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Adaptive Diet Strategy of the Wolf (*Canis lupus* L.) in Europe: a Review

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Abstract: The diet strategy of the wolf in Europe is reviewed on the basis of 74 basic and 14 additional literature sources. The comparative analysis reveals clear dependence on the latitude (and, therefore, on the changing environmental conditions) correlated with the wild ungulate abundance and diversity. Following a geographic pattern, the wolf is specialised on different species of ungulates: moose and reindeer in Scandinavia, red deer in Central and Eastern Europe and wild boar in Southern Europe. Where this large prey is taken, the roe deer is hunted with almost the same frequency in every region. The wolf diet in Europe shows two ecological adaptations formed by a complex of variables: 1. Wolves living in natural habitats with abundance of wild ungulates feed mainly on wild prey. 2. In highly anthropogenic habitats, with low abundance of wild prey, wolves feed on livestock (where husbandry of domestic animals is available) and take also a lot of plant food, smaller prey (hares and rodents) and garbage food. The frequency of occurrence of wild ungulates in the diet of wolves in North Europe varies from 54.0% in Belarus to 132.7% in Poland, while that of livestock is in the range from 0.4% in Norway to 74.9% in Belarus. In South Europe, the frequency of occurrence of wild prey varies from 0% in Italy and Spain to 136.0% in Italy, while of domestic ungulates ranges between 0% and 100% in Spain. The low density or lack of wild prey triggers the switch of the wolf diet to livestock, plant food (32.2-85% in Italy) or even garbage (up to 41.5% in Italy).

Keywords: Wolf, *Canis lupus*, prey, adaptive strategy

Introduction

The wolf (*Canis lupus* L.) has always been a competitor with humans for the wild prey as well as a conflict species, which attacks domestic animals. It is also one of the wild species, which spreads diseases and parasites, such as rabies, tapeworms and others. Therefore, the strong opposition and fight against this species through the centuries with all available means was inevitable. As a result of this, the wolf was exterminated in Great Britain in the 14th century and in many countries in Western Europe as early as the 18th century (Aybes, Yalden 1995). This could happen also in the Balkans in the 20th century but due to the relatively less disturbed nature and the high adaptability of the species to the constantly changing environmental conditions, the wolf managed to survive till the time when its important role in nature was properly assessed. The first assessments of the wolf's role in the ecosystems were published in the 1960s by Pimlot (1967) and Mech (1970). These assessements were further developed by Filonov, Kaletskaya (1985), Rukovsky (1985), several Russian authors in Anonymous (1986), Boitani (1996), Mech, Boitani (2003), Ferrari (2012) and others. Many studies on the wolf diet have been conducted since the 1950s, aiming to assess the wolf impact on nature, especially in countries as Italy, where the wolf numbers were reduced to about 100 in the 1970s and afterwards increased.

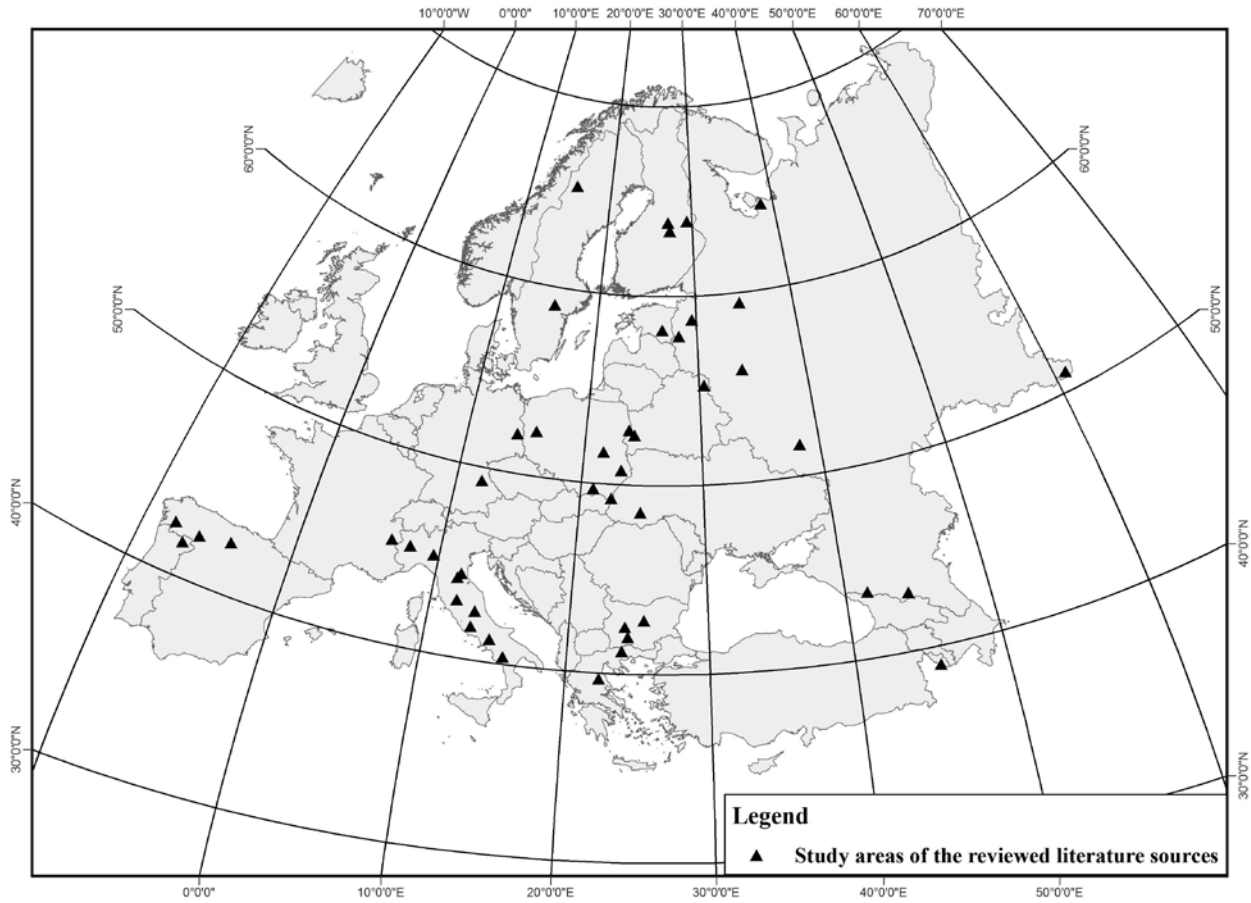

Fig. 1. Map of the reviewed literature sources study areas

Several papers reviewed the wolf preybase preferences in Europe (Okarma 1995, Meriggi, Lovari 1996, Marsili 2007, Meriggi *et al.* 2011) but these articles usually omitted data and analyses published in Cyrillic alphabet and in grey literature (papers, study reports, theses).

