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Research article

Carnivore guild utilization of hunter-provided food sources in boreal forest

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Scavenging is an alternative foraging strategy to predation for many carnivore species, as they shift between predation and scavenging in response to changes in resource availability. The use of carrion may lead to interspecific competition and is thus influenced by a risk–reward trade-off to balance coexistence with guild-members, where smaller species are expected to be more vigilant due to their vulnerability to larger competitors. We used cameras to investigate the utilization of viscera from the annual moose *Alces alces* hunt by four sympatric carnivore species: wolf *Canis lupus*, wolverine *Gulo gulo*, red fox *Vulpes vulpes* and pine marten *Martes martes* in south–central Scandinavia, in relation to body size and habitat. Red foxes had highest probability of visiting viscera sites in both open and forested habitats. Visits by both red foxes and pine martens were longer in open habitats, while number of visits or activity did not differ between habitats. For pine martens, the probability of visiting viscera sites was twice as high in forest compared to open habitat; consequently, red foxes showed the highest overall use of viscera. Red foxes were most vigilant, especially in open habitat, whereas wolverines and pine martens spent a higher proportion of time feeding. Increased vigilance of red foxes facilitates extended resources use in open habitat, while for pine martens, the risk–reward decision occurs before leaving forest cover and entering open habitats. Viscera were not used to a large extent by wolves or wolverines. Wolves are generally less prone to scavenging and wolverines probably use other food resources, more suitable for caching. Overall, competition did not prevent use of viscera, probably due to small-scale temporal segregation and limited use by the larger carnivores. Consequently, this pulse of human-subsidized food resources before winter may have important implications for the smaller facultative scavengers.

Keywords: carrion use, interspecific competition, pine marten, red fox, wolf, wolverine

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Introduction

Scavenging is an alternative foraging strategy to predation and most carnivore species opportunistically utilize carrion when available, making it an important food resource (DeVault et al. 2003, Wilson and Wolkovich 2011, Sebastián-González et al. 2021). Carnivores are able to shift between predation and scavenging, allowing them to adapt to changes in resource availability (Wilson and Wolkovich 2011, Pereira et al. 2014). However, smaller species are limited by their foraging range and the benefits from scavenging may not outweigh the associated costs (DeVault et al. 2003). Scavenging may also lead to increased competition within the scavenger guild, and risk of intra- and/or interspecific aggression from dominant carnivores nearby carrion (Selva et al. 2005). Thereby, carnivore feeding strategies are influenced by both resource availability and risk–reward trade-off to balance coexistence with guild-members and their foraging strategies. Fights can cause injury or death, and the outcome of this type of competition is often determined by differences in body or group size (Donadio and Buskirk 2006). Smaller and solitary species are thus expected to be more vigilant as they are subject to a higher risks than larger competitors (Caro 1987).

The accessibility of carrion and risks associated with scavenging can be influenced by habitat structure and composition: for example, carrion is easier to detect in open spaces, but also more exposed to competitors. Hence, the most accessible feeding habitat may also be the riskiest, resulting in animals being more vigilant in those habitats and spending less time feeding (Lima and Dill 1990). Nevertheless, the detection and accessibility of carrion, as well as the risks associated with scavenging in different habitats, vary among different species, being affected by habitat use (Selva et al. 2005) and escape strategies.

In Scandinavia, moose *Alces alces* is the largest wild ungulate and an important game species (Storaas et al. 2001, Boman et al. 2011). Remains from the annual moose hunt during autumn provide an important scavenging resource for many carnivore species (Wikenros et al. 2013, Gomo et al. 2017). After a moose is shot, it is common practice to eviscerate it on site before the body is removed from the forest, and viscera from the moose hunt results in an annual biomass of 16–22 kg km^{-2} available to scavengers (Wikenros et al. 2013).

Wolverines *Gulo gulo*, red foxes *Vulpes vulpes* and pine martens *Martes martes* are – together with the common raven *Corvus corax*, northern goshawk *Accipiter gentilis* and golden eagle *Aquila chrysaetos* – the most common scavengers within the wolf *Canis lupus* distribution in Scandinavia (van Dijk et al. 2008, Wikenros et al. 2013). Wolves, with their larger size, are expected to exhibit dominance over the other scavenger species. Wolves are known to kill red foxes (Wikenros et al. 2023), and occasionally wolverines (Wallace et al. 2021). Wolverines have been documented to sporadically kill both red foxes and pine martens (Mattisson et al. 2016, Aronsson et al. 2022). Red foxes have been observed killing pine martens, and when the red fox population declined as a result of a sarcoptic mange outbreak in the 1980s, the pine marten population increased, suggesting that red fox is an important predator on pine marten (Storch et al. 1990, Lindström et al. 1995). Pine martens avoid open areas and are selective regarding forest age and composition (Storch et al. 1990, Brainerd and Rolstad 2002). Furthermore, pine martens have been found to be more vigilant than red foxes at carrion sites, as well as more vigilant in open habitats (Wikenros et al. 2014). The red fox is a habitat generalist (Hersteinsson and Macdonald 1992) and its abundance is positively related to the amount of viscera from moose harvest (Jahren et al. 2020) and likely also the absence of large carnivores (Selås and Vik 2006).

