UNIVERSITY OF LATVIA

AGRITA ŽUNNA

Population status of wolf *Canis lupus* after the implementation of the Action Plan for Conservation of Species in Latvia

SUMMARY OF DOCTORAL THESIS

Submitted for the Doctoral degree in Biology
Subfield of Zoology

Riga, 2023

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The doctoral thesis was carried out at the Latvian State Forest Research Institue "Silava", from 2015 to 2022.

The thesis contains the introduction, four chapters, conclusions, reference list and an appendice.

Form of the thesis: dissertation in Biology, subfield of Zoology

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The thesis will be defended at the public session of the Doctoral Committee of Biology, the University of Latvia, at 14.00 on 10.11.2023., Riga, Jelgavas 1, room 335.-336.

The thesis is available at the Library of the University of Latvia, Raiņa blvd. 19.

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SUMMARY

Wolf (*Canis lupus* L.) is an especially protected species that can be exploited in Latvia to a limited extent. Before Latvia's entry into the European Union and the implementation of the Habitats Directive 92/43/EEC of the Council of Europe, wolves were hunted without any restrictions, and at the beginning of the 2000s, the number of these predators was significantly reduced. In 2000, the development of the first wolf species conservation plan in Latvia was started, and according to it, since 2004, the annual maximum allowable limit of hunted wolves has been determined, as well as the wolf hunting season from July 15 to March 31 has been specified. Although the number of wolves gradually increased after the introduction of restrictions, it is still necessary to constantly monitor the status of the wolf population and adjust the species management measures accordingly to ensure the conservation of a non-threatened and sustainable wolf population that is able to perform its natural functions in the ecosystem as much as possible without causing significant damage to the national economy.

In this thesis, data on the population status of Latvian wolves in the period from 1998 to 2022 have been collected and analysed in order to identify possible changes in the distribution of animals and the size of the population, to assess the demographic, social and kinship structure, the species' reproductive capabilities and feeding conditions, and to evaluate existing conflicts with public interests and clarify the public's attitude towards wolves and their population management.

The main results show that the distribution of the Latvian wolf population has improved and the number of individuals has increased due to the population's ability to restore the number of individuals lost as a result of hunting. The population has high genetic diversity. The impact of hunting on the demographic, territorial and social structure of the wolf population has been established. Feeding conditions do not limit the population. Wolves feed mainly on roe deer and wild boar and are able to quickly adapt to changes in the food base. The amount and number of reported cases of depredation caused by wolves in the country is small, but local losses can be significant. Better results in the protection of livestock would be provided by the use of appropriate preventive measures at the moment, since the effectiveness of hunting in reducing damage is affected by various factors. The public attitude towards wolves in Latvia is mostly favourable to the conservation of the species and the existing population management practices.

Key words: wolf, population status, demography, kinship structure, feeding ecology, depredation, public attitude

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1. INTRODUCTION

In today's scenery, large carnivores must share their living space with humans and their interests, and the survival of these species often depends on successful coexistence with humans, which is influenced by species management measures, human attitudes, appropriate legislation and the resolution of predator-related conflicts (Fritts et al. 2003, Chapron 2014). Wolf (*Canis lupus* L.) is an important species of large carnivore in Europe, which has been exterminated in many parts of its former area. Wolves have never been completely exterminated in Latvia. They are still found in relatively large numbers and are an important part of the Baltic wolf population, which is significant on a pan-European scale (Boitani et al. 2022). Nowadays, the attitude towards wolves is improving in some parts of society, however the successful existence of this species still largely depends on the willingness of people to co-exist with this predator, since human actions are the main cause of wolf mortality (Fritts et al. 2003). Wolf conservation experts recognise that strictly controlled wolf hunting is permissible in regions where it does not threaten the favourable status of the population and is carried out in accordance with the species management plan (Linnell et al. 2008). However, the reasons for hunting wolves are not always sufficiently justified and in accordance with the sustainable management of the species (Frank and Woodroffe 2001, Ginsberg 2001, Vucetich and Nelson 2014, Allen et al. 2017). Mutual adaptation is necessary for large carnivores and humans to co-exist (Carter and Linnell 2016), but in order to facilitate this, it is necessary to have as complete knowledge as possible about the status of carnivore populations, the processes taking place in them and the impact of human activities on them.

Wolf is included in Annex II (Specially Protected Fauna Species) of the Berne Convention (Convention on the Conservation of European Wildlife and Natural Habitats) and the Directive of the Council of Europe on the Protection of Natural Habitats, Wild Fauna and Flora. Latvia is bound by the requirements of these documents. Therefore, it is necessary to constantly monitor the status of the wolf population in order to ensure the existence of a sustainable population.

Since the introduction of hunting restrictions in 2004, there have been improvements in some parameters characterising the status of the population (Ozoliņš et al. 2017). However, it is still necessary to obtain current data on distribution, demographics and feeding habits, to monitor the impact of hunting on the population, to analyse conflicts related to wolves in more detail and to evaluate so far unstudied population indicators as a genetic and kinship structure in order to expand knowledge about the Latvian wolf population, to assess the impact of the existing management system and, if necessary, to make decisions based on scientific research about changes in it.

Scientific novelty

This research collected and analysed data on a sample set of a unique European scale in terms of the number of individuals, collected material, research

area and time period from a hunted, but long-term growing wolf population in the middle of the European range of the species.

The kinship structure and genetic parameters of the Latvian wolf population have been analysed for the first time. The most long-term data on the feeding habits of wolves has been analysed so far and an insight has been gained into their changes due to the decline of important prey species.

The damages caused by wolves in conditions that are not characteristic of other European wolf populations – when wolf hunting is allowed for a minimally limited period and territory, determining only the annual permissible amount of hunting – has been assessed in more depth, and the further directions of research in this field have been clarified. Information on public attitude towards wolves and their management measures in Latvia has been updated.

