since harvest we did not combine the two variables in the same model but rather viewed them as competing models, evaluated by AIC_c values. The effect of age and density was evaluated through a second order polynomial, and AIC was used to determine if the non-linear (second order) was better than the linear (first order). Gut piles were removed from the analyses when only rumen content remained.

Results

The gut pile parts with high energy content (class 1) were depleted at significantly higher rate compared to parts with low energy content (class 2) (coxph: $z = -7.504$, $p < 0.001$). Already 10 days after the moose were killed, only 15% of the gut piles contained parts with high energy content, although 90% still had remains. Ten percent were depleted (i.e. only rumen content left) (Fig. 2).

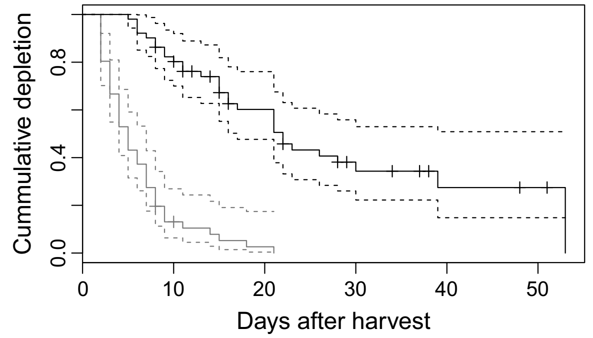

Fig. 2 Depletion of gut pile parts with high and low energy content. *Grey* high energy content, *black* low energy content. *Dashed lines* show 95% confidence intervals

There was no significant difference (coxph: $z = 1.333$, $p = 0.183$) in depletion of the class 2 parts between the hunting periods. Depletion of the class 1 part tended to go faster in the second hunting period, but differences could not be estimated because coxph model assumptions were violated.

Density of gut piles with high energy content parts remaining was highest during the first hunting period, whereas low energy parts lasted longer and at higher density (Fig. 3).

Scavenging patterns

In total, 15 species scavenged on the gut piles. Magpie, Eurasian jay, hooded crow and common raven were the most common avian scavengers while red fox was the most common mammal (Table 1). In addition to species in Table 1, arctic fox, American mink (*Neovison vison*) and domestic dog (*Canis lupus familiarizes*) were registered scavenging on one gut pile each. Pine martens only visited a quarter of the available gut piles but were often observed many days to the same gut pile (Table 1). The same pattern (high species revisiting rate) was also observed for several corvids species. Crows, and partly ravens and magpie, were the only species aggregating in groups, up to 27, 16 and 12 individuals were recorded at one time respectively. Jays, raptors and mammals were usually only present one individual at a time (Table 1). Interestingly, even domestic cats (*Felis catus*) visited some of the gut piles, and returned frequently to the same gut pile.

Scavenging birds (raptors, large corvids and small corvids) arrived 5–8 days earlier at gut piles than mammals did (ANOVA: $F_{3,258} = 30.5$, $p < 0.001$), while there was no difference in arrival time between groups of birds (eagle sp.; TukeysHSD: $p = 0.08–0.4$; Fig. 4). The probability of mammals to visit gut piles was best explained by density of gut piles, showing a strong non-linear response

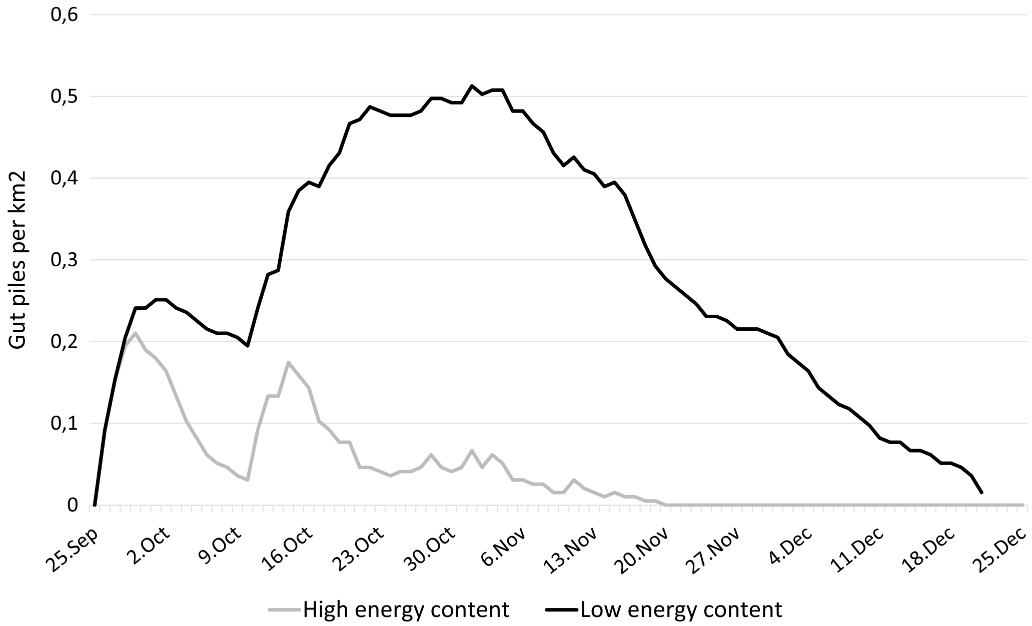

Fig. 3 Temporal development of the availability of gut pile parts with high and low energy content. Years are pooled

Table 1 Species documented on gut piles (N = 50) from moose harvest in Central Norway in 2012–2014

Species[a]	Latin name	% visited	Days present	Max no. ind.
Birds				
Magpie	*Pica pica*	100	10.9 (7.1)	3 (1–12)
Eurasian jay	*Garrulus glandarius*	90 (82–96)	7.6 (7.9)	1 (1–5)
Hooded crow	*Corvus cornix*	90 (82–94)	5.2 (3.2)	8 (1–27)
Raven	*Corvus corax*	70 (55–81)	2.8 (2.1)	3 (1–16)
Siberian jay	*Perisoreus infaustus*	10 (6–18)	2.6 (0.9)	1 (1–2)
White-tailed eagle	*Haliaeetus albicilla*	20 (17–27)	2.6 (2.3)	1 (1–2)
Golden eagle	*Aquila chrysaetos*	16 (9–27)	1.4 (0.5)	1 (1–2)
Goshawk	*Accipiter gentilis*	6 (0–19)	2.3 (1.3)	1
Mammals				
Red fox	*Vulpes vulpes*	68 (45–78)	4.0 (2.6)	1 (1–3)
Badger	*Meles meles*	40 (35–55)	4.4 (3.5)	1 (1–2)
Pine marten	*Martes martes*	24 (6–35)	7.5 (4.9)	1 (1–2)
Domestic cat	*Felis catus*	6 (0–13)	9.0 (4.6)	1

