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Original Investigation

Wolf (*Canis lupus*) feeding habits during the first eight years of its occurrence in Germany

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ABSTRACT

Due to the fact that the feeding habits of large carnivores are the main contentious point when they start resettling regions they were absent from for several decades, the diet composition of the wolves in Germany was analysed from the beginning of this process. Wolves in Germany primarily feed on wild ungulates, which make up more than 96% of their diet. The dominating prey species is the roe deer (55.3%), followed by red deer (20.8%) and wild boar (17.7%). The second important food category are the leporids (2.9% of Biomass), whereas livestock makes up only 0.6% of all biomass consumed. Wolves clearly prefer hunting on juvenile to adult red deer; roe deer are not selected after their age. We found seasonal differences in the diet composition with a higher amount of wild boar in spring and winter, when a high amount of juveniles and weakened animals, respectively, are available. In the first years of the study the percentage of red deer was much higher, and the percentage of roe deer therefore was lower than the following years. The amount of wild boar in the wolf diet fluctuated most in the first three years. Diet composition remained constant during the last five years. Wolves needed less than two generations for adapting to the new conditions in the cultivated landscape of eastern Germany.

Introduction

Originally widespread across the northern hemisphere, the wolf was extirpated in most of the west and middle European countries till the 19th century. Mostly the fear of livestock damages and mythologisation of the wolf as pest led to large-scale persecution of this predator (Fritts, 1982; Fritts et al., 2003; Butzeck et al., 1988; Boitani, 1995, 2003; Mech, 1995). Additional extinction of wild ungulates in some regions accelerated this process (Fernández and de Azua, 2010). During recent decades and with the legal protection of the wolf in most European countries, wolves have started resettling regions they had been displaced from (Wabakken et al., 2001; Boitani, 2003; Valière et al., 2003; Nowak and Mysłajek, 2006).

In the late 18th century the wolf was eliminated from Germany due to organized persecution (Butzeck et al., 1988; Ansorge and Schellenberg, 2007). Since then single wolves immigrated, rarely but regularly, to eastern Germany, but none succeeded in establishing a new population until they were placed under legal protection in the whole of Germany in 1990. It took ten more years until the first reproduction of wolves could be recorded in the Muskau heath in north eastern Saxony. From that point the wolves in Germany reared pups every year and the population started growing (Ansorge and Schellenberg, 2007).

The feeding habits of the wolves as large carnivores and their influence on wild ungulate populations and livestock farming are at the center of the tensions between man and wolves (Kleiven et al., 2004). Particularly in regions where the wolf was absent for more than one human generation, people have to relearn accepting a large predator in their neighbourhood (Linnell et al., 2001; Williams et al., 2002; Gärtner and Hauptmann, 2005). To prevent speculations and exaggerations it is of huge importance to get precise information about the diet composition of the returned wolves and its development during the adaptation to their new environment, as basis of wolf and game management.

The diet of the wolf generally depends on the availability of potential prey species, especially large wild ungulates. Studies in North America (Rogers et al., 1980; Hughard, 1993; Messier 1994; Kunkel et al., 1999; Peterson, 1999; Nelson and Mech, 2000; Arjo et al., 2002, a.o.) and Europe (Meriggi et al., 1991; Okarma, 1997; Jędrzejewski et al., 2000; Andersone and Ozolins, 2004; Fejklova et al., 2004; Gazzola et al., 2005; Nowak et al., 2005, a.o.) show, that wild ungulates are the main prey of wolves living in game-rich regions. If there are not enough wild ungulates available and other food resources like livestock or waste are frequent, wolves are able to change their feeding habits towards these categories

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(Boitani, 1982; Meriggi et al., 1991; Vos, 2000; Peterson and Ciucci, 2003; Hovens and Tungalaktuja, 2005). With a seasonal surplus of other prey like salmon in costal British Columbia (North America) (Darimont et al., 2003) they can adapt to using quite nontypical food.

The German wolves originated from Poland, where the diet of the predators has been intensively studied from the lowlands of Bialowieza primeval forest to the mountainous regions in southern and southeastern Poland (Jędrzejewski et al., 2000, 2002; Nowak et al., 2005; Śmietana, 2005). There, red deer *Cervus elaphus* is the main prey and the only one positively selected regarding their share in ungulate community, whereas roe deer *Capreolus capreolus* and wild boar *Sus scrofa* are used to a lesser extent. However, wolves in western Poland, who belong to the same wolf population as German wolves, seem to hunt red deer according to its relative abundance (Nowak et al., 2011).

