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Consistent specialization on roe deer across contrasting prey communities: diet and prey selection of Eurasian lynx in the Western Carpathians

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The Carpathian population of the Eurasian lynx (*Lynx lynx carpathicus*) represents one of the most important native source populations for lynx conservation and reinforcement in Central Europe, yet ecological drivers of prey selection remain poorly understood. We investigated diet composition, and factors influencing prey selection in the Western Carpathians using an integrated approach combining GPS telemetry and systematic kill-site inspections, snow tracking, scat analysis, camera trapping and microsatellite genotyping for individual lynx identification from scats. Based on 446 prey remains and 386 scat samples collected across several mountain regions, we found that the lynx diet was overwhelmingly dominated by wild ungulates, which accounted for 96.0% of prey remains and 96.3% of total consumed biomass. Roe deer (*Capreolus capreolus*) was the main prey species, representing 64.6% of prey remains and 69.0% of consumed biomass, followed by red deer (*Cervus elaphus*; 27.6% and 24.8%, respectively). Despite substantial variation in ungulate community composition and the availability of alternative prey, roe deer remained consistently positively selected across all study areas. In contrast, red deer consumption increased with its relative availability and was more frequent in males, particularly during winter, indicating context-dependent flexibility in prey use. Non-ungulate prey contributed only marginally to the diet, and we found little evidence that lynx age, social status or population density substantially influenced prey selection. Our results demonstrate that Carpathian lynx remain strongly specialized on roe deer while retaining capacity to exploit alternative ungulate prey under specific ecological conditions. These findings improve our understanding of predator–prey interactions in a key

European lynx population and provide an important scientific basis for conservation and management of lynx and its prey. Our integrated approach and findings also provide an ecological benchmark for anticipating predator–prey relationships as lynx recover across their former range through natural recolonization, reinforcement and reintroduction.

KEYWORDS

diet, GPS telemetry, *Lynx lynx*, prey selection, scat analyses, Western Carpathians

Introduction

Predation can fundamentally structure ecological communities by regulating prey populations and generating cascading effects across trophic levels, particularly where predator populations persist at ecologically functional densities. The strength of these effects therefore depends not only on predator presence, but also on predator abundance and the intensity of predator–prey interactions (Terborgh and Estes, 2013; Ripple et al., 2014). Predators do not hunt randomly: optimal foraging theory—grounded in considerations of prey availability, vulnerability, energy yield, risk, and habitat—predicts that predators prioritize prey that maximize energy gain while minimizing risk (MacArthur and Pianka, 1966; Stephens and Krebs, 1986). Empirical studies have confirmed that prey selection varies across ecological gradients (e.g. Ståhlberg et al., 2017), yet several carnivore diet studies remain descriptive, often ignoring intraspecific variation and ecological context.

Many large carnivores are considered dietary specialists despite inhabiting ecosystems containing diverse and abundant alternative prey (Molinari-Jobin et al., 2007). Optimal foraging theory predicts that predators should adjust prey use according to prey profitability and availability (Stephens and Krebs, 1986), yet empirical studies have repeatedly shown persistent prey preferences across contrasting ecological contexts (Odden et al., 2006; Nagl et al., 2022). Understanding how predators balance such specialization with the capacity for flexible prey use remains an important challenge in predator ecology.

Understanding the factors that shape predator–prey interactions is fundamental for explaining the ecological role of large carnivores within ecosystems. Predators can influence prey populations directly through predation and indirectly through behavioral responses, with consequences that may extend across trophic levels (Treves and Karanth, 2003; Terborgh and Estes, 2013; Ripple et al., 2014). Because prey selection determines the strength and distribution of these effects, understanding the mechanisms underlying predator foraging decisions is essential for predicting predator impacts on prey communities and ecosystem dynamics. Importantly, feeding ecology also has a strong human dimension, because perceptions of what large carnivores prey upon often shape attitudes towards their presence and management. Misconceptions about diet and predation impacts can therefore contribute to negative public attitudes and hinder conservation efforts, particularly in human-dominated landscapes where large carnivores are returning after historical declines (Chapron et al., 2014; Kaczensky et al., 2024a). A precise understanding of their feeding ecology is thus important not only for assessing their ecological role, but also for informing evidence-based management and improving public acceptance. The Eurasian lynx (*Lynx lynx*) is widely regarded as a specialized predator of roe deer (*Capreolus capreolus*) across much of its European range (e.g. Breitenmoser and Haller, 1993; Nowicki, 1997; Molinari-Jobin et al., 2007; Krofel et al., 2011). However, the importance of alternative prey such as red deer (*Cervus elaphus*), chamois (*Rupicapra rupicapra*), lagomorphs or livestock varies substantially among regions (Nowicki, 1997; Breitenmoser and Haller, 1993; Belotti et al., 2015; Khorozyan and Heurich, 2023; Buzan et al., 2024). This variation suggests that prey selection reflects a balance between specialization on preferred prey and flexibility in the use of locally available alternatives, making the Eurasian lynx (hereafter lynx) a useful model for investigating the ecological drivers of prey selection.

Although the diet and predation ecology of lynx have been widely studied across Europe (e.g. Jędrzejewski et al., 1993; Nowicki, 1997; Odden et al., 2006; Molinari-Jobin et al., 2007; Krofel et al., 2011; Belotti et al., 2015; Melovski et al., 2022; Khorozyan and Heurich, 2023), Carpathians, one of the most important native strongholds of lynx in Europe, remain comparatively underrepresented. Despite its major conservation significance, quantitative evidence on diet composition, prey selection, and feeding behavior from this region is remarkably limited (e.g. Okarma, 1984; Hell et al., 2004; Duľa et al., 2023). Consequently, it remains unclear whether Carpathian lynx (*Lynx lynx carpathicus)* exhibit the same degree of roe deer specialization reported elsewhere in Europe or whether they respond more flexibly to the region's diverse ungulate communities. Addressing this gap is important for both ecological theory and applied conservation. Carpathian lynx represent one of the principal source populations for ongoing reinforcement and translocation programs across Central and Western Europe (Bonn Lynx expert Group, 2021; Krofel et al., 2025), making a detailed understanding of their feeding ecology particularly relevant. Quantifying prey preferences and trophic flexibility can improve our understanding of predator–prey dynamics while also informing conservation planning, population management, and long-term viability of both source and restored populations.

We expected the diet of lynx to be dominated by wild ungulates, with roe deer representing the primary prey species throughout the study area. Given the strong specialization on roe deer reported across much of the species European range (Nowicki, 1997; Odden et al., 2006; Molinari-Jobin et al., 2007; Krofel et al., 2011; Belotti et al., 2015; Khorozyan and Heurich, 2023), we hypothesized roe deer would remain positively selected even in areas where alternative ungulate prey were abundant (Nowicki, 1997; Belotti et al., 2015; Duľa and Krofel, 2020). At the same time, we expected prey use to vary according to local prey communities. Specifically, we

predicted that the contribution of red deer to the lynx diet would increase with its local availability, reflecting context-dependent flexibility in prey use (Nagl et al., 2022). Because larger-bodied prey may be more accessible to individuals with greater hunting capacity, we further expected red deer to occur more frequently in the diet of adult lynx, particularly males, and during periods of increased prey vulnerability. Finally, we explored whether local lynx density and individual characteristics influenced prey selection and whether evidence of individual variation in prey use could be detected (Gossow and Honsig-Erlenburg, 1985; Okarma et al., 1997; Belotti et al., 2015).