The aim of this study was to investigate the extent to which a carnivore guild utilized viscera from moose shot during the annual autumn harvest. We used remote wildlife cameras mounted near viscera sites to compare utilization patterns by wolves, wolverines, red foxes and pine martens. We investigated 1) the probability of visiting a viscera site, the number, and duration of visits; 2) behaviour with focus on vigilance and feeding; and 3) circadian activity pattern at viscera sites. We also examined 4) how the utilization, behaviour and activity varied between viscera sites in forested and open habitat, and hence the presumed risk of interference competition and potentially intra-guild predation. We predicted 1) higher utilization of viscera by pine martens and red foxes compared to wolverines and wolves; 2) that the proportion of vigilant behaviour would be inversely related to body size; 3) that smaller carnivores would show different circadian activity patterns compared to the larger carnivores, to reduce the risk of interference competition; and 4) that the proportion of vigilant behaviour would be higher in open habitat compared to forest habitat for the tree climbing species (pine martens and wolverines), due to lack of escape cover.

Material and methods

Study area

The study was carried out in two areas (60°97′N–12°23′E, 60°42′N–15°19′E) in south-central Scandinavia (Fig. 1), a region with a continental climate where snow generally covers the ground from December to March (SMHI 2023). The area is primarily boreal forest, interspersed with bogs and lakes. Norway spruce *Picea abies* and Scots pine *Pinus sylvestris* are dominating tree species, alongside with deciduous species, mainly birch *Betula* spp. and locally also aspen *Populus tremula*. In most of the area the forest is intensively managed, generating a vast forest-road network, and creating a patchwork of tree stands in various succession stages.

Within the study area, moose are the main prey of wolves but they also prey on roe deer *Capreolus capreolus*, and occasionally red deer *Cervus elaphus* and wild boar *Sus scrofa* (Zimmermann et al. 2015, Sand et al. 2016). Moose occur at an average winter density of 1.3 moose km^{-2} within Scandinavian wolf territories (Zimmermann et al. 2015). Also, wolves scavenge during 6–13% of their

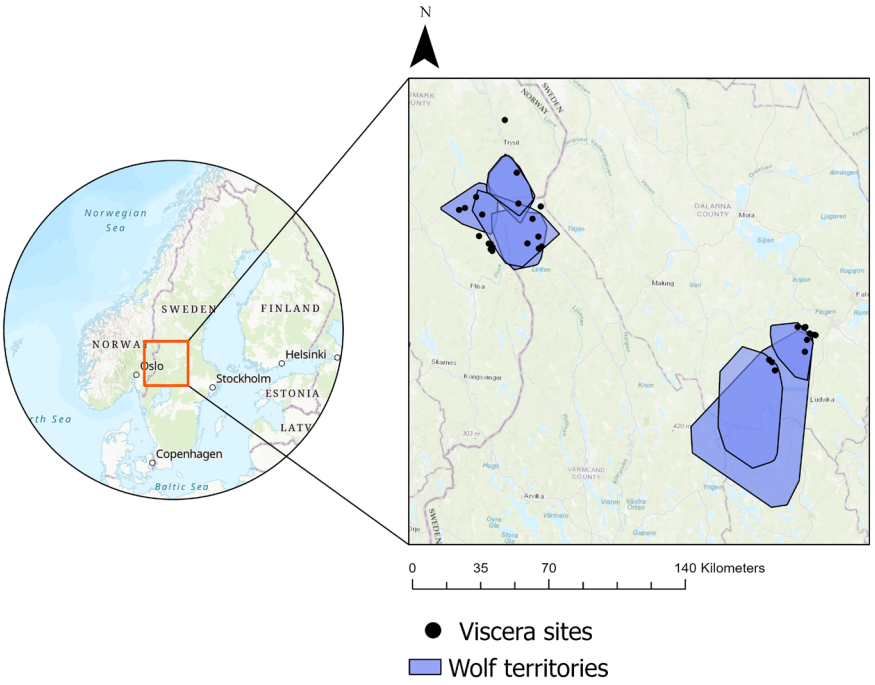

Figure 1. Location of viscera sites from harvested moose in south–central Scandinavia where movement-triggered cameras were set up (black circles) from October to November 2019–2020. Annual (2018–2020) wolf territories with at least one GPS-collared wolf are shown in blue polygons. Wolverines, red foxes and pine martens were present in all areas where cameras were set up.

consumption time and utilize viscera from the moose hunt (Wikenros et al. 2023).

The wolverine is a facultative predator and scavenger (Inman et al. 2012, Mattisson et al. 2016). In the study area, moose are the main food source, mainly obtained by scavenging hunting remains and wolf-kills, but wolverines also feed on smaller mammals and birds, such as mountain hare *Lepus timidus* and capercaillie *Tetrao urogallus*.

