LATVIJAS UNIVERSITĀTE

Žanete Andersone *

Vilks (*Canis lupus* L., 1758) Latvijā: populācijas stāvoklis, demogrāfija, morfometrija, trofiskā ekoloģija un ģenētika saistībā ar pašreizējo apsaimniekošanas praksi

The wolf (*Canis lupus* L., 1758) in Latvia: status, demography, morphometry, trophic ecology, and genetics in relation to current management practices

Promocijas darbs
bioloģijas doktora zinātniskā grāda iegūšanai

Thesis for doctoral degree in Biology

Rīga, 2002

Introduction

Recent ecological studies indicate that top-down processes are very important in terrestrial ecology (Oksanen et al. 1981, Burns 1989, Polis and Strong 1996, Polis et al. 1997, Pace et al. 1999, Schmitz et al. 2000, Halaj and Wise 2001), which implies that top predators can significantly influence processes in lower trophic levels (Begon et al. 1986). The wolf-prey-vegetation relationship is an example of such an intrinsic complex, which requires an integrated approach (Бибиков и Караваева 1989, Железнов 1990, Skogland 1991, Berger 1999, Post et al. 1999, Smith et al. 1999, Ripple et al. 2001).

Although the ecology of large carnivores has been a popular study subject in both Eurasia and North America (Bibikov 1985, Carbyn et al. 1995, Mech 1995, Jędrzejewska and Jędrzejewski 1998), it has never been properly studied in Latvia despite the great practical significance of carnivores and their impact on human economic activities – game management and livestock husbandry. The very limited studies on wolf-prey relationships have been done only in a study area in western Latvia (Gaross 1997). Some preliminary studies have also been carried out in Lithuania (Prusaite 1961a, 1961b) and Estonia (Valdmann et al. 1998). Understanding population ecology is important not only from theoretical but also from the practical point of view of wildlife management (Odum 1959, Caughley and Sinclair 1994, Bookhout 1996). Moreover, ecosystem functioning is strongly linked to biodiversity (Hector et al. 2001) species richness positively correlating with ecosystem function (Schwartz et al. 2000).

Wolves were traditionally regarded as pests, which should be eliminated by all means possible (Новиков 1956, Павлов 1982, 1990). A different opinion appeared only recently when it was realised that wolves are endangered in large parts of their present distribution (Promberger and Schröder 1992, Boitani 2000, Delibes 2000), which is significantly smaller than their original one (Bibikov 1985, Mitchell-Jones et al. 1999) resulting from a centuries-long persecution by humans. The Baltic countries still host a strong wolf population compared to Western Europe (Boitani 2000) and can serve as a source for a potential dispersal of wolves westwards.

Wolves are one of the most controversial predators (Lopez 1995), which have been persecuted using a wide range of hunting methods (Bibikov et al. 1983, Frkovic et al. 1992, Jędrzejewska et al. 1996b, Okarma 1996, Elgmork 2000). The reason of such an attitude toward the species is that wolves have been feared for centuries due to the potential threat they pose to human life (Peterson 1947, Осмоловская и Приклонский 1975, Vanags 1989, Корытин 1990, Павлов 1990, Jhala and Sharma 1997, Корытин 1997, Linnell et al. 2002), livestock (Pulliainen 1965, Priklonsky 1985, Delibes 2000) and game resources exploited by people (Filonov and Kaletskaya 1985, Nowak and Myslajek 1999a, Delibes 2000). Therefore, the problems of human – wolf conflicts, especially depredation on livestock, cannot be viewed in isolation from the socio-economic context (Cozza et al. 1996, Breitenmoser 1998, Ciucci and Boitani 1998, Boitani 2000).

As wolf control is a politically sensitive issue (Carbyn 1983, Anonymous 1997, Sharpe et al. 2001), it is clear that carnivore conservation requires a complex approach, addressing biological, ethical, emotional and economical aspects (Mills 1987, Naess and Musterud 1987, Boman and Bostedt 1994, Boman 1995, Mech 1995, Mech et al. 1996, Linnell et al. 2000). In Latvia, the first attempt to use different aspects of wolf – human relationships in carnivore management was applied in the recent Wolf Action Plan (Ozoliņš and Andersone 2000).

In the mid-1990s, when the conflict between hunters and predators in Latvia was aggravated due to the competition for the depleted prey base, unlimited and even promoted hunting of large carnivores created a unique situation for research. In 1998, the first national wolf research project was started. It was important to answer the basic questions – what is the current situation with the wolf population, how do the wolves in Latvia compare to the neighbouring wolf populations, what is their diet and population structure, and what is the impact of unlimited hunting on the population? The analysis of population dynamics, distribution, demographic structure, morphometrics and genetics contribute to understanding of the impact of unlimited hunting on the wolf population. The study on wolf trophic ecology is a first step toward a more detailed research of predator – prey interactions in Latvia, which is important for the future management planning, considering carnivore share in the total ungulate mortality. All these issues required a comprehensive study on the wolf in Latvia, which has been the aim of the present work.

The specific objectives of this study were as follows:

- To analyse the present status of wolves in Latvia, taking into account changes in the species' distribution range and population size in time;
- To find out the impact of intensive hunting on the demographic structure of wolves in Latvia by sampling harvested animals;
- To investigate morphometrical and craniometrical characteristics of wolves from Latvia in comparison with wolf populations in the neighbouring countries;
- To analyse the diet of wolves including its seasonal, sexual and geographical variations within Latvia and to compare it with the diet of the country's second most common large carnivore species – lynx *Lynx lynx*;
- To verify the occurrence of wolf – dog hybrids in Latvia;
- To analyse past and present wolf – human conflicts in the Baltic region.

Summary

The study summarises data collected in Latvia from 1997 to 2001. It covers the following aspects of the wolf *Canis lupus* L., 1758 biology: demography, morphometrical and craniometrical characteristics, trophic ecology and genetics. The study was based mainly on harvested animals as well as on scats collected in the field in different parts of Latvia. The study also includes the analysis of the human – wolf conflicts in the Baltic and the current wolf status and recent changes in its dynamics and distribution based on the official data on census and hunting bag from the State Forest Service dated from 1923.

Currently, wolves occur in most of the Latvian territory except the south of the country and the region to the north from Rīga along the Rīga Gulf. In total, there are about 300-500 wolves in Latvia. Distribution and dynamics of the wolf population in the country are directly connected with the intensity of persecution by humans. Wolves were close to extinction by 1940 and were very scarce in the 1960s when an intensive anti-wolf campaign occurred. However, they were able to recover quickly due to the presence of the core population to the east of Latvia. After another significant post-war peak in the 1990s, wolves have decreased during the study period both in numbers and range following the intensive harvesting in the mid-1990s.

The main reason for the wolf - human conflicts nowadays originates from the fact that hunters perceive wolves as their competitors for wild ungulate resources. In the past, livestock depredation and a potential threat to humans was another source of the interest conflict. Nowadays, livestock depredation occurs only locally and seasonally, sheep (70.8%), calves (21.9%) and dogs (5.2%) being the most often victims.

In order to find out the current population's demographic structure and the possible impact of hunting on its sex and age structure, a sub-sample of 84 harvested individuals (36 ♂♂, 48 ♀♀) was investigated, determining precise age of the animals and reproductive status of females. Sex ratio showed the prevalence of females (♂♂ : ♀♀ = 0.77), which, along with the high fecundity (on average, six embryos per female), may be an indication of heavy exploitation of the population, because increased fecundity and female production is known as a compensatory mechanism for high mortality rates. The prevalence of females in the 3rd and the 4th age groups suggests that increased female production started in 1996-1997, which coincided with the peak of wolves' persecution. The age structure showed a relatively low proportion of subadult wolves – juveniles

constituted only about 20% of the total hunting bag. That suggests there are other pre- and neonatal mortality factors, possibly related to elimination of pregnant and lactating females during the summer hunting. The low proportion of old animals is another indication of the population's over-exploitation as intensive hunting tends to decrease the average age of populations.

Craniometrical analysis of 187 wolf skulls (115 ♂♂, 72 ♀♀) was carried out, measuring 19 parameters, including skull weight. Skull parameters of males exceeded those of females. The average condylobasal length of male and female skulls was accordingly 23.7 and 22.5 cm, total length – 26.5 and 24.8 cm, zygomatic breadth - 14.3 and 13.2 cm. Thus, cranial parameters of Latvian wolves did not differ significantly from those of wolves from the neighbouring countries like Belarus, Lithuania and Poland. Deviations from the normal tooth pattern were found in 9.5% of the skulls investigated, congenital oligodonty and polydonty were found in 7.9% of skulls, polydonty being the most common tooth anomaly (71.4%). Tooth anomalies were more common in males. A few skulls bore evidences of traumatic injury, probably through encounters with ungulates. Within the country, the difference in most of the cranial parameters was found between wolves from north-eastern Latvia and wolves from the Kurland Peninsula in the west. Wolves from the east of the country had generally bigger characteristics (in total, 13 parameters), while only two parameters, facial length and length of *incisura palatina,* were bigger in wolves from the west. It is suggested that the differences in cranial parameters indicate some degree of isolation of the Kurland Peninsula's wolves due to the hampered migration from the east. That is indirectly supported by the data on the distribution of wolves in Latvia, which was decreasing for the last few years due to over-hunting in vast territories, including the area naturally serving as an ecological corridor between east and west of the country. However, the craniometrical disruption has most likely been caused by the differences in the average age of the population in the west and east due to different hunting intensity. This hypothesis requires more research on wolf demography.

Morphometrical measurements were taken from 496 harvested wolves (244 ♂♂, 252 ♀♀), 90% of the measurements being taking by hunters according to a specially developed questionnaire. Sexual dimorphism was found in body parameters, males being bigger than females. The average weight of males and females was accordingly 41.2 and 34 kg, height – 77 and 71 cm, total body length – 159.2 and 150.5 cm, tail length – 42.6 and 40.8 cm. Sex ratio of this sample also showed female prevalence (♂♂ : ♀♀ = 0.97).

1.4% of wolves investigated had signs of scabies. The high proportion of the animals with old injuries (8.3% in total, of which 46.3% of injuries were of obvious anthropogenic origin) is another evidence of the high hunting pressure on wolves in Latvia. Age structure of the harvested wolves as determined by hunters showed a lower proportion of juvenile wolves than the sub-sample of 84 animals. Although having been proved as an inappropriate method for age determination, the questionnaire method demonstrated that it could be a useful tool for morphometrical studies on a large scale provided that measurements to be taken are simple.

Trophic ecology of wolves in Latvia was studied by analysing 302 scats and 107 stomachs of harvested animals collected from different parts of Latvia in both winter and summer seasons. Wild ungulates (cervids and wild boar) were the staple food for wolves in both seasons (55.7% of frequency of occurrence in summer and 76.6% in winter), while beavers were the second most important prey in summer (18.8%). Due to its abundance in Latvia, beaver is an important alternative prey for wolves, its significance being much higher than elsewhere in Europe. However, it seems to have gained such a role in the wolf diet only in the last decade following the decline in ungulate populations in the early 1990s caused by the cumulative effect of hunting, poaching and predation. Male wolves were found to prey on beavers considerably more than females did. Some seasonal variations in the wolf diet were observed, the proportion of ungulates increasing in winter. Cervids occurred in 49.4% of summer samples and 51.2% of winter samples, wild boar – 20% and 33.9% accordingly. Wild boar were a preferred prey, the significance of which increased in winter. Wild boar was a more common prey for wolves in the east of Latvia, while cervids and livestock (mainly as carrion) were most often preyed on in the west. Summer diet was characterised by a broader food niche including minor prey items such as rodents, medium-sized carnivores, reptiles, berries etc. Domestic animals rarely featured on the predator' menu except for during winter when livestock was consumed as carrion (13.1%). Winter diet of wolves was compared with that of lynx (49 stomachs), revealing that the trophic competition between the two large carnivore species was moderate. Food niche was narrower for lynx, which relied almost entirely on roe deer as prey (86.5%), while also other prey species were available to wolves due to the differences in their size and hunting strategy. 36.7% of wolf and 34.7% of lynx stomachs checked were empty. The average weight of stomach content in wolves was 990.3 g, ranging from 20 to 4350 g.

Genetic samples (muscle or blood tissue) from Latvian wolves were taken (n = 39). Hybridisation between wolves and free-ranging dogs in Latvia was analysed based on 31 harvested individual, six samples originating from a litter of suspected hybrid origin due to the pups' abnormal morphological features. Eight samples from Latvian male wolves were used in a methodological comparative study using a combination of mtDNA, autosomal and Y-chromosome markers for the most precise identification of wolf - dog hybrids. The hybrid origin of the six pups, their putative mother and a male from the same area in northern Latvia was confirmed using the mtDNA control region and autosomal microsatellites. Only one potential hybrid was found in western Latvia. Hence, eight hybridisation cases (of nine cases in total) came from the same region where wolf density was low, therefore, supporting the idea that wolves cross-breed with stray dogs when the local spatial and demographic structure of the wolf population is disturbed. Hybridisation seems to be more common in Latvia than elsewhere in Western Europe, which can be possibly explained by the high abundance of stray dogs in the countryside, and indiscriminate and unlimited wolf hunting. However, genetic diversity of wolves from Latvia proved to be higher compared to the isolated population of Scandinavia.

