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Wolf hunting in Latvia in the light of population continuity in the Baltics

Key words: wolves, population, demography, hunting

Introduction

Within previous two centuries the wolves *Canis lupus* vanished from the major part of Western and Central Europe (Bibikov 1985). However, species always had better prospect in the eastern coast of the Baltic Sea. Impressive hunting bags of wolves have been reported from the former Baltic provinces in 1825 and 1826 – 577 and 935 respectively (Grevé 1909). The hunting bags have been quite accurately reported in most countries whilst harvest took place (Bluzma 2000; Ozoliņš et al. 2001; Lõhmus 2002). Recently, the wolves inhabit a wide range in Eastern Europe from the Baltic Sea to central regions of European Russia. The so called Baltic population covers Baltic countries, NE Poland, Belarus, N-Ukraine and some regions in the Russian Federation (Leningrad, Novgorod, Pskov, Tver, Smolensk, Brjansk, Moscow, Kaliningrad, Kursk, Belgorod and Orel). According to the latest update (Linnell et al. 2008), the Baltic population counts about 3,600 individuals and is considered to be probably most viable in Europe. The wolves in Poland have got the worst status estimation (Jedrzejewski et al. 2010). The northern part of the Baltic wolf population is linked to the Karelian population of about 750 individuals which are separated by a geographic barrier – Karelian lakes. Some weak link possibly exists with the Carpathian population in SW Poland (Linnell et al. 2008). In Latvia, wolves never have been completely extinct and recovered soon after weakening of hunting pressure. As far as known from history, in the previous periods of particularly drastic wolf control, population remnants survived just in locally continuous woodland and bog areas in the east of Latvia. For instance, only 17 wolves were counted in 1940 and all of them in the east (Kalniņš 1943). However, a gap in the wolf distribution in central Latvia (Priedītis & Ozoliņš 2001) still is a cause for concern. The morphological data from skulls show that animals of the same age are bigger in the east (Andersone & Ozoliņš 2000). In the long term, disrupted distribution pattern can increase isolation between these two micro-populations resulting in decreased genetic diversity (Randi 1993) unless ecological corridors are ensured. Roads and railways are known as most unconquerable human built barriers for wolves in Poland (Jedrzejewski et al. 2004). In Lithuania, wolves are rare along highways and main roads too (Balčiauskas 2008). Although roads and traffic in Latvia are supposed to be less laden, hunting on wolves is very intensive. Over 100 wolves are killed annually since the late 1990s, but

maximum hunting bag was nearly 400 in 1996 (Ozoliņš et al. 2008). Successful recruitment in a heavily harvested population might depend on influx of new matured individuals from adjacent territories (Ozoliņš et al. 2001). Therefore landscape barriers in such circumstances can be of bigger importance than in cases when wolves are protected or moderately persecuted. For instance in Spain, wolves from an expanding population even established home ranges on both sides of a fenced four-lane highway (Blanco et al. 2005). It has been also acknowledged that wolves can survive in disjunctive populations providing moving between populations when human persecution is not excessive and prey is abundant (Haight et al. 1998).
The aim of this study is to examine whether the most obvious barriers in landscape really hinder demographic processes in wolf population, and might it be that current intensity of wolf control is a threat to population continuity in the Baltic region. Other important question addressed is: either the wolf management within territory of Latvia supplement the Baltic population or sink in the immigrants from neighbouring areas? The answers would provide important implications for national level and trans-boundary management plans.

Material and methods

Study area

In order to reveal possible discontinuity of wolf population, the territory of Latvia was divided into three districts (Fig. 1) – West Latvia or Courland plus Semigallia (W-Latvia) 21080 km², North-Eastern Latvia or Livland plus Latgale (NE-Latvia) 35990 km² and South-Eastern Latvia or Selonia (SE-Latvia) 7510 km². Total approximated area of Latvia is 64580 km². It was displayed in digital map as polygon, cut by road and river lines, after that the areas were calculated by *ArcGis* software tools.
W-Latvia has a fairly long coastal border in the north and west, relatively ranking this area in status of peninsula, and terrestrial border with adjacent Lithuania in the south. This district is rich in forest, particularly in its northern part where forest cover locally reaches 63.9 % (Anonymous 2004). Vast woodland of the Courland is separated in the east from SE-Latvia by comparatively deforested central part of the country and a developing motor road A7 'Via Baltica' crossing the whole territory of Latvia from Riga to Lithuanian border. Traffic intensity on this road amounts 17 462 units per day near Riga and 3 801 unit per day at the state border (data browsed from www.lvceli.lv in 2010). SE-Latvia verges to Lithuania and Belarus in the south. It is a long stretched district more scarcely covered by forest in the west (31.1 %) and east (33.8 %) while the most forested locality in central part holds 54.7 % of woodland (Anonymous 2004). Northern border of Selonia is the few hundred meters wide River Daugava.
NE-Latvia is the largest and most northern district separated from SE-Latvia by the River Daugava and a parallel railway as well as a motor way A6. Traffic intensity on A6 is between 3 000 and 10 000 vehicle units per day. Livland has a coastal border in the west. Estonia shares the borderland with this district in the north but Russia and Belarus provide a long eastern frontier. District is well forested (up to 56.6 %) in the north, although forest cover declines to 29.2 % in the east.
All the three territorial districts are not absolutely isolated and could be passable for large mammals. There are no considerable barriers at all for dispersal inside each of the selected territories.

