



Low contribution of livestock in the grey wolf diet in the area with high availability of free-ranging cattle and horses

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Abstract

The recovery of the wolf (*Canis lupus*) population in Europe is progressing, and predators settle in vast forests as well as in areas intensively used for agriculture, where interactions between wolves and livestock are frequent, often leading to conflicts with local communities. In 2020–2022, we studied the wolf diet composition in the Warta River Mouth (WRM hereinafter) region (western Poland), where herds of cattle (ca. 4,000) and horses (ca. 700) are freely grazed. Using genetic fingerprinting based on microsatellite DNA markers, tracking, and camera trapping, we confirmed that the area is used by two wolf family groups. Through the analysis of scat content ($n=109$), we found that in the WRM, wolves feed primarily on wild ungulates (81.9% of the consumed food biomass) and wild medium-sized mammals (14.5%). Domestic animals were eaten rarely, and cattle and dogs comprised 3% and 0.4% of the consumed food biomass, respectively. During these two years of research, only three cattle calves consumed by wolves were found. The diet of wolves in the WRM did not significantly differ from the food composition of these predators in six other study areas within the Central European wolf population. Our research shows that despite the high availability of unguarded herds of cattle and horses, wolves prey mainly on wild mammals. Managers searching to solve wolf-livestock conflicts should consider that wolf depredation is not a simple function of livestock availability but is also influenced by other factors, such as the species and breed of livestock, grazing methods, landscape, and availability of wild prey.

Keywords *Canis lupus* · Predation · Livestock damage · Diet composition

Introduction

Humanity has a massive impact on all environments of the Earth, which is well illustrated by the fact that human-made mass has recently surpassed the mass of living organisms (Elhacham et al. 2020). Furthermore, the biomass of livestock and humans far exceeds that of all wild mammals (Bar-On et al. 2018). Even among wild mammals, the artiodactyls, often the game species artificially supported by

humans, prevail (Greenspoon et al. 2023). Among numerous other threats to nature worldwide, agriculture, including animal husbandry, is considered one of the most harmful (Gordon 2018; Cravino et al. 2024). This threat is intensified by the growing demand for food (Tilman et al. 2011) and the continuous expansion of people into natural areas (Williams et al. 2020; Li et al. 2022).

On a continent as densely populated and transformed by people as Europe, it is impossible to create extensive protected areas that can adequately safeguard biodiversity (Pacheco et al. 2024). This is particularly obvious in the case of species with high space requirements, such as large carnivores (Di Minin et al. 2016; Diserens et al. 2017). Therefore, the land-sharing approach, when people and wild species co-occur, is promoted as an adequate solution in a human-dominated landscape (Grass et al. 2021). The introduction of various protection measures for large carnivores resulted in the recovery of their populations across Europe (Chapron et al. 2014). However, in some regions, large

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carnivores are declining (Gómez-Sánchez et al. 2018), or the effective size of their populations remains insufficient (Mergeay et al. 2024).

This is particularly evident in the case of the grey wolf (*Canis lupus*), which was deliberately exterminated for centuries and is now naturally returning to its former territories (Di Bernardi et al. 2025). Such process is the most intense in Central Europe, where due to the species's strict protection introduced in Poland already in 1998 (Nowak and Mysłajek 2017), wolves recolonized areas west to Vistula River (Nowak and Mysłajek 2016; Nowak et al. 2017; Szweczyk et al. 2019) and established stable populations in Germany, Czech Republic, Belgium, the Netherlands, and Denmark (Di Bernardi et al. 2025).

