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Original Investigation

Diet and prey selection of wolves (*Canis lupus*) recolonising Western and Central Poland

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ABSTRACT

Wolf *Canis lupus* diet was studied by scat analysis in four main and several other locations recolonised by this species in Central and Western Poland between 2002 and 2009. Wild ungulates made up 94.8% of the total biomass of food consumed, with the most common being roe deer *Capreolus capreolus* (42.8%), wild boar *Sus scrofa* (22.6%) and red deer *Cervus elaphus* (22.2%). Supplementary prey were: fallow deer *Dama dama* (2.7%), brown hare *Lepus europeus* (2.5%) and Eurasian beaver *Castor fiber* (1.4%). Domestic animals, exclusively dogs and cats, made up 1.0% of food biomass. A high similarity in the ratio of wild ungulate species in wolf food biomass between study sites was observed. Wolves hunted wild ungulate species accordingly to their relative abundance in the community. As wild ungulates are abundant and livestock density is low the large forest tracts of Western Poland seems to be very good habitat for wolves. Therefore, with more dispersing wolves from Eastern Poland and Eastern Germany, wolf recovery could significantly accelerate in the next few years in this region.

Introduction

In Europe the diet of wolves (*Canis lupus*) recolonising areas from which they were extirpated long ago has been studied mostly in Italy (Meriggi et al. 1991; Patalano and Lovari 1993; Meriggi et al. 1996; Capitani et al. 2004), the Scandinavian Peninsula (Müller 2006) and Germany (Ansorge et al. 2006). In Italy wolves which were studied in eight locations fed, depending on local food base, on very diverse foods, from garbage and fruits to livestock and wild ungulates, such as roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) (Meriggi and Lovari 1996). In the Scandinavian Peninsula moose (*Alces alces*) dominated the diet of wolves (Müller 2006). Other prey species like roe deer, Eurasian beaver (*Castor fiber*), European badger (*Meles meles*) and brown hare (*Lepus europaeus*) constituted a much lower proportion of diet, but some differences between territories were found. In Germany wolves, belonging to one newly established pack, preyed mainly on roe deer, with red deer and wild boar preyed on less frequently, and mouflon (*Ovis gmelinii*) and brown hares taken rarely (Ansorge et al. 2006).

In Poland studies on wolf diet have so far been conducted mostly in the main wolf range. They indicated that wolves fed primarily on wild ungulates, often positively selected red deer, preyed on roe deer proportionally to its relative abundance, and avoided wild boar. The share of domestic ungulates in wolf diet was diverse but relatively small within the country (Jędrzejewski et al. 1992, 2000, 2010; Śmietana and Klimek 1993; Nowak et al. 2005).

The main range of wolves in Poland has been recently restricted to large forests in eastern, north-eastern and southern (the Carpathian Mts.) parts of the country (east of the Vistula river). In the western part of country wolves have been very scarce during the last 30 years, mostly due to regular hunting, poaching, barriers to dispersal and separation from the source population in Eastern Poland (Jędrzejewski et al. 2004, 2005). Since 1998, when wolves had became protected in the whole of the country, a recolonisation of forests of Central and Western Poland has been intensified. However, the process is slow and restrained by development of urbanised areas, increasing road traffic and expanding transportation infrastructure in Central Poland (Jędrzejewski et al. 2004). Nevertheless there are still functional ecological corridors allowing the long distance dispersal of terrestrial mammals, which support wolf recovery in Poland (Jędrzejewski et al. 2004, 2005; Huck et al. 2010, 2011). A habitat suitability model for Polish wolves showed that in the regions west of the Vistula river there are about 39,000 km^2 of forest tracts suitable for wolf habitation, where more than 900 individuals are able to live, while the main wolf range in Eastern Poland comprises 22,600 km^2 and the current wolf population recorded for the whole country is 600 individuals (Jędrzejewski et al. 2008).

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Forests in Western Poland are inhabited by three native wild ungulate species: red deer, roe deer and wild boar, and their densities in this region are the highest in the country. In some areas alien species, such as fallow deer (*Dama dama*) and mouflon, have been introduced for hunting purposes, however with limited success, so they occur only in low densities (Central Statistical Office 2009; Wawrzyniak et al. 2010). The density of livestock in Western Poland is low compared to other regions. The mean density of the main husbandry animals in the western part of the country is: 24.9 cattle/km^2, 1.2 sheep and goats/km^2, 1.1 horses/km^2 of agricultural lands, while the mean density for the whole of Poland is: 35.4, 1.8 and 1.8 indiv./km^2, respectively. The highest density of cattle is found in North-Eastern (44.4–78.4 cattle/km^2) and Central Poland (45.2 cattle/km^2), sheep and goat farming is most intense in the Carpathian Mts. (1.8–13.7 indiv./km^2) and horses are bred mostly in the eastern, northern and southern part of the country (1.8–4.2 horses/km^2) (Central Statistical Office 2010).