Data set for analysis

All available records on killed or dead-found wolves were collected from 1997 to 2010. According to preciseness and reliability, all records can be divided into 3 groups.
1. Voluntary reported information on date and place of hunted wolves. These reports we received from local forestry districts by contacting people dealing with game management and hunting supervision. There was no specially defined neither temporal nor spatial system for this reporting and it concerns the period from 1997 till April 2004.
2. Completely reported information on date and place of hunted wolves. Since May 2004,

Fig. 1 Location of the three districts compared in this study: A – W-Latvia (Courland & Semigallia); B – SE-Latvia (Selonia); C – NE-Latvia (Livland & Latgale). Internal borders drawn by disrupted black line.

reporting system is supported by legislation and every dead wolf has been recorded through the State Forest Service network.

3. Information on the wolves sampled for investigation by researchers. This information includes sex, age and reproductive status of individuals. The carcasses of killed or dead-found wolves were collected. Sample was selected using information from the two above mentioned groups. We strove to avoid bias of sampling selectivity concerning survey regularity, distance to destination, preliminary estimated age or sex. Legal status of the wolf has changed over the study period. In order to reduce population, hunting was promoted by paying bounties from state budget until 1999. Bounties were cancelled although there was no restriction for culls and season was open all year around from 2000 till 2003. Since 2004, the season is closed from 1st April till 14th July and annual quota is set adapting culls to the changes in population (Ozoliņš et al. 2008).

Examination of carcasses

The heads of the collected carcasses were cut off. Usually only the head was available for study from carcasses heavily shot or damaged in vehicle collision. Then we included it in our sample if sex of the animal was certainly known. One of the canines was extracted boiling the skull and ca. 1.5 cm long tip of the root was sawn off. Techniques described by Klevezal (1988), including decalcification, freezing, sectioning, staining and mounting on a glass slide, were used. Counting of incremental lines of the tooth cement was performed microscopically. Those animals that were not aged precisely for various technical reasons we determined as adults with unknown absolute age. Canine was placed back in the skull to not spoil the trophy that encouraged the hunters to provide material. In female wolves above 1 year of age, reproductive organs were removed. Examination of ovaries and uterus was used to determine if a female had been reproducing (Kirkpatrick 1980).

The uterine horns were opened for checking internal walls. Placental scars or swelled post-birth sites were counted for fecundity index.
In some cases, it became necessary to press the uterus walls between two glass plates and to look through against a light source. If an adult female was killed late in winter and found to be freshly ovulated, and uterus walls were all swelled and not appropriated for counting anything, the animal was registered as breeding (fertile) but not included in the sub-sample for fecundity assessment. In most of females taken in March, well visible foetuses were discovered.

Analysis of hunting pressure and success

It is assumed that information on wolf abundance and distribution gained by their hunting should be analysed in comparison with data on hunting effort (Sutherland 2000).
Unfortunately, we were not able to measure complete hunting effort. We do not know number of hunts or hunting days spent without success. We also do not know how many wolves were shot by occasion during hunting for another game and how many by deliberate chase. Therefore hunting efficiency was measured by the number of shot wolves divided by days of successful wolf hunting. The bigger is study area, the more hunters are involved and total time spent.
Since the numbers of days spent for hunting depend on the area considered, for a better comparison we divided this figure by area and related to 1000 km². Thus we used a formula for calculation, assuming that hunting is more efficient if more wolves are shot over shorter period (less number of days) and inside smaller territory:

$$HE = N/D * S * 0.001 \qquad (1)$$

where HE – hunting efficiency
N – number of killed wolves within study period
D – number of those days when the wolves were killed
S – area where the wolves were killed in km²

