Food habits of the wolf *Canis lupus* in Latvia based on stomach analyses

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Abstract. The diet of *Canis lupus* in Latvia was studied from December 2001 to April 2008 based on analyses of 165 stomachs. Wild ungulates (cervids and wild boar) were the main food of the wolves. Cervids were found in 64.7% of the samples (69.7% of the biomass), wild boar in 25.9% of the samples (22.6% of the biomass), and beavers in 8.6% of the samples (6.4% of the biomass). The average mass of stomach contents was 824.1 g. Empty stomachs made up 26.7% of all stomachs. Statistically significant differences were found comparing variances of stomach content biomass between 1–2-year-old and adult animals and also in beaver remains in the diet of male and female wolves (12.9% and 3.2% of the stomach content biomass, respectively). There were no other significant differences in the diet composition, stomach content biomass, and percentage of empty stomachs among age groups, between sexes, and between eastern and western parts of Latvia. Interpretation and implications to wolf conservation policy based on the given results are suggested.

Key words: Canis lupus, diet, stomach content, Latvia.

INTRODUCTION

Foraging of the wolf *Canis lupus* is fairly well studied for the Palaearctic and the North American range (Bibikov, 1985; Pavlov, 1990; Jędrzejewska & Jędrzejewski, 1998; Mech, 2003). The few studies conducted in the Baltic region (Valdmann et al., 1998, 2005; Andersone, 1999; Andersone & Ozoliņš, 2004) confirm the existing knowledge; however, they have significant implications related to the species conservation policy.

Wolf conservation is a totally new and comparatively lately implemented initiative for the Baltics and Latvia in particular (Ozoliņš, 2001, 2006). Nevertheless, the wolf population has never been assessed as endangered. Promotion of wolf killing by paying bounties was abolished in 2000 while the legal restrictions on hunting, including a short ban during the breeding season, were introduced for the first time in 2004. Due to the never disrupted human–wolf coexistence in this area, the so-called wolf conflict is rather moderate and mainly related to the fear of the hunters that any protection measures towards wolves will reduce their bags

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of wild ungulates or just make them harder to hunt. Livestock depredation is considered probably to less extent than elsewhere as preventive measures are so far completely ignored by the farmers despite the fact that tens of sheep and cattle are killed annually. Since 1998, the policy makers have succeeded in involving most of the relevant stakeholders in a joint wolf population monitoring that provides data on its current distribution, demographic viability, and records of damage to livestock. Since 2004, these data have been used in order to adjust the wolf hunting quota to the actual population status to enable sustainable wolf harvesting. The point of interactions between the wolf and other game species persists hence all details of wolf diet and amount of consumed prey are important to deal with controversial interests of wildlife managers.

This study examines the food eaten by wolves, who afterwards were killed by hunters so that the sex, age, date of hunting, and place of individuals are known. As hunting pressure may change the demographic structure of the wolf population (Bondarev, 2002; Mech, 2003) it is important to understand how far and whether at all it has consequences in foraging, which is the main reason of the 'wolf conflict' (Treves & Karanth, 2003). Our latest material will help to make a temporally and spatially related analysis on wolf diet and prey consumption for quite a considerable time period because preliminary data were gathered and summarized already from 1998 to 2001 (Andersone & Ozoliņš, 2004). At that time wolves were persecuted without any restriction and ungulate populations just started to recover after the fast decline in the 1990s (Andersone-Lilley & Ozoliņš, 2005). Recently, ungulate populations have shown an obvious increase and the wolf population is controlled at a more or less stable level. Thus we expected some changes in the wolf diet as well.

MATERIAL AND METHODS

Food habits of wolves in Latvia were studied from December 2001 to April 2008. The study was based on analyses of 165 stomachs obtained from harvested wolves all over the country. As wolves were rarely hunted in the summer season, there were only 17 stomachs from this time of year. Therefore differences between summer and winter diets were not analysed.