Aim of the thesis

The aim of the thesis is to evaluate the development of the wolf population status in Latvia since the introduction of the species conservation plan, to find out the impact of restricted hunting on it and to assess the effectiveness of the management system in maintaining a sustainable population and solving conflict situations.

Research objectives of the thesis

1. To characterise the spatial, demographic and genetic structure of the population.
2. To assess the food base of wolves and the impact of the reduction in the number of wild boars caused by African swine fever on it.
3. To analyse the damage caused by wolves.
4. To find out the public attitude towards wolves and the current population management system.

Arguments of the thesis

1. The Latvian wolf population currently has a favourable number dynamics and indicators characterizing distribution and the genetic diversity of the population, and the population is able to restore the number of individuals lost as a result of hunting. The impact of hunting on the demographic, territorial and social structure of the wolf population is observed.
2. The amount and variety of available food does not limit the wolf population, and predators are able to quickly adapt to changes in the food base. The main food objects of wolves are wild ungulates, mainly roe deer, and wild boar.
3. The recorded amount and number of depredation cases in the country is small, however locally caused losses can be significant. The effectiveness of wolf hunting in mitigating the damage is still unclear, and the best results at this time would provide the use of effective preventive measures.

4. The public attitude towards wolves in Latvia is mostly favourable to the conservation of the species and existing population management practices, and the majority of respondents do not want significant changes in the current situation.

Methodology

The research used information and material from wolves legally hunted or otherwise killed between April 1998 and March 2022. Various types of samples were collected – canine roots for exact age determination, reproductive organs of females for evaluation of reproductive status, muscle tissue samples for genetic analysis and stomach contents for food composition research.

Data on the damage caused by wolves between 2000 and 2020 are obtained from reports of wolf attacks on domestic animals collected by the State Forest Service.

The public attitude study "Survey on large carnivores in Latvia" was conducted in 2017, using the questionnaire method to clarify the opinions of various groups of society.

Published study results

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∗ Research funded by the Game Management Development Foundation "Impact of hunting on the grey wolf (*Canis lupus*) population status in Latvia" (2022)

∗ Research funded by European Social Fund „ Developing a system for genetic monitoring of wildlife species" Nr. 2014/0002/1DP/1.1.1.2.0/13/APIA/VIAA/053 (2014-2015)

∗ Research funded by the Latvian Environmental Protection Fund "Updating of Species Conservation Plan for the grey wolf in Latvia" (Nr. 1-20/117) (2016-2017)

∗ Research funded by the Latvian Environmental Protection Fund "Training of the responsible surveyors for carnivore species identification in the cases of livestock depredation, including both sign identification skills in nature and sampling for DNA analyses" (Nr. 1-20/134) (2018-2019)

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2. MATERIAL AND METHODS

1. The wolf population demography and kinship structure research used information and material from wolves legally hunted or otherwise killed (traffic accidents, mange) from April 1998 to March 2022. Different types of samples were obtained from 2730 wolves for further research.

1.1. The exact age according to the number of growth lines in tooth cementum (canine root samples) was determined for 1995 animals, which were divided into three age groups – up to one year old (pups) (n=1049), one year old (n=205) and adult wolves (older than 2 years) (n=886). Another 145 animals were identified as adults, but their exact age could not be determined.

1.2. Reproductive organs (uterus and ovaries) were collected from 580 females, of which 313 females were adults of known age. According to the number of placental scars or embryos in the uterus, the average number of pups per litter of each hunting season was calculated. The proportion of reproductive females was calculated from the number of females that were older than two years and showed signs of reproduction (placental scars or signs of rutting).

1.3. For genetic analyses, 1363 muscle tissue samples were collected between 15 July 2009 and 31 March 2021. A total of 1269 individuals (662 males, 607 females) were successfully genotyped. The exact age was known for 985 animals. Population genetic indicators (expected and observed heterozygosity, inbreeding coefficient, allelic diversity, genetic distance and differentiation, mutual kinship, number of migrants per generation) were calculated and 16 autosomal microsatellite loci were analysed to determine the kinship of individuals. Kinship analyses examined direct sibling relationships and parent-offspring relationships. In order to compare the western and eastern parts of the population, the genetic samples were divided into two groups according to the geographical location of the harvest.

2. The wolf food composition research analysed the stomachs of hunted wolves collected from July 2001 to March 2020 (n=887). Based on the remains of the hair and bones of the eaten animals found in the stomach contents of the wolves, the food objects of the predators were determined, and, if necessary, microscopic analyses of the animal hair were carried out. The frequency of occurrence of food objects (%) and the biomass consumed were calculated.

3. Data on damages caused by wolves in Latvia were obtained from reports on wolf attacks on domestic animals, which are collected centrally by the State Forest Service (SFS). The thesis analyses data on damage from 2000 to 2020 at the level of both the forestries and the parishes. The data analysis also used SFS data on the number of counted and hunted wolves in the country during this time period.

4. The public attitude study “Survey on large carnivores in Latvia” was conducted in 2017. Questions from the previously conducted public survey in Latvia (2002) and the survey of the project “Large carnivores in northern landscapes: an interdisciplinary approach to their regional conservation” (2005) were used in the compilation of the questionnaire. This survey was designed and planned with the support of Human Dimenssions expert Dr. Alistair J. Bath (Canada, Memorial University of Newfoundland). The questionnaire contained 36 questions about residents' attitudes, beliefs and knowledge about wolves, as well as respondents' demographic information. According to the previously used methodology, 1000 printed survey questionnaires were distributed to the families of Latvian residents through 27 randomly selected schools. Questionnaires were distributed electronically to hunters, farmers and nature protection organisations. For data collection and analysis, a sufficient number of questionnaires were received from the school group (595 questionnaires) and the hunter group (510 questionnaires).