As wolves are known to adopt their feeding preferences from their parents (Packard, 2003), the implication would be that wolves in Germany show a comparable pattern. Otherwise, the process of adaptation to new conditions in the availability of prey and environmental circumstances could lead to specialization on and preference for other prey species and therefore to a shift in the feeding habits. This ability to adapt on new conditions makes the wolf one of the most widespread mammalian species. Following this approach adaptation to the new environment should take approximately one wolf-generation, two years.

The development of diet composition since wolves resettled regions they have been displaced from before, has not been continuously studied yet. This study gives new insights into the recovery and adaptation strategies of wolves and would be very helpful in regard to game and wolf management and public relation.

Study area

The study area of about 2500 km^2 is located in the Lusatian heath in north eastern Saxony and parts of southern Brandenburg in Germany and covers the entire area occupied by wolves in Germany during the examination period (Fig. 1).

Characterised by large former and still operating opencast coal mines, an intensively used military training area (145 km^2) and pine forest monocultures, the region is under strong anthropogenic influence. But compared to whole Saxony the area has a much higher amount of forest cover (52%; Saxony: 26.8%) and open areas (6%; Saxony: 0.6%) than average and a lower amount of settlement and traffic area (3%; Saxony: 10.3%). The region is flat (elevation: 120–170 m asl.) with dry, sandy grounds covered by pine forests, mixed pine-oak forest and open or scattered heathland including larger parts of the biosphere reserve Upper Lusatian Heath and Pond Landscape in the south.

The area is located in the temperate zone with a semi-continental climate. During the study period from spring 2001 to spring 2009 the mean annual temperature was 9.3 °C and the mean annual precipitation was 631.5 mm. The duration of snow cover differed from 11 to 68 days (mean 35.1 days) per winter.

Wolves in Germany coexist with 5 wild ungulate species; two of them (moufflon *Ovis ammon musimon* and fallow deer *Cervus dama*) were introduced by humans as game species. Their share of the ungulate community is very low in the study area; moufflon disappeared from the main areas with permanent wolf occurrence until 2003. With a mean hunting bag of 1.0 animals per km^2 the wild boar makes up the largest part of the general hunting bag in the area, together with roe deer with 0.97, followed by red deer with a mean of 0.78 animals per km^2. The hunting bag is used as indication for the development of ungulate density, because no useful data on the population densities of these ungulates are available.

By establishing in this area the wolves recolonised exactly the region where the last eastern German wolves were extirpated in the 18th century. After the first reproduction in the year 2000 in the Muskau heath, a second pack established in 2005, henceforward every year at least one more new pack could be confirmed. In the year 2009 six packs and one territorial pair of wolves without offspring occupied about 2500 km^2.

Methods

Scat collection and analysis

The diet analysis was conducted using wolf scats, which were collected during all seasons from April 2001 till March 2009, by walking or driving transects on forest roads and fire belts. General characteristics of collectable wolf scats are a high amount of good visible hairs and bone fragments and a diameter of at least 25 mm (Weaver and Fritts, 1979; Ciucci et al., 1996). Additionally, there is no sign for feral dogs in the study area, which would regularly feed on game.

In total 1890 scats were evaluated. After collection, the scats were frozen until further analysis, then heated to free them from pathogenic organisms like parasites, washed through a sieve with 1 mm meshes and oven dried at 46 °C. The nondigested parts of the prey items like bone fragments and hairs were separated. Hairs were identified using keys of Teerink (1991) and Meyer et al. (2002) as well as our own determination key and reference collections. Criteria for the identification of hair were macroscopic characteristics like hair length, colour and structure, and microscopic features like the structure of the hair medulla and cuticular patterns. Bone fragments, teeth and claws or hooves were also used for determining scat content. For the differentiation of cervid species we used our large reference collection of hairs from different parts of the animal body of different age, sex and season.

