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Animal Ecology

All you can eat: Artificial feeding sites affect large herbivores and their predator in a human-dominated landscape

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Abstract

The re-expansion of large mammals in European human-dominated landscapes poses new challenges for wildlife conservation and management practices. Supplementary feeding of ungulates is a widespread practice with several motivations, including hunting, yet the known effects on target and non-target species have yet to be disentangled. According to optimal foraging theory, such concentrated food sources may attract herbivores and carnivores in turn. As such, feeding sites may skew the spatial distribution of wildlife and alter intra-and interspecific interactions, including predator–prey dynamics. Here, we investigated the use of ungulate-specific feeding sites by target and non-target species in a human-dominated and touristic area of the Alps, using systematic camera trapping. We assessed potential temporal segregation between roe deer and red deer at feeding sites and whether these concentrated artificial food sources influenced the occurrence and site use intensity of ungulates and wolves at the broader scale. We found that feeding site frequentation by roe deer was influenced by the presence of red deer, with a higher crepuscular and diurnal activity and a longer time span between visits at feeding stations strongly used by red deer, indicating potential temporal niche partitioning between the two ungulates. We also found that ungulates occurred with a higher probability at shorter distances from feeding sites and used sites with high human outdoor activity less intensively than less disturbed ones. Wolves' site use intensity was higher closer to feeding sites, indicating a potential effect of supplemental feeding sites on both prey's and predators' space use. Our results reveal side effects of artificial feeding sites, thus contributing to a more informed and evidence-based management, with high relevance especially in light of the considerable recovery of large

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Marco Salvatori and Giulia Bombieri contributed equally to the work reported here.

mammals across anthropized regions of Europe and the popularity of artificial feeding of ungulates for hunting or recreational purposes. We thus advise limiting this practice in areas where large herbivores, predators, and humans closely coexist.

KEYWORDS
artificial feeding, *Canis lupus*, *Capreolus capreolus*, *Cervus elaphus*, human disturbance, intra-guild competition, *Ovis musimon*, predation, prey–predator interactions, supplementary feeding, ungulates, wolf, wildlife management

INTRODUCTION

The re-expansion of large mammals in European human-dominated landscapes is a conservation success story. Yet, it poses new challenges for wildlife management practices that have to adapt to unprecedented conditions (Chapron et al., 2014; Passoni et al., 2024). Supplementary feeding of wildlife is popular across Europe and is implemented for a range of reasons, including recreation (hunting, viewing/photography), management, conservation, and research (Dubois & Fraser, 2013; Garshelis et al., 2017). Supplemental food is usually placed at specific feeding sites, may consist of different types of resources (e.g., corn, grain, fruits, hay, and carrion) depending on the target species, and may be provided all year long or in specific seasons or limited periods depending on its purpose. Feeding of ungulates and other game species is often aimed at maximizing survival, maintaining high population densities, as well as improving body condition and trophy quality (Milner et al., 2014; Putman & Staines, 2004). Artificial feeding may also aim at redistributing or luring animals away from certain areas (i.e., diversionary feeding) where they could engage in conflicts with humans and their activities (Kubasiewicz et al., 2016), for example, to reduce road collisions (Andreassen et al., 2005) or damages to vegetation and human properties (Arnold et al., 2018; Ziegltrum, 2004). The practice has also been implemented to support conservation and recovery of threatened or reintroduced species (Kowalczyk et al., 2011; López-Bao et al., 2008; Moreno-Opo et al., 2015). With the rapid growth of wildlife tourism worldwide, supplemental feeding has also become a common strategy to ensure easy viewing opportunities (Orams, 2002; Penteriani et al., 2017).

However, the effectiveness of supplemental feeding to achieve the intended purposes has often been questioned, with the concurrent observation of several drawbacks (Arnold et al., 2018; Kavčič et al., 2013; Morehouse & Boyce, 2017). For example, feeding sites have been shown to cause significant alterations to the spatial distribution and home range behavior of ungulates and consequently to the natural dynamics of herbivory (Felton et al., 2017; Ranc et al., 2020). Other reported impacts include lower genetic quality due to weakened natural selection during winter months (Milner et al., 2014), deteriorated body conditions, and increased pathogen transmission (Becker et al., 2015; Sorensen et al., 2014). Artificial wildlife aggregations may also increase the opportunity for negative interactions and conflicts with humans and domestic animals (Jerina et al., 2012; Milner et al., 2014; Steyaert et al., 2014), especially when located close to human settlements, roads, or highly frequented areas.

Several studies have recorded the use of artificial feeding sites by multiple taxa, often up to 20 species in the same study area (Bowman et al., 2015; Candler et al., 2019; Fležar et al., 2019; Popova et al., 2017; Selva et al., 2014). These include a variety of non-target species, which can be directly or indirectly attracted or repelled by them (Belotti et al., 2014; Campbell et al., 2013; Lambert & Demarais, 2001; Pascual-Rico et al., 2018; Selva et al., 2017). Even backyard bird feeders may become unsuspected attractants for non-target species, from gray squirrels to white-tailed deer (Reed & Bonter, 2018), and even black bears, leading in extreme cases to serious conflicts with humans (Bombieri et al., 2018).

Such human-driven aggregations of different taxa inevitably amplify the impacts found for single species to the whole community, altering animal behavior with consequences on inter-and intraspecific interactions, including predation and competition. Foraging theory predicts that predators should choose predation strategies that maximize food intake while minimizing energetic costs (Charnov, 1976; MacArthur & Pianka, 1966). In contexts where prey is distributed in an aggregated manner, predators are expected to focus their search efforts in areas of high prey concentration (Valeix et al., 2010). Indeed, higher predation rates of ground nesting birds, including protected species, have been reported as a consequence of artificial feeding (Cortés-Avizanda et al., 2009; Oja et al., 2015; Selva et al., 2014). Large carnivores' behavior can also be affected by the occurrence of feeding sites. Artificial feeding has been found to affect brown bear movements (Penteriani et al., 2021), denning behavior (Krofel et al., 2017) and increase bear kleptoparasitism on Eurasian lynx (*Lynx lynx*; Krofel & Jerina, 2016), eventually impacting lynx predatory and movement behavior (Oliveira et al., 2023). Two studies have, to our knowledge, investigated the effect that artificial feeding can have on predator–prey interactions between large mammals. Woodruff et al. (2018) found that wolf kill rates increased closer to winter supplemental feed grounds for elk *Cervus elaphus*, whilst Belotti et al. (2014) observed no influence of fenced feeding enclosures used for red deer in winter on Eurasian lynx' spatial and predatory behavior. Whether ungulate feeding sites really attract large carnivores, potentially due to the spatial predictability and the high local density of prey, is therefore still unclear.