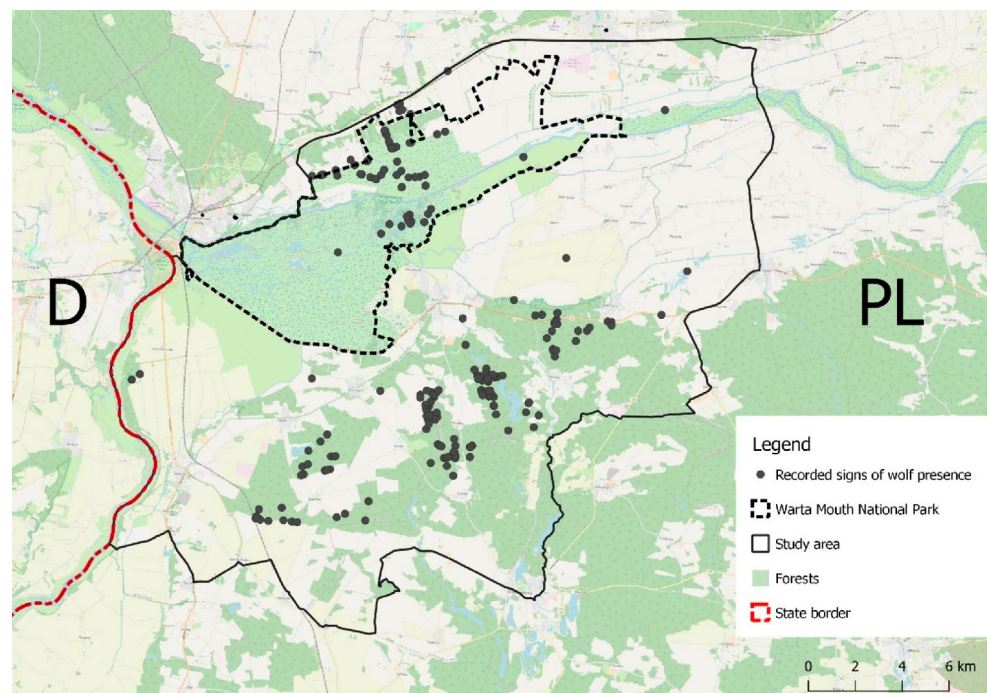
Despite the numerous benefits for nature, a land-sharing approach may lead to many conflicts, especially in the livestock-wildlife interface (Pe'er et al. 2022; VerCauteren and Breck 2024). In the case of large carnivores, it is primarily connected with livestock depredation (Singer et al. 2023). Wolves prey on various livestock species and scavenge on their carcasses left in the environment by farmers or used as bait by hunters (Jędrzejewski et al. 2002, 2012; Mateo-Tomás et al. 2023). Depredation level, however, may differ between dispersing individuals and members of stable family groups (Mayer et al. 2022) and is widely affected by environmental features (Gervasi et al. 2021). The level of wolf damage to livestock is also highly variable and influenced by species, breeds, grazing methods, and the implementation of mitigation measures (Nowak et al. 2005; Oliveira et al. 2021; Khorozyan and Heurich 2022).

A growing trend of wolf-related livestock depredation is being recorded in most European regions (Singer et al. 2023), likely reflecting the ongoing recovery of the species across the continent (Di Bernardi et al. 2025). In Poland alone, the share of livestock in the wolf's diet varies from 0 to 15.3% of their food biomass (Jędrzejewski et al. 2012). However, the predatory patterns of wolves on livestock still require in-depth research (Mayer et al. 2022; Petridou et al. 2023). Therefore, in this study, we attempted to assess the impact of predation of recently recovered wolves on domestic animals in the Warta River Mouth region (western Poland) (Nowak et al. 2017; Di Bernardi et al. 2025); the area grazed by large free-ranging and unprotected herds of cattle and horses. We hypothesize that in such circumstances, wolves intensively prey on readily available livestock. To verify this assumption, we studied the food composition of local wolves and compared it with the diet of carnivores living in areas without free-ranging grazing, which are also situated within the Central European wolf subpopulation (Nowak et al. 2011; Wagner et al. 2012; Mysłajek et al. 2019).

Study area

The study area (ca. 500 km²), called Warta River Mouth (hereinafter WRM), is located in Western Poland, along the state border with Germany (52°35'N 14°42'E) (Fig. 1). It includes the Natura 2000 site "Ujście Warty" PLC080001 (332.2 km²) and its vicinities. The central part of the Natura 2000 site is the Warta Mouth National Park (hereinafter WMNP) (80.7 km²), established in 2001. The Natura 2000 site, designated in 2004, protects the final section of the

Fig. 1 The Warta River Mouth region, with the depiction of the Warta Mouth National Park and Natura 2000 site "Ujście Warty" (PLC080001). D – Germany, PL – Poland



Warta River at its confluence with the Odra River. The area is covered mainly by humid grasslands (56%) and farmlands (35%), while forest cover is scarce (5%). The annual fluctuations of the Warta River level might be as great as 4 m. Thus, large patches of grasslands are seasonally flooded. The Natura 2000 site is surrounded by a mosaic of managed forests dominated by Scots pines (*Pinus sylvestris*), agricultural lands, and human settlements. It is one of the most critical areas for waterfowl in Central Europe, and the national park itself is protected by the Ramsar Convention. The average temperature in January is -2.4 °C, while in July, it is 19.4 °C, and the mean annual precipitation is 550 mm (Standard Data Form 2025).

