Diet of the grey wolf Canis lupus in Roztocze and Solska Forest, south-east Poland

Authors: Mysłajek, Robert W., Stachyra, Przemysław, Figura, Michał, Nędzyńska-Stygar, Monika, Stefański, Robert, et al.

Source: Journal of Vertebrate Biology, 71(22040)

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/jvb.22040

Journal of Vertebrate Biology

Open Access

J. Vertebr. Biol. 2022, 71: 22040

DOI: 10.25225/jvb.22040

RESEARCH PAPER

Diet of the grey wolf *Canis lupus* in Roztocze and Solska Forest, south-east Poland

Robert W. MYSŁAJEK[1*], Przemysław STACHYRA[2], Michał FIGURA[1,3], Monika NĘDZYŃSKA-STYGAR[4], Robert STEFAŃSKI[2], Michał KORGA[5], Iga KWIATKOWSKA[1], Kinga M. STĘPNIAK[1], Katarzyna TOŁKACZ[6] and Sabina NOWAK[1]

[1] *Department of Ecology, Institute of Functional Biology and Ecology, Faculty of Biology, University of Warsaw, Biological and Chemical Research Centre, Warszawa, Poland; e-mail: r.myslajek@uw.edu.pl*

[2] *Roztocze National Park, Zwierzyniec, Poland*

[3] *Association for Nature "Wolf", Twardorzeczka, Poland*

[4] *Faculty of Biology, Adam Mickiewicz University of Poznań, Poznań, Poland*

[5] *Lublin Ornithological Society, Lublin, Poland*

[6] *Institute of Biochemistry and Biophysics, Polish Academy of Sciences, Warszawa, Poland*

Received 28 June 2022; Accepted 24 August 2022; Published online 3 October 2022

Abstract. The diet composition and prey selection of grey wolves (*Canis lupus*) inhabiting the Roztocze and Solska Forest (south-east Poland) was studied based on an analysis of scats collected in 2001-2002 (n = 84) and 2017-2020 (n = 302). In both periods, wolves preyed mainly on wild ungulates (96.5-96.7% of consumed biomass). Roe deer (*Capreolus capreolus*) was the most critical wolf prey accounting for 57.8% of consumed biomass in 2001-2002 and 49.2% and 2017-2020, but wolves positively select only wild boar (Jacob's selectivity index $D = 0.213$ in 2001-2002 and 0.710 in 2017-2020) and fallow deer ($D = 0.588$ only in 2017-2020). The largest species – moose *Alces alces* and red deer *Cervus elaphus* – were consumed less than expected from their share in the ungulate community. Predation on medium-sized wild mammals and domestic animals was low, 0.8-2.2% and 1.1-2.7% of the biomass consumed, respectively. The breadth of the wolf diet was very narrow and identical in both study periods ($B = 1.07$), while the similarity of diet composition was high ($\alpha = 0.999$). This study indicated the stability of the wolf diet over two decades and the importance of wild boar as a food source for this carnivore.

Key words: food habits, prey selection, diet composition

Introduction

Grey wolves (*Canis lupus*) have been persecuted for centuries, which has led to their extinction in many regions (Mech & Boitani 2003). Nowadays, natural recovery of this canid has been observed in Europe (Chapron et al. 2014), mainly due to the introduction of legal instruments at national and international levels (Trouwborst 2015, Nowak & Mysłajek 2017) and the implementation of numerous projects of non-governmental organisations and governmental agencies working to ease wolf-human coexistence (Salvatori & Mertens 2012, Salvatori et al. 2020). Nonetheless, the widespread illegal killing of legally

* *Corresponding Author*

protected wolves (Musto et al. 2021, Nowak et al. 2021) indicates that further actions are needed to secure the persistence of this large carnivore in human-dominated European landscapes.

One of the main reasons for the lack of wolf acceptance among some stakeholders, particularly hunters and animal breeders, is predation on game and domestic animals (Krange et al. 2017, van Heel et al. 2017, Arbieu et al. 2019). The share of these food categories in the wolf diet might vary enormously, both spatially (Jędrzejewski et al. 2012, Zlatanova et al. 2014) and temporally (Sidorovich et al. 2003, Meriggi et al. 2011). Therefore, implementing solutions to improve the coexistence of wolves and local communities requires constant monitoring of their food habits (Mysłajek et al. 2021).

In Central Europe, wolves prey primarily upon red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), and in some locations also on the Eurasian beaver (*Castor fiber*) (Valdmann et al. 2005, Žunna et al. 2009, Jędrzejewski et al. 2012, Špinkytė-Bačkaitienė & Pėtelis 2012, Wagner et al. 2012, Sidorovich et al. 2017). However, the diet of wolves in this part of Europe is influenced by multiple factors, including ungulate abundance (Sidorovich et al. 2003), the number of wolves in a family group (Jędrzejewski et al. 2002b), season (Mysłajek et al. 2021), the rearing of pups (Mysłajek et al. 2019), and outbreaks of ungulate diseases (Valdmann & Saarma 2020). In some studies, a correlation between genetic distances and dietary differentiation of wolf subpopulations was also found (Jędrzejewski et al. 2012, Pilot et al. 2012).

Several wolf management units – so-called Baltic, Central European and Carpathian subpopulations – were identified in Central Europe based mainly on species distribution, landscape features, suitability of habitats, dispersal abilities and differences in population management (Linnell et al. 2008, Boitani 2018). Recently, this differentiation has also been supported by studies on the genetic structure of the wolf population (Szewczyk et al. 2019, 2021b). Moreover, genetic studies indicated that in south-eastern Poland, between Baltic and Carpathian subpopulations, there is a cline of genetically distinct wolf subgroups (Pilot et al. 2006, Czarnomska et al. 2013, Szewczyk et al. 2019) extending eastwards roughly along the Belarussian-Ukrainian borderland (Pilot et al. 2006). In this study, wolf scat samples collected in south-eastern Poland during two periods (2001-2002 and 2017-2020) were analysed to reveal potential temporal changes in the diet of this carnivore.

