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Feeding dynamics of the wolf (*Canis lupus*) in the anthropogenic landscape of Germany: a 20-year survey

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Abstract
In Germany, wolves live in a human-dominated landscape. The return of the wolf to Germany more than 20 years ago is a prime example of successful nature conservation; however, it has also led to conflict due to the high degree of landscape fragmentation and the feeding habits of the wolf. Here, the wolf diet composition was studied based on an analysis of 11,225 scats. Wolves in Germany mainly feed on wild ungulates, which comprise more than 94% of their diet. The predominant species are roe deer and wild boar, whereby in most territories roe deer dominate the diet composition. Depending on availability, red deer and fallow deer may also make up a high proportion of the diet. Seasonal and territorial variation in diet composition has been noted even in directly neighboring territories. Wolves preferentially hunt juveniles of the main prey species. With the exception of the mouflon, which has all but disappeared locally, no other ungulate species has vanished from the wolf's diet. This study provides an overview of the varied diet of wolves in Germany since recolonization more than 20 years ago.

Keywords Feeding ecology · Flexible adaptation · Long-term study · Prey selection · Scat analysis · Wolves

Introduction

By the mid-nineteenth century, the wolf had been completely eradicated in Germany and large parts of Western and Central Europe (Mech and Boitani 2003; Ansorge and Schellenberg 2007). Following recovery of wolf populations in eastern Poland in the twentieth century (Nowak and Mysłajek 2017), individual animals also dispersed to eastern Germany, did not, however, become established, because wolves were officially killed to prevent their settlement (Reinhardt and Kluth 2007). It was only after strict protection of the wolf in Poland in 1998 (Czarnomska et al. 2013; Nowak and Mysłajek 2016), and reunification of Germany in 1990, when the wolf was also placed under protection in the eastern federal states in accordance with European legislation, that a natural recolonization began.

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For the first time in 150 years, wolves were able to reproduce in Saxony close to the German-Polish border (Kluth et al. 2002). Over the years, the wolf population in Germany has grown steadily, spreading mainly in a north-west direction. In 2020/21, wolves were detected in 10 German federal states, and the population numbered 215 wolf territories (packs, pairs, territorial individuals) (DBBW 2023, Fig. 1).

Dietary studies of wolves have been conducted around the world for almost 80 years (Mech and Boitani 2003), often focusing on conflicts with livestock and the perceived negative impact on wild ungulates (Naughton-Treves et al. 2003; Kleiven et al. 2004; Bergstrom et al. 2009). In general, the diet composition depends on the availability of prey (Baudrot et al. 2016; Newsome et al. 2016). Wild ungulates are preferred (Meriggi et al. 1996, 2011), although wolves are opportunistic in their prey choice. They feed on domestic ungulates if wild ungulate populations are depleted by humans (Boitani 1982; Peterson and Ciucci 2003; Gazzola et al. 2007; Stahler et al. 2006) or are easily available when unprotected (Linnel and Cretois 2018). In past decades, food analyses have been published in several European countries (summarized in Newsome et al. 2016). More recently in SItaly (Mori et al. 2017; Ciucci et al. 2018; Ferretti et al. 2019), Norway (Ståhlberg et al. 2017), Poland (Mysłajek et al. 2018, 2019, 2022), Serbia (Ćirović and Penezić 2019), Greece (Petridou et al. 2019), Romania (Sin et al. 2019), Portugal (Figueiredo et al. 2020), Bosnia and Herzegovina (Trbojević et al. 2020), Estonia (Valdmann and Saarma 2020) and Germany (Ansorge et al. 2006; Wagner et al. 2012; Lippitsch et al. 2021; Reinhardt et al. 2021).

However, most of the existing studies we know of examined only a few areas and over short periods of time. Often, only estimates of frequency of occurrence of prey species in the diet of wolves were made. However, for a complete analysis, biomass calculations are also necessary to estimate how many animals are eaten by wolves. Long-term studies have been conducted in Poland (Nowak et al. 2011; Jędrzejewski et al. 2012) and Belarus (Sidorovich et al. 2003, 2017), which also took the biomass calculation into consideration. Since wolf scats have been collected for dietary analyses since the very beginning of wolf recolonization in Germany, we had the unique opportunity to conduct a long-term study on wolf feeding habits in Central Europe. This study presents a systematic assessment of the dietary habits of wolves in Germany over 20 years and provides a detailed overview of the spatial and temporal patterns and dynamics of prey selection and diet composition.

Material and methods

Study area

The study area includes parts of the wolf range in Germany, mainly in the eastern part of the country (Fig. 1). Until the early 2010s, scat was collected in all the existing territories. Later, sample collection focused on selected territories. Wolves primarily colonize the North German Lowland and partly the Central German Upland. A recent habitat suitability model (Kramer-Schadt et al. 2020) suggests that both landscapes are very suitable for wolves and at the same time highly anthropogenically shaped. The North German Lowland is a flat region with few hills formed during the last ice age. It is crossed by many rivers, such as the Elbe, Weser, Oder and Ems. It is characterized by heathlands and extensive forests, especially in eastern Saxony (SN) and southern Brandenburg (BB) (Fig. 1) and is an important region for agriculture and livestock farming. In addition, there are several active military training grounds, which played an important role in the colonization of the region by wolves (Reinhardt et al. 2019). In the initial settlement areas of north-eastern Saxony and southern Brandenburg, active and former opencast coal mines also characterize the landscape. The human population density in the North German Lowland is relatively low, with the exception of the metropolitan regions of Berlin, Hamburg, Bremen and the Ruhr area. The Central Upland extends to the south is characterized by hilly terrain. Agriculture is less pronounced, while urban density is generally higher. Compared to the lowland, levels of snow can be high until April in the Central Upland. Most of the territories studied are located in the Lowland.