The management regime has so far been unfavourable for the species conservation, as legal all-year-round hunting resulted from a public perception of the wolf as a pest. The recent proposed changes in hunting legislation provide a closed season on wolves from April to mid-July, which is a first step toward a sustainable management of the species. Introduction of a longer seasonal ban and hunting quotas in the future would be a valuable input into wolf conservation. Several above-mentioned features of the population revealed during the present study indicate to population's over-exploitation. The results of the study, therefore, imply that the wolf management practice should be changed toward a more sustainable approach.

The following conclusions can be made from the present study:

- For the last few decades, wolves have been widely distributed and numerous in Latvia, however, both a numerical and distribution decline has been observed in the last three years as a consequence of unregulated persecution by humans.

- Mophologically, both in body size and weight, and craniometrical characteristics, Latvian wolves are similar to those of the neighbouring countries hosting the forest zone's race of the species. The degree of sexual dimorphism typical to wolves from Latvia was revealed, males being bigger than females.

- Craniometrical parameters show some morphological disruption between wolves in Kurland Peninsula and the rest of the country, wolves in the east having bigger skulls.

- The sex and age structure of the harvest bag, i.e., low proportion of old animals, female predominance and their high fecundity (6 embryos on average), all point towards the current over-exploitation of the population. A relatively low ratio of juveniles (20%) is an indication of additional pre- and neonatal mortality factors, possibly elimination of pregnant and lactating females through summer hunting. The high proportion of animals with human-caused injuries (3.8%) is another evidence of the strong hunting pressure.

- Wild ungulates (cervids and wild boar) are the staple food for wolves both in winter (76.6%) and summer (55.7%) seasons, beaver being the second most important prey category in summer (18.8%). Livestock depredation is a relatively rare event, and livestock is mainly consumed in winter as carrion (13.1%). Wolves in Latvia prey on beavers considerably more than elsewhere in Europe. Beavers may have been a buffer prey during ungulate declines in the mid-1990s, helping to maintain high wolf densities.

- Hybridisation between wolves and stray dogs has been confirmed in Latvia. Most of the cases were found in northern Latvia in an area with low wolf density, which is an evidence of the importance of maintaining the proper spatial and demographic structure of the wolf population in order to prevent further hybridisation.

- Although on the whole, the Latvian wolf population is still numerous (totalling currently about 300-500 individuals), some negative consequences of the unregulated wolf hunting have been observed such as numerical and distributional decline, deviations in the demographic structure, hybridisation with dogs etc. Conservation of wolves in Latvia can be most effective through changing the current hunting legislation and wolf management practice toward a more sustainable system.

Kopsavilkums

Pētījumā ir apkopoti no 1997.g. līdz 2001.g. Latvijā ievāktie dati par sekojošajiem vilka *Canis lupus* L., 1758 bioloģijas aspektiem: demogrāfiju, morfometriskajiem un kraniometriskajiem rādītājiem, trofisko ekoloģiju un ģenētiku. Pētījums tika balstīts galvenokārt uz dažādās Latvijas daļās nomedītajiem vilkiem un ievākto ekskrementu analīzēm. Pētījumā tiek analizēti konflikti starp cilvēku un vilku Baltijā, kā arī pašreizējais vilku stāvoklis un izmaiņas populācijas dinamikā un izplatībā, balstoties uz Valsts Meža dienesta oficiālajiem uzskaites un nomedīšanas datiem sākot no 1923.gada.

Pašreiz vilki ir sastopami Latvijas teritorijas lielākajā daļā, izņemot valsts dienvidu daļu un Vidzemi gar Rīgas jūras līci. Pavisam Latvijā ir ap 300-500 vilki. Populācijas izplatība un dinamika valstī ir cieši saistītas ar vilku medīšanas intensitāti. Līdz 1940.gadam vilki Latvijā bija gandrīz izzuduši, un to skaits bija ļoti zems 1960.gados, kad ar vilkiem intensīvi cīnījās. Tomēr pateicoties kodola populācijai uz austrumiem no Latvijas, tie spēja ātri atgūt iepriekšējo skaitu. Pēc otrā lielākā pēckara vilku populācijas pieauguma 1990.gados, pētījumu veikšanas laikā vilku skaits un izplatība samazinājās dekādes vidū sākušās intensīvās apmedīšanas rezultātā.

Mūsdienās galvenais iemesls konfliktiem starp vilku un cilvēku ir tas, ka mednieki uzskata vilku par konkurentu par savvaļas pārnadžu resursiem. Agrāk svarīgs konflikta cēlonis bija uzbrukumi mājlopiem un vilku potenciālā bīstamība cilvēkiem. Mūsdienās uzbrukumi mājlopiem ir tikai lokāla un sezonāla problēma, visbiežāk no vilkiem cieš aitas (70.8%), teļi (21.9%) un suņi (5.2%).

Lai noteiktu pašreizējo populācijas demogrāfisko struktūru un medību iespējamo ietekmi uz to, tika izpētīti 84 nomedītie īpatņi (36 ♂♂, 48 ♀♀). Dzimumu attiecība uzrādīja mātīšu pārsvaru (♂♂ : ♀♀ = 0.77), kas kopā ar augstu auglību (vidēji 6 embriji vienai reproduktīvā vecuma mātītei) norāda uz populācijas pārmedīšanu, jo paaugstināta auglība un mātīšu pārsvars populācijā darbojas parasti kā kompensācijas mehānisms pret lielu mirstību. Mātīšu pārsvars 3. un 4.vecuma grupās nozīmē, ka lielāka mātīšu dzimšana sākās 1996.-1997.g., kas sakrīt ar intensīvas vilku apkarošanas sākumu. Vecuma struktūra uzrādīja relatīvi zemu jaunu vilku īpatsvaru – vilki līdz gada vecumam sastādīja tikai ap 20% no visiem nomedītajiem īpatņiem. Tas liek domāt, ka pastāv citi pre- un neonatālās mirstības faktori, iespējams, saistīti ar grūsno un zīdošo mātīšu elimināciju vasaras medību laikā. Vecu dzīvnieku zemais īpatsvars ir vēl viena norāde uz populācijas pārāk intensīvu apmedīšanu, jo tā parasti samazina populācijas vidējo vecumu.

Tika veikta 187 vilku galvaskausu (115 ♂♂, 72 ♀♀) kraniometriskā analīze, izmantojot 19 parametrus, t.sk. galvaskausa svaru. Tēviņu galvaskausu parametri bija lielāki par mātīšu. Vidējais kondilobazālais garums tēviņu un mātīšu galvaskausiem bija attiecīgi 23.7 un 22.5 cm, kopējais garums – 26.5 un 24.8 cm, zigomātiskais platums – 14.3 un 13.2 cm. Tādējādi, Latvijas vilku galvaskausu parametri būtiski neatšķīrās no attiecīgajiem rādītājiem vilkiem no tādām kaimiņu zemēm, kā Baltkrievija, Lietuva un Polija. Novirzes no normālās zobu formulas tika atrastas 9.5% izpētīto galvaskausu, iedzimtā oligodontija un polidontija konstatētas 7.9% galvaskausu. Polidontija bija visbiežāk sastopamā zobu anomālija (71.4%). Zobu formulas anomālijas biežāk bija sastopamas tēviņiem. Dažiem galvaskausiem bija traumu pazīmes, kas varētu būt radušās no kontaktiem ar pārnadžiem. Republikas robežās tika atrastas atšķirības lielākajai daļai galvaskausu parametru vilkiem no Kurzemes un no pārējās Latvijas teritorijas. Vilkiem no valsts austrumiem bija lielāki galvaskausu rādītāji (pavisam 13 parametri), kamēr tikai divi parametri, sejas daļas garums un *incisura palatina* garums, bija lielāki Kurzemes vilkiem. Tiek izteikta hipotēze, ka atšķirības galvaskausu parametros atspoguļo Kurzemes vilku izolāciju, ko ir izraisījusi apgrūtināta migrācija no Latvijas austrumiem. Šo hipotēzi netieši apstiprina dati par vilku izplatību Latvijā, kas ir samazinājusies pēdējo dažu gadu laikā intensīvas vilku apkarošanas dēļ, t.sk. arī teritorijās, kas dabīgi kalpo kā ekoloģiskais koridors starp valsts austrumu un rietumu daļām. Tomēr visdrīzāk kraniometrisko rādītāju sadalījumu ir izraisījušas populācijas vidējā vecuma atšķirības Latvijas austrumu un rietumu daļās dažādas medību intensitātes dēļ. Šīs hipotēzes pārbaudīšanai ir nepieciešami papildus pētījumi par vilku demogrāfiju.

Morfometriskie mērījumi tika veikti 496 nomedītajiem vilkiem (244 ♂♂, 252 ♀♀), 90% mērījumu veica mednieki pēc īpaši izstrādātās anketas. Tāpat kā galvaskausos, arī ķermeņa izmēros bija izteikts dzimumu dimorfisms – tēviņi bija lielāki par mātītēm. Vidējais svars tēviņiem un mātītēm bija attiecīgi 41.2 un 34 kg, augstums skaustā – 77 un 71 cm, kopējais ķermeņa garums - 159.2 un 150.5 cm, astes garums - 42.6 un 40.8 cm. Šīs paraugkopas dzimumu attiecībā arī dominēja mātītes (♂♂ : ♀♀ = 0.97). 1.4% apsekoto vilku bija kašķa pazīmes. Liels skaits dzīvnieku ar veciem ievainojumiem (kopā 8.3%, no kuriem 46,3% ievainojumu bija nepārprotami antropogēnas izcelsmes) ir vēl viena norāde uz intensīvu vilku apkarošanu Latvijā. Nomedīto vilku vecuma struktūra pēc mednieku noteiktajiem vecumiem uzrādīja zemāku nepieaugušo vilku īpatsvaru nekā 84 īpatņu paraugkopa. Kaut arī anketēšanas metode izrādījās neatbilstoša vecuma noteikšanai, tā var būt noderīga plaša mēroga morfometriskajos pētījumos, pie nosacījuma, ka veicamie mērījumi ir vienkārši.

Vilku trofiskā ekoloģija Latvijā tika pētīta, analizējot 302 ievāktos ekskrementus un 107 nomedīto vilku kuņģus no dažādām Latvijas daļām gan no ziemas, gan vasaras sezonas. Vilku pamatbarība abās sezonās bija savvaļas pārnadži – briežveidīgie dzīvnieki un mežacūkas (55.7% vasaras un 76.6% ziemas paraugu), kamēr bebrs bija otrais pēc svarīguma barības objekts vasarā (18.8%). Pateicoties bebru lielajam skaitam Latvijā tie ir kļuvuši par svarīgu alternatīvu barības avotu vilkiem, daudz nozīmīgāku nekā citur Eiropā. Iespējams, ka šādu lomu bebrs ir ieguvis tikai pēdējās dekādes laikā pēc pārnadžu skaita samazināšanās 1990.gadu sākumā, ko bija izraisījusi medību, malu medību un plēsonības apvienotā ietekme. Vilku tēviņu barībā bebrs bija sastopams ievērojami biežāk. Vilku barošanās nedaudz mainījās sezonāli, pārnadžu īpatsvaram palielinoties ziemas sezonā. Briežveidīgie bija sastopami 49.4% vasaras un 51.2% ziemas paraugu, mežacūkas – attiecīgi 20 un 33.9%. Mežacūkas vilki medīja ievērojami vairāk salīdzinot ar to īpatsvaru pārnadžu sabiedrībā, īpaši ziemā. Mežacūku īpatsvars vilku barībā bija augstāks Latvijas austrumu daļā, bet rietumu daļā plēsēju uzturā dominēja briežveidīgie un mājdzīvnieki (galvenokārt kritušie). Vasarā vilkiem bija raksturīga plašāka barošanās niša, kas iekļāva mazākus barības objektus, tādus kā grauzēji, vidēja lieluma plēsēji, rāpuļi, ogas utt. Ar mājdzīvniekiem vilki barojās reti, izņemot ziemas sezonu, kad plēsēji papildināja ēdienkarti ar galvenokārt izgāztuvēs atrodamajiem kritušajiem mājlopiem (13.1%). Vilku ziemas barošanās tika salīdzināta ar lūšu barošanos (49 kuņģi), pierādot, ka barības konkurence starp šīm divām lielo plēsēju sugām bija mērena. Lūsim, kas gandrīz pilnībā pārtika no stirnām (86.5%), barības niša bija šaurāka nekā vilkam, kuram pateicoties atšķirībām izmēros un medību stratēģijā bija pieejams arī cits medījums. 36.7% vilku un 34.7% lūšu kuņģu bija tukši. Vidējais kuņģa satura svars vilkiem bija 990.3 g, robežās no 20 g līdz 4350 g.