The aim of this study was to find out the diet composition and prey selection by wolves in Western Poland. We assumed that because the densities of wild ungulates are high and livestock are not abundant, wolves recolonising Western Poland would primarily feed on wild species of ungulates. We also attempted to verify whether the prey selection of these wolves fits the general pattern of predation described by Okarma (1995), and shows clear preference toward red deer.

Material and methods

Study area

Data on wolf diet composition were collected in the lowland part of Western and Central Poland, the region between Vistula river and Polish-German border (N 50°08′–54°19′, E 14°09′–21°04′). Most of the wolf scats were found in four large forests tracts: the Bydgoszcz Forest (Central Poland), the Wałcz Forest (North West Poland), the Rzepin Forest and the Lower Silesian Forest (West Poland). During the study period in each of our study sites only one, or eventually two resident wolf packs were present. Some samples were also collected in the Noteć Forest (N 52°39′–52°53′, E 15°30′–16°49′, ca. 1350 km^2), the Sława Forest (N 52°39′–52°53′, E 15°30′–16°49′, ca. 150 km^2), the Rudy Forest (N 50°07′–50°22′, E 18°13′–18°30′, ca. 415 km^2) and the Święty Krzyż Forest (N 50°55′–51°07′, E 20°29′–21°08′, ca. 770 km^2) where wolf presence was only temporary (the Sława Forest and the Rudy Forest) or areas were recently recolonised by this species (the Noteć Forest and the Święty Krzyż Forest) (Fig. 1).

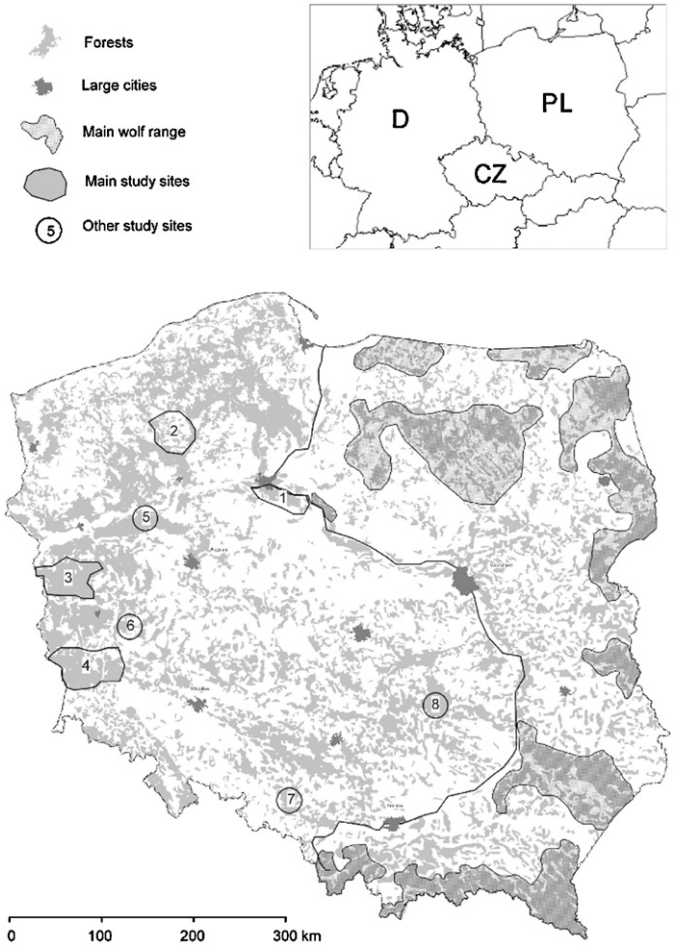

Fig. 1. Study area. Sites of scat collecting in Central and Western Poland, 2002–2009. (1) Bydgoszcz Forest, (2) Wałcz Forest, (3) Rzepin Forest, (4) Lower Silesian Forest, (5) Noteć Forest, (6) Sława Forest, (7) Rudy Forest, and (8) Świety Krzyż Forest.

Bydgoszcz Forest

A forest complex (total area 640 km^2) located south of Bydgoszcz (N 52°50′–53°07′, E 17°41′–18°45′), between the basins of the Vistula river and the Noteć river. The highest altitude is 116 m a.s.l. The region is characterized by parabolic sand dunes covered by Scots pine *Pinus sylvestris* forest (90%) with admixture of oak *Quercus petrea* and hornbeam *Carpinus betulus*. The annual mean temperature is 8.4 °C (July 18.2 °C and January −2.7 °C), the annual rainfall is 525 mm, and snow cover persists on the ground from 50 to 80 days. There is a large area (29 km^2) burnt in 1992, and now covered with thickets of Scots pine trees, in the centre of the forest. In the eastern part there is also an active military training area (38 km^2) used for artillery purposes. Permanent wolf presence has been recorded there since 2004. Livestock density in agricultural land outside the forest is: 44.4 cattle/km^2, 1.4 sheep and goats/km^2 and 1 horse/km^2.