Potential prey species such as roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) are present in high densities throughout the study area. Red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) are not present in all territories of the study area, but occasionally present in high densities. Mouflon (*Ovis musimon*) and sika deer (*Cervus nippon*) are only found sporadically. Other medium-sized mammals may be present in large densities in a small area, such as the beaver (*Castor fiber*) and coypu (*Myocastor coypus*), which are found naturally along rivers and in wetlands, as well as the European hare (*Lepus europaeus*).

Collection and analysis of wolf scats

A total of 11,225 wolf scats collected throughout all four seasons from May 2001 to April 2021 were used for the

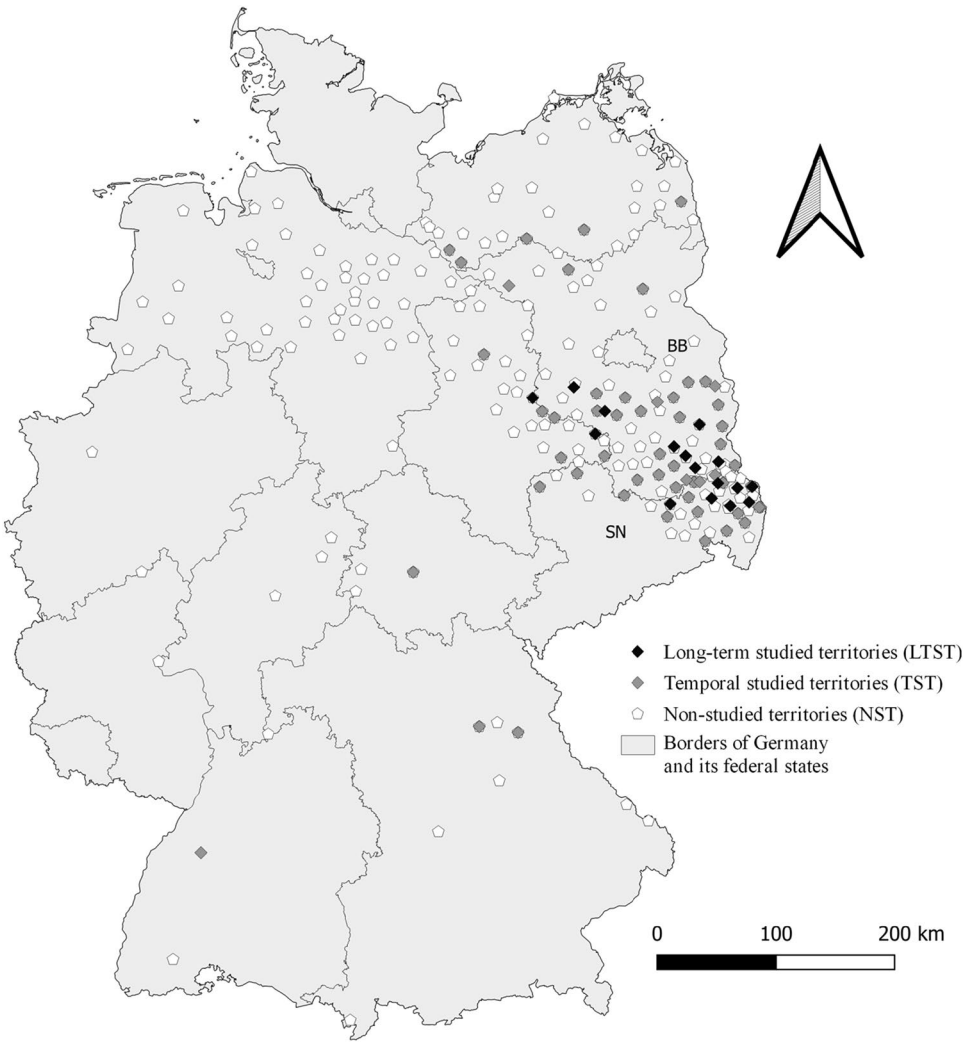

Fig. 1 Distribution of all wolf territories documented in Germany in 2020 (data from DBBW 2023); long-term studied territories (LTST) ≙ territories with more than 180 analyzed scats sampled over at least 3 years (Table 3); temporal studied territories (TST) ≙ territories from which scats were analyzed but fewer than in LTST (see Electronic appendix Table D)

diet analysis. Most of the samples were collected within the frame of the national wolf monitoring programme that is conducted annually at federal state level (Kaczensky et al. 2009; Reinhardt et al. 2015). Data evaluation took place according to monitoring years (MY, from 1st May to 30th April of the following year), which follows the biological cycle of wolves. Presence signs of wolves, such as scats or tracks were searched along forest paths on foot or driving slowly by bicycle or car. For diet analyses, the wolf scats found were collected in plastic bags, labelled with date, territory name and coordinates and stored frozen until sent to the laboratory. Identification of wolf scat followed the standards for the monitoring of wolves by Reinhardt et al. (2015). Thus, to avoid confusion with fox or dog scat, only scat that scored at least C2 (confirmed findings using the SCALP criteria) was included in the analysis. Scat that narrowly missed the C2 characteristics but had been assessed by an experienced person was also included in the analysis.

To eliminate potential pathogens, the collected scat was frozen at − 80 °C and then heated to + 70 °C. Next, the scat was treated according to the description of Jędrzejewska and Jędrzejewski (1998) following the standard methods of Lockie (1959) and Goszczyński (1974). The scat was soaked in water, washed in a sieve with a 1 mm mesh width and oven-dried at + 40 °C. After drying, soil and stones were removed. The dry weight (0.1 g precision) of all indigestible food items in a sample such as hairs, bones, hooves, claws, feathers, fruit remains and stones, was determined.

Prey remains of mammals were identified using reference collections. The hairs were examined microscopically using the atlas keys of Teerink (1991) and Meyer et al. (2002). Other macro components in the scats (e.g., hooves, teeth, bones) were also used for species determination, however, also to estimate prey age. Prey remains were classified into three age classes: "small juvenile" (from birth to 3 months), "juvenile" (3–12 months) and "adult" (older than 12 months).