The main prey of the red fox are voles *Microtus* spp., and pine martens primarily feed on small rodents, birds, eggs, insects and carrion, but ungulate remains can also constitute an important food source for both species (Hagström and Hagström 2010, Needham et al. 2014, Pasanen-Mortensen and Elmhagen 2015).

Data collection

In collaboration with local hunters, movement and time-lapse triggered cameras were set up at viscera sites during the two first months of the annual moose harvest (October–November) during 2019 and 2020 (Fig. 1). A shot moose is often eviscerated at the site, leaving internal organs such as lungs, spleen, rumen, intestines and sexual organs, and often including the heart, liver, kidneys and rumen (Supporting information). At each viscera site, one camera was deployed no later than the day after the moose was shot. We used three different camera models (HF2 PRO COVERT, HyperFire HC600 and HyperFire PC800 Professional), all from Reconyx. The cameras were programmed to take a series of three consecutive photos at 1-s intervals when triggered by movement, and to take a new series of photos after 1 min if movement continued. In addition, an image was taken every 5 min to have a standardized sampling schedule that would also photograph smaller species that would not trigger the camera's motion detector. Cameras were placed at a total of 42 sites within the study area. We included data from the first 28 days following camera setup, resulting in data from a total of 1062 camera days. Thirty cameras were active for 28 days and the remaining 12 cameras were active for 7–23 days (mean 18 ± 5.5 (SD) days) due to malfunctioning.

Compilations of photos and habitat classification

The date and time of all photos were obtained via the Reconyx Map View Professional software (ver. 3.7.2.2). The content of each photo was reviewed manually to assess the presence of the focal species and the number of individuals (hereafter, presence-photos). We classified photos where no species was observed as absence-photos, while images taken when the camera was not functioning or covered with snow were classified as failed photos (Supporting information). Based on the photos from each camera, the habitat of the site was classified as either forested or open based on the presence or absence of trees in the vicinity of the viscera site (Supporting information). Of the 42 sites included in this study, 29 were located in forested habitat and 13 in open habitat.

Utilization, behaviour and activity at viscera sites

We included three measurements of utilization: probability of visiting a viscera site, number of visits and visit duration. We defined a visit as a sequence of photos documenting

presence of the species in question, interrupted by less than 30 min of absence-photos (Lamichhane et al. 2019). This was to account for animals remaining at the site but moving out of range of the camera. We rounded visit duration to the nearest minute (1 min for all visits < 60 s).

We classified individual behaviours per photo as feeding, vigilant or other (Supporting information). We defined 'feeding' as being when the individual had its head down near the viscera, 'vigilant' as being when it had its head up in an alert position (Atwood and Gese 2008) and as 'other' when individuals were, for example, walking, running or climbing trees. For all visits consisting of > 1 photo, we calculated the proportion of each behaviour per visit as the number of photos per individual where the behaviour was displayed, divided by the total number of photos per individual. In cases with two or more individuals in the same photo, the behaviour was classified separately for each individual.

To investigate temporal activity patterns of the focal species and temporal partitioning between species, we used all presence-photos from the 5-min time-lapse photos.

Statistical analyses

Utilization and behaviour

We analysed utilization and proportion of vigilant and feeding behaviour using Bayesian modelling in JAGS (Plummer 2003) called from R using the 'rjags' package (Plummer et al. 2016). See Supporting information for detailed model specification. For probability of visiting a viscera site, we coded each site as either visited (1) or not visited (0) by each species and used a Bernoulli distribution with a logit-link function. For number of visits, we used a Poisson distribution with a log-link function. For visit duration, we used a negative binomial distribution with a log-link function. We modelled proportion of vigilant and feeding behaviour separately, using a beta distribution with a logit-link function. To fit the beta distribution we changed zeros to 0.014 (smallest non-zero proportion in our data) and ones to 0.95 (largest proportion excluding one in our data). For each model, we included species, habitat and their interaction as explanatory variables. To account for the differences in deployment time between cameras, we included number of camera days as an explanatory variable for probability of visiting a viscera site and as a log-transformed offset for number of visits. Furthermore, we included a group-level effect of viscera sites in the number of visit models (i.e. allowing the relationship between the different species to be different for each site) to account for over-dispersion in the data. Wolves were excluded in the two behaviour models due to the limited number of sites visited.

We ran two independent chains with different starting values and after discarding the first 100 000 iterations we extracted parameter estimates at every 1000th step from a total of 1 000 000 accumulated samples from each chain. Convergence was assessed by visual inspection of trace plots to assure stability and homogeneous mixing, and by using the Gelman and Rubin diagnostic (< 1.1) (Gelman and Rubin 1992). We evaluated model fit using posterior predictive checks, comparing the mean and coefficient of variation of data sets simulated from each model to the original data used to estimate the model coefficients (Hobbs and Hooten 2015; Supporting information). For model predictions we present posterior means with associated 95% credible intervals (CRI). To assess differences between groups we subtracted their posterior distributions (i.e. A–B). The proportion of the resulting posterior distribution > 0 is then the probability for group A > group B. A probability of 50% indicated that the mean estimate for the difference equals 0 and has no predictive value.