Wałcz Forest

A large forest complex (about 1000 km^2) located north to Piła, between the Gwda river valley and the Drawska plain (N 53°03′–53°38′, E 16°04′–16°56′). The altitude ranges from 100 to 205 m a.s.l. Most of the area is covered by Scots pine forest (94%) with admixtures of birch *Betula pubescens*, alder *Alnus glutinosa* and *A. incana*, oak and Norway spruce *Picea abies*. The mean annual temperature is 8.1 °C, the annual rainfall is 520 mm and the vegetation season length is 200–213 days. The landscape is undulating, with sandy hills created by a retreating glacier. There are many large and small lakes and pit bogs within the forest. In the centre there is a large old military training area (175.5 km^2) used since 1935 by the German army and after the World War II by the Soviet army, since 1993 recultivated and managed by a forest service. Currently it is the biggest area of heath in Europe. Wolves recolonised the area in 2002. The livestock density in agricultural land outside the forest is: 28.5 cattle/km^2, 1.4 sheep and goats/km^2 and 1 horse/km^2.

Rzepin Forest

A forest complex (950 km^2) located south east of Słubice, along the Polish-German border, between the Odra, Warta and Obra rivers (N 52°02′–52°21′, E 14°35′–15°28′). It is sparsely inhabited by people, without any large towns within the forest. Numerous sandy dunes are covered with Scots pine monocultures with a small admixture of oaks and beech *Fagus sylvatica* trees, which are more abundant adjacent to lakes and the two rivers; Pliszka and Ilanka. There are also small areas covered with deciduous forests of horn-

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beam, lime *Tilia cordata*, oaks and willows *Salix* sp. The mean annual temperature is 8.3 °C, the annual rainfall is 550 mm, and the vegetation season length is 230–260 days. The highest point is 106 m a.s.l. Wolves have been resident there since 2004. The livestock density in agricultural land within and outside the forest is: 12.4 cattle/km^2, 1.3 sheep and goats/km^2 and 1.3 horse/km^2.

Lower Silesian Forest

A largest forest tract (ca. 1700 km^2) in Western Poland, located along the Polish–German border, between Olszyna, Zgorzelec and Legnica (N 51°14′–51°37′, E 14°44′–15°54′). Part of the Silesian-Muskauer Plain, its western edge adjoins the Niese river. Human density is very low within the forest—only several small towns and villages are located there. The area is mostly covered by Scots pine (ca. 90%), but there is also birch and oak admixture in wet locations, spruce and alder is common near rivers. There are two large rivers: Bóbr and Kwisa, but also several smaller watercourses. There are several former and active military training areas. The largest and still active is the Żagań-Świętoszów military area covering 380 km^2 in the centre of the forest. The mean annual temperature is 8 °C, the annual rainfall is 520–700 mm, and the vegetation season length is about 220 days. The lowest point is 107 m a.s.l., while the highest is 235 m a.s.l. Near the Polish–German border the presence of individual wolves has been recorded since 2001, but the first resident pack was established in 2007 in the eastern part of the forest. Livestock density in agricultural land within and outside the forest is: 11.7 cattle/km^2, 1 sheep and goat/km^2 and 1.3 horse/km^2.

The species structure of wild ungulate communities in these four study areas is described in Table 2.

Analysis of wolf diet composition

Wolf diet was studied on the basis of analysis of 474 wolf scats, which were collected between 2002 and 2009 in areas newly recolonised by wolves in Central and Western Poland. Scats were gathered during snow tracking of wolves in winter and by walking along the dense grid of forest roads year round. The largest number of faeces (443 samples) was collected in four large forests: the Wałcz Forest (112), the Bydgoszcz Forest (81), the Rzepin Forest (126), and the Lower Silesian Forest (124). Scats were also collected in the Noteć Forest (7 samples), the Sława Forest (2), the Rudy Forest (13) and the Święty Krzyż Forest (9) (Fig. 1).

Analysis of scats followed the standard method of drying and washing through a 0.5 mm-mesh sieve (Lockie 1959; Goszczyński 1974; Jędrzejewska and Jędrzejewski 1998). Prey was identified by bone remains, hooves, claws, feathers and hair, according to the taxonomic keys (Dziurdzik 1973; Debrot et al. 1982; Pucek 1984; Teerink 1991) and by comparison to the reference material of the Association for Nature "Wolf".