3. RESULTS

3.1. Demographic and kinship structure of the wolf population and population management

Within the period from April 1998 to March 2022, the proportion of juveniles among wolves hunted or otherwise killed varied from 25.6% to 62.2%, with an average of 49.2% (Fig. 1). The proportion of yearlings in all hunting seasons was small, on average – 9.6%. The proportion of adult wolves ranged from 31.3% to 61.5%, with an average of 41.2%. During these years, there is a statistically significant trend for the proportion of juveniles to increase ($F(1, 22)=15.91$, $p=0.001$, $R2=0.42$), while the proportion of yearlings ($F(1, 22)=5.76$, $p= 0.025$, $R2=0.21$) and the proportion of adult animals ($F(1, 22)=6.23$, $p=0.021$, $R2=0.22$) decreased accordingly.

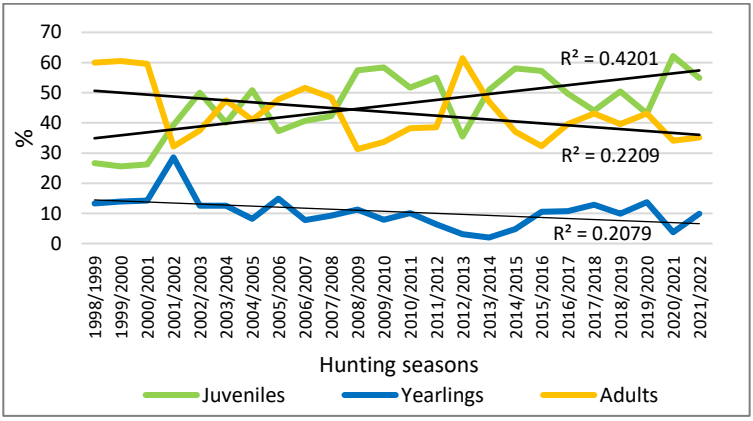


Figure 1. Trends in the proportion of age groups among wolves (n=2151) hunted in Latvia from 1998/1999 to 2021/2022 hunting season (juveniles – p=0.001, yearlings – p=0.025, adults – p=0.021).

The number of placental scars found in females harvested between April 1998 and March 2022 ranged from 1 to 14. The mean number was 6.3 ± 0.98, with a range of 4.0 to 7.7 across years. The proportion of reproductive females during these years varied from 44.4% to 100%, with an average of 67.7% (Fig. 2).

A large proportion of females (46.4%) were already involved in the reproduction process at a young age – two to three years. It was found that younger females had on average smaller litters than older females, and there was a statistically significant correlation between the proportion of reproductive females and the number of placental scars ($r=-0.508$, $p=0.011$) – smaller litters were observed with a larger proportion of breeding females in the population.

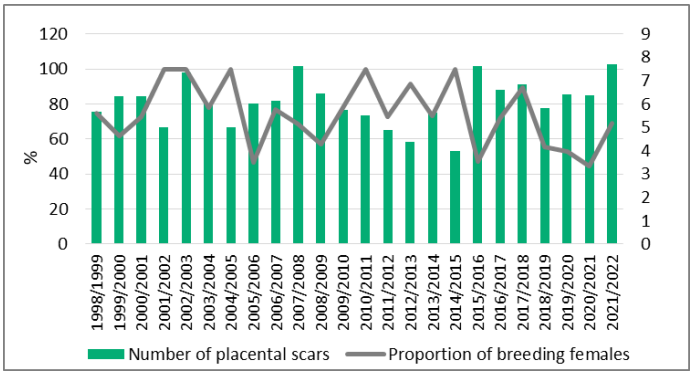


Figure 2. The average number of placental scars (n=185) and the proportion of females involved in reproduction (n=313) of the wolves hunted in Latvia from 1998/1999 to 2021/2022 hunting seasons.

Within the period from 2009 to 2021, the expected heterozygosity (He) of the population was 0.732±0.018, the observed heterozygosity (Ho) was 0.713±0.018. The inbreeding coefficient was low at 0.026±0.006. Allelic diversity by year ranged from 5.81 to 6.39 and was not statistically significantly different ($F(13, 210)=0.24$, $p=0.997$).

Comparing the eastern and western parts of the population, the expected and observed heterozygosity did not differ significantly – 0.737±0.019 and 0.722±0.020 in the eastern part and 0.706±0.018 and 0.700±0.022 in the western part, respectively. Allelic diversity was also not significantly different between parts of the population (in the eastern part – 8.15, in the western part – 7.74; $t(30)=0.51$, $p=0.611$). The eastern and western parts of the population are genetically little differentiated ($Fst=0.019$, $p=0.001$). Inbreeding coefficients in both parts of the population were low, 0.020±0.008 in the eastern part and 0.010±0.008 in the western part. Between the parts of the population, 13 migrants within a generation were found.

Within the period from 2009 to 2021, 223 groups of related wolves were determined. Kinship groups can be formed by animals from one or more wolf packs (Fig. 3). In the majority of groups, related individuals were found only during one or two hunting seasons (respectively 46.1% and 15.6% of all groups). The longest time when related animals were hunted within the same group was 11 years. According to kinship analyses, the movement of individuals across the central part of Latvia was found in 19 related wolf groups.