The area has high densities of native wild ungulates – red deer (*Cervus elaphus*) 8–10 individuals/10km², roe deer (*Capreolus capreolus*) 27–31 indiv./10km², and wild boar (*Sus scrofa*) 2–3 indiv./10km² (data for 2021–2023, Statistics Poland 2024; Bank Danych o Lasach <https://www.bdl.lasy.gov.pl>). Additionally, the population density of the Eurasian beaver (*Castor fiber*) is among the highest recorded in Poland (8–9 indiv./10km², Yanuta et al. 2022). Furthermore, the local grasslands are pastures for numerous herds of livestock. In the grazing season, which usually lasts from mid-June to the end of November (after waterfowl breeding season), ca. 4,000 beef cattle (including calves) and 700 cold-blooded horses are grazing in the WMNP. The livestock is free-ranging within the national park, and no protection measures are applied against wolf depredation (Fig. 2).

Methods

Estimation of the number of Wolf family groups

We applied tracking, camera trapping, and genetic fingerprinting based on microsatellite DNA sequences to estimate

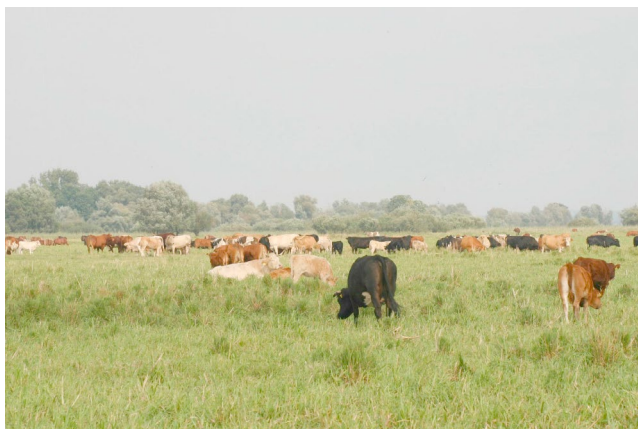


Fig. 2 Free-ranging cattle grazing inside the Warta Mouth National Park (Photo by P. Baranowski)

the number of wolves and discriminate wolf family groups within the study area in 2020–2022. Wolves frequently use dirt roads and trails to move across their territories (Zimmermann et al. 2014) and often mark them with scats, urine, and ground-scratching (Stępniaik et al. 2020). Therefore, we followed roads and trails, searching for evidence of the wolf's presence in the mud and sand. However, during winter, we also tracked wolves in the snow outside the trails. All signs of wolf presence, such as tracks, resting places, urine marking, bloody vaginal discharge by females during mating season, ground scratching, scats, and prey remains, were recorded and computed in the database. A total of 260 signs of wolf presence were recorded, of which the majority were scats and tracks (Fig. 1, Supplementary Information S1).

We set up four camera traps (Ereagle E1B) to obtain additional information on the number of wolves in the study area. Camera traps operated from December 2020 to February 2022. We chose the location of camera traps based on the traces of the recent presence of wolves in a given location. The camera trap was left in each of them for about three weeks. If a camera trap recorded wolves, it was left in its current location for another 3 weeks, but if there were no recordings of wolves, the camera trap was moved to a new location. Recordings were made in total in 36 locations – ten in the WMNP and another 26 in the forests adjacent to the national park. Following the recommendation of Zimmermann et al. (2014), we set up camera traps on trees near forest roads or at intersections of dirt roads at a height of approximately 1 m.

Genetic fingerprinting was mainly based on DNA isolated from the non-invasive samples or tissues of dead or injured individuals found within the study area between 2014 and 2022 ($n=63$). Scat and tissue samples were preserved with 96% ethanol and stored at $+4$ °C. Blood was collected on FTA cards (Whatman) and kept at room temperature in dry paper envelopes containing desiccant. Urine samples were mixed with 2 volumes of 96% ethanol and sodium acetate (100 mM final concentration) and kept at -20 °C. We isolated DNA from scats either with QIAamp DNA Stool Mini Kit (Qiagen) or Exgene™ Stool DNA Mini Kit (GeneAll Biotechnology). For FTA cards, we used Exgene™ Genomic DNA Micro kit (GeneAll Biotechnology) or QIAamp DNA Investigator Kit (Qiagen). For tissues and precipitated urine samples, we applied Exgene™ Tissue SV kit (GeneAll Biotechnology).

