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Research article

# Wolf diet in the Notecka Forest, western Poland

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We assessed the diet composition of wolves inhabiting Notecka Forest (ca 1400 km$^2$) in western Poland based on the analysis of scats (n = 261) collected in 2008–2021. The study revealed that wolves in this large forest tract, consisting mainly of pine monocultures, consumed primarily wild ungulates (95.2% of consumed biomass). The roe deer was the essential food item (47.8%), followed by the red deer *Cervus elaphus* (25.1%) and the wild boar *Sus scrofa*) (18.4%). Wolves supplemented their diet with medium-sized wild mammals, mainly the European hare *Lepus europaeus* (2.8%) and the Eurasian beaver *Castor fiber* (1.9%). The food niche was narrow (*B* = 1.1), and there was no difference in food composition between the spring–summer and autumn–winter seasons. We emphasize the significance of the smallest European wild ruminant, roe deer, in the diet of wolves inhabiting Central European Plains.

Keywords: *Canis lupus*, *Capreolus capreolus*, *Cervus elaphus*, diet composition, *Sus scrofa*, wolf recovery

## Introduction

Large carnivores play a crucial role in ecosystems, directly and indirectly shaping interactions among species (Ford and Goheen 2015, Suraci et al. 2016, Hoeks et al. 2020). They also provide essential ecosystem services generating economic returns to local communities (O'Bryan et al. 2018, Raynor et al. 2021, Giergiczny et al. 2022). In the past, the relationship between humans and carnivores was often seen in the context of their impact on domestic and game animals, resulting in the extinction of many carnivore species globally (Treves and Karanth 2003, Ripple et al. 2014). Nevertheless, due to protective measures, large carnivores are making a comeback even in areas with high human density after being absent for decades or even centuries (Chapron et al. 2014, Ingeman et al. 2022).

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One of the most spectacular example of large carnivore recovery is the recent comeback of grey wolf *Canis lupus* in the western part of the Central European Plains (Nowak and Mysłajek 2016, Reinhardt et al. 2019). Completely vanished in the Netherlands, Belgium, Denmark, Luxembourg, and Germany, wolves survived only in extensive forests east of the Vistula River in Poland and neighboring Eastern European countries (Wolsan et al. 1992). Even there, in the 1970s, the species abundancy and range were severely restricted after decades of deliberate extermination (Sumiński 1975, Nowak and Mysłajek 2017). Socio-economic changes after the fall of communism at the turn of the 1980s and 1990s enabled the emergence of non-governmental organizations that conducted campaigns to protect large carnivores (Niedziałkowski and Putkowska-Smoter 2020, Niedziałkowski et al. 2021). As a result, wolves became strictly protected in Poland in 1998, six years before this country joined the European Union and implemented the EU Habitats Directive (Mysłajek and Nowak 2015). It stimulated the increase of the wolf population and their recovery first in western Poland (Nowak et al. 2017), then in Germany (Jarausch et al. 2021) and the neighboring countries of northwestern Europe (Lelieveld et al. 2016, Sunde et al. 2021).

The western part of the European Plains offers to wolves plenty of suitable habitats and abundant prey populations (Jędrzejewski et al. 2008, Borowik et al. 2013, Cimatti et al. 2021). The area, though, is heavily altered by humans; thus, the presence of wolves is connected with numerous management issues such as livestock depredation (Mayer et al. 2022), road mortality (Nowak and Mysłajek 2016), and illegal killing (Nowak et al. 2021). The debates on wolf conservation often relate to the predator's impact on the livestock and game animals as breeders and hunters are stakeholders least accepting the return of the wolves and emphasizing the threat to their economic interests (Dressel et al. 2015, Pates and Leser 2021). On the other hand, the wolf is protected under the Habitats Directive, and EU member countries are required to ensure favorable conservation status for this species (Trouwborst 2010). Therefore, to inform decisions about managing species constituting a wolf's food base and to recognize the potential impact of this predator on game and domestic animals, high-quality data on its diet are needed.