Food remains were found in 121 stomachs. Fresh stomach contents were weighed (1 g precision) and microscopic slides of hair found in stomachs were prepared in order to identify prey species according to the keys by Teerink (1991) and our own reference collection. In our former (Andersone & Ozoliņš, 2004) as well as recent experience, in the majority of cases the contents of wolf stomachs consist of remains of a single prey species. As a maximum, remains of two different prey were found in the same stomach. Eleven samples contained two food items including plant remains. In those samples the relative volume (in percents) was estimated for each item by sight. Then the relative volume index and the total mass of stomach content in grams were used to calculate the weight of each item. Two cervid species, *Cervus elaphus* and *Capreolus capreolus*, were not separated

in some cases during the analysis because of their very similar hair structure and consequently possible identification mistakes. The elk *Alces alces* was not found with certainty within our sample. Also species of small rodents (e.g. *Arvicola terrestris, Clethrionomys glareolus, Microtus* sp., and *Apodemus* sp.) and birds were not identified.

The diet was quantified by two indices: frequency of occurrence and ratio of stomach content biomass. Frequency of occurrence was calculated dividing the number of stomachs containing a particular prey item by the total number of stomachs containing food remains. Ratio of stomach content biomass was calculated dividing the total weight of a particular food item in the sample (the total weight of a prey species or category) by the total weight of the stomach contents.

Sex of the animals was determined during the examination and autopsy of 164 harvested wolves (for one animal sex remained undetermined). Stomachs of 46 males and 118 females were available. The difference between sexes in our sample did not result from a shaped sex ratio in the population but our sample was biased by the main aim of monitoring the wolf population – the demographic status (Ozoliņš et al., 2001). Therefore the whole carcasses of female wolves were collected in order to determine the reproductive status while collecting skulls from the male wolves was sufficient.

The absolute age of the animals was determined by counting cement increment lines in root slices of a canine as approved in our preliminary investigations of wolves collected for monitoring the demographic status of a wolf population (Ozoliņš et al., 2001). According to that the wolves for which age could be determined were divided into three age groups – animals under age 1 (n = 34), 1–2-year-old animals (n = 35), and adult animals (≥ 3 years old) (n = 43).

Geographical differences in diets between wolves in east and west Latvia were also verified. Similarly to the study by Andersone & Ozoliņš (2004), the border between both study areas ran from Riga city southwards to the frontier with Lithuania. Of the harvested wolves 78 were from the eastern part, and 87 from the western part. Abundance of prey species is characterized by the game statistics recorded by Latvian State Forest Service (SFS) (Andersone-Lilley & Ozoliņš, 2005). As the number of the hunters and their hunting efforts are quite stable, the annual hunting bags are suggested to be the least biased indices.

The Kolmogorov–Smirnov test was used to test normality of the samples and the Mann–Whitney U-test was used to test statistical differences between samples (Fowler et al., 2006). The proportion validity test was used to test statistical differences in empty stomachs (Liepa, 1974).

RESULTS

Wild ungulates (cervids and the wild boar *Sus scrofa*) were the main food of the wolves (Table 1). Cervids were found in 64.7% of the samples, comprising 69.6% of the stomach content biomass, while wild boar were found in 25.9% of the samples, comprising 22.6% of the biomass. Inter alia, stomach analyses showed

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Table 1. Diet composition of wolves from December 2001 to April 2008

Food item	Frequency of occurrence, %	Stomach content biomass, %
Roe deer	32.8	41.5
Unidentified cervids	31.9	28.1
Wild boar	25.9	22.6
Beaver	8.6	6.4
Medium-sized and small carnivores	1.7	0.4
Small rodents	0.9	0.02
Domestic animals	1.7	0.2
Birds	1.7	0.6
Plants and berries	4.3	0.1

that roe deer constituted undoubtedly at least 41.5% of the biomass while unidentified cervids amounted to 28.1%. The abundance of roe deer and wild boar has increased considerably during the last decade (Fig. 1). Another significant food item was the beaver *Castor fiber*, which was found in 8.6% of the samples (6.4% of the biomass).