Other remains, e.g., of birds and fish were identified using museum collections. Finally, plant matter such as berries and fruits were also considered as food.

Data analysis

For each food category and prey species, the frequency of occurrence (F %) was calculated:

$$F_i[\%] = \frac{n_i * 100\%}{n_{\text{scats}}}, \tag{1}$$

where n_i is the number of scats containing a certain food item and n_{scats} is the total number of samples examined. The biomass (BM_i) consumed was calculated following Goszczyński (1974):

$$\text{BM}_i = \text{DM}_i[\text{kg}] * \text{DC}_i, \tag{2}$$

based on specific digestion-coefficients DC_i (Table 1) and the summarized dry mass of each prey category DM_i of washed scat. Both estimations were applied to the general, annual and territorial diet composition. To evaluate annual differences, the collected scats were assigned according to a MY. We used the given coordinates to assign each scat to a certain wolf territory. For more detailed analyses, only scats from long-term studied territories (LTST) were considered. The χ^2-test was used for statistical validation of the seasonal, territorial and annual differences in the main prey species (MPS). Annual changes were also tested with a linear model ($y = ax + b$) to determine the presence of trends in the MPS.

The dietary overlap or the similarity between diets of different territories was assessed using the Morisita index (Morisita 1959) modified by Horn (1966):

$$C = \frac{2 + \sum (x_i * y_i)}{\sum x_i^2 + \sum y_i^2}, \tag{3}$$

where x_i and y_i are amounts of the ith prey species/category in the diet of the territory x and y, respectively. The value of the index varies between 0 (no overlap) and 1 (complete overlap).

Furthermore, the prey preference was calculated using the Ivlev selection index D by Jacobs (1974) with a significance level of 0.2 or − 0.2 (Mattioli et al. 2004). Since reliable density estimates of the prey species are not available for our study area, we used hunting bag data instead. The availability of the MPS was linked its proportion in the wolf diet:

$$D_i = \frac{r_i - p_i}{r_i + p_i - 2r_i p_i}, \tag{4}$$

where r is the biomass of the prey species i consumed by the wolf in the calculated wolf diet, and p the mean supply of the prey species i in the study period of the individual packs computed from the hunting bags of the individual areas (DBU Natural Heritage 2023 pers. comm.; Ministry for Infrastructure and Agriculture of the State of Brandenburg 2009, 2011, 2013; Ministry of Regional Development, Environment and Agriculture of the State of Brandenburg 2015, 2018; Ministry of Agriculture, Environment and Climate Protection of the State of Brandenburg 2021; Supreme Hunting Authority of the Federal State of Saxony 2023 pers. comm.) and usable net weight of the prey (Table 2).

The mean weights of the MPS were used to convert the consumed biomass to the number of preyed animals. A daily rate per wolf of 3 kg of live prey is assumed (Wotschikowsky 2017).

The mean number of wolves in each pack was available from the monitoring data collected annually at federal state level (data of the environmental agencies of the federal states, Table 3). The pack sizes used are not estimates; rather, the minimum number of wolves confirmed in a

Table 1 Digestion-coefficients (DC) according to L: Lockie (1961); G: Goszczynski (1974); F: Fairley et al. (1987); A: Ansorge et al. (2006)

Prey category	*DC*
Ungulates > 3 month	118
Capreolus capreolus < 3 month	50[A]
Sus scrofa < 3 month	50[A]
Cervus elaphus < 3 month	118[A]
Dama dama < 3 month	50[A]
Livestock	118[G]
Medium sized mammals	50[G]
Small mammals	23[G]
Birds	35[G]
Fish	25[F]
Fruits	14[L]

Table 2 Mean weights (kg) of the main prey species (MPS) according to Wotschikowsky (2017)

	Net weight (kg)	
	Small juvenile (< 3 month)	Juvenile, adult (> 3 month)
Capreolus capreolus	6	12
Sus scrofa	11	25
Cervus elaphus	19	40
Dama dama	9	25

Table 3 Number of analyzed scats (*n*) and the mean pack sizes in the long-term studied territories (LTST) during the period under observation

Territory	Acronym	*n*	Study period	Mean minimum pack size
Altengrabow	AG	637	2008/09–2015/16	8.6
Dauban	DN	273	2007/08–2016/17	7.7
Daubitz/Muskauer Heide	DZ	1367	2001/02–2020/21	6.6
Gluecksburger Heide	GLH	421	2012/13–2018/19	5.6
Altdoebern-Großraeschen	GR	188	2012/13–2019/20	4.9
Hornow	HO	185	2013/14–2018/19	3.8
Koenigsbruecker Heide	KH	357	2011/12–2020/21	6.2
Lehnin	LE	435	2009/10–2018/19	6.2
Lieberose	LB	190	2009/10–2017/18	4.6
Milkel	MI	961	2008/09–2020/21	7.1
Neustadt	N	615	2002/03–2008/09	5.4
Nochten	NO	919	2005/06–2020/21	7.5
Niesky	NY	458	2010/11–2017/18	5.5
Seese	SE	191	2010/11–2018/19	2.9
Sperenberg-Jueterbog	SPJ	325	2011/12–2017/18	5.4
Welzow	WE	343	2009/10–2013/14	7.0

pack in a single monitoring year according to the rigorous national monitoring standards (Reinhardt et al. 2015). For the calculations of ungulate individuals consumed by wolves per pack, pack sizes were recalculated to wolf units, where one adult wolf or yearling constitutes one wolf unit and pups are counted as 0.5 wolf units. The calculation was carried out for the MPS for LTST. To calculate the number of prey consumed by the individual packs, a mean territory size of 200 km^2 was assumed (Jędrzejewski et al. 2007; Reinhardt and Kluth 2016).