In the present paper, we assess the diet strategy of the wolf in Europe based on a review of the latitudinal and londitudinal gradients of the prey and the real wolf preferences in relation to multiple factors. We also try to summarise the wolf hunting strategies by using commonly accessible published sources and by including some grey literature, which is generally inaccessible to the West-European authors.

Material and Methods

We reviewed 74 scientific papers (Appendix 1) on the wolf preybase in Europe, published in the period 1953-2010 and originating from various countries (Fig. 1). These papers are written in 7 languages: 32 in English, 13 in Italian, 17 in Russian, 8 in Bulgarian, one in German, one in Portuguese and one in Ukrainian. These are 44 papers published in scientific journals, 8 in books, 7 reported at conferences or symposia, 3 PhD theses, 6 MSc theses and 5 project reports. In addition, 19 further sources were used to clarify the wolf adaptability.

The reviewed papers include diverse methods of wolf diet assessment, the scat analyses being most frequently used, followed by the analyses of the stomach content and prey remains. The papers also report different indices which describe the utilisation and selectivity of the food components.

Two main methods used for the scat analyses are: 1) Diet diversity following the method of Ciucci *et al.* (1996); 2) Diet volume percentage over dry weight.

The stomach content analyses are rarely used, especially if the species is not hunted because dead specimens are difficult to retrieve. Several papers deal with data on prey remains, as a result of snow tracking during winter or tracking based on telemetry study. The prey animals are sexed, and the age and physical condition of the prey are identified.

The main statistical analyses in the reviewed papers follow the standard procedures of Lockie (1959), namely: frequency of occurrence ($\mathbf{F_i}$%) of the different types of food **(1)**; relative frequency of occurrence ($\mathbf{rF_i}$%) **(2);** mean volume ($\mathbf{V_i}$) of the food remains in %. **(3)**

(1) Fi%=ni/N.100
(2) rFi%= Fi/Fn
(3) Vi%=∑vi/N

where: $\mathbf{F_i\%}$ **–** frequency of occurrence of one type of food; $\mathbf{n_i}$ – number of samples containing the particular type of food; **i** – type of food; **N** – number of all samples; $\mathbf{rF_i\%}$ – relative frequency of occurrence; $\mathbf{F_n}$ – overall frequency of occurrence of the particular type of food; $\mathbf{V_i\%}$ – volume of the particular food; $\mathbf{V_i}$ – volume of the different types of food

In the cases when more than one type of food is found in the samples, the percentage of food is defined according to the 7-scale method of Kruuk (1989).

This standardised approach allows for a comparison of the data between the different studies, published in the papers. Some of the papers also deal with the seasonal importance of the different prey base. However, these analyses are not consistent though all the studies and are not taken into consideration in the current paper. For the aims of the current review we consider mainly the frequency of occurrence ($F_i\%$) of the different types of food as a basic comparison tool for the wolf preferences in the different parts of Europe. The diverse methods of wolf diet assessment do not allow for a sound statistical cross country/ wolf study approach. Therefore, we mainly consider the type of preybase and frequency of occurrence ranges as a basis for comparison.

Results

The first systematic analyses of the current wolf distribution and basic wild preybase (ungulates) in Europe were made by Peters (1993) and Okarma (1995). Both authors state that the main wolf preybase in Europe consists of 8 species: reindeer (*Rangifer tarandus*), moose (*Alces alces*), European bison (*Bison bonasus*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), fallow deer (*Dama dama*) and saiga (*Saiga tatarica*). Additionally, several other species play an important role for the wolf in some regions, owing to their isolated distribution but high abundance locally: the chamois (*Rupicapra rupicapra*), the Pyrenean chamois *(Rupicapra pyrenaica),* the Alpine ibex (*Capra ibex*), the Caucasian tur (*Capra caucasica*), the Iberian ibex (*Capra pyrenaica*), the Common ibex (*Capra aegagrus*), and some introduced species such as the mouflon (*Ovis orientalis musimon*) (Genov, pers. comm). The mentioned species do not play a vital role for the wolf but they may constitute an important food source in case of deficiency of other preys in certain periods. The most widely distributed and abundant prey species, which are the main prey for the wolf in many places, are the following three species: the red deer, the roe deer and the wild boar.

According to its distribution from the Polar circle to 40˚ N latitude, the wolf feeds mainly on the ungulates, which are most abundant in the area. In the most northern parts near the Polar circle up to 50˚ N latitude, the main prey is the reindeer, which in many areas is semi-domesticated (Kojola *et. al*. 2004), followed by the moose. In South Sweden, the preybase is enriched by added values of the roe deer and wild boar. Between 60˚ and 50˚ N, the reindeer is replaced by the red deer, which is the most abundant and significant food source. Although the food base in Bialowieza Primary Forest is very rich (there are 5 prey species, i.e. red deer, moose, European bison, wild boar and roe deer), the red deer has been selected by the wolf (Jedrzejewski *et al*. 2000).

The main prey of the wolf from the Polar circle to 50˚ N latitude is the wild ungulates, $F_i\%$ of which ranges from 40.3% to 100% of all the food sources and constitute from 78.8 to 99.9% of the volume of the food taken ($V_i\%$) (Table 1).