Other food items found in wolf diet were small rodents, medium-sized and small carnivores (such as the fox *Vulpes vulpes*, the racoon-dog *Nyctereutes procyonoides*, and animals from the Mustelidae family), birds, domestic animals (a dog and a cat in this case), and plants and berries. However, none of these items exceeded 4.3% of the occurrence and 0.6% of the stomach content biomass.

The mass of stomach contents varied from 10 to 5152 g; the average mass was 824.1 g. Mass of the stomach contents was not normally distributed (Kolmogorov–Smirnov test, P < 0.001) as for the most part it was under 400 g (Fig. 2). A little over a quarter (26.7%) of all stomachs were empty.

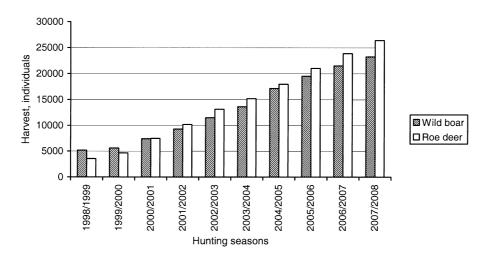


Fig. 1. Changes in the abundance of two main ungulate species within the last decade.

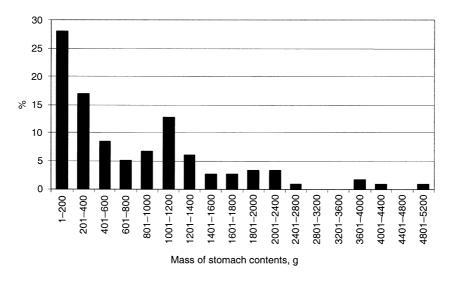


Fig. 2. Distribution of biomass from examined stomach contents (totally empty stomachs are excluded).

There were slight differences in the diets of different age groups of wolves, mostly concerning the consumption of beaver (Table 2); however, none of them were statistically significant (U-test, P > 0.05).

Among variances of stomach content biomass a significant difference was found only between 1–2-year-old and adult animals (U-test, P < 0.05).

Stomach contents of yearlings were on average lighter (593 g; 35–4000 g) than those of younger (705.1 g; 10–2050 g) and adult wolves (964.5 g; 15–2400 g); however, due to the variance distribution pattern (Fig. 2) comparison of mean values was not applicable. Furthermore, the yearlings had more often empty

Food item	Wolves under age 1		1-2-year-old wolves		Adult wolves	
	Frequency of occurrence, %	Stomach content biomass, %	Frequency of occurrence, %	Stomach content biomass, %	Frequency of occurrence, %	Stomach content biomass, %
Roe deer	30.8	49.1	42.9	67.8	40.7	44.0
Unidentified cervids	34.6	19.4	23.8	10.9	22.2	14.5
Wild boar	19.2	19.9	28.6	17.1	29.6	32.7
Beaver	15.4	8.9	4.8	2.9	11.1	8.8
Domestic animals	0.0	0.0	4.8	1.0	0.0	0.0
Birds	7.7	2.7	0.0	0.0	0.0	0.0
Plants and berries	3.8	0.1	4.8	0.3	0.0	0.0

Table 2. Diet composition of different age groups of wolves

stomachs (37.1%) than younger (20.6%) and adult animals (32.6%), although differences were not statistically significant (P > 0.1). The ratio of different age groups varied within the study period (Fig. 3). For sex ratio, the deviation from 1:1 was not significant in none of the three age groups (χ^2 test with Yates' correction, P = 0.05).

The diets of male and female wolves were rather similar (Table 3). A statistically significant difference was found only in beaver remains in the stomach (12.9% in the male diet and only 3.2% in the female diet) (U-test, P < 0.05).

The average mass of stomach contents of male wolves was larger (882.3 g; 40–5152 g) than that of female wolves (792.4 g; 10–3640 g). No significant differences were found in the percentage of empty stomachs between male (21.7%) and female (28.8%) wolves (P > 0.1).