Results

Diet composition

The wolves under investigation in Germany fed almost exclusively on wild ungulates, which were detected in 96.0% of the scats, corresponding to a 94.5% share of the biomass consumed (Table 4). The main prey was roe deer with a biomass share of 45.1%, followed by wild boar at 27.3%. Red and fallow deer, which do not occur in all parts of the study area, accounted for 11.7% and 5.4% of the biomass, respectively. Mouflon was only detected sporadically in the wolves' diet. With a biomass share of 3.4%, medium sized mammals represented another food category, where hare was mainly identified, followed by coypu and beaver. Livestock, especially sheep and cattle, was confirmed in 1.6% of the scat and accounted for a biomass share of 1.8%. Occasionally, small mammals, wild birds, fish and various fruits were also detected in the scats. Taken together, these food categories were found in 8.3% of the scats, but only made up 0.2% of the biomass consumed, and thus play a minor role.

Table 4 Frequency (*F*) and biomass (BM) of prey species in the wolf diet in Germany ($n = 11{,}125$)

	F (%)	BM (%)
Capreolus capreolus	51.1	45.1
Sus scrofa	33.5	27.3
Cervus elaphus	12.2	11.7
Dama dama	5.4	5.4
Ovis musimon	0.3	0.3
Cervidae indeterminable	7.5	4.7
Medium-sized mammals	7.0	3.4
Small mammals	4.3	0.1
Livestock	1.6	1.8
Mammalia indeterminable	0.5	0.1
Birds	1.0	0.0
Fish	0.1	0.0
Fruits	2.8	0.1

Temporal variation in MPS of long-term analyzed LTST

In the territories studied over a 10-year period, the diet of the wolves was analyzed for changes in composition of the MPS (Fig. 2). Very different trends could be observed in the individual territories. No particular trend was detected in the DZ territory. The use of roe deer, red deer and wild boar

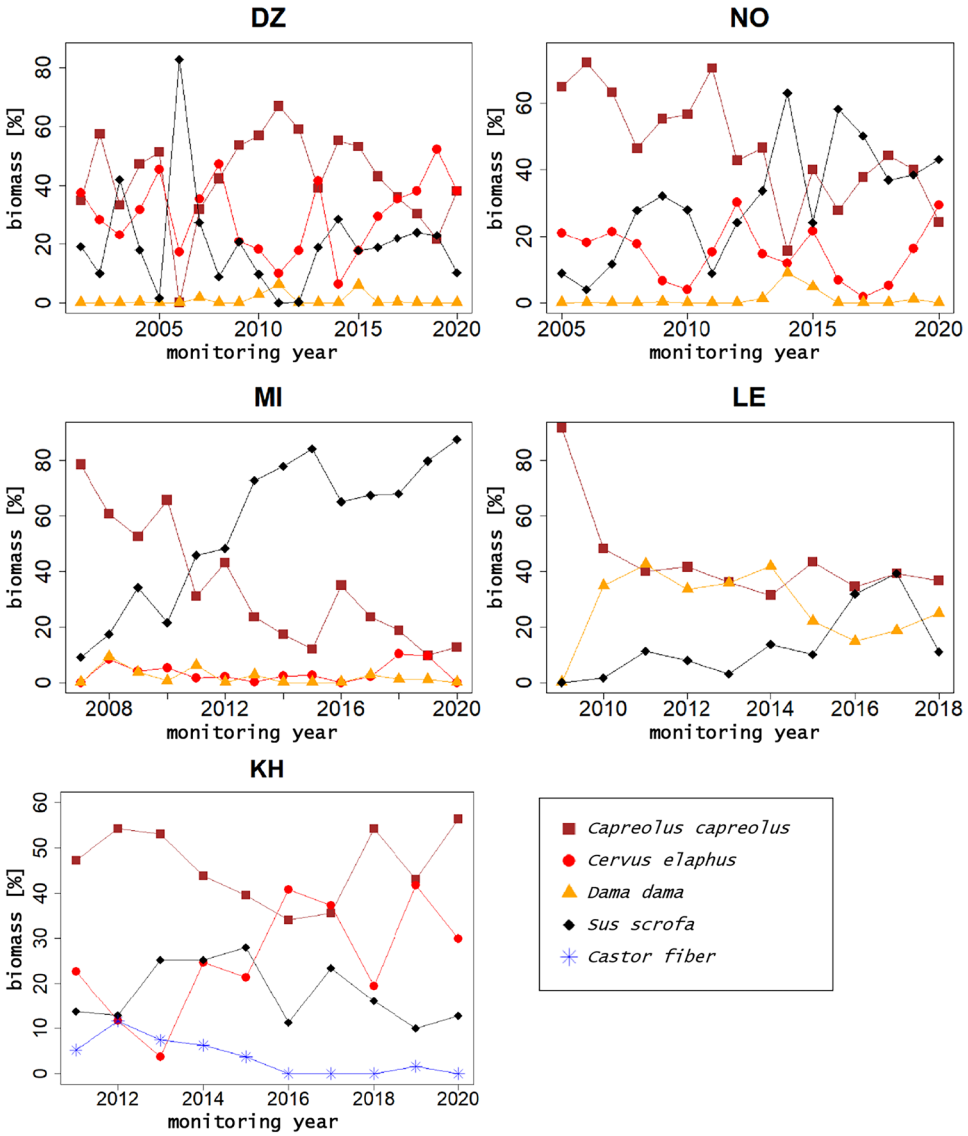

Fig. 2 Diet composition of main prey species (MPS) in five wolf territories studied over time for at least 10 years (sample size of scats per MY are summarized in Electronic appendix Table E)

fluctuated strongly over the years. Fallow deer were only occasionally preyed on. In the NO territory, a significant positive trend towards wild boar ($r = 0.71$, $p < 0.01$) and a significant negative trend toward roe deer ($r = 0.75$, $p < 0.001$) was found. Roe deer were the main prey in NO until MY 2013, and red deer rates fluctuated strongly. Very clear trends could be confirmed in the MI territory. A significant decrease in roe deer ($r = 0.87$, $p < 0.001$) and a significant increase in wild boar ($r = 0.89$, $p < 0.001$) were also recorded. At 71.6%, the wild boar was clearly the main prey since MY 2011. Except for the first year of the study, balanced proportions in the MPS were observed in LE. The KH territory was a special case. A relatively high proportion (9.0%) of beaver was found here until 2015, after which there was only sporadic evidence of beaver in the wolf diet. A slight non-significant increase in the proportion of red deer ($r = 0.61$, $p = 0.06$) was observed.