To test these hypotheses, we combined GPS telemetry, systematic kill-site investigation, scat analysis, camera trapping and microsatellite genotyping. By integrating complementary methods that differ in their strengths and detection biases, this approach provides a comprehensive assessment of lynx diet composition and prey selection. Our study therefore offers new insights into how a specialized large carnivore balances persistent prey preferences with ecological flexibility within one of its most important strongholds in Europe.

Materials and methods

Study area

The study was conducted across several mountain ranges at the western edge of the Carpathian lynx distribution (Figure 1), spanning an edge-core gradient of lynx densities ranging from 0.26 to 1.85 lynx/100 km^2 (Duľa et al., 2021). The study region exhibits significant altitudinal variation, with elevations ranging from 350 to 1709 m.a.s.l., contributing to a cold mountain climate characterized by persistent snow cover from mid-November to late March or April (Tolasz et al., 2007; Bochníček and Hrušková, 2015). The entire study area is predominantly forested. In the peripheral regions of the Beskydy and Javorníky Mountains, forests are dominated by the Norway spruce (*Picea abies*), while natural forests are primarily confined to protected nature reserves. In contrast, the Strážov Mts., are predominantly covered by European beech (*Fagus sylvatica*) forests. Human land use, including forestry, hunting, tourism and agriculture, has created a heterogeneous landscape with varying levels of habitat fragmentation and anthropogenic influence (Kubala et al., 2020; Duľa et al., 2021).

Within the core lynx distribution area, comprising the Kysucká vrchovina, Kysucké Beskydy, Oravská Magura, Malá Fatra, and Strážov Mountains, the permanent occurrence and long-term reproduction of Eurasian lynx, grey wolf (*Canis lupus*), and brown bear (*Ursus arctos*) have been consistently documented. By contrast, in the Javorníky Mountains, which represent an intermediate part of the distribution range, and in the Beskydy Mountains, situated near its periphery, confirmed reproduction has been reported primarily for lynx and wolves (Kutal et al., 2017; Kubala et al., 2020; Duľa et al., 2021, 2023; authors' unpublished data; Figure 1).The study area hosts a diverse and abundant ungulate community, including roe deer, red deer, fallow deer (*Dama dama*), mouflon (*Ovis gmelini*), and wild boar (*Sus scrofa*). Additionally, a variety of medium-sized (e.g., brown hare) and small mammals (e.g., rodents or insectivores) serve as potential prey for lynx

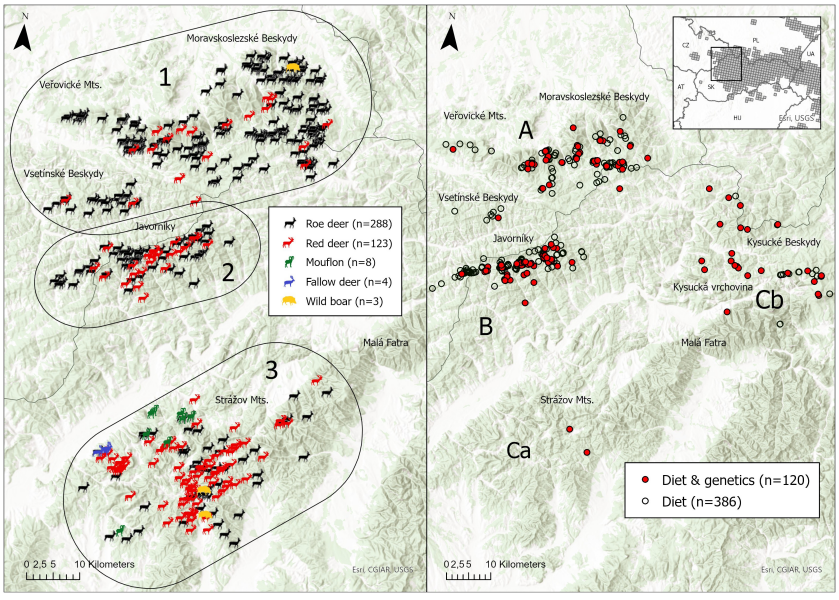


FIGURE 1
Study area, sampling sites, and spatial distribution of lynx ungulate prey remains recorded between 1/2011–11/2021 (left) and scat samples collected during 2/2010–2/2021 (right). Numbers 1–3 and the corresponding polygons denote the three study areas: (1) the Beskydy Mts., (2) the Javorníky Mts., and (3) the Strážov Mts. Within these areas, intensive prey searches and assessments of prey availability were conducted to quantify prey selection using Jacobs' selectivity index D (Jacobs, 1974). The letters A, B, C represent lynx density gradient, with A corresponding to the edge (0.26 –1.08 lynx/100 km^2), B to the middle (0.59–1.19 lynx/100 km^2), C (Ca, Cb) to the core (0.97–1.85 lynx/100 km^2) according to density estimates in Duľa et al. (2021) and Kubala et al. (2020). The inset, using EEA squares (10 × 10 km), shows the lynx distribution according to Kaczensky et al. (2024b). The green-shaded background layer represents suitable lynx habitat according to Duľa et al. (2021). The image was created in ArcGis Pro (ESRI, 2025).

throughout the region as indicated by hunters' inventories, harvest reports, and author's unpublished data. Together with differences in lynx population density and large carnivore occurrence, this variation provided an opportunity to evaluate prey selection and dietary flexibility across contrasting ecological conditions.