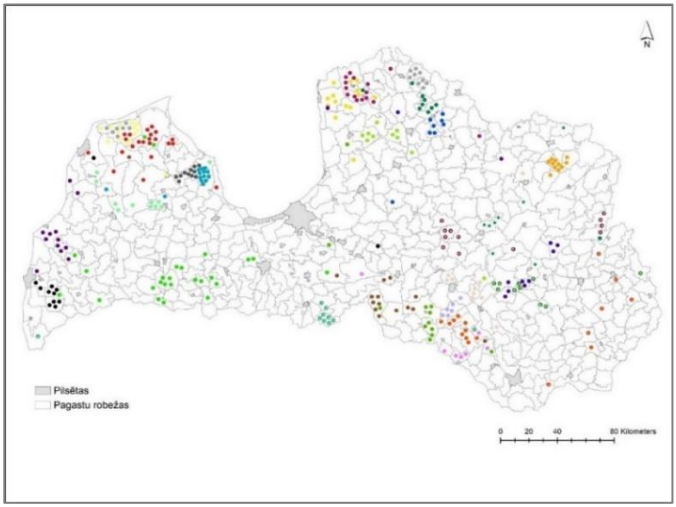
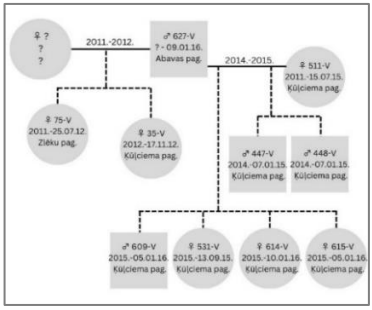


Figure 3. The largest related groups of wolves (n=27), whose individuals were hunted in Latvia between 2009 and 2021. Colours represent separate groups of related animals.

The loss of at least one breeder was found in 64.6% of the groups of relatives. The replacement of breeding partners lost during hunting was also observed, and in four families it was found that after one of the breeders and at least part of the other animals of the pack were hunted, the other breeder was hunted within one to two years in a relatively distant place (35 – 110 km) (Fig. 4.).

a)



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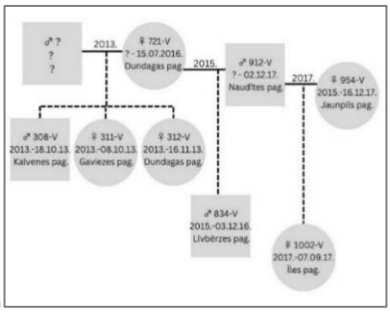

Figure 4. Kinship relationships in two Kurzeme wolf packs. The continuous line represents the relationship between the breeders, the numbers of years above them – the known duration of the existence of the couples. Dashed lines represent offspring. For each wolf, the sample number, year of birth, hunting date and hunting location are indicated. Individuals that have not been sampled or unknown information from existing samples are marked with "?".

3.2. Wolf feeding ecology

Analyses of the stomach contents of hunted wolves found that the main food items for wolves in Latvia are wild ungulates – cervids (red deer, roe deer) and wild boar. The other food items are less common (Fig. 5).

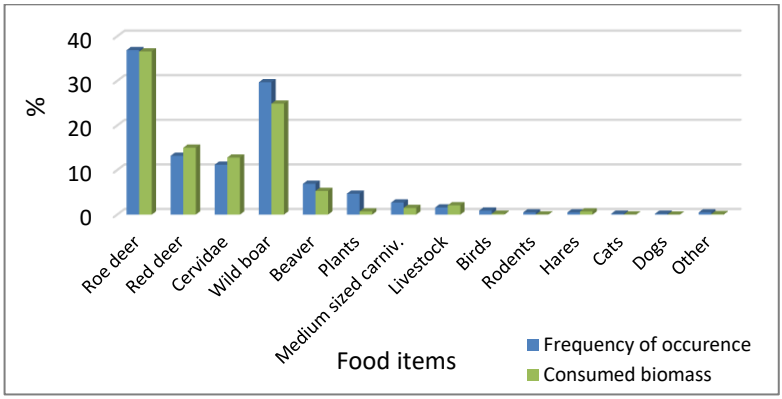

Figure 5. Occurrence of wolf food items and consumed biomass in the stomachs of wolves hunted in Latvia (n=656) between July 2001 and March 2020.

Less than a third of stomachs were empty (26.0%), the difference from full stomachs was statistically significant (χ^2=203,6, 95% TI from 23,3% to 29,0%, p<0,001).

The consumption of the major food items was not constant from year to year. Relationships in changes in consumption of cervids and wild boar were observed, which were examined in three periods – before, during and after the reduction in animal numbers. In 2010, when the number of roe deer decreased due to harsh winter conditions, the consumption of wild boars and to a lesser extent red deer increased (Fig. 6). Whereas, as the number of wild boars decreased from 2014 due to the spread of African swine fever (ASF), wolves hunted roe deer more intensively (Fig. 7). Changes in roe deer and wild boar consumption between periods were statistically significant (χ^2=18.90, 2 df, p<0.001 and χ^2=27.25, 2 df, p<0.001, respectively).

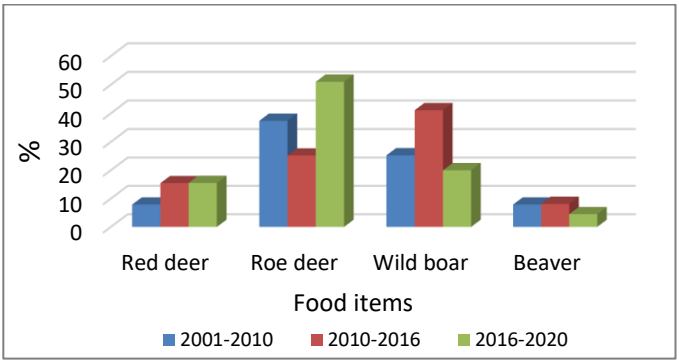

Figure 6. Changes in the food composition of wolves in Latvia in connection with changes in the number of animals in the roe deer population between July 2001 and March 2020. Changes between periods were statistically significant (in red deer – $\chi^2(2)=7.34$, $p=0.025$; in roe deer – $\chi^2(2)=31.41$, $p<0.001$; in wild boar – $\chi2(2)=26.50$, $p <0.001$).