Selection of MPS and territorial differences

When pooling data for all territories and years (see Electronic appendix Table A), the Ivlev selection index shows clear and significant preference for roe deer. Wild boar was not preferred in any territory compared to availability. Preferential use of red deer and fallow deer could only be observed in individual territories. Thus, red deer were preyed upon significantly more often than is suggested by their proportion in the hunting bag in DZ, LB and N, while fallow deer were preyed upon more often in DN, GR and SE. On the other hand, red deer were used in significantly lower proportions in seven territories (AG, GLH, GR, HO, NY, SE and WE) as compared to their proportion in the hunting bag. Fallow deer was avoided completely in HO and used to a lesser degree in NY. Although a high proportion of fallow deer was found in the diet of wolves in AG and LE,

preferential use of this species was not detected there. The same applies to red deer in GLH and KH.

In many cases, characteristic differences in the food composition of the individual territories could be identified (see Electronic appendix Table C). A total of 6 clusters were obtained from the Morisita distances (see Electronic appendix Table B), with a spacing of at least 0.1 (Fig. 3). In most of the territories, roe deer was the main prey, but in very different proportions (37.1–62.8%, Table 5). Wolf territories that are directly next to each other can sometimes show significant differences in food composition (Fig. 4). Generally, the packs or clusters were all similar in their basic food composition, on account of their very high use of ungulates. Specific features were found in the GR/HO/MI cluster due to the high use of wild boar. Another clear distinction from the other clusters was observed in the AG/LE cluster as a result of the high use of fallow deer. All other differences between the clusters can be attributed to minor differences in the use of the various ungulates.

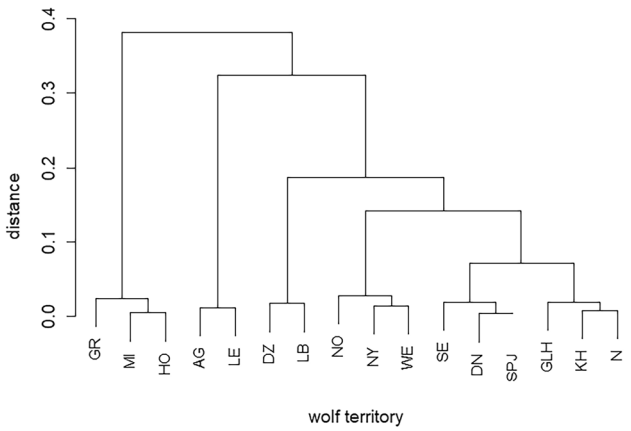

Fig. 3 Distances according to Morisita (1959) between the diet compositions of long-term studied territories (LTST) using the complete linkage clustering method

Juvenile ungulates in wolf diet

Juveniles (under 12 months) make up a significant proportion of the MPS in the wolf diet (Table 6). About 26% of the food remains from roe deer, 32% from wild boar and 20% from fallow deer could be reliably identified as fawns, piglets or calves. In red deer, almost half of the samples were identified as calves, representing 50% of the red deer biomass consumed. Increased proportions of small juveniles were observed in all MPS in connection with the respective rearing periods. Thus, a clear tendency toward the use of roe deer fawns and fallow deer calves was observed during summer months and of piglets in spring and summer. Red deer calves were frequently used throughout the year, with the exception of the winter months.

Number of preyed individuals

At a daily amount of 3 kg, a wolf needs about 1095 kg of live prey per year. Thus, considering the calculated biomass proportions of MPS (see Table 5), and based on the assumed mean territory size of 200 km^2 (Jędrzejewski et al. 2007; Reinhardt and Kluth 2016), as well as the mean pack sizes (Table 3), wolves consumed 0.66–1.76 roe deer,

Table 5 Food categories and diet composition (%) of wolves in long-term studied territories (LTST); other food ≙ small mammals, fish, wild birds, fruits

	AG	DN	DZ	GLH	GR	HO	KH	LB
n scats	637	273	1367	421	188	185	357	190
Capreolus capreolus	44.5	59.5	40.2	49.8	39.2	39.8	48.2	49.1
Sus scrofa	9.2	13.3	20.9	7.1	41.6	54.1	16.4	16.8
Cervus elaphus	1.3	16.4	33.3	18.6	6.9	3.0	21.4	28.9
Dama dama	27.4	5.4	0.5	2.0	2.7		1.1	0.9
Cervidae indet	11.7	0.6	2.1	11.7	4.8	0.9	1.6	1.7
Medium sized mammals	4.2	4.4	2.0	8.7	2.6	0.3	9.3	1.7
Other food	1.9	0.3	1.0	2.2	2.3	2.0	2.1	0.9
	LE	MI	N	NO	NY	SE	SPJ	WE
n scats	435	961	615	919	458	191	325	343
Capreolus capreolus	39.5	37.1	52.9	53.4	46.3	62.8	60.1	53.6
Sus scrofa	13.8	50.4	15.7	24.4	34.4	15.5	11.1	30.7
Cervus elaphus	1.7	4.6	23.6	15.1	8.5	4.7	12.9	5.2
Dama dama	28.9	3.3	0.8	0.4	1.3	4.9	3.6	0.8
Cervidae indet	7.0	1.2	0.1	1.2	3.8	5.9	4.3	0.4
Medium sized mammals	3.2	2.3	4.8	3.7	2.9	5.5	4.2	7.4
Other food	6.0	1.1	2.2	1.7	2.8	0.7	3.9	1.9