Prey remain detection and scat collection

Lynx prey remains were systematically detected through GPS telemetry monitoring of eleven lynx individuals (12/2018–11/2021) and opportunistically as well as by chance following lynx tracks on snow cover (2/2010–2/2021) across three study areas: Javorníky Mts., Beskydy Mts. (including Moravskoslezské Beskydy, Vsetínské Beskydy, Veřovické Mts) and Strážov Mts. (including part of Lučánská Malá Fatra; Figure 1). A total of nine males and two females were equipped with GPS GSM/Iridium collars (Lotek Small WildCell/Litetrack Iridium 250, Lotek Wireless, Newmarket, Ontario, Canada; Vertex lite, Vectronic Aerospace, Berlin, Germany; Tellus Iridium, Followit AB Sweden; Supplementary Table 1; Supplementary Data Sheet 1). Permits for animal capture and handling were obtained from the PLA Beskydy Administration, the Ministry of Environment of the Czech Republic (permit numbers: SR/0031/BE/2019; MZP/2020/630/167) and the Ministry of Environment of the Slovak Republic (permit number: 7402/2013-2.2366/2016-2.3; 6933/2019-9.2 [7/19-rozkl.]). Potential kill sites were identified through the clustering service mode provided by Inventa Wildlife monitoring system (Vectronic Aerospace), Followit GEO monitoring system (Followit AB) and GPS Web Service (Lotek Wireless) or by conducting location cluster analysis of telemetry data (Krofel et al., 2013) using ArcGis software (ESRI, Redlands, CA, USA). These clusters were systematically surveyed in the field to locate prey remains, with inspections taking place between 3/2019 and 11/2019 in the Javorníky Mts, 4/2020 and 10/2021 in the Beskydy Mts, and 12/2018 and 9/2021 in the Strážov Mts. At each identified kill site, data on the sex (male, female) and age category (juvenile, individuals < 1 year old and adult) of prey were recorded (Duľa and Krofel, 2020; Duľa et al., 2023). Where feasible, camera traps were deployed at the kill site to document lynx visits to the prey remains, capturing images or videos to assist in lynx identification.

To document also small and medium-sized prey in the lynx diet, as well as to facilitate genetic analyses for lynx individual and sex identification, scat samples were collected across various mountain regions from January 2009 to April 2021 (Figure 1; Supplementary Data Sheet 1). Scat detection was carried out through snow tracking of lynx during the winter months and by walking along forest roads, trails, rocky ridges, or known "lynx latrines" primarily located at marking sites during the warmer season (Sidorovich, 2006). A total of 446 prey remains, and 386 scat samples were collected for subsequent analyses. Due to variations in sample condition and age, 134 scat samples were utilized exclusively for dietary analyses and 120 for dietary analyses and microsatellite genotyping of lynx individuals (Figure 1; Supplementary Data Sheet 1).

Analyses of diet composition

Scats were processed and analyzed using standardized protocols, including washing through a 0.5 mesh sieve, oven drying at 60–70 °C, and weighing as described by Krofel et al. (2011). Prey identification was conducted through macroscopic examination of bones, hooves, hind-hooves, claws, feathers and microscopic analysis of hairs using determination keys (De Marinis and Asprea, 2006; Teerink, 1991; Tóth, 2017), and by comparing with reference hair samples collected from various ungulate species, covering different body parts, age classes, and seasons. When multiple food items were identified within a single scat sample, each item was weighed separately, or its proportion was estimated visually. Diet composition was quantified using frequency of occurrence (*%FO*), relative frequency of occurrence (*%RFO*), and percentage of total consumed biomass (*%TCB)* following the methods outlined by Krofel et al. (2011) and Melovski et al. (2022). Because frequency-based metrics and biomass estimates capture different aspects of diet composition, all three measures are reported. Total consumed biomass (%TCB) was considered particularly informative for evaluating the energetic contribution of prey categories, whereas %FO and %RFO facilitate comparison with previous studies of Eurasian lynx diet. Biomass estimates for dietary components were derived by multiplying dry matter weight by digestibility coefficients (Table 1; Supplementary Data Sheet 1) according to Rühe et al. (2008). Plant material was excluded from TCB calculations (Krofel et al., 2011).

Variations in feeding patterns

We examined whether the occurrence of the main species (roe deer, red deer, brown hare) and prey demographic characteristics (sex and age class) varied according to lynx sex, age class and social status. We used binomial generalized linear mixed models (GLMMs) with a logit link, treating the detection of each species as a binary response variable (1 = detected, 0 = not detected; Supplementary Data Sheet 2). For analyses of prey sex and age, the response was similarly binary, with male/juvenile prey coded as 1 and female or adult prey coded as 0. Lynx sex, age class, and social status were included as fixed effects, while individual lynx identity was included as a random intercept to account for repeated samples from the same individual. Model terms were evaluated using likelihood ratio tests comparing the full model with reduced models excluding each predictor. All models converged successfully without singularity, showed no evidence of overdispersion, and collinearity among predictors was low. Random effects for individual lynx captured inter-individual variability, increasing the reliability of the estimated effects and indicating that the detected patterns were not driven by differences among individual lynx.

We further examined inter-individual variation in prey use among male lynx by evaluating differences in the relative frequency of red deer occurrence in individual diets. Analyses were restricted to individuals with at least ten prey observations to ensure robust estimates of individual prey-use patterns (Supplementary Data

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TABLE 1 Diet composition of lynx in the Western Carpathians, based on scat analyses (n=386) expressed as frequency of occurrence (*%FO*), relative frequency of occurrence (*%RFO*), and percentage of total consumed biomass (*%TCB*).

Prey item	*%FO*	*%RFO*	*%TCB*	*TCB (g)*	*CF*
Undetermined cervids	32.38	28.94	30.97	48880.66	81
Roe deer *Capreolus capreolus*	46.89	41.9	47.64	75199.19	81
Red deer *Cervus elaphus*	13.21	11.81	17.14	27058.05	81
Wild boar *Sus scrofa*	2.07	1.85	0.59	930.69	81
Wild ungulates total	**94.56**	**84.49**	**96.34**	**152068.59**	**81**
Brown hare *Lepus europaeus*	4.67	4.17	2.66	4193.94	48
Not determined medium mammal	0.26	0.23	0.07	104.64	48
Medium mammals total	**4.92**	**4.4**	**2.72**	**4298.58**	**48**
European water vole *Arvicola amphibius*	0.26	0.23	≤ 0.05	23.52	24
Bank vole *Clethrionomys glareolus*	0.26	0.23	≤ 0.05	59.76	24
Least weasel *Mustela nivalis*	0.26	0.23	≤ 0.05	11.28	24
Edible dormouse *Glis glis*	0.52	0.46	0.19	295.44	24
Mice *Apodemus* sp.	1.3	1.16	0.14	221.76	24
Shrew *Sorex* sp.	0.52	0.46	≤ 0.05	54.42	24
Weasel *Mustela* sp.	0.26	0.23	≤ 0.05	1.92	24
Vole *Microtus* sp.	1.3	1.16	0.18	288.24	24
Undetermined small mammal	1.3	1.16	0.29	458.16	24
Small mammals total	**5.96**	**5.32**	**0.90**	**1414.5**	**24**
Domestic goat *Capra hircus*	0.26	0.23	≤ 0.05	65.61	81
Plant material	6.22	5.56	–	–	–
Others total	**6.48**	**5.79**	**≤ 0.05**	**65.61**	**Variable**
Total scats	**386**				

Biomass estimates were calculated following correction factors (*CF*) determined by Rühe et al. (2008). Plant material was excluded from TCB calculations.
Bold text and values indicate the main prey categories.