## Study area

The study area encompassed the forests located at the fork of Noteć and Warta rivers in north-western Poland (52°35′–52°53′N, 15°21′–16°59′E) (Fig. 1). It includes the Notecka Forest (from now on NF), which size is about 1400 km$^2$ and of elongated shape (length ca 100 km, width ca 20 km). The forests grow on glacier–river terraces with dunes of a relative height of 20–40 m (> 90 m a.s.l.). The majority (95%) of stands are Scots pine *Pinus silvestris* monocultures intensively managed by the Polish State Forest Service. The forest interior almost lacks watercourses, but some natural lakes and artificial water reservoirs occur at the edges. The NF is situated in the temperate climate zone, with an oceanic characteristic, where the mean temperature is −1°C in January and 16°C in July, and annual precipitations are

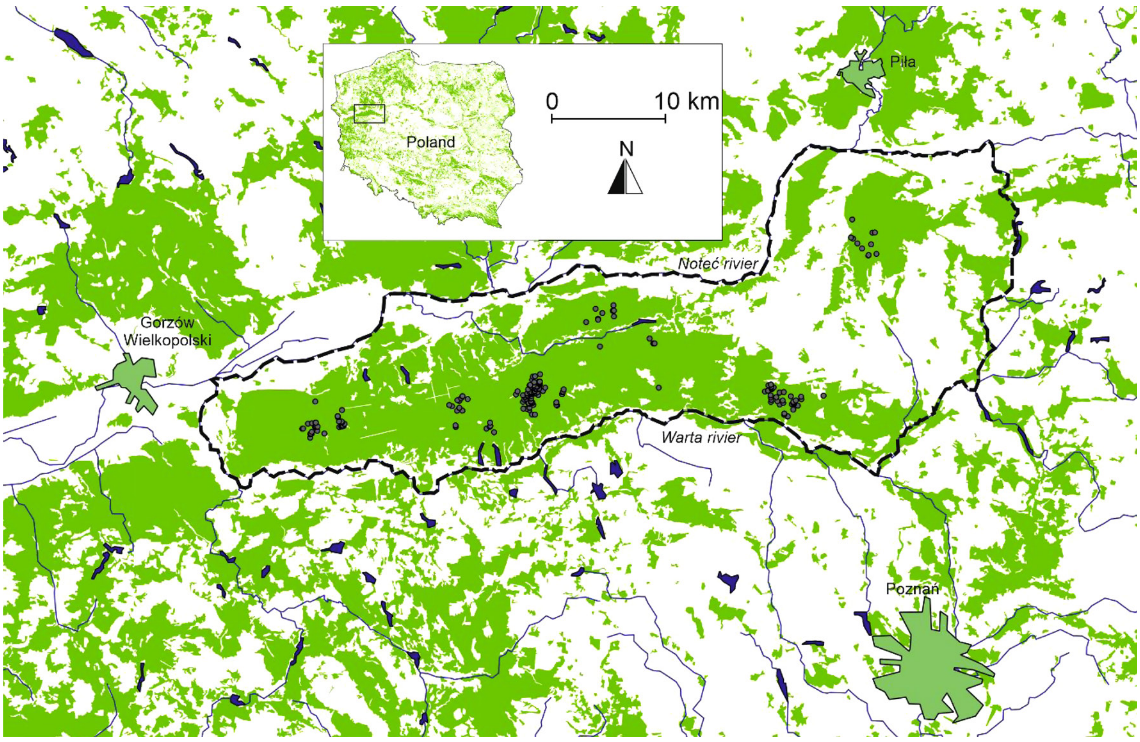


Figure 1. Location of scats (grey dots) used for the wolf diet assessment in the Notecka Forest and its vicinity in western Poland.

500–600 mm (Kusiak and Dymek-Kusiak 2002, Miś 2003, Okoński and Dreger 2022).