Material and Methods

Study area

The study area covers large parts (ca. 1,300 km^2) of two neighbouring, although topographically different, regions; the Roztocze and Solska Forest; situated in south-eastern Poland (central point 50° 30′ N, 23° 00′ E), near the border with Ukraine (Fig. 1). Roztocze is an upland area, with hills reaching a maximum altitude of ca. 390 m a.s.l. Local forests consist mainly of Scots pine *Pinus silvestris* stands, but there are several patches of beech *Fagus sylvatica*, oak *Quercus* ssp. and fir *Abies alba* forests. Forest tracts are heavily fragmented and interspersed with large agricultural areas and villages. Conversely, the Solska Forest is a compact forest tract dominated by managed Scots pine stands with small patches of black alder *Alnus glutinosa* swamp forests in wetter locations (Chmielewski & Sowińska 2011, Maciejewski & Szwagrzyk 2011). The area's climate is transitional between Atlantic and continental, with an average temperature of –2.9 °C in January, and 19.1 °C in July, with annual precipitation of 691 mm (Tittenbrun 2019).

There are several protected areas within the study area. The most important is the Roztocze National Park (84.8 km^2), which protects patches of mainly deciduous forests in the central part of Roztocze (Tittenbrun 2019). The national park overlaps with the Natura 2000 special area of conservation "Roztocze Środkowe" (PLH060017). Another Natura 2000 site located on the Biłgoraj Plain "Uroczyska Puszczy Solskiej" (PLH060034) protects vast areas (346.7 km^2) of the Solska Forest. Both Natura 2000 sites are, among other purposes, dedicated to the protection of the wolf habitats (Diserens et al. 2017). The network of local protected areas are complemented by landscape parks (Szczebrzeszyński, Krasnobrodzki and Puszczy Solskiej), several small nature reserves and some minor Natura 2000 sites.

The region is inhabited by several species recognised as a primary wolf food base (Jędrzejewski et al. 2012, Mysłajek et al. 2019), including both native (moose *Alces alces*, red deer, roe deer and wild boar and alien (fallow deer *Dama dama*) ungulate species (Borowik et al. 2013), as well as Eurasian beaver (Halley et al. 2021). During vegetation season, cattle, horses and sheep are grazed on pastures surrounding forest tracks, especially in the Roztocze region (Dziaducha 2021). Furthermore, the Roztocze National Park supports small herds of heritage breeds of horses, cattle and sheep (altogether ca. 120 individuals) grazed on pasture inside the park.

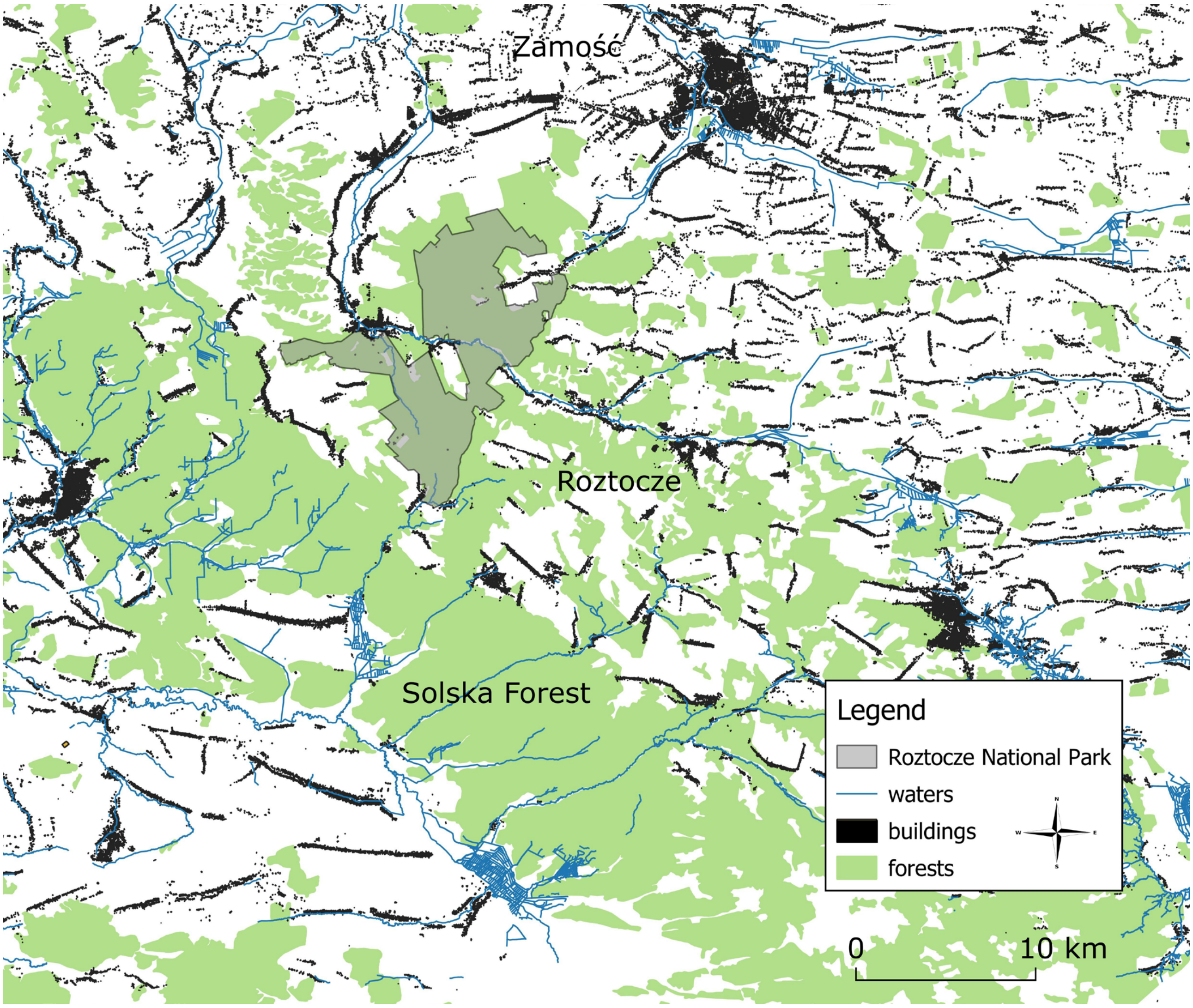

Fig. 1. The study area – Roztocze and Solska Forest in south-east Poland.