Sheet 2). Permutation-based tests were used to evaluate whether the observed among-male variation exceeded random expectation. In each permutation, red deer labels were randomly redistributed among prey records while preserving both the total number of red deer records and the number of prey records per male. This generated a null distribution in which red deer occurrence was independent of male identity. First, a global permutation test was applied using the standard deviation of individual red deer RFO values as the test statistic. This tested whether males differed in red deer use more than expected by chance. Second, a robust max-statistic permutation test was used to identify whether the most extreme observed male was more extreme than expected under random prey assignment. In this test, the maximum positive deviation from the mean RFO of all other males was recalculated in each permutation. This procedure accounts for the *post hoc* selection of the most extreme individual and provides a conservative test of individual specialization. Finally, individual-level max-corrected p-values were calculated by comparing each male's observed deviation from the mean of all other males against the permutation distribution of the maximum deviation. Males were classified as robust potential red deer specialists only if their deviation was positive and remained significant after max-statistic correction. All analyses were performed in R (R Core Team, 2025).

Calculation of prey availability

The species composition and relative abundance of the ungulate community in each study area (Beskydy Mts., Javorníky Mts., Strážov Mts; Figure 1) were estimated based on hunters' inventories and harvest reports. Data were sourced from the National Forest Centre official databases (Strážov Mts, Slovak part of Beskydy and Javorníky Mts) and from seven local administrative bodies in the Czech part of the Beskydy and Javorníky Mts (PLA Beskydy). Only data from hunting grounds within the area where prey remains and scats were collected were considered. To minimize errors from potential underestimation of ungulate populations, the reverse calculation method developed by Plhal and Kamler (2012) was employed, utilizing the expected reproduction rate (RR) for each species and the anticipated sex ratio of the population. The following RR values were applied for roe deer, red deer, wild boar, mouflon and fallow deer: 0.80, 0.75, 3.20, 0.85 and 0.85 respectively (values extracted from the Regulation of Czech Ministry of Agriculture; No. 491/2002 Coll. about the creation of hunting plans). These values were selected from the lower end of the available range for each species, accounting for reduced productivity in mountain forests according to Kutal et al. (2016). Finally, we calculated the relative abundance (percentage) and density (ind./

km^2) of selected ungulate species (roe deer, red deer, fallow deer, mouflon, wild boar) for each study site and time period separately and use these values to characterize prey availability across the study areas (Supplementary Data Sheet 2, 3).

Individual identification and assignment of demographic characteristics

To assess the diet composition and prey selection at the individual level, telemetry data were supplemented with microsatellite genotyping of collected scats following Krojerová-Prokešová et al. (2019) and Gajdárová et al. (2021). Individual identity and demographic characteristics (sex, age class and social status) were determined using a combination of genetic analyses, telemetry monitoring and photographic identification from camera-trap records obtained at marking sites or snow tracking (n=10) and kill sites (n=46; Figure 2; Supplementary Data Sheet 1). Lynx age class was classified into two categories: adult (A), defined as an individual older than two years, and subadult (S), defined as an independent individual in its second year of life with a known life history, including known maternal identity and year of birth (Duľa et al., 2021). Social status was classified into two categories: solitary individuals, comprising all independent adult or subadult lynx older than one year, and family groups, comprising adult females accompanied by kittens (Duľa et al., 2021). Assignments were cross-validated using a long-term photographic database generated through multi-seasonal systematic camera-trapping (Krojerová-Prokešová et al., 2019; Kubala et al., 2020; Duľa et al., 2021; author's unpublished data).

Assessment of prey selection and analysis of influencing factors

Prey selection analyses were based on identified ungulates from prey remains and scats and estimates of prey availability. Preferences for individual ungulate species relative to their availability in the prey community were quantified using Jacobs' selectivity index D (Jacobs, 1974) for each area sites (Beskydy Mts., Javorníky Mts., Strážov Mts.). The formula for calculating the selectivity index is as follows: $D= (r-p)/(r + p-2rp)$, where r represents the proportion of a specific prey species in the total number of ungulates killed by lynx, and p represents the proportion of that species in the ungulate community. D values range from -1 (indicating complete avoidance of the species) to 1 (indicating maximum positive selection of the species). The selectivity index was calculated for three lynx categories: 1) all individuals (males, females/family groups, unknown), 2) males, 3) females (including family groups; Supplementary Data Sheet 3).

To identify the potential factors associated with the variation in prey selection between roe and red deer, we modelled prey identity as a binary response variable (red deer = 1; roe deer = 0). Because mouflon, fallow deer, and wild boar were infrequently represented among identified prey remains, subsequent analyses were restricted to the two dominant ungulate species. An information-theoretic approach was used to evaluate prey availability, prey density, lynx density and lynx demographic characteristics on prey selection. We developed 31 competing models, incorporating combinations of continuous covariates (e.g. prey availability/density and lynx density) and categorical predictors (e.g., lynx sex, lynx social status, and season; Supplementary Table 2; Supplementary Data Sheet 2). Models were ranked using the Akaike's Information Criterion (AIC), with models differing by less than two AIC units (ΔAIC < 2.0) considered to have similar empirical support. Generalized Additive Mixed Effect Models (GAMMs) with binomial error distribution and logit link function (GAMM-b) were used because non-linear relationships were anticipated (Baudrot et al., 2016). Given that red deer densities had only six unique values, the number of knots was limited to five. Individual lynx identity was included as random effects in all models. To evaluate prey selection, we examined whether confidence intervals of fitted relationships overlapped the theoretical line representing equal selection of roe deer and red deer (Baudrot et al., 2016). GAMMs and GLMMs were fitted using the 'gam' function from the R package 'mgcv' (Wood, 2017), which allows the inclusion of simple random effects (Pekar and Brabec, 2019). Model diagnostics indicated no effect of overdispersion (φ = 1.0.). Statistical inference was based on

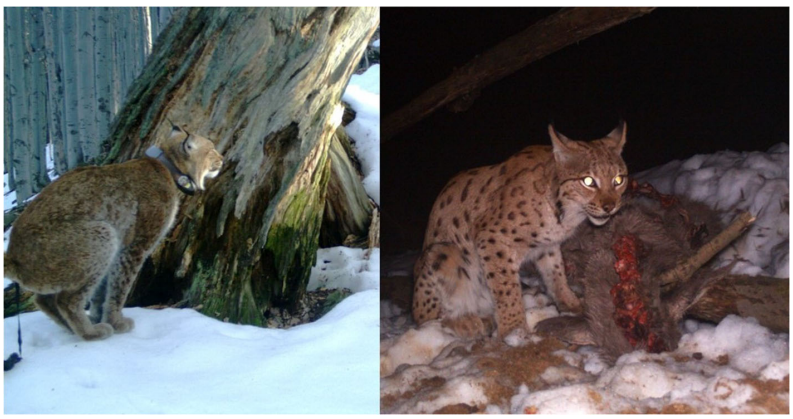


FIGURE 2
Adult resident male lynx "František", defecating at marking site in Moravskoslezské Beskydy Mts (left) and adult resident male "Olda" feeding on a red deer carcass in the Javorníky Mts (right).

estimated effect sizes, associated uncertainty and test statistics, with $\alpha = 0.05$ used as a conventional reference threshold. All analyses were performed in R (R Core Team, 2022).