The low frequency of occurrence of the wild ungulates ($F_i\%$=40.3%) and the high frequency of domestic ungulates ($F_i\%$=31.7%) presented by Gavrin, Donaurov (1954) for the Belorussian part of Bialowieza at that time results from the high wolf density (due to less cull), on the one hand, and the low wild ungulate density due to poaching and mismanagement, on the other hand.

The wolf diet between 50˚ and 40˚ N latitude is more complicated. There are three wolf prey species, which represent different shares: the red deer, roe deer and wild boar. In the semi-desert regions of the lower Volga River, the main food source for the wolf is the saiga antelope. Further southwards, the more important is the share of domestic ungulates and other animals. The main wolf prey species there are the wild boar and the roe deer, with a lesser share of the red deer. Some other species appear as an alternative prey, such as the fallow deer, chamois and the mouflon (Table 2).

There are several areas, in which the wild boar is a prevailing prey. In Italy, in the Casentino forest, the species constitutes 52.5% of the samples and 45.6% of the volume (Mattioli *et al.* 1995). In the Western Rhodope Mountains, Bulgaria, the wild boar occurs in 38.5 % (Fi) of the wolf diet (Serafimov *et. al.* 2009), being prefered to the roe deer.

In this part of Europe the frequency of occurrence and share of the domestic ungulates is rising. In some region as the Northern Caucasus the livestock F_i is 94.5% of all samples (Bibikov *et al.* 1985),

Table 1. Frequency of occurrence (%) of different types of food in the wolf diet in Northern Europe above 50° N latitude: 1. Wild ungulates; 2. Domestic ungulates; 3. Plant food; 4. Others

Country	Region	1	2	3	4	Source
Scandinavia	South-central	102.0*	0.4	-	40.0	Olsson *et al*. (1997)
	Sweden	91.1	-	-	48.9	Müller (2006)
Finland	East-central Karelia	72.0	3.0	2.0	24.5	Gade-Jørgensen, Stategaard (2000)
	Kainuu	75.0	-	-	35.8	Huitu (2000)
German	Sassonia	110.5	-	-	9.8	Ansorge *et al.* (2006)
Poland	Bieszczady	79.9	-	-	29.1	Suminski, Filipiak (1977)
	Bialowieza	132.7	0.6	30.5	26.6	Jedrzejewski *et al*.(2000)
	Western Beskids	99.4	4.4	57.2	24.5	Nowak *et al.* (2005)
Estonia	Alam-Pedja Reserve	79.6	5.0	3.0	23.1	Kübarsepp, Valdmann (2003)
Latvia	Latvia	75.0	13.0	6.5	33.3	Andersone, Ozolins (2004)
Belarus	Polesija	46.9	25.2[a]			Gatah (1979)
	Bialowieża	40.3	31.7	1.1	27.9	Gavrin, Donaurov (1954)
		90.2	7.9	2.4	10.7	Bunevič (1988)
	North-eastern part	94.7	10.5	3.4	27.2	Sidorovich *et al*. (2003)
Russia	Voronezh state reserve	18.6	10.1	-	71.3[b]	Mertz (1953)
		89.5	2.9	3.3	16.9[c]	Likhatcky *et al.* (1995)
	Arkhangelsk, Onega peninsula	24.4	-	5.5	78.7[d]	Rukovski, Kupriyanov *et. al.* (1972)
	Verhnevolzie	68.8	11.3	5.2	28.9	Kočetkov, Sokolov (1979),
	Pskovski region	60.5	10.4	-	36.2	Russakov (1979)
		62.1	12.1	7.7	33.5	Russakov, Timofeeva (1984)

*The values above 100% are due to the fact that in a single sample (scat or stomach) there is more than one type of food [a] dog; [b] hare *(Lepus sp.)* 20.4%, dog 19.1% and beaver 14.0%; [c] beaver 3.0%; [d] mountain hare (*Lepus timidus*) and muskrat (*Ondatra zibethicus*).

while in the Northeastern Portugal 76.8% of F_i in the scats (V_i = 84.7%) is due to domestic ungulates.

The synanthropisation of the wolf in that latitude is not only based on the take of livestock but also on the usage of garbage dumps. According to Boitani (1996), the analysis of 220 scat samples in Italy reveal that the F_i in the food of garbage dumps is 33.4% (V_i= 44.1%). The consumption of fruits is increased as in the Northern Italy the dog rose (*Rosa canina*) constitutes 31.5% of all the food (Meriggi *et al.* 1991), while Pezzo *et al*. (2003) report that the fruits of hawthorn (*Crataegus monogyna*) are the most frequent plant food in the wolf diet. In Bulgaria, in the lowland, the wolf is also feeding on grapes and sweet corn (Genov, pers. comm).

The wolf in Italy is more anthropogenically influenced in the lowlands. The results of Macdonald *et al.* (1980) in the Majella National Park show a higher take of plant food (F_i = 64.7%), domestic ungulates (F_i = 41.0%), garbage dumps (F_i = 14.2%), and others (F_i = 37.8%). Almost the same results are obtained by Ragni *et al.* (1985) during a study in Umbria, where the F_i of domestic ungulates is extremely high (71.0%) owing to the lack of wild ungulates. In Abruzzo NP, the F_i of wild ungulates (38.0%) is almost equal to the F_i of domestic ungulates (34.5%), with a high share of plant food (32.8%) and garbage (12.0%) (Patalano, Lovari 1993). A recent review of the wolf diet in Italy (Meriggi *et al.* 2011) reported significant variable trends in the frequency of occurrence of the wild boars, roe deer, red deer, and the chamois in the wolf diet over time. The authors discovered significant and positive relationships between the ungulate abundance and the ungulate presence in the wolf diet only for wild boars and roe deer. These two species are pointed out as the most important prey for the wolf in Italy.

The frequency of occurrence of domestic ungulates, plant food and garbage is high in other countries as well. In Spain, F_i of wild ungulates is 2/3 less than that of the livestock (52.3%); the plant food and garbage are also frequent food (8.5% to 41.5%, respectively) (Salvador, Abad 1987). In Greece, the ratio wild / domestic ungulates is 1:8 (F_i domestic ungulates = 64.3%) and the plant food consumption is extremely high (Fi = 57.1%) (Papageorgiu *et al.* 1994).