The wolf population has been present in this region continuously throughout the second half of the 20th century (Wolsan et al. 1992, Głowaciński & Profus 1997). However, it was intensively hunted until it became protected in most of Poland (including our study area) in 1995 and then in the whole country in 1998 (Mysłajek & Nowak 2015). The survey conducted at the beginning of the 21st century revealed that the region is inhabited by at least five wolf family groups (Jędrzejewski et al. 2002a). Analyses of environmental factors proved that this area is rich in habitats suitable for large carnivores (Jędrzejewski et al. 2005, 2008) and has a good connection with other forests through ecological corridors (Huck et al. 2010, 2011). Along with wolves, the Eurasian lynx *Lynx lynx* also occurs in the study area (Niedziałkowska et al. 2006).

Assessment of the wolf diet

To assess the composition of the wolf diet, we analysed the content of wolf scats. Between 2017-2020 302 scats of wolves were opportunistically collected (Roztocze n = 146 and Solska Forest n = 156). Ongoing studies based on tracking, genetic analyses and telemetry (Mysłajek et al. 2018, S. Nowak and R.W. Mysłajek, unpublished data) revealed that territories of local wolf family groups include fragments of both Roztocze and Solska Forest. Thus, in our analyses, data were polled from both regions. Scats were picked up mainly along forest roads frequently used by wolves for movement and marking hot spots (Stępniak et al. 2020). Genetic samples were obtained from 192 fresh scats, and a fragment of the mtDNA control region and 13 polymorphic autosomal microsatellite loci were analysed to confirm proper species identification (see Szewczyk et al. 2019 for details of the DNA analysis). Every sample was placed in a paper envelope and dried for five days at 70 °C in a laboratory drier, then washed through a 0.5 mm-mesh sieve and redried.

Prey species were identified using hair identification keys (Debrot et al. 1982, Pucek 1984, Teerink 1991, De Marinis & Asprea 2006) and compared with reference material. The composition of food was expressed as: 1) the 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 item relative to the total biomass consumed by wolves. The biomass of food items was calculated by multiplying the weight of prey remains identified in scats by the following coefficients of digestibility: ungulates (118), medium-sized mammals (50), small rodents and insectivores (23), plant material (4) (Jędrzejewska & Jędrzejewski 1998).

Levins' (1968) formula was applied to estimate the breadth of the wolf food niche:

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

where *pi* is the contribution of group *i* of wolf prey to the total biomass of food consumed by wolves. Identified wolf prey was classified into the following groups: 1) wild ungulates, 2) domestic animals, 3) medium-sized wild mammals, and 4) others (e.g. small mammals, plants, etc.). Therefore, the *B* index could range from 1 (strong specialisation on one prey group) to 4 (opportunistic, preying on all prey groups).

The similarity of diet composition was calculated between spring-summer (April-September, n = 68 scats) and autumn-winter (October-March, n = 234) in 2017-2020 and between two study periods 2001-2002 (Jędrzejewski et al. 2012) and 2017-2020 (this study). The seasonal differences in wolf diet were analysed only for 2017-2020, as data for 2001-2002 were insufficient. The calculation was based on two levels: 1) general food groups (wild ungulates, domestic animals, medium-sized wild mammals, and others), and 2) ungulate species (moose, red deer, roe deer, fallow deer and wild boar). The species structure of wild ungulates eaten by wolves was assessed based on the proportion of consumed biomass. In cases of the category "Cervidae undetermined", proportions of given cervid species (red deer, roe deer, fallow deer and moose) in the whole sample were determined based on proportions of these species among accurately identified samples. Pianka's (1973) formula was applied to calculate diet similarity:

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

where α_{ij} is the degree of similarity of food composition between the first (*i*) and second (*j*) time period, p_{ia} is the contribution of prey category *a* in the total biomass of prey consumed by wolves in the first time period, p_{ja} is the contribution of prey category *a* in the total biomass of prey consumed by wolves in the second period. To calculate Pianka's index, we used the software TimeOverlap 1.0., which employs a randomisation algorithm to calculate the amount of overlap of each group of randomised distributions for each iteration. The significance is determined by comparing randomised overlap values to the amount of empirical overlap (Castro-Arellano et al. 2010). We used 10,000 iterations to generate null distributions and considered significance at $\alpha = 0.05$.

For wild ungulates, the selectivity index *D* was assessed utilising the formula of Jacobs (1974):

$$D = \frac{r - p}{r + p - 2rp}$$

where *r* is the fraction of a species in the wolf diet and *p* is the fraction of that species in the ungulate community. Selectivity index *D* range from –1 (minimum negative selection) to 1 (maximum positive selection). Species structure of wild ungulates eaten by wolves was assessed based on the proportion of their occurrence in scats. The occurrence of a given species in a scat was treated as one specimen. In cases where we were unable to accurately classify cervid species ("Cervidae undetermined" category), proportions of given cervid species (red deer, roe deer, fallow deer and moose) in the whole sample were determined based on the proportions of these species among accurately identified samples. The structure of ungulate communities in the study area was estimated using data on game inventories for 2017-2020 provided by the Roztocze National Park and hunting grounds no. 277, 278, 279, 280, 281, 295, 296, 297, 306 and 319 published in the Forest Data Bank (State Forests 2021), while for 2001-2002, it was obtained from Jędrzejewski et al. (2012). Official data on ungulate numbers are derived from various methods of censuses, including winter tracking after a fresh snowfall, drive counts and year-round observations (Wawrzyniak et al. 2010).

Results

Grey wolves inhabiting the Roztocze and Solska Forest primarily prey on wild ungulates, comprising 96.5% and 96.7% consumed biomass in 2001-2002 and 2017-2020, respectively (Table 1). The roe deer was the most important prey, which made up 57.8% of the biomass consumed in 2001-2002 and 49.2% in 2017-2020. Between the two study periods, consumption of roe deer and red deer slightly decreased. However,

Table 1. Wolf diet in the Roztocze and Solska Forest in 2001-2002 (Jędrzejewski et al. 2012) and 2017-2020 (this study). %O: percentage of occurrence in scats, %B: percentage of total biomass consumed. (+) Contribution to diet < 0.05%.