There were no significant differences in the diet composition between eastern and western Latvia (U-test, P > 0.05) although the consumption of cervids was slightly higher in the west while the consumption of wild boar was higher in the east (Table 4).

The average mass of stomach contents in the eastern part of the country (776.4 g; 10–3640 g) differs only slightly from that in the western part (784.6 g; 10–5152 g). Also the percentage of empty stomachs was similar in east and west Latvia (26.9% and 26.4%, respectively) and no statistically significant differences were found (P > 0.1).

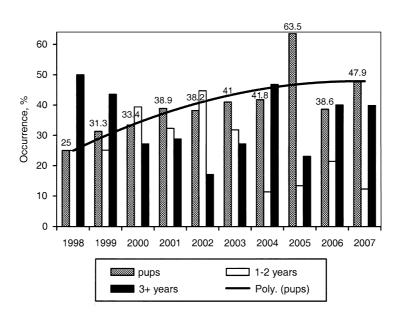


Fig. 3. Dynamics of three age groups in the wolf population according to their occurrence in the hunting bag. Pup percentage (increasing trend) is indicated by figures on the top of the corresponding bars.

Food item	Male	wolves	Female wolves		
	Frequency of occurrence, %	Stomach content biomass, %	Frequency of occurrence, %	Stomach content biomass, %	
Roe deer	34.3	38.4	32.5	43.2	
Unidentified cervids	31.4	30.1	31.3	27.0	
Wild boar	22.9	17.3	27.5	25.4	
Beaver	8.6	12.9	8.8	3.2	
Medium-sized and small carnivores	2.9	1.0	1.3	0.1	
Small rodents	2.9	0.1	0.0	0.0	
Domestic animals	2.9	0.2	1.3	0.2	
Birds	0.0	0.0	2.5	0.8	
Plants and berries	2.9	0.04	5.0	0.1	

Table 3. Diet composition of male and female wolves

Table 4. Diet composition of wolves in east and west parts of Latvia

Food item	East Latvia		West Latvia		
	Frequency of occurrence, %	Stomach content biomass, %	Frequency of occurrence, %	Stomach content biomass, %	
Roe deer	43.4	46.4	23.8	37.3	
Unidentified cervids	24.5	19.9	38.1	35.3	
Wild boar	24.5	26.9	27.0	19.0	
Beaver	7.5	5.3	9.5	7.4	
Medium-sized and small carnivores	1.9	0.2	1.6	0.6	
Small rodents	0.0	0.0	1.6	0.04	
Domestic animals	1.9	0.1	1.6	0.3	
Birds	3.8	1.2	0.0	0.0	
Plants and berries	5.7	0.1	3.2	0.1	

DISCUSSION

The diet of wolves in Latvia is rather diverse although they mainly preyed upon wild ungulates as in other areas where the natural prey base is rich (Bibikov, 1985; Jędrzejewska & Jędrzejewski, 1998; Kübarsepp & Valdmann, 2003; Mech 2003). Consumption of beaver is mentioned also in other studies of wolves (Pavlov, 1990; Kohira & Rexstad, 1997; Jędrzejewska & Jędrzejewski, 1998; Valdmann et al., 1998; Mech, 2003; Sidorovich et al., 2003) although the proportion of beaver in the wolf diet was seldom as high as in Latvia. Occurrence of other food items is similar to the data from studies in other European countries (Jędrzejewski et al., 1992; Valdmann et al., 1998; Kübarsepp & Valdmann, 2003; Sidorovich et al., 2003).

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In comparison with previous studies of wolf food habits in Latvia (Andersone & Ozoliņš, 2004), the consumption of cervids was somewhat higher during this research period while the consumption of beavers had decreased. Low density of ungulates in Latvia in the first half of the 1990s coincided with the growth of the beaver population (Balodis et al., 1999) and beavers were considered to be an alternative prey for wolves at that time (Andersone, 1999). As the population status of wild ungulates has improved since the beginning of the 2000s (Fig. 1), wolves most likely prey more on available ungulates as they are more suitable for their body size, life in packs, and social hunting pattern (Mech, 2003).