To date, few studies have investigated interspecific interactions among ungulates at feeding sites (Kavčić et al., 2021; Payne et al., 2017; Popova et al., 2017), mainly because in most study areas only one ungulate species was detected (but see Fležar et al., 2019). Available evidence suggests that roe deer *Capreolus capreolus* tend to temporally avoid both wild boars *Sus scrofa* and red deer at feeding stations (Popova et al., 2017). Among European ungulates, red deer has indeed been indicated as a dominant species when it coexists with smaller sized wild ungulates (Borkowski et al., 2021; Corlatti et al., 2019; Ferretti et al., 2015, 2018; Franchini et al., 2023; Gamelon et al., 2020). When feeding stations are located in areas where multiple ungulate species live in sympatry, intra-guild dynamics may be altered, affecting not only the spatial distribution of the species, but also potentially increasing occasions of inter-and intraspecific disease transmission, increasing stress levels in less dominant species, and eventually intensifying competition.

The practice of supplemental feeding is thus controversial, has the potential to alter important intra-and interspecific dynamics, and calls for scientific investigation to assess the effects of such practice, especially in light of the recent comeback of large predators in many areas of Europe (Cimatti et al., 2021), where this practice is widespread and often unregulated. We contributed to filling this gap by investigating the use of ungulate-specific feeding sites (i.e., supplied with hay only) by target and non-target species, especially focusing on ungulates and wolves and their potential interactions, in an area of the Eastern Italian Alps characterized by a high density of feeding sites, located within a matrix of forest roads, ski slopes, trails, settlements, roads, and tourist facilities. Three species of alpine ungulates (roe deer, red deer and alpine chamois *Rupicapra rupicapra*) coexist here with an introduced non-native species, the mouflon *Ovis musimon*, and with resident wolf packs. Insights on wildlife frequentation of feeding sites thus appear fundamental to assess direct and indirect effects on target and non-target species, and to inform policy regarding the management and regulation of this practice in areas where ungulates, large predators, and humans closely coexist.

Specifically, we addressed these issues by (1) identifying the target and non-target species visiting feeding stations and quantifying the intensity of use both in time and space; (2) focusing on interspecific dynamics among ungulates at the feeding sites, measuring potential temporal segregation between roe deer and red deer; and (3) assessing whether the presence of supplementary feeding stations influenced the space use of ungulates and wolves in the broader context of the whole study area. We predicted that feeding sites, though supplied with herbivore-specific food, would be used by a large number of non-target species (Prediction P1) and trigger temporal segregation of different ungulate species using feeding sites (Prediction P2). We also predicted that artificial feeding stations would attract ungulates, shaping their space use (Prediction P3) and creating a ripple effect that would draw wolves due to the high concentration of prey (Prediction P4).

METHODS

Study area

The study area was located in Val di Fassa, Trento province, Eastern Italian Alps (centered on 46° 26′ 48.3936″ N, 11° 41′ 51.054″ E). Human settlements and infrastructures are concentrated along the valley bottom, creating an urban continuum surrounded by open fields and pastures. Slopes are dominated by forest cover, mainly composed of spruce *Picea abies* until the tree line, at approximately 2000 m elevation. Shrubs with *Pinus mugo*, alpine grasslands, and rocky dolomitic massifs make up the high elevation environment. Fassa valley is a popular destination for winter sports and tourism (over 200,000 tourists between January and March 2023; https://statweb.provincia.tn.it/movturistico/data.asp?db=annuarioturismo&sp=spArrPresEsAlbXAmbProvMes&var=0&a=2023), with numerous ski facilities and infrastructures and a dense network of trails and forestry roads which are intensely used by outdoor recreationists year-round. After a century-long absence (Marucco et al., 2023), wolves have reoccupied the area in 2017, with two resident packs recorded in the valley in the study period. Supplemental feeding stations are located in forest environments or within small clearings and are supplied with hay by local hunters between November and April. The average density of supplemental feeding stations in the study area is 2.60 per 10 km^2. This management practice is currently mainly intended to improve winter survival of roe deer, though their efficacy in reaching this objective and the presence of possible side effects have never been scientifically tested.

Data collection

To test prediction P1 (use of feeding sites by non-target species) and P2 (competition between red and roe deer at the feeding sites) we used camera traps to monitor 14 supplementary feeding stations located throughout the study area during January–March 2022 (Step 1). Though these 14 stations represent only a subset of the 27 feeding stations active in the area, they were selected to be geographically and environmentally representative, covering the whole north–south gradient of the valley (Figure 1). Prediction P3 and P4 were instead tested by systematic camera trapping at 40 non-baited sampling sites, active during January–February 2023, located along forestry roads throughout the study area (Step 2), and aimed at measuring ungulates' and wolves' space use at different distances from the feeding stations.