The composition of food was expressed as: (1) a percentage of faeces which contains different prey species relative to the total number of fecal samples (% occurrence) and (2) a percentage of biomass of particular food component relative to the total biomass consumed by wolves (% biomass). The biomass of food components was obtained by multiplying the weight of prey remains found in scats by coefficients of digestibility (Goszczyński 1974). The following coefficients of digestibility were used: rodents and insectivores—23, medium-sized mammals—50, ungulates—118, insects—5, plant material—4 (after Lockie 1961; Goszczyński 1974; Roger et al. 1991; Jędrzejewski and Jędrzejewska 1992).

The breadth of the food niche was calculated followed the Levins (1968) method according to formula $B = 1/\sum p_i^2$, where p_i is a contribution of every group of wolf prey in the total biomass of food consumed by wolves. To estimate the breadth of food niche, wolf prey was classified into the following groups: (1) wild ungulates; (2) domestic animals; (3) medium-sized mammals (hare, badger, fox); (4) others (small mammals, plants, etc.). Thus Index B could achieve values from 1 (strong specialization in one group of prey) to 4 (opportunistic preying on all groups).

Similarity of diet composition between forests was calculated following the formula of Pianka (1973): $\alpha_{lz} = (\sum p_{la} p_{za})\ [(\sum p_{la}{}^2)\ (\sum p_{za}{}^2)]^{-1/2}$, where α_{lz} is a degree of similarity of food composition in the first forest complex (l) and the second forest complex (z), p_{la} is a contribution of a prey a in the total biomass of prey consumed by wolves in the first forest complex, p_{za}—contribution of prey a in the total prey biomass consumed by wolves in the second forest complex.

In order to minimize errors in estimating wolf preferences toward prey species (Jędrzejewski et al. in press) the structure of the wild ungulates (red deer, roe deer, wild boar and fallow deer) in the four study areas were estimated based on: (1) annual game inventories, and (2) hunter's harvest reports, both provided by local State Forest divisions. During game inventories the number of animals of each game species was calculated by hunters using a combination of winter tracking on constant transects and direct observations of individuals throughout the year. The winter game census was based on snow tracking after new snowfall, when hunters walked a constant grid of transects, counted all tracks of ungulates and recorded their direction on maps. The difference between the number of tracks entering and leaving a grid cell (part of a forest surrounded by transects) gave the number of animals present in the cell (Pucek et al. 1975; Jędrzejewska et al. 1997). The results were compared and verified using results of year-round observations and so-called "common-sense guesses" done in the forest divisions. As there is a possibility that ungulate numbers were underestimated (Pucek et al. 1975; Wawrzyniak et al. 2010), we considered them as minimum values. We therefore assessed the percentage of a given ungulate species in the ungulate community for all four forests. We only took into account data from those hunting divisions that were located within wolf territories.

Preferences for particular ungulate species were calculated on the basis of the selectivity index D of Jacobs (1974): $D = (r - p)/(r + p - 2rp)$, where r means the percentage of this species in the ungulate structure found in wolf faeces (relative frequency), and p means: (1) percentage of this species in the whole ungulate community in the study area, and (2) percentage of this species in the hunting harvest within the study area. The species structure of wild ungulates killed by wolves was based on the proportion of ungulate occurrences in scats. Occurrence of a given species in one scat was treated as one specimen. In cases where deer could not accurately be classified (Cervidae undetermined), the proportions of red and roe deer were determined based on a sample of identified specimens.

Results

Wild ungulates made up 94.8% of the total biomass of food consumed by wolves in Western Poland (range 89.1–97.9%) (Table 1). Roe deer comprised the highest proportion with 42.8% of food biomass (range 29.6–57.6%). The next most common species were: wild boar which comprised 22.6% of food biomass (range 9.4–35.7%), and red deer, which constituted 22.2% of food consumed by wolves (range 17.8–27.8%). Fallow deer where less frequently consumed, which constituting just 2.7% (range 0–7.0%) of wolf food (Table 1). Of the medium-sized mammals, only brown hare and Eurasian beaver were significant as wolf prey, consisting 2.5% (range 1.7–3.8%) and 1.4% (range 0–5.1%) of total biomass, respectively. The only remains of domestic animals found in wolf scats, were those of dogs and cats, which made up 1.0% of biomass (Table 1).

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Table 1
Diet composition of wolves *Canis lupus* in four main study areas (localities 1–4 in Fig. 1) and other localities combined (5–8 in Fig. 1) in Western and Central Poland, 2002–2009. %Occ—percentage of occurrence in scats, %Bio—percentage of the total biomass consumed. (+) Contribution to diet <0.05%. Categories to estimate the breadth of food niche (after Levins 1968): (1) wild ungulates, (2) domestic medium-sized animals (cats, dogs), (3) wild living medium-sized mammals, and (4) others (small mammals, plants, etc.).