No Latvijas vilkiem tika ievākti ģenētiskie paraugi (muskuļu vai asiņu audi) (n = 39). Balstoties uz paraugiem no 31 nomedītā vilka, tika analizēta hibridizācija starp vilkiem un klaiņojošiem suņiem Latvijā. Seši paraugi tika paņemti no viena metiena no Latvijas ziemeļu daļas, par kura hibrīdo izcelsmi radās aizdomas kucēnu neparasto morfoloģisko pazīmju dēļ. Astoņi paraugi no Latvijas vilku tēviņiem tika izmantoti metodoloģiskajā salīdzinošā pētījumā, precīzākai vilku – suņu hibrīdu identifikācijai izmantojot mtDNS, autosomālos un Y-hromosomas marķierus. Kucēnu, to potenciālās mātes un tēviņa no viena Ziemeļvidzemes rajona hibrīdā izcelsme tika pierādīta, izmantojot mtDNS kontroles reģiona un autosomālo mikrosatelītu marķierus. Tikai viens potenciāls hibrīds tika atrasts Latvijas rietumos. Tādējādi, astoņi hibridizācijas gadījumi (no deviņiem pierādītajiem) nāk no viena rajona ar zemu vilku blīvumu, atbilstoši teorijai par to, ka vilki krustojas ar klaiņojošiem suņiem, ja ir izjaukta vilku populācijas vietējā telpiskā un demogrāfiskā struktūra. Hibridizācijas gadījumi Latvijā bija relatīvi biežāki salīdzinājumā ar Rietumeiropu, ko var izskaidrot ar lielu klaiņojošu suņu skaitu lauku teritorijās un neierobežotām vilku medībām. Tomēr vilku ģenētiskā daudzveidība Latvijā bija augstāka salīdzinājumā ar Skandināvijas izolēto populāciju.

Līdz šim vilku apsaimniekošanas režīms sugas aizsardzību neveicināja, jo vilks tika uzskatīts par kaitīgu dzīvnieku, ko atļauts medīt cauru gadu. Pašreizējais medību likumdošanas grozījumu projekts paredz vilku medību aizliegšanu no aprīļa līdz jūlijam, ko var uzskatīt par pirmo soli sugas ilgtspējīgas apsaimniekošanas virzienā. Nomedīšanas limitu un garākas vasaras medību aizlieguma sezonas ieviešana nākotne būtu vērtīgs ieguldījums vilku saglabāšanā. Vairākas augstāk minētās pazīmes, kas tika atklātas šī pētījuma gaitā, liecina par populācijas pārekspluatāciju. Tādējādi, no pētījuma rezultātiem izriet, ka ir jāmaina vilku populācijas apsaimniekošanas prakse, pārejot uz ilgtspējīgas apsaimniekošanas principiem.

No šī pētījuma var izdarīt sekojošus secinājumus:

- Pēdējo dekāžu laikā vilki ir bijuši plaši izplatīti Latvijā, tomēr pēdējo trīs gadu laikā tiek novērota to skaita un izplatības samazināšanās neierobežotu medību dēļ.

- Morfoloģiski, gan pēc ķermeņa izmēriem un svara, gan pēc galvaskausu parametriem, Latvijas vilki ir līdzīgi citu kaimiņu valstu mežu zonas vilkiem. Noskaidrots Latvijas vilku populācijai raksturīgais dzimumu dimorfisma līmenis.

- Kraniometriskie parametri uzrādīja morfoloģisku sadalījumu starp vilkiem no Kurzemes un Latvijas ziemeļaustrumiem. Vilkiem no Latvijas austrumiem bija lielāki galvaskausi.

- Uz pārāk intensīvu populācijas apmedīšanu norāda nomedīto vilku dzimuma un vecuma struktūra, t.i., vecu dzīvnieku zemais īpatsvars, mātīšu skaitliskais pārsvars un to augsta auglība (6 embriji uz vienu mātīti). Relatīvi zemais nepieaugušo dzīvnieku īpatsvars (20%) norāda uz papildus pre- un neonatālās mirstības faktoriem, kas var būt saistīti ar grūsno un zīdošu mātīšu nomedīšanu. Liels dzīvnieku īpatsvars ar antropogēnas izcelsmes traumām (3.8%) arī liecina par stipru medību slodzi.

- Savvaļas pārnadži (briežveidīgie dzīvnieki un mežacūkas) ir vilku pamata barība Latvijā gan ziemas (76.6%), gan vasaras (55.7%) sezonās. Bebrs ir otrais svarīgākais barības objekts vasarā (18.8%). Uzbrukumi mājlopiem ir salīdzinoši reti, un galvenokārt tiek lietoti uzturā izgāztuvēs atrodamie kritušie mājdzīvnieki ziemā (13.1%). Latvijā vilki ievērojami vairāk barojas ar bebriem nekā citviet Eiropā. Iespējams, bebri kalpoja par bufera barību pārnadžu skaita samazināšanās laikā 1990 gadu vidū, palīdzot uzturēt augstu vilku skaitu.

- Tika apstiprināta hibridizācija starp vilkiem un klaiņojošiem suņiem Latvijā. Vairums gadījumu tika konstatēti Latvijas ziemeļos, rajonā ar zemu vilku blīvumu, kas vēlreiz norāda uz nepieciešamību uzturēt vilku populācijas dabisku telpisko un demogrāfisko struktūru, lai novērstu turpmāku hibridizāciju.

- Kaut arī kopumā Latvijas vilku populācija joprojām ir samērā liela (ap 300-500 vilki), ir novērotas neierobežotu vilku medību dažas negatīvas sekas, tādas kā skaita un izplatības samazināšanās, novirzes demogrāfiskajā struktūrā, hibridizācija ar suņiem utt. Lai nodrošinātu vilku aizsardzību Latvijā, ir nepieciešams mainīt pašreizējo medību likumdošanu un praksi, balstot to uz ilgtspējīgas apsaimniekošanas principiem.

Резюме

Волк (*Canis lupus* L., 1758) в Латвии: статус популяции, демография, морфометрия, трофическая экология и генетика в связи с настоящей практикой использования вида

В настоящей работе обобщены данные, собранные в Латвии с 1997 по 2001 гг., охватывающие следующие аспекты биологии волка *Canis lupus* L., 1758: демографию, морфометрию и краниометрию, питание и генетику. Исследование основывалось главным образом на добытых животных и экскрементах, собранных в различных частях Латвии. Работа также включает анализ конфликтов между волком и человеком в Прибалтике, анализ настоящего статуса волка, динамики его численности и распространения на основе официальных данных учета и добычи с 1923 г., предоставленных Государственной Лесной службой.

В настоящее время волк встречается на большей части территории Латвии за исключением юга страны и области к северу от Риги вдоль Рижского залива. Общая популяция волка в Латвии насчитывает около 300-500 особей. Распространение и динамика численности волка в Латвии непосредственно связаны с интенсивностью преследования его человеком. Волки были на грани исчезновения к 1940 г. и очень малочисленны в 1960-х гг. во время интенсивной борьбы с ними. Однако благодаря ядру популяции к востоку от Латвии волк сумел быстро восстановить свою численность. После второго наиболее значительного послевоенного пика в 1990-х гг. численность и ареал волка в Латвии стали уменьшаться в результате интенсивной добычи в середине последней декады.

Основной причиной современного конфликта между волком и человеком является восприятие этого хищника охотниками как конкурента на диких копытных. В прошлом актуальны были также ущерб животноводству и потенциальная угроза жизни людей. В настоящее время нападения на скот случаются эпизодически, локально и сезонно, чаще всего от хищничества страдают овцы (70.8%), телята (21.9%) и собаки (5.2%).

Чтобы изучить демографическую структуру популяции и влияние на нее охотничьего пресса, была проанализирована выборка из 84 добытых особей (36 ♂♂, 48 ♀♀). Соотношение полов показало доминирование самок (♂♂ : ♀♀ = 0.77), что вместе с высокой плодовитостью (в среднем 6 эмбрионов на самку) является показателем сильного промыслового пресса на популяцию, так как повышенная

плодовитость и рождаемость самок известны как механизм компенсации в условиях высокой антропогенной смертности. Преобладание самок в 3-й и 4-й возрастных группах предполагает, что повышенная рождаемость самок началась в 1996-1997 гг., что совпадает с пиком преследования волка. Возрастная структура показала относительно низкую долю неполовозрелых особей – прибылые составляли около 20% добычи. Это предполагает наличие дополнительных факторов пре- и неонатальной смертности, возможно, связанных с элиминацией беременных и кормящих самок во время летней охоты. Низкая доля старых животных является еще одним подтверждением чрезмерной эксплуатации популяции волка человеком, так как интенсивная добыча обычно снижает средний возраст популяции.

Краниометрический анализ 187 черепов (115 ♂♂, 72 ♀♀) включал в себя 19 параметров, в том числе и вес черепа. Параметры черепа самцов превышали таковые у самок. Средняя кондилобазальная длина черепа самцов и самок была соответственно 23.7 и 22.5 см, общая длина – 26.5 и 24.8 см, зигоматическая ширина – 14.3 и 13.2 см. Таким образом, краниальные параметры латвийских волков не отличались значительно от таковых у волков из соседних регионов – Беларуси, Литвы, Польши. У 9.5% исследованных черепов были найдены отклонения от нормальной зубной формулы. Врожденные олиго- и полидонтия встречались у 7.9% черепов, полидонтия являлась наиболее частой аномалией (71.4%). Аномалии зубной формулы чаще встречались у самцов. У нескольких черепов были найдены травмы, вероятно, свидетельствующие о конфронтациях с копытными. В пределах Латвии были найдены различия параметров черепа у волков с северо-востока и запада республики. У волков из восточной части республики размеры черепа были больше (всего 13 параметров). Только два показателя, длина лицевой части и длина *incisura palatina,* были больше у волков с Курляндского полуострова. Предполагается, что различия в краниальных параметрах указывают на некоторую степень изоляции волков полуострова по причине затрудненной миграции с востока. Это подтверждается также данными о распространении волка в Латвии, ареал которого из-за чрезмерной добычи сократился в течение нескольких последних лет, в том числе и на территориях, служащих естественным экологическим коридором между восточной и западной частями республики. Однако, вероятнее всего, разделение краниометрических показателей было вызвано различиями в среднем возрасте популяции на западе и востоке вследствие различной интенсивности добычи. Эта гипотеза требует дополнительных исследований демографии волка.

У 496 добытых волков (244 ♂♂, 252 ♀♀) были взяты морфометрические промеры, 90% измерений производилось охотниками в соответствии со специально разработанной анкетой. Морфометрические показатели также выявили половой диморфизм, самцы были больше самок. Средний вес самцов и самок составлял соответственно 41.2 и 34 кг, высота в холке - 77 и 71 см, общая длина тела – 159.2 и 150.5 см, длина хвоста – 42.6 и 40.8 см. Соотношение полов в этой выборке также показало преобладание самок (♂♂ : ♀♀ = 0.97). У 1.4% обследованных волков были найдены признаки чесотки. Высокая доля животных со старыми ранениями (всего 8.3%, из которых 46.3% были несомненно антропогенного происхождения) является очередным свидетельством сильного промыслового пресса на волка в Латвии. Возрастная структура добытых волков, основывающаяся на определении возраста охотниками, показала более низкую долю прибылых волков по сравнению с выборкой из 84 особей. Хотя метод анкетирования показал свою непригодность для определения возраста добытых волков, он является полезным инструменом для широкомасштабных морфометрических исследований, при условии что измерения достаточно упрощены.