For Step 1, we placed one camera trap (CT) per feeding site, set to take three consecutive photos when triggered, and to remain inactive for 5 min after each three-picture shot, to avoid SD card saturation and rapid battery depletion. Each camera was set to point directly toward the feeding station, from a distance of 5–8 m, and was positioned on trees at about 80–100 cm above the ground. This setup is ideal to detect medium and large species directly using the station, but likely under-detects small vertebrates such as rodents and passerines, and also large predators such as wolves, which are not directly attracted by the food provided but rather could be attracted by the concentration of ungulates and are thus

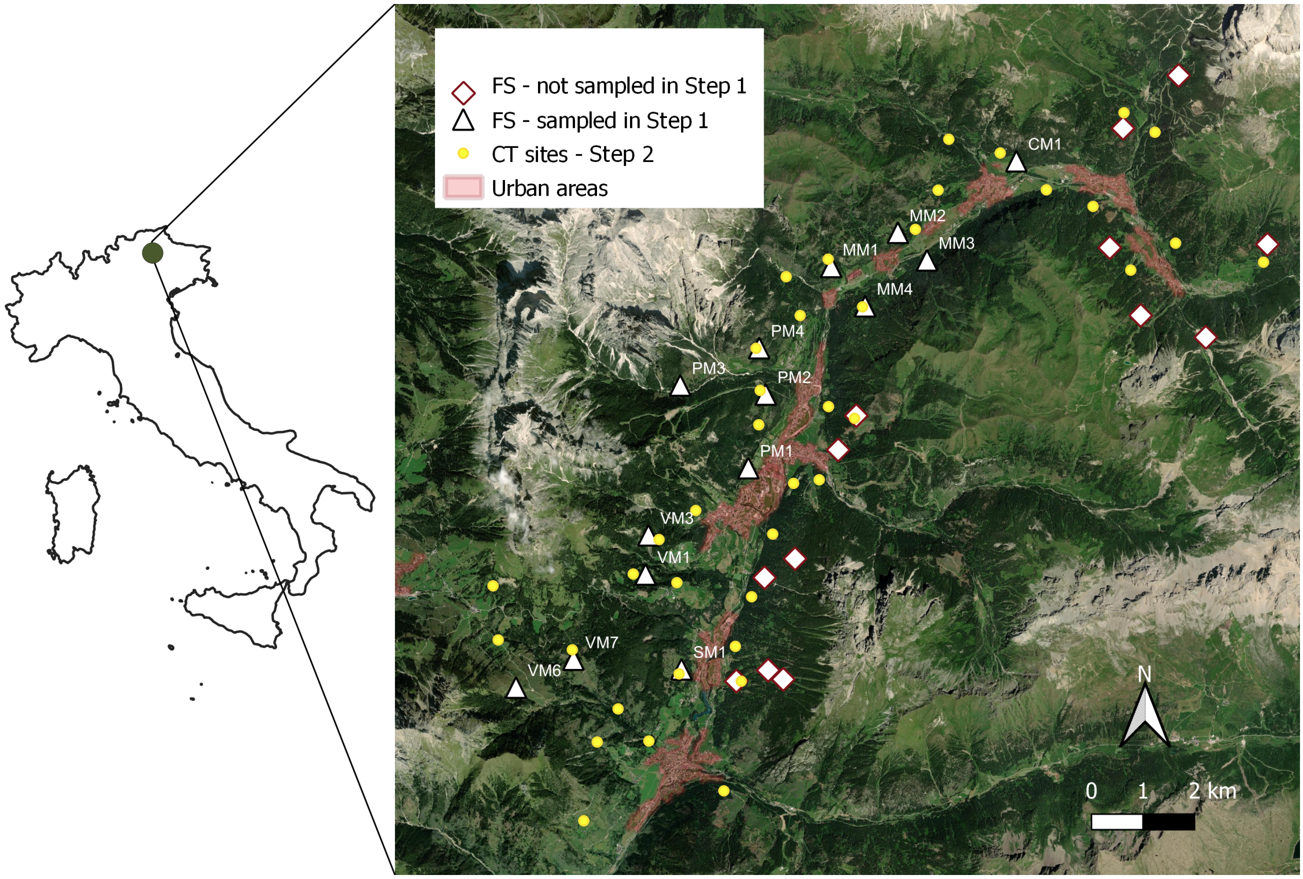

FIGURE 1 Map of the study area in Val di Fassa, Eastern Italian Alps. Active artificial feeding sites (FS) are indicated by white triangles if they were sampled during Step 1, by white diamonds otherwise. Yellow dots indicate camera trapping sampling sites of Step 2. Urban areas in the valley bottom have been highlighted in red following Corine Land Cover classification. Satellite map was obtained from ESRI Satellite (https://server.arcgisonline.com/ArcGIS/rest/services/World_Imagery/MapServer/tile/{z}/{y}/{x}). The panel on the left-hand side shows the location of the study area within Italy.

unlikely to get close enough to be detected by the camera traps (Popova et al., 2017). Each camera trap was checked, and SD cards and batteries were replaced each week from mid-January to mid-March 2022.

During Step 2, we laid over the study area a regular grid with 40 cells sized 1 × 1 km and positioned a sampling site along a forestry road within each cell. The position of the sampling sites was stratified following a gradient of distance to the closest feeding station, thus ensuring that the 40 sampling sites were located at different distances from feeding stations, creating a set of 40 random distances in the interval 0–3500 m through the *sf* package (Pebesma & Bivand, 2023) in the RStudio environment (Posit Team, 2025). CTs were positioned in the field as close as possible to the theoretical points, attached to trees at a height of approximately 60–80 cm, at 2–3 m from the target forestry road. CTs were set to take three pictures per trigger in continuous mode, were checked regularly to avoid battery depletion, and remained active for a median of 37 days (range 9–39) from mid-January to the end of February, with total sampling effort reaching 1336 camera days. No bait was used.