Only a few small human settlements and oil and gas mine installations are inside this forest tract. In its vicinity, however, numerous villages and towns are located, including two large cities: Gorzów Wielkopolski (120 000 inhabitants) and Poznań (540 000 inhabitants) (Statistics Poland 2022a). The NF is a popular touristic destination, especially in summer and autumn during the mushroom-picking season (Kusiak and Dymek-Kusiak 2002). The area is protected within the European Union's network of nature protection areas Natura 2000. The NF is included in the EU Birds Directive Site 'Puszcza Notecka' (PLB 300015, 1783 km$^2$). Some forest fragments are also protected within several small EU Habitats Directive Sites (Fig. 1), and the wolf is one of the target species (Diserens et al. 2017).

There is a large and diverse ungulate prey base for wolves. Among native species, the most abundant are the red deer *Cervus elaphus*, the roe deer *Capreolus capreolus*, and the wild boar *Sus scrofa*, while moose *Alces alces* and European bison *Bison bonasus* are recorded occasionally. Moreover, the fallow deer *Dama dama* – an alien species, was introduced here for hunting purposes (Solarz 2012). Based on hunting statistics, the mean population densities of major ungulate species between 1998 and 2003 reached 0.5–1.5 individuals km$^{-2}$ for red deer, 1.5–4.5 ind. km$^{-2}$ for roe deer and 0.5–1.5 ind. km$^{-2}$ for wild boar (Borowik et al. 2013). In the following years, a constant increase in the number of all deer species was recorded, and only recently, a substantial decrease in the wild boar numbers was observed due to African Swine Disease (Morelle et al. 2020, Statistics Poland 2022b). Vicinities of the NF, especially along river valleys, are used for cattle grazing. In central Poland, free-roaming dog densities range from 2.2 to 3.1 ind. km$^{-2}$ (Krauze-Gryz and Gryz 2014), and because of climate changes, they sometimes breed and raise pups in the wild (Krauze-Gryz and Gryz 2022).

There were several reproducing wolf family groups recorded in the NF in the 21st century (Nowak and Mysłajek 2016, Nowak et al. 2017). The area is located within a central European wolf population (sensu Linnell et al. 2008, Szewczyk et al. 2019, 2021 for the genetic basis of delimitation of this subpopulation), which has a category 'Vulnerable' (D1) according to the IUCN red list of threatened species (Boitani 2018). Apart from wolves, the dispersing individuals of Eurasian lynx *Lynx lynx* sporadically roamed throughout NF but did not establish a breeding population yet (Mysłajek et al. 2019a, Tracz et al. 2021).

## Material and methods

We estimated the composition of the wolf diet by analyzing the content of their scats (n = 261) collected opportunistically across the entire NF from 2008 to 2021 (Fig. 1 for scat locations and Dryad Digital Repository for years of scat collection). Fieldwork was performed within long-term projects dedicated to the assessment of population dynamics (Nowak and Mysłajek 2016), habitat selection (Nowak et al. 2017), and genetics (Hulva et al. 2018, Szewczyk et al. 2019, Kloch et al. 2021) of wolves recovering in western Poland. The gathering of samples over many years allows us to take into account long-term fluctuations of wild ungulate numbers. Scats were collected while walking or driving along forest roads, and special attention was paid to junctions of roads often used by wolves for marking territory (Stępniak et al. 2020). Such an approach gives the same results as the analyses of scats collected at home sites or at clusters of telemetry locations (Gable et al. 2017). Scats were identified based on size, shape, and location near wolf tracks and ground scratchings (Jędrzejewski and Sidorovich 2010). Along with studies on the diet composition, the authors also conducted studies on wolf genetics, thus from fresh scats, non-invasive genetic samples were taken and subsequently analysed using a fragment of mitochondrial DNA and a set of autosomal microsatellite markers to ensure proper identification of the species – see Hulva et al. (2018), Szewczyk et al. (2019) and Kloch et al. (2021) for further details. Collected scats were placed in paper envelopes and dried in a laboratory drier at 70°C for five days to kill parasites often recorded in feces (Popiołek et al. 2007). Subsequently, scats were soaked and washed on the dense sieve. The remaining elements – hair, fragments of bones, teeth, hooves, etc. – were used to recognize food items eaten by wolves. Prey species were identified using hair (Debrot et al. 1982, Teerink 1991, De Marinis and Asprea 2006) and skull (Pucek 1984) identification keys and reference material.