Proportion of gut piles visited (% visited) is presented with all years pooled and range for the different years, while numbers of days with visits per gut pile (days present) is presented as mean (±SD) and daily maximum number of individuals recorded at one time (Max no. ind) as the median and range (min–max)

[a] Arctic fox (*Vulpes lagopus*), American mink (*Nivea vision*) and domestic dog (*Canis lupus familiaris*) were registered scavenging on one gut pile each

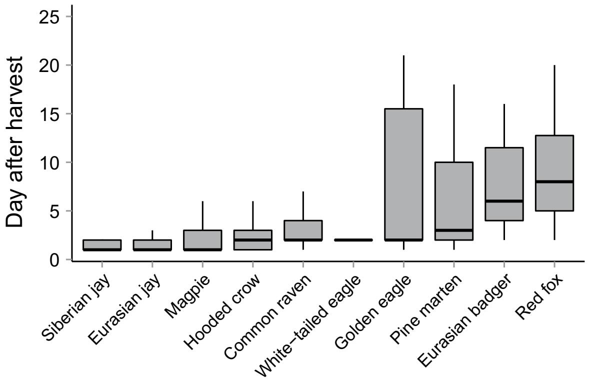

Fig. 4 Arrival time at gut piles from moose harvest (days after harvest) by different scavenger species. Based on 50 harvested moose in central Norway in 2012–2014. Box plots show median (*bold horizontal lines*), interquartile range (*box*), and range up to 1.5 times interquartile range (*bars*)

peaking at around median densities (Fig. 5; $\beta1 = -3.3$, $SE = 3.7$; $\beta2 = -19.0$, $SE = 3.8$). Gut pile age had no effect on daily visits by mammals ($\Delta AIC_c = 29.9$, c.f. Null model: $\Delta AIC_c = 29.5$). There were some variance in random intercept between gut piles (1.4, 1.2 SD) and a tendency for variation between years (0.06, 0.24 SD).

In contrast, the probability of both small and large corvids to visit gut piles was only influenced by days since harvest. Model with gut pile density increased AIC_c by 172 and 108 for small and large corvids respectively. The

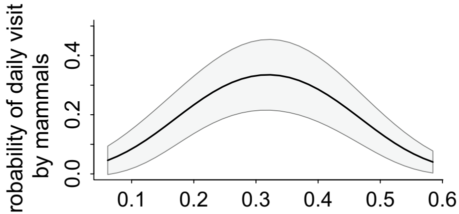

Fig. 5 Probability of scavenging mammals to visit gut piles in relation to gut pile density. Gut piles remaining after field dressing of hunted moose in Central Norway in 2012–2014

daily presence of small corvids decreased rapidly (Fig. 6; $\beta 1 = -46$, $SE = 4.2$; $\beta 2 = 29$, $SE = 3.1$), while the daily presence of large corvids decreased in a linear manner and more gradually with increasing age of the gut pile (non-linear $\Delta AIC_c = 1.4$, $\beta = -0.09$, $SE = 0.009$).

The general probability of visits varied between gut piles (4.3, SD 2.1 for small corvids and 1.3, 1.2 SD for large) but there was no variance between years thus this variable was removed from the analyses.

Discussion

We have shown that gut piles from moose hunt are rapidly detected, and parts with high energy content are removed in less than 3 weeks. Gut piles constitute a large amount of food and are likely to have a positive influence on several of the scavenger populations. This pulse of food increased resource availability for scavenging species during a 3-month period. It seems safe to conclude that moose gut piles fit the PAFS concept.

In this study, corvids, red fox, pine marten and badger were the main scavenger species. Northern ecosystems lack obligate scavengers and the low abundances of large scavenging carnivores opens up for smaller carnivores [13, 18, 48, 49]. The high moose harvest in Scandinavia is one, if not the most, important food resource for scavengers, making it unique compared to boreal areas in other parts of the world. There has been high moose harvest for about 40 years, and the harvest periods do not change much between years. We believe that the scavenging species in this ecosystem have adapted to this resource, and it may be an important food buffer potentially reducing juvenile mortality [21–25, 50]. The high energy content of the visceral fat in the gut piles is easily converted to body fat storage in mammals, reducing the risk of starvation during winter bottle-necks [30]. Alternatively, the remains can be cached and utilized later [26–29, 51–53].

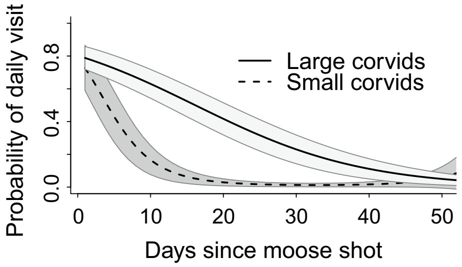

Fig. 6 Probability of scavenging corvids to visit gut piles in relation to gut pile age. Gut piles remaining after field dressing of hunted moose in Central Norway in 2012–2014

In our study, gut pile parts with high energy content were utilized rapidly, primarily by corvids. Corvids were present at all gut piles shortly after harvest, and had access to all parts of the gut pile. Corvid presence declined with time probably reflecting reduction in gut pile quality. Optimal foraging theory predicts that only the energy rich parts should be utilized before moving to a new patch if available, as observed in both predators and scavengers [38, 40, 41]. Our results suggest that corvids move to a more recent harvest site nearby rather than staying and feeding on remains of poorer quality. Stomachs and intestines have high content of connective tissue, and corvids might have limited ability to digest collagen compared to mammal scavengers [54]. Dependent on size, corvid species might also be restricted by limited beak strength [55]. This also reflects the benefits of direct access to harvest remains for birds compared to whole carrions where access to parts with high energy content may require opening by larger species [56].

The late arrival of mammals seems to limit their access to parts with high energy content, already consumed by avian scavengers. Mammals responded primarily to gut pile density and daily presence peaked at intermediate densities. Reduced mammal presence at high gut pile densities might indicate a saturation effect, comparable to seed predation during masting events [57]. On the other hand, accumulation of gut pile parts with low energy content lead to longer resource pulse duration, with possible prolonged positive effects on mammal scavengers [37]. Hence, even a reduction in gut pile density may reduce the potential positive effects on the density of mammalian scavengers. Nonetheless, corvids probably have an important ecological impact in limiting gut pile availability to other scavengers through resource competition [58]. Hence, lower corvid abundance may benefit mammalian scavengers. Large scavenging predators (wolverine, brown bear) were only present sporadically in our study area and were not observed at any of the gut piles. This contrasts to comparable studies on autumn pulses of gut piles, where bear species were the main mammal scavengers [12, 59]. Red fox is the main mammal scavenger in other studies from northern Europe [18, 19, 48], and in studies of human provided subsidies in general [60].