Our data do not confirm the statement of Polish researchers (Jedrzejewska & Jedrzejewski, 1998; Nowak et al., 2005) that red deer is preferred to roe deer and wild boar. The share of roe deer and wild boar in the live ungulate community of Latvia seems to be relatively higher than in Poland both in terms of numbers and biomass. While the roe deer numbers in southern Poland are three- to four-fold bigger than those of red deer (Nowak et al., 2005), the roe deer population in Latvia exceeds the red deer population 6-7 times (SFS data). Furthermore, the abundance only of roe deer and wild boar increased five-fold during the last decade (Fig. 1); no such increase was observed for red deer or elk. The compliance with Estonian results convinces us about actual differences in prey selectivity that probably is not necessarily related only to prey availability but also to different predation patterns in various parts of the population range that are under different wolf management systems by humans. In Estonia, the most preferred wolf prey is wild boar followed by roe deer while elk is the least taken ungulate species (Valdmann et al., 1998). It should be noted that the red deer population is marginal in Estonia but the wolf population is harvested like in Latvia while in Poland wolves are protected thus enabling them to live in larger packs. All these facts taken together do not exclude the possibility that wolf predation simultaneously affects the growth rate of the red deer population in Latvia and Estonia because the wolf population is well supported by particularly abundant roe deer and wild boar.

The average mass of stomach contents was similar to that found in previous studies (Andersone & Ozoliņš, 2004). The heaviest stomach content (5152 g) was heavier than ever documented in Latvia; however, it was lighter than those found in Russia and North America (Pavlov, 1990; Mech, 2003).

The high proportion of light stomach contents found in this study (Fig. 2) may be explained by wolf's ability to digest a large amount of food in a short period (Mech, 2003). Therefore, if a wolf is not hunted shortly after its meal, there will not be much food left in its stomach.

The percentage of empty stomachs was lower than found in studies in Russia (Bibikov, 1985) but similar to that in Estonia, where it was reported that 27 out of 37 stomachs (73%) contain prey remains (Valdmann et al., 1998). In comparison with previous studies in Latvia (Andersone & Ozoliņš, 2004) the percentage of empty stomachs had decreased. Together with an increase in wild ungulate consumption and decrease in beaver consumption this may indicate a slight improvement of general feeding conditions of wolves in Latvia.

Differences in diet among different age groups

The statistically significant difference found in the stomach content biomass between yearlings and adult wolves and also other differences in the diet that were nonsignificant (probably due to the comparatively small sample size) may be explained by different feeding conditions in different age groups. Adult wolves are good at hunting, their diet consists mostly of wild ungulates and beavers (Table 2) and they have no need to prey for smaller animals. Wolf pups are fed by their parents and sometimes other pack members (Schmidt & Mech, 1997), thus there is a high proportion of wild ungulates and beaver in their diet as well. The more varied diet of yearlings may be related to the fact that because of their lower rank in the pack hierarchy they are usually the last to join the consumption of the pack's prey (Mech, 1999), and so they have more reasons than other pack members to prey upon small animals. Also when hunting on their own they are not as successful as adult wolves – especially when preying upon beaver young animals may lack the skills and experience to catch that animal.

For the same reasons 1–2-year-old wolves more often have empty stomachs. Although those differences were not significant it is worth continuing this research with increasing the sample size.