See definitions of different territories in Table 3

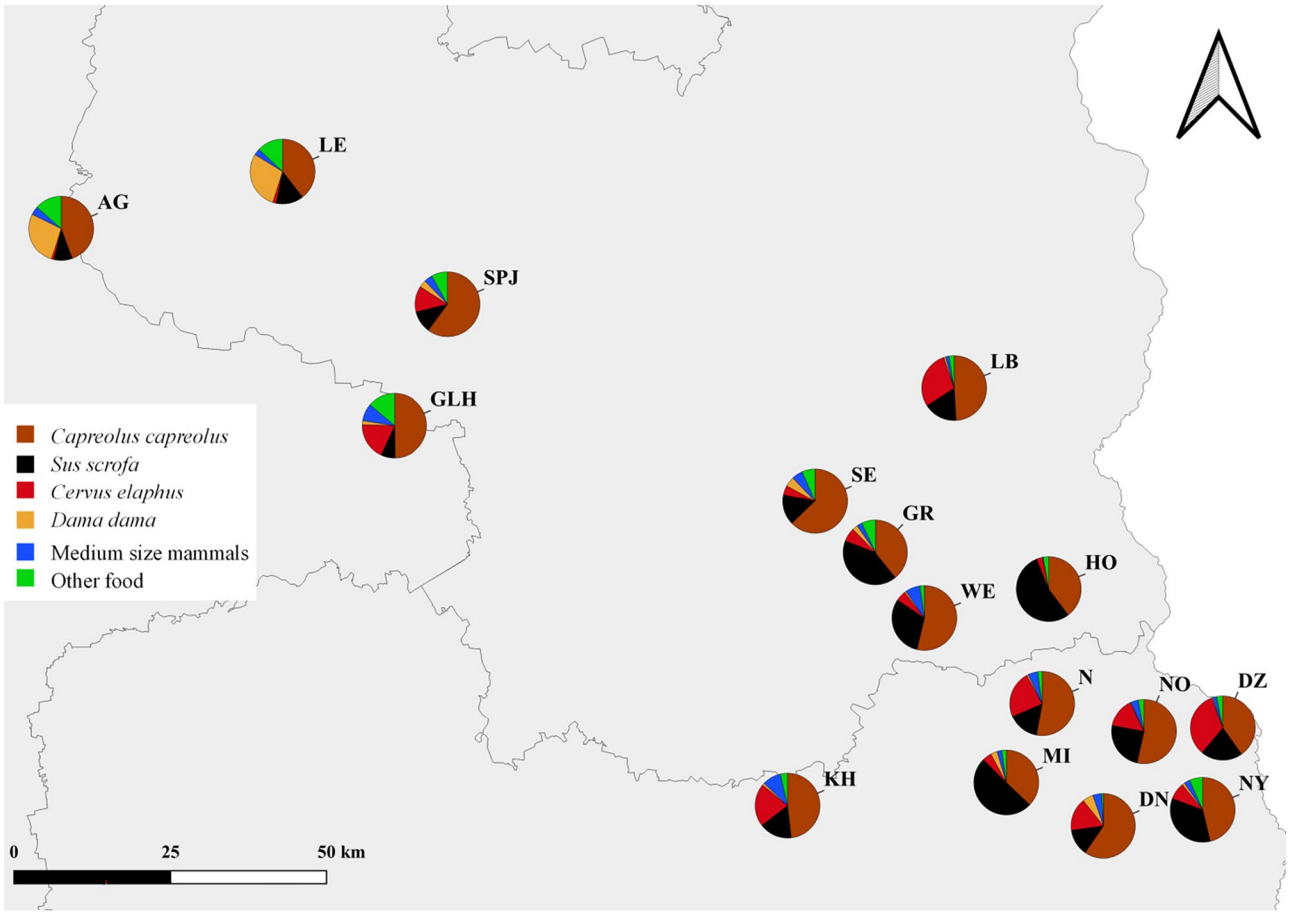

Fig. 4 Diet compositions of the long-term studied territories (LTST) as listed in Table 3 (see Fig. 1)

Table 6 Percentage of juveniles (under 12 months) in the four main prey species (MPS) calculated as the consumed biomass for all and throughout the seasons

Age class	*Capreolus capreolus*		*Sus scrofa*		*Cervus elaphus*		*Dama dama*	
	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult
All	25.8	74.2	32.2	67.8	50.0	50.0	19.5	80.5
Spring	15.4	84.6	34.4	65.6	37.3	62.7	13.3	86.7
Summer	50.7	49.3	43.6	56.4	71.6	28.4	42.5	57.5
Autumn	25.0	75.0	18.1	81.9	36.6	63.4	18.1	81.9
Winter	12.4	87.6	16.2	83.8	12.3	87.7	11.6	88.4

0.09–0.59 wild boar, 0.01–0.36 red deer and 0.00–0.36 fallow deer per 1 km^2 yearly in the studied areas (Table 7).

This implies that, on average, in our study area, a wolf consumed 47 roe deer (of which 12 were "small juveniles"), 14 wild boars (of which 3 were "small juveniles"), 5 red deer (of which 3 were "small juveniles") and 3 fallow deer (of which 1 was a "small juvenile") per year. Compared to the hunting bag, more roe deer were eaten by wolves in the territories DN, DZ, N and NO than hunted by humans. In all the territories, red deer, fallow deer and wild boar were hunted more frequently by humans.

Discussion

Basics

From the analysis of wolf scats, it is evident that wolves in Germany, like their conspecifics in several other parts of Europe, feed predominantly on wild ungulates (Jędrzejewski et al. 2012; Wagner et al. 2012; Imbert et al. 2016; Ståhlberg et al. 2017; Mysłajek et al. 2018; 2022; Mengüllüoğlu et al. 2019; Sin et al. 2019; Figueiredo et al. 2020; Valdmann and Saarma 2020; Reinhardt et al. 2021).