Statistical analyses

Step 1

Intensity of feeding site use by the detected species was measured as the number of detection events at each site and as the number of sites visited by each species, also accounting for group size. To estimate the temporal activity pattern of the wild ungulates that regularly used feeding sites, we first subsampled the detection data considering photographs that were taken less than 30 min apart as a single event, thereby ensuring independence between events (Rovero & Zimmermann, 2016). We then estimated temporal activity curves non-parametrically through kernel density estimation with the bandwidth set at one using the R package *activity* (Rowcliffe, 2016), both over all feeding sites and for each site separately (in this latter case a threshold of 20 minimum events was used to estimate the activity curve of each species). To assess if the temporal activity of the roe deer varied depending on the intensity of use of the potentially dominant red deer, we estimated its activity curve both at lower and higher red deer visitation rates, taking the across-site mean value of 52 red deer events as the threshold. We then tested whether the two roe deer curves differed, calculating the overlap index Δ_4 (Ridout & Linkie, 2009) and comparing it against a null distribution of overlap indices derived by randomly sampling with replacement from the combined data. To evaluate if this potential difference in roe deer activity patterns at low and high red deer intensity of use corresponded to different temporal overlap in activity of the two species, we also estimated the overlap index Δ_4 between the two cervids, again separating feeding sites with low and high red deer use, using the mean value as the threshold. We did not evaluate temporal interactions between mouflon and cervids since they rarely co-occurred at the same feeding sites (see Appendix S1: Figure S2). To further explore potential interspecific competition between the two cervid species, we applied time lag analysis (Parsons et al., 2016) to successive independent roe deer events (with 1-h temporal resolution) considering the presence or absence of red deer detections between them. In the hypothesis of interspecific competition and dominance of red deer over roe deer, the presence of red deer would delay the return of roe deer to the feeding site, increasing the time lag between consecutive roe deer detections. We therefore calculated time intervals between successive roe deer sequences without red deer in the middle and compared them against those that had a red deer event in between through a Wilcoxon sum ranked test. We discarded all intervals longer than 48 h in both categories as outliers to avoid that a few very long time lags exerted an excessive influence on the statistical comparison.

Step 2

To evaluate whether ungulates and wolves space use was influenced by the presence of active feeding sites, we used occupancy models, that is, hierarchical models that correct the probability of occurrence of a species at a site with information on its detection probability (MacKenzie et al., 2003). Occupancy models were originally meant to describe wildlife use of discontinuous habitat patches and, following Efford and Dawson (2012), we acknowledge that when applied to animal detections in continuous habitat, the closure assumption is violated, and that detection probability is strongly influenced by population density and movement parameters. We therefore interpret detection probability as the intensity of site use and occupancy as site use probability (see Nickel et al., 2020). To build our occupancy models, we considered a set of temporally dynamic variables that could potentially affect detection probability and a separate set of habitat variables that we hypothesized could influence stable site use, based on known ecological preferences of the target species. We included feeding sites-related variables both on detection and occupancy probability, since they might influence animals' space use both in terms of fine-scale movements within the home range and of large-scale spatial distribution. We tested the following set of covariates on detection probability, hypothesizing potential effects on behavior and consequently on the intensity of site use (see Appendix S1: Table S2): *effort*, sampling effort in terms of the number of days each camera remained active; *humans*, number of daily events of humans at each site to account for the potential effect of human disturbance; *predators*, number of daily events of wolves at each site to include the potential effect of fear of predation by ungulates; *prey*, number of daily events of ungulates at each site as predator detection probability is likely affected by the presence of prey. For the occurrence probability (site use probability), we selected a set of landscape covariates that could have potential effects on the stable spatial distribution of ungulates and wolves in the study area: *dist_town*, distance from the closest urban area; *slope*, terrain slope, extracted from COPERNICUS EU-DEM, a Digital Elevation Model raster layer with 25-m pixel resolution; *northing*, topographic orientation calculated as arcsine of the aspect (i.e., the orientation angle in relation to the north); *edge*, density of forest edges calculated with the COPERNICUS European forest cover layer Tree Cover Density (https://doi.org/10.2909/486f77da-d605-423e-93a9-680760ab6791) in R through the package *landscapemetrics* (Hesselbarth et al., 2019). We calculated forest density for each 1 × 1 km cell in which a camera was deployed, considering as forest habitat each pixel with more than 10% of tree cover density (following the FAO definition of forest; Food and Agriculture Organization, Global Forest Resources Assessment, 2020). We also calculated the distance to the closest feeding station (*dist_FS*) and the number of feeding stations within a 2-km circular buffer around each CT (*N_FS*), and we included them both on occupancy and detection probability sub-models. The choice of buffer width for *N_FS* was taken as a compromise between having a reasonable number of feeding stations included in the buffers and avoiding excessive overlap between adjacent buffers. A full list of hypothesized effects of covariates is provided in Appendix S1: Table S2. All variables included were not correlated according to the Spearman correlation test with $r < |0.5|$.

The detections of red deer, roe deer, mouflon, and chamois were merged because the number of sequences was too low to allow a separate occupancy model for each species, and given that we were interested in potential effects of feeding sites over the whole guild of large herbivores. We therefore merged into a single entity the detections of roe deer, red deer, mouflon, and chamois and calculated daily detection matrices for wolves and all ungulates combined to build occupancy models in R through the package *unmarked* (Kellner et al., 2023). Since testing all combinations of the selected covariates on both levels of the occupancy models would result in a too large number of models, we followed a stepwise model selection procedure: keeping occupancy probability constant, we added one variable at a time to the detection probability component and compared the Akaike informative criterion (AIC) value against the more parsimonious model without that variable. If the AIC value was lower than in the previous model, we included the variable in the model formulation and proceeded by adding a new variable. Once we obtained the best model structure in terms of AIC for the detection probability, we repeated the same procedure for occupancy. For the final model selection phase, if more than two models had ΔAIC values <2, we considered the most parsimonious one. Exploratory analysis showed that one sampling site had a value of human events 2 orders of magnitude higher than all other sites; we therefore excluded this site from the analysis to avoid spurious statistical patterns and likelihood convergence failure (Crawley, 2012).