Analysis of demography in wolf population

To describe sex-age structure of samples from various time periods or territories, we used both absolute figures and percentages. By pooling ageing data we drew the sex-age pyramids for our samples and compared the distribution of age classes by χ^2 test. In particular, we focused on wolves younger than 1 year, 1–2 years old or yearlings as well as complete 2 years old and older (2+). These age groups were examined for their presence in hunting bags according the months when animals were killed. Sex ratio as females to males (F/M) was calculated for selected areas and age groups. Deviation from 1:1 is checked for statistical significance by χ^2 test with Yates' correction ($P = 0.05$). Data were processed according to advises by Fowler et al. (2006) and using SigmaStat software, version 3.0.
Knowledge of female fertility and fecundity was used to calculate the theoretical number of juveniles in the given sample of wolf population. Following formula was used:

$$N_J = N_F * F * P \qquad (2)$$

where N_J – theoretical number of born pups
N_F – number of adult females
P – mean number of pups produced by one female
F – ratio of 2+ year old females involved in reproduction (fertile females)

Assuming that proportions among age classes have not changed with time too fast, as well as excluding migration bias, we tried to figure out survival rate in wolf population from the first to second year of life (Skalski et al. 2005):

$$S_J = N_{1Y} / N_J \qquad (3)$$

where S_J – survival of pups
N_{1Y} – number of yearlings

Results

A total of 1219 records on killed wolves were available for this study. Average ratio of our research sample amounts 65.1 % of reported material. From the Table 1 one can see there is no concern that our sample would be biased regarding study districts. None of them was significantly overrepresented by data sampling. Consequently, we can assume that the numbers and demographic structure of killed wolves rather reflect their abundance and population structure in corresponding territories.

More or less equal number of wolves was taken throughout the country per successful hunting day. In W-Latvia it is 1.500 ± 0.049 (max. 7), in NE-Latvia – 1.635±0.062 (max. 8), in SE-Latvia – 1.393 ± 0.084 (max. 5). None of the three samples is normally distributed. Comparing the treatment groups by Kruskal-Wallis one way analysis of variance on ranks, the differences among them are not statistically significant ($P = 0.174$). A bit different view we have got by looking at data regarding different size of selected territories. Hunting efficiency calculated by formula (1) has been considerably higher in SE-Latvia – 0.186 wolves per 1000 km², while it was only 0.071 and 0.044 in W and NE respectively. So, ignoring statistical validity (mean values are invalid, non-parametric test (Fowler et al. 2006) required) we can declare that the best hunting success or biggest number of wolves shot per day is in NE-Latvia but hunting pressure towards wolves or cull per day and per area is the highest in SE-Latvia. Yet, absolutely largest number of dead wolves was reported and sampled from W-Latvia (Tab. 1).

There are differences among districts when we take into consideration distribution of killed wolves according months (Fig. 2). Comparing the patterns by χ^2 test, statistically significant difference is verified between NE and SE ($\chi^2 = 17.569 > 15.51$ d.f. = 8, $P = 0.05$) as well as between W and NE ($\chi^2 = 49.268 > 20.09$ d.f. = 8, $P = 0.01$). Patterns from SE and W do not differ significantly ($\chi^2 = 13.094 < 15.51$ d.f. = 8, $P > 0.05$). It is noticeable that biggest number

Table 1 The numbers of killed wolves in Latvia available for the study

District	Reported dead wolves		Sampled dead wolves		Ratio of sampled wolves out of reported ones %
	numbers 2000–2010	percentage %	numbers 1997–2010	percentage %	
NE-Latvia	528	43,3	324	40,8	61,4
W-Latvia	567	46,5	389	49,0	68,6
SE-Latvia	124	10,2	81	10,2	65,3
Total	1219	100,0	794	100,0	65,1