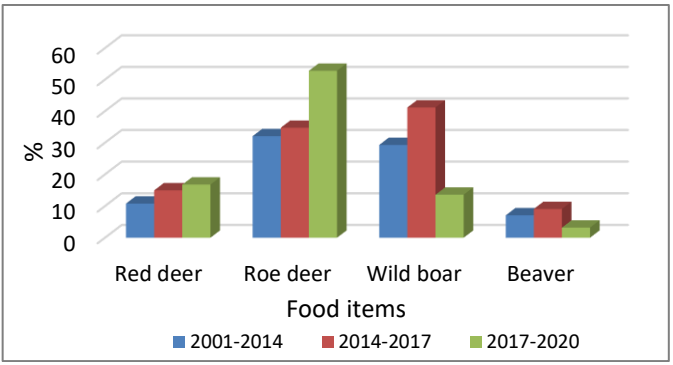

Figure 7. Main wolf food items in Latvia in relation to changes in the number of animals in the wild boar population between July 2001 and March 2020. Changes in roe deer and wild boar consumption between periods were statistically significant ($\chi^2=18,90$, 2 df, $p<0,001$ and $\chi^2=27,25$, 2 df, $p<0,001$, respectively).

3.3. Damages caused by wolves in Latvia and the ecological and economic factors affecting them

Within the period from 2000 to 2020, 531 depredation cases in which a wolf was identified as the attacker were reported to the SFS. The number of cases of damage caused by wolves varied from 9 to 62 per year (Fig. 8), with an average of 25 attacks per year.

The main victims of wolf attacks were sheep (killed – 84.3% of all domestic animals, injured – 90.4%), cattle and goats were killed and injured less often, and dogs least often.

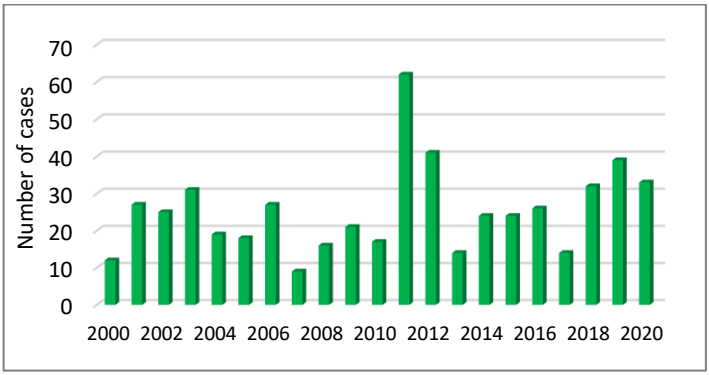

Figure 8. The number of wolf attacks on domestic animals in Latvia from 2000 to 2020.

The attacks mostly took place between May and November (93.3%). In the other months of the year, they were very rare (Fig. 9). Differences in the number of attacks between months were statistically significant (Friedman test, χ^2 (11)=147.19, p<0.001).

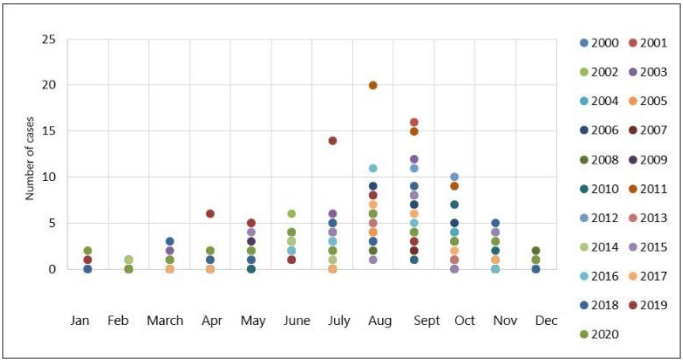

Figure 9. Distribution of the number of wolf attacks by month in Latvia from 2000 to 2020 (p<0.001).

Damages do not occur evenly throughout the entire country, their number in forestries varies from year to year, and damages occur more often in some parishes than in others.

Examining the number of wolves counted and hunted during the research period compared to the amount of damage caused throughout the country, no statistically significant correlations were found either in specific years (with counted wolves – r=0.302, p=0.184; with hunted wolves – r=0.169, p=0.465), nor when comparing the data with a year shift, when the number of damages follows the number of counted or hunted wolves (with counted wolves – r

=0.187, p=0.431; with hunted wolves – r=0.194, p=0.411). Looking in more detail at the number of wolves hunted in each forestry and the number of depredation cases caused by wolves during the period of six hunting seasons (2015/2016 – 2020/2021), no clear connection between the intensity of hunting and the amount of damage can be observed.

Summarising the information available to the SFS on the use of preventive measures on farms where domestic animals were attacked, it was found that ineffective preventive measures were used in 52.6% of cases, while in 35.8% of cases no protective measures were used at all.

3.4. Public attitude towards wolves in Latvia

The attitude towards wolves was mostly neutral or positive in both school and hunter groups (Fig. 10), but the hunter group was more positive. The results of the groups were statistically significantly different ($\chi^2(6)=43,47$, $p<0,001$).

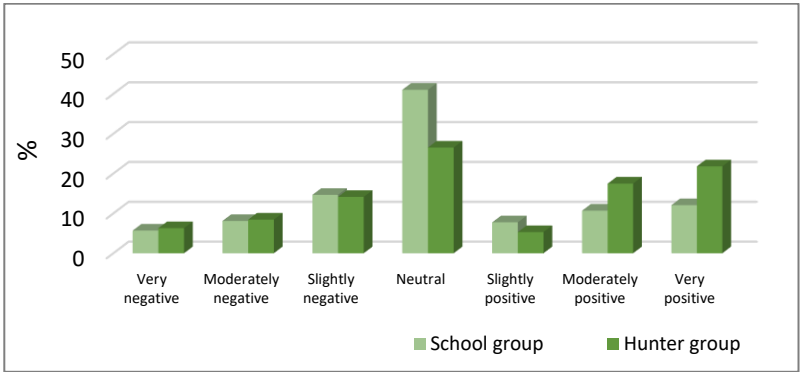

Figure 10. The attitude of school and hunter group respondents towards wolves in Latvia ($p<0.001$) according to the results of the survey conducted in 2017.