Between the 1980s and 1990s, there was a clear dependence of the wolf in the Southern Europe on

Table 2. Frequency of occurrence (%) of the different types of food in the region between 40˚ and 50˚ N latitude (South Europe): 1. Wild ungulates; 2. Domestic ungulates; 3. Plant food; 4. Garbage food; 5. Others

Country	Region	1	2	3	4	5	Source
Portugal	North-East	8.6	76.8	-	-	14.8	Roque *et al*. (2001)
Spain	León	35.3	52.3	85.0	41.5	14.3	Salvador, Abad (1987)
	Galicia	-	80.0	10.0	-	38.3	Cuesta *et al.* (1991)
	Cantabria	82.0	10.0	1.3	-	18.0	Cuesta *et al.* (1991)
	Douro Meseta	107.7	3.8	6.3	2.5	106.0	Cuesta *et al.* (1991)
	Demanda mountains	62.0	57.0	-	-	5.0	Cuesta *et al.* (1991)
	Sierra Morena	100.0	-	-	-	-	Cuesta *et al.* (1991)
France	Alpi Marittime	80.0	18.0	-	-	3.0	Poulle *et al.* (1997)
Italy	Abruzo NP	38.0	34.5	32.8	12.0	52.3	Patalano, Lovari (1993)
	Majella NP	-	41.0	64.7	14.2	37.8	Macdonald *et al.* (1980)
	Umbria	-	71.0	-	-	29.0	Ragni *et al.* (1985)
	Forli	107.7	3.8	6.3	2.5	6.3	Mattioli *et al.* (1995)
	Arezzo – Foreste Casentinesi- FC	105.0	5.0	-	-	5.0	Mattioli *et al.* (1995), (2004), Gazzola (2000); Avanzinelli (2001)
	Arezo – lto Mugello (SAF)	110.0	1.0	-	-	5.0	
	Arezzo – Vallesanta (VS)	107.0	7.0	-	-	5.0	Gazzola (2000); Avanzinelli (2001); Giustini (2002)
	Arezo – Pratomagno (PM)	103.0	1.0	-	-	6.0	Capitani *et al*. (2004); Mattioli *et al*. (2004)
	Arezo – Alpe della Luna -Valtiberina	102.0	6.0	-	-	5.0	Mattioli et al. (2004)
	Arezo – Alpe di Catenaia	122.0	1.0	-	-	6.0	Alboni 2004, Lamberti 2004; Colombo 2005
	Genova	17.2	22.9	64.9	9.5	76.3	Meriggi *et al.* (1996)
	La Spezia	36.0	56.3	42.2	-	21.9	
	Val di Susa- Alpi Cozie	86.4	6.7	1.7	-	4.5	Gazzola *et al.* (2005)
	Val di Cecina	110.9	9.3	-	-	9.3	Capitani *et al.* (2004)
	Val di Susa	91.4	5.7	-	-	3.0	Capitani *et al.* (2004)
	PN Orechella	136.0	32.0	11.0	-	73.0	Ciucci *et al*. (1996)
	Central Italy*	55.3	28.6	38.2	-	33.1	Pezzo *et al*. (2003)
Greece	North Greece**	7.8	64.3	57.1	-	53.4	Papageorgiu *et al.* (1994)[a]
	Central Greece**	22.2	154.6	8.3	-	2.8	Migli *et al.* (2005)[b]
Bulgaria	Central Balkan, Rositsa	65.0	22.0	-	-	13.0	Stepanov (2009)
	West Rhodopi, Shiroka poljana	80.3	11.9	-	-	2.4	Genov *et al*. (2008)
	West Rhodopi, Beglika	74.2	20.9	2.0	-	5.5	Serafimov *et al*. (2008)
	West Rhodopi, Chepino	93.0	5.0	-	-	2.0	Georgiev *et al*. (2008)
	West Rhodopi, Laki	88.1	9.6	2.7	-	1.8	Genov *et al*. 2010
Ukraine	East Carpathians	32.6	48.9	48.1		66.2	Korneev, 1950
Azerbajdzan	Caucas	37.0	35.0	8.0		20.0	Gidayatov, 1970
Russia	West Caucas	1.0	95.2	2.9	-	2.9	Bibikov *et. al.* (1985)
	Voronz Region*	2.0	99.5	81.0[c]	-	16.3	
	Caucas reserve	78.7	-	5.4	-	15.9	Kudaktin, 1978
	Caucas reserve	85.9		6.0		8.1	Kudaktin, 1986
	Sayano-Shushenski reserve	98.7		1.1		0.2	Zavazkiy, 1981

[a] Autumn and winter; [b] winter; [c] 48.4% pears; * stomachs/ guts; ** stomachs.

the livestock due to the rapid decline of wild prey. This is one of the reasons for the elevated conflict. This is the time of appearance of the so called 'synanthropic' wolves and the differentiation between the 'wild' and 'synanthropic' packs (Bibikov *et. al.* 1985, Okarma 1995). The reversed situation is observed in the Eastern Europe, and in particular in Bialowieza (Jedrzejewski *et. al.* 2000), where the wolf diet consists mainly of wild prey (F_i=132.7%) with insignificant consumption of livestock (0.6%) but still with high consumption of plant food (30.5%).

The clear adaptable nature of the wolf to the availability of prey is confirmed also by Mattioli *et al.* (1995) in a study in Casentino forest in Italy, where the high wild prey consumption (F_i = 107.7%) correlates with the wild prey abundance, resulting also in very low livestock losses (F_i = 3.8%) and garbage usage (2.5%). Another study of Meriggi *et al.* (1996) in three different regions in Italy with different wild ungulate abundance also shows clear correlation between the low wild prey densities due to hunting and Fi of wild ungulates = 17.2% to F_i domestic = 22.9%, garbage = 9.5 and plant food = 64.9% (Genova region). With clear wild prey abundance (Casentino forest, Flori) the situation changes to F_i of wild prey = 107.7% and F_i of domestic animals = 3.8%

Meriggi, Lovari (1996) have found a significant inverse correlation between the F_i% of wild and domestic ungulates in the diet. This was later confirmed by Meriggi *et al.* (2011) and shows that when wolves can choose between the two prey categories, they may prefer wild prey. In Italy, the consumption of rubbish / fruit and that of ungulates are significantly negatively correlated (Meriggi *et al.* 2011). When the wild herbivores are scarce, the wolves are forced to use alternative food sources (*e.g.* small mammals, lagomorphs, fruits and garbage). The same results are obtained by Cuesta *et al.* (1991), who compared 5 regions with different wild prey abundance in Spain: the F_i of wild prey varies from 0% (Galicia) to 100% (Sierra Morena) according to its abundance.