Food item	2001-2002		2017-2020	
	%B	%O	%B	%O
Red deer *Cervus elaphus*	19.5	15.5	15.9	13.6
Roe deer *Capreolus capreolus*	57.8	51.2	49.2	43.4
Fallow deer *Dama dama*	-	-	2.9	3.0
Moose *Alces alces*	-	-	0.3	0.7
Undetermined cervids	13.4	27.4	2.3	6.0
Wild boar *Sus scrofa*	5.8	17.9	26.1	34.4
Wild ungulates total	96.5	97.6	96.7	96.4
European hare *Lepus europaeus*	0.8	2.4	1.0	1.7
Red fox *Vulpes vulpes*	-	-	0.4	0.3
European beaver *Castor fiber*	-	-	0.8	1.3
Medium-sized mammals total	0.8	2.4	2.2	3.3
Domestic dog *Canis lupus familiaris*	2.1	4.8	1.1	1.3
Cattle	0.6	1.2	-	-
Domestic animals total	2.7	6.0	1.1	1.3
Small rodents	+	6.0	+	0.7
Birds	+	1.2	-	-
Plant material	+	34.5	+	14.9
Plastic, rope	-	-	0.0	0.7
Number of scats analysed	84		302	
Biomass of food consumed (kg)	160.0		327.6	

the opposite trend was recorded for wild boar, with the biomass of this species consumed by wolves being four times higher in 2017-2020 than two decades earlier. Both moose and fallow deer were recorded in the wolf diet only in 2017-2020 (Table 1).

Among medium-sized mammals, only European hare reached ca. 1% of the consumed biomass in both study periods, while red fox and Eurasian beaver were sporadically eaten only in 2017-2020 (Table 1). Domestic dogs comprised 2.1% consumed biomass in 2001-2002 and only 1.1% in 2017-2020. Livestock – exclusively cattle – was consumed only in 2001-2002 and constituted 0.8% of the biomass consumed. The biomass of other food items, such as small rodents or birds, was negligible (Table 1).

The breadth of the wolf diet was very narrow and identical in both study periods (B = 1.07). The similarity of diet composition between the two study periods was high when four general food categories were considered (α = 0.999) and when only ungulates were considered (α = 0.930). The breadth of the food niche was narrow in both spring-summer and autumn-winter (B = 1.09 and B = 1.07, respectively) (Table 2). Similarity of diet composition was high (α = 0.999) for general food categories but moderate (α = 0.710) for ungulates.

From 2001-2002 the wild ungulate community in the Roztocze and Solska Forest consisted of four species: moose (0.3%), red deer (24.0%), roe deer (64.7%) and wild boar (11.0%), while in 2017-2020 it consisted of five species: moose (7.5%), red deer (28.8%), fallow deer (0.8%), roe deer (52.7%) and wild boar (10.1%). Jacob's selectivity indexes (D) revealed that wolves in 2001-2002 positively selected wild boar (D = 0.213), preyed on roe deer proportionally to its occurrence in the environment (D = 0.004), and avoided, although to a different extent, moose (D = –1.0), and red deer (D = –0.144). In 2017-2020, however, wolves positively select wild boar (D = 0.710) and fallow deer (D = 0.588), and avoided moose (D = –0.862), red deer (D = –0.446) and roe deer (D = –0.193).

Table 2. Comparison of the wolf diet in the Roztocze and Solska Forest in spring-summer (April-September) and autumn-winter (October-March) seasons, 2017-2020. %O: percentage of occurrence in scats, %B: percentage of total biomass consumed. (+) Contribution to diet < 0.05%.

Food item	Spring-summer		Autumn-winter	
	%B	%O	%B	%O
Red deer *Cervus elaphus*	28.3	17.6	13.1	10.7
Roe deer *Capreolus capreolus*	19.7	17.6	55.9	50.9
Fallow deer *Dama dama*	-	-	3.5	3.8
Moose *Alces alces*	1.5	2.9	-	-
Undetermined cervids	2.3	7.4	2.3	5.6
Wild boar *Sus scrofa*	43.9	50.0	22.0	29.9
Wild ungulates total	95.7	98.5	96.8	95.7
European hare *Lepus europaeus*	1.6	2.9	0.9	1.3
Red fox *Vulpes vulpes*	-	-	0.5	0.4
European beaver *Castor fiber*	2.6	2.9	0.4	0.9
Medium-sized mammals total	4.2	5.8	1.8	2.6
Domestic dog *Canis lupus familiaris*	-	-	1.4	1.7
Domestic animals total	-	-	1.4	1.7
Small rodents	+	1.5	+	0.4
Plant material	0.1	19.1	+	13.7
Plastic, rope	-	-	-	0.9
Number of scats analysed	68		234	
Biomass of food consumed (kg)	61.0		266.6	

Discussion

The grey wolf is an opportunistic predator displaying extensive dietary plasticity. Although it preys mainly on wild ungulates across its range, the wolf frequently supplements its diet with smaller vertebrates and even plant material (Zlatanova et al. 2014, Newsome et al. 2016, Homkes et al. 2020). Moreover, numerous studies demonstrated temporal and spatial changes in food habits (Meriggi et al. 2011, Lafferty et al. 2014, Lodberg-Holm et al. 2021). In Central Europe, wolves primarily hunt medium and small wild ungulates (i.e. red deer, roe deer and wild boar) but avoid large ungulate species such as moose and European bison (Jędrzejewski et al. 2012). Regionally, however, the Eurasian beaver became one of the most important food items in the wolf diet (Špinkytė-Bačkaitienė & Pėtelis 2012, Sidorovich et al. 2017, Mysłajek et al. 2019, 2021).