Трофическая экология волка в Латвии изучалась на основе анализа 302 экскрементов и 107 желудков добытых волков из различных частей республики, собранных в зимний и летний сезоны. Основной пищей волка в Латвии являлись дикие копытные (оленевые и кабаны) (55.7% встречаемости в летних и 76.6% в зимних пробах), в то время как бобр был второй наиболее значимой добычей летом (18.8%). Благодаря высокой численности бобра в Латвии, он являлся важной альтернативной добычей волка, по значению намного превышающей таковое где-либо в Европе. Предполагается, что бобр приобрел столь важную роль в питании волка лишь в течение последнего десятилетия вследствие падения численности копытных в начале 1990-х гг., вызванного суммарным эффектом охотничьего пресса, браконьерства и хищничества. Самцы волка питались бобрами чаще, чем самки. Также наблюдались некоторые сезонные изменения в питании волка, доля копытных возрастала в зимний период. Оленевые встречались в 49.4% летних и 51.2% зимних проб, кабан - соответственно в 20% и 33.9%. Кабану, особенно в зимнее время, отдавалось предпочтение. Кабан был более частой добычей волка на востоке Латвии, а оленевые и домашний скот (в основном в виде падали) – на западе. Летнее питание волка отличалось большим разнообразием и включало в себя более мелкую добычу, такую как грызуны, средние хищники, пресмыкающиеся, ягоды и т.д. Домашние животные в питании волка встречались нечасто, за исключением зимнего периода, когда они потреблялись в виде падали (13.1%). Зимний рацион волка сравнивался с таковым у рыси (49 желудков). Было показано, что трофическая конкуренция между двумя видами крупных хищников умеренная. Для рыси, которая почти стопроцентно питалась косулей, была характерна более узкая пищевая ниша, в то время как волку в связи с разницей в размерах и охотничьей стратегии была доступна и другая добыча. 36.7% волчьих и 34.7% рысьих желудков были пустые. Средний вес содержимого желудка волка составлял 990.3 г, в пределах от 20 до 4350 г.

Были собраны генетические образцы (кровь или мышцы) латвийских волков (n = 39). Гибридизация между волками и бродячими собаками в Латвии была проверена на пробах тканей 31 добытого волка. Шесть образцов были взяты у предположительно гибридных щенков из одного помета с севера Латвии, отличающихся необычными морфологическими чертами. Восемь проб от самцов волка из Латвии были использованы в методическом сравнительном исследовании по использованию маркеров митохондриальной, аутосомальной ДНК и ДНК Y-хромосомы для наиболее точной идентификации волко-собачьих гибридов. Гибридное происхождение шести щенков, их потенциальной матери и самца из того же района северной Латвии было подтверждено путем использования маркеров контрольного региона ДНК и аутосомальных микросателлитов. Таким образом, восемь из девяти доказанных случаев гибридизации происходят из одного района с низкой плотностью волков, тем самым подтверждая существующую теорию, что волки скрещиваются с бродячими собаками, если нарушена местная пространственная и демографическая структура популяции. Предположительно, гибридизация волка с собакой в Латвии является более частым феноменом, чем в Западной Европе, что может быть объяснено многочисленностью бродячих собак в сельской местности и неограниченным отстрелом волков. Однако генетическое разнообразие латвийских волков было выше, чем у изолированной скандинавской популяции.

До сих пор статус волка в Латвии с точки зрения его охраны был неблагоприятным, так как волк считался вредителем, охота на которого разрешена круглый год. Недавний проект изменений охотничьего законодательства предусматривает запрет охоты на волка с апреля до середины июля, что можно считать первым шагом на пути к рациональному использованию вида. Введение охотничьих квот и более продолжительного закрытого летнего сезона в будущем еще более бы способствовали охране волка. Многочисленные вышеупомянутые характеристики популяции, полученные в результате данного исследования, свидетельствуют о чрезмерной эксплуатации вида в Латвии. Таким образом, результаты исследования показывают, что практика управления популяции волка человеком должна быть изменена в сторону более рационального ее использования.

На основе настоящей работы можно сделать следующие выводы:

- В течение нескольких последних десятилетий волки в Латвии были широко распространены и многочисленны, однако за последние три года в результате неограниченного преследования человеком численность и ареал волка в республике сократились.

- Морфологически, как по размеру тела и весу, так и по краниометрическим показателям, латвийские волки сходны с волками лесной расы из сопредельных территорий. Была определена степень полового диморфизма, характерная для волков Латвии.

- Анализ краниометрических показателей выявил некоторое морфологическое разделение между волками из западной и восточной частей Латвии, для волков с северо-востока республики были характерны более крупные черепа.

- Половозрастная структура добытых зверей, а именно: низкая доля старых особей, преобладание самок и их высокая плодовитость (в среднем по шесть эмбрионов), указывает на сильный промысловый пресс в популяции. Сравнительно низкая доля прибылых (20%) указывает на наличие дополнительных факторов пре- и неонатальной смертности, возможно, связанных с добычей беременных и кормящих самок во время летней охоты. Высокая доля животных со старыми ранениями антропогенного характера (3.8%) служит дополнительным свидетельством сильного охотничьего пресса.

* Дикие копытные (оленевые и кабаны) составляют основу питания волка как в зимний (76.6%), так и в летний (55.7%) сезоны. Бобр является вторым важнейшим объектом летнего питания хищника (18.8%). Нападения на домашний скот сравнительно редки. В основном скот входит в рацион волка в виде падали в зимний период (13.1%). Волки в Латвии питаются бобрами в значительно большей мере, чем где-либо в Европе. Вероятно, бобр служил буфером во время падения численности копытных в середине 1990-х гг., поддерживая таким образом высокую плотность популяции волка.

* Было подтверждено наличие волко-собачьих гибридов в Латвии. Большинство случаев гибридизации было обнаружено на севере республики в местности с низкой плотностью волка, что лишний раз свидетельствует о важности поддержания нормальной пространственной и демографической структуры популяции хищника для предотвращения случаев гибридизации в дальнейшем.

* Хотя в целом латвийская популяция волка по-прежнему многочисленна (около 300-500 особей), наблюдаются некоторые негативные последствия неограниченной охоты на волка, такие как спад численности, отклонения в демографической структуре, появление волко-собачьих гибридов и т.п. Охране волка в Латвии может способствовать изменение охотничьего законодательства и настоящей практики управления популяцией в сторону более рационального ее использования.

Acknowledgements

This research was carried out within the framework of several projects of the former State Forest Inventory Institute, DARUDEC, Forest Research Institute "Silava", Latvian and Estonian Funds for Nature. I am very grateful for the opportunity to participate in them and thank all those people I worked with.

I would like to thank my supervisor, Dr.hab.biol. Henryk Okarma (Institute of Nature Conservation of the Polish Academy of Sciences, Kraków) for the encouragement and his valuable suggestions on my thesis.

The greatest appreciation I owe to my colleague, Dr. Jānis Ozoliņš, with whom I started to work on wolves within the project in the State Forest Inventory Institute and with whom we've been working together shoulder to shoulder all these years. The work would be impossible without his enthusiastic help of providing wolf carcasses through the system of the State Forest Service, participation in the material analysing and discussing the ideas. He has really been a key person to the success of this work. I also thank the former colleagues from the State Forest Inventory Institute for their help both at the very early stage of the project and afterwards – Agris Starzds, Edgars Doniks, Juris Tauriņš, Juris and Jānis Rankevici, Mikus Rantiņš. I am very grateful to Jānis Baumanis, the chief of the Game Department of the State Forest Service, many anonymous employees of the State Forest Service, hunters, nature photographer Andris Eglītis and all those people who helped me with data collection and practical arrangements during all these years for their practical help and enthusiastic co-operation.

I thank Alda Pupila and Guna Bagrade for their practical help in material analysing, and Dr. Uģis Bergmanis from the Teiči Nature Reserve for his help with material collection in that region as well as Aivars Dundurs and Valdis Rēders for providing some material for the study and their practical help. I thank my colleagues from the Ķemeri National Park for understanding and helping out with practical things when necessary – Aivars Ornicāns, Andis Liepa, Janis Ķuze, Aivars Tomaševics and all the others. I am most grateful to the staff of the Riga Zoo (P.Petrovs, B.Drapča, R. Sieriņa) and to Velga Vītola from the Gauja National Park for their practical help with wolf-dog hybrids. I am very grateful to Drs. Bogumila and Wlodzimierz Jedrzejewski for introduction to the diet analysis' techniques.

Lots of "grazia" undoubtedly deserve my Italian colleagues – Dr. Ettore Randi and Dr. Vittorio Lucchini from Istituto Nazionale per la Fauna Selvatica - for their invaluable help in analysing the genetic samples from Latvia and fruitful co-operation. I also thank the Swedish colleagues from Uppsala University, especially Dr. Carles Vilà for analysing samples from Latvia. I thank the colleagues from the Department of Animal Ecology of the Faculty of Biology (University of Latvia) who helped during my PhD studies.

The Research Council of Norway should be acknowledged. Their financial support made possible my stay at the Norwegian Institute for Nature Research (Trondheim) to work on the finalisation of this thesis. I am very thankful to NINA's staff for helping with practical arrangements, especially to Dr. John Linnell for helping to found a way in the statistical jungle and for his critical comments on my manuscripts, and Dr. Arild Landa and Elizabeth Davies for their hospitality during my stay in Trondheim.

I am very grateful to the Scottish nature photographer and writer Niall Benvie for improving the English of the thesis' summary.

Last but not least I would like to thank my parents for their understanding and support to my wolf-oriented lifestyle – my mother Zofija Andersone and father Eduards Andersons, who taught me to appreciate the wonders of nature since my very early childhood.

List of papers included into thesis

I. Andersone, Ž., Ozoliņš, J. 2000. Big game and large carnivores in Latvia: present status and future prospects. *Journal of Wildlife Management*. [In press]

II. Ozoliņš, J., Andersone, Ž., Pupila, A. 2001. Status and management prospects of the wolf *Canis lupus* L. in Latvia. *Baltic Forestry* 7, No. 2(13): 63-69.

III. Andersone, Ž., Balčiauskas, L., Valdmann, H. 2002. Human-Wolf Conflicts in the East Baltic - past, present and future. *Proceedings of the 2nd International Wildlife Management Congress*. [In press]

IV. Andersone, Ž., Ozoliņš, J. Morphometrical characteristics of wolves from Latvia: experience of hunters' involvement in data collection. *Submitted manuscript.*

V. Andersone, Ž., Ozoliņš, J. 2000. Craniometrical characteristics and dental anomalies in wolves *Canis lupus* from Latvia. *Acta Theriologica* 45 (4): 549-558.

VI. Valdmann, H., Andersone, Ž., Koppa, O., Ozoliņš, J., Bagrade, G. Winter diets of wolf and lynx in Estonia and Latvia – implications for predator-prey management. *Submitted manuscript.*

VII. Andersone, Ž., Ozoliņš, J. Seasonal, geographical and sexual variations of the diet of wolves (*Canis lupus*) in Latvia. *Submitted manuscript.*

VIII. Vilà, C., Walker, C., Sundqvist, A.-K., Flagstad, Ø., Andersone, Ž., Casulli, A., Kojola, I., Valdmann, H., Halverson, J., Ellegren, H. Combined use of maternal, paternal and bi-parental genetic markers for the identification of wolf-dog hybrids. *Submitted manuscript.*

IX. Andersone, Ž., Lucchini, V., Randi, E., Ozoliņš, J. 2002. Hybridisation between wolves and dogs in Latvia as documented using mitochondrial and microsatellite DNA markers. *Zeitschrieft für Säugetierkunde* 67: 79-90.

1. Status of the wolf population in Latvia

1.1. Introduction

Despite the originally vast distribution range, wolves became endangered in many countries (Wabakken et al. 1983, 1984, Boitani 1992, Promberger and Schröder 1992, Butzeck 1993, Findo 1995, Li et al. 1996, Nader 1996, Nitsche 1996, Cerveny et al. 2000, Delibes 2000). In most cases, large carnivores have been heavily persecuted in Europe. Conservation measures and a more favourable legal status facilitating natural re-colonisation within the former range borders have only recently been instigated (Okarma 1989, Wolsan et al. 1992, Okarma 1993, Adamic 1996, Adamic et al. 1998, Bienek et al. 1998, Breitenmoser 1998). As the status of the wolf largely depends on the intensity of persecution by humans, carnivore conservation often requires favourable management policy more than habitat conservation (Linnell et al. 2000, 2001).

Perception of wolves as competitors for wild game and livestock (Nowak and Myslajek 1999a) is the main cause for the intensive persecution of wolves. Hunting, both legal hunting and poaching, was, and still is, the main mortality factor affecting wolf populations throughout most of their distribution (Mech 1995, Jędrzejewska et al. 1996a, Smietana and Wajda 1997, Boitani 2000), natural factors playing a relatively minor role. Although intra-guild predation and aggressive interactions are common among carnivores (Boles 1977, Paquet and Carbyn 1986, Route and Peterson 1991, Kehoe 1995, Peterson 1995), wolves are rarely killed by their few natural enemies (Matjushkin 1985, Hayes and Baer 1992, Bergmanis 2000). To understand population regulation of wolves as well as the impact of harvest on the population structure, the demography of the population should be studied (Mech and Hertel 1983, Hayes and Harestad 2000a). Long-term monitoring of the demographic structure of populations can help to predict dynamics and can be applied in the species' management (Danilov et al. 1985).