RESULTS

Step 1

We recorded a total of 5541 animal photographic sequences at the feeding sites, detecting 11 wild species and 1 domestic species (domestic cat *Felis catus*), confirming prediction P1 (use of artificial feeding sites by non-target species). High variation was detected in the number of species across sites, which ranged from 1 to 8 species per site (mean 4.7; median 5; Appendix S1: Figures S1 and S2). Red deer was the species that used feeding sites most intensively ($n_{\text{seq}} = 2736$; 49% of all recorded sequences), followed by roe deer ($n_{\text{seq}} = 1494$; 27%), mouflon ($n_{\text{seq}} = 828$; 15%), and the other species recorded (Figure 2). The red fox *Vulpes vulpes* was the species visiting the highest number of sites (100%), followed by roe deer (79%), mouflon (64%), and red deer (57%; Figure 2).

Red deer was the species that exploited artificial feeding more intensively, but visited 8 feeding sites out of 14, while roe deer and mouflon visited 11 and 9, respectively. Alpine chamois, although present in the area, was never recorded at the sites. One site was never visited by any ungulate, three sites were visited by only one species, five sites were visited by two species, whereas five sites were visited by all three species (roe deer, red deer, mouflon).

Ungulate group size recorded differed among species and sites (Appendix S1: Table S1; Figure S3). Overall,

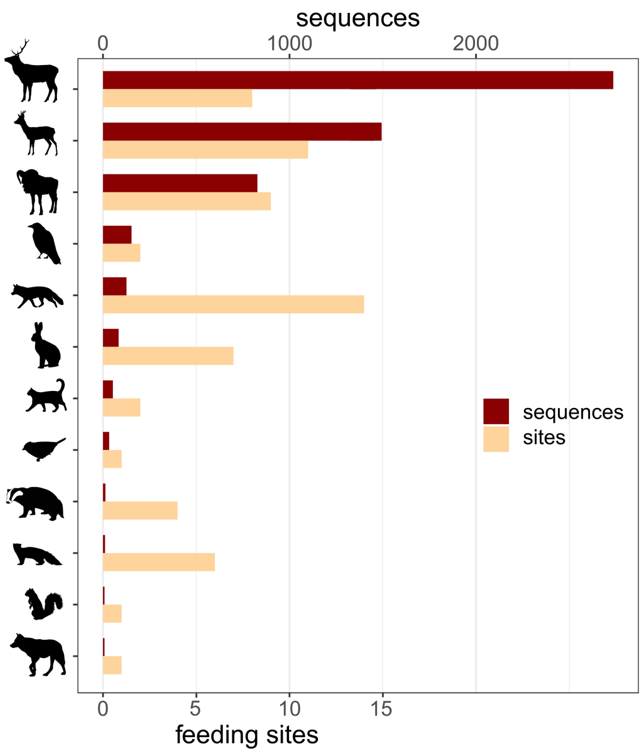

FIGURE 2 Barplot of number of photographic sequences (red, top *y* axis) and number of visited feeding sites (orange, bottom *y* axis) for each species detected during Step 1, indicated by their silhouettes. Species are listed from most to least detected in the following order: *Cervus elaphus, Capreolus capreolus, Ovis musimon, Corvus corone, Vulpes vulpes, Lepus* spp., *Felis catus, Fringilla coelebs, Meles meles, Martes foina, Sciurus vulgaris, Canis lupus.*

mouflon was the species with the largest group sizes ($\text{mean}_{\text{groupsize}} = 4.85$; median = 4; range = 1–24), whereas roe deer and red deer group size were similar (roe deer: $\text{mean}_{\text{groupsize}} = 1.33$, median = 1, range = 1–6; red deer: $\text{mean}_{\text{groupsize}} = 1.3$, median = 1, range = 1–4).

The temporal pattern of mouflon was markedly diurnal, with activity peaking around midmorning and rapidly declining after noon, while a pronouncedly nocturnal pattern was found for red deer, with an activity peak around midnight and the lowest values around noon. Roe deer showed an intermediate curve in comparison to the other two species, with the peak of activity occurring after midnight and a lower but constant activity during daylight hours (Appendix S1: Figure S1). Despite our sample of feeding sites being too limited to make any robust comparison among sites, we can still observe variation both in the number of species visiting the sites and in the patterns of daily use of the sites by ungulates. Whereas red deer seem more consistent in their nocturnal use of the sites, roe deer and mouflons show variations across sites, with some sites being used mainly at twilight/night hours, and other sites being used mainly during the day (Appendix S1: Figure S5).

By comparing the activity pattern of roe deer at lower and higher intensity of use by red deer, we found that the two roe deer curves were significantly different (observed overlap = 0.61, expected overlap = 0.91 ± 0.02 SE, $p < 0.001$). Roe deer were more diurnal and crepuscular where red deer visitation rate was higher, showing an activity peak at dusk that was absent at sites with low red deer presence (Figure 3A). Where red deer visitation rate was lower, roe deer activity pattern showed a nocturnal shape, maintaining however a low but non-null activity level even during the central hours of the day. The overlap coefficient between roe and red deer was halved in sites intensely used by red deer (overlap at high red deer use = 0.34, 0.29–0.40 95% CI) compared with sites where red deer were scarcely present (overlap at low red deer use = 0.69, 0.60–0.77 95% CI). Prediction P2 (avoidance of red deer by roe deer) was further corroborated by the time lag analysis: time lags between successive independent roe deer events without presence of red deer in between had a median duration of 3.18 h ($Q1 = 1.63$, $Q3 = 7.95$; Figure 3B), whereas those with red deer events in the middle had a median duration of 15.01 h ($Q1 = 9.42$, $Q3 = 22.24$). The two distributions were significantly different according to a Wilcoxon sum rank test ($W = 6158$, $p < 0.001$).