Our study in the Roztocze and Solska Forest revealed stability in wolf food habits, as they focused on wild ungulates in two study periods over two decades. However, changes in the species composition of wild ungulates in the wolf diet were recorded, i.e. a decrease in red deer and roe deer and an increase in wild boar, as well as a preference of wolves for wild boar; this pattern is unexpected, considering earlier studies; red deer were thought to be the preferred prey of wolves in Central and East Europe (Okarma 1995). Moreover, based on long-term data from the Białowieża Forest (north-east Poland), Jędrzejewski et al. (2000) suggested that with an increase in red deer density, wolves hunt less roe deer and wild boar. In our study area, the red deer population showed a three-fold increase over the first two decades of the 21st century (Central Statistical Office 2021), though it was not accompanied by an increase in the share of this ungulate in the wolf diet. A similar pattern was recorded in the eastern part of the Polish Carpathians, where in 1989-1992, roe deer were eaten less frequently than red deer (Śmietana & Klimek 1993), while in 2013-2014, the opposite situation was recorded (Gorzelewska et al. 2017). These observations, along with several other studies, reveal the dominance of roe deer in the wolf diet over red deer in Central Europe (Nowak et al. 2011, Wagner et al. 2012, Mysłajek et al. 2019, 2021) despite a high abundance of red deer (Central Statistical Office 2021). These findings prompt a rethink of previously proposed (Okarma 1995, Jędrzejewski et al. 2012) patterns of wolf preferences for red deer.

In the Roztocze and Solska Forest, wolves have shown selection towards fallow deer, which is an alien species introduced for hunting purposes (Głowaciński et al. 2011). Despite its competition with native cervids (Focardi et al. 2006, Dolman & Wäber 2008, Obidziński et al. 2013), this species has not been listed as an invasive alien species in Poland, and the introduction of fallow deer is continued in different regions of the country (Kopij et al. 2017). Wolves may help to eliminate this alien species, but the growing popularity of this species as game, and the behaviour of hunters to increase its range and numbers, makes this goal unlikely.

Wild boar were rarely positively selected from the ungulate community in Central Europe (Jędrzejewski et al. 2012), except for some parts of the Carpathians (Lanszki et al. 2012, Sin et al. 2019). This species, however, is an essential and often dominant part of the wolf diet in southern Europe (Nores et al. 2008, Meriggi et al. 2011, Mori et al. 2017, Dolapchiev et al. 2022). Wild boar are a sociable, conspicuous and locally abundant species, readily detectable to a predator (Mori et al. 2017). Mech et al. (2015) considered wild boar as rather difficult prey for wolves, but recent studies have shown that wolves prey mainly on young individuals, especially piglets, which are easier to capture (Nores et al. 2008). It is also supported by our observations of a high proportion of wild boar in the wolf diet in spring-summer when piglets are abundant. Moreover, an increase of wild boar in the wolf diet in the Roztocze and Solska Forest coincided with an outbreak of the African Swine Disease (ASF) in this area (Woźniakowski et al. 2021). ASF causes high wild boar mortality, and wolves may not only easily kill individuals weakened by the disease but also consume carcasses of dead individuals. A recent study (Szewczyk et al. 2021a) showed that the utilisation of carcasses of wild boar infected by the ASF virus should be considered a valuable ecosystem service provided by wolves.

Contrary to other studies on the food habits of wolves from the Baltic subpopulation, which indicated the importance of the Eurasian beaver as a prey alternative to ungulates (Jędrzejewski et al. 2012, Špinkytė-Bačkaitienė & Pėtelis 2012, Sidorovich et al. 2017, Mysłajek et al. 2021), consumption of this species by wolves inhabiting the Roztocze and Solska Forest was low. The abundance of the Eurasian beaver in our study area, however, is much lower than in north-eastern Europe (Halley et al. 2021), and in southern Poland this species does not occur in the wolf diet (Nowak et al. 2005, Gorzelewska et al. 2017, Mysłajek et al. 2021).

Wolves in the Roztocze and Solska Forest rarely prey on livestock, and this pattern was visible for both study periods. Overall, the proportion of livestock in the wolf diet in Poland varies enormously, both spatially and temporarily (Śmietana & Klimek 1993, Nowak et al. 2005, 2011, Jędrzejewski et al. 2012, Gorzelewska et al. 2017), and is significantly affected by the implementation of proper livestock protection measures (Nowak et al. 2005). However, domestic dogs were consumed in 2001-2002 and 2017-2020 in our study area. The killing of dogs by wolves is considered a significant source of conflict between predators and humans (Bassi et al. 2021, Iliopoulos et al. 2021). Nonetheless, free-ranging dogs are abundant in natural habitats across Poland, being important predators of wild species, including game animals and livestock (Krauze-Gryz & Gryz 2014, Wierzbowska et al. 2016). Thus wolf predation on dogs may be seen as having a conservation benefit for native species in local Natura 2000 sites (O'Bryan et al. 2018).

In south-eastern Poland, the grey wolf co-exists with the Eurasian lynx, which also hunts wild ungulates. In contrast to wolves, which kill a large variety of prey species, the lynx preys almost exclusively on roe deer (Mysłajek et al. 2022). This species is the most abundant ungulate in Poland, and its population is steadily increasing (Central Statistical Office 2021); therefore, potential wolf-lynx competition over prey is unlikely (Schmidt et al. 2009).

Our study confirmed that wolves in south-eastern Poland rely mainly on wild ungulates for prey and only occasionally kill domestic ungulates. Taking into consideration the rich food base, i.e. numerous and increasing populations of wild ungulates (Central Statistical Office 2021), rare incidents of livestock depredation, and availability of large patches of suitable habitats (Jędrzejewski et al. 2005, 2008, Huck et al. 2010), the persistence of wolves in the Roztocze and Solska Forest is so far secure. This situation will aid in keeping a favourable conservation status of the wolf in the local Natura 2000 sites, where this species is one of the conservation targets (Diserens et al. 2017).

Acknowledgements

We thank the staff of the Roztocze National Park for their help during our field studies. Project funded by the Forest Fund of the Polish Forest Holding "State Forests" (grants EZ.0290.1.27.2018, EZ.0290.1.15.2019, EZ.0290.1.16.2020 and EZ.0290.1.16.2021). The study was co-financed by the National Science Centre, Poland (grant No. 2020/39/B/NZ9/01829).

Author Contributions

R.W. Mysłajek – conceptualisation, methodology, investigation, formal analysis, writing original draft, review and editing, P. Stachyra – investigation, funding acquisition, M. Figura – investigation, M. Nędzyńska-Stygar – investigation, formal analysis, R. Stefański – investigation, M. Korga – investigation, I. Kwiatkowska – investigation, K.M. Stępniak – investigation, K. Tołkacz – investigation, review and editing, S. Nowak – conceptualisation, methodology, investigation, review and editing.