Item	Bydgoszcz Forest		Wałcz Forest		Rzepin Forest		Lower Silesian Forest		Other localities		Total	
	%Occ	%Bio	%Occ	%Bio	%Occ	%Bio	%Occ	%Bio	%Occ	%Bio	%Occ	%Bio
Roe deer *Capreolus capreolus*	32.1	29.6	40.2	42.9	27.0	33.1	60.5	57.6	38.7	43.6	40.5	42.8
Red deer *Cervus elaphus*	16.0	18.2	21.4	24.9	21.4	26.7	18.5	17.8	22.6	27.8	19.8	22.2
Fallow deer *Dama dama*	1.2	0.2	–	–	7.1	7.0	2.4	2.0	6.5	6.7	3.2	2.7
Undetermined *Cervidae*	16.0	12.1	13.4	5.1	8.7	3.2	4.0	0.9	9.7	2.4	9.9	4.5
Wild boar *Sus scrofa*	38.3	35.7	23.2	16.2	46.8	26.8	25.0	19.6	12.9	9.4	31.9	22.6
Wild ungulates total	96.3	95.8	86.6	89.1	96.0	96.8	95.2	97.9	87.1	89.9	94.1	94.8
Raccoon dog *Nyctereutes procyonoides*	–	–	0.9	1.0	0.8	0.2	–	–	–	–	0.4	0.3
Red fox *Vulpes vulpes*	–	–	–	–	0.8	+	–	–	–	–	0.2	+
Badger *Meles meles*	–	–	–	–	–	–	0.8	0.2	–	–	0.2	+
Domestic dog *Canis lupus familiaris*	1.2	0.4	3.6	1.6	1.6	0.8	–	–	12.9	6.0	2.3	1.0
Domestic cat *Felis sylvestris catus*	–	–	0.9	+	–	–	–	–	–	–	0.2	+
Brown hare *Lepus europaeus*	4.9	3.8	5.4	3.2	2.4	1.9	3.2	1.8	3.2	1.7	3.8	2.5
Eurasian beaver *Castor fiber*	–	–	8.9	5.1	0.8	0.3	0.8	0.1	3.2	2.4	2.7	1.4
Red squirrel *Sciurus vulgaris*	–	–	0.9	+	–	–	–	–	–	–	0.2	+
Undetermined mouse *Apodemus* sp.	–	–	1.8	+	0.8	+	3.2	+	3.2	+	1.7	+
Undetermined Insectivora	–	–	0.9	+	–	–	–	–	–	–	0.2	+
Birds	–	–	0.9	+	3.2	+	–	–	–	–	1.1	+
Insects	1.2	+	–	–	–	–	–	–	–	–	0.2	+
Plant material	2.5	+	24.1	+	46.0	+	8.9	+	25.8	+	22.4	+
Anthropogenic material[a]	1.2	–	0.9	–	–	–	0.8	–	–	–	0.4	–
Number of scats analysed	81		112		126		124		31		474	
Biomass of food consumed [kg]	91.5		122.9		117.3		152.7		35.1		519.5	
Breadth of food niche *B*	1.09		1.25		1.07		1.04		1.23		1.14	

[a] Pieces of plastic and glass.

Feeding niches of wolves in all study areas were narrow (mean 1.14, range 1.0–1.2, SE = 0.043) (Table 1). This indicates a strong specialization of wolves in one group of prey–wild ungulates. The similarity of the proportion of wild ungulate species in wolf food biomass between study sites was high, the mean α was 0.94 (range 0.91–0.98, SE = 0.013). The Wałcz forest was the only study site where the biomass of medium-sized wild mammals (European beaver, brown hare and raccoon dog combined—9.3% of food biomass) was a significant component of diet. In the remaining forests wolves utilized this source of food occasionally (Table 1).

According to figures provided by game inventories the wild ungulate communities in the study sites were dominated by roe deer (mean 56.1%, range 52.8–59.6%) (Table 2). The next most common species were red deer (mean 22.2%, range 17.6–25.9%) and wild boar (mean 21.2, range 14.5–28.0%). Fallow deer presence was sparse (mean 1%, range 0.1–1.6%). The structure of wild ungulates harvested in Western Poland revealed a significantly higher proportion of wild boars, which reached on average 42.7% (range 35.0–53.6%) and a lower proportion of roe deer (mean 33.7%, range 28.2–40.1%). The overlap of the ungulate community structure amongst study sites was high, mean $\alpha = 0.99$ (range 0.97–1.00, SE = 0.005), there were also strong similarities amongst species structures in game harvest data (mean $\alpha = 0.97$, range 0.93–0.99, SE = 0.008).