Activity pattern

To analyse temporal activity patterns of the focal species and assess whether there was temporal partitioning between species at the viscera sites, we used the R package 'Overlap' (Ridout and Linkie 2009). We compiled presence-photos of the species from the 5-min time-lapse photos as the replication unit, and transformed time of day to radians (circular time variable) and fitted second-degree kernel density curves of activity to determine the coefficient of overlap (Δ) (Meredith and Ridout 2021). We estimated the mean coefficient of overlap using *Dhat1* (Δ_1) for small sample sizes and bootstrapped this for each pairwise species combination to 10 000 replications from the R package 'boot' (www.r-project.org, Canty 2002). Following Monterroso et al. (2014) we considered overlap estimates together with associated 95% confidence intervals of $\Delta_1 \leq 0.50$ to be of low overlap value (high temporal partitioning), $\Delta_1 < 0.70$ to be moderate (moderate temporal partitioning) and $\Delta_1 \geq 0.70$ to be high (low temporal partitioning).

Results

We received a total of 315 589 photos during the study period, of which 5953 photos were of our focal species (98 of wolves, 1239 of wolverines, 1671 of red foxes and 2945 of pine martens); 37 670 photos were of other species (see Supporting information for details of number of photos and complete species list).

Probability of visiting a viscera

Of the 42 viscera sites (29 in forest and 13 in open habitat), 38 were visited by at least one of the focal species (Table 1); six by wolves (three in forest, three in open habitat), 12 by wolverines (nine in forest, three in the open), 32 by red foxes (23 in forest, nine in the open) and 21 by pine martens (17 in forest, four in the open). One of the sites was visited by all four focal species (Table 1). Of the six visits by wolves, eight individuals were present in the same photo during one visit. Two red foxes were present in the same photo during two visits, but we never observed more than one wolverine or pine marten in the same photo.

Table 1. Number of viscera sites visited by the different combinations of focal species (wolf, wolverine, red fox and pine marten) in forest and open habitat in south-central Scandinavia during October to November 2019–2020.

Species	Forest habitat	Open habitat
Wolf, wolverine, red fox, pine marten	1	0
Wolf, wolverine, red fox	1	0
Wolf, wolverine, pine marten	0	0
Wolf, red fox, pine marten	1	0
Wolverine, red fox, pine marten	4	2
Wolf, wolverine	0	0
Wolf, red fox	0	2
Wolf, pine marten	0	0
Wolverine, red fox	0	1
Wolverine, pine marten	2	0
Red fox, pine marten	7	2
Wolf	0	1
Wolverine	1	0
Red fox	9	2
Pine marten	2	0
None	1	3

We found a higher probability of visiting a viscera site by red foxes than by all other focal species (82% probability in forest and 74% in open habitat) (Fig. 2). In forest habitat, the probability of visiting a viscera site by pine martens (61%) was higher than for both wolves (10%) and wolverines (32%), and the probability for wolverines was higher than for wolves. In open habitat, there were no differences in probability of visiting a viscera site between wolves (24%), wolverines (24%) or pine martens (33%). The pine marten was the only species where the probability differed between habitats, with almost twice as high probability in forest compared to in open habitat.

Number of visits and visit duration

We recorded a total of 617 visits at viscera sites: 12 visits by wolves (six visits at three sites in both habitats), 51 visits by wolverines (39 and 12 visits at nine and three sites in forest and open habitat, respectively), 234 visits by red foxes (155 and 79 visits at 23 and nine sites in forest and open habitat, respectively) and 320 by pine martens (270 and 50 visits at 17 and four sites in forest and open habitat, respectively). The number of visits by red foxes and pine martens varied greatly between sites (red foxes: 1–26 visits at the same site in forest, 1–33 in the open; pine martens: 1–55 visits in forest, 1–28 in the open). For wolves and wolverines, we recorded 1–4 and 1–8 visits at the same site in both habitats. Pine martens had more visits compared to wolves at sites in both habitats, and red foxes had more visits compared to wolves in open habitat (Fig. 2). There were no differences between number of visits for the other species, or between habitats for the same species.

There was variation in visit duration for all species; 1–20 min for wolves, 1–48 min for wolverines, 1–65 min for red foxes and 1–90 min for pine martens. In forest habitat, visit duration for red foxes was shorter than for both wolverines and pine martens (Fig. 2). Visit duration for red foxes was shorter than for pine martens also in open habitat but did not differ from wolverines. Additionally, pine martens had longer visits compared to wolves in open habitat, but not in forest. For both red foxes and pine martens, visits were longer in open habitat compared to visits in forest (Fig. 2).