We amplified 13 polymorphic microsatellite loci: CPH5 (Fredholm and Winterø 1995), vWF (Shibuya et al. 1994), FH2001, FH2010, FH2017, FH2137, FH2087, FH2088, FH2096, FH2140, FH2054, FH2161 (Francisco et al. 1996), and PEZ17 (Neff et al. 1999). Additionally, we amplified chromosome fragments DBX intron 6 and DBY intron 7 (Seddon 2005) as sex markers. Amplifications were carried

out in three 10 µl multiplex reactions, each containing 5 µl KAPA2G Fast Multiplex Mix (Kapa Biosystems, USA), 10 µg/µl BSA, primers at concentration 0.2 µM each and 3.6 µl of DNA extract. PCR was started with initial denaturation (95 °C, 15 min) followed by 4 cycles of 94 °C (30 s), 60 °C (90 s) and 72 °C (60 s); another 5 cycles of 94 °C (30 s), 58 °C (90 s) and 72 °C (60 s), 5 cycles of 94 °C (30 s), 54 °C (90 s) and 72 °C (60 s), 25 cycles of 94 °C (30 s), 50 °C (90 s) and 72 °C (60 s), and a final elongation 30 min at 72 °C. The quality of PCR products was then assessed based on the electrophoresis results in agarose gel. At this stage, samples that were too diluted, contaminated, or contained DNA from several wolves were rejected ($n=49$). Good-quality samples were sequenced, and DNA fragments were separated by electrophoresis using a genetic analyzer ABI3730/xl with the internal size standard GS600 LIZ™ (Applied Biosystems, USA). Allele sizes were binned using PeakScanner 1.0 software.

Multilocus genotypes were compared in GenAlEx ver. 6.5 (Peakall and Smouse 2012). The genotypes with one mismatching allele were considered to originate from the same individual. Differences in three or more loci were treated as the samples came from different individuals. In the case of two mismatching alleles, further analysis was performed to determine the origin of the samples from the same or different wolves. Closely related individuals were identified by estimating relatedness between pairs of individuals using the estimator of Lynch and Ritland (1999) implemented in GeneAlEx and by direct genotypes comparison (Supplementary Information S1).

Assessment of the Wolf diet composition

Wolf diet was assessed by analysing 109 scats collected between 2020 and 2022. Scats were placed in paper envelopes, dried in a laboratory drier at 70 °C for five days to eradicate intestinal parasites often recorded in wolf scats in Poland (Popiołek et al. 2007), and stored until the analysis. Subsequently, dry scats were soaked, washed through a 0.5 mm-mesh sieve, dried, and weighed. Food items eaten by wolves were recognized by the remaining elements – hair, fragments of bones, hooves, claws, teeth, and feathers (Lockie 1959; Goszczyński 1974).

We identified prey species and/or genera according to the taxonomic keys (Debrot et al. 1982; Pucek 1984; Teerink 1991; De Marinis and Asprea 2006; Tóth 2017) as well as the comparison to the reference material. In case of doubt ($n=5$ samples), DNA isolation and mitochondrial DNA sequencing were performed from the prey remains to identify the species. Genetic material was extracted using the Exgene™ Genomic DNA micro isolation kit, following the manufacturer's instructions and recommendations. The

products were then sequenced, and the obtained nucleotide sequences were identified using the Basic Local Alignment Search Tool (<https://blast.ncbi.nlm.nih.gov>).

The composition of food was expressed as (1) a percentage of occurrence – the percentage of scats containing different prey species relative to the total number of scats, and (2) the percentage of biomass – the percentage of biomass of a particular food component relative to the total biomass consumed by wolves. The biomass of food items was calculated by multiplying the weight of prey remains found in scats by the following coefficients of digestibility: rodents and insectivores – 23, medium-sized mammals – 50, ungulates – 118, insects – 5, plant material – 4, birds – 35 (Jędrzejewska and Jędrzejewski 1998).