The comparison of the relative frequency of four wild ungulate species in wolf diet to their frequency in the communities in the study sites revealed that wolves slightly avoided roe deer (*D* mean −0.23, range −0.48 to 0.06, SE = 0.119) and preferred wild boar (*D* mean 0.26, range 0.07–0.55, SE = 0.108) (Table 2). However, the comparison of wolf diet to the harvest structure in the study sites showed that, conversely, wolves slightly preferred roe deer (*D* mean 0.28, range 0–0.5, SE = 0.127) and avoided wild boar (*D* mean −0.25, range −0.43 to 0.04, SE = 0.105). For red deer the Jacob's selectivity indices *D* showed that wolves generally hunted the species according to its relative abundance in the wild living community (mean 0.03, range −0.20 to 0.33, SE = 0.124) and to its proportion in the game harvest structure (mean −0.03, range −0.25 to 0.22, SE = 0.126) (Table 2). In case of fallow deer wolves generally hunted this species according to its relative abundance (*D* mean = 0.1, range −1 to 0.66, SE = 25.503) or selected this species when compared to game harvest structure (*D* mean = 0.44, range −1 to 1, SE = 29.881). Generally, in the four main study areas the proportions of various species of ungulates correlated positively with their relative abundance in the wild living communities, both for census and harvest data (Fig. 2).

Discussion

Wolves recolonising forests of Western Poland predominantly preyed on wild ungulates. This result was consistent with other studies on wolf diet in the rest of Poland and Eastern Germany (Table 3). Wild ungulates were the staple food of wolves also in other regions of Europe (Andersone 1999; Finďo 2002; Sidorovich et al. 2003; Andersone and Ozoliņš 2004; Gazzola et al. 2005; Barja 2009; Žunna et al. 2009; Jędrzejewski et al. 2010). The absence of domestic ungulates distinguishes wolf diet in Western Poland from the diet of populations in Eastern and Southern Poland (Table 3) and in several regions of Europe (Finďo and Hood 2001; Finďo 2002; Sidorovich et al. 2003; Gazzola et al. 2005; Migli et al. 2005). The most likely reasons for this were low densities of livestock and a high abundance of wild ungulates within the wolf range in Western Poland (Jędrzejewski et al. 2008; Central Statistical Office 2010; Wawrzyniak et al. 2010). The same phenomenon was recorded in Eastern Germany, where ungulates densities are comparable to those in Western Poland (Ansorge et al. 2006).

In North-Eastern, Eastern and Southern Poland wolves hunted all ungulate species, although with a general positive selection of red deer and avoidance of wild boar, when considering species composition in the community and their relative frequency in wolf scats (Table 4). In our study areas no obvious preferences for any of the four species of ungulates emerged, but in general they were preyed proportionally to their relative abundance in the wild living communities (Fig. 2). The possibility of using game inventories as a source for estimating structures of wild ungulate communities was presented by Jędrzejewski et al. (in press). They discussed likely errors that arise when data on wolf prey structure obtained

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Table 2
Species structure of wild ungulate communities based on game inventories (Census) and based on harvest reports (Harvest), and percentage of a given species in the wild ungulate structure found in wolf scats (Wolf scats) in four main study sites (localities 1–4 in Fig. 1). Prey selectivity index *D* after Jacobs (1974).

Community or wolf scats	Percentage of a given species in the community or wolf prey			
	Red deer	Roe deer	Fallow deer	Wild boar
Bydgoska Forest				
Census	25.9	59.6	0.1	14.5
Harvest	30.2	34.8	0	35.0
Wolf scats	20.6	40.9	1.7	36.8
Selectivity *D* Scats-Census	−0.15	−0.36	0.26	0.55
Selectivity *D* Scats-Harvest	−0.25	0.13	1.00	0.04
Wałcz Forest				
Census	21.9	57.5	1.6	19.1
Harvest	18.5	40.1	1.3	40.1
Wolf scats	26.4	50.0	0	23.6
Selectivity *D* Scats-Census	0.12	−0.15	−1.00	0.13
Selectivity *D* Scats-Harvest	0.22	0.50	−1.00	−0.37
Rzepin Forest				
Census	17.6	52.8	1.6	28.0
Harvest	17.8	28.2	0.4	53.6
Wolf scats	22.7	28.1	7.4	42.1
Selectivity *D* Scats-Census	0.33	−0.48	0.66	0.30
Selectivity *D* Scats-Harvest	0.15	0.00	0.90	−0.23
Lower Silesian Forest				
Census	24.2	54.7	0.8	20.4
Harvest	26.2	31.6	0.1	42.1
Wolf scats	17.5	57.7	2.2	22.6
Selectivity *D* Scats-Census	−0.20	0.06	0.47	0.07
Selectivity *D* Scats-Harvest	−0.25	0.49	0.84	−0.43
Total				
Census	22.4	56.1	1.0	20.5
Harvest	23.2	33.7	0.45	42.7
Wolf scats	21.8	44.2	2.8	31.2
Selectivity *D* Scats-Census	0.02	−0.22	0.10	0.26
Selectivity *D* Scats-Harvest	−0.03	0.28	0.44	−0.25

Table 3
Diet composition (mean percentage of consumed biomass) of wolves in different regions of Poland and Germany based on analysis of scats (from Jędrzejewski et al. in press; Ansorge et al. 2006, and this study).