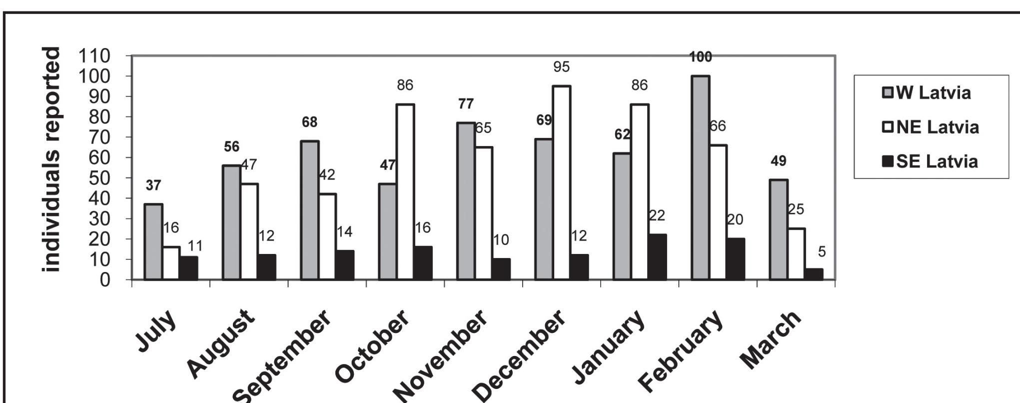

Fig. 2 Reports on wolf numbers shot in the three selected districts of Latvia during the hunting seasons from 2000 till 2010.

of wolves in W and SE Latvia was killed in late winter. In NE-Latvia, major wolf hunting takes place in December, although many are shot in October and January.

Patterns of sex and age structure (Fig. 3) are statistically similar (χ^2 test, $P > 0.05$) in all the three districts, however few peculiarities can be detected when looking at particular age groups. The oldest wolf shot in NE-Latvia was 13 years old. In W-Latvia, wolves may survive until 9 years of age, in SE-Latvia the oldest had only 7.

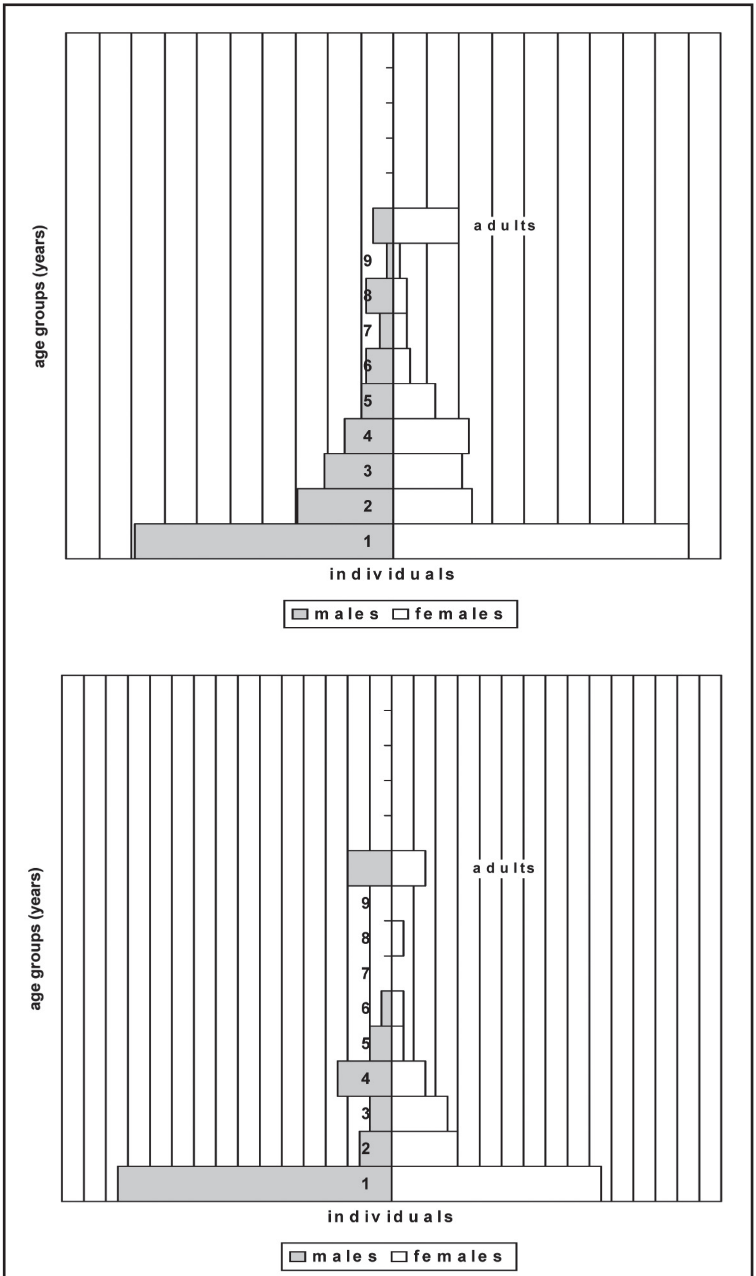

Fig. 3 Sex-age structure of wolf samples from W-Latvia (above, n=389) and SE-Latvia (below, n=81). The age groups start from 1 (up to 1 year olds) and end with the adults of undetermined age. Patterns are statistically similar ($\chi^2 = 3.898 > 3.49$, d.f. = 8, P = 0.90).