Step 2

During Step 2, we collected 8900 photographic sequences, of which 5148 depicted humans, 226 roe deer, 144 wolves, 121 red deer, 3 mouflons, and 1 chamois. Regarding domestic species, we also recorded 1051 sequences of dogs *Canis lupus familiaris* (always with humans) and 405 of equines (mostly with humans; 398 *Equus caballus* and 7 *Equus asinus*). The stepwise model selection procedure for ungulates led to two models within ΔAIC < 2. They both included effort and humans on the detection probability component and terrain slope and distance from the closest feeding site on the occupancy component, and differed only for the inclusion of northing on occupancy (Appendix S1: Table S3A). The first and the most parsimonious between these two models indicated that ungulates had a mean occupancy of 0.74, with a positive relation with terrain slope ($\beta_{\text{slope}} = 0.92 \pm 0.51$), and a negative one with distance from the closest feeding site ($\beta_{\text{dist\_FS}} = -1.64 \pm 0.59$). Their mean detection probability was 0.24, with negative relations with human daily events ($\alpha_{\text{humans}} = -0.07 \pm 0.03$) and sampling effort ($\alpha_{\text{effort}} = -0.16 \pm 0.09$; Table 1; Figure 4).

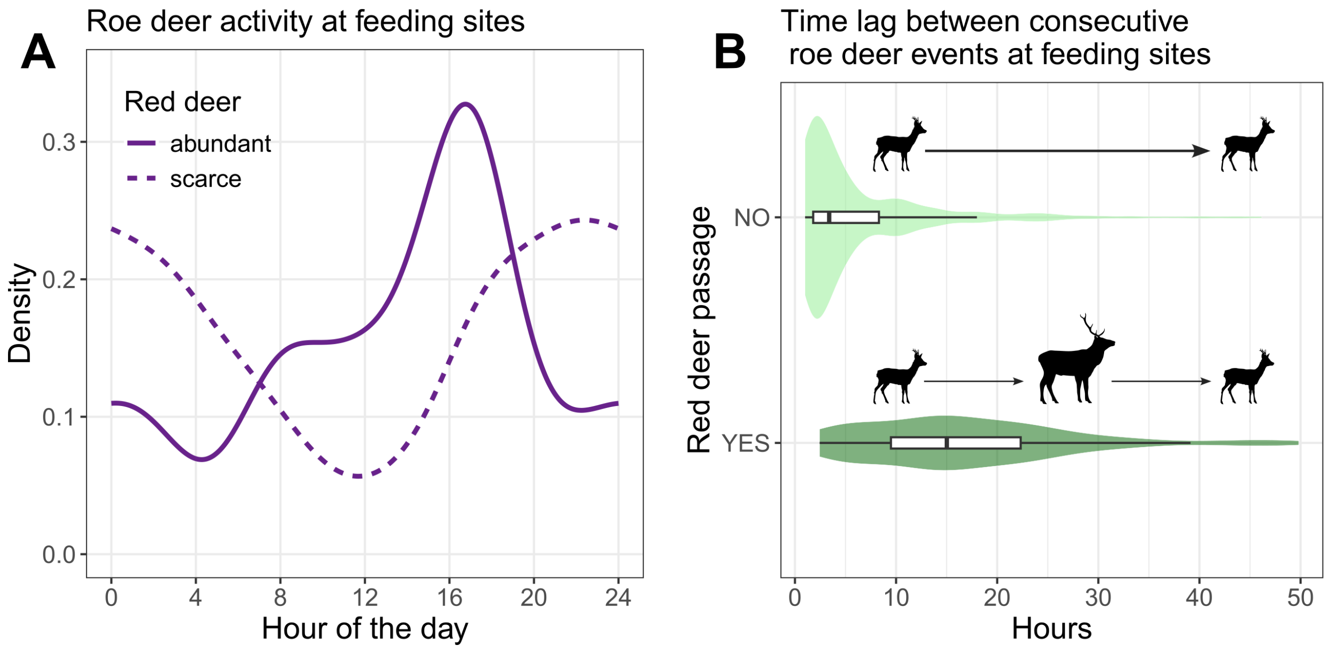

FIGURE 3 (A) Roe deer temporal activity curves at higher (solid line) and lower (dashed lines) red deer intensity of use of feeding sites. The two curves are different with $p < 0.001$. (B) Boxplots and violin plots for the time lags as hours between successive roe deer events with (light green) or without (dark green) a red deer detection in between.

TABLE 1 Best occupancy model for ungulates.

Parameter	Estimate	SE	*p*
Occupancy			
Intercept	1.35	0.49	<0.01
Slope	0.92	0.51	0.07
dist_FS	−1.64	0.59	<0.01
Detection probability			
Intercept	−0.98	0.09	<0.01
Humans	−0.07	0.03	0.01
Effort	−0.16	0.09	0.09

Abbreviation: dist_FS, distance to the closest feeding station; SE, standard error.

The best model for wolf (Table 2; Appendix S1: Table S3B) indicated that mean detection probability was 0.10, with a positive relationship with sampling effort ($\alpha_{\text{effort}} = 0.33 \pm 0.21$) and daily human events ($\alpha_{\text{humans}} = 0.05 \pm 0.03$), and a negative relationship with ungulates' daily events ($\alpha_{\text{ungulates}} = -0.45 \pm 0.29$) and distance from the closest feeding site ($\alpha_{\text{dist\_FS}} = -0.38 \pm 0.15$; Figure 4). Wolf occupancy was negatively related to the density of forest edges ($\beta_{\text{edge}} = -0.63 \pm 0.43$) and had a mean of 0.76.

Considering the most relevant covariates as those whose 95% CI did not overlap 0, ungulates' site use intensity seemed to be mostly influenced by the daily rate of human passage and their site use probability by the distance to the closest feeding site, both with negative regression coefficients, confirming prediction P3 (spatial attraction of ungulates towards feeding sites). Wolves' site use intensity had a markedly negative association with the distance from the closest feeding site, supporting prediction P4 (cascading attraction of feeding sites on wolves).

DISCUSSION

The recovery of large carnivores in European, human-dominated landscapes calls for evidence-based adaptations of current wildlife management practices to minimize human-carnivore conflicts and enhance the regulating top-down effect large predators can have on ecosystems (Marshall et al., 2016; van Beeck Calkoen et al., 2023). By sampling the wildlife community visiting artificial feeding sites and by assessing the space use of wolves and ungulates in a touristic valley of the Eastern Alps, we found that these concentrated, artificial food sources have the potential to alter both predator and prey behavior and space use, affect intra-guild diel use of resources, and influence a vast array of target and non-target species.