Item	Southern Poland (Carpathian Mts.) ($n=2$)	Eastern Poland ($n=2$)	North-eastern Poland ($n=8$)	Western Poland ($n=4$)	Eastern Germany ($n=1$)
Wild ungulates	95.4	95.5	82.7	94.8	97.4
Wild-living medium sized mammals	0.9	0.8	9.3	4.2	2.6
Domestic animals	3.6	3.9	6.9	1.0	–

from scat investigation or from prey remains was compared to the structure of wild ungulates assessed by hunting inventories or to the game harvest structure. They concluded that in order to minimise bias, results of scat analyses should be compared to harvest structure, as both harvest and scat analyses overestimate the proportions of smaller species or highly productive species. In our study, when diet composition was compared to the ungulate community structure obtained from game inventories, roe deer were avoided, wild boar preferred and red deer hunted accordingly to its share in the community (Table 2). However, the species structure

Table 4
Species composition of ungulates (in %) in the community based on game inventories (Census) and on harvest reports (Harvest) and frequency of ungulates in wolf scats in different regions of Poland and Eastern Germany (from Ansorge et al. 2006; Jędrzejewski et al. in press; and this study). *n*—number of study areas. Numbers are percentage of occurrence of a given species of ungulates in the community, in harvest or percentage of this species in the ungulate structure found in wolf scats.

Species	Southern Poland (Carpathian Mts.) ($n=2$)	Eastern Poland ($n=2$)	North-eastern Poland ($n=7$)	Western Poland ($n=4$)	Eastern Germany ($n=1$)
Moose					
Census/Harvest	–	1.6/0	5.1/0	–	–
Wolf scats	–	–	1.7	–	–
Red deer					
Census/Harvest	36.5/46.2	18.7/15.6	30.6/21.4	22.4/23.2	23.6/?
Wolf scats	50.8	29.0	22.2	21.8	29.9
Roe deer					
Census/Harvest	57.3/?	63.5/54.1	45.3/34.4	56.2/33.7	49/?
Wolf scats	37.3	58.8	50.7	44.2	46.6
Fallow deer					
Census/Harvest	–	–	–	1.0/0.4	–
Wolf scats	–	–	–	2.8	–
Wild boar					
Census/Harvest	5.6/?	14.4/29.8	21.3/44.2	20.5/42.7	27.4/?
Wolf scats	12.0	12.5	26.7	31.2	23.5

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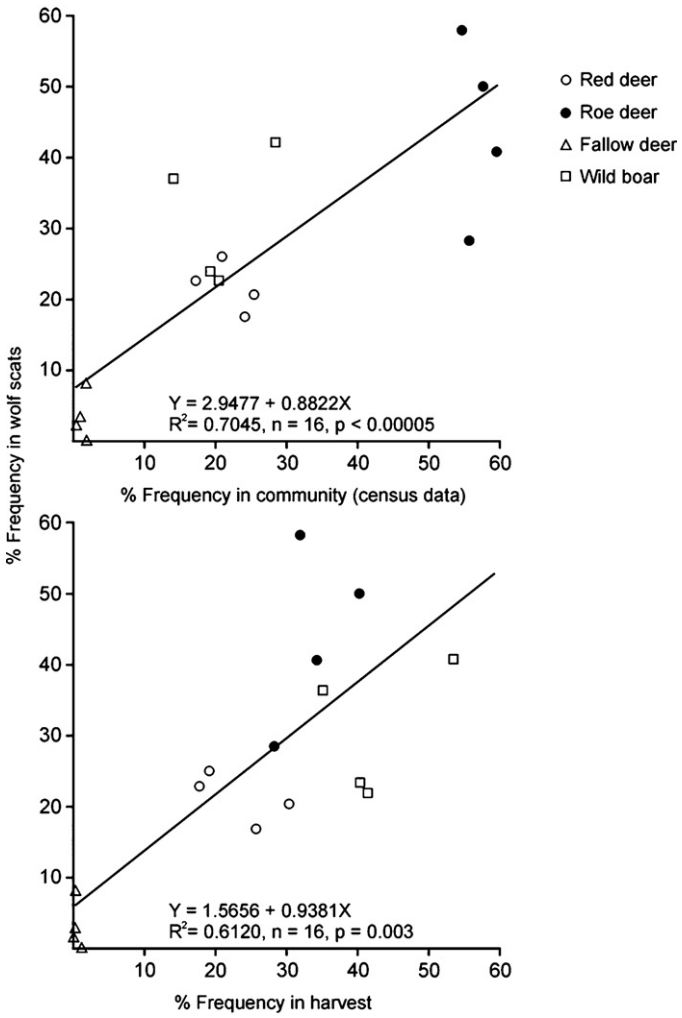