Digestable plant material, like berries and other fruits were regarded as food, whereas nondigested plant material like grass or pine-needles were not regarded as food components. Neither were insects, which were either dung or carrion beetles or parasites of the prey and therefore ingested by chance.

Age determination

For the determination of the age of the wolf prey we used the scat analysis and, additionally, the analysis of wolf kills found during field work.

If suitable bone fragments, teeth and hairs of the prey in the wolf scats were used to determine the age of the prey. Regarding the analysis of the scats it was possible to distinguish young ungulates to the age of three months from adults. Furthermore, the age of the prey animals found as wolf kills during field work (roe deer $n = 34$, red deer $n = 55$) was determined through stage of dentition and classified as young (up to one year old) and adult (more than one year old). Due to the fact, that very young ungulates are consumed completely and no remains can be found, we combined data from scat analysis and wolf kills to estimate the percentage of young animals in wolf diet (P_j) for the main prey species roe deer and red deer.

For that we used formula (1):

$$P_j = \frac{P_{jp} \times B_{as} + B_{js}}{B_t} \quad (1)$$

where P_{jp} is the percentage of biomass of juveniles older than three months, from prey remains, B_{as} the biomass of non juveniles calculated from scat analysis [kg] and B_{js} is the biomass of very young juveniles from scat analysis [kg] and B_t is the total biomass of these species.

Fig. 1. Location of the study area in Central Europe.

Table 1
Average usable net weight of the main prey species, weight of small juveniles (age less than three months) in brackets.

	Net weight [kg]	
	Juveniles	Adults
Roe deer	(4)8	14
Red deer	(15)30	50
Wild boar	(5)10	40

We used average usable prey mass as specified in Table 1 for translating biomass into numbers of animals killed.

Statistics

We calculated the frequency of occurrence as well as the percentage of biomass consumed referring to the general, seasonal and the annual diet composition. For the latter we used the hunting year running from first of April to the end of March. The percentage of biomass consumed was calculated using the method of Goszczyński (1974), where dry mass of washed scats is multiplied by coefficients of digestibility (Table 2).

Table 2
Coefficients of digestibility according to L, Lockie (1961); G, Goszczyński (1974); F, Fairley et al. (1987) (cited in Jędrzejewska and Jedrzejewski, 1998); A, Ansorge et al. (2006); juv. Juvenile.

Prey category	Coefficient of digestibility
Adult ungulates	118_G
Capreolus capreolus juv.	$50_{G,A}$
Sus scrofa juv.	$50_{G,A}$
Livestock	118_G
Medium sized mammals	50_G
Small mammals	23_G
Birds	35_G
Fish	25_F
Fruits	14_L

Furthermore we calculated niche breadth B (Levins, 1968) and standardized niche breadth B_a (Hurlbert 1978, cited in Hofmann, 1999)

$$B = \frac{1}{\sum(p_j^2)} \quad (2)$$

where p_j is the percentage of biomass of prey taxa.

$$B_a = \frac{B-1}{n-1} \quad (3)$$

where n is the number of prey categories.

Furthermore we used the selectivity index D of Jacobs (1974) (formula (4)) to quantify the different pattern of utilization of the game species by hunters and wolf and the selection of juveniles referring to the age structure of an average cervid population:

$$D = \frac{r-p}{r+p-2rp} \quad (4)$$

where r means the fraction of a prey species in the total number of ungulates killed by the wolf, and p is the contribution of this species in the hunting bag/of this age class in ungulate community.

For evaluating the difference between the diet composition (Frequency) of different years, packs or seasons we used the Chi square test.

Results

Diet composition

In total, 33 different food objects, combined to 8 food categories were detected in the scats (Table 3). The most dominant category, concerning both, frequency (F = 97.0%) and percentage of biomass (B = 96.2%), are wild ungulates. With a frequency of occurrence of 56.2% and a percentage of biomass of 55.3%, roe deer are the main prey of the wolves in Germany, followed by red deer and wild boar, with a biomass percentage of 20.8% and 17.7%, respectively. Two more species of ungulates, fallow deer and moufflon, are rarely found in the wolf scats, as they are in ungulate community in the study area.

The majority of all scats contained remains of only one food object (64%), in 28% of all faeces two different food objects were

Table 3
Food categories and diet composition of wolves in a eight year development and in total (calculated after Goszczyński, 1974); +, less than 0.05%.