Investigating the space use drivers of ungulates at the study area scale, we found that they occurred with a higher probability at sites closer to artificial feeding stations and that their site use intensity was negatively

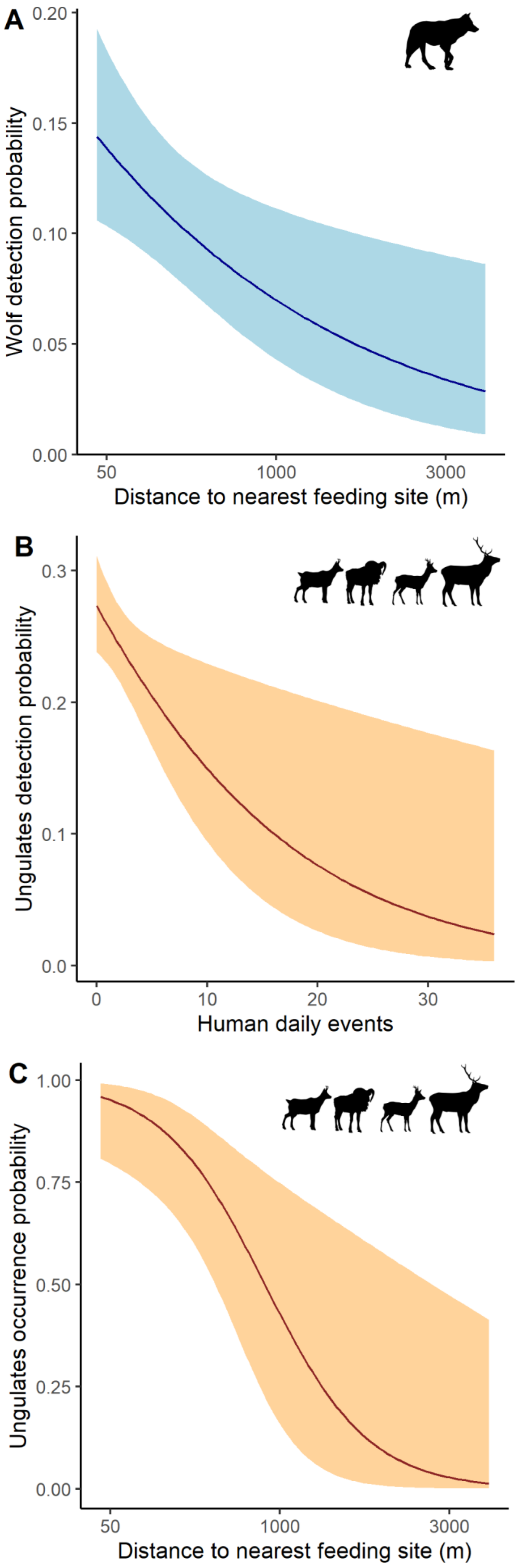

FIGURE 4 Plots of the prediction from the best models showing the covariates with 95% CI that did not overlap 0. (A) Wolf and (B) ungulate detection probability; (C) ungulate occurrence probability. Lines describe mean predictions and ribbons 95% confidence intervals (in light blue for wolf and light brown for ungulates). Species identities are indicated by their silhouettes.

TABLE 2 Best occupancy model for wolves.

Parameter	Estimate	SE	*p*
Occupancy			
Intercept	1.22	0.45	<0.01
Edge	−0.63	0.43	0.15
Detection probability			
Intercept	−23.73	0.17	<0.001
dist_FS	−0.38	0.15	<0.01
Ungulates	−0.45	0.29	0.13
Humans	0.05	0.03	0.07
Effort	0.33	0.21	0.16

Abbreviation: dist_FS, distance to the closest feeding station; SE, standard error.

related to the daily rate of human passage recorded by the camera trap. Large herbivores in our human-dominated study area thus tended to spatiotemporally avoid forestry roads highly frequented by humans and to spatially select areas closer to artificial feeding sites. The behavior of large herbivores is known to be influenced by the level of nonlethal human outdoor activities, with spatiotemporal avoidance of human presence often reported (Courbin et al., 2022; Salvatori et al., 2024; Visscher et al., 2023). Although in certain case studies large herbivores have been shown to benefit from the shielding potential of humans towards large predators (e.g., Shannon et al., 2014), in regions where they are subjected to hunting their avoidance towards humans can surpass that exhibited towards large carnivores (Ciuti et al., 2012; van Beeck Calkoen et al., 2022). Though our study took place in winter, after the closure of the autumn hunting season, the ungulates inhabiting our study area are regularly subject to hunting activities that can exacerbate avoidance behaviors even towards other, nonlethal, human activities such as outdoor recreation (Burton et al., 2024; Paton et al., 2017). The fact that ungulate site use probability increased closer to feeding sites matches experimental evidence indicating that concentrated artificial food sources can lead to major modifications of home range and individual movement rates in large herbivores (Ossi et al., 2017; Ranc et al., 2020). Our data also show that the cases where multiple individuals of the same species were observed using the feeding site simultaneously were not rare, confirming the potential for spatial aggregation of ungulates around feeding sites' areas (e.g., Ossi et al., 2020).