Behaviour

Of 605 visits to viscera sites by wolverines, red foxes and pine martens, 518 (86%) consisted of more than one photo. For wolverines, all 39 visits in forest and all 12 visits in open habitat consisted of >1 photo; for red foxes, there were 124 (80%) visits in forest and 64 (81%) visits in open habitat; and, for pine martens, there were 235 (87%) visits in forest habitat and 44 (88%) in open habitat. Wolverines, red foxes and pine martens spent the same amount of time being vigilant in forest habitat, approximately 35% of the visit (Fig. 3). In open habitat, vigilance for red foxes increased to approximately 50%, resulting in higher vigilance than for both wolverines and pine martens (Fig. 3). The proportion of time feeding was higher for both wolverines and pine martens (45–55%) compared to red foxes (30%) in both habitats (Fig. 3), and in forest habitat pine martens spent more time feeding (55%) than wolverines (45%). We did not find any differences in the proportion of time spent feeding in forest versus open habitat for any of the species. When comparing the different habitats, pine martens spent more time feeding compared to being vigilant in both forest and open habitat. Wolverines spent more time feeding than being vigilant in forest habitat, and red foxes were more vigilant than feeding in open habitat.

Activity pattern

All species exhibited a nocturnal activity pattern at viscera sites, with increasing activity in the periods surrounding dawn and dusk and highest activity during night (Table 2; Supporting information). The estimated degree of overlap varied between the species combinations (Table 2). Wolverines showed low to medium temporal partitioning with red foxes and pine martens in both open and forested habitat, and low to high temporal partitioning with wolves, depending on habitat type (Table 2; Supporting information). Wolves showed similar temporal partitioning but also high variation with red foxes and pine martens in both habitats. Similarly, red foxes and pine martens showed low temporal partitioning in both habitats. Wolves exhibited a shift in activity towards dusk in open habitat compared to forest habitat (Table 2; Supporting information), whereas wolverines, red foxes and pine martens retained a similar activity pattern in both habitats.

Discussion

We recorded visits to viscera sites by wolves, wolverines, red foxes and pine martens. The sites were also visited by a wide range of other mammal and bird species, of which many

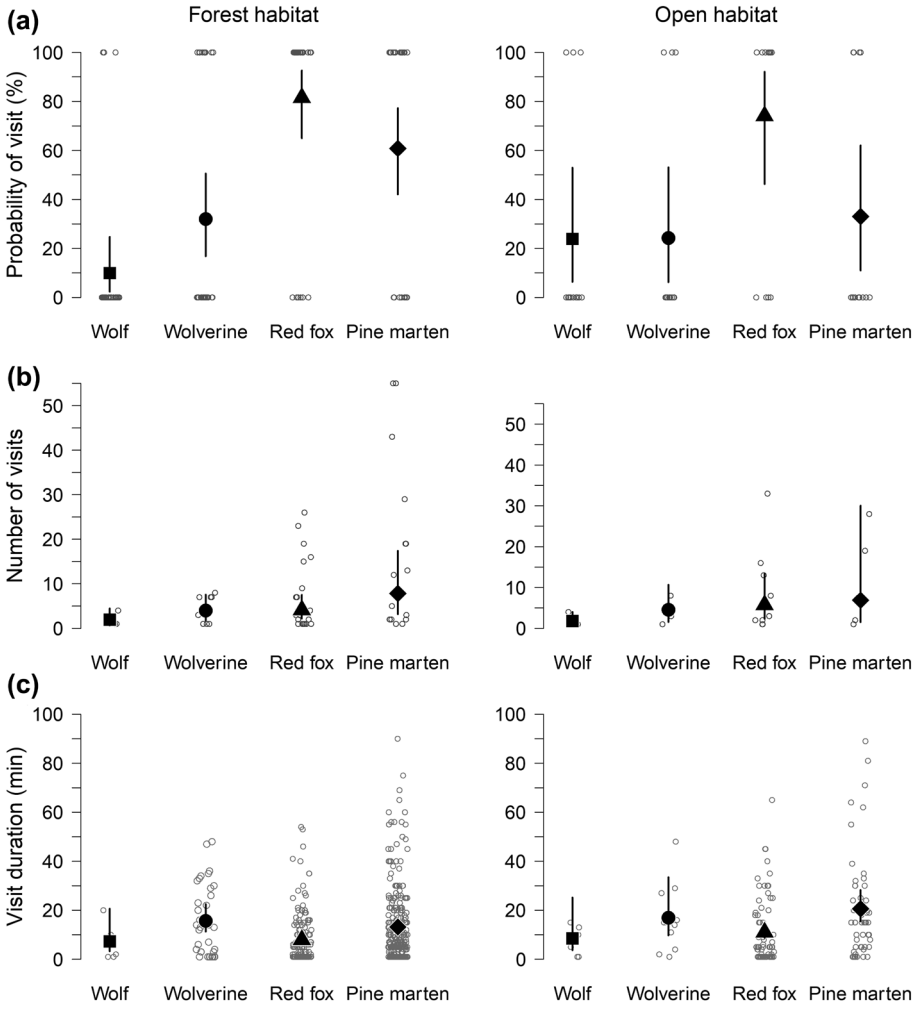

Figure 2. Predicted mean ± 95% credible interval (CRI) for (a) probability of visit, (b) number of visits and (c) visit duration at viscera sites by wolves, wolverines, red foxes and pine martens in forest (left) and open habitat (right), in south-central Scandinavia during October to November 2019–2020. Raw data are shown as dots outlined with dark grey. See Supporting information for numeric predictions and probabilities of differences between predicted means.