	Percentage of biomass								
	01/02	02/03	03/04	04/05	05/06	06/07	07/08	08/09	Total
Capreolus capreolus	36.0	49.9	40.2	48.7	63.8	53.7	53.0	50.8	55.3
Cervus elaphus	34.9	39.3	19.6	28.0	19.4	25.1	23.2	26.4	20.8
Sus scrofa	19.2	8.9	36.1	19.4	11.1	12.6	17.1	15.2	17.7
Ovis ammon musimon	8.6			0.3		0.7	1.4		0.9
Cervus dama				0.3		1.1	2.3	3.5	1.5
Artiodactyla	98.7	98.1	95.9	96.6	94.4	93.1	97.0	95.9	96.2
Leporidae	1.3	1.7	3.8	2.9	4.1	4.9	2.5	3.9	2.9
Nyctereutes procyonoides					0.1	0.1			+
Vulpes vulpes			0.1						+
Mustela erminea						+			+
Ondatra zibethicus					0.4				0.1
Medium sized mammals			0.1		0.4	0.1			0.1
Apodemus sylvaticus			+						+
Apodemus spec.							+		+
Arvicola terrestris			+	+				+	+
Clethrionomys glareolus					+			+	+
Microtus agrestris					+		+		+
Microtus arvalis						+	+		+
Microtus spec.		+	0.1	+	0.1	0.2	0.1	+	0.1
Rattus norvegicus						+			+
Erinaceus europaeus					0.1				+
Small mammals indet					+			+	+
Small mammals		+	0.2	+	0.3	0.2	0.1	+	0.1
Felis sylvestris f. catus						0.2			+
Gallus gallus f. domestica			+		+	+			+
Ovis ammon f. aries		0.2			0.5	1.1	0.2	0.1	0.4
Oryctolagus cuniculus f. domestica				0.5	0.2			0.1	0.1
Domesticated animals		0.2	+	0.5	0.7	1.3	0.2	0.2	0.6
Aves			+	+	+	+	+	+	+
Rubus fruticosus					0.1	+	+		+
Malus domestica						0.2	+	+	+
Zea mays					+	+		+	+
Prunus cerasus							+		+
Pyrus communis						+	+		+
Fruits					0.1	0.3	0.1	+	0.1
Pisces			+			+			+

detected and only 8% of all samples consisted of more than two different items (up to four).

With a percentage of biomass of less than 5%, leporids are by far the second most important food category. Remains of domesticated animals were found in 1.4% of all scats, making up 0.6% of the biomass consumed. Among the domesticated animals, the domestic sheep dominated with a proportion of 74% of this category, followed by rabbit (17%) and one type of domestic cat (8%). Barn fowl appears occasionally, but makes only 1% of the biomass in this food category.

Two percent of all faeces contained fruit, such as apple (*Malus domestica*) and pear (*Pyrus* sp.) which appeared mainly in autumn and winter when they are used for attracting game to feeding sites. In summer, blackberry (*Rubus fruticosus*) and cherry (*Prunus* sp.) could be determined in some wolf scats. Other items like small mammals (several species of Muridae and Arvicolidae), medium sized mammals, birds and fish were found in the wolves' diet too, but with a percentage of biomass less than 0.2%, so their proportion was very low. Anthropogenic waste did not play any role in the diet of wolves in Saxony.

Juvenile ungulates in wolf diet

Regarding the percentage of biomass, calves make up to 49.5% of all red deer consumed, while just 15.4% of roe deer biomass is made up by fawns. Assessing a healthy and average cervid population with a growth rate of 25% in red deer and 30% in roe deer (Niethammer and Krapp, 1986), red deer calves are clearly positively selected ($D = 0.75$), whereas roe deer fawns are chosen according to their share in ungulate community ($D = 0.0$).

Every third roe deer killed is juvenile, whereas about 70% of all red deer killed by the wolves are less than one year old (Table 4, Fig. 2).

The percentage of very young wild boar in the wolf diet is even higher than in the red deer (Table 4), suggesting that the percentage of all juveniles is even higher for wild boar, too. But due to the fact that we do not have enough data on wild boar wolf-kills, the real percentage of juvenile boar in the wolf diet remains unknown.