The breadth of the food niche was calculated using the Levins (1968) formula:

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

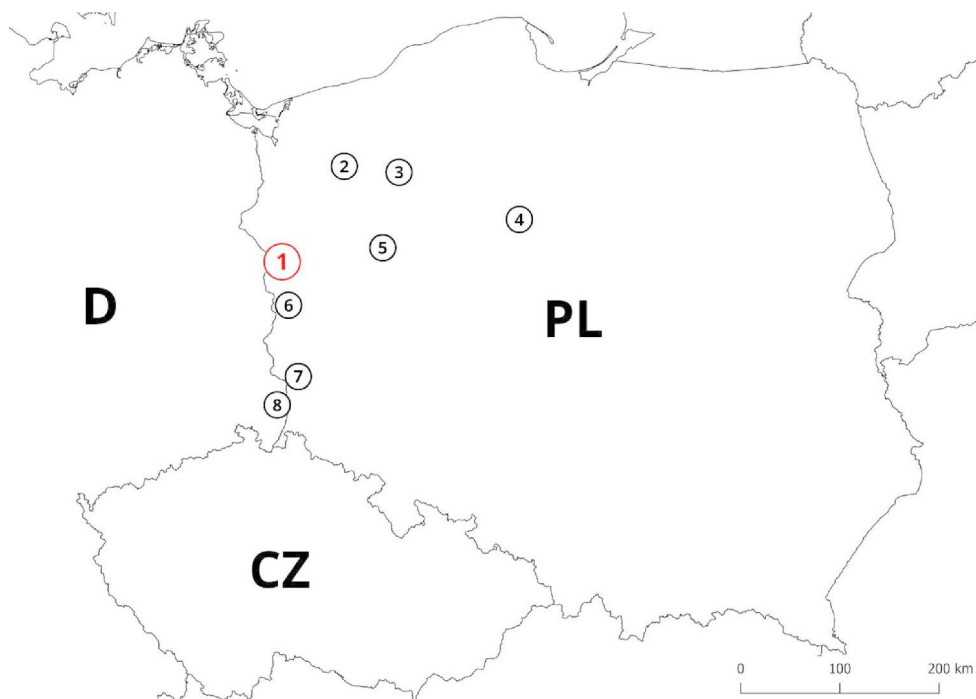
where pi is the contribution of group i of wolf prey in the total biomass of food consumed by wolves. The prey was classified into the following groups: (1) wild ungulates (cervids, suids); (2) medium-sized mammals; (3) domestic animals (livestock and pets); (4) others (small mammals, plants, birds, etc.). Thus, B can achieve values from 1 (strong specialization in one prey group) to 4 (opportunistic preying on all food categories).

To check out the possible difference between the diet of local wolves and others, we compared our data with the results of the wolf diet studies conducted in several parts of the Central European wolf subpopulation (for the delimitation of wolf subpopulations in Europe, see Szewczyk et al. 2021b): Bydgoszcz Forest, Wałcz Forest, Rzepin Forest, Lower Silesian Forest (Nowak et al. 2011), Drawa Forest (Mysłajek et al. 2019), Notecka Forest (Nowak et al. 2024b), and East Germany (Wagner et al. 2012) (Fig. 3). The similarity of diet composition between study areas was calculated following the formula of Pianka (1973):

$$\alpha_{lz} = \left(\sum p_{la} \times p_{za} \right) \times \left[\left(\sum p_{la}^2 \right) \times \left(\sum p_{za}^2 \right) \right]^{-1/2},$$

where α_{lz} is a degree of similarity of food composition between the first (l) and the second (z) study area, p_{la} is a contribution of a prey a in the total biomass of prey consumed by wolves in the first study area, p_{za} is a contribution of a prey a in the total biomass of prey consumed by wolves in the second study area. For these calculations we used four food categories: wild ungulates, medium-sized mammals, domestic animals and others. Thus, index can take values from 0 (no similarity in food composition between complexes) to 1 (complete overlap of diet in both complexes).

Fig. 3 Locations of study areas used to compare the food composition of wolves from the Central European subpopulation. (1) Warta River Mouth, (2) Drawa Forest, (3) Wałcz Forest, (4) Bydgoszcz Forest, (5) Notecka Forest, (6) Rzepin Forest, (7) Lower Silesian Forest, (8) Eastern Germany



We also obtained data on wolf predation on livestock within the study area, recorded by the Warta Mouth National Park and Regional Directorate for Environmental Protection.