The aim of the study was to summarise the existing information on wolf population dynamics and distribution (official data from the State Forest Service) as well as to investigate the current age and sex structure of the population of wolves in Latvia based on investigation of the harvested animals.

Paper I

1.2.1. Big game and large carnivores in Latvia: present status and future prospects

BIG GAME AND LARGE CARNIVORES IN LATVIA: PRESENT STATUS AND FUTURE PROSPECTS

ŽANETE ANDERSONE
Kemeri National Park, "Meza maja", Kemeri - Jurmala, LV-2012, Latvia

JĀNIS OZOLIŅŠ
State Forest Service, 13.Janvara iela 15, Riga, LV-1932, Latvia

Abstract: The game fauna of Latvia is typical for the east Baltic region: it includes 17 mammal and 31 bird species. There is a shooting season for most species and for some species there are quotas. The community of wild ungulates includes four species - elk (*Alces alces*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and wild boar (*Sus scrofa*). Roe deer is the most numerous cervid in Latvia. Large carnivores are wolf (*Canis lupus*), lynx (*Lynx lynx*), brown bear (*Ursus arctos*). The latter is a protected species, found mainly in northeastern Latvia. A drastic decline in ungulate numbers during the last decade combined with a simultaneous increase in wolf and lynx populations resulted in heavy hunting pressure on the predators, especially the wolves. The first country-wide project on wolf ecology was started in 1997. A semi-aquatic mammal of special interest from the management point of view is the beaver (*Castor fiber*) which is another problem species. It has become abundant and causes damages to silviculture and agriculture. It is the only game species that has been properly studied since the 1950s. There is an urgent need for serious studies on game fauna in Latvia and for broad international co-operation, especially in the field of large carnivores.

Key words: game fauna, large carnivores, Latvia, semi-aquatic mammals, wild ungulates.

J. Wildl. Res. 5 (1): 000 – 000, 2000.

INTRODUCTION

Latvia belongs to the Baltic region, which lies in the transition zone between boreal and mixed forests, the total area being 64,600 km^2 (Fig.1). It is characterized by high proportion of forests, consisting of pine, spruce, birch, aspen and alder, and of bogs - 41.4% and 10% accordingly. Latvia is situated on lowland: the highest point scarcely exceeds 300 m above sea level. The climate is temperate, precipitation 550 - 850 mm/year, snow cover 75 - 115 days/year.

The fauna of Latvia is similar to that of the other Baltic states. Its formation started at the end of the last glaciation about 10,000 - 15,000 years ago. The mammal fauna of Latvia numbers 63 species and includes both taiga elements and those of broadleaf forest fauna (Timm et al. 1998). Seventeen mammal and 31 bird species are hunted.

LEGAL STATUS

Hunting in Latvia is regulated by the Hunting Law, the Hunting Regulations and documents of the State Forest Service. In nature reserves and national parks those regulations are supplemented by the rules of the protected territory approved by the Ministry of Environment Protection and Regional Development (MEPRD). Thus, there are three levels of regulation: the Hunting Law ratified in the Parliament (Saeima), the Hunting Regulations confirmed at prime ministerial level, and supplementary documents within the frame of mentioned rules issued by the State Forest Service, which is administered by the Ministry of Agriculture. Consequently, the permanent responsibility over hunting and protection of hunting resources belongs to the State Forest Service and partly to the MEPRD as well (Anonymous 1998).

The Hunting Regulations specify hunting species and divide them into two categories: limited and unlimited hunting resources. The first group of species includes elk *Alces alces*, red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, wild boar *Sus scrofa*, beaver *Castor fiber*, males capercaillie *Tetrao urogallus* and black grouse *Tetrao tetrix*. Shooting limits of those species are set every year by the State Forest Service depending on the population size. Hunters need a special permit for shooting each individual of the mentioned species.

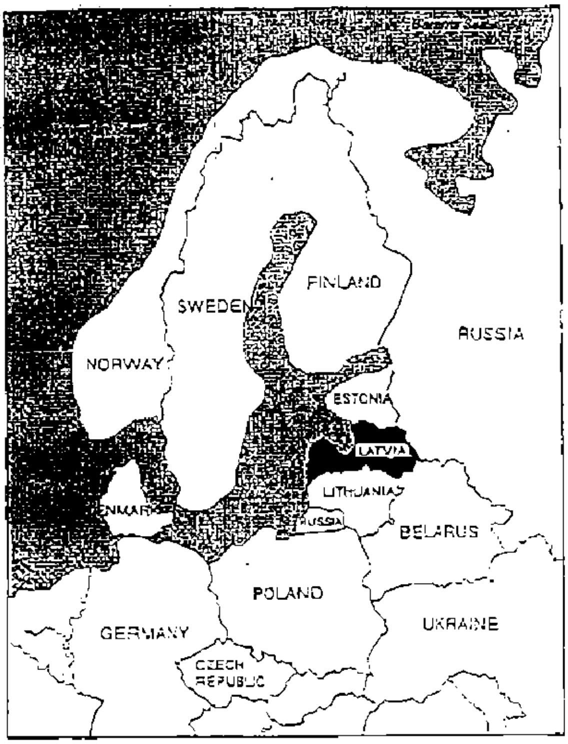


Fig.1. Geographical position of Latvia.

For the second group hunting limits are not specified. This group includes following bird and mammal species: bean goose *Anser fabalis*, white-fronted goose *A. albifrons*, 20 species of wild ducks (excluding shelduck *Tadorna tadorna* and species from the genus *Mergus*), hazel grouse *Bonasa bonasia*, moorhen *Gallinula chloropus*, common coot *Fulica atra*, woodcock *Scolopax rusticola*, common snipe *Gallinago gallinago*, feral pigeon *Columba livea*, wood pigeon *C. palumbus*, hybrids of capercaillie and black grouse, brown hare *Lepus europaeus*, mountain hare *L. timidus*, red squirrel *Sciurus vulgaris*, muskrat *Ondatra zibethica*, polecat *Mustela putorius*, American mink *M. vison*, pine marten *Martes martes*, badger *Meles meles*, lynx *Lynx lynx*, wolf *Canis lupus*, fox *Vulpes vulpes*, raccoon dog *Nyctereutes procyonoides*. For those species, hunters need a seasonal permit that specifies place, time and other conditions of hunting.

In some cases it is allowed to hunt animals over the shooting season or quota, e. g., if there has been considerable damage to the forest or agriculture the State Forest Service gives an additional permit. Also, in epizootic regions hunting terms can be changed or hunting can be completely prohibited. From the management point of view, wild ungulates and large predators, as well as such habitat-building species as beaver, are of special interest. However, very few studies have been carried out on game mammals - mostly on beaver (Balodis 1990, 1994) and cervids (Skriba 1975), and also on small and medium-sized carnivores (Ozolins, Pilats 1995). Almost nothing has been done on large predators. Some regional studies in restricted areas were carried out on wolves (Gaross 1994, Andersone 1998), no reliable data available on lynx and brown bear.

UNGULATE COMMUNITY

In Latvia, there are four native species of wild ungulates: elk, red deer, roe deer, and wild boar. After the last glaciation during the Atlantic and subboreal climatic period, the species composition included also European bison *Bison bonasus*, aurochs *Bos primigenius*, and wild horse *Equus gmelini sylvaticus*. In Latvia, the latter two species are thought to have gone extinct about 1000 years ago (Kalnins 1943), while European bison likely survived until the 18th century when it was eradicated by over-hunting (Taurins 1982). However, according to another source, the aurochs and the European bison were badly confused in the historical annals of German feudals about hunting bags (Lange 1970). Recently, WWF-Latvia started a project of re-introduction of European bison, Beck cattle and wild horse *konik* in southwestern Latvia. The aim of the project is to improve management of the area and thus to prevent over-growing of the Lake Pape by reeds (U. Rotbergs, pers. comm.).

The recent ungulate species have also experienced numerical changes in time both due to natural and anthropogenic factors.

Elk is the only ungulate species that has been constantly present in the territory of Latvia since it first appeared here at the end of the Ice Age. It was very abundant in northern Latvia in the 17th century and there were still 2,000 individuals at the end of the last century (Kalnins 1943). During World War I population size decreased drastically to some 100 animals. The species became abundant again in the 1970s - 1980s (Fig. 2).

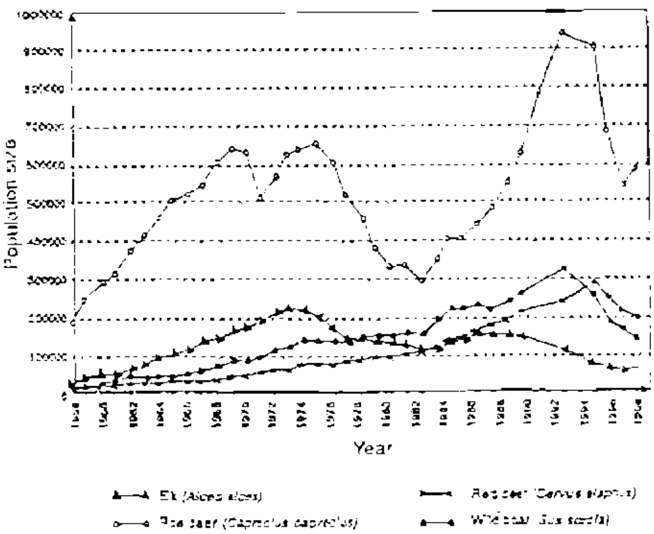


Fig.2. Population dynamics of for ungulate species in Latvia during the last 30 years (according to the official census data).

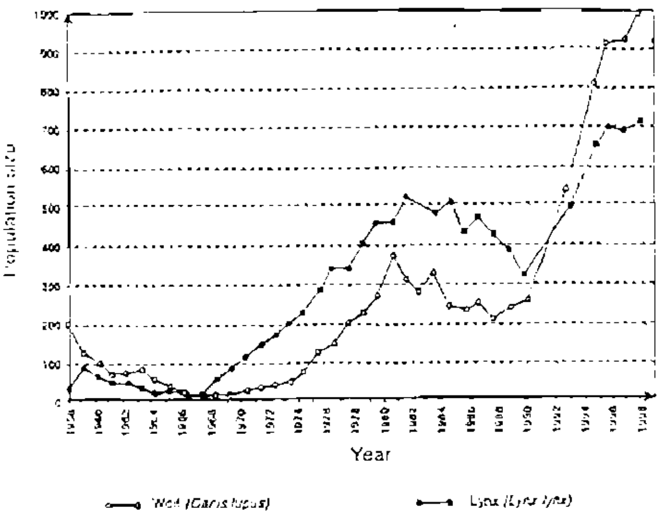


Fig.3. Population dynamics of wolf (*Canis lupus*) and lynx (*Lynx lynx*) in Latvia during the last 30 years (according to the official census data).

Red deer reached maximum in Latvia five to six thousand years ago (the boreal - Atlantic period). The local population of red deer went extinct by the 10th century (Skriba 1975). Artificial re-introduction started already in the 17th century. Initially animals were kept in enclosures. At the very beginning of this century some individuals escaped and started to reproduce in the wild (Kalnins 1943, Skriba 1975). Later several animals were released on purpose. They established several local micropopulations of red deer in western and southern Latvia which were not connected with each other. Gradually, red deer spread over the territory, and by World War II there were about 1,500 red deer in Latvia (Skriba 1975). Now the species occurs practically everywhere in the country, however the population density is likely to have decreased recently (Fig. 2).

Roe deer in Latvia went extinct by the 17th - 18th century. The extinction was explained as a natural process caused by climate cooling simultaneously with an increase of wolf density. Natural re-population started in the 19th century, especially in its second part, when the climate became warmer and also the number of wolves was considerably reduced (Taurins 1982). Lange (1970) was of the opinion that population recovery was considerably supported also by intentional release and occasional escape of introduced individuals. In this century, the population size of roe deer has fluctuated according to climate and especially the number of predators (Fig. 2).

Wild boar was found in Latvia in the boreal time (Taurins 1982) until the 19th century when, due to natural reasons, species range retreated to the south (Greve 1909). Wild boar started to disperse towards the north in the end of the 19th and in the beginning of this century. Since the 1940s, it has occurred all over the country (Taurins 1982).

At present, elk, red deer, roe deer, and wild boar occur in the whole territory of Latvia, in all forestry administrative districts. However, during the last decade, there has been a general decline in population size (Fig. 2). Possible causes of such a depression include poaching, especially in the beginning of the 1990s (unstable period of political changes and difficult socio-economic conditions), and high density of predators, especially wolves.