There are also some studies of the conflict with farmers in regions where the wolf appears for the first time since its local extinction – Poulle *et al.* (1997) in Mercantour, the French Alps, with F_i of domestic ungulates of 17.0%; Gazzola *et al.* (2005) in Val di Susa, with F_i of domestic ungulates of 6.7%; and Capitani *et al.* (2004) in Val di Cecina, with F_i of domestic ungulates of 9.3%. In all of these studies, there is also a high F_i for the wild prey (above 80%), which is a clear sign of wild prey preference. Sidorovich *et al*. (2003) in Belarus also studied two regions, with high wild prey abundance (F_i for wild prey = 94.7%; domestic = 10.5 %) and with low wild prey abundance (F_i for wild prey = 54.0%; domestic = 74.9 %).

In all cases of low wild prey density, the share of other prey (smaller alternative prey) is becoming high and (or) the wolf feeds more on livestock (Table 3 and 4). Regarding the volume (V_i) of the different food, the domestic ungulates (usually sheep) are taking around 4.5%, while the rest is taken by hares/ rabbits, rodents, fruits, grass and garbage food.

According to the reviewed published sources, the wolves found between 40° and 50° N latitude show a clear preference for the wild boar, with the roe deer as a secondary prey in cases the red deer is scarce or absent. F_i of the wild boar compared to that of the other species shows an increment correlated with the decrease in the latitude. In some places, the two prey species may have the same share or there may be a slight prevalence of the roe deer (in Arezzo – Vallesanta, Gazzola *et. al.* 2000, or Val Tiberina, Mattioli *et al.* 2004) but, in general, the prevalence in most of the regions in Italy is for the wild boar (F_i > 60%, for example in Pratomagno – Capitani *et al.* 2004, Mattioli *et al.* 2004, or in Alpe di Catenaia – Alboni 2004, Lamberti 2004, Colombo 2006). This is probably due to the wider distribution, higher productivity and abundance of the wild boar, followed by the roe deer, the red deer and the mouflon. Yet, there are some local deviations where the wild boar is not always preferred by the wolf and this is most probably a consequence of other variables (local persecution, low habitat quality, etc.), which are not studied.

The longitudinal review in the east of 17° E (Central and East Europe) shows a different situation. The main prey there is the deer species, roe deer as the most important in the south and red deer and moose in the north.

Discussion

The studies on the wolf diet are numerous but they are usually using a similar approach. They reveal that the wolf preybase strategy in Europe differs significantly from that of their counterparts in North America and Asia, mainly due to the highly fragmented habitats and the lack of enough wild ungulates to feed upon. In many places, the original ungulate diversity of 5-6 species is decreased to 2 or 3 species (Okarma 1995).

The fluctuation in the abundance of the wild undulates due to anthropogenic pressure led to the complexity of the wolf feeding ecology (Spassov 2007). The wolf uses all available sources and shows flexibility in its attempts to survive.

Table 3. Wolf diet (Fi%) in the region above 50˚ N latitude
1. N – number of samples; 2. Reindeer; 3. Moose; 4. Red deer; 5. Roe deer; 6. Wild boar; 7. Others; 8. Wild ungulates, total; 9. other food

Source	1	2	3	4	5	6	7	8	9
Müller (2006)	1594	92.3	-	-	-	-	-	92.3	7.7
Gade-Yorgensen, Stagegaard (2000)	370		92.0	-	-	-	-	92.0	8.0
Huitu (2000)	120	34.5	44.3	-	-	-	-	78.8	21.2
Ansorge *et al.* (2006)	152	-	-	43.0	34.0	16.0	3.2[a]	92.2	3.8
Kübarsepp, Valdmann (2003)	119	-	77.5	2.0	20.4	-	-	99.9	0.1
Andersone, Ozolinš (2004)	?	-	-	59.0	-	26.0	-	85.0	15.0*
Jędrzejewski *et al.* (2000)	411	-	-	60.9	2.9	15.4	18.2[b]	97.4	2.6**
Danailov *et al.* 1979	978	-	47.0	-	0.7	-	15.4[c]	47.7	36.9

[a] mouflon; [b] European bison; [c] mountain hare; * 2.3% domestic ungulates; ** 1.2% domestic ungulates.

Table 4. Wolf diet (Fi%) between 40˚ and 50˚ N latitude (Southern Europe)
1. N – number of samples; 2. Red deer; 3. Roe deer; 4. Wild boar; 5. Others; 6. Wild ungulates; 7. Domestic ungulates; 8. Plant food; 9. Other food

Source	1	2	3	4	5	6	7	8	9
Nores *et al*. (2008)	1456	16.6	16.7	12.9	11.0	57.2	33.2	-	9.6
Merggi *et al*. 1996.	519	0.8	5.0	27.3	12.5	45.6	24.1	11.5	17.9
Mattioli *et al*. (1995)	240	14.6	32.9	44.8	3.9	92.6	6.1	0.3	1.0
Pezzo *et al*. (2003)	38/45*	14.7	-	35.6	-	46.0	23.5	7.0[b]	23.5-
Migli *et al.* 2005[a]	36**	-	2.45	10.42	-	12.87	74.3	12.14	0.69
Cellina (2001)	58	-	45.0	28.7	-	73.7	9.7	7.6	9.0
Palumbo (2003)	50***	-	28. 0	62.0	8.0	98.0	-	-	2.0
Marucco *et al.* (2010)	2806	-	-	-	-	82.1	15.2	-	2.7
Stepanov (2009)	84	27.0	13.5	24.5	-	65.0	22.2	-	12.8[c]
Serafimov *et al.* (2008)	197	9.7	26.4	36.4	-	72.5	20.6	-	6.9
Genov *et al.* (2008)	84	-	35.7	50.0	-	85.7	11.9	-	2.4
Georgiev *et al.* (2008)	80	22.5	46.3	25.0	-	93.8	5.0	-	1.2
Genov *et al.* (2010)	109	13.8	24.8	40.3	8.2	87.1	9.2	1.9	1.8

[a] winter; [b] fruits (*Crataegus monogyna)*; [c] food remains bear/ wolf;
* stomachs / guts; ** stomachs; *** prey remains.