Results

Diet composition

In total, 22 distinct prey items were identified from 446 prey remains and 386 scats (Tables 1, 2; Supplementary Data Sheet 1). Roe deer was the most frequent prey species, accounting for 64.6% (n = 288) of all identified prey remains followed by red deer 27.6%; n=123), and mouflon (2.2%; n=10). All remaining prey species individually contributed less than 2% of recorded prey items (Table 2; Supplementary Table 1).

Marked geographic variation in prey composition was observed among study areas. Roe deer dominated the diet in Beskydy Mts. (83.3% of prey remains) and Javorníky Mts. (67,9%), whereas red deer was the main prey species in the Strážov Mts., accounting for 55.9% identified prey remains compared with 33.6% roe deer. Mouflon and fallow deer contributed locally to the diet in the Strážov Mts., while wild boar and other prey species occurred only rarely across all study areas (Table 2; Supplementary Table 1).

Analysis of lynx scats revealed a dietary pattern similar to that observed from prey remains. Wild ungulates accounted for 96.3% of total consumed biomass (TCB), whereas medium-sized mammals and small mammals contributed only 2.7% *and* 0.9% of TCB, respectively. Among identified ungulate prey (n=261), roe deer represented the largest proportion of consumed biomass, followed by red deer (24.8%). Brown hare was the most important non-ungulate prey species but contributed only 2.7% of total consumed biomass. All other prey items, including rodents, insectivores, and small mustelids, occurred only rarely and collectively contributed negligibly to the overall diet (Table 1).

A total of 392 prey remains (87.9%) and 142 scats (36.8%) were assigned to 61 individual lynx (40 males and 21 females) enabling subsequent analyses of variation in prey use among demographic groups (Supplementary Data Sheet 1). Wild ungulates dominated individual diets, accounting for 96.5% of frequency of occurrence (FO), whereas medium-sized mammals and small mammals were considerably less common, representing 2.4% and 1.3% of FO, respectively.

Predation patterns were generally consistent across lynx demographic categories (Figure 3). Among red deer prey, lynx males consumed red deer more frequently than females (23.3% vs. 6.6%; OR ≈ 4.3; GLMMs, $\chi^2 = 4.28$, $p = 0.0385$). In contrast, the occurrence of roe deer and brown hare did not differ significantly according to lynx sex, age class or social status. (Figure 3). Lynx primarily preyed upon adult (68.4%) and female (74.3%) ungulates (Supplementary Table 1). No significant differences in prey age-class or sex composition were detected among lynx categories, except for juvenile prey consumption. Adult lynx exhibited higher probability of consuming juvenile ungulates than subadults (36.6% vs. 19.5%; GLMMs, $\chi^2 = 4.61$, $p = 0.0318$). Social status was also retained as a significant predictor of juvenile prey occurrence (GLMMs, $\chi^2 = 5.10$, $p = 0.024$), but this is likely influenced by the small sample size in the family-group category (n = 5).

Male lynx showed substantial inter-individual variation in the relative frequency of occurrence (RFO) of red deer. Individual Red deer RFO ranged from 0.060 to 0.793 (n=10; Figure 4A). The global permutation test showed that among-male variation in red deer RFO was far greater than expected under random assignment of red deer records. The observed standard deviation of individual RFO values was 0.280, whereas permuted values were substantially lower. This difference was highly significant ($p = 0.0001$), demonstrating pronounced individual heterogeneity in red deer use among male lynx (Supplementary Figure 1). The robust max-statistic permutation test confirmed that the strongest observed individual deviation was unlikely to arise by chance. The observed maximum difference between the most extreme male and the mean RFO of all other

TABLE 2 Prey remains identified from lynx, across three study areas in the Western Carpathians: Beskydy Mts. (including Moravskoslezské Beskydy, Veřovické Mts. and Vsetínské Beskydy), Javorníky Mts. and Strážov Mts. (including part of Lučanská Malá Fatra).

	Beskydy Mts.		Javorníky Mts.		Strážov Mts.		Total	
Prey species	Count	%	Count	%	Count	%	Count	%
Roe deer (*Capreolus capreolus*)	185	83,3	55	67,9	48	33,6	**288**	**64,6**
Red deer (*Cervus elaphus*)	20	9,0	23	28,4	80	55,9	**123**	**27,6**
Mouflon (*Ovis gmelini)*	1	0,5	0	0,0	9	6,3	**10**	**2,2**
Brown hare (*Lepus europaeus*)	6	2,7	2	2,5	0	0,0	**8**	**1,8**
Domestic pigeon (*Columba livia f. domestica*)	4	1,8	1	1,2	0	0,0	**5**	**1,1**
Fallow deer (*Dama dama*)	0	0,0	0	0,0	4	2,8	**4**	**0,9**
Red fox (*Vulpes vulpes*)	3	1,4	0	0,0	0	0,0	**3**	**0,7**
Wild boar (*Sus scrofa*)	1	0,5	0	0,0	2	1,4	**3**	**0,7**
Domestic chicken (*Gallus gallus domesticus*)	1	0,5	0	0,0	0	0,0	**1**	**0,2**
The common blackbird (*Turdus merula*)	1	0,5	0	0,0	0	0,0	**1**	**0,2**

Data were obtained from eleven GPS monitored lynx through inspections of kill sites (12/2018–11/2021) and opportunistic snow-tracking surveys (2/2010–2/2021).
Bold values indicate the total number of records for each prey species.

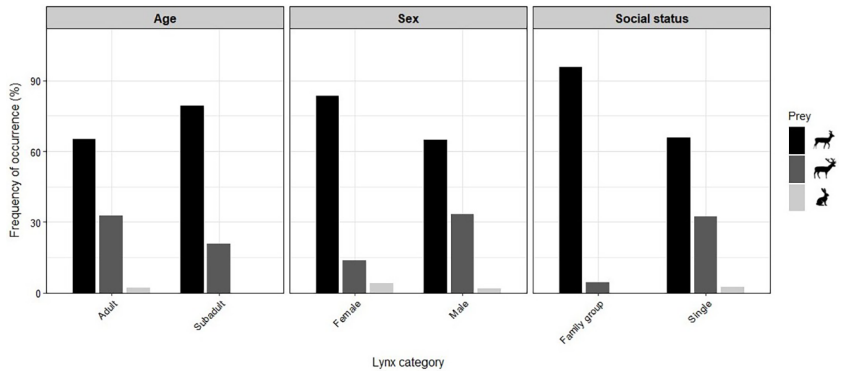


FIGURE 3
Frequency of occurrence (FO%) roe deer, red deer, brown hare in the diet of lynx according to lynx age class, sex and social status.