The preservation of the existing wolf population management system was supported by 30.4% of the school group and 54.6% of the hunter group (Fig. 11).

When expressing an opinion about what should be done with wolves in Latvia, the answers of the groups differed statistically significantly ($\chi^2(6)=185.54$, $p<0.001$). It was noted in the hunter group, much more often (61.9%) than in the school group (27.6%), that the number of wolves should be slightly or strongly reduced (Fig. 12).

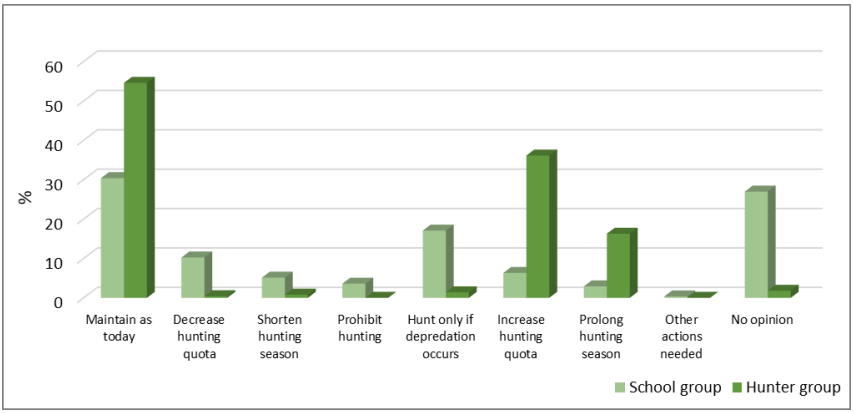

Figure 11. Opinions of school and hunter group respondents about the wolf population management system in Latvia ($p<0.001$) according to the results of the survey conducted in 2017.

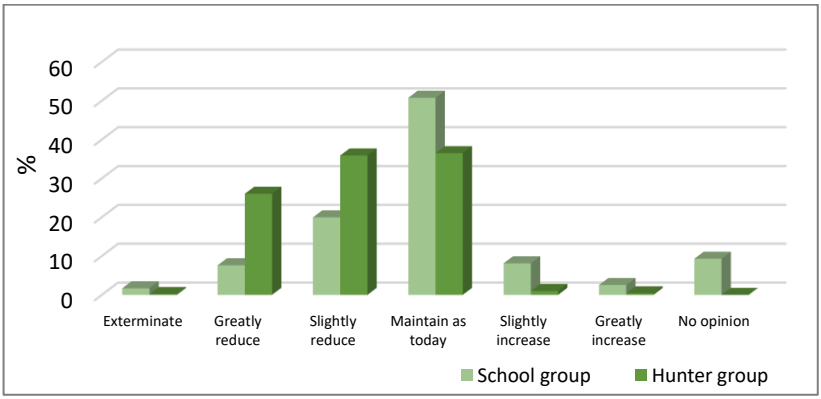

Figure 12. The opinion of school and hunter group respondents about what should be done with the number of wolves in Latvia ($p<0.001$) according to the results of the survey conducted in 2017.

Relationships between the attitude expressed by the respondents, the desired behaviour towards wolves and the opinions expressed in several other questions of the questionnaire were found. If the respondents believed that wolves are dangerous, their number in the country is large or they cause damage to farmers, the attitude towards them was more negative and the opinion that the number of wolves in the country should be reduced was expressed more often.

4. DISCUSSION

4.1. Demographic and kinship structure of the wolf population and population management

The proportions of age groups among the hunted wolves with an increased proportion of juveniles (Fig. 1) indicate a population exposed to a relatively intense hunting pressure. A large proportion of pups has been found in places where wolves are intensively hunted (Jedrzejwska et al. 1996, Fuller et al. 2003). An increase in the proportion of pups in the population indicates active reproduction and larger litters to restore the number of lost individuals.

Increased reproductive activity is evidenced by the early involvement of females in the reproduction process, the high proportion of reproductively active females and the detected average number of placental scars (Fig. 2), which allows us to judge the size of the litters. Similar litter sizes (5-8 pups) have also been found in wolf populations hunted elsewhere in Europe and Russia (Rjabov 1988, Balčiauskas 2002, Kojola 2005, Jędrzejewska and Jędrzejewski 1998, Sidorovich et al. 2007).

Hunting can provoke an increase in the number of animals, because in an attempt to restore the number of lost individuals, animals increase their reproductive activity (Fryxell et al. 2014). At a high density of wolves, moderately intensive hunting can create free spaces for dispersing wolves and facilitate the finding of a mate and territory and, accordingly, the rapid start of reproduction. In addition, good feeding conditions help ensure larger litters and female involvement in reproduction at a young age, and the ability to quickly restore their numbers helps to maintain the current population size.

The genetic diversity of the Latvian wolf population can currently be assessed as high, and the population is not at risk of inbreeding. The allelic diversity of the population has not decreased over the years, which can be considered a favourable indicator for the population, as it often responds more sensitively to processes in the population than changes in heterozygosity (Mills 2007, Allendorf et al. 2008). The observed heterozygosity in Latvia is higher than in several European (Vilà et al. 2002, Caniglia et al. 2014, Fabbri et al. 2014, Hindrikson et al. 2017) and some North American populations (Wayne and Vilà 2003). The western and eastern parts of the population are not isolated. There is an exchange of individuals between them, which is confirmed by the genetic indicators and the dispersal of animals across the central part of Latvia found in the kinship analysis.