Merging the age groups into three classes (pups, yearlings and adults), we studied their occurrence over the recently open hunting season – from July till March. In NE-Latvia, maximum number of wolf pups is shot in autumn (Fig. 4). By late winter (February, March), pup ratio declined but adult ratio increased. Similar patterns can be observed in W and SE, just in those districts the pups occur in hunting bags earlier – already in July reaching maximum occurrence in September (Fig. 5 & 6). Statistically significant differences we found in pup

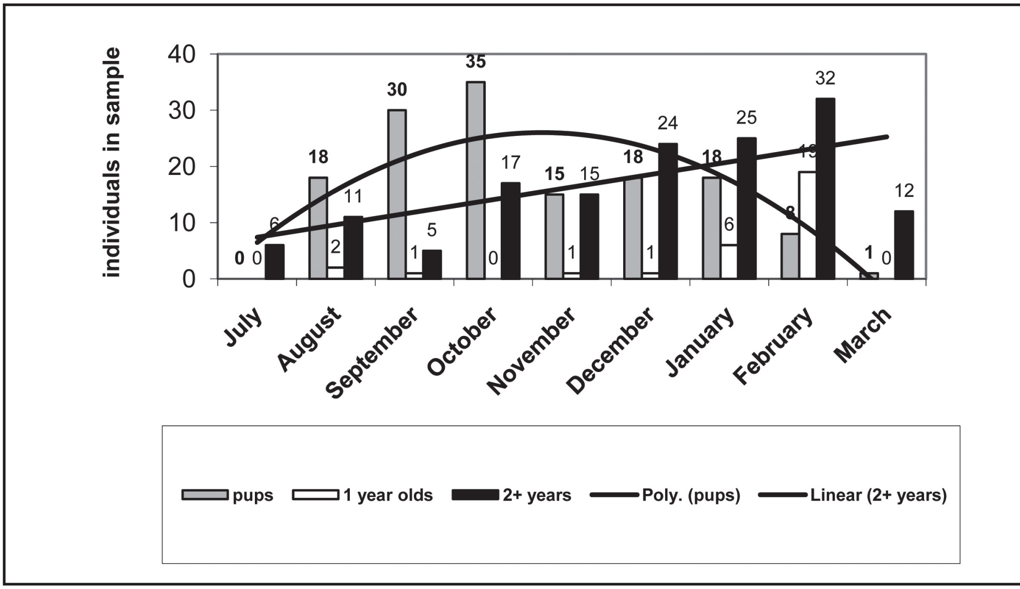

Fig. 4 Changes in occurrence of the three age classes of wolves over the hunting season in NE-Latvia.

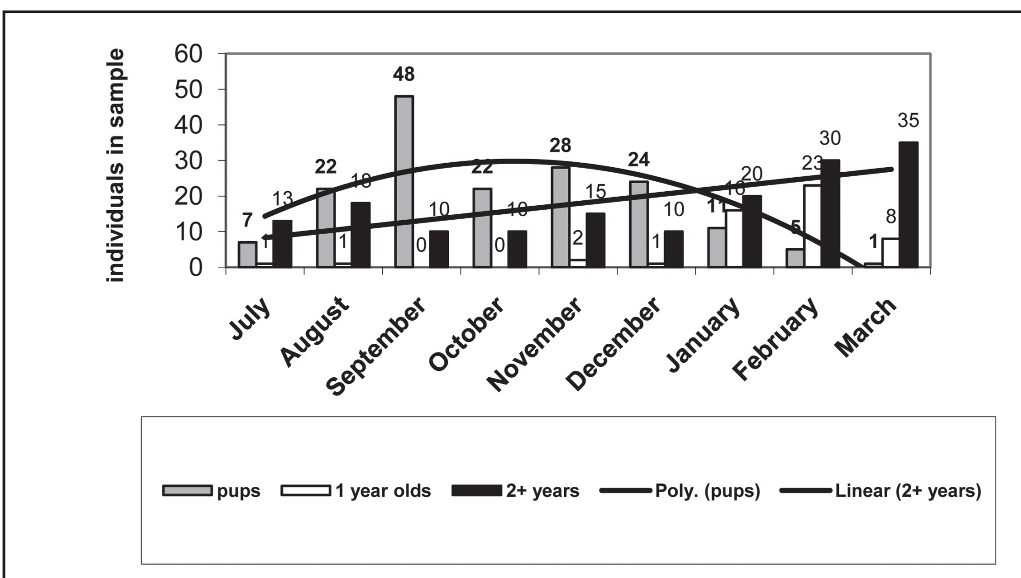

Fig. 5 Changes in occurrence of the three age classes of wolves over the hunting season in W-Latvia.