There are various ways of interpreting data from scat analysis. The most reliable approximation can be obtained using the biomass calculation model developed for the same or a closely related species. However, to document rare food items, frequency of occurrence is also recommended (Klare et al. 2011). Therefore, we presented the diet composition using the frequency of occurrence and the percentage of biomass. The frequency of occurrence was expressed as the percentage of scat samples containing a given food item, including items contributing less than < 5% to scat volume (i.e. trace amounts) (Klare et al. 2011). The percentage of biomass was expressed as the percentage of biomass of a particular food item relative to the total biomass consumed by wolves. Ingested biomass was calculated using the following coefficients of digestibility: 118 for ungulates (all deer species and wild boar), 50 for medium-sized mammals (domestic dog, European hare, European badger, and European beaver), 23 for small rodents, 35 for birds, and 4 for plant material (Goszczyński 1974, Jędrzejewska and Jędrzejewski 1998).

We estimated the differences in food composition between two seasons – spring–summer (April–September, n = 162 scats) and autumn–winter (October–March, n = 99 scats) – using Pianka's (1973) formula:

$$\alpha_{ij} = \left(\sum p_{ia} \times \sum p_{ja}\right) \times \left[\left(\sum p_{ia}{}^2\right) \times \left(\sum p_{ja}{}^2\right)\right]^{-1/2}$$

Table 1. Diet composition of wolves in the Notecka Forest, 2008–2021 (n = 261 scats). %O: percentage occurrence in scats, %B: percentage of total biomass consumed. (+) Contribution to diet < 0.05%.

| Food item | Spring–summer | | Autumn–winter | | Total | |
|---|---|---|---|---|---|---|
| | %B | %O | %B | %O | %B | %O |
| Red deer *Cervus elaphus* | 26.7 | 17.9 | 21.2 | 16.2 | 25.1 | 17.2 |
| Roe deer *Capreolus capreolus* | 45.8 | 50.6 | 52.6 | 45.5 | 47.8 | 48.7 |
| Fallow deer *Dama dama* | 0.5 | 0.6 | – | – | 0.4 | 0.4 |
| Undetermined cervids | 2.5 | 6.12 | 6.3 | 16.2 | 3.6 | 10.0 |
| Wild boar *Sus scrofa* | 20.2 | 19.8 | 13.9 | 18.2 | 18.3 | 19.2 |
| Wild ungulates total | 95.7 | 93.8 | 94.0 | 91.9 | 95.2 | 93.1 |
| European hare *Lepus europaeus* | 3.4 | 2.5 | 1.2 | 4.0 | 2.8 | 3.1 |
| European badger *Meles meles* | – | – | 0.4 | 1.0 | 0.1 | 0.4 |
| Eurasian beaver *Castor fiber* | 0.9 | 3.1 | 4.3 | 8.1 | 1.9 | 5.0 |
| Medium-sized wild mammals total | 4.3 | 5.6 | 5.9 | 13.1 | 4.8 | 8.1 |
| Domestic dog *Canis lupus familiaris* | + | 0.6 | – | – | + | 0.4 |
| Small rodents | – | – | + | 2.0 | + | 0.8 |
| Birds | + | 0.6 | – | – | + | 0.4 |
| Plant material | + | 5.6 | 0.1 | 11.1 | + | 7.6 |
| The number of scats analysed | 162 | | 99 | | 261 | |
| Biomass of food consumed (kg) | 258.8 | | 108.7 | | 367.5 | |