Direct negative impacts of scavenging on gut piles from harvested moose is potential lead poisoning arising from bullet remains [59, 61]. An estimated deposit of 182 kg of lead in moose gut piles yearly in Scandinavia could be a management concern regarding scavenging species [62]. For example, golden eagles show an increase in blood lead levels during the moose hunting season, and might experience increased mortality both through lethal and sub lethal doses of lead [63]. Legislation banning the use of lead ammunition or forcing removal of gut piles would effectively reduce the risk of lead poisoning. However, the latter would in addition result in a radical reduction regarding food abundance for scavenging species, possibly with larger ecosystem impact [64, 65]. In addition, anthropogenic resources can alter wildlife–pathogen dynamics and create opportunities for cross-species transmission of pathogens [66]. The protozoan parasites *Toxoplasmoso gondii*, *Giardia* spp. and *Cryptosporidium* spp. found in moose and other cervids [67, 68] can infect several scavenger species [69–71]. On the other hand, red fox use of anthropogenic food sources may indirectly reduce the prevalence of the zoonotic tapeworm *Echinococcus multilocularis* in foxes if it results in reduced predation on small rodents, the intermediate hosts of the parasite [72, 73]. Interestingly, prevalence of *E. multilocularis* in small rodents increases during autumn and winter [74], the period gut piles are present. However, possible effects of gut piles on wildlife–pathogen dynamics are probably diverse [66], but should be considered.

Conclusions

In this study, we show that gut piles left at the kill site after moose harvest are an intensively used food source by a range of scavenging birds and mammals during autumn and early winter. This study also provides novel insight into how quality and density of carrion affect scavenging patterns among functional groups of scavengers. Enforcing a removal of gut piles by hunters will reduce food supply in a critical period for several scavenging species. This may have direct negatively effects on several scavenging species utilizing this predictable food resource, but it is difficult to predict the long-term effect on the relative abundance of scavengers. It could potentially reduce less wanted species as corvids and red fox, but also impact eagles and wolverines. Reducing the amount of gut piles in the landscape would reduce the potential risk of lead poisoning [59, 61], but could also be mitigated by using lead free bullets. However, to what extend this pulsed resource is important for the overall survival, reproduction and population dynamics of both scavenging and potential prey species needs further investigation. Ignoring these PAFS would make the understanding of the food web structure and dynamics in the boreal forest difficult.

Authors' contributions

GG conceived the study, participated in its design, performed statistical analyses and drafted the manuscript. TW participated in the design of the study and helped drafting the manuscript. JM performed statistical analyses and helped drafting the manuscript. PFM helped drafting the manuscript and collecting data. BRH collected data. All authors read and approved the final manuscript.

Author details

[1] Nord University, 8049 Bodø, Norway. [2] Norwegian Institute for Nature Research (NINA), 7484 Trondheim, Norway. [3] Inland Norway University of Applied Sciences, 2418 Elverum, Norway.

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Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

The datasets used and analyzed during the current study are available from the corresponding author on reasonable request.

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Paper III

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Gjermund Gomo
Inland Norway University of Applied Sciences
P.O. Box 400
NO-2418 Elverum, Norway
+47 97 07 17 12
gjermg@gmail.com

Spatiotemporal patterns of red fox scavenging in forest and tundra: the influence of prey fluctuations and winter conditions

GJERMUND GOMO[1], *Inland Norway University of Applied Sciences (HINN), Faculty of Applied Ecology, Agricultural Sciences and Biotechnology (Fac. Appl. Ecol.), NO-2480 Evenstad, Norway*
JENNY MATTISSON, *Norwegian Institute for Nature Research (NINA), P.O. Box 5685 Torgarden, NO-7485 Trondheim, Norway*
LARS RØD-ERIKSEN, *Norwegian Institute for Nature Research (NINA), P.O. Box 5685 Torgarden, NO-7485 Trondheim, Norway*
NINA E. EIDE, *Norwegian Institute for Nature Research (NINA), P.O. Box 5685 Torgarden, NO-7485 Trondheim, Norway*
MORTEN ODDEN, *HINN, Fac. Appl. Ecol., NO-2480 Evenstad, Norway*

ABSTRACT

The red fox (*Vulpes Vulpes*) is an adaptable species with a wide distribution range. Concern has been raised regarding increased red fox abundance and range expansion, directly and indirectly enhanced by human activities, including carrion supply, and its negative impact on native fauna. In this study, we used camera traps to investigate how red fox scavenging was influenced by fluctuations in small rodent abundance, habitat type, season, snow depth and environmental productivity. We predicted two main alternate patterns: (i) An inverse relationship between scavenging and small rodent abundance due to diet shifts, i.e. a functional response. Scavenging should increase when small rodent abundance is low and when deep snow reduces prey accessibility, and decrease in productive areas. (ii) Scavenging should be higher following summers of high small rodent abundance if the visitation patterns mainly reflect red fox abundance.

We found contrasting patterns of scavenging during winter between alpine and forest habitat. In the former, scavenging increased when small rodent abundance was high and snow cover was low, i.e. as in prediction (ii). In forest, the influence of small rodents and snow was the opposite, i.e. as in prediction (i). Productivity did not appear in the best models, and small rodent abundance had no marked influence on scavenging in autumn. Our results suggest that diet shifts due to low small rodent abundance and accessibility is a main determinant of scavenging in forests. The numerical response in alpine areas is probably due to deeper snow, increasing the importance of carrion resources.

KEY WORDS red fox, scavenging, small rodents, habitat, climate, camera traps

INTRODUCTION

Ecosystems are subsidized to a varying degree with energy, matter and organisms from neighboring sources (Polis, Anderson et al. 1997, Leroux and Loreau 2008), or by anthropogenic activity (Oro, Genovart et al. 2013). Such subsidies can cause an increase in abundance and distribution of opportunistic species which, in turn, may result in trophic cascades altering communities, or ecological processes such as competition and predator-prey interactions (Tylianakis, Didham et al. 2008, Oro, Genovart et al. 2013). Generalist predators may depend on resource subsidies in periods when their primary prey species are less abundant, less vulnerable or unavailable (Pereira, Owen-Smith et al. 2014). Subsidies can therefore alter predator populations dynamics, with consecutive effects on prey populations (Newsome, Dellinger et al. 2015).