Literature

Arbieu U., Mehring M., Bunnefeld N. et al. 2019: Attitudes towards returning wolves (*Canis lupus*) in Germany: exposure, information sources and trust matter. *Biol. Conserv. 234: 202–210.*

Bassi E., Pervan I., Ugarković D. et al. 2021: Attacks on hunting dogs: the case of wolf – dog interactions in Croatia. *Eur. J. Wildl. Res. 67: 4.*

Boitani L. 2018: *Canis lupus*. The IUCN Red List of Threatened Species 2018: e.T3746A133234888. Downloaded on 20 November 2021. *https://10.2305/IUCN.UK.2018-2.RLTS.T3746A133234888.en*

Borowik T., Cornulier T. & Jędrzejewska B. 2013: Environmental factors shaping ungulate abundances in Poland. *Acta Theriol. 58: 403–413.*

Castro-Arellano I., Lacher T.E., Willing M.R. & Rangel T.F. 2010: Assessment of assemblage-wide temporal niche segregation using null models. *Methods Ecol. Evol. 1: 311–318.*

Central Statistical Office 2021: Local data bank. *https://bdl.stat.gov.pl*

Chapron G., Kaczensky P., Linnell J.D.C. et al. 2014: Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science 346: 1517–1519.*

Chmielewski T.J. & Sowińska B. 2011: Landscape ecological structure of the Roztocze and Solska Forest regions: a comparative study of models from 1988 and 2011. *Teka Kom. Ochr. Kszt. Środ. Przyr. 8: 13–23.*

Czarnomska S., Jędrzejewska B., Borowik T. et al. 2013: Concordant mitochondrial and microsatellite DNA structuring between Polish lowland and Carpathian Mountain wolves. *Conserv. Genet. 14: 573–588.*

De Marinis A.M. & Asprea A. 2006: Hair identification key of wild and domestic ungulates from southern Europe. *Wildl. Biol. 12: 305–320.*

Debrot S., Mermod S., Fivaz G. & Weber J.-M. 1982. Atlas des poils de mammifères d'Europe. *Université de Neuchâtel, Neuchâtel, Switzerland.*

Diserens T.A., Borowik T., Nowak S. et al. 2017: Deficiencies in Natura 2000 for protecting recovering large carnivores: a spotlight on the wolf *Canis lupus* in Poland. *PLOS ONE 12: e0184144.*

Dolapchiev N.P., Zlatanova D.P., Popova E.D. et al. 2022: Apostatic or anti-apostatic? Prey selection of wolf *Canis lupus* L. (Mammalia: Canidae) in the Osogovo Mountain, Bulgaria. *Acta Zool. Bulg. 74: 235–244.*

Dolman P.M. & Wäber K. 2008: Ecosystem and competition impacts of introduced deer. *Wildl. Res. 35: 202–214.*

Dziaducha S. 2021: Statistical yearbook of Lubelskie Voivodship. *Statistical Office, Lublin, Poland.*

Focardi S., Aragno P., Montanaro P. & Riga F. 2006: Inter-specific competition from fallow deer *Dama dama* reduces habitat quality for the Italian roe deer *Capreolus capreolus italicus*. *Ecography 29: 407–417.*

Głowaciński Z. & Profus P. 1997: Potential impact of wolves *Canis lupus* on prey populations in eastern Poland. *Biol. Conserv. 80: 99–106.*

Głowaciński Z., Okarma H., Pawłowski J. & Solarz W. 2011: Alien species in the fauna of Poland. *Instytut Ochrony Przyrody PAN, Kraków, Poland. (in Polish)*

Gorzelewska A., Moska M., Pirga B. & Piróg A. 2017: Diet of the wolf *Canis lupus* (Linnaeus, 1758) in the Bieszczady Mountains, Poland. *Roczniki Bieszczadzkie 25: 309–320.*

Halley D., Rosell F. & Saveljev A. 2021: Population and distribution of Eurasian beaver (*Castor fiber*). *Balt. For. 18: 168–175.*

Homkes A.T., Gable T.D., Windels S.K. & Bump J.K. 2020: Berry important? Wolf provisions pups with berries in Northern Minnesota. *Wildl. Soc. Bull. 44: 221–223.*

Huck M., Jędrzejewski W., Borowik T. et al. 2010: Habitat suitability, corridors and dispersal barriers for large carnivores in Poland. *Acta Theriol. 55: 177–192.*

Huck M., Jędrzejewski W., Borowik T. et al. 2011: Analyses of least cost paths for determining effects of habitat types on landscape permeability: wolves in Poland. *Acta Theriol. 56: 91–101.*

Iliopoulos Y., Antoniardi E., Kret E. et al. 2021: Wolf–hunting dog interactions in a biodiversity hot spot area in Northern Greece: preliminary assessment and implications for conservation in the Dadia-Lefkimi-Soufli Forest National Park and adjacent areas. *Animals 11: 3235.*

Jacob J. 1974: Quantitative measurement of food selection. A modification of the forage ratio and Ivlev's selectivity index. *Oecologia 14: 413–417.*

Jędrzejewska B. & Jędrzejewski W. 1998: Predation in vertebrate communities. The Białowieża Primeval Forest as a case study. *Springer, Berlin, Germany.*

Jędrzejewski W., Jędrzejewska B., Okarma H. et al. 2000: Prey selection and predation by wolves in Białowieża Primeval Forest, Poland. *J. Mammal. 81: 197–212.*

Jędrzejewski W., Jędrzejewska B., Zawadzka B. et al. 2008: Habitat suitability model for Polish wolves *Canis lupus* based on long-term national census. *Anim. Conserv. 11: 377–390.*

Jędrzejewski W., Niedziałkowska M., Hayward M.W. et al. 2012: Prey choice and diet of wolves related to ungulate communities and wolf subpopulations in Poland. *J. Mammal. 93: 1480–1492.*

Jędrzejewski W., Niedziałkowska M., Mysłajek R.W. et al. 2005: Habitat selection by wolves *Canis lupus* in the uplands and mountains of southern Poland. *Acta Theriol. 50: 417–428.*

Jędrzejewski W., Nowak S., Schmidt K. & Jędrzejewska B. 2002a: The wolf and the lynx in Poland – results of a census conducted in 2001. *Kosmos 51: 491–499.*