Results

The number of Wolf family groups

Genotypes of sufficient quality were obtained for 14 samples belonging to 12 wolves. Based on the relatedness analysis, these individuals were divided into two family groups (Supplementary Information S1). Since the genetic samples used in this study were collected over several years and the lack of samples from one season from both family groups, it was not possible to assess the size of particular family groups (samples may originate from individuals from different generations). Wolves, mainly single individuals, were recorded via camera traps in seven locations, one in WMNP and the rest in the adjacent forests. However, one recording documented seven individuals, most likely a pair of breeders and their offspring from the previous year.

Wolf diet composition

Wolves in the WRM area primarily consumed wild ungulates, comprising 81.9% of the food biomass. The most frequent prey was roe deer, constituting 59.8% of the biomass consumed, followed by wild boar (20.5%). The share of the

red deer was negligible and made up only 0.7% of food biomass. Among medium-sized mammals, wolves consumed European beavers (6.8% of food biomass) and European hares *Lepus europaeus* (7.7% of biomass consumed). Scats also contained remains of domestic animals (cattle 3% and domestic dogs 0.4% of food biomass), plant material, small rodents, and birds (Table 1).

The similarity of the wolf diet between WRM and other forest tracts across the Central European wolf subpopulation (Table 2) was very high (mean $\alpha = 0.991$, SD=0.003, range 0.987–0.997). Wolves in the study area had the widest food niche ($B=1.44$) compared to the other forest complexes included in analyses ($B=1.04$ – 1.25) (Table 2), which was due to the higher proportion of medium-sized wild mammals in their diet.

Three cattle calves were reported to Warta Mouth National Park as being eaten by wolves, one in 2020 and two in 2022 (Fig. 4). However, the reasons for their deaths were not unambiguously determined.

Discussion

Our sample size ($n=109$ scats) was sufficient to properly assess the share of main food categories in the wolf diet according to recommendations from the recent literature (Trites and Joy 2005; Dellinger et al. 2011). However, we are aware that wolves may scavenge the carrion of wild and domestic animals found within their home ranges (Śmietana and Klimek 1993; Selva et al. 2005). Therefore, it should be

Table 1 Diet composition of wolves *Canis lupus* in warta mouth river region, 2020–2022, revealed through scat content analysis ($n=109$). %B – the percentage of total biomass consumed, %O – the percentage of occurrence in scats. (+) contribution to diet <0,1%. Categories to estimate the breadth of food niche (after Levins 1968): (1) wild ungulates, (2) medium-sized mammals, (3) domestic animals, (4) others

Food item	Total	
	%B	%O
Wild boar <i>Sus scrofa</i>	20.5	35.8
Red deer <i>Cervus elaphus</i>	0.7	0.9
Roe deer <i>Capreolus capreolus</i>	59.8	63.3
Undetermined cervids	0.9	3.7
Wild ungulates total	81.9	88.1
European beaver <i>Castor fiber</i>	6.8	7.3
European hare <i>Lepus europaeus</i>	7.7	5.5
Medium-sized mammals total	14.5	12.8
Cattle <i>Bos</i> sp.	3.0	2.8
Domestic dog <i>Canis lupus familiaris</i>	0.4	1.8
Domestic animals total	3.4	4.6
Birds	+	0.9
Plant material	0.1	15.6
Small rodents	0.1	3.7

considered that the food composition assessed by scat analysis can overstate the actual level of predation of a given species.

Contrary to our expectations, livestock constituted only a small part of the wolf's diet in WRM (3% of the food biomass, Table 1), which corresponds well with the results of other studies conducted across Central Poland, where wolves rarely prey upon farm animals (Nowak et al. 2011, 2024b; Mysłajek et al. 2019) despite their availability (Statistics Poland 2024). Considering the lack of claims for compensation from animal breeders in WRM, we may assume that most livestock remains in wolf scats in this area come from scavenging. It is supported by the observation that in cattle grazing within the Warta River Mouth National Park, losses of calves as still-born or dead during the first day after birth is on average 1.5%, and may even reach 2.3% in Charolais breed (Dobicki et al. 2007). Since their owners do not continuously supervise cattle, dead calves can be available to wolves for extended periods. The low



Fig. 4 Limousin cattle calve eaten by wolves at the Warta Mouth National Park in 2022 (Photo by P. Baranowski)

levels of wolf predation on cattle and lack of predation on horses in the WRM may be due to the grazing methods. Living in conditions similar to natural allows both species of domestic animals to show and ameliorate behavior typical for large free-living herbivores, such as gathering in large herds and self-defencing (Krueger et al. 2023; Smit and Kuijper 2024). Another factor may be that within the WRM, mainly beef cattle breeds such as Limousin, Hereford, Red and Aberdeen Angus, and Blonde d'Aquitaine are grazed. Such breeds are much heavier and more muscular than dairy cattle, posing a more significant threat (Byard 2024). The next reason may be that in the WRM area, most cows are not dehorned (Fig. 5). Cattle dehorning can reduce their ability to defend themselves against predators, and this practice is particularly intense in northern and central Europe (Cozzi et al. 2015), where the wolf population is developing (Di Bernardi et al. 2025).