Shooting limits are largely biased by the imprecise annual official census of ungulates that usually over-estimates population sizes. Census data for large mammals can be over-estimated due to the fact that every forestry unit (on average 250 km^2) is counting animals separately, usually without any co-ordination with neighbouring units. Afterwards numbers from all forestry districts are simply summed up. During the last 30 years shooting quotas varied from 12 to 60% for elk, from 5 to 27% for red deer, from 1 to 24% for roe deer, and from 31 to 72% for wild boar. Thus, over-harvesting of cervids may have also caused their depression. Retaining unreasonably high shooting quotas during the last decade can hardly lead to improvement of the situation.

Each species has its own shooting period. Elks may be hunted from 15 August till 30 November. Red deer stags are hunted from 1 September till 31 December, while for red deer hinds and calves the season is open y from 15 July. Also, selective hunting of less valuable young red deer stags (up to two years old) is allowed from 15 July. Roe deer males are hunted from 15 June till 30 September, and roe deer females and the young - from 1 September till 30 November. The longest shooting season is for wild boar - from 15 July till 31 January.

LARGE PREDATORS

There are three species of large predators in Latvia - wolf, lynx, and brown bear. Wolf has always been a part of the post-glacial mammal fauna of Latvia. Fluctuations of population dynamics reflect the intensity of persecution by humans. Population maximum was registered in the 18th and in the first part of the 19th century (Kalnins 1943). Then the number decreased because fire-arms started to be used widely to hunt wolves (Taurins 1982). In this century, population size has also varied significantly. It rose after World War I and World War II, as well as during the last decade (Fig. 3). In 1997, according to the official inventory, there were 997 wolves in Latvia. In the hunting season of 1997/1998, 369 wolves were harvested. Taking into account that the same wolf pack inhabits the territory of several forestry units, the real number of predators (the same equally refers to the lynx) should be somewhat lower than the official data indicate because of the mentioned census problems. Over-estimation of populations of large predators by official inventories is a widespread problem (Okarma, 1994).

Wolves occur practically everywhere in Latvia, excluding the region to the north from Riga along the coast of the Riga Bay. It is of interest that in the very same area another predator - lynx - is present. According to hunting bag data, the highest density of wolves is in western and eastern Latvia. However, it may also reflect hunting activity rather than the real density of animals.

Lynx is the second most numerous large predator in Latvia (Fig. 3). It appeared in the territory of the country together with boreal forests. Since then it has always been a part of the Latvian fauna. During population depressions, species range in the country was limited to northern Latvia (Taurins 1982). Now lynx is found in most parts of the country. However, its distribution is mainly related to the large forests.

Brown bear was a common species in Latvia until the beginning of the 19th century when, due to intensive forest cutting and strong hunting pressure, the population size decreased rapidly. In the second part of the 19th century the last individuals of the local population were shot in western Latvia (Taurins 1982). However, W. L. Lange (1970) has recorded remains of a brown bear population in northeastern Latvia by 1900. Since 1970 brown bears have been found in Latvia again, e.g., in 1978, they were observed 17 times, in 1979 - 34 times (Taurins 1982). According to the official census data, in 1997 there were six brown bears in Latvia. Most of the reports on encounters with bears or their footprints come from northern or northeastern Latvia. The status of those animals is uncertain. It is not known whether they are residents or come into Latvia from Estonia and Russia. In Estonia, where natural conditions are quite similar to those in Latvia, there are 250 - 300 brown bears (H. Valdmann, pers. comm.), while in Latvia we have only few individuals of uncertain status. The reason for such a drastic difference is probably a high disturbance level because in Latvia a half of the human population lives in the countryside (Timm et al. 1998). However, a special study should be proposed to clarify the real causes of such a difference.

One can hardly talk about management of large predators in Latvia because official policy is to keep their number as low as possible to prevent decline in wild ungulates. It does not refer to the brown bear, which is a protected and rare species in Latvia (Ingeldg et al. 1993). The public attitude towards predators is rather negative, especially in regard to the wolf. This, together with insufficient information on biology of the local populations of carnivores, makes it difficult to pursue a sound policy towards the species.

Wolf and lynx belong to so-called unlimited hunting resources. However, shooting season for lynx is from 1 October till 15 March, while wolf is regarded as a pest species (like fox, raccoon dog, raven *Corvus corax*, hooded crow *Corvus corone*, magpie *Pica pica* and stray dogs and cats) which may be hunted all year round without any limitation. Moreover, in 1997-1999, a reward of Ls 75 (ca. USD 125) was paid for each killed wolf. In some places with high wolf density, e.g., in eastern Latvia, where increased migration from the east is probable, wolves can cause problems, attacking domestic livestock and dogs. However, the negative attitude is mostly due to the fact that the wolf is regarded by hunters as their competitor for wild ungulates. Since ungulate population declined significantly during the last years, hunters blame wolves and lynxes and try to reduce number of predators as much as possible.

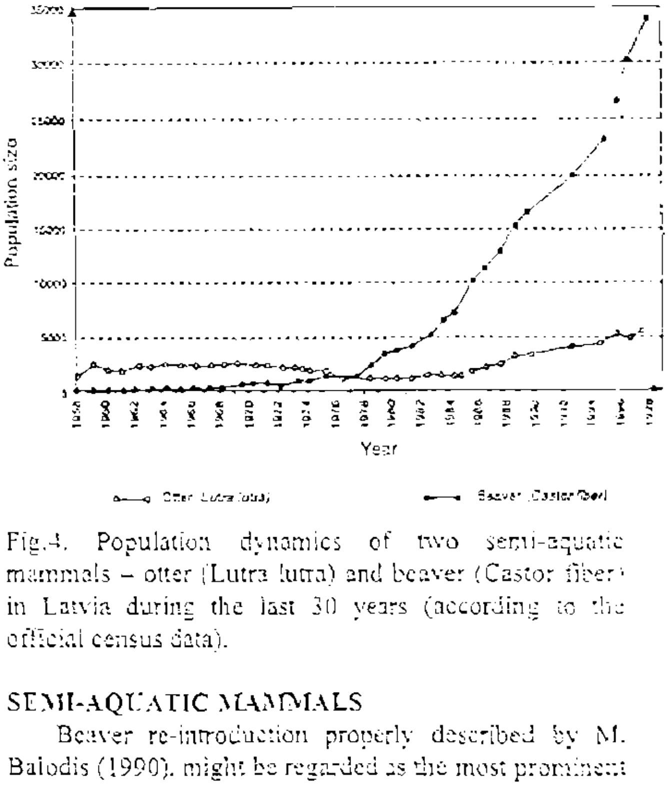


Fig.4. Population dynamics of two semi-aquatic mammals – otter (Lutra lutra) and beaver (Castor fiber) in Latvia during the last 30 years (according to the official census data).

SEMI-AQUATIC MAMMALS

Beaver re-introduction properly described by M. Balodis (1990), might be regarded as the most prominent wildlife management action in Latvian history. Beavers densely inhabited the territory of Latvia since the boreal climatic period (ca. 8,000 years ago). Drastic decline of the population caused mainly by over-hunting started in the 17th century. In 1871 or 1873, the last beaver was killed and for 50 years no beavers were recorded. In 1927, four European beavers were brought from Norway and released in the Kurland Peninsula. Two other Norwegian beavers were released in the northeastern part of Latvia in 1935. After World War II, ten beavers were brought from Voronezh Reserve (Russia) and about 150 beavers were displaced from the already successful re-acclimatization sites to other waterbodies. Now beavers are common throughout Latvia and their population size, according to the expert's estimation (Balodis 1994), is at least twice as big as the official number (Fig.4). Although initial studies of the positive role of beavers in habitat improvement had been carried out (Balodis 1990, 1994), the species was more often regarded as a pest in regard to forestry and agriculture. In the 1980s, the population was controlled significantly by trapping beavers for pelts (up to 6.000 beavers per year). Nowadays, hunting of beavers has been reduced due to the collapse of fur market, and the main factor, diminishing population growth, is probably predation by wolves (unpubl. data).

The activity of beavers has likely favoured an increase in the otter *Lutra lutra* population, which is a currently protected species in Latvia (Fig. 4).

FUTURE PROSPECTS

In Europe, the most important species management and conservation problem at the moment is the status of large predators and settlement of interests of both humans and wild animals (Anonymous 1994). The aim of studies on carnivores is out of simple scientific interest, but they should also provide arguments to change the general attitude towards predators. In Latvia, the wolf is the main problem species nowadays, which urgently needs a sound management policy. At least rewards should be abandoned and a closed shooting season established. However, implementation of such a goal will definitely encounter a strong opposition. Therefore, each conservation action has to be especially well-supported by scientific studies.

In 1997, the first wolf project in Latvia started. The aim of the project was to understand the real situation of the species and the damage it causes. Within the project we have already collected data on morphology, diet of the local wolf population, and to some extent on demographic and spatial structure (this information is based on harvested animals). This project was finished in 1999. Such information is essential for creating a management plan for the species on the country scale.

In future, we are planning to extend the study to all large predators, including lynx and brown bear. The northern part of Latvia, along the border with Estonia, is of special interest. The border of the wolf micropopulation crosses the area - in the coastal region only lynx occurs, while further inland both species are found. Also, along the border with Estonia, appearance of brown bear is possible. Thus, it could be a good area to study co-existance of all three species of large predators.

Studies on large carnivores require international co-operation (Anonymous 1994). The comparative aspect of such projects would be of special interest since natural conditions even within Europe differ significantly and so do management practices.

LITERATURE CITED

ANDERSONE, Z. 1998. Summer Nutrition of Wolf (*Canis lupus*) in the Slitere Nature Reserve, Latvia. Proceedings of the Latvian Academy of Sciences. Section B, 52 (1 - 2): 137-139.

ANONYMOUS. 1994. Seminar on the management of small populations of threatened mammals. Environmental encounters, No. 17. 128 pp.

ANONYMOUS. 1998. National Report on Biological Diversity. Latvia. Ministry of Environmental Protection and Regional Development. Riga. 48 pp.

BALODIS, M. 1990. [The Beaver. Biology and Management in Latvia]. Zinatne, Riga. 271 pp. (In Russian with English summary).

BALODIS, M. 1994. Beaver Population of Latvia: History, Development and Management. *Proceedings of the Latvian Academy of Sciences* Section B, No. 7/8: 122 - 127.

GAROSS, V. 1994. [The effect of wolves and lynxes on cervids in Kurzeme]. *Meza Dzive*. No. 5 (208): 10 - 15. (In Latvian).

GREVE, K 1909. Säugetiere Kur-, Liv-, Estlands. W. Mellin u. Co. Riga. 183 S.

INGELÖG, T., R. ANDERSSON, AND M. TJERNBERG (eds.). 1993. Red Data Book of the Baltic Region. Part1. Lists of threatened vascular plants and vertebrates. Swedish Threatened Species Unit, Uppsala. 95 pp.

KALNINS, A. 1943. [Huntsmanship]. Latvju gramata, Riga. 704 lpp. (In Latvian).

LANGE, W. L. 1970. Wild und Jagd in Lettland. Harro von Hirscheydt Vrlg., Hannover-Döhren. 280 S.

OKARMA, H. 1994. Protection and management of large carnivores (wolf, lynx) in Bialowieza Primeval Forest, Poland. Seminar on the management of small populations of threatened mammals. Environmental encounters. No. 17: 56 - 59.

OZOLINS, J., AND V. PILATS 1995. Distribution and status of small and medium-sized carnivores in Latvia. Ann. Zool. Fennici. 32: 21 - 29.

SKRIBA, G. 1975. [History and results of reacclimatization of red deer in Latvian SSR]. Ochrana i vosproizvodstvo prirodnych resursov (Proceedings of the Latvian Academy of Agriculture), 83: 29-40. (In Russian).

TAURINS, E. 1982. [Mammals of Latvia]. Zvaigzne, Riga. 256 lpp. (In Latvian).

TIMM, U., V. PILATS, AND L. BALCIAUSKAS. 1998. Mammals of the East Baltic. Proceedings of the Latvian Academy of Sciences. Section B, 52. No.1/2 (594/595): 1-9.

Paper II

1.2.2. Status and management prospects of the wolf *Canis lupus* L. in Latvia

Status and Management Prospects of the Wolf *Canis lupus* L. in Latvia

JĀNIS OZOLIŅŠ
State Forest Service
13. Janvāra iela 15, 1932 Rīga, Latvia
ŽANETE ANDERSONE
Ķemeri National Park
"Meža māja", 2012 Ķemeri-Jūrmala, Latvia
ALDA PUPILA
Teiči State Nature Reserve
Aiviekstes iela 3, 4862 Ļaudona, Madonas raj., Latvia

Ozoliņš J., Andersone Ž., Pupila A. 2001. Status and Management Prospects of the Wolf *Canis lupus* L. in Latvia. *Baltic Forestry*, 7 (2): 63–69.