ratio between NE and SE-Latvia ($\chi^2 = 19.683 > 17.530$, d.f. = 8, P = 0.025), and NE and W-Latvia ($\chi^2 = 19.806 > 17.530$, d.f. = 8, P=0.025) but not between W and SE-Latvia ($\chi^2 = 11.706 > 10.22$, d.f. = 8, P = 0.25). The only significant difference in adult ratio was revealed between W and SE-Latvia ($\chi^2 = 24.805 > 20.09$, d.f. = 8, P = 0.01).

Sex ratio deviates from 1:1 least in W-Latvia and most in SE (Fig. 7) but none of the deviations appeared statistically significant. There is also no significant difference of merged sex ratios in all age groups among selected three districts (χ^2 test, P > 0.05).

The number of placental scars was the biggest in female wolves from NE-Latvia and the smallest from SE however Kruskal-Wallis test does not confirm significance of these differences (H = 2.248, d.f. = 2, P = 0.325). Nearly the same share of adult females took a part at reproduction in all study districts (Tab. 2). At last we found that the wolves in W-Latvia expose

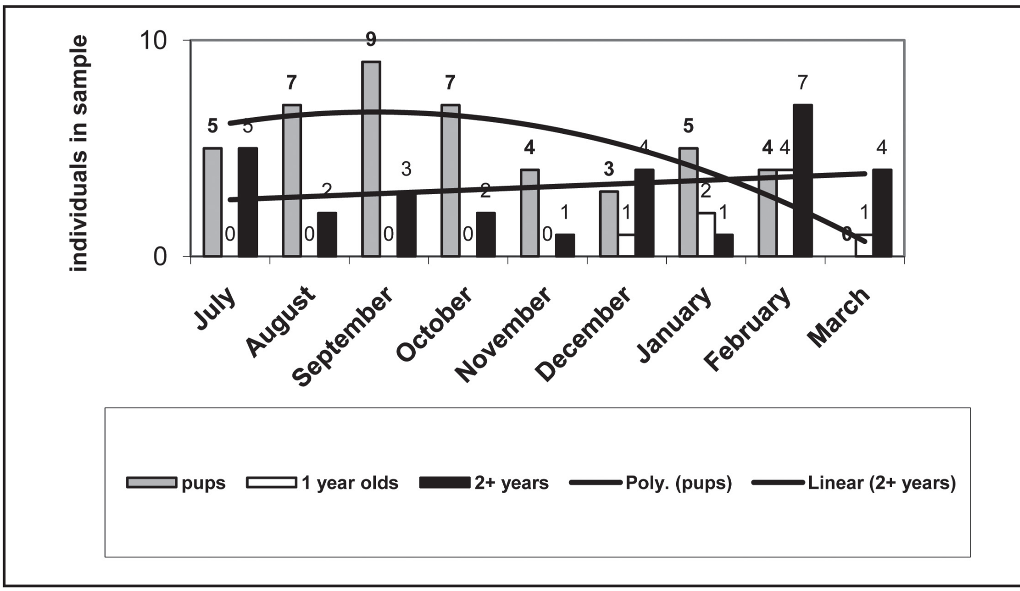

Fig. 6 Changes in occurrence of the three age classes of wolves over the hunting season in SE-Latvia.

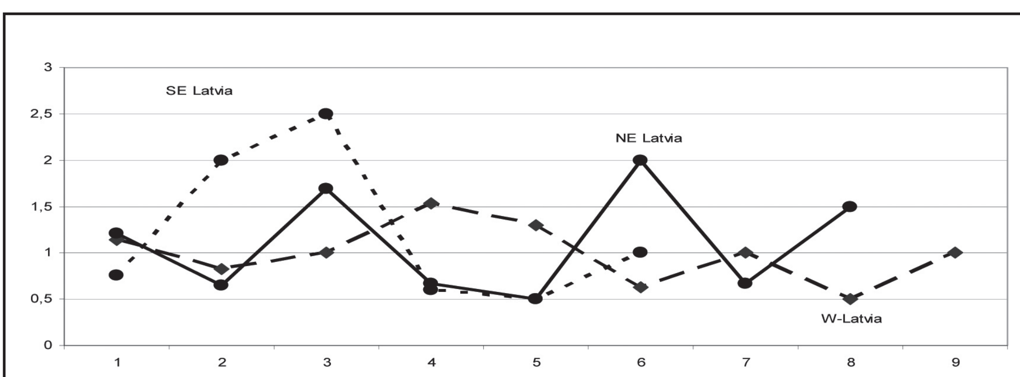

Fig. 7 Fluctuations of female/male sex ratio (ordinate) in wolves over nine age classes (abscissa) in three territorial districts of Latvia. Continued line – NE Latvia, interrupted line – W Latvia, dot line – SE Latvia.