where $\alpha_{ij}$ was the degree of similarity of food composition between the first (*i*) and second (*j*) periods, $p_{ia}$ is the contribution of prey category *a* in the total biomass of prey consumed by wolves in the first period, $p_{ja}$ was the contribution of prey category *a* in the total biomass of prey consumed by wolves in the second period. We obtained diet similarities for general food groups (wild ungulates, domestic animals, medium-sized wild mammals, and others) and ungulate species (all cervids and suids). The species structure of wild ungulates consumed by wolves was based on the proportion of biomass of given species in the wolf diet. Proportions of each cervid species in the 'Cervidae undetermined' category were estimated based on the proportions of these species in the identified samples (Jędrzejewski et al. 2012). We deepened this analysis by applying the Chi-square test for the absolute frequency of occurrence of main prey species among seasons (Wright 2010). The Kolmogorov–Smirnov test indicates that the number of food items per scat does not follow a normal distribution, D(261) = 0.519, p < 0.001; therefore, to reveal seasonal differences for this parameter, we used the non-parametric Mann–Whitney U-test (Sokal and Rohlf 1995).

Based on food biomass we calculated the breadth of the wolf food niche using Levins' (1968) formula:

$$B = \frac{1}{\Sigma pi^2}$$

where *pi* is the contribution of group *i* of wolf prey to the total biomass of food consumed by wolves. We divided wolf prey into four main groups: 1) wild ungulates (cervids, suids), 2) domestic animals (both livestock and pets), 3) medium-sized wild mammals, and 4) others (i.e. small mammals, plants, etc.). Therefore, when $B = 1$, it indicates strong specialization in one prey group, while when $B = 4$, it shows opportunistic utilization of all prey groups.

## Results

We recorded 12 food items in the wolf diet in NF, 2008–2021, including wild ungulates (three species of cervids – red deer, roe deer, and fallow deer, as well as unidentified cervids, and the wild boar), lagomorphs (European hare *Lepus europaeus*), wild carnivores (European badger *Meles meles*), domestic pets (dog *Canis lupus familiaris*), large semiaquatic rodents (Eurasian beaver *Castor fiber*), small terrestrial rodents, birds and plant matter (Table 1).

Overall, wolves in NF consumed mainly wild ungulates (95.2% of biomass), among which the most important was the roe deer (47.8%), followed by the red deer (25.1%) and wild boar (18.4%), while the share of the fallow deer (0.4%) was negligible. Although medium-sized wild mammals, such as European hare, European badger, and Eurasian beaver, were recorded in 8.1% of scats, their biomass constituted only 4.8%. We recorded no livestock remains in the wolf scats in the NF whatsoever, and the only domestic animals consumed by those predators, however rarely, were dogs. Other food items (e.g. small rodents, birds, plants) were negligible (Table 1).

There was no seasonal difference in food composition between both seasons, considering all food components (Pianka's $\alpha = 1.0$) and ungulates alone ($\alpha = 0.982$). The average number of food items per scat was 1.1 (SD = 0.36, range 1–3), with slightly higher score in autumn–winter ($\bar{x} = 1.22$, SD = 0.46) than in spring–summer ($\bar{x} = 1.07$, SD = 0.29), however, this difference was statistically negligible (Mann–Whitney U-test, U = 6942.5, z = −1.81835, NS). The $\chi^2$ test revealed no difference in the absolute frequency of occurrence of main food items between seasons (Table 2).

Due to the substantial share of wild ungulates in the wolf diet in NF, the breadth of the food niche was narrow ($B = 1.1$) in both seasons and overall.