Historically, wolves in Latvia were considered as a pest to be exterminated by all means possible. To assess the impact of unlimited persecution, wolf demography was studied between 1998 and 2000 by collection of samples from harvested animals. Laboratory examination of ovaries and uterus was used to determine if a female was in reproductive condition. Placental scars, swelled post-birth sites in uterine horns or fetuses were counted. The skulls were collected and the age of harvested wolves was determined by counting the number of incremental lines in the tooth cement. The main demographic indices are the following: sex ratio – 1:1.3 (n=84); the average number of embryos per female wolf - 6.0 (n=10, SD = 1.89). The ratio of young wolves in hunting bag is smaller than expected taking into account the fertility of females. Unlimited hunting is believed to have a reflection in the age and sex structure of the wolf population. Certain suggestions concerning sustainable wolf management with presumably lesser impact on population structure are given. They provide for closed hunting during the breeding season and for a legally prescribed opportunity to close the hunting comprehensively after appointed hunting bag is reached.

Key words: wolf, hunting, population structure, species conservation

Introduction

The wolf is a typical representative of the carnivorous mammals of the eastern Baltic. It has inhabited the land area of present-day Latvia since the post-glacial era, dating back to the 9th millennium BC (Tauriņš 1982; Timm et al. 1998). Humans have from time immemorial held wolf as his competitor in hunting wild ungulates. More recent animal husbandry has only intensified this conflict. The attacks on domestic animals were the principal reason why humans exterminated wolves, though their pelt and meat could be of use (Von Ende 1982, Сибанеев 1998). Occasional assaults on people, especially children, only aggravated the situation (Корытин 1990; Павлов 1990; Jhala, Sharma 1997).

In the modern times, the dynamics of the wolf population over the most part of its natural distribution range essentially depends on hunting policy. According to the hunting statistics, in the 1930s and 1960s, the wolf population of Latvia was on the verge of extinction. It gradually stabilised again by the end of the 1970s. During the 1980s, the wolf population was stable and distributed evenly throughout Latvia, contrary to the situation in most of the countries of west Europe, where wolf was found only in Spain and Italy (Boitani 2000). In the early 1990s, greatly due to the changing political situation in Latvia, there was for some years no control over the wolf population. Viable populations of ungulates of the late 1980s and early 1990s created excellent feed resources for carnivores. This situation resulted in another rapid growth of the wolf population, reaching nearly 1,000 individuals in official statistics. In Europe, the 1990s also were noted for an increase in the wolf population and widening of its distribution range. As a result of natural migration, wolf appeared in such countries as Switzerland, France, Austria, etc., where it had been absent for more than a century (Boitani 2000).

Currently, wolves are recognized as an intrinsic part and parcel of natural ecosystems, and a number of countries favour its re-introduction. In Latvia, however, it is vice versa, wolves are considered a nuisance to be exterminated by all means possible, resulting in another anti-wolf campaign launched in the mid-1990s.

A pronounced population decrease was reflected in the game statistics of late 1990s. However, the wolf population is not considerably threatened yet. Suggestions about initiation of sustainable management and conservation strategy were caused by political choice of Baltic nations of joining the EU. The new political way should be accompanied by development of the new economy, new international liability and new attitude to nature management. That is why in controlling wolf we should be guided by the good data on population status rather than emotions.

The goal of the given study is to contribute to the conservation of wolf, done against the background of sweeping changes in the country's political and economic situation. Hereby we inform the management and policy-making institutions about some specific features of the population ecology found out in wolves of Latvia during the last two years.

Material and methods

The age structure of the wolf population of Latvia was studied between 1998 and 2000. The State Forest Service helped us find hunters who volunteered in providing information on the animals killed and their skulls for research. Initial co-operation with hunters was started already in 1997 when State Forest Service distributed questionnaires about morphometric characteristics of shot wolves and their division into three easier definable age classes: juveniles, yearlings, and wolves aged two years and older. Preliminary knowledge about body weight, height, length as well as the length of tail and hind foot was obtained (Andersone, Ozoliņš 2000a) from the whole Latvia. The animals used for the given study were collected both in east and west Latvia. However, the distribution of the samples collected was not really random and depended on how successfully it was managed to motivate the local hunters to assist in the research work. The sub-sample from the harvested animals (sample number = 84 wolves) was taken starting from the autumn of 1998 and until the spring of 2000 (Fig. 1), and accounts for 19% of the total harvested animals in this period. Eighteen freshly killed adult female wolves of total 31 were available for necropsy. Visual examination of ovaries and uterus was used to determine if a female had been reproducing (Kirkpatrick 1980). Placental scars, swelled post-birth sites in uterine horns or fetuses were counted. The uterine horns were opened before visual examination. Sometimes it became necessary to press them between two glass plates and to look through against a light source. The scars of previous pregnancy stood out as darkened purple or violet spots. To determine what proportion of adult females was reproductively active, the date, when a wolf was killed, was taken into account as well. Adult females without fresh breeding evidences in uterus and ovaries from March till December were assumed as non-breeding.

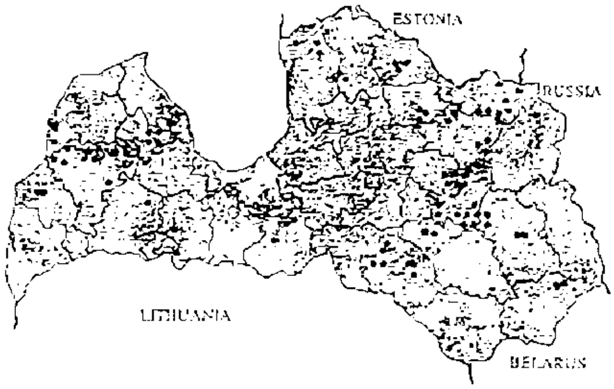


Figure 1. Black dots show the localities in Latvia where the wolves, included in this study, were hunted down, years 1998-2000. The distribution of forest and administrative borders of forestry districts are shown in grey

To determine the age of the individual, each of the skulls collected for research purposes had one canine removed and its root (1-1.5cm long) sawn off. The tooth was then placed back in the jaw in order not to spoil the trophy. The individual's age was determined by counting the number of incremental lines in the tooth cement of the given piece of tooth root. Techniques recommended by Kunz et al. (1996) or Sutherland (2000) and properly described by Klevezal were used (Клевезаль 1988), including decalcification, freezing, sectioning, staining and mounting on a glass slide for microscopic examination.

Official hunting statistics available from the monograph by A. Kalniņš (1943) about the period before World War II were compared with more recent information published by J. Ziediņš (1990) and provided by State Forest Service (1990-2000). Supposedly biased trends in statistics by any economical or political reason were discussed on the base of personal communication with officials who previously worked on game management issues (Krūmiņš et al.).

Results

The total sex ratio in our sub-sample was 1:1,3 (males : females). However statistically, the difference from equal distribution was not of high significance at this sample size (χ^2=0,862; P<0,3; d.f.=1; n.s.). This ratio was not equal for all age classes (Fig. 2). The largest numerical predominance of females over males was found within wolf cubs aged up to 1 year (1:2,4 - χ^2=1,505; P<0,25; d.f.=1) and in the 4th year of life (1:2,7

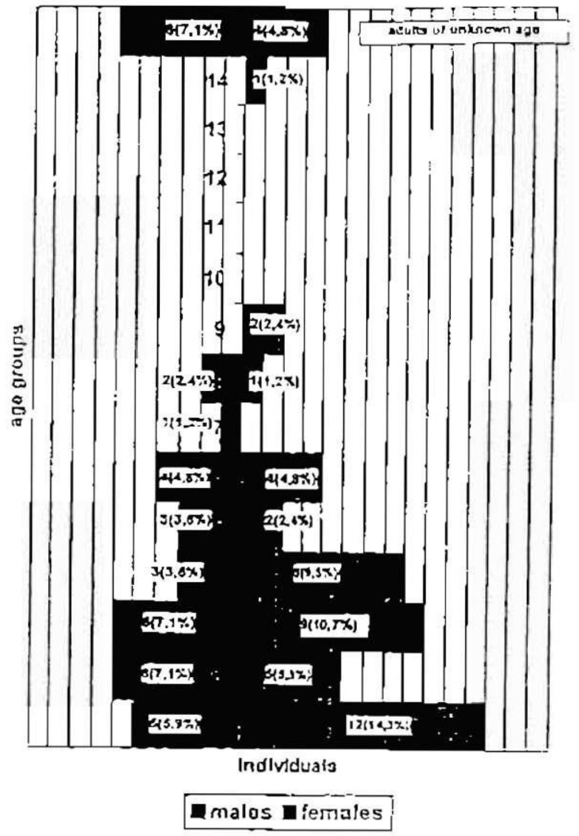


Figure 2. The age and sex structure of hunted wolves (n=84)

- χ^2=1.198; P<0.3; d.f.=1; n.s.). By the comparing the general age distribution of all females with that of males, no statistically significant differences were found (χ^2=8.018; P<0.5; d.f.=9; n.s.). The oldest wolf was 13 years old. That animal appeared to be a still reproductively active female having 6 fresh placental scars and lactating till being shot in May.

Assuming that the number of fresh placental scars is equal to that of embryos during last pregnancy, the average number of embryos per female wolf was 6.0 (n=10; SD = 1.89). In one case a female wolf was shot in spring and 10 equally developed embryos were found in the uterus. The wolf was 5 years old. Besides, no relationship between fertility and age was found in our sample. Reproduction evidences (fresh placental scars, lactation, rut) were found in 83% of 18 checked female wolves being at least 2 years old. Thirteen other adult females were not checked for this purpose mostly because of heavily damaged internal organs.

Our own experience with estimating wolf age confirms that the age was rather over than underestimated by hunters. Therefore we, decided to not use preliminary data on age structure of earlier measured wolves in this analysis but just to demonstrate that differences in body size between young and adult animals might be not remarkable. Measurements of wolf bodies were collected since 1997 when we at the beginning mostly used assistance of hunters (see for data Andersone, Ozoliņš 2000a). The data were pooled according to a rough estimate of animal's age class by hunters and summarized in the frame of other study. For example, comparing body length, the cubs aged up to 1 year were outstanding as the smallest ones (♂♂ juveniles/yearlings: t=5.081; P<0.01, ♀♀ juveniles/yearlings: t=3.724; P<0.01), while yearlings were quite similar to adults, especially in females (♂♂ yearlings/adults: t=2.533; P=0.05; ♀♀ yearlings/adults: t=1.411; P>0.1 n.s.).

Discussion and conclusions

The research, based on a sub-sample from the harvested animals, has indicated that there are few peculiarities in the population structure of this sample compared to classic patterns of typical stable or increasing population (Одум 1975). Attention should be drawn to the age distribution, illustrated by percentage of the whole sample population. For the age above 3 years, the pyramid is regarded as optimal, while an insufficient number of the youngsters stands out quite clearly (Fig. 2). When adding up all adult females in the representative sample (n = 31) and by knowing that 83% of them were capable of having cubs, and the average number of embryos was 6, one has to conclude that, theoretically, the number of cubs in their first year should have amounted to 154 that might be 70% of the population. However, the existing figures are very different, and cubs of the first year only represent 20% of the total hunting bag. There is no reason to believe that cubs have a better survival rate than older animals during hunting. Instead, it may have something to do with the mortality of cubs and/or embryos showing results different from the indices of potential fertility in females, estimated by counting placental scars and embryos. In addition, the killing of pregnant and lactating females by hunters also reduces the number of cubs survived. A disruption of the population structure, both spatial and social, caused by hunting could be a reason for the existing age distribution. It is mentioned in the literature that the spatial distribution of wolf is most strongly affected by the intensity of hunting. It disrupts the integrity of the pack's territory, as the animals increase their home range to avoid hunters (Bibikov 1985). The total wolf population includes also individuals that live solitary. Under normal conditions, about 60% of all the wolves live in packs (Bibikov 1985). Stamping out established packs of wolves enlarges the ratio of solitary animals, disrupting the balance in the system predators – ungulates. For stray wolves, entering a territory, it may take years to adapt themselves to the groupings of ungulates there (Кудактин 1984).

The "right" shape of age pyramid of 2-year old and older wolves might indicate that the native population of wolves has reproduced more successfully in 1996 and 1997 – i.e. 3 years ago. This assumption agrees with the curve of population dynamics (Fig. 3) and the fact that snow conditions in winter 1995/96 were comparatively hard for ungulates providing rich food for wolves in their turn. Additionally, there might be an influx of those wolves from Belarus and Russia that have just reached sexual maturity – the 3rd age group - and are roaming about in search of new territories.

could be mistaken for adults and therefore provided to researchers.

The proportion of females increases in the populations under a strong hunting pressure. It seems to be an attempt to compensate for the damage sustained by the population (Bibikov 1985). Therefore, we concluded that predominance of females in hunting bag from Latvia could be also a consequence of the effect of the high hunting pressure unless the next years of continued study might confirm that samples would be too small to find out the true trends.