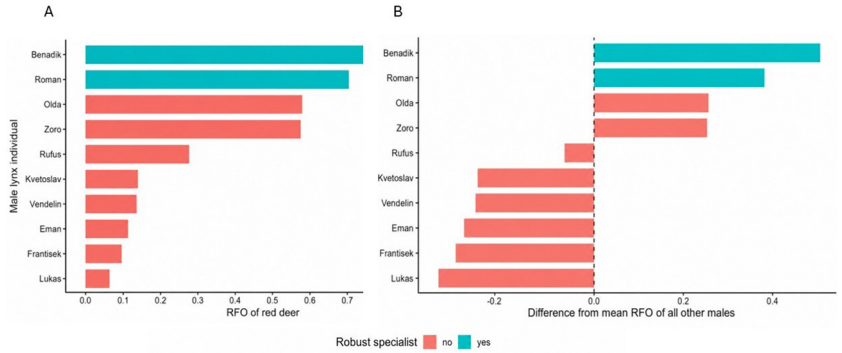


FIGURE 4
Bars in panel **(A)** show the proportion (RFO) of red deer records among all prey records assigned to each male. Bars in panel **(B)** show the difference between each male's red deer RFO and the mean red deer RFO of all other males. Positive values indicate higher-than-average red deer occurrence, whereas negative values indicate lower-than-average occurrence. Colors indicate whether an individual was classified as a robust potential red deer specialist after max-statistic correction.

males was 0.503, and this remained significant after max-statistic correction (p = 0.0012). Thus, even after accounting for the *post hoc* selection of the most extreme individual, the data supported the presence of unusually high red deer use in a subset of males (Supplementary Figure 2). Individual-level max-corrected tests identified two males as robust potential red deer specialists. The first male Benadik, showed the strongest positive deviation from the remaining males (difference = 0.503, p = 0.0012; Figure 4B), followed by Roman (difference = 0.383, p = 0.0084; Figure 4B). Although male Olda and Zoro also showed elevated red deer RFO, their deviations were not significant after max-statistic correction (p = 0.0841 and p = 0.0895, respectively; Figure 4B). These individuals should therefore be interpreted as males with high red deer occurrence, but not as statistically robust specialists.

Prey selection and effect of influencing factors

Jacob's selectivity index indicated consistent positive selection of roe deer across all study areas (D_{overall}=0.46–0.78), despite its relatively low representation within ungulate communities (3.71–14.67%; Supplementary Table 3). In contrast, red deer exhibited positive selection in the Javorníky and Strážov Mts. (D_{overall}=0.28 and 0.25, respectively) but was negatively selected in Beskydy Mts. (D_{overall}=-0.35). Mouflon was strongly selected where available (Strážov Mts.; $D_{overall}$ = 0.73), wild boar was consistently avoided across study areas (Figure 5; Supplementary Table 3). Patterns of prey selection were generally similar between sexes. Both male and female lynx exhibited strong positive selection for roe deer, across all study areas (D_{males}=0.46–0.75; D_{females}=0.46–0.83). However, positive selection for red deer was observed only in males in the Javorníky and Strážov Mts. (D = 0.40 and 0.27, respectively), while both sexes showed negative selection for red deer in Beskydy Mts. (D = -0.32; Figure 5; Supplementary Table 3).

Although Jacobs' selectivity index indicated persistent positive selection of roe deer across study areas, GAMM analyses identified factors associated with increased red deer use relative to roe deer. The best-performing model included red deer relative availability, lynx sex and season (Supplementary Table 2; R^{2adj} = 0.26). The probability of red deer occurrence in diet increased with red deer relative availability (GAMM-b; χ^2 = 40.2, P < 0.001; Figure 6A). Male lynx exhibited a higher probability of consuming red deer than females (GAMM-b; χ^{22} = 13.4, P = 0.001; Figure 6A). In addition, prey selection varied among seasons (GAMM-b; χ^{23} = 12.8, P = 0.005; Figure 6B), with the lowest probability of red deer use occurring during summer and the highest during the winter.

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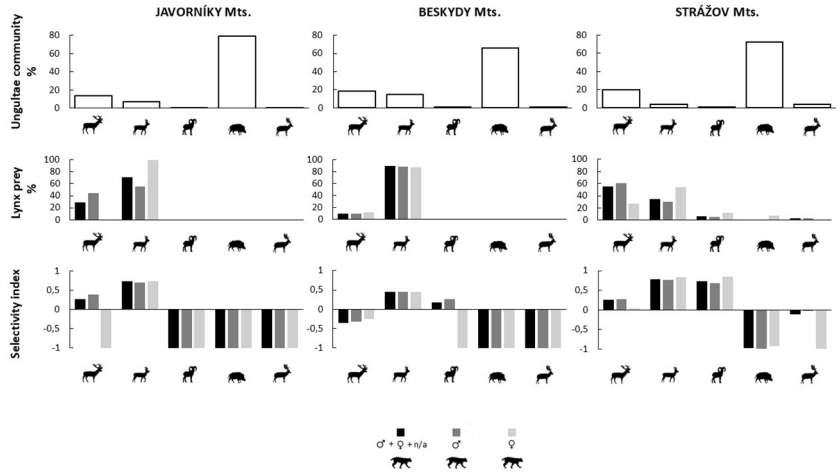


FIGURE 5
Relative composition of the ungulate communities (prey availability), lynx prey composition, and Jacobs' selectivity index *D* (Jacobs, 1974) in three study areas. Selectivity estimates were derived from prey remains identified through GPS (telemetry) based kill-site investigations and snow tracking surveys. Results are shown for all lynx combined, males, and females (including family groups).

Although the probability of red deer occurrence increased with its relative availability, roe deer remained the predominant prey across most of the observed availability gradient, particularly among females (Figure 6A). This effect was substantially stronger in males than in females. Female lynx continued to consume predominantly roe deer, even where red deer represented the dominant ungulate species in the prey community (Figure 6A).

Discussion

Using a comprehensive, multi-method dataset from three study areas of the Western Carpathians, we evaluated diet composition and the ecological factors shaping prey selection in the native Carpathian population of Eurasian lynx. Our results revealed a strongly ungulate-based diet, with wild ungulates accounting for 96% of both identified prey remains and consumed biomass. Despite marked spatial variation in ungulate community composition, roe deer remained consistently positively selected across all study areas, whereas the use of red deer increased with its relative availability and varied with predator sex and season. In contrast, non-ungulate prey contributed only marginally to the diet, and we found little evidence that lynx age, social status or population density substantially influenced prey selection. Overall, these findings support the general pattern reported from many European lynx populations, where roe deer represents the principal prey, while also demonstrating considerable context-dependent flexibility in the use of alternative ungulates where these are locally abundant. A central finding of our study is that roe deer remained positively selected across all study areas despite representing only a small proportion of local ungulate communities. Although roe deer constituted a smaller proportion of the diet than reported from several other European populations, it remained the most frequently consumed and consistently selected prey species. The lower dietary contribution of roe deer likely reflects the greater diversity and availability of alternative ungulate prey in the Western Carpathians. Nevertheless, despite the presence of abundant