The red fox is a generalist predator occupying a wide range of ecosystems around the globe (Schipper, Chanson et al. 2008), and is listed among the 100 most invasive species outside its original range (Lowe, Browne et al. 2000). Increasing and expanding populations of red fox raise concern, as they may negatively affect both populations of endangered species and important game species (Fletcher, Aebischer et al. 2010, Jahren, Storaas et al. 2016, Elmhagen, Berteaux et al. 2017, Marolla, Aarvak et al. 2019). In Fennoscandia, both direct and indirect factors connected to anthropogenic activity have been linked to red fox range expansion and increased abundance. For example, top-down regulation of red foxes have been reduced both due to intense lethal control of large carnivores and reduced hunting pressure from humans (Selas and Vik 2006, Pasanen-Mortensen, Pyykonen et al. 2013). Land use changes have increased areas of crop production and clear-cuts in the forests which, in turn, benefits small rodents and roe deer (*Capreolus capreolus*), which are important food resources for the red fox (Pasanen-Mortensen, Elmhagen et al. 2017). Moreover, red foxes might benefit from increased availability of anthropogenic food resources through the expansion of human settlements, cabin areas and infrastructure (Gallant, Lecomte et al. 2019, Rød-Eriksen, Skrutvold et al. 2020). Species of facultative scavengers in northern ecosystems often utilize carrion during winter, creating possibilities for food web interactions between species that otherwise have weak connections in these ecosystems (Ims and Fuglei 2005). Red foxes are facultative scavengers, and ungulate carrion are often an important part of their diet, especially during winter (Jędrzejewski and Jędrzejewska 1992, Killengreen, Lecomte et al. 2011, Needham, Odden et al. 2014) when the availability of prey is lower (Cagnacci, Lovari et al. 2003). Hence, increasing densities of ungulate populations, and thereby carrion, have been linked to increased winter survival and elevated carrying capacity of red foxes in Fennoscandia during the last century (Selas and Vik 2006). More recent data from the arctic tundra in Scandinavia also links higher abundance of carrion from semi-domesticated reindeer (*Rangifer tarandus*) to higher occupancy and range expansion of scavenging species including red fox, corvids, and eagles (Henden, Stien et al. 2014, Sokolov, Sokolova et al. 2016). Remains from hunting of ungulates is another source of food that can subsidise scavengers during harvest periods (Wikenros, Sand et al. 2013, Gomo, Mattisson et al. 2017).

Elevated carrying capacities due to climate change are expected for some boreal generalist predator species in northern ecosystems (Elmhagen, Kindberg et al. 2015). Since climate change affects a wide range of species and ecological processes, the overall outcome is likely to be diverse, and vary among regions. For example, small rodent cyclicity is an important component of northern ecosystems, where many mammalian and avian predators are adapted to respond quickly to high small rodent abundances (Ims and Fuglei 2005, Gilg, Kovacs et al. 2017). Since the reproductive success of many of these species are closely dependent on small rodent abundance, dampening of multiannual small rodent population cycles due to climate change has been a matter of concern during the last decades (Kausrud, Mysterud et al. 2008, Henden, Ims et al. 2009, Schmidt, Ims et al. 2012, Ehrich, Schmidt et al. 2020). Elevated winter temperatures alter snow conditions and may lead to a collapse of subnivean space, which in turn entails higher winter mortality in small rodents (Kausrud, Mysterud et al. 2008). Changes in snow conditions might also affect the availability of small rodents for predators (Jędrzejewski and Jędrzejewska 1992, Lindström and Hörnfeldt 1994). Climate driven changes in small rodent abundance and availability may thus affect red fox survival and carrying capacity, and possibly affect the importance of carrion and anthropogenic food resources in their diet.

The aim of this paper was to investigate patterns of red fox scavenging under contrasting environmental conditions during a period of fluctuating small rodent abundance in Scandinavia. By including both forest and alpine areas in winter and moose (*Alces alces*) gut piles in autumn, the study covers contrasting environmental conditions regarding snow depth, small rodent abundance and carrion availability (Hagen 2014, Gomo, Mattisson et al. 2017). Based on camera trap data, we investigated how temporal variation in prey abundance, and other environmental factors, affected red fox visitation rates at bait stations and hunting remains. We predict two main alternate patterns: (i) An inverse relationship between scavenging and small rodent abundance due to diet shifts, i.e. a functional response and ii) A positive relationship between scavenging and small rodent abundance due to a numerical response of red foxes to increasing food resource availability. Scavenging by red foxes have been shown to be inversely related to prey availability, and carrion use by red foxes may thus be negatively correlated with small rodent abundance through a functional response (i.e. prey switching). Small rodent fluctuations have also been linked to red fox reproduction (Englund 1970), and population dynamics of foxes may be positively related to small rodent abundance through a delayed numerical response (Englund 1980). Hence, red fox visitation rates at carrion should be higher following summers of high small rodent abundance if the scavenging patterns mainly reflect red fox abundance. Opposite patterns of carrion use may therefore be expected, depending on the relative importance of functional and numerical responses of foxes to small rodent fluctuations. We expect that two main environmental factors may influence the relationship between red fox utilization of small rodents and carrion: landscape productivity and snow cover. The positive relationship between small rodent dynamics and red fox reproduction appear to be stronger in marginal (Englund 1970), i.e. alpine habitats, probably due to a higher dependency on small rodents in areas with less alternative prey. We thus expect that the impact of small rodent abundance on carrion use by foxes will be inversely correlated with landscape productivity and hence higher in the alpine tundra. Snow cover can influence red fox foraging success on small rodents. While red foxes are well adapted to locate prey beneath snow, their hunting success probably decreases with increasing snow depth. We therefore expect snow depth to influence red fox carrion use.

STUDY AREA

Our study was conducted in central Norway from 2012 to 2014 (Fig. 1). The bait study took place in winter between January and April, and the gut piles study (Gomo, Mattisson et al. 2017) in autumn between 25th September to 14th December i.e. during and after the moose hunting season. The area covers an elevational gradient ranging from 90 to 850 m.a.s.l., with the forest line at approximately 560 m.a.s.l. (Fig 1b). Alpine habitats are dominated by dwarf birch (*Betula nana*) and shrubs of willow (*Salix sp.*), whereas forested habitats are dominated by pine (*Pinus sylvestris*), spruce (*Picea abies*) and mountain birch (*Betula pubescens*) (Moen 1998). Semi-domesticated reindeer have perennial pastures in the region, including calving areas within or bordering our study area. Wild ungulates are mainly moose and roe deer. Carrion from ungulates provide an estimated biomass of 29.1 kg/km^2 in boreal forest and 3.6 kg/km^2 in alpine areas during the cold season (November to April) (Hagen 2014). Estimated biomass of moose gut piles in the gut pile study area was 33 kg/km^2 (25th September to 14th November). For details, see (Gomo, Mattisson et al. 2017).