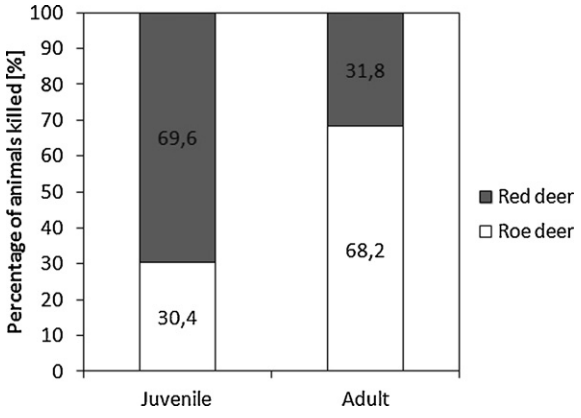

Fig. 2. Percentage of juveniles in the two main prey species red deer and roe deer calculated as percentage of animals killed.

Table 4
Percentages of biomass and number of individuals from scat analysis ($n = 1384$) and prey remains found during wolf monitoring (Roe deer: $n = 42$, Red deer: $n = 47$); n.d., no data.

		Biomass [%]			Number [%]		
		Scat analysis	Prey remains	Combined	Scat analysis	Prey remains	Combined
Capreolus capreolus	Juvenile	5.7	5.6	15.4	16.9	9.3	30.4
	Adult	94.3	94.4	84.6	83.1	90.6	69.6
Cervus elaphus	Juvenile	21.9	39.4	49.5	32.4	47.0	68.2
	Adult	78.1	60.6	50.5	67.6	53.0	31.8
Sus scrofa	Juvenile	15.3	n.d.		49.6	n.d.	
	Adult	84.7	n.d.		50.4	n.d.	

Development of diet composition

Wild ungulates are the main prey of the wolves during the whole time period 2001–2009, amounting to at least 93.1% of the diet.

The percentage of roe deer in the wolf diet is increasing in the first years of the examination period and then it remains constant with a peak in the hunting year 05/06. The role of red deer however is decreasing after two years of high proportion, and the percentage of wild boar is fluctuating throughout the years without any obvious trend. Other food categories did not show any trend during the eight year development (Fig. 3, Table 3). Medium-sized mammals, small mammals, fish and birds as well as fruits are supposed to be fed on by occasion and are not actively searched for by the wolves.

Only the frequency of prey species in the first year 01/02 shows significant differences to the others ($p = 0.031$). The frequency of roe deer in the diet was much less than in the following years and the amount of wild boar and red deer was comparably high. Furthermore mouflon was quite an important prey, which became much less important in the following years.

The niche breadth was the highest in the first year of the study (2001/02), with $B = 3.3$ ($B_a = 0.6$) and decreases to an index level between $B = 2.2$ ($B_a = 0.1$) and $B = 2.8$ ($B_a = 0.2$) (Table 5).

Livestock in the diet of the wolves did occur in seven out of eight years with a peak in the year 06/07 (1.3% of biomass consumed) but there no trend could be confirmed. Sheep as the main domestic prey species peaked in the year 06/07 too, with 1.1% of the biomass consumed.

Utilization of the game species by hunters and wolf

The composition of the wolf diet in relation to the percentages of the same species in the hunting bag shows the differences in the utilization of the ungulate game species. Whereas hunters shot nearly the same amount of roe deer and wild boar and only a few less red deer, wolf diet is more based on roe deer, being the main prey. As the hunting bag depends on the different reproduction rates and lots of other parameters, it is just a weak indication of the real ungulate density. But this high index value (Fig. 4) indicates, that roe deer might be positively selected by the wolves, whereas red deer and wild boar are not. During the eight year development this pattern remains stable, with a positive trend of the roe deer index value.

Table 5
Niche breadth (Levins, 1968) and standardized niche breadth (Hofmann, 1999) over an eight year development.