Wild or domestic animals?

The studies on the wolf diet in Europe from the 1980s till today showed two ecological tendencies: 1. Wolves living in natural habitats with a high abundance of wild ungulates feed mainly on wild prey. 2. If the habitats are highly anthropogenic, with low abundance of wild prey, the wolves feed on livestock, also taking a lot of plant food, smaller prey (hare and rodents) and garbage food.

On the European scale, there is a clear geographic pattern showing a different diet strategy between North (above 50˚ N latitude), where the wolf hunts on reindeer, moose and red deer (Bjarvall *et al*. 1982, Filonov 1989, Jedrzejewski *et al*. 2000, Kočetkov 1988, Okarma 1995, Ozolinš, Andersone 2003, Smietana, Klimek 1993), and South (below 50˚ N), where the wolf preys upon a variety of wild ungulates, anthropogenic food and fruits (Macdonald *et al.* 1980, Ragni *et al.* 1985, Salvator, Abad 1987, Cuesta *et al.* 1991, Patalano, Lovari 1993, Papageorgiu *et al.* 1994). Yet, over time there is a clear tendency to an increased use of wild ungulates in Southern Europe (Meriggi *et al.* 2011).

There is another split between Western and Eastern Europe (around 17°E longitude) affecting the choice of prey, especially in Ukraine and Moldova, where large forests have been converted into agricultural lands and open fields, forcing the wolf to adapt to new spatial, diet and reproductive conditions (including hybridisation with dogs) (Bibikov *et al.* 1985, Ryabov 1993)

In Southern Europe, where all wolf habitats

have been destroyed, the species uses both types of the feeding strategies mentioned above, and the flexibility depends on the level of anthropogenic influence. In Spain in the mountain regions, the wolf is specialised on wild ungulates, while in the lowlands it feeds more on domestic ungulates (Cuesta *et al.* 1991). In Italy the first studies (around 1960s and 1970s) showed a large share of livestock in the wolf diet, but with an increase in the wild prey abundance, the wolf switches to the wild prey as more risk-free source of food (Mattioli *et al.* 1995, Ciucci *et al.* 1996, Meriggi *et al.* 1996, Capitani et al. 2004, Mattioli *et al.* 2004, Gazzola *et al.* 2005, Marsili 2007). This is confirmed by Meriggi, Lovari (1996), Meriggi *et al*. 2011 and Sidorovich *et al.* (2003), who state that the selection of wild and domestic ungulate prey is influenced mainly by their local abundance, but also by their accessibility. Therefore, the diet breadth increases with the decrease in the presence of large prey in the diet. Furhermore, in areas (for example in Bulgaria and France), where the wolf had a local extinction and reappeared again, with the increase in the wolf numbers, the livestock damages also increase (Spassov 2007, Poulle *et al.* 1997). This is mainly due to the loss of livestock protection habits and skills in shepherds. The restocking of wild ungulates in many regions led to a significant decrease in the conflict wolf-man (Meriggi, Lovari 1996, Poulle *et al.* 1997, Vos 2000). Since the 1990s, there has been a constant and persistent increase in the share of the wild ungulates in the wolf diet in Europe. On the European scale, this phenomenon is linked to the increase in the distribution and abundance of wild ungulates since the 1970s and the total protection of the wolf in many European countries. This is followed by the appearance of the wolf in new regions, but also by the formation of negative attitudes in farmers and other local people in these regions, and therefore, to illegal persecution (Poulle *et al*. 1997, Gazzola *et al*. 2005).

A critical element of the quick wolf recovery in many areas is the ability of performing long distance travels compared to that of the prey. As a result, the wolf may recolonise areas with low densities of wild prey and later to switch to livestock as alternative prey. Noting this remarkable adaptability in the wolf expansion, Linnell *et al.* (2008) point out that in the future the conflict wolf-man will be increased by including newly recolonised areas with higher human population density.

Specificity of diet in the different regions

The review of the literature shows a clear difference in the diet strategy corresponding to the ecological conditions. On latitudinal gradient, the wolf is mainly taking a larger prey: moose and reindeer in Scandinavia (Ansorge *et al.* 2006, Gade-Yorgensen, Stagegaard 2000, Huitu 2000, Müller 2006), red deer in Central and Eastern Europe (Okarma *et. al.* 1995, Ivanov 1988; Jedrzejewski *et. al.*2000; Spassov *et al.* 2000, Spassov 2007) and wild boar in Southern Europe. The review shows that although this is generally true, the wolf may show a local adaptation to another type of prey and even carrion in relation to miltiple variables. Thus, the wolf offen plays a vital sanitary role in the prevention of spread of deseases (Ivanov 1988), especially during the outbreak of zoonoses, such as the swine plague.

Where this large prey is taken, the roe deer is hunted with almost a similar frequency in every region. The other ungulate species are with local importance only.