Wolves in the WRM also consumed domestic dogs, however rarely (Table 1). No complaints of wolf predation on dogs were submitted to either the Warta Mouth National Park or the Regional Directorate for Environmental Protection, which are both institutions responsible

Table 2 Share of the main food categories (reflected as a percentage of the food biomass), breath of the food niche, and similarity between Wolf diet in the warta mouth river region and seven other study areas across the central European Wolf population. Data after: warta river mouth region (this study), Bydgoszcz forest, Wałcz forest, Rzepin forest, and lower Silesian forest (Nowak et al. 2011), Drawa forest (Mysłajek et al. 2019), Notecka forest (Nowak et al. 2024b), Eastern Germany (Wagner et al. 2012)

Food item	Warta River Mouth	Bydgoszcz Forest	Wałcz Forest	Rzepin Forest	Lower Silesian Forest	Drawa Forest	Notecka Forest	Eastern Germany
Wild ungulates	81.9	95.8	89.1	96.8	97.9	94.8	95.2	96.2
Medium-sized mammals	14.5	3.8	9.3	2.4	2.1	5.2	4.8	3.0
Domestic animals	3.4	0.4	1.6	0.8	0.0	0.0	0	0.5
Others	0.2	0.0	0.0	0.0	0.0	0.0	0	0.2
Food niche breadth <i>B</i>	1.44	1.09	1.25	1.07	1.04	1.11	1.10	1.08
Overlap with Warta River Mouth	-	0.990	0.997	0.988	0.987	0.992	0.991	0.989



Fig. 5 Horned cow in the Warta Mouth National Park (Photo by P. Baranowski)

for compensation. Thus, we can assume that dogs eaten by wolves were stray or free-roaming individuals. According to data gathered by Polish hunters, ca. 138,000 free-ranging dogs are recorded on hunting grounds, killing over 33,000 game species and 280 livestock annually (Wierzbowska et al. 2016). Free-ranging dogs have a negative impact on wildlife (Krauze-Gryz and Gryz 2014; Wierzbowska et al. 2016); thus, wolves' predation on free-ranging dogs may be considered an essential ecosystem service rather than a nuisance. It is imperative due to the lack of effective mitigation measures and simultaneous strong social opposition to solutions involving the capture or shooting of dogs (Holmes et al. 2015; Krauze-Gryz and Gryz 2023). However, wolf predation on owned dogs, especially those used for guarding and hunting, may increase conflicts with local societies and, therefore, requires special attention (Bassi et al. 2021).

The food niche of wolves in the WMR region was relatively narrow, as they predominantly consumed wild ungulates. This finding is consistent with other studies on wolf diet composition worldwide, underscoring the wolf's preference for large and medium-sized wild ungulates (see reviews by Zlatanova et al. 2014 and Newsome et al. 2016). A comparison of the wolf diet in the WMR and other areas across the Central European wolf subpopulation showed no significant differences. However, the share of wild ungulates (81.9%) was slightly lower than in other locations (Nowak et al. 2011, 2024b; Wagner et al. 2012; Mysłajek et al. 2019). The wolf diet in the WMR was dominated by roe deer (59.8%), which is also the most abundant species among the ungulate community across Poland (Borowik et al. 2013), and the primary wolf prey in numerous localities across the entire Central European Plains (Jędrzejewski et al. 2012; Nowak et al. 2011, 2024b; Mysłajek et al. 2019, 2022). The second most important food for wolves was the wild boar (20.5%).