Table 7 Utilization of the main prey species (MPS) by wolves and hunters per 1 km^2 and year

	Capreolus capreolus		*Sus scrofa*		*Cervus elaphus*		*Dama dama*	
	Wolf prey	Hunting bag	Wolf prey	Hunting bag	Wolf prey	Hunting bag	Wolf prey	Hunting bag
AG	1.18	1.84	0.12	1.90	0.01	0.20	0.36	1.59
DN	1.76	1.44	0.25	2.70	0.16	0.28	0.07	0.16
DZ	0.99	0.69	0.24	1.57	0.36	1.18	0.01	0.00
GLH	0.96	1.48	0.09	2.72	0.12	2.38	0.02	0.15
GR	0.74	2.25	0.43	3.38	0.04	0.42	0.02	0.07
HO	0.66	2.56	0.43	2.57	0.02	0.31	0.00	0.07
KH	1.19	1.34	0.20	2.17	0.21	0.64	0.01	0.07
LB	0.82	2.67	0.15	1.91	0.20	0.39	0.01	0.04
LE	0.78	2.36	0.15	2.05	0.03	0.08	0.31	1.46
MI	0.93	1.66	0.59	2.60	0.04	0.10	0.04	0.17
N	0.95	0.70	0.15	1.90	0.13	0.16	0.01	0.03
NO	1.39	0.72	0.31	2.44	0.14	0.37	0.01	0.01
NY	0.94	1.39	0.30	2.65	0.08	0.48	0.01	0.15
SE	0.80	2.25	0.14	3.38	0.02	0.42	0.04	0.07
SPJ	1.30	2.07	0.11	2.29	0.10	0.31	0.04	0.17
WE	1.37	2.25	0.38	3.38	0.05	0.42	0.01	0.07

See definitions of different territories in Table 3

In this context, roe deer are the main prey species (MPS) in most wolf territories in Germany. This is probably due to the wide distribution of roe deer and limited defensive behavior of the species in comparison to larger ungulates. Across Europe, this is not a special phenomenon, because wherever they occur in high densities roe deer are often used by wolves as the main food source (Gazzola et al. 2007; Žunna et al. 2009; Nowak et al. 2011; Jędrzejewski et al. 2012; Figueiredo et al. 2020; Mysłajek et al. 2019, 2022; Valdmann and Saarma 2020). Roe deer were also the MPS in the individual study years, while wild boar has become more important in recent years.

It is often observed that the largest ungulate species present are preyed upon by wolves (Okarma 1995), if present in higher densities relative to other ungulates. Assuming that long-term hunting bags are an indicator of ungulate densities, red deer should make up a high proportion of the diet of wolves in some of the territories in Germany. This was only found in the territories of DZ, GLH, KH, LB, and N, whereby a positive selection could only be determined in DZ, LB and N. In all the other territories, except LE and MI, the hunting bag statistics also indicate high red deer densities; however, equivalent use of red deer by wolves was not detected. A correlation with pack size could not be determined either, as the estimated pack size for DZ, GLH, KH, LB and N was not above average.

A special situation is seen in the diet composition of wolves in GR, HO and MI, which to a high degree (41.6–54.1%) feed on wild boar, and thus constitute the main prey. Due to its defensive behavior (greater body size of adult wild boar and fangs), the wolf usually avoids this species (Okarma 1995), even in areas with very high densities (Jędrzejewski et al. 2000).Wild boar has been identified as MPS in Italy, Anatolia and South-East Europe (Mattioli et al. 2011; Zlatanova et al. 2014; Ciucci et al. 2018; Mengüllüoğlu et al. 2019; Sin et al. 2019; Trbojević et al 2020). The subspecies *Sus scrofa majori* found in Italy is relatively small (Niethammer and Krapp 1986; Mattioli et al. 2011; Imbert et al. 2016) and may be easier to catch than the *Sus scrofa scrofa* subspecies found in Germany. In Anatolia, the wild boar is often the only wild ungulate species that occurs in high densities. This is mainly due to the fact that for religious reasons wild boar are not used as human food, and other ungulates have been intensively and uncontrollably hunted in recent decades (Mengüllüoğlu et al. 2019). An increase in the proportion of wild boar in the diet of wolves is evident in four out of five territories monitored long-term in Germany (Fig. 2). The increase is also reflected in hunting bags (Ministry of Agriculture, Environment and Climate Protection of the State of Brandenburg 2021; Supreme Hunting Authority of the Federal State of Saxony 2023 pers. comm.). However, the question arises as to whether the wolves prey on adult wild boar, as indicated by scat analyses. In 20 years of opportunistic collection of ungulates killed by wolves in Saxony, no adult wild boar were found, and until 2020, neither were any adult boar found during several months' systematic search for the prey remains of radio collared wolves. However, during the telemetry cluster searches, several adult wild boars were found that had been shot by hunters but not recovered.

These carcasses were found by wolves and then scavenged. It is likely that the use of wild boar by wolves will continue to increase due to high reproduction rates and concomitant increase in the wild boar population. Lower densities of wild boar could on the other hand cause wolves to change their feeding habits (Klich et al. 2021). Either as a consequence of increased wild boar hunting due to African swine fever (ASF), or an increase in the ASF-associated mortality rate of wild boar (Valdmann and Saarma 2020). In turn, this would decrease the prey range available to wolves. However, wild boar hunting in Germany, would have to be very intensive for wild boar populations to decline sharply enough for this effect to occur.

Red and fallow deer calves, piglets and roe deer fawns are important components of the wolf diet, and their remains have been found in scats throughout the year. Other studies in Europe also attribute high importance to juveniles as wolf prey (Zlatanova et al. 2014; Newsome et al. 2016; Ciucci et al. 2018). Analysis of wolf kills in Saxony (Wagner et al. 2011) shows a clear preference for red deer calves in proportions higher than in the present scat analysis. Roe deer fawns are also frequently preyed upon, but with similar proportions as in the present scat analysis. Given that fawns are often eaten completely by wolves, the proportions in the kill analysis are likely to be underestimated. The situation with regard to wild boar piglets is similar. However, when interpreting the data on juvenile proportions, it should be noted that these are minimum values. The proportion of very young prey (< 3 months), which are usually consumed completely, can be clearly determined from the prey samples, while a precise distinction between juvenile (< 12 months) and adult animals is often difficult or impossible.