species are known scavengers (e.g. common raven, golden eagle, brown bear *Ursus arctos* and wild boar), but also several non-carnivorous species that passed by the site without feeding on the viscera (e.g. roe deer, red deer, black grouse *Lyrurus tetrix* and capercaillie). Red fox was the most common scavenger in both forest and open habitats. As predicted, the probability of visiting viscera sites was higher for red foxes and pine martens compared to wolves and wolverines in forested habitat. Pine martens and red foxes generally occur at higher densities and have smaller home ranges (pine martens: 7 km^2 on average (Brainerd 1997) and red foxes: 1–44 km^2 (Walton et al. 2017)) than wolverines: 100–200 and 600–1000 km^2 (for females and males, respectively) (Persson et al. 2010, Aronsson et al. 2022) and wolves: (1017 km^2) (Mattisson et al. 2013), i.e. the viscera are accessible to more individuals of the two smaller species.

The pine marten was the only species for which habitat influenced the probability of visiting viscera sites. Pine martens are more habitat specialists compared to the other three species, with a selection for old coniferous forest and ruggedness, and avoidance of open areas like bogs and clearcuts (Storch et al. 1990, Kurki et al. 1998, Brainerd and Rolstad 2002, Willebrand et al. 2017, Angoh et al. 2023). Open habitat presumably represents higher risk for pine martens, due to their smaller body size and the absence of structures that provide protection from both mammalian and avian predators (Pulliainen 1981, Lindström et al. 1995), as they tend to stay close to forest cover even when using open habitat (Pereboom et al. 2008). Therefore, the lower probability of visits to carrion in open habitat by pine martens is presumably driven by their arboreal nature and limited escape opportunities. Because of the pine martens' preference for ruggedness and old forested habitats (Angoh et al. 2023), their detection of food sources in open habitats may be lowered due to their overall habitat use. Red foxes, on the other hand, are habitat generalists (Hersteinsson and Macdonald 1992) and their broader use of different habitats allows them to use alternative food sources more than habitat-specialists such as pine

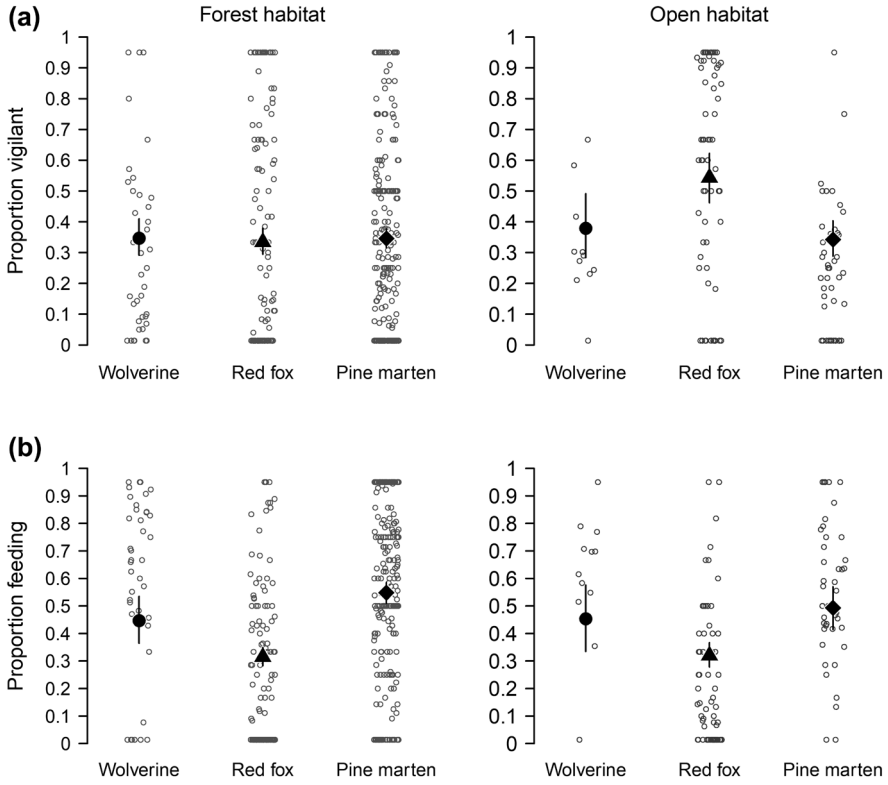

Figure 3. Predicted mean ± 95% credible interval (CRI) proportion (a) vigilant behaviour and (b) feeding behaviour by wolverines, red foxes and pine martens during visits to viscera sites in forest (left) and open habitat (right), in south–central Scandinavia during October to November 2019–2020. Raw data are shown by dots outlined with dark grey. For numeric predictions and probabilities of differences between predicted means, see Supporting information.

martens (Willebrand et al. 2017). This was supported by our findings showing that red foxes had the highest probability of visiting viscera sites, independent of habitat.