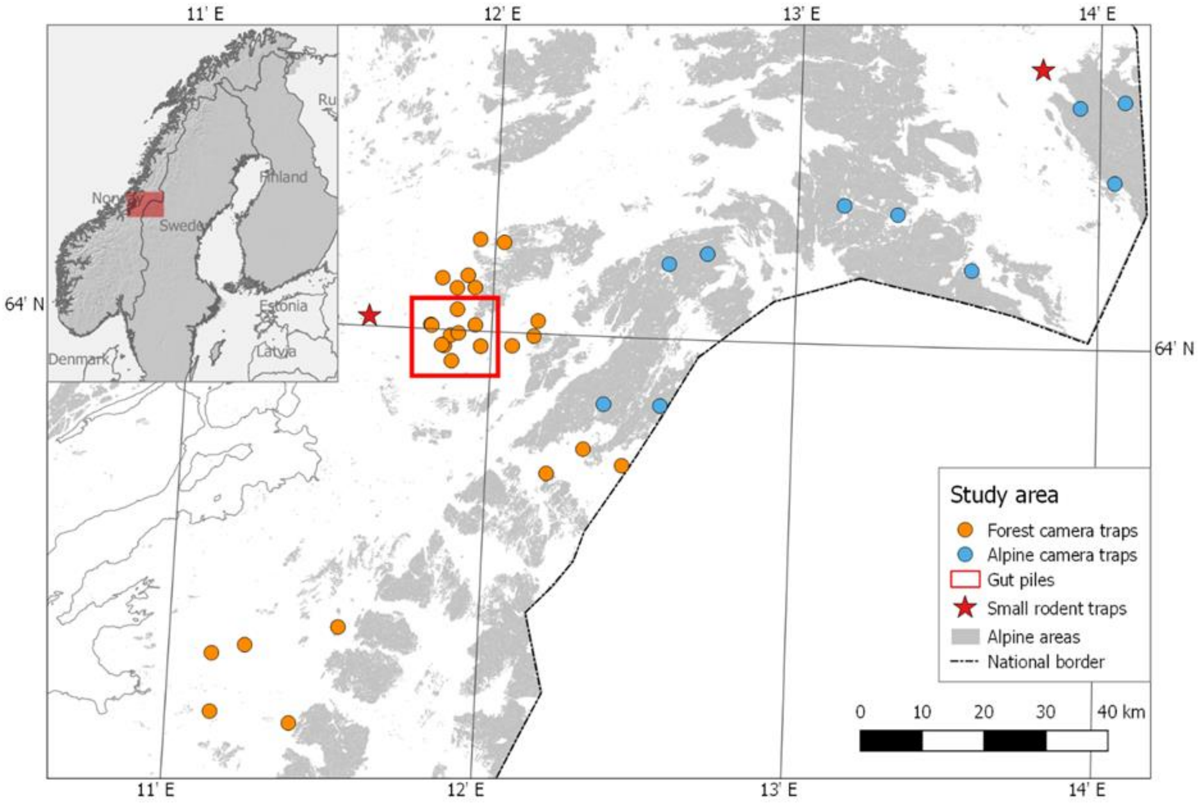

Figure *1*. Spatial distribution of bait study sites in central Norway. Circles show the placement of camera traps in boreal habitats (orange) and alpine habitats (blue) in winter. Grey areas represent alpine habitat. The red square shows the area of the gut pile study in autumn (details in (Gomo, Mattisson et al. 2017)), whereas red stars represent small rodent trapping locations.

FIELD SAMPLING

Camera traps (Reconyx Hyperfire Professional PC 800 and PC 900, Reconyx Inc., Wisconsin, USA) were set up at 38 bait locations in winter (29 in forest and 9 in alpine habitat) for a total of 65 bait sessions (42 in forest and 23 in alpine habitat), i.e. some bait locations were reused several years. This resulted in a total of 1253 monitoring days between January and April, 2012-2014. The average duration of a bait session was 19 ± 4 days (mean ± 2SE) in forested and 20 ± 5 days in alpine habitats, ranging from 4 – 62 days. Bait consisted of frozen blocks of discarded reindeer meat, fat and connective tissue weighing between 10 and 20 kg and measuring approximately 60 x 40 x 15 cm. To ensure that the bait was not removed immediately by large scavengers, and to keep the bait frozen, the bait was buried in the snow in a vertical position (only 5 cm of the top was visible). In the autumn camera traps (Reconyx Hyperfire PC 900 and Wingcam II TL) was mounted at 50 moose gut piles during the moose hunting seasons of 2012-2014, totaling 1043 monitoring days. The hunters set up the cameras before they left the dressing site (1 camera per site (Gomo, Mattisson et al. 2017)). Cameras were placed 4–6 m from the baits/gut piles at approximately 1−1.5 m above the ground and tilted slightly downwards towards the bait. Camera traps for the winter study were programmed to take a picture every 10 minutes to increase capture probability of elusive species (c.f. Hamel, Killengreen et al. 2013). The cameras at gut piles were in addition triggered by a motion sensor, with a 2 min delay between triggers to maintain battery and memory card capacity. All pictures were examined and the number of individuals of each species in each picture was recorded. To reduce sampling bias, only images where the bait was still present (i.e. not fully consumed) and thus acting as an attractant to animals were included in the analyses. Complete consumption was estimated based on visual examination of the pictures.

Small rodent phases

Small rodent phases were categorized based on autumn snap trapping in two locations within the study area (Fig 1) (Sørensen 2019, Sørensen 2020). The two snap-trapping indexes showed similar cyclicity, however the amplitudes at the eastern location (representing the alpine study area, Fig. 2) were higher than at the western location (representing the forest study area, Fig. 2), probably due to differences in altitude, latitude and winter length between the trapping areas (Andreassen, Johnsen et al. 2020). Bank vole (*Myodes glareolus*) was the dominating species, and Norwegian lemming (*Lemmus lemmus*) was caught only in the eastern location in 2011 during a pronounced lemming peak in alpine areas. We defined the winter small rodent phases as post-peak in 2012, low in 2013 and pre-peak in 2014 based on the trapping in the preceding autumn following Stoessel, Elmhagen et al. (2019), and autumn small rodent phases as low in 2012, pre-peak in 2013 and peak in 2014. Small rodent phases in winter were included in the analyses of red fox visitation at bait locations while autumn phases were used for gut piles.