Hunting year	B	B_a
01/02	3.3	0.6
02/03	2.4	0.3
03/04	3	0.3
04/05	2.8	0.2
05/06	2.2	0.1
06/07	2.7	0.2
07/08	2.7	0.2
08/09	2.8	0.2
Total	2.6	0.1

Seasonal differences in the wolf diet

For eliminating errors based on differences between the years we used the data of only one year (08/09) who are corroborating the data of the whole study period: We found significant differences between the average and the diet composition of spring ($p = 0.027$) and winter ($p = 0.045$). The main difference between these seasons is that the amount of wild boar is higher and the percentage of deer is lower in spring and winter (Fig. 5). Furthermore the niche breadth is the highest in spring ($B = 3.1$; $B_a = 0.35$) and winter ($B = 3.2$; $B_a = 0.31$) too, meaning that the wolf diet was

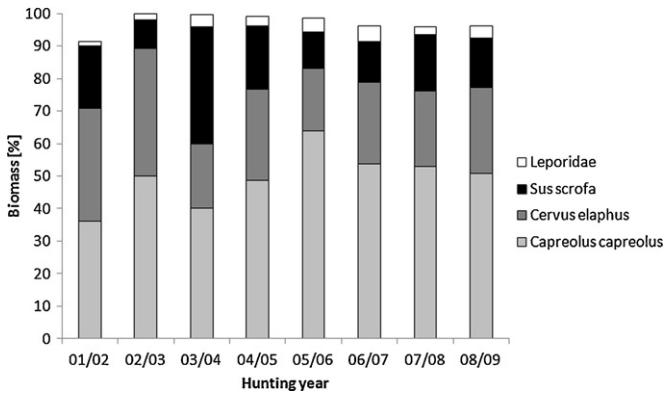

Fig. 3. Eight year development of diet composition.

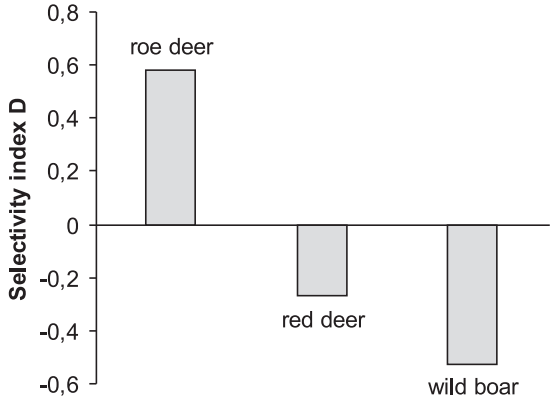

Fig. 4. Comparison between the utilization of the three main prey species by hunters and wolf; positive values mean a higher percentage of the prey species in the wolf diet, negative values a higher percentage in the hunting bag.

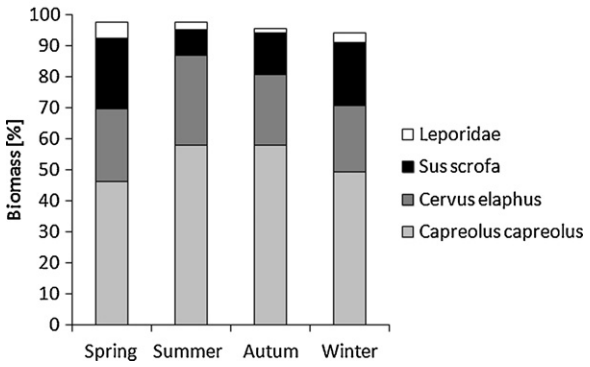

Fig. 5. Diet composition in different seasons in the year 08/09.

more diverse in these seasons than in summer ($B = 2.6$; $B_a = 0.23$) and autumn ($B = 2.5$; $B_a = 0.19$).

Discussion

Diet composition

The diet of the wolves in Germany is dominated by wild ungulates, as it is characteristic for wolves living in game rich regions. Studies in eastern and central Europe agree that wolves hunt for wild or domestic ungulates (i.e. Jędrzejewski et al., 2000; Kübarsepp and Valdmann, 2003; Sidorovich et al., 2003; Andersone and Ozolins, 2004; Gazzola et al., 2005; Nowak et al., 2005; Hovens and Tungalaktuja, 2005) depending on game abundance (Meriggi et al., 1991; Mattioli et al., 1995; Sidorovich et al., 2003). But unlike our results from German wolves, who primarily hunt on roe deer, most of the other studies confirmed the wolf hunt preferably on the largest ungulate species in high abundance, available in the region. Jędrzejewski et al. (2000) and Nowak et al. (2005) report that wolves in Bialowieza primeval forest and the Beskid mountains in Poland, where the composition of the ungulate community is comparable to that in our study area, clearly prefer hunting on red deer. On the other hand in western Poland roe deer is the most consumed prey and red deer is obviously not preferred by the wolf (Nowak et al., 2011). The percentage of red deer in the ungulate community is given with 38.5% in Bialowieza (Jędrzejewski et al., 2000), 21% in the Beskid mountains (Nowak et al., 2005) and in western Poland 22.2% (Nowak et al., 2011) respectively. As we do not have comparable data about the real density of red deer in Lusatia, we can only use the hunting bag, where 21% are red deer, and 41% are roe deer.