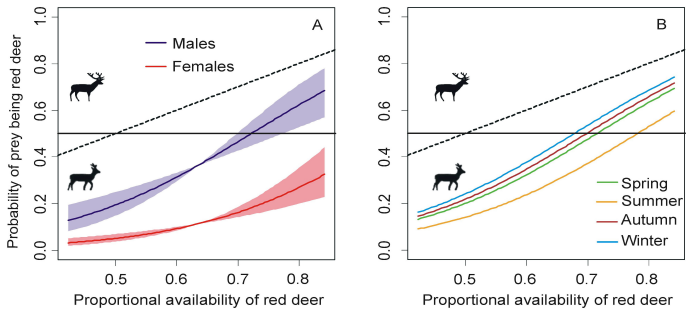


FIGURE 6
Predicted probability that a prey item was red deer rather than roe deer as a function of the relative availability of red deer in the ungulate community, stratified by lynx sex **(A)** and season **(B)**. Values above 0.5 indicate a predominance of red deer in the diet, whereas values below 0.5 a predominance of roe deer. Colored lines represent fitted GAMM predictions and shaded area denote 95% confidence intervals (CI). The horizontal solid line indicates equal representation of both prey species in the diet (0.5), while the dashed line represents the expected relationship under no prey preference. The relationships in panel A are the mean predation of males and females. The relationships in panel B are the estimates for the winter season when the predicted probability of red deer occurrence was highest.

alternative prey, roe deer consistently exhibited the highest selectivity values, indicating that increased prey diversity promotes dietary flexibility without eliminating the underlying preference for roe deer. Similar preferences have been from other European populations and are generally attributed to the body size, behavior and vulnerability of roe deer, which closely match the hunting strategy and energetic requirements of lynx (Jędrzejewski et al., 1993; Jobin et al., 2000; Krofel et al., 2011; Mysłajek et al., 2021; Odden et al., 2006).

Red deer was the second most important prey species overall and constituted a substantial component of the lynx diet in areas where it occurred at high densities. While roe deer dominated the diet in Beskydy Mts.and Javorníky Mts., red deer became the most frequently consumed prey species in the Strážov Mts., reflecting marked regional differences in prey availability. Similar patterns have been reported from other European regions supporting sympatric populations of roe and red deer, including Bialowieza Forest (Jędrzejewski et al., 1993; Okarma et al., 1997) and the Bohemian Forest (Červený and Bufka, 1996; Belotti et al., 2015). In addition, mouflon and fallow deer contributed locally to the diet in the Strážov Mts., indicating that lynx can readily exploit alternative ungulate prey when available. Comparable patterns have been reported from regions supporting mouflon populations, such as the Moravian Karst and the Šumava region (Červený and Bufka, 1996; Duľa and Krofel, 2020). Importantly, increased use of alternative prey did not eliminate the underlying preference for roe deer. Despite substantial regional variation in prey composition and the local dominance of red deer in some areas, roe deer remained consistently selected across all study sites. Together with the GAMM results, these findings suggested that lynx exhibit considerable trophic flexibility in response to local prey availability while retaining a persistent preference for roe deer. In contrast, wild boar and livestock contributed negligibly to the diet throughout the study areas. Although both prey types may become locally important in some European populations However, in other regions, such Bialowieza National Park or Balkan region, lynx have been observed to hunt wild boar more frequently (Jędrzejewski et al., 1993; Melovski et al., 2022). Furthermore, although livestock, particularly sheep, constitutes a relatively important food component for lynx in Scandinavia during the vegetation season (Sunde et al., 2000; Odden et al., 2002, 2006; Gervasi et al., 2014), their low occurrence in our study indicates that abundant wild ungulate largely satisfy the energetic requirements of the lynx in the Western Carpathians.

The majority of identified ungulate prey were adult individuals and females, a pattern consistent with observations from other European populations, including Dinaric Mts (Krofel et al., 2011), Bialowieza Forest (Jędrzejewski et al., 1993), Swiss Jura Mountains (Molinari-Jobin et al., 2002) and central, and southeastern Norway (Andersen et al., 2007). Similar patterns have often been attributed to differences in vulnerability among prey demographic groups, as adult females and juveniles may be more susceptible to predation under certain ecological conditions (Andersen et al., 2007; Krofel et al., 2011; Mattison et al., 2014). Although differences among lynx demographic categories were generally weak, adult lynx showed a higher frequency of juvenile ungulates in their diet than subadult individuals. This contrasts with results from southern Norway, where the opposite pattern was observed (Mejlgaard et al., 2013). In the present study, however, this finding should be treated with caution, as it may be driven by the relatively small number of subadult individuals in the dataset rather than by a biologically consistent age-related difference in prey use within the study area. Previous studies have shown that lynx prey selection can vary seasonally, with increased predation on juveniles during the birthing season and shifts in ungulate prey composition associated with seasonal changes in prey behavior and vulnerability (Molinari-Jobin et al., 2004; Breitenmoser et al., 2010; Mattison et al., 2014). Together, these findings suggest that prey demographic characteristics may contribute to variation in prey use, although the underlying mechanisms require further investigation.

Although lynx primarily specialize on ungulate preys, a broad range of alternative prey items, including lagomorphs, rodents and birds, has been reported throughout its European range (Jobin et al., 2000; Krofel et al., 2011; Molinari-Jobin et al., 2007; Odden et al., 2006; Okarma et al., 1997; Valdmann et al., 2005; Sidorovich, 2006; Vogt et al., 2018; Khorozyan and Heurich, 2023). In our study, non-ungulate prey contributed only a minor proportion of the diet, accounting for 4% of prey remains and 3.7% of consumed biomass. Brown hare was the most frequently recorded alternative prey species, but its contribution remained low and was comparable to values reported from the Slovak Carpathians (2.5% of consumed biomass, Hell et al., 2004), Dinaric Mts. (2% of consumed biomass, Krofel et al., 2011) and Swiss Jura (2% of prey remains found, Jobin et al., 2000). Absence of tetraonids from the diet was unexpected given their occurrence in previous studies from Slovakia but likely reflects their low densities or local absence in the study areas compared with core mountain habitats where these species remain more common (Hell et al., 2004; Mikoláš et al., 2018a, b). Overall, the limited importance of alternative prey further emphasizes the strong dependence of lynx on wild ungulates in the Western Carpathians.