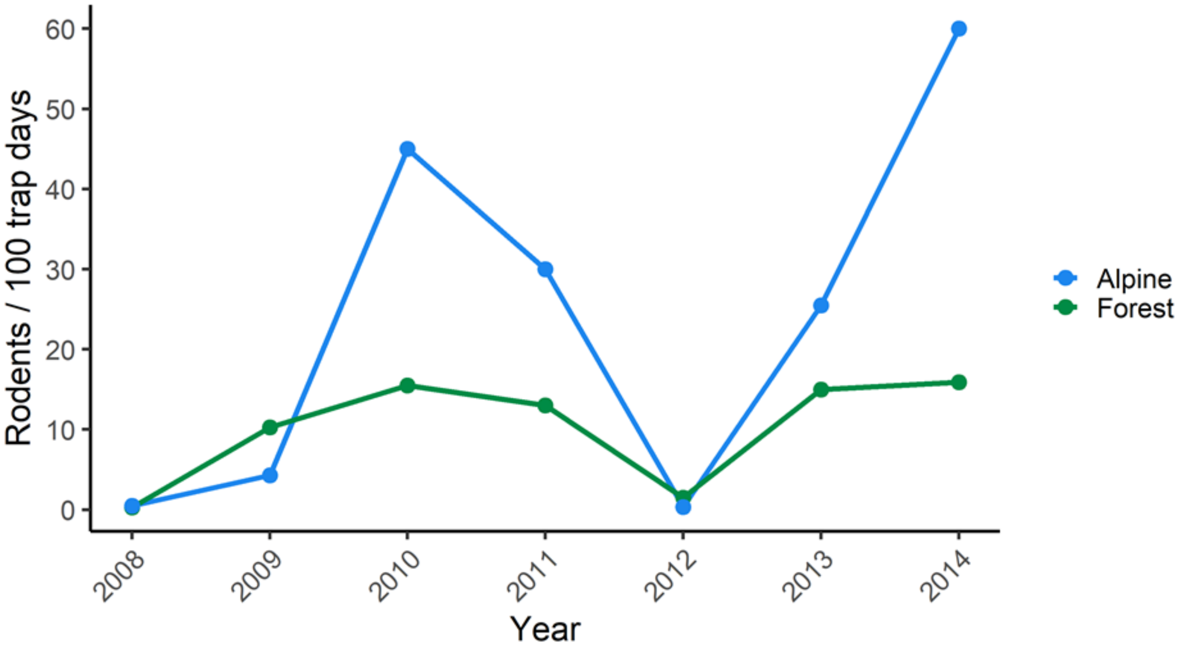

Figure 2. Autumn snap-trapping indices for small rodents in forest (the westernmost trapping location of Ogndal; green line) and alpine (the easternmost trapping location of Lierne; blue line) habitats. During our winter study period, a post-peak rodent phase occurred in winter 2011/12, a low rodent phase in winter 2012/13, and a pre-peak rodent phase in winter 2013/14.

Environmental variables

Snow depth was extracted from interpolated maps (NMI, 2019) with a resolution of 1 km pixels, and calculated as an average within a 1.5 km buffer (~7 km^2) around each camera site for each bait session. Mean site snow depth (± 2SE) was 32 cm (± 9.9) at forested and 108 cm (± 9.9) at alpine sites but varied between years (Fig. 3). For primary productivity we used a measure of peak plant productivity (average Enhanced Vegetation Index EVI; (Tveraa, Stien et al. 2013)), averaged over the years 2000-2018, at a resolution of 210 m pixels.

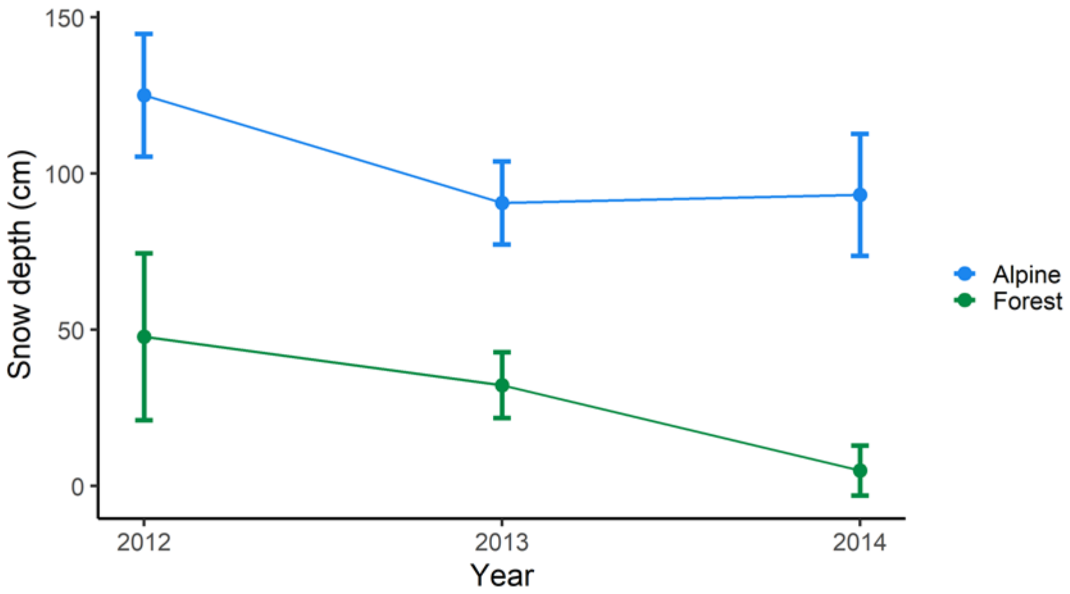

Figure 3. Mean snowdepth in centimeters (± SD) for bait stations per year within forest and alpine habitats.

STATISTICAL ANALYSES

To investigate the influence of small rodent phases, snow depth or primary productivity on carrion use by red foxes, we used binomial generalized linear mixed-effects models (GLMM; in R-package lme4 (Bates, Maechler et al. 2015)). As the dependent variable we used daily presence of red fox to gut piles/baits (0 or 1, where 1 is defined as ≥1 red fox picture). We included gut pile/bait ID (N = 50 for gut piles, N = 23 for alpine baits, N = 42 for forest baits, Fig.1.) as random intercept in the model to account for repeated measures within and between years. We analyzed gut piles, forest baits and alpine baits separately, as the sample size was too small to support three-way interactions. We included productivity, small rodent population phase, snow depth and an interaction between small rodent phase and snow depth as explanatory variables in the bait models. The gut pile models included only productivity and small rodent phase as explanatory variables, as snow cover was limited to a few days during the autumn study period. In addition, we included an estimate of local gut pile density, as this parameter was shown to affect mammal scavenging in this study area (for more details see (Gomo, Mattisson et al. 2017)).

To compare the probability of red fox use between the three sources (gut piles, forest baits, alpine baits), we ran an additional GLMM model, including gut pile/bait ID as a random intercept.

RESULTS

The probability of daily use of carrion by red fox was in general higher at alpine baits in winter (predicted probabilities: 0.24 ± 0.04 SE) than on forest baits in winter (0.12 ± 0.02 SE) and gut piles in autumn (0.10 ± 0.01 SE).

The probability of daily use by foxes at alpine baits where primarily influenced by a combination of small rodent phases and snow depth (Table 1 & 2). Use was highest during the post-peak small rodent phase but decreased with increasing snow depth. The same pattern was observed also during the pre-peak phases, while snow depth had no effect during the low small rodent phase (Fig 4a, Table 2). The second best model additionally included productivity, but the increased in AICc with almost 2 (1.85) and the significantly lower AICc-weight (0.55 vs 0.22) indicate that this variable had little effect on daily use. Further, the probability of daily use by foxes at forest baits was best explained by small rodent phase alone (Table 1). Use was lower in the pre-peak rodent phase compared to the post-peak (β= -1.31192, SE= 0.31452, p<0.001) , but not different from the low phases (β= 0.04248, SE=0.346, p=0.902). However, the model including an interaction with snow depth performed almost equally well (ΔAICc=0.18; Table 1). In contrast to alpine baits, red fox daily use of forest baits increased with increasing snow depth during the low small rodent phase while snow had little effect in the two other small rodent phases (Fig 4b, Table 2).