The wolf is often referred to as an opportunistic species, which takes the most abundant and easy to acquire prey species (Okarma 1995, Meriggi, Lovari 1996). This is generally argued by Barja (2009) who states that the trophic position of the wolf in Galicia, Spain, is closer to a facultative specialist (feeding mainly on roe deer in the presence of other alternatives – red deer and wild boar), than to an opportunistic species. This is supported by data from Osogovo Mountain, Bulgaria, where the roe deer is mostly preferred (more than 70% of the prey) in the presence of the extremely abundant wild boar (Alexander Dutsov, unpublished). This may be due to the inability or unwillingness of the wolf pack to undertake the risk attacking large, potentially dangerous prey, when smaller but enough profitable prey is available. Yet, Barja (2009) states that the wolf may change the key food item when other profitable prey, not so dangerous as the wild boar, is available. The red deer preference in Poland also confirms that hypothesis (Jedrzejewski *et al.* 2000, Nowak *et al.* 2005),

There is also a difference in 'where' the prey is taken. In Scandinavia, the moose is preyed upon in the forests (Filonov 1989), while the roe deer and the wild reindeer – in the open areas and fields (Bjärvall, Isackson 1981, Olsson *et al.* 1997). The red deer is mainly taken by the wolf in coniferous forests with patches of mixed forests and also in the lowlands (Okarma 1995). The wild boar and the roe deer in Southern Europe are hunted mainly in mountainous areas. So the local specificity may be also a result of the types of habitat available and their coverage.

One important question is the risk taking by the wolf while hunting the prey. The study in Arezzo Province in Italy (Capitani *et al.* 2004) reveals a

great fluctuation in the wolf prey's preference under different circumstances in six areas with different prey availability (as species and as abundance). The observed fluctuations are not only due to the different temporary prey densities but also to the fitness of the pack. The wolf packs might be specialised on certain prey species according to the body size of the individuals in the pack and the numbers of the pack members. This is closely connected with the size of the prey (body mass) and fitness, so the energy expenditure during hunting is balanced on income-outcome level. The predator assesses every victim prior to the attack for the probability of killing it with minimum efforts. There is also a risk injuries or even death involved when attacking a larger prey. According to Mech, Peterson (2003), a great role in the selection of the prey is played by a combination of efficiency of the attack and amount of food to be obtained and the risk of injury involved, when the prey is actively resisting.

This gives the roe deer a second place in many areas as it is a difficult prey to get – it leads more or less solitary life (gathering in small herds only in winter or in open fields) and represents a smaller amount of food for one take (Gerard *et al*. 1995). Although the moose is much more risky to get, it is preferred by the wolf in the north (Ollsson *et al.* 1997) by presenting a large portion of food for one take.

More complex is the question why the wild boar is not preferred since the abundance in Central and Eastern Europe (Poland in particular) is similar as in Southern Europe. The wolves prefer to take down wild boars with a weight between 10 to 35 kg. (Mattioli *et al.* 1995 Meriggi *et al.* 1996, Mattioli *et al.* 2011). The juveniles with this weight are poorly defended by the mothers, live in a big herd, which is easily seen by the predators, or can be separateed from the mothers before the end of their first year. The juveniles with smaller weight (below 10 kg) are better defended by the mother and do not worth the risk as supply small amount of food (Meriggi *et al.* 1991, 1996, 2011).

The preferred prey in Central and Eastern Europe – the red deer is also carefully chosen by the wolf. These are usually subadults (1-2 years old) with a body weight around or a bit higher than that of the wild boar (Jedrzejewski *et al.* 2000, Nowak *et al.* 2005). The hypothesis is that the red deer is preferred because of the bigger biomass at one take and the greater pack size of the northern wolves compared to their southern counterparts. These bigger packs can be supported by the extensive forests of Bialowieza, where most of the studies on the wolf prey were done, while the fragmented forests of Southern Europe (Italy in particular) can sustain only smaller packs. Additionally, the red deer populations are not as dependent to the forest mast productivity as the wild boar whose number may greatly vary after years with low mast production and this could provide more stable income for the bigger packs.

Conclusions

The wolf is one of the most flexible species of large mammals which is able to survive in diverse habitats and food conditions. In the northern part of its distribution it feeds mainly on wild ungulates (reindeer, moose and red deer) and livestock is not of significance to its diet. In Southern Europe the wolf diet is more diverse, as wild ungulates (mostly wild boar and the share of roe and red deer) are still predominantly taken. In some regions the wolf also feeds on livestock, which may constitute a greater share of its diet. It is especially true for regions where the species recolonises back after extinction and important reason for higher livestock losses is the loss of preventing habits in livestock husbandry.

The species may adapt its hunting/ food aquisition strategy in every region according to the status of the prey, the habitat allowance and anthropogenic factors. In regions, in which the wild ungulates are abundant the wolf chooses its strategy in a balance of the prey biomass, energy spent in catching the prey, and the defence capabilities of the prey itself. The wolf may quickly switch its main prey from one type to another according to the shifts of prey density and the anthropogenic factors. Nowadays, because of that adaptability, it is able to expand, reestablish and gain some of the lost territories of his historical distribution in Europe.

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Appendix 1. Literature review of the main sources on the wolf diet strategy in Europe