The attraction potential of feeding sites towards ungulates seemingly affected large predators in turn: wolves' site use intensity increased closer to them, indicating the potential positive effect of the predictable presence of ungulates around feeding stations in reducing wolf energy expenditure to locate prey. Optimal foraging theory predicts that predators should concentrate their activity in areas with the highest local abundance of prey, that is, prey hotspots (Roth & Lima, 2007). Especially when the resources exploited by the prey are patchy and fixed in space, as is the case with artificial feeding stations, both predators and prey distribution are expected to match resource locations (Sih, 2005). In our case, the higher occurrence probability of ungulates around feeding sites seems to directly translate into higher wolf detection probability, fitting theory expectations. We detected wolves at feeding sites only sporadically during Step 1 since, even when their presence signs were recorded in the sites' surroundings, they did not come close enough to the feeding stations to be detected by the camera traps, as also suggested by Popova et al. (2017). However, when we assessed drivers of wolf space use across the whole study area during Step 2, the distance to the closest feeding station emerged as the most relevant variable in explaining their detection probability. Previous research has shown that wolves tend to directly exploit prey-rich areas (Kittle et al., 2017) and that killing rate tends to be related to prey density (Messier, 1994). Woodruff et al. (2018) found that wolf killing sites were located with higher probability at shorter distances from the areas where ungulate supplemental food was provided. Though we did not measure predation events directly, the higher site use intensity of wolves closer to ungulate feeding sites we recorded suggests a potential facilitation effect for these predators that might exploit feeding stations as predation hotspots, leading to side effects of the artificial feeding practice that could spread along the food web through altered predator–prey interactions. Although interpretation of habitat and space use patterns from camera trap data requires caution (Ferrer-Ferrando et al., 2023), we believe our sampling design provides reliable insights in this regard. Further research, ideally involving GPS tracking of both wolves and their prey and/or experimental closure of artificial feeding sites, is needed to better test for wolf spatial selection of feeding sites as well as understand whether these sites translate into predation clusters. Telemetry data would also allow studying hunting strategies employed by wolves to decrease hunting predictability in such highly predictable predation hotspots and the antipredator behaviors ungulates employ, trading off the considerable nutritional reward and the high predation risk associated with feeding sites (Bassing et al., 2024).

Behavior of predators and preys with respect to feeding sites was not the sole ecological process potentially affected by supplementary feeding in our study area: the different activity patterns found for roe deer at feeding sites with different intensity of red deer use may indicate a form of time partitioning in the use of concentrated resources between the two species. Indeed, the temporal overlap of the activity patterns of the two species at sites intensely used by red deer was half that found at sites where red deer was only sporadically present. Our results evidence that roe deer tend to avoid red deer at artificial feeding sites, as had already been suggested by previous research: Popova et al. (2017) reported that roe deer activity peak during the visitation of feeding sites tended to be shifted so as not to coincide with red deer's; Kavčič et al. (2021) found results compatible with avoidance of red deer by chamois at artificial mineral stations; Ossi et al. (2020) anecdotally reported temporal niche segregation by roe and red deer at feeding sites; Ossi et al. (2017) showed that the presence of larger ungulates is one of the key variables decreasing the probability of feeding site use by roe deer at a continental scale. We hypothesize that in our study area roe deer need to cope with two opposite drivers when using feeding sites: the occurrence of red deer, highly concentrated during the night, and the exposure to human disturbance, strongly diurnal. We therefore propose that, at feeding sites where red deer was absent or rarely present, roe deer minimized human-related risk by shifting towards darkness hours, while at feeding sites intensely used by the bigger sized cervid the result of the two opposite drivers led to higher crepuscularity. Evidence shows that ungulates' reliance on feeding sites diminishes as vegetation green-up advances during spring (Ossi et al., 2020); however, intensified interspecific interaction during winter might have negative consequences on roe deer fitness (Ferretti et al., 2011, 2015). Such evidence is particularly relevant for our study area where supplemental feeding is intended to support roe deer rather than red deer, and this strategy could prove counterproductive in reaching its expected outcome. Our data also highlight the intense use of the sites by the mouflon, a non-native species that may particularly benefit from feeding sites given its scarce adaptation to harsh winters.

Though supplied with hay, the feeding sites we targeted were visited by a wide array of wild and domestic mammals and by two bird species, indicating that the attraction potential of feeding stations targeted for herbivores is not drastically dissimilar from those supplied with corn, fruits, or carrion. Indeed, the number of species we observed here is similar to that found by Fležar et al. (2019), who already reported similar visitation rates of feeding sites supplied with plant-based and mixed food items in Slovenia. The aggregation of numerous individuals of the same species and of several different species at feeding stations could lay the ground for increased intra-and interspecies pathogen transmission (Becker et al., 2015; Sorensen et al., 2014) and spread of altered predation dynamics (Cooper & Ginnett, 2000; Cortés-Avizanda et al., 2009; Oja et al., 2015; Selva et al., 2014). Indeed, even though the species that exploited feeding stations more intensely were three large herbivores, medium-sized carnivores and omnivores also visited the sites, possibly attracted by the concentration of prey, like rodents or small birds.

Legislation on supplemental feeding of wildlife is highly heterogeneous, differing across European countries and even regions of the same country, with a real legal vacuum and absence of regulation in some cases, despite mounting evidence suggesting that the drawbacks often outweigh the benefits and intended objectives in wildlife management (ISPRA, 2013; Kavčič et al., 2013; Milner et al., 2014). In our study area, feeding sites: (1) attracted both wild and domestic non-target species, (2) were used with specific, interactive patterns by roe deer and red deer, when both occurred, (3) were used by the mouflon, a non-native species whose population containment is recommended in the study area, (4) were a major driver of ungulate space use, and (5) increased the site use intensity of wolves, potentially altering their space use and predation patterns. Moreover, in a context where winter outdoor activities are widespread and feeding sites are often located close to hiking trails, ski slopes, and even paved roads and settlements, the potential to generate negative interactions between large mammals and humans or domestic animals (e.g., pathogen transmission, negative interactions between dogs and wildlife) needs to be carefully considered. Our results reveal side effects of artificial feeding sites that can spread at the ecosystem level and thus potential flaws in current management of this practice at the local scale, contributing to a more informed and evidence-based management. These findings are also highly relevant at the broader scale, especially in light of the considerable recovery of both ungulates and large predators across anthropized regions of Europe (Linnell et al., 2020), and the popularity of artificial feeding of ungulates for hunting or recreational purposes.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Salvatori & Bombieri, 2025) are openly available from Figshare: https://doi.org/10.6084/m9.figshare.29557670.v1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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