Table 2. Evaluation of the differences in the absolute frequency of occurrence of main food items in the wolf diet in the Notecka Forest in spring–summer (n = 162 scats) and autumn–winter (n = 99 scats) seasons, 2008–2021. Yate's continuity correction was applied to calculate $\chi^2$.

| Food item | Detected | Seasons | | $\chi^2$ | p-value |
|---|---|---|---|---|---|
| | | Spring–summer | Autumn–winter | | |
| Wild boar *Sus scrofa* | Yes | 32 | 18 | 0.023 | 0.88 |
| | No | 130 | 81 | | |
| Red deer *Cervus elaphus* | Yes | 29 | 16 | 0.037 | 0.85 |
| | No | 133 | 83 | | |
| Roe deer *Capreolus capreolus* | Yes | 82 | 45 | 0.465 | 0.50 |
| | No | 80 | 54 | | |
| Eurasian beaver *Castor fiber* | Yes | 5 | 8 | 2.269 | 0.13 |
| | No | 157 | 91 | | |
| European hare *Lepus europaeus* | Yes | 4 | 4 | 0.119 | 0.73 |
| | No | 158 | 95 | | |

## Discussion

We understand that drawing conclusions from a sample of 261 scat over a 13-year period may be biased when connected to both ungulate and wolf population dynamics. Additionally, opportunistic collection may have over-represented certain killing events, especially when scats are found concentrated. Nevertheless, for both the spring–summer and autumn–winter seasons, our sample size was above the threshold (n > 94) suggested as sufficient to effectively estimate the diet of carnivores (Trites and Joy 2005, Dellinger et al. 2011). Moreover, we interpreted data by applying the most recommended methods for such analyses (Klare et al. 2011). Therefore, we believe that our study's results correctly assessed the wolf diet's composition in NF.

Across the entire central European wolf population, wolves consume primarily wild ungulates (Nowak et al. 2011, Wagner et al. 2012), which was the case in our study, as the remaining food items were negligibly represented in the diet of wolves in NF. Therefore, their food niche is profoundly narrow, as has already been found in other studies (Nowak et al. 2011, Wagner et al. 2012, Mysłajek et al. 2019b, Van Der Veken et al. 2021). The roe deer is the most important prey in Germany (Ansorge et al. 2006, Wagner et al. 2012, Lippitsch et al. 2024), Belgium (Van Der Veken et al. 2021), as well as in the majority of study areas in western Poland (Nowak et al. 2011, Mysłajek et al. 2019b). Interestingly, in some forests in western Poland, the wild boar prevails in the wolf diet, but roe deer is always second in importance (Nowak et al. 2011). Moreover, wolves inhabiting Central European Plains consume fewer red deer than their counterparts from northeast Poland (Jędrzejewski et al. 2012) despite the substantial availability of this species across the country (Borowik et al. 2013). The dominance of roe deer in the diet of wolves (Nowak et al. 2011, Lippitsch et al. 2024) is probably due to its largest share in the structure of ungulate communities across Central European Plains (Borowik et al. 2013). To support this conclusion, however, we need more accurate data on the population densities of ungulates (Valente et al. 2020). Interestingly, we found no seasonal differences in the wolf diet composition in NF. In other study areas, seasonal variations arose mainly from the larger biomass of beavers eaten mainly in periods with low water levels (Sidorovich et al. 2017, Mysłajek et al. 2021, Nowak et al. 2024a). In NF, beavers were eaten at similar rate in both seasons (Table 1–2).

Earlier research emphasized the wolf's predilection towards red deer (Okarma 1995, Jędrzejewski et al. 2000). However, current studies conducted in Central European, Baltic, and Carpathian wolf subpopulations, documented rather diverse patterns of the wolf diet, reflected in substantial temporal changes in diet composition (Sidorovich et al. 2017, Mysłajek et al. 2021) as well as in spatial heterogeneity in prey consumption even in closely located areas (Andersone and Ozoliņš 2004, Nowak et al. 2005, Valdman et al. 2005, Sin et al. 2019, Guimarães et al. 2022, Mysłajek et al. 2022). Also, southern European studies highlighted significant temporal and spatial differences in the wolf diet (Capitani et al. 2004, Meriggi et al. 2011). Thus, long-term research projects on wolf diet are necessary to provide knowledge for making informed decisions related to both wolf conservation and game management.