likely the largest contribution to reproduction of population. Despite their range covers just one third of the country, they hold above 47 % of all females in reproductive age and give birth to 47 % of all pups (Tab. 3). Due to a better survival, W-Latvia contributes to total recruitment by 57 % of yearlings. This statement, of course, is true only assuming that there is no bias in our sampling.

Discussion

By shooting more than 100 wolves annually and comparatively long open season for hunting (Ozoliņš et al. 2008), Latvia seems to cause a threat to population continuity within Baltic region. Only in Russia and Belarus wolves are persecuted even more ruthlessly (Sidorovich et al. 2003; Danilov 2005). In neighbouring oblasts of Russian Federation, 4,962 wolves had been shot during six years from 2001 till 2006 (Lomanov 2004; Gubarj 2007).

On other hand, Latvia is located at the sea coast and can not be a hindrance for wolf dispersal towards west unless population distribution would recover around Baltic Sea. Recent concern is about spatial fragmentation north-southwards i.e. from Estonia to Lithuania as well as between Courland and eastern Latvia.

In this study, we did not examine significance or features of landscape barriers but focused on indices of population abundance and demography caused likely by these supposed barriers. Our first finding is the four fold greater density of killed wolves in SE-Latvia comparing to NE. Looking for reasons, attention is attracted by differences in monthly distribution of shot animals. In SE, comparatively more wolves are taken in July, January and February while in NE – in October and December (Fig. 2). In this aspect, wolf harvest in SE-Latvia is more in line with that in W-Latvia. For successful wolf hunting, tracking in snow conditions is traditionally considered of importance. Differences in the hunting efficiency might be explained by various duration of snow cover among the districts. In W-Latvia, the mean snow period lasted from 66 to 100 days over the years 1945–2004 (Draveniece et al. 2007). In NE-Latvia, snow may persist until 134 days on average. SE-Latvia in term of snow period stays in between with mean duration of snow cover from 77 to 111 days. This could mean equal hunting circumstances throughout the country in January and February but a better chance for the hunters in NE in autumn and late winter. January and February is known as mating season for wolves (Tumanov 2003), and from this point of view sex and age of the killed individuals is an impor-

*Table 2 Female fertility and fecundity indices in wolf population: **mean fecundity** is mean number of placental scars or embryos; **n** is number of females with countable placental scars or embryos; **fertility %** is ratio of females with evidences of reproduction amongst 2+ year old females; N_J is theoretical number of pups calculated by formula (2); S_J is survival of pups calculated by formula (3)*

Districts	Mean fecundity	±SE	N	Min.	Max.	Fertility %	N_J	S_J
W-Latvia	6.088	0.339	34	3	10	73.7	256	0.207
NE-Latvia	6.600	0.342	25	3	10	70.0	231	0.134
SE-Latvia	5.429	0.812	7	2	8	76.9	54	0.167

Table 3 Comparative share in percents of the three studied districts in total population recruitment in Latvia

Districts	Range	Females at age 2+	Pups theoretically born	Yearlings survived
W-Latvia	32.6	47.5	47.3	57.0
NE-Latvia	55.7	41.7	42.7	33.3
SE-Latvia	11.6	10.8	10.0	9.7