Jędrzejewski W., Schmidt K., Theuerkauf J. et al. 2002b: Kill rates and predation by wolves on ungulate populations in Białowieża Primeval Forest (Poland). *Ecology 83: 1341–1356.*

Kopij G. 2017: Expansion of alien carnivore and ungulate species in SW Poland. *Rus. J. Biol. Invasions 8: 290–299.*

Krange O., Sandström C., Tangeland T. & Ericsson G. 2017: Approval of wolves in Scandinavia: a comparison between Norway and Sweden. *Soc. Nat. Resour. 30: 1127–1140.*

Krauze-Gryz D. & Gryz J. 2014: Free-ranging domestic dogs (*Canis familiaris*) in Central Poland: density, penetration range and diet composition. *Pol. J. Ecol. 62: 183–193.*

Lafferty D.J.R., Belant J.L., White K.S. et al. 2014: Linking wolf diet to changes in marine and terrestrial prey abundance. *Arctic 67: 143–148.*

Lanszki J., Márkus M., Újváry D. et al. 2012: Diet of wolves *Canis lupus* returning to Hungary. *Acta Theriol. 57: 189–193.*

Levins R. 1968: Evolution in changing environments. *Princeton University, Princeton, USA.*

Linnell J., Salvatori V. & Boitani L. 2008: Guidelines for population level management plans for large carnivores in Europe. *https://ec.europa.eu/environment/nature/conservation/species/carnivores/pdf/guidelines_for_population_level_management.pdf*

Lodberg-Holm H.K., Teglas B.S., Tyers D.B. et al. 2021: Spatial and temporal variability in summer diet of gray wolves (*Canis lupus*) in the Greater Yellowstone Ecosystem. *J. Mammal. 102: 1030–1041.*

Maciejewski Z. & Szwagrzyk J. 2011: Long-term changes in stand composition of natural forest associations on the Roztocze highlands (eastern Poland). *Pol. J. Ecol. 59: 535–549.*

Mech L.D. & Boitani L. 2003: Wolves: behavior, ecology and conservation. *University of Chicago Press, Chicago-London.*

Mech L.D., Smith D.W. & MacNulty D.R. 2015: Wolves on the hunt. The behavior of wolves hunting wild prey. *University of Chicago Press, Chicago-London.*

Meriggi A., Brangi A., Schenone L. et al. 2011: Changes of wolf (*Canis lupus*) diet in Italy in relation to the increase of wild ungulate abundance. *Ethol. Ecol. Evol. 23: 195–210.*

Mori E., Benatti L., Lovari S. & Ferretti F. 2017: What does the wild boar mean to the wolf? *Eur. J. Wildl. Res. 63: 9.*

Musto C., Cerri J., Galaverni M. et al. 2021: Men and wolves: anthropogenic causes are an important driver of wolf mortality in human-dominated landscapes in Italy. *Glob. Ecol. Conserv. 32: e01892.*

Mysłajek R.W. & Nowak S. 2015: Not an easy road to success: the history of exploitation and restoration of the wolf population in Poland after World War Two. In: Masius M. & Sprenger J. (eds.), Fairytale in question: historical interactions between humans and wolves. *White Horse Press, Cambridge, UK: 247–258.*

Mysłajek R.W., Romański M., Kwiatkowska I. et al. 2021: Temporal changes in the wolf *Canis lupus* diet in Wigry National Park (northeast Poland). *Ethol. Ecol. Evol. 33: 628–635.*

Mysłajek R.W., Stachyra P., Figura M. & Nowak S. 2022: Food habits of the Eurasian lynx *Lynx lynx* in south-east Poland. *J. Vertebr. Biol. 71: 21061.*

Mysłajek R.W., Stachyra P., Szewczyk M. et al. 2018: Wolf *Canis lupus* and lynx *Lynx lynx* in Roztocze National Park, 2016-2017. *Przegląd Przyrodniczy 29: 71–83.*

Mysłajek R.W., Tomczak P., Tołkacz K. et al. 2019: The best snacks for kids: the importance of beavers *Castor fiber* in the diet of wolf *Canis lupus* pups in north-western Poland. *Ethol. Ecol. Evol. 31: 506–513.*

Newsome T.M., Boitani L., Chapron G. et al. 2016: Food habits of the world's grey wolves. *Mammal Rev. 46: 255–269.*

Niedziałkowska M., Jędrzejewski W., Mysłajek R.W. et al. 2006: Environmental correlates of Eurasian lynx occurrence in Poland – large scale census and GIS mapping. *Biol. Conserv. 133: 63–69.*

Nores C., Llaneza L. & Álvarez Á. 2008: Wild boar *Sus scrofa* mortality by hunting and wolf *Canis lupus* predation: an example in northern Spain. *Wildl. Biol. 14: 44–51.*

Nowak S. & Mysłajek R.W. 2017: Response of the wolf (*Canis lupus* Linnaeus, 1758) population to various management regimes at the edge of its distribution range in Western Poland, 1951–2012. *Appl. Ecol. Environ. Res. 15: 187–203.*

Nowak S., Mysłajek R.W. & Jędrzejewska B. 2005: Patterns of wolf *Canis lupus* predation on wild and domestic ungulates in the Western Carpathian Mountains (S Poland). *Acta Theriol. 50: 263–276.*

Nowak S., Mysłajek R.W., Kłosińska A. & Gabryś G. 2011: Diet and prey selection of wolves *Canis lupus* recolonising Western and Central Poland. *Mamm. Biol. 76: 709–715.*

Nowak S., Żmihorski M., Figura M. et al. 2021: The illegal shooting and snaring of legally protected wolves in Poland. *Biol. Conserv. 264: 109367.*

O'Bryan C.J., Braczkowski A.R., Beyer H.L. et al. 2018: The contribution of predators and scavengers to human well-being. *Nat. Ecol. Evol. 2: 229–236.*

Obidziński A., Kiełtyk P., Borkowski J. et al. 2013: Autumn-winter diet overlap of fallow, red, and roe deer in forest ecosystems, Southern Poland. *Centr. Eur. J. Biol. 8: 8–17.*