Contrary to the Baltic subpopulation (Andersone and Ozoliņš 2004, Jędrzejewski et al. 2012, Mysłajek et al. 2021, Nowak et al. 2024a), wolves from the Central European Plains consume much fewer beavers despite their availability (Yanuta et al. 2022). Interestingly, in contrast to other studies (Latham et al. 2013, Sidorovich et al. 2017, Gable et al. 2018, Mysłajek et al. 2021), in NF we recorded a larger amount of beavers eaten by wolves in autumn–winter seasons than in spring–summer. Consumption of beavers seems to be affected by several factors, including local topography, water level, and availability of other prey species (Gable et al. 2016, 2018), which impact may be difficult to untangle. Although this semiaquatic species may be crucial during the pup-rearing season to provision offspring (Mysłajek et al. 2019b), in areas with abundant ungulate populations, such as central Europe (Borowik et al. 2013), it seemed to be less important. Therefore, in central Europe, more attention should be paid to the sustainable management of wild ungulates, which are the primary food base for wolves but, at the same time, also game species.

Our study documented a lack of livestock remains in the wolf scats in NF. Low livestock consumption by well-established wolf packs seems to be characteristic for the central European subpopulation (Ansorge et al. 2006, Nowak et al. 2011, Wagner et al. 2012, Mysłajek et al. 2019b). Use of livestock, however, is highly context-dependent and may increase due to lack of proper protection measures (Nowak et al. 2005), deterioration of the wild ungulate populations (Sidorovich et al. 2003), or dispersal of wolves across agricultural lands with high livestock densities (Mayer et al. 2022). Thus, further studies investigating the impact of various factors on wolves' impact on livestock are necessary.

As observed in other European localities, wolves in NF occasionally consumed domestic dogs (Sidorovich et al. 2003, Nowak et al. 2011, Van Der Veken et al. 2021). Although wolves may attack dogs of hunters or dogs near buildings (Bassi et al. 2021, Kojola et al. 2022), in central Europe, they most probably kill and consume free-ranging individuals, which frequently roam through forests and agricultural lands and kill wild animals (Wierzbowska et al. 2016, Krauze-Gryz and Gryz 2022). Therefore, the killing of free-ranging dogs by wolves may be treated as an essential ecosystem service similar to those delivered by large felids (Braczkowski et al. 2018). Also, predation on the fallow deer in Central European Plains should be considered an ecosystem service, as this cervid is an alien species competing with native ungulates (Ferretti et al. 2011, Obidziński et al. 2013).

Our research supported previous observations indicating that wolves inhabiting the vast forest tracts of central Europe consume primarily wild ungulates, especially the roe deer (Nowak et al. 2011, Wagner et al. 2012, Mysłajek et al. 2019b, Van Der Veken et al. 2021, Lippitsch et al. 2024). Recently, however, these predators often settle in areas with lower forest cover (Nowak et al. 2017, Planillo et al. 2024). Mattioli et al. (2004) already revealed that predation on roe deer is negatively correlated with the percentage of forest cover. Therefore, we suggest that future research projects should pay more attention to understanding the diet of wolves in such landscapes. This will allow us to better understand the adaptability of wolves to environments under greater human pressure and guide future management actions.

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## Author contributions

**Sabina Nowak**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Supervision (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Patrycja Tomczak**: Data curation (supporting); Investigation (supporting); Writing – review and editing (supporting). **Aleksandra Kraśkiewicz**: Data curation (supporting); Investigation (supporting). **Jacek Więckowski**: Data curation (supporting); Investigation (supporting). **Katarzyna Tołkacz**: Investigation (supporting); Writing – review and editing (supporting). **Weronika Baranowska**: Investigation (supporting). **Antoni Kasprzak**: Investigation (supporting). **Robert W. Mysłajek**: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Project administration (equal); Resources (equal); Supervision (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal).

## Transparent peer review

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## Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.vq83bk427 (Nowak et al. 2024b).

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