Fig. 2. Frequency of ungulate species in the wolf diet (percentage of a given ungulate species in the ungulate structure found in wolf scats) in areas 1–4 (see Fig. 1) in relation to their frequency in the community and the game harvest reports.

of harvested ungulates suggested that the proportion of wild boar in the community was seriously underestimated by game inventories, while roe deer were overestimated. Thus, we set the wolf diet composition against harvest data. In that case wolves in Western Poland generally positively selected roe deer, avoided wild boar and once again hunted red deer accordingly to their ratio in the harvest structure (Fig. 2). These findings were consistent with studies in Poland and Eastern Germany conducted in intensively managed forests, where roe deer predominated in the ungulate community and wolves preyed on this species proportionally to its relative abundance or even more intensively (Ansorge et al. 2006; Nowak et al. 2005; Jędrzejewski et al. in press; Table 4). In other regions of Europe, where roe deer share the forest with wild boar and/or moose, they can also be intensively preyed on by wolves, especially where they are present in high densities (Hell 1990; Mattioli et al. 1995; Olsson et al. 1997; Mattioli et al. 2004; Barja 2009; Žunna et al. 2009). Wild boar are generally avoided by wolves in Europe (Okarma 1995), but positively selected in a few places such as Italy or Central Estonia (Meriggi et al. 1996; Kübarsepp and Valdmann 2003) where red deer was rare, or hunted in accordance to their relative abundance (Brtek and Voskár 1987; Finďo 2002; Nowak et al. 2005). In the Białowieża Primeval Forest, where structure of wild ungulates was obtained both from game inventories and driving census, wolves hunted wild boar less than expected from their abundance and showed an increasing avoidance of wild boar with growing density of red deer (Jędrzejewski et al. 2000). Thus, the most interesting findings from our analyses was the lack of a clear preference toward red deer, despite high densities of this species in the field reported by local forest divisions (mean 2.7 indiv./km^2 range 1.6–4 indiv./km^2). The possible explanation is that in recovering, not saturated populations as found in Western Poland, where packs have been established by young dispersers (Kojola et al. 2006), and family groups were relatively small (mostly breeding pairs and their pups of the year, Nowak and Mysłajek 2011), hunting red deer can be risky or requires high energy expenditures. Thus predation on abundant smaller prey such as roe deer and wild boar piglets was easier and more efficient. The only wolves that showed preferences toward red deer were those from the Wałcz Forest and the Rzepin Forest (Table 2), where packs were larger (5–7 individuals) and established earlier (4–5 years) (Nowak and Mysłajek 2011). Similar habits were reported from the Białowieża Primeval Forest where smaller packs killed larger prey less frequently than bigger packs (Jędrzejewski et al. 2002) or from Latvia, where packs were small and young due to intensive exploitation, and preyed mostly on roe deer and wild boar (Žunna et al. 2009). Furthermore, in Scandinavia success of wolves in moose hunting was correlated with age of breeding males and their body mass (Sand et al. 2006). Thus, with ageing of wolves, gaining experience and efficiency in hunting and increasing of pack size, the diet composition can change toward higher preferences for red deer.

The low proportion of medium-sized wild animals in wolf diet in Western Poland corresponds well to results of other studies in Poland and Eastern Germany (Table 3). The only site where European beavers and brown hares were important prey to wolves was the Wałcz Forest, where beavers are abundant on rivers and lakes. The same was reported from some regions of NE Poland, where beavers are also common (Jędrzejewski et al. in press), and other locations within the wolf range in Northern and Eastern Europe, e.g. Latvia (Andersone 1999, 2003; Andersone and Ozoliņš 2004; Žunna et al. 2009), Belarus (Sidorovich et al. 2003) and Scandinavian Peninsula (Müller 2006).

With regard to food resources the forest tracts of Western Poland seems to be very good habitat for wolves, as was predicted by the habitat suitability model for this species in Poland (Jędrzejewski et al. 2008; Huck et al. 2010). The wild ungulate communities include three to four species and are abundant. The low density of domestic animals in the region assures the low level of damage to livestock, which may support the acceptance toward wolves in local communities. Therefore, if the ecological corridors which are already defined in the country (Jędrzejewski et al. 2009; Huck et al. 2010, 2011) are effective and result in more wolves dispersing from Eastern Poland and Eastern Germany, in the future we could experience an acceleration in development of the wolf population in the western part of the country.

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