During the observed 12 hunting seasons, groups of related wolves were found in all regions of Latvia, and in individual groups where a sufficient number of genetic samples were collected, the typical wolf pack structure was observed – a breeding pair and their offspring of two years (Mech 1970, Mech and Boitani 2003). A negative impact of hunting on the social and territorial structure of the

population was also observed, in contrast to populations not hunted, where wolf packs have relatively stable pack territories and social structure of the population (Mech and Boitani 2003). The loss of at least one parent in kinship groups was often found. Despite the early loss of a parent at least some of the pups are able to survive due to other adult members of the pack continuing to provide for them, however the loss of even one parent can make it difficult for remaining adults to care and provide for the pups, and can affect the social and spatial structure of the pack and encourage attacks on livestock by inexperienced young wolves (Frank and Woodroffe 2001, Brainerd et al. 2008, Eklund et al. 2017). The loss of breeders or other pack members can also lead to the splitting of the pack, the loss of its territory and the early dispersal of juvenile animals, sometimes even over considerable distances, which reduces the social and territorial stability of the population, increases the turn-over of individuals in packs, and reduces the degree of relatedness in the population characteristic to the species.

4.2. Wolf feeding ecology

The species composition of the main food base of wolves in Latvia has not changed, compared to the results of previous studies (Andersone and Ozoliņš 2004). Wild ungulates are still the main food of wolves (Fig. 5), as it has also been found in the rest of Europe and other parts of the world (Jedrzejewski et al. 2002, Kübarsepp and Valdmann 2003, Peterson and Ciucci 2003, Pezzo et al. 2003, Capitani et al. 2004, Štrbenac 2005, Lanszki et al. 2012). Compared to the initial research period (Andersone and Ozoliņš 2004), the proportion of wild ungulates in the food of Latvian wolves has slightly increased, while the proportion of another food object – beaver – has decreased. This is most likely explained by the increase in the number of wild ungulates in Latvia since the beginning of 2000, when wolves no longer needed to prey on alternative sources of food.

Significant changes in the choice of wolves' prey were found in the consumption of roe deer and wild boar in the periods when the number of roe deer decreased in the winter of 2010/2011 (Fig. 6) and when the number of wild boar in Latvia began to decrease due to ASF from the summer of 2014 (Fig. 7). Wolves are able to quickly adapt to significant changes in the food base, and in both periods it was found that when the availability of one species decreased, the consumption of the other species increased by 16-18%, thus compensating for the shortage, and in the short term leaving no visible negative impact on the population size of the more heavily hunted species. Similar processes have been observed in Estonia (Valdmann and Saarma 2020), Poland (Klich et al. 2021a) and Belarus (Klich et al. 2021b) after the spread of ASF in these regions.

4.3. Damages caused by wolves in Latvia and the ecological and economic factors affecting them

Data on damages caused by wolves in Latvia has been collected since 2000, but it is not known how much damage is not reported. The registered cases show

that damages caused by wolves are relatively rare in Latvia and, compared to other countries, the amount of depredation is still small (Štrbenac 2005, Krofel et al. 2011, Männil and Kont 2012, Widman and Elofsson 2018). The number of damage cases has fluctuated over the years (Fig. 8). Most wolf attacks on livestock are random in nature, when the animals take advantage of the opportunity (Gula 2008).

Similar to what was observed in other studies (Wydeven et al. 2004, Gula 2008), wolves do not cause damage in the entire area of their distribution in Latvia. In some parishes, damage occurred more often, while in others, no damage was detected at all during these years. The territorial distribution of depredation cases in Latvia is predictable to some extent, and such information can help farmers to evaluate the need to use protective measures on their farms.

A couple of the factors that can affect the extent and territorial distribution of depredation is availability of wild prey and climatic conditions that can affect the wild prey base. In several regions within the territories of eight forestries, the amount of damage increased during the hunting seasons of 2011/2012 and 2012/2013, when the number of roe deer in Latvia decreased significantly, but in general, the lack of wild game in Latvia is not the reason for significant depredation. The impact of several other factors that may contribute to attacks in Latvia cannot be clearly evaluated at the moment (for example, the size of wolf packs and their territories, the relationship between the density and number of wolves and the amount of damage in specific regions, the amount of wolf-dog hybrids in the population, the status of the social structure of the wolf population), and at least some of these factors, like local landscape conditions, are not easily influenced. Therefore, measures to protect domestic animals play an important role in preventing damage, because unprotected or insufficiently protected animals suffer most often (Pavlov 1990, Blanco et al. 1992, Ciucci and Boitani 1998, Kaczensky 1999, Boitani 2000, Balčiauskas et al. 2002, Gula 2008).

Similar to other studies (Pavlov 1990, Ciucci and Boitani 1998, Balčiauskas et al. 2002, Štrbenac 2005, Musiani et al. 2005), attacks in Latvia were mainly detected from May to November (Fig. 9). During this time, livestock is more easily accessible because animals are in pastures, and they are mostly poorly guarded. The frequency of attacks in all years increased between July and October, when wolves, compelled by some circumstances, are more likely to prey on livestock in order provide food for pups (Fritts et al. 1992, Anderson et al. 2001, Harper et al. 2008).

The effectiveness of predator hunting in preventing depredation is still not clearly known. Some studies have found that lethal control of predators can be less effective than other protection methods (Treves et al. 2016, Bruns et al. 2020), and livestock keeping conditions are often more important in reducing damage than decreasing the number of wolves (Kaczensky 1996). Moreover, the effectiveness of hunting in reducing damage may depend on various factors, such as the social status of hunted individuals in the pack and whether problem

individuals, the whole pack or only part of the pack are hunted (Eklund et al. 2017). In some cases, predator hunting can increase the amount of depredation (Frank and Woodroffe 2001, Treves et al. 2016, Eklund et al. 2017).