Table 1. GLMM-models for assessing the effect of small rodent phases (Low, pre-peak, post-peak), snow depth and environmental productivity on red foxes' daily use (0,1) of alpine- and forest bait stations. Models were fitted with a binomial distribution and included bait ID as a random intercept.

	Alpine baits			**Forest baits**		
Model	**ΔAICc**	**K**	AICω	**ΔAICc**	**K**	AICω

Rodent:snow	0.00	7	0.546	0.18	7	0.257
Rodent:snow + prod	1.85	8	0.216	1.95	8	0.106
Rodent+snow	2.50	5	0.156	1.09	5	0.164
Rodent+snow + prod	4.00	6	0.074	3.12	6	0.059
Rodent	8.90	4	0.006	0.00	4	0.282
Rodent + prod	10.93	5	0.002	1.97	5	0.105
Snow	38.86	3	<0.001	5.46	3	0.018
Snow+prod	40.79	4	<0.001	7.28	4	0.007
Null	45.82	2	<0.001	20.37	2	<0.001
Prod	47.84	3	<0.001	22.30	3	<0.001

Table 2. Results from the GLMM model assessing the probability of red fox daily use at alpine- and forest bait station during winter including the variable snow depth and small rodent phase (low, pre-peak and post-peak and their interaction.

	Alpine baits				Forest baits			
Model variables	β	SE	z-value	Pr(>|z|)	β	SE	z-value	Pr(>|z|)
Intercept	1.83	0.954	1.92	0.05	-1.23	0.194	-6.33	<0.001 ***
Snow depth	-1.58	0.638	-2.47	0.01 *	0.19	0.365	0.51	0.6
Low rodent	-3.21	0.825	-3.89	<0.001 ***	1.71	0.743	2.30	0.02 *
Pre-peak rodent	-3.07	0.915	-3.35	<0.001 ***	-1.41	1.596	-0.88	0.4
Snow: low rodent	1.79	0.740	2.42	0.02 *	2.52	1.215	2.07	0.04 *
Snow: pre-peak rodent	0.19	0.771	0.24	0.8	-0.28	1.278	-0.22	0.8

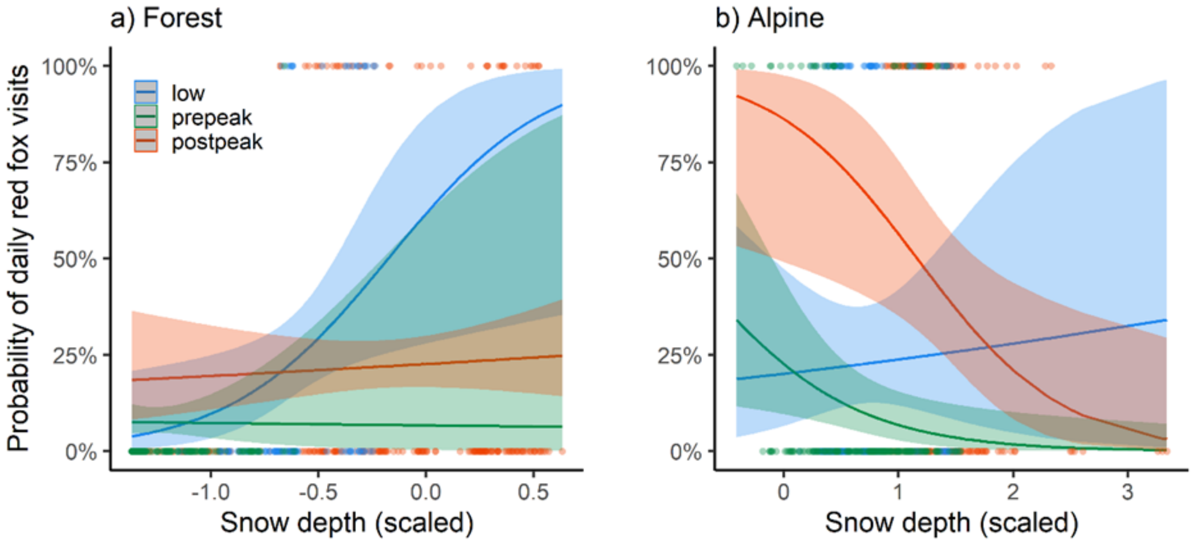

Figure 4. Predicted probabilities of red fox daily use of bait stations in forest (a) and alpine (b) habitats during winter. The predictions are based on the model including the interaction between small rodent phases (low, pre-peak, post-peak) and snow depth (top ranked model for alpine and

second-ranked model for forest following AIC; Table 1). Dots are daily non-detections (bottom) and detections (top) from the raw data, color-coded for each rodent phase.

None of the models of the probability of daily use by red fox at gut piles during the autumn performed well and the best model was only 1.29 AIC_c-units from the NULL model (Table S1). The best model included only the estimated density of gut piles where red fox use was highest at intermediate densities of gut piles. The second-best model (**ΔAICc =0.25**) additionally included small rodent phase which showed a tendency for higher use of gut piles during the pre-peak small rodent phase (predicted probability: 0.14 ± 0.036SE) compared to the low phase (0.06 ± 0.028). Use of gut piles during the peak year was at intermediate levels (0.08 ± 0.031).

DISCUSSION

This study presents novel insight into spatial and temporal patterns of red fox scavenging and its relationship with small rodent dynamics, snow depth, habitat and season in central Fennoscandia. We predicted two contrasting pattens of red fox scavenging depending on the relative importance of numerical- and functional responses to fluctuations in small rodent abundance. Interestingly, we found evidence of both responses, but their influence on red fox scavenging seemed to differ between forests and alpine areas.

In alpine areas, use of baits was highest in the small rodent post-peak winter. This probably reflected relatively higher red fox abundance, as red foxes have been shown to respond numerically to small rodents by increased reproduction in peak years in northern areas (Englund 1980). This assumption is further supported by a study in northern Fennoscandia during the same time period, where a red fox abundance index based on snow-track counts showed a similar pattern through the small rodent cycle (Stoessel, Elmhagen et al. 2019). Small rodent phase also had an influence on red fox presence at forest baits during winter, the effect was however less clear. Small rodent amplitudes were lower in our forest study area compared to the alpine area, and it is likely that both lower between-year variation in small rodent abundance and hence less variation in red fox reproductivity (Englund 1980, Lindström 1989) may result in less marked fluctuations in red fox use of carrion. In contrast to alpine baits, red fox use of forest baits did not decrease from the post-peak to the low small rodent phase. This might reflect a higher dependency of carrion during the low small rodent phase in forest habitat, compared to phases when small rodents are more abundant, in accordance with (Englund 1965, Jędrzejewski and Jędrzejewska 1992).