Looking at the ratio of the considered age groups in our sample, we can see that since the beginning of our study the proportion of pups has been increasing, that of adults was fluctuating but the share of 1–2-year-old wolves declined after 2003 (Fig. 3). If we assume that the year 2000 was a turning point since when the food supply has improved (Fig. 1), this fact as well as the changes of the population structure might be an explanation for the successful population recovery after harvesting. The favourable foraging conditions and inter-population response to human control (Bondarev, 2002; Mech, 2003) might support good reproduction of the wolf population. The breeding wolves got higher fecundity and fed successfully their pups. However, the survival of pups until 1–2 years of age was rather low because of hunting pressure, in particular since 2003. Thus, keeping the wolf population at a stable level by hunting probably stimulates total consumption of prey biomass meaning that the same number of wolves eat more when the pup ratio is high and the ratio of yearlings is low.

Depredation upon domestic animals constituted two cases in this study when a dog and a cat had been eaten. In both cases it was done by 1–2-year-old wolves in the winter season when young animals start to hunt on their own. As observed in other studies (Andersone, 2003; Andersone & Ozoliņš, 2004) livestock constitutes a small part of the wolf diet in Latvia and it is secondary prey to wolves when wild prey is available.

Differences in diet between sexes

The slight differences in the diet of male and female wolves, which were significant concerning the consumption of beaver, may be explained by their possibly different hunting behaviour, especially while taking care of the pups. During this time the female wolf mostly stays with the litter and is fed by other pack members (Mech, 2003).

Differences in the consumption of beaver were also found in previous studies (Andersone, 2003) where similarly male wolves consumed beaver more often than female wolves. As beaver is hunted during individual rather than pack hunting these differences may be due to the fact that male wolves wander around more often than female wolves, especially during the lactation period.

The higher proportion of empty stomachs in female wolves may be related to the fact that the majority of empty female stomachs belonged to young animals that had a higher proportion of empty stomachs anyway.

Geographical differences in wolf diet

Absence of statistically significant differences in the composition of wolf diet, stomach content biomass, and percentage of empty stomachs between east and west Latvia shows that in general feeding conditions and availability of different prey are similar all over the country. Higher consumption of cervids in the west in comparison to higher consumption of wild boar in the east (Table 4) can be explained by slight local differences in the distribution and density of wild ungulate species as explained earlier by Andersone & Ozolinš (2004).

CONCLUSIONS

In the last decade the management of wolf population in Latvia changed from unlimited persecution to restricted control at a stable population level. This coincided with an obvious population increase of two main prey species – the roe deer and wild boar. This coincidence was politically a very favourable background for the implementation of wolf conservation policy because hunters easily accepted new restrictions of wolf hunting. However, two aspects should not be overlooked in the further strategy of wolf conservation and they might require solutions in the future. First, although recent staple food (roe deer and wild boar) was rich, wolves might still affect other species, especially those known as preference food in other parts of the population range, e.g. the red deer. Second, the attempt to control the wolf population at a stable level probably may cause an increase in prey consumption due to the changes in the population structure and reproduction.

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Huntide (Canis lupus) toitumine Lätis maosisu analüüsi põhjal

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Huntide (*Canis lupus*) toitumist Lätis uuriti 165 maosisu analüüsi põhjal 2001. aasta detsembrist kuni 2008. aasta aprillini. Huntide põhitoiduks olid metsikud sõralised (hirvlased ja metssead). Hirvlasi leiti 64,7% proovidest (69,7% biomassist), metssigu 25,9% proovidest (22,6% biomassist) ja kopraid 8,6% proovidest (6,4% biomassist). Maosisu keskmine mass oli 824,1 g ja 26,7% kõikidest magudest olid tühjad. Statistiliselt olulisi erinevusi leiti maosisu biomassi puhul 1–2 aasta vanuste ja täiskasvanud loomade vahel ning koprajäänuste biomassi puhul isas- ja emashuntide vahel (vastavalt 12,9% ning 3,2%). Teisi olulisi erinevusi toidu koostises, maosisu biomassis ja tühjade magude osakaalus eri vanuserühmade, sugude ning Ida- ja Lääne-Läti populatsioonide vahel ei esinenud. Saadud tulemuste põhjal tehti ettepanekuid hundi kaitsmise strateegia kohta.