Red foxes and pine martens exhibited significant differences in the duration of their visits at viscera sites, and these differences were also related to habitat type. However, because both the number and duration of visits are conditional on visiting a site, our results regarding number and duration of visits need to be interpreted by considering the probability of a visit. For example, both pine martens and red foxes spent a longer time at viscera sites located in open habitats compared to those in forest, and pine martens generally spent longer times at sites than did red foxes in both habitats. Also, for the lack of difference in number of visits between habitats for pine martens, the lower probability of visiting viscera in open habitat needs to be considered. As there is a large variation in the number of visits to individual viscera sites, and only four sites in open habitat visited by pine martens, there is no difference in the number of visits to individual viscera sites despite the total number of visits being more than five times higher in forest habitat. This suggests that, during the rare occasions on which pine martens utilize viscera in open habitats, they visit it to the same extent as in forest habitat but stay longer at the site. Red foxes, on the other hand, are equally likely to visit viscera sites in both habitats and have a higher visit probability than pine martens in both habitats. Consequently, even though red foxes had shorter visit durations compared to pine martens in both habitats, their overall use of viscera was higher.

Wolverines, red foxes and pine martens are all opportunistic species, relying on both predation and scavenging (Mattisson et al. 2016, Willebrand et al. 2017, Nordli et al. 2024), while wolves generally spend less time scavenging compared to predation (Wikenros et al. 2023). Considering the opportunistic nature of wolverines, we found that they utilized viscera sites to a low extent (approximately 25–30% probability of visit). This might be because wolverines also utilize other sites of remains with more biomass (heads, bones and hides) brought back to the area after slaughter (Aronsson et al. 2022). Furthermore, wolverines frequently cache food as a strategy to buffer for unpredictable food availability (Inman et al. 2012, van der Veen et al. 2020). Most of the viscera are hard to cache, hence wolverines might use other, larger and more predictable slaughter remains more frequently.

In contrast to our predictions, the proportion of time spent vigilant during a visit was not related to body size, and the proportion of time spent vigilant did not increase in open habitat for wolverines or pine martens. The only difference in vigilance between species was found in open habitat, where red foxes were more vigilant than both wolverines and pine martens. The higher vigilance exhibited by red foxes in

Table 2 Estimated temporal overlap Δ_1 with 95% CI in activity pattern for pairwise combinations of wolf, wolverine, red fox and pine marten at viscera sites in forest (a) and open habitat (b), as well as between habitat for each species (c) from 5-min time-lapse camera photos on the circular transformed variable time of day, in south–central Scandinavia during October to November 2019–2020. For graphic representation of diel activity overlap see Supporting information.

Combination	Overlap Δ_1	95% CI	Temporal partitioning
a) Forest			
Wolf–Wolverine	0.58	0.41–0.84	High–Low
Wolf–Red fox	0.55	0.37–0.79	High–Low
Wolf–Pine marten	0.67	0.58–0.98	Moderate–Low
Wolverine–Red fox	0.89	0.87–0.99	Low
Wolverine–Pine marten	0.86	0.81–0.94	Low
Red fox–Pine marten	0.84	0.77–0.87	Low
b) Open			
Wolf–Wolverine	0.63	0.53–0.91	Moderate–Low
Wolf–Red fox	0.65	0.48–0.85	High–Low
Wolf–Pine marten	0.69	0.58–0.91	Low–Moderate
Wolverine–Red fox	0.75	0.66–0.90	Low–Moderate
Wolverine–Pine marten	0.77	0.68–0.92	Low
Red fox–Pine marten	0.86	0.80–0.93	Low
c) Forest | Open			
Wolf–Wolf	0.58	0.34–0.83	Low–High
Wolverine–Wolverine	0.74	0.62–0.89	Low–Moderate
Red fox–Red fox	0.90	0.84–0.95	Low
Pine marten–Pine marten	0.88	0.82–0.93	Low