Wild boar are highly social animals, and their tendency to live in groups with a large number of piglets, depending on the protection of their mothers, makes them easier to hunt (Mattioli et al. 1995; Meriggi et al. 2011). However, this result deserves attention due to the recent approaches to wild boar management in Poland related to the spread of the African Swine Disease (hereinafter ASF). Due to massive sanitary culling (over 1,5 million wild boar in 2019–2024, 760 thousand in 2020–2022), the wild boar population has significantly declined (European Food Safety Authority et al. 2024; Statistics Poland 2024). As the ASF zones also covered the area of the WMR in 2020–2022, the intense culling lowered the number of wild boar there, and it became the least numerous ungulate within the WRM (Statistics Poland 2024; Bank Danych o Lasach <https://www.bdl.lasy.gov.pl>). Despite that, wild boar were still the second most important food item for wolves. Such a large consumption of wild boar may be caused by the presence of individuals infected with the ASF virus, as wolves may take an opportunity to kill weakened individuals or consume carrions of already dead animals. The intense consumption of wild boar within active ASF zones should be considered a valuable ecosystem service provided by wolves to the pig breeding industry (Szewczyk et al. 2021a).

The red deer, the largest wild ungulate living in the WRM, was rarely eaten by local wolves (Table 1). Earlier papers suggested that wolves prefer this species (Okarma 1995; Jędrzejewski et al. 2002). In more forested areas, it actually may become the staple food for wolves (Jędrzejewski et al. 2002; Belardi et al. 2024), and the density of its population may be the most significant factor explaining wolf occurrence (Roder et al. 2020). However, recent studies indicate that in Central Europe, wolves primarily prey on roe deer and wild boar, with a lesser focus on red deer (Nowak et al. 2011; Sin et al. 2019; Lippitsch et al. 2024). It is unlikely that such patterns emerge from pack size, as this parameter is similar in areas recently recolonized and long inhabited by wolves (Jędrzejewski et al. 2002; Nowak et al. 2008; Nowak and Mysłajek 2016; Mysłajek et al. 2018). However, this may be partly explained by the increasing occurrence of wolves in a mosaic of forests and farmlands (Di Bernardi et al. 2025), where roe deer find favorable habitats and a rich food base (Kamieniarz et al. 2024). Agricultural food subsidies significantly enhance the reproductive performance of roe deer and increase their body mass (Brunot et al. 2025), thereby expanding the food base for large carnivores. Furthermore, the functional response of wolves on larger ungulates is strongly dependent on the density of a smaller ungulate prey (Sand et al. 2016). The wolf's predation on red deer may, therefore, be modest in areas with a high density of roe deer, as is the case in Central Europe (Borowik et al. 2013).

In WRM, medium-sized mammals (Eurasian beaver and European hare) comprised 14.5% of wolves' total food biomass. The share of the hare in the wolf diet (7.7% of the food biomass) corresponds well with other results from Central Europe (Ansorge et al. 2006; Špinkytė Bačkaitienė and Pételis 2012). In Poland alone, hare makes, on average, 1.3% of wolf's food biomass (Jędrzejewski et al. 2012), while in the western part of the country 2.5% (Nowak et al. 2011). The beaver, whose share in the wolf's diet in WRM accounted for 6.8% of the food biomass, is also widely used as an additional food source (Jędrzejewski et al. 2012; Nowak et al. 2011), especially in areas with higher availability of wetlands (Mysłajek et al. 2021; Nowak et al. 2024a). Water levels significantly influence predation intensity on beavers, and this species is most susceptible to predation during ice-free periods (Gable et al. 2018) and during summer droughts (Sidorovich et al. 2017). Therefore, an increased frequency of droughts across Europe (Ciais et al. 2005; Hari et al. 2020) may boost the susceptibility of beavers to predation.

Our research confirmed that wolf predation on farm animals is context-dependent. In the case of free grazing of large livestock, such as beef cattle and cold-blooded horses, the impact of wolves may be lower than expected. Previous studies have indicated that interactions between wolves and livestock depend highly on the environment (König et al. 2023), grazing methods (Petridou et al. 2023; Kelava Ugarković et al. 2023), knowledge of farmers about mitigation methods (Durá-Alemaña et al. 2024), availability of wild prey species (Meriggi et al. 2011; Janeiro-Otero et al. 2020), and the stability of wolf family groups (Imbert et al. 2016; Fabbri et al. 2018). For these reasons, when counteracting potential conflict situations, it is essential to consider all these aspects before proceeding with solutions that involve lethal methods (Kutal et al. 2024).

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Data availability The data will be available at the electronic data repository of the University of Warsaw after the paper is published.

Declarations

Competing interests The authors declare no competing interests.

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