Okarma H. 1995: The trophic ecology of wolves and their predatory role in ungulate communities of forest ecosystems in Europe. *Acta Theriol. 40: 335–386.*

Pianka E.R. 1973: The structure of lizard communities. *Annu. Rev. Ecol. Syst. 4: 53–74.*

Pilot M., Jędrzejewski W., Branicki W. et al. 2006: Ecological factors influence population genetic structure of European grey wolves. *Mol. Ecol. 15: 4533–4553.*

Pilot M., Jędrzejewski W., Sidorovich V.E. et al. 2012: Dietary differentiation and the evolution of population genetic structure in a highly mobile carnivore. *PLOS ONE 7: e39341.*

Pucek Z. 1984: Key for identification of Polish mammals. *Polish Scientific Publishers PWN, Warszawa, Poland.*

Salvatori V., Balian E., Blanco J.C. et al. 2020: Applying participatory processes to address conflicts over the conservation of large carnivores: understanding conditions for successful management. *Front. Ecol. Evol. 8: 182.*

Salvatori V. & Mertens A.D. 2012: Damage prevention methods in Europe: experiences from LIFE nature projects. *Hystrix 23: 73–79.*

Schmidt K., Jędrzejewski W., Okarma H. & Kowalczyk R. 2009: Spatial interactions between grey wolves and Eurasian lynx in Białowieża Primeval Forest, Poland. *Ecol. Res. 24: 207–214.*

Sidorovich V., Schnitzler A., Schnitzler C. et al. 2017: Responses of wolf feeding habits after adverse climatic events in central-western Belarus. *Mamm. Biol. 83: 1–7.*

Sidorovich V.E., Tikhomirova L.L. & Jędrzejewska B. 2003: Wolf *Canis lupus* numbers, diet and damage to livestock in relation to hunting and ungulate abundance in north-eastern Belarus during 1990–2000. *Wildl. Biol. 9: 103–111.*

Sin T., Gazzola A., Chiriac S. & Rîșnoveanu G. 2019: Wolf diet and prey selection in the South-Eastern Carpathian Mountains, Romania. *PLOS ONE 14: e0225424.*

State Forests 2021: Forest data bank. *https://www.bdl.lasy.gov.pl*

Stępniak K.M., Szewczyk M., Niedźwiecka N. & Mysłajek R.W. 2020: Scent marking in wolves *Canis lupus* inhabiting managed lowland forests in Poland. *Mammal Res. 65: 629–638.*

Szewczyk M., Łepek K., Nowak S. et al. 2021a: Evaluation of the presence of ASFV in wolf feces collected from areas in Poland with ASFV persistence. *Viruses 13: 2062.*

Szewczyk M., Nowak C., Hulva P. et al. 2021b: Genetic support for the current discrete conservation unit of the Central European wolf population. *Wildl. Biol. 2021: wlb.00809.*

Szewczyk M., Nowak S., Niedźwiecka N. et al. 2019: Dynamic range expansion leads to establishment of a new, genetically distinct wolf population in Central Europe. *Sci. Rep. 9: 19003.*

Śmietana W. & Klimek A. 1993: Diet of wolves in the Bieszczady Mountains, Poland. *Acta Theriol. 38: 245–251.*

Špinkytė-Bačkaitienė R. & Pėtelis K. 2012: Diet composition of wolves (*Canis lupus* L.) in Lithuania. *Acta Biol. Univ. Daugavp. 12: 100–105.*

Teerink B.J. 1991: Atlas and identification key. Hair of west European mammals. *Cambridge University Press, Cambridge, UK.*

Tittenbrun A. 2019: Protection pln of the Roztocze National Park with materials used to its elaboration. *Roztoczański Park Narodowy, Zwierzyniec, Poland. (in Polish)*

Trouwborst A. 2015: Global large carnivore conservation and international law. *Biodivers. Conserv. 24: 1567–1588.*

Valdmann H., Andersone-Lilley Z., Koppa O. et al. 2005: Winter diets of wolf *Canis lupus* and lynx *Lynx lynx* in Estonia and Latvia. *Acta Theriol. 50: 521–527.*

Valdmann H. & Saarma U. 2020: Winter diet of wolf (*Canis lupus*) after the outbreak of African swine fever and under the severely reduced densities of wild boar (*Sus scrofa*). *Hystrix 31: 154–156.*

van Heel B.F., Boerboom A.M., Fliervoet J.M. et al. 2017: Analysing stakeholders' perceptions of wolf, lynx and fox in a Dutch riverine area. *Biodivers. Conserv. 26: 1723–1743.*

Wagner C., Holzapfel M., Kluth G. et al. 2012: Wolf (*Canis lupus*) feeding habits during the first eight years of its occurrence in Germany. *Mamm. Biol. 77: 196–203.*

Wawrzyniak P., Jędrzejewski W., Jędrzejewska B. & Borowik T. 2010: Ungulate management in Poland. In: Apollonio M., Putman R. & Andersen R. (eds.), Ungulate management in Europe in the 21st century. *Cambridge University Press, Cambridge, UK: 223–242.*

Wierzbowska I.A., Hędrzak M., Popczyk B. et al. 2016: Predation of wildlife by free-ranging domestic dogs in Polish hunting grounds and potential competition with the grey wolf. *Biol. Conserv. 201: 1–9.*

Wolsan M., Bieniek M. & Buchalczyk T. 1992: The history of distributional and numerical changes of the wolf *Canis lupus* L. in Poland. In: Bobek B., Perzanowski K. & Regelin W. (eds.), Transactions of the 18th IUGB Congress, Kraków 1987. *Świay Press, Kraków-Warszawa, Poland: 375–380.*

Woźniakowski G., Pejsak Z. & Jabłoński A. 2021: Emergence of African swine fever in Poland (2014–2021). Successes and failures in disease eradication. *Agriculture 11: 738.*

Zlatanova D., Ahmed A., Valasseva A. & Genov P. 2014: Adaptive diet strategy of the wolf (*Canis lupus* L.) in Europe: a review. *Acta Zool. Bulg. 66: 439–452.*

Žunna A., Ozoliņš J. & Pupila A. 2009: Food habits of the wolf *Canis lupus* in Latvia based on stomach analyses. *Estonian J. Ecol. 58: 141–152.*