The influence of snow depth on use of baits also differed markedly between forests and alpine areas. At alpine baits, red fox presence decreased with increasing snow depth in the post-peak and pre-peak small rodent phases. Red fox space use has been shown to be influenced by snow conditions (Pozzanghera, Sivy et al. 2016), and by an interaction between snow conditions and abundance of prey and carrion (Carricondo-Sanchez, Samelius et al. 2016). Differences in small rodent abundance throughout the small rodent cycle might hence result in different patterns of red fox area use between years (Stoessel, Elmhagen et al. 2019). Red foxes are capable of locating even small remains of carrion beneath the snow (Mullen and Pitelka 1972), but successful hunting and digging may be difficult when snow is too deep (Willebrand, Willebrand et al. 2017). Hence, less use of baits with increasing snow depth in mountains might be caused by foxes avoiding these areas when deep snow reduces accessibility of food resources. On the contrary, red fox presence at baits in forests was only influenced by snow depth in the low small rodent phase, where presence at baits increased with snow depth. This pattern might be explained by a functional response where red foxes in forest habitat switch to search for carrion when a combination of both low abundance, and reduced accessibility, of small rodents is present. Since carrion is a temporarily and spatially unpredictable food source, restricting space use to areas with less snow might not be a good strategy. Interestingly, the whole scavenger community showed a positive response to reindeer density in low arctic tundra (Henden, Stien et al. 2014), and this response was much stronger in a year that correspond to a low small rodent phase in this particular area (Ims, Yoccoz et al. 2011). Our results further suggest that red fox are less restricted by snow depth in their use of alpine areas during years with low abundance of small rodents, which might increase spatial overlap and interactions with the endangered arctic fox (Stoessel, Elmhagen et al. 2019), with potentially negative effects on the arctic fox (Killengreen, Strømseng et al. 2012, Hamel, Killengreen et al. 2013). Higher use of carrion in less productive alpine habitat compared to forest habitat is in accordance with the prediction that carrion is more important to red foxes when other prey is less abundant or less available. The deep snow in the alpine study area probably limited access to small rodents in general (Jędrzejewski and Jędrzejewska 1992, Lindström and Hörnfeldt 1994, Willebrand, Willebrand et al. 2017), increasing the importance of carrion regardless of small rodent abundance. Another mechanism which may favor scavenging over hunting, is increased energy cost of travel in deep snow (Crête and Larivière 2003). Carrion biomass was also lower in the alpine area compared to the forest (Hagen 2014), which might increase the probability of foxes utilizing individual alpine baits.

In contrast to baits during winter, we did not observe any notable influence of small rodent abundance on red fox use of gut piles in the autumn. Red fox use of gut piles tended to be higher in years with increasing small rodent abundance but was more influenced by gut pile density. Our results thus suggest that red foxes utilize this resource equally between years, regardless of small rodent density. Gut piles are a pulsed but predictable resource, both in term of abundance and distribution compared to other carrion resources (Wikenros, Sand et al. 2013, Gomo, Mattisson et al. 2017). This may lead to behavioral adaptations (Tsukada 1997) where red foxes independent of alternative prey abundance actively search for gut piles when the moose hunting season begins. Resource subsidies are shown to increase red fox carrying capacity (Bino, Dolev et al. 2010) and high gut pile abundance may result in higher red fox abundance (Jahren, Odden et al. 2020).

In this study, we showed that small rodent dynamics influenced red fox scavenging during winter. In the forests, scavenging increased during periods of low small rodent abundance and when accessibility to this food resource was limited by deep snow. In contrast to the marked functional response in scavenging observed in forests, scavenging in alpine areas followed patterns predicted by a numerical response, i.e. scavenging increased when the abundance of small rodents was high the preceding summer, and when accessibility of small rodents was high due to relatively low snow depths . Snow in alpine areas was more than twice as deep than in forests during all three winters of this study, and thus probably often above a threshold where red foxes efficiently can access resources on the ground. These harsh environmental conditions reduce the attractiveness of the alpine habitat for the red fox, but could be modified by changes in access to carrion resources. Snow depth further seemed to be a key factor that modifies the effects of small rodents on red fox scavenging and creates differences in patterns of scavenging between habitats.

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Conflicts of interest/Competing interests

The authors declare that they have no conflicts of interest/competing interests.

Ethics approval

Not applicable

Consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and material

The datasets used and analysed during the current study are available from the corresponding author on reasonable request.

Code availability

The codes used in R during the current study are available from the corresponding author on reasonable request.

Authors' contributions

GG, JM and MO conceived the idea of this study. GG, NEE, LRE collected and compiled the data; GG, JM & LRE performed statistical analyses. GG, JM, LRE, NEE & MO all contributed in the writing of the manuscript. All authors read and approved the final manuscript.

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APPENDIX

Table S1. GLMM-models evaluated to assess the effect of small rodent phases (Low, pre-peak, peak), gut pile density and environmental productivity on daily use (0,1) of gut piles by red fox. Models were fitted with a binomial distribution and included gut pile ID as a random intercept.

Model	**ΔAICc**	**K**	AICω
Gut pile density	0.00	4	0.178
Gut pile density + Rodent	0.25	6	0.157
Rodent	0.37	4	0.148
Gut pile density + prod	0.63	5	0.130
Gut pile density + prod + Rodent	0.69	7	0.126
Rodent + prod	1.02	5	0.107
Null	1.29	2	0.093
Prod	2.15	3	0.061

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University of
Applied Sciences

The objectives of my thesis were to investigate 1) the structure of the winter scavenger community across a forest-alpine gradient in central Scandinavia and the effects of temperature and snow depth; 2) effects of large quantities of gut piles left behind during the moose harvest on scavenging communities and the influence of energy content and gut pile density on scavenging patterns; 3) how fluctuating small rodent abundance, landscape productivity and snow depth affected red fox scavenging in forest and alpine habitat.

Spatial variation in snow depth along the forest-alpine gradient interact with habitat to shape the structure of the scavenger community, and individual species occurrence at baits. Habitat generalists dominated as scavengers in both habitats. Increasing snow depth only had negative effect on occurrence at baits for the species with stronghold in forest. Depletion of gut piles was dependent on the different quality of gut pile parts, the energy rich parts were depleted first, mostly by corvids, and several times faster than the parts with lower energy content. This resulted in large differences in the magnitude and the duration between the parts with high and low energy content, where the latter accumulated to higher densities and was present a long time after the end of the moose hunting season. Corvids presence at gut piles was best explained by gut pile age, while mammal presence was best explained by gut pile density. Patterns of red fox scavenging differed between forest and alpine habitat. Red fox scavenging in alpine areas during winter was highest following the peak in rodent abundance the preceding summer. In forest, red fox scavenging during winter increased when small rodent availability was low. However, red fox scavenging of moose gut piles in autumn was not affected by small rodent abundance.