The composition lynx diet varies considerably across environmental gradient (Jędrzejewski et al., 1993; Nowicki, 1997; Khorozyan and Heurich, 2023) and is influenced by multiple interacting factors, including the availability and density of ungulate prey, the abundance of alternative prey species, predator demographic characteristics and seasonal conditions (Jędrzejewski et al., 1993; Pulliainen et al., 1995; Molinari-Jobin et al., 2007; Krofel et al., 2011; Odden et al., 2006; Melovski et al., 2020; Khorozyan and Heurich, 2023). In regions where ungulate prey is scarce, lynx may reduce kill rates and rely more heavily on alternative prey resources (e.g., in Mavrovo National Park, Macedonia, Melovski et al., 2020). In contrast, the Western Carpathians support exceptionally abundant populations of both roe and red deer, creating conditions in which lynx can maintain a highly ungulate-based diet and sustain some of the highest ungulate kill rates in Europe (Duľa et al., 2023; Oliveira et al., 2025). Our results suggest that under such conditions, variation in prey use is driven primarily by differences in ungulate community composition rather than shifts toward alternative prey.

Our results provide evidence of context-dependent trophic flexibility of lynx. Although roe deer remained consistently selected across all study areas, the use of red deer increased with its relative availability and in Strážov Mts., constituted a larger proportion of the diet than roe deer. Similar shifts towards alternative ungulate prey have been documented in other European populations,

including Alpine lynx populations where chamois become an important dietary component (Breitenmoser and Haller, 1993; Jobin et al., 2000; Molinari-Jobin et al., 2007; Vogt et al., 2018; Nagl et al., 2022). Importantly, increased use of red deer did not eliminate the underlying preference for roe deer, which remained positively selected even where its relative abundance was low. This pattern suggests that lynx adjust prey use according to local prey availability while retaining a persistent preference for roe deer. In contrast to our prediction, we found no evidence that variation in lynx population density influenced the probability of red deer versus roe deer occurrence in the diet. These results therefore do not support a major role of intraspecific competition in shaping prey selection within our study system. However, density-dependent dietary shifts have been reported elsewhere, most probably in Alpine lynx populations where increased use of chamois has been linked to elevated lynx densities (Nagl et al., 2022). The role of intraspecific competition in shaping lynx prey selection may therefore be context dependent and warrants further investigation.

Previous studies have reported variation in lynx diet according to sex, age and social status, in several European populations (e.g., Molinari-Jobin et al., 2007; Okarma et al., 1997; Krofel et al., 2011), although such differences appear less pronounced in Scandinavia and Karelia (Pulliainen et al., 1995; Sunde and Kvam, 1997; Odden et al., 2006). Consistent with these studies we detected relatively limited demographic variation on prey use. Roe deer consumption remained remarkably stable across lynx categories, whereas significant differences were detected primarily in red deer use. Male lynx exhibited a higher probability of consuming red deer than females, suggesting that predator sex may influence the use of larger alternative prey species. Although male lynx showed pronounced inter-individual variation in red deer use, with statistical analyses indicating apparent individual specialization and earlier anecdotal observations pointing in the same direction (Gossow and Honsig-Erlenburg, 1985), this pattern should be interpreted cautiously. Two males identified as potential red deer specialists occurred in the Strážov Mts., where red deer availability was highest among all study areas. This spatial coincidence strongly suggests that the observed differences may be driven primarily by local prey availability and associated encounter opportunities rather than by intrinsic specialization of individual lynx. In addition, red deer use varied seasonally, with the highest probability of occurrence in the diet during winter. Similar sex specific and seasonal patterns have been reported from Bohemian Forest, Białowieża Forest and in Southern Norway (Okarma et al., 1997; Belotti et al., 2013, 2014; Gervasi et al., 2014). A plausible explanation is that winter conditions increase the vulnerability of red deer through reduced mobility and poorer physical condition, thereby improving hunting opportunities for lynx (Gossow and Honsig-Erlenburg, 1985; Nilsen et al., 2009). More generally, seasonal changes in weather conditions and prey vulnerability are known to influence predator–prey interactions in a wide range of large carnivore systems (Huggard, 1993).

Recent studies have demonstrated that molecular approaches, particularly DNA metabarcoding, can improve the detection of rare or low-frequency dietary components that may remain undetected using conventional scat analyses (McInnes et al. 2017; Massey et al., 2021; Buzan et al., 2024). Consequently, some minor prey items may have been underestimated in our study. However, conventional methods provide information on consumed biomass and facilitate direct comparison with the extensive body of previous research on lynx feeding ecology. Future studies would benefit from integrating molecular and conventional approaches to improve both taxonomic resolution and quantitative assessment of diet. In addition, prey availability was estimated from hunting statistics and reverse-calculation procedures rather than direct population surveys. These estimates should therefore be interpreted as standardized indices of relative prey availability and may not fully capture local variation in ungulate abundance. Also, sex-specific comparisons should be interpreted with caution because the number of GPS-collared females and female-assigned prey records was lower than for males. Although the analyses incorporated a broader dataset combining multiple sampling approaches, this imbalance may have reduced statistical power to detect sex-related differences.

Although only 31% of scats were deemed suitable for the combined analyses (dietary and genetic) and 65.2% of the samples (36.8% scats and 87.9% prey remains) could be assigned to individual lynx, the integration of telemetry, prey-remains analyses, scat analyses, camera trapping and genetic identification provided a robust framework for investigating individual-level variation in prey use. By combining multiple complementary methods with different strengths and limitations, our study offers one of the most comprehensive assessments of Eurasian lynx feeding ecology currently available from the Carpathian region.

Data availability statement

The original contributions presented in the study are included in the article and its Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

The animal study was approved by Permits for animal capture and handling were obtained from the PLA Beskydy Administration, the Ministry of Environment of the Czech Republic (permit numbers: SR/0031/BE/2019; MZP/2020/630/167) and the Ministry of Environment of the Slovak Republic (permit number: 7402/2013-2.2366/2016-2.3; 6933/2019-9.2 [7/19-rozkl.]). The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

MD'A: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Validation, Visualization, Writing – original draft, Writing – review & editing. RM: Formal analysis, Investigation, Writing – review & editing, Methodology, Visualization. JK: Data curation, Funding acquisition, Investigation, Project administration,

Resources, Validation, Writing – review & editing. JK-P: Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Validation, Writing – review & editing. BG: Data curation, Formal analysis, Investigation, Validation, Writing – review & editing. MB: Data curation, Investigation, Validation, Writing – review & editing. JB: Data curation, Funding acquisition, Investigation, Resources, Validation, Writing – review & editing. MH: Data curation, Formal analysis, Investigation, Validation, Writing – review & editing. JL: Data curation, Investigation, Validation, Writing – review & editing. BM: Data curation, Investigation, Validation, Writing – review & editing. MS: Data curation, Funding acquisition, Project administration, Resources, Validation, Writing – review & editing. BT: Data curation, Investigation, Resources, Validation, Writing – review & editing. MK: Data curation, Funding acquisition, Investigation, Project administration, Resources, Supervision, Validation, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2026.1951546/full#supplementary-material

SUPPLEMENTARY DATA SHEET 1
Raw dataset of scats and prey remains.

SUPPLEMENTARY DATA SHEET 2
Raw dataset used for GAMM, GLMM and Permutation test analyses.

SUPPLEMENTARY DATA SHEET 3
Prey availability and selectivity index calculation.

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