According to Okarma (1995) roe deer is the main prey of wolves in Europe when it is very frequent, and larger cervids like red deer or reindeer are rare. Nonetheless, Bunewich (1988) found wolves in Belarus preying preferentially on roe deer. He refers to the smaller pack sizes due to legal hunting of the wolf in Belarus to explain the preference of roe deer in presence of high numbers of red deer. As wolves in Germany are a strictly protected species, packs are normal in size (about eight in annual mean), so this should not be the reason for the preference of roe deer in this case. The roe deer is one of the two most common cervid game species in the study area and occurs all throughout the country extensively. In the whole of Saxony, the yearly hunting bag of the roe deer doubled since 1990. Typical habitats of roe deer are widely distributed in the wolf region: edges of woods with dense undergrowth and access to field, grassland or scrub. Thus roe deer is the prey species which wolves encounter most frequently during their ramble. Furthermore, the smaller deer species is of a suitable prey size with low risk for the wolf. Nevertheless, the anti-predator behavior of roe deer such as vigilance and barking (Reby et al., 1999) impedes the wolf hunting success. Quoting a recent study from Scandinavia, wolves run only 47% successful attacks on roe deer, but none of the roe deer escaped after being injured by a wolf (Wikenros et al., 2009).

The seasonal differences in the diet result from a high availability of young wild boar in spring and more weakened boar in winter. Particularly a higher amount of wild boar in the wolf diet in spring was reported from other regions (Meriggi et al., 1991; Okarma, 1995; Jędrzejewski et al., 2000) and results from a positive selection of juveniles due to the potential risk in killing a well fortified adult wild boar.

Potential for conflict

Livestock makes up only a very small part of the diet of wolves in eastern Germany. This fact is based on very efficient livestock protection methods like fencing and livestock guarding dogs, which are financially supported. In the flat regions, flocks are fenced behind 90 cm high electrical mash for keeping the livestock and protection against wild boar and dogs, so a basic wolf protection is quite common. Several authors (Meriggi et al., 1991; Mattioli et al., 1995; Sidorovich et al., 2003; Nowak et al., 2005 and others) prove that damage to livestock by wolves mainly depends on the quality of livestock protection methods (Okarma, 1995; Nowak and Mysłajek, 2004) and the availability of wild ungulates (Okarma, 1995; Capitani et al., 2004; Nowak et al., 2005). The wildlife stock in the study area is high, so that the wolves do not need to prey on livestock and thereby take the risk of a confrontation with shepherds, guarding dogs or fences.

Even during the eight year study period, where the wolf population was growing from one to seven packs within Lusatia, wolf attacks on domestic animals never exceeded 22 per year and the last two years of the examination period, damage declined. According to Jędrzejewski et al. (2000) and Nowak et al. (2005) the potential for conflicts in Germany is comparably low.

Juvenile ungulates in the wolf diet

Lots of studies prove that juveniles, females, old animals and those with bad condition, especially of the larger prey species, are used by wolves above average (Mattioli et al., 1995; Okarma, 1995; Jędrzejewski et al., 1992, 2000, 2002; Gula, 2004; Gazzola et al., 2005; Nowak et al., 2005, and others). This corresponds well to our first results combining the analysis of the wolfkills and scat analysis, where juvenile red deer are clearly preferred, whereas neither the female roe deer nor the fawns are preferred by the wolf. In the opposite a study from Italy shows preference of young individuals within the roe deer prey (Mattioli et al., 2004). The percentage of very young juvenile wild boar in the wolf scats indicates that juvenile wild boars are even more positively selected by the wolves than young red deer, as observed in other studies (Jędrzejewski et al., 2000, 2002; Capitani et al., 2004; Nowak et al., 2005). But without data from wild boar prey remains we cannot give an imperative statement on the percentage of juvenile wild boar in the wolf diet.