Country	Location	Latitude (°N)	Longitude (°E or °W)	Source
-	Europe – overall comparison	-	-	Meriggi, Lovari (1996)
-	Europe – overall comparison	-	-	Okarma (1995)
Azerbajdzan	Caucas			Gidayatov, 1970
Belarus	Bialowieza	52°2′-52°4′	23°2′-24°2′ E	Gavrin, Donaurov (1954)
Belarus	Bialowieza	52°2′-52°4′	23°2′-24°2′ E	Bunevich (1988)
Belarus	North-eastern Belarus	55°0′	29°3′ E	Sidorovich *et. al.* (2003)
Belarus	various regions	53°3′-56°0′	23°0′ -32°5′ E	Gatah (1979)
Bulgaria	Western Rhodopes	41°5′	24°5′ E	Genov *et. al.* (2010)
Bulgaria	Western Rhodopes	41°5′	24°1′ E	Genov *et. al.* (2008)
Bulgaria	Western Rhodopes	41°5′	23°6′ E	Georgiev *et. al.* (2008)
Bulgaria	Western Rhodopes	41°5′	24°0′ E	Serafimov *et. al.* (2009)
Bulgaria	Central Balkan region	42°5′	25°0′ E	Spassov *et al.* 2000; Stepanov (2009)
Bulgaria	Ihtimanska Sredna Gora mountain	42°5′	23°8′ E	Ivanov (1988)
Estonia	Alam-Pedja Nature Reserve	58°2′	26°1′ E	Kübarsepp, Valdmann (2003)
Finland	Central Finland	62°3′	25°5′ E	Gade-jorgensen, Stagegaard (2000)
Finland	Kainuu	64°2′	28°3′ E	Huitu (2000)
Finland	East-Central Finland	62°3′	26°3′ E	Kojola *et. al.* (2004)
France	Southern France	44°1′	7°10′ E	Poulle *et. al.* (1997)
Germany	all country	51°0′	13°1′ E	Ansorge *et. al.* (2006).
Greece	Central Greece	39°4′	21°3′ E	Migli *et. al.* (2005)
Greece	North Greece	41°1′	24°1′ E	Papageorgiou *et. al.* (1994)
Italy	Provincia di Arezzo	43°3′	11°5′ E	Alboni (2004)
Italy	Parco Nazionale, Monte Falterone	43°6′	11°4′ E	Avanzinelli (2001)
Italy	all country	37°-47°	7°3′ -17°3′ E	Boitani (1996)
Italy	North-Eastern Apennines	46°1′	12°5′ E	Capitani *et. al.* (2003)
Italy	three different Italian ecosys-tems	43°3′	11°5′ E	Capitani *et. al.* (2004)
Italy	Parco Regionale dei Cento Laghi	44°3′	10°1′ E	Cellina (2001)
Italy	all country	37°-47°	7°3′ -17°3′ E	Ciucci *et. al.* (1996)
Italy	Provincia di Arezzo	43°3′	11°5′ E	Colombo (2005)
Italy	Western Alps	44°1′	7°1′ E	Gazzola *et. al.* (2005)
Italy	Parco Nazionale, Monte Falterone	43°6′	11°4′ E	Gazzola *et. al.* (2000)
Italy	Foreste Casentinesi, Monte Falterona e Valle Santa	43°6′	11°5′ E	Giustini (2002)
Italy	Alpe di Catenaia	43°4′	11°6′ E	Lamberti (2004)
Italy	Abruzzo mountains	41°4′	13°5′ E	MacDonald *et. al.* (1980)
Italy	Central-East Apennine	43°4′	12°4′ E	Marsili (2007)
Italy	Piemonte region	44°1′	7°2′ E	Marucco *et. al.* (2010)
Italy	Foreste Casentinesi National Park	43°6′	11°4′ E	Mattioli *et. al.* (1995)
Italy	North-eastern Apennine	46°1′	12°5′ E	Mattioli *et. al.* (2004)
Italy	Northern Italy	46°0′	10°0′ E	Meriggi *et. al.* (1996)
Italy	all country	37°-47°	7°3′ -17°3′ E	Meriggi *et. al.* (2011)
Italy	BolognesеAppenne	44°3′	11°2′ E	Palumbo (2003)
Italy	Abruzzo NP, Central Italy	41°4′	13°5′ E	Patalano & Lovari (1993)
Italy	Central Italy	43°3′	11°5′ E	Pezzo *et. al.* (2003)
Italy	Umbria, Central Italy	44°5′	12°4′ E	Ragni *et. al.* (1985)
Latvia	all country	55°4′- 58°0′	20°5′- 28°1′ E	Andersone, OZOLINŠ (2004)

Appendix 1. Continued

Country	Location	Latitude (°N)	Longitude (°E or °W)	Source
Latvia	all country	55°4′- 58°0′	20°5′- 28°1′ E	Ozolinš, Andersone (2003)
Poland	Bialowieza	52°3′- 55°0′	23°3′- 23°5′ E	Jedrzejewski *et. al.* (2000)
Poland	Western Carpathian Mnts	49°3′- 50°0′	19°0′- 23°3′ E	Nowak *et. al.* (2005)
Poland	Bieszczady Mountains	49°3′	22°5′E	Smietana, Klimek (1993)
Poland	all Poland	49°3′-54°5′	15°0′E-23°3′ E	Suminski, Filipiak (1977)
Portugal	North-east Portugal	41°4′	7°3′W	Roque *et. al.* (2001)
Russia	West Caucasus Voronz Region	43°0′	42°1′ E	Bibikov *et. al.* (1985)
Russia	Darvinskii Reserve	58°5′	37°3′E	Filonov (1989)
Russia	all Russia	-	-	Rukovsky (1985); Filonov, Kaletskaya (1985)
Russia	Voronezh state reserve	51°5′	39°2′E	Likhatcky *et. al.* (1995)
Russia	Arkhangelsk, Onega peninsula	64°3′	38°0′E	Rukovski, Kupriyanov *et. al.* (1972)
Russia	North-West USSR	-	-	Danilov *et. al.* (1979)
Russia	Tversk region	56°5′	34°5′E	Kočetkov, Sokolov (1979)
Russia	Caucas reserve			Kudaktin, 1978
Russia	Caucas reserve			Kudaktin, 1986
Russia	Voronez region	51°5′	39°2′E	Mertz (1953)
Russia	North Pskov region	58°3′	28°4′E	Rusakov (1979)
Russia	Pskov region	58°0′	28°4′E	RUSSAKOV, TIMOFEEVA (1984)
Russia	Sayano-Shushenski reserve			Zavazkiy, 1981
Spain	five areas to cover all country	36°0-43°5′	9°0′W-3°0′ E	Cuesta *et. al.* (1991)
Spain	Northern Spain	43°0′	4°5′W	Nores *et. al.* (2008)
Spain	León province	42°4′	5°5′W	Salvador, Abad (1987)
Spain	Galicia (North-western Spain)	42°3′	8°1′W	Barja (2009)
Sweden	South central Scandinavia	60°3′	15°0′E	Olsson *et. al.* (1997)
Sweden	North-Western Sweden	65°1′	16°0′E	Bjarvall, Isakson (1982)
Sweden	all country	55°0′-68°3′	11°0′-19°0′ E	Müller (2005)
Ukraine	East Carpathians			Korneev, 1950