tant index for demographic status of population. In all districts, February and March are strongly dominated by occurrence of matured individuals. Hunting bag from NE contains a large proportion of adult wolves also in December and January. Death of individuals with high reproductive value (Begon et al. 1986) may impact population more than loss of pups or yearlings. Therefore NE district may be threatened by over-harvesting rather than SE and W-Latvia. It has also very unstable female to male ratio while in the W district sex deviates less from 1:1 but in SE district deviation could be due to smaller sample size (Fig. 7). Interesting, that in W and NE females slightly dominate over males of the first age class but likely more males were born in SE. Prevalence of male pups is mentioned as characteristic in wolves by Bondarev (2002) and Tumanov (2003) but birth of more females is observed in thinned populations (Bondarev 2002). Also by this index NE district seems to be worse than SE, however difference is not approved statistically. Fecundity in female wolves from SE is lower and fertility higher comparing to other districts. Also these differences are not approved statistically but again – SE district got the best and NE district – the worst assessment. Namely higher fecundity is a phenomenon caused by over-harvesting and well known from other studies. For Karelian region, mean litter size of 5.0 is mentioned (Danilov 2005). The author emphasizes that increase of fecundity can be related to heavier hunting pressure. Despite the heightened productivity, wolves in NE-Latvia are able to contribute less in population recovering after harvest. Comparing to size of range, they produce little number of pups and yearlings (Tab. 3) that may substitute for the killed individuals. SE-Latvia can ensure nearly the same proportion in reproduction as its territory amounts from total country area. W-Latvia is reproducing more wolves than expected from its area. Thus, we concluded that W and SE-Latvia do not provide any threat by over-harvesting to the Baltic wolf population. More concern is about NE-Latvia, where less pups are born and survived than expected from a territory that occupies nearly 56 % of the country. Results show that wolves in NE-Latvia probably are eradicated on more systemic basis because despite generally worse hunting efficiency, the greatest number of individuals was killed per day of successful hunt. This is not necessarily due to better snow conditions. Quite many wolves are killed from August to September, especially pups. Supposedly, the high mortality is compensated by heightened fecundity and opportunity for matured individuals to disperse from less harvested spots to vacated areas. It might be enabled by suitable habitat and sufficient food supply. Surprisingly, east Latvia is considered as an important territory with suitable habitats and so called low conflict potential for another important carnivore species – Eurasian otter *Lutra lutra* (Reuther et al. 2004).

In conclusion, we acknowledged that wolf hunting in Latvia is hardly an obstacle for their conservation in the countries located southwards. Lithuania might even benefit from successful reproduction in W-Latvia and possible wolf dispersal from this area. The only problem for the wolves in this district is their weak connectivity to eastern part of Latvia. Assessing potential threat to continuity of the entire Baltic wolf population, just eastern Latvia, especially NE, is conspicuous for most intensive harvest and least reproduction. It concerns also lowest survival of pups until one year age. Pup mortality is always high, even in not harvested populations. By Danilov (2005) 30–60 % of annual offspring are lost until beginning of winter. According data reviewed by Mech (2003), natural survival rate can be 20–88 % for pups from birth to period of exploitation. Nevertheless, the wolves in the NE according our former data (Ozoliņš 2008) have first signs of troubled demographic processes and their distribution is more uneven. On the other hand, those wolves have a better chance to be recruited with immigrants from adjacent Estonia, Russia and Belarus. This blending might be a reason for morphometric distinction of the wolves in east Latvia (Andersone & Ozoliņš 2000). Such statement appears controversial because Estonian researchers have noticed the opposite – immigration of the wolves from Latvia to Estonia (Valdmann et al. 2004). Thus, we can not confirm that real threat to population continuity exists so far. Furthermore, one should consider that data were collected over more than ten year long period and population status has not changed meanwhile (Ozoliņš et al.

2008). Obviously good geographical connectivity has ensured sustainable wolf hunting. Since trans-boundary wolf management planning is required in future (Linnell et al. 2008), we recommend to take into account, that population in Latvia is slightly over-harvested within territory from the north-eastern border to the River Daugava (about 56 % of total country). In the rest of the country, wolves are exposed to a moderate hunting pressure not affecting demographic processes.

Summary

By shooting more than 100 wolves annually and comparatively long open season for hunting, Latvia seems to cause a threat to population continuity within Baltic region. The aim of the study is to examine whether the most obvious barriers in landscape hinder demographic processes in wolf population. Territory of Latvia is divided into three districts: West Latvia – 21 080 km², North-Eastern Latvia – 35 990 km² and South-Eastern Latvia – 7510 km². Territories are mutually separated by motor ways and a river. A total of 1219 records on killed wolves between 1997 and 2010 were used for an analysis. 794 carcasses were examined for sex, age and reproductive status. Four fold more wolves appeared killed per successful hunting day on 1000 km² in SE-Latvia comparing to NE. Nevertheless, hunting impact on wolves from SE and W Latvia is moderate. Sub-population from W-Latvia is reproducing even more wolf pups and yearlings than expected from its range comparing to the ranges of other sub-populations. Wolves in NE-Latvia despite highest fecundity rate are most suffering from intensive harvest and least reproduction, as well as lowest survival of pups until one year age. Wolf hunting in Latvia is unlikely an obstacle for their conservation in the countries located southwards. However, sub-population in eastern Latvia depends on a good geographical connectivity to Estonia, Russia and Belarus obviously enabling compensation of lost individuals by dispersing ones.

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