Development of diet composition

In the eight year development of the food composition the percentage of roe deer shows an upward trend during the first years without any indication of growing roe deer density in the region. On the other hand the proportion of red deer in the wolf diet declines to a lower level after two years, while the amount of wild boar is fluctuating. Especially the percentage of wild boar in the eight year development can be explained by the different availability of this prey species because of changing density and availability of juveniles due to weather conditions and acorn crop.

Because of the changing wild boar density (Bieber and Ruf, 2005), this species only in few cases becomes the main prey of wolves (Mattioli et al., 1995; Okarma, 1995). But if it occurs in constant very high densities, while other ungulate prey species are rare, wild boar can play a prominent role. For example Sidorovich et al. (2003) reports that from Belarus and Meriggi et al. (1991) and Mattioli et al. (1995) from two different regions in Italy, where the density of wild boar is particularly high because of the access to anthropogenic food resources.

The crucial question in the adaptation of the wolves' diet to new conditions in the composition of ungulate community and environmental features is: do they adopt the hunting and therefore diet traditions from their source-population, or do they immediately adapt to changed prey availability? But the first question should be: did the conditions actually change? The western Poland-German wolf population originates from the Baltic wolf population. Compared to conditions in eastern Poland (Nowak and Mysłajek, 2006) the percentage of forest cover is lower, whereas the proportion of agricultural areas, streets and settlement areas is higher in the Lusatian heath. The forests mainly are fragmented in smaller patches, only few larger continuous forest districts occur in the German wolf area. So the roe deer and wild boar have perfect living conditions (Niethammer and Krapp, 1986) and are widely distributed, whereas red deer is mainly restricted to the larger forested areas. Therefore wolves do have perfect conditions for hunting roe deer, which are easy to prey on and almost evenly distributed. Nowak et al. (2011) show a comparable tendency for wolves in western Poland, who are closely related to German wolves belonging to the same population and living in a comparable landscape. Wild boar are quite common in the whole study area too, but their numbers are fluctuating due to weather conditions and acorn crop (Bieber and Ruf, 2005) and adult boar are well-fortified and not easy to be killed for a single or young wolf.

As wolves in the first two years preferentially preyed on red deer, roe deer became more important with expanding wolf area into agricultural used areas, opencast pits and the biosphere reserve. So the adaptation to the new conditions did occur very fast in one generation of wolves. That means, that not only the diet composition changed, but also the hunting behavior had to be adapted. While one adult red deer is enough to feed the pack for several days (Głowaciński and Profus, 1997; Jędrzejewski et al., 2000, and others), one roe deer can be completely eaten by two wolves in one night. Furthermore: killing a smaller roe deer is possible for a single wolf, whereas it is more likely to kill a much stronger red deer if more wolves take part in the hunt.

Different authors reported, that larger packs prefer hunting on larger game like red deer, moose or reindeer (Okarma, 1995; Peterson and Ciucci, 2003; Jedrzejewski et al., 2004), whereas single wolves, pairs and small packs prefer hunting on smaller deer, hares or livestock, because the risk of injuries and failure is lower.

In the first years of the study period the moufflon was an important food resource with 8.6% of the diet made up by this prey species. Moufflon, native in Corsica and Sardinia, were introduced in the 1970s for hunting (Niethammer and Krapp, 1986), but as this wild sheep is adapted to a rocky and dry environment the flat region is not suitable for them. They disappeared from the main parts of the study area because of illnesses and wolf predation. The moufflon are easy to prey on, because they are not able to escape from predators in steep rocky areas, as they do in their original environment.

This adaptation of wolves to cultivated landscape with comparably high human population density, density of streets and build up areas, and large-scale utilization of the landscape by industry, agriculture and military, shows that wolves do not need wilderness. They can cope with any kind of landscape without causing invincible conflicts (Mech, 1995; Fritts et al., 2003), if they do have wild ungulates to prey on. From the beginning of resettlement it took less than two generations to adapt to the new conditions.

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