open habitats, coupled with long visit durations, may suggest that increased vigilance in open habitat facilitates extended resources use. However, the proportion of time spent feeding was lower for red foxes compared to wolverines and pine martens in both habitats, even though all species exhibited similar activity patterns. We found, similar to Ståhlberg and Apollonio (2023) in Italy, that the increase in vigilance by red foxes did not come at the cost of feeding, as it was compensated for by a reduction in other behaviours (e.g. walking and running). Pine martens spent more time feeding compared to being vigilant in both habitats, and in contrast to Wikenros et al. (2014), pine martens did not increase vigilance in open habitats, even though visit duration was longer. However, the low probability of pine martens visiting a viscera site in open habitat in our study suggests that the risk–reward decision for them occurs before entering open habitat that lacks the potential to escape larger predators by climbing trees; while, at the site, pine martens focus on utilizing the food resource. The study in Italy showed that pine martens spent more time feeding compared to being vigilant at carcass sites, which was attributed to the absence of avian predators (Ståhlberg and Apollonio 2023). In our study area, avian predators are present, indicating that additional mechanisms are driving the behavioural choices of pine martens. That red foxes display higher level of vigilance behaviour than the other focal species in open habitat may be attributed both to avoidance of direct intraguild with guild members, as red foxes need to outrun imminent threats, and to differences in the risk of human-induced mortality between the focal species. Red foxes are heavily hunted in Scandinavia, targeted either at bait sites or pursued with dogs, where roads and open landscapes are frequently chosen due to the higher visibility. Conversely, pine martens are typically targeted with traps positioned in trees within forests, and wolverines are protected in most of the study area. Consequently, the higher risk of being shot in open habitats may induce higher vigilance among red foxes.

Wolverines spent more time feeding compared to being vigilant in forested habitat, but there was no difference in open habitat. A possible explanation for this is that trees provide an escape strategy for wolverines in the presence of wolves. Nevertheless, as the probability of visiting viscera by wolverines was low in both habitats, the lack of significant differences in behaviours displayed in open habitats could also be an effect of low sample size.

In general, all four species exhibited a nocturnal activity pattern with very few visits mid-day. Wolves differed somewhat from the other species with a more pronounced peak in activity at dusk compared to dawn. These patterns confirm the general species-specific activity patterns documented in other studies (Theuerkauf et al. 2003, Diaz-Ruiz et al. 2016, Thiel et al. 2019, Mori et al. 2022). However, wolves had a larger shift in activity towards dusk in open habitat compared to forest habitat, whereas wolverines retained a similar activity pattern in both habitats.

In Scandinavia, available biomass for scavengers from viscera is highest during autumn. Other food sources for scavengers that are available year-round, but to a lesser extent in terms of biomass, are remains after wolf-killed ungulates, and from vehicle collisions and natural death of ungulates (Wikenros et al. 2013). Wolves are more prone to scavenging in winter than during autumn, despite the pulse of available biomass from viscera during this time period (Wikenros et al. 2023). This may be due to wolves avoiding viscera sites in autumn due to human hunting activity during this time. Such avoidance could also be expected when considering that the mortality of wolves is largely due to anthropogenic factors (legal hunting, poaching and vehicle collisions) (Liberg et al. 2020). All except one of our monitored viscera sites were located within established territories of a breeding pair, with high hunting success, subsidizing the most recent litter of pups (Sand et al. 2006a, b, Nordli et al. 2023), while excluding non-territorial dispersing wolves that are more prone to scavenging (Wikenros et al. 2023).

This study showed that viscera from the annual moose hunt supply mammalian facultative scavengers. This applies particularly to the smaller carnivores, pine marten and red fox, but also to the wolverine. Wolves, however, which to a higher degree rely on predation than on scavenging, were more infrequent visitors at viscera sites. The activity patterns suggest that the large-scale temporal separation plays a limited role in avoidance of competition among our study

species, while the lack of simultaneous observations of several species at viscera sites suggests that temporal segregation probably occurs at a smaller scale. The large-scale, but short-term, pulse of human-subsidized food resources may have important ecological implications. This may especially be so for generalist facultative scavengers and predators before the bottleneck of the winter months, and in turn for their their prey, potentially altering numerical and functional responses, and affecting population dynamics of mammals in the Scandinavian boreal forest.

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Author contributions

Camilla Wikenros: Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Methodology (equal); Project administration (lead); Supervision (lead); Writing – original draft (lead); Writing – review and editing (lead). **Kristoffer Nordli**: Conceptualization (supporting); Data curation (supporting); Formal analysis (equal); Methodology (supporting); Supervision (supporting); Visualization (supporting); Writing – original draft (supporting). **Giulia Amato**: Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Methodology (equal); Writing – review and editing (supporting). **Jens Persson**: Funding acquisition (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Giorgia Ausilio**: Data curation (supporting); Writing – review and editing (equal). **Erik Versluijs**: Data curation (supporting); Writing – review and editing (supporting). **Ane Eriksen**: Funding acquisition (equal); Writing – review and editing (supporting). **Petter Wabakken**: Funding acquisition (equal); Writing – review and editing (supporting). **Malin Aronsson**: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Funding acquisition (equal); Methodology (equal); Project administration (supporting); Supervision (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.44j0zpcn1 (Wikenros et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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