No significant correlations between the number of hunted wolves and the number of damage cases have been established during the research period, and also no clear correlations between the damage caused and the spatial distribution of wolf hunting can be observed. Damage occurs both in areas with high and relatively low hunting intensity. According to these data, there is no reason to claim that hunting in all conditions and regions helps to reduce the amount of depredation. There is no direct, easily detectable relationship between the number of wolves hunted and the amount of damage caused in Latvia. Depredation is most likely influenced by various factors, and to obtain more complete information a more extensive study of local situations over a longer period of time is required.

4.4. Public attitude towards wolves in Latvia

The chosen method of distribution of survey questionnaires through schools had a certain impact on the sample group of respondents, as only members of families with school-aged children participated in the survey. It is also not known whether the rules for the choice of the person filling in the questionnaire were always followed, as a higher proportion of women and young people was found in the sample group than in the general population of the country. Despite this, it is believed that the obtained information gives an idea of the public attitude towards wolves and enables the identification of specific population groups whose attitudes and opinions may be important in the conservation of large carnivores and population management.

In general, the public attitude towards wolves can be characterised as neutral or positive (Fig. 10). The respondents were mostly satisfied with the existing situation and current wolf population management system (Fig. 11). A neutral attitude can be considered a positive trait as it may indicate less potential for conflict (Majìć and Bath 2010). However, this group of people should be taken into account when planning management measures for the species, as a neutral attitude can be turned in both positive and negative directions with appropriate publicity or strongly expressed opinions (Williams et al. 2002, Ericsson and Heberlein 2003).

Similar to the study in Croatia (Bath and Majic 2000), hunters in Latvia expressed a positive attitude towards wolves slightly more often than school group respondents (Fig. 10). However, they also more often claimed that wolves cause financial losses and damage to farmers, and expressed desire for a longer hunting season and larger limits of wolves to be hunted (Fig. 12). Even if the evaluative part of hunters' attitude towards wolves is positive, their beliefs and subjective knowledge can influence behavioural intentions towards reducing the number of wolves.

The established relationship between negative attitudes towards wolves and the beliefs that there are many wolves in Latvia, that wolves are dangerous and that they cause damage to farmers, show how subjective beliefs and knowledge can shape attitudes and indicate the directions of action in order to improve them.

Although attitude is not the only determinant of behaviour (Heberlein 2012), it can to some extent predict people's behavioural intentions and behaviour (Manfredo 2008). This research found this in the opinions about what should be done about the number of wolves in the country. In both groups of respondents, a negative attitude correlated with the desire to reduce the number of wolves, and also, if the respondents thought that there were many wolves, they were more likely to express the opinion that the number of animals should be reduced. A similar relationship was also found in a study in Norway (Bjerke et al. 2008), where opinions (beliefs) about the number of wolves influenced desired actions (behaviour), which is in accordance with the principles of cognitive hierarchy (Fulton et al. 1996).

5. CONCLUSIONS

- ✓ Since the development of the species conservation plan and the implementation of appropriate population management in 2004, the geographical structure of the wolf population has improved and the number of individuals has increased, as the population is able to restore the number of individuals lost as a result of hunting, due to high reproductive activity, good supply of food resources and, possibly, ongoing immigration of animals from less intensively hunted areas.
- ✓ Frequent loss of breeding animals and disintegration of the social and territorial structure of the packs were found. However, in part of the population kinship analyses showed the typical structure of wolf packs and long-standing groups of related animals. The migration of animals between the west and east of the country currently is not disturbed, and parts of the population are not isolated.
- ✓ The major food items of wolves in Latvia are wild ungulates, mainly roe deer and wild boar. The importance of beavers in wolf food has decreased compared to the earlier study period.
- ✓ Currently, the feeding conditions of wolves in Latvia do not limit the population, and wolves are able to quickly adapt to significant changes in their prey base.
- ✓ The amount and number of reported wolf depredation cases in the country is small, and their seasonality, as well as their territorial distribution in Latvia, is predictable, thus farmers have the opportunity to adjust animal husbandry conditions and the use of preventive measures.

- ✓ In order to reduce the damage caused by wolves, it is necessary to use effective preventive measures, as the importance of wolf hunting in reducing damage can depend on various factors. The resolution of conflict situations and the successful coexistence of the species in a human-populated environment could be facilitated by both informative measures and practical and financial support for the protection of domestic animals.
- ✓ The public attitude towards wolves in Latvia is mostly favourable to the conservation of the species and current population management practices, as the majority of respondents did not express the desire for significant changes in the existing situation.

6. RECOMMENDATIONS

1. Study the immigration of animals from neighbouring countries in order to establish to what extent such immigration takes place and how significantly it helps to maintain the Latvian wolf population, as well as the evaluation of the effects of potential migration threats *(Rail Baltica*, national border fences, etc.) is necessary after their implementation.

2. Collect genetic material from neighbouring countries (Lithuania, Estonia) in order to clarify the kinship and social structure of wolves in the border areas.

3. Develop non-invasive research methods and non-invasive genetic monitoring, as the data obtained in this way would provide information about current processes in the population.

4. In order to reduce the depredation caused by wolves and to create a balance between the protection of wolves, the economic interests of the people and the well-being of both predators and domestic animals, within the limits of professional competence, promote the successful cooperation among the respective institutions and organisations and provide a basis for the implementation of practical support measures for farmers and political decision making.

5. When determining the wolf hunting limit in the future, also take into account the food resources available to predators and the possible influence of national border fences on the wolf population.

6. When determining the length of wolf hunting season, take into account the impact of hunting on the social and spatial structure of the population and the possibilities of preserving functional wolf packs.

7. Periodically repeat the research on the public attitude towards large carnivores in order to get an insight in the current situation in the country.

8. Informative and financial support is needed for people whose economic activity is affected by the presence of wolves.

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