Besides ungulates, other smaller prey categories can also play an important role in the diet of wolves, which has been documented in several European (Andersone and Ozoliņš 2004; Žunna et al. 2009; Sidorovich et al. 2017; Mysłajek et al. 2019) and worldwide studies (resumed in Gable et al. 2018). In this context, Sidorovich et al. (2017), Gable et al. (2018) and Mysłajek et al. (2019) in particular focus on the importance of beavers for wolf pups. Our investigations revealed one territory (KH) with a relatively high proportion of beaver in the wolves' diet. This area called Koenigsbrueck Heath was a military training ground until 1992 after which it became a nature reserve. In the absence of large predators, beavers were able to expand strongly there until 2011 (a total of 54 beaver territories equals 4.44 beaver territories per km^2) (Kneis et al. 2013). Since then, beaver population losses of 60% were recorded by 2015 and of 90% by 2021. Besides predation by wolves, the decrease in the beaver population has been caused by a steep decline in the food supply near water bodies combined with a sharp decline in available beaver habitat due to long-term drought and disease (Stein 2023). This decrease could also be documented in the diet composition of the KH wolves (see Fig. 2), where beaver remains have rarely been found in scat since 2015. Heavy use of another medium-sized mammal, in this case the coypu, was noted in GLH. Beaver, coypu and hare were also identified in other territories. Despite in part very high game densities (Table 7), wolves in Germany also prey on smaller species.

Among ungulate species, the number of animals killed by wolves is generally lower than the number killed by hunters. Only in five territories did wolves kill more roe deer than hunters. In general, our calculations do not show a decline in hoofed game, as measured by their proportion in the wolves' diet. Although the current hunting bag statistics show a decline in the number of roe deer, red deer and fallow deer hunted in some regions, the hunting bags are still at a high level. Assuming that ungulate hunting bags are an indicator of wildlife densities, the diet composition of the wolves shows territorial differences relative to available prey, but no disappearance of prey species (Ministry of Agriculture, Environment and Climate Protection of the State of Brandenburg 2021; Superior Authority for Hunting of Saxony 2023 pers. comm.). However, hunting bags provide only a rough estimate of ungulate densities; more reliable density estimates of prey species are not available. In eastern Saxony, for example, roe deer hunting has been reduced in several areas because of people's fears that together hunting, and the presence of wolves might lead to a collapse of the roe deer population. At the same time, in hunting areas with a high red deer population, roe deer are not the primary hunting target and as a consequence are underrepresented in the hunting bag. The mouflon, however, is an exception. In eastern Saxony, for example, relatively high biomass proportions were found in diet analyses at the start of the wolf's territorial expansion. Today, the mouflon has all but disappeared in eastern Saxony, because the mouflon is an introduced species that is not well adapted to the given habitat and has limited defensive behavior against wolves, which makes it vulnerable. In Brandenburg, the hunting bag of mouflon is also declining sharply.

In some areas of Europe, predation of livestock plays an important role in the wolf diet (Petridou et al. 2019; Trbojević et al. 2020). However, in the study presented here, livestock make up only a minor proportion of the wolf diet. When looking at individual territories, only LE (3.4% of frequency) has a slightly higher share of livestock than all other territories (< 2.5%). Several studies have shown that wolves use fewer livestock when a sufficiently high number of ungulates are available (Meriggi et al. 1996, 2011; Barja 2009; Bassi et al. 2012), and especially when several species of wild prey are present (Meriggi and Lovari 1996; Tiralla et al. 2021). However, the main factor influencing wolf predation on livestock is how well protected domestic prey are. According to the hunting bag in our study region,

ungulate densities are high, which likely results in a low level of predation on livestock. Furthermore, livestock are often well protected by fences and guard dogs, presenting a barrier to the wolf.

Outlook and conclusions

Further studies need to be carried out, particularly in long-term territories, to detect changes in diet composition (e.g., due to ASF) and adjust wildlife management accordingly. The spread of ASF could result in reduced wild boar densities, and thus increase pressure on other ungulates and livestock. A potential effect of ASF is not detectable in the data on hand. Data on this problem are not yet available. So-called "ASF protection fences" are being used in Germany to reduce the migration of wild boar, contain the spread of ASF and protect domestic pigs. However, these fences also drastically restrict the movement range of all larger animals and at least in the short-term pose an extreme restriction on migration. Therefore, additional integrative monitoring of all larger mammals is necessary to obtain more accurate information on wildlife densities. This should also improve the calculations carried out and provide better information to both nature conservation and hunting authorities.

The various analyses in this study have once again shown that wolves are opportunistic carnivores, and that the composition of wolf diet depends primarily on the availability and density of prey. The study also confirmed that wolves in Germany mainly feed on wild ungulates and rarely use domestic ungulates. Thus, the diet composition can vary significantly from territory to territory, especially in the wild ungulates category, although the territories may be located close to each other. In the study presented here, the available data did not reveal the wolf diet to influence the population dynamics of autochthonous wild ungulates.

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Author contributions Material preparation was performed by IR, GK, FB, MK, F-UM, HS, JT, JT, MT and HW. Data collection and analysis was performed by PL. HK, HA and PL were involved in the study conception and design. The first draft of the manuscript was written by PL. All authors commented on earlier versions of the manuscript, and all authors read and approved the final version of this manuscript.

Data availability The datasets used in the current study are available from corresponding author on reasonable request.

Declarations

Conflict of interest All the authors declare that they have no conflict of interest. No funding was received to conduct this study.

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