Generally, wolf can actually tolerate a high hunting pressure. Ballard et al. (1987) state that first when the population loss exceeds 30-40% of the size of a stable population, decrease in numbers is unavoidable. Each year from the 1960s until the late 1970s, the number of killed wolves even exceeded officially esti-

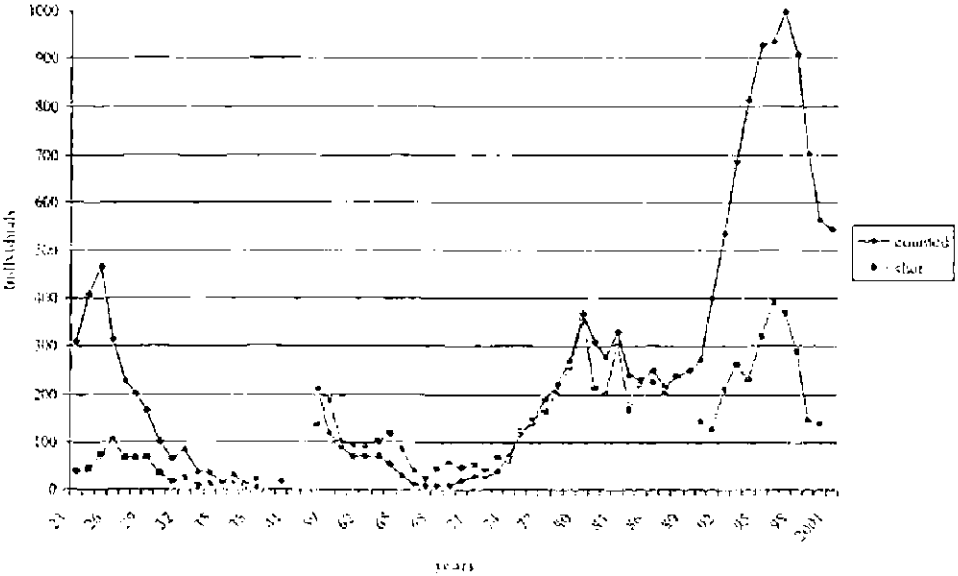


Figure 3. The population dynamics of wolf in Latvia (official statistics). Data are missing for the WWII period and 1989

Nearly over the entire range of wolf's distribution, the number of males is higher than females (Bibikov 1985; Рябов 1988; Okarma 1989; Павлов 1990). The natural mortality is higher for females, whereas males are hunted down more frequently (Павлов 1990). In Latvia we found the opposite, the predominance of females over males in several age groups, especially the first year group in the harvest (Fig. 2). Although the statistical significance of this phenomenon was very low, it is remarkable that females greatly dominated in 5 of the total 10 age classes but males dominate in 4 only with comparatively lesser numerical prevalence. A reason may be that females during the first year generally grow so fast that they almost reach the size of an adult. Sometimes we particularly required hunters to report about shot adult females to raise information on fertility in wolves. Consequently, young females

mated population size (Fig. 3). This situation is difficult to explain. The population was really small during that decade. Two reasons, why the hunting bag was higher than the estimated population size, could be mentioned. First, hunters were interested to hide the real wolf number as possible result of Soviet regulations; the more wolves counted the less shooting permits were issued to harvest ungulates. Second, it is possible that the wolves, after the persecution campaign in the post-war period, continually invaded Latvia's territory from Russia, because the hunting intensity in Latvia presumably was higher than in the east, thus providing many spare areas for immigrating wolves, and wolf density in Russia was bigger. We can not tell when exactly the wolf population started to recover in Latvia but by the late 1970s the hunting bag of wolves had increased considerably. It is simply impossible to shoot more than 90% of the wolf population (200-300 animals) and still observe a population increase as shown in Figure 3. Thus, it is more likely that the wolf population amounted to about 800 individuals already in the early 1980s. One reason for the increase in population size was probably that the ungulate populations also were rich during that period (Ziediņš 1990). The ungulate populations were so big during that period that they could probably support the increase in the wolf population without the hunters feeling any kind of actual competition from the wolf. Then in the 1990s, the situation changed. As a consequence of the collapse of Soviet economy, the ungulate resources were overexploited. Hunters again experienced the wolf as a serious competitor. The hunting statistics of mid 1990s, when 200-300 wolves were killed per season, allow us to assume that the population estimate (of approximately 900 animals in 1994-96) made before harvesting (by late summer but not on March 1 as declared officially) was correct, since the population tolerated without obvious decline such a high hunting pressure from 1992 till 1995. However, the rapid increase in the wolf population during the 1990s might be not true. What is more likely, as stated earlier, the wolf population had already reached 800-900 individuals in the early 80s and then it remained stable until 1996-1997 when almost 400 wolves were shot. The following fast decline in population size occurred, because the critical hunting pressure of over 40% was overstepped. Consequently, in the past few years there has been a decline in the wolf population.

The recent period is noted for a tendency towards fragmentation of the range inhabited by wolf (Fig. 4). North Kurzeme (north-west Latvia) and Latgale (south-east) are becoming the regions where the density of wolf is highest. The sparsely forested Zemgale Plain, lying between the above mentioned regions, hamper east – west migration of wolves. Approximately one thousand years ago wolves lived in the open landscape (Bibikov 1985). The fact that wolf has become a typical forest dweller is of less importance here. Nowadays, in Europe the forest is the most essential habitat for wolf, where it feels safe. If the isolation between the two populations will increase, reducing the genetic diversity of wolf (Randi 1993) may be a result. Already now the morphometric data of skulls show the individuals of the eastern population to be bigger than western ones (Andersone, Ozoliņš 2000b).

In conclusion we propose certain improvements in the management system of wolves in Latvia fitting better into the context of modern species' conservation requirements.

• The hunting season should be closed between April 1 and August 31. In this season, wolf, upon

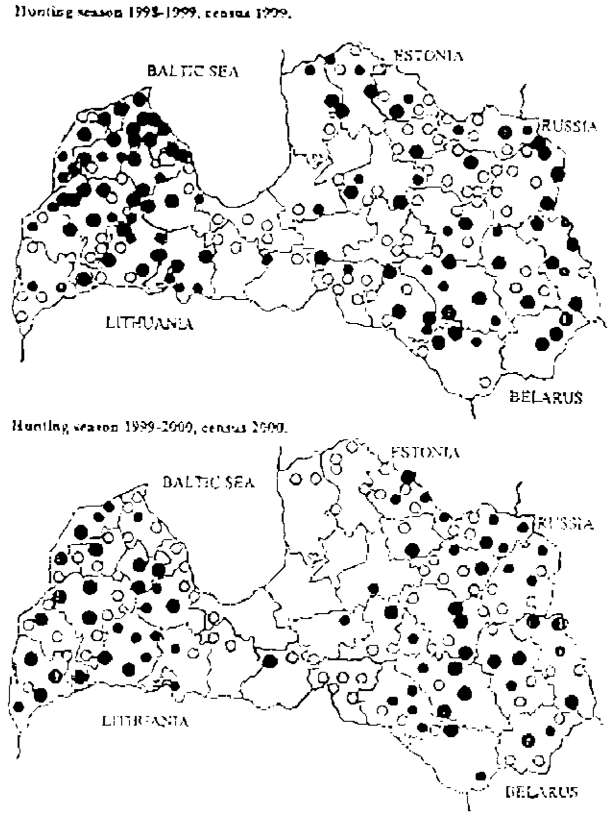


Figure 4. The distribution of wolf in Latvia for the study period. The bigger dark circles stand for the forest districts where more than one wolf was killed; the forest districts where only one wolf was hunted are marked by smaller dark circles; the white circles denote the forest districts where wolves are recorded but none hunted down

drawing up a statement as provided by the regulations, may be harvested only in the places it has inflicted damage, or when found in human settlements, or attacking domestic animals and man (the statement is drawn up *post factum* after the wolf is killed).

• In specially protected areas wolf hunting is allowed only with a permit of the Ministry of Environmental Protection and Regional Development (for research purposes, in places, were wolf has inflicted serious damage, etc.).

• Opportunity to collect wolf carcasses for further investigations should be guaranteed by law. Therefore, the fact of hunting down a wolf must, within 3 days, be reported to the nearest Forest District Office. A case of accidentally killing a wolf or finding it dead (run down, killed during an assault to livestock, etc.) must, within a day, be recorded by drawing up statement and reporting to the respective Forest District Office.

• Hunting quotas on wolf should be introduced along with the demand for compliance with the above provisions. For the time being it is difficult to establish definite hunting quotas, since it is impossible to evaluate the effect of closed season for wolf, moreover, we have no means of comparison as in Latvia the wolf has over centuries been persecuted without any restrictions. We suggest that the current population status and the results of the hunting season of 1999/2000 should be set as a benchmark in this respect. This is possible as the present population density poses no significant danger to the animal husbandry and most of the hunters' collectives seem accepting it, too. At the same time, the very existence of the species is not under a threat, except for possible isolation between the eastern and western metapopulations. All this implies that for the hunting season to come there is no special reason to decrease the hunting quota for wolf compared to the previous season (150 individuals). As we have no experience of how to divide the hunting quota between the regions of the country, and taking into account that population migration can lead to a high concentration of wolf in some localities, it is suggested that the hunting season should be closed as soon as the number of the previous season is hunted, but not later than by March 31. This can only be done if the State Forest Service sums up the hunting data on a regular basis and the hunters inform the forest authorities on the hunting results within 3 days. The hunting data should be linked to the monitoring research for the given species. In the future, when a clear picture of the population size is available, hunting quotas may be either increased or reduced in addition to changing the duration of the hunting season.

• A unified formal procedure must be established for reporting, recording and checking the damage done by carnivores. In the localities, where regular substantial damage is inflicted by carnivores, special short-term hunting permits may be issued, thus legalising the hunting, done outside the time frame of the hunting season. At the same time, solutions should be sought for compensating the damage caused by wolves to the domestic animal holders. Priority should be given, and the compensation mechanism tested first of all, in relation to protected areas.

Acknowledgements

This study was possible due to the financing from Danish Co-operation for Environment in Eastern Europe DANCEE, Latvian Environmental Fund and the budget of Latvian Academy of Sciences. The co-operation was kindly provided by following institutions: Latvian State Forest Service, Forestry Research Institute "Silava", Faculty of Biology at Latvian University, Ziemeļvidzeme's Biosphere Reserve, Latvian Forest Inventory Ltd., Danish company DARUDEC and State Stock Holding Company "Latvijas valsts meži". We particularly thank Dr. Imants Baumanis, Jānis Baumanis, Dainis Blūmentāls, Māris Bondars, Edgars Doniks, Gunārs Freimanis, Dr. Otars Opermanis, Per Egge Rasmussen, Agris Strazds, Dr. Kārlis Vismanis and Arnis Žeiers for their enthusiastic assistance as well as two anonymous reviewers for their valuable input.

References

Andersone Z., Ozolins J. 2000a. First results of public involvement in wolf research in Latvia. Folia Theriologica Estonica, 5: 7-14.

Andersone Z., Ozolins J. 2000b. Craniometrical characteristics and dental anomalies in wolves *Canis lupus* from Latvia. Acta Theriologica, 45 (4): 549-558.

Bibikov D. I. (ed.). 1985. The Wolf: History, Systematics, Morphology, Ecology. Nauka, Moskva, 606 p.

Boitani L. 2000. Action plan for the conservation of wolves (Canis lupus) in Europe. Council of Europe Publishing. Nature and environment No.113, 86 pp.

Jhala Y. V., Sharma D. K. 1997. Child-lifting by wolves in eastern Uttar Pradesh, India. Journal of Wildlife Research, 2 (2): 94-101.

Kalniņš A. 1943. Medniecība [Hunting]. Latvju grāmata, Rīga, 703 p. (in Latvian)

Kirkpatrick L. 1980. Physiological indices in wildlife management. In: S.D. Schemnitz (Editor), Wildlife management techniques manual. The Wildlife Society, Washington, p. 99-112.

Kunz T.H., Wemmer C. and Hayssen V. 1996. Sex, age, and reproductive condition of mammals. In: D.E. Wilson, F.R. Cole, J.D. Nichols, R. Rudran and M.S. Foster (Editors), Measuring and Monitoring Biological Diversity. Standard Methods for Mammals. Smithsonian Inst. Press, Washington and London, p. 279-290.

Okarma H. 1989. Distribution and numbers of wolves in Poland. Acta Theriologica, 34, 35: 497-503.

Sutherland W.J. 2000. The Conservation Handbook: Research, Management and Policy. Blackwell Science, Cambridge, 278 p.

Tauriņš E. 1982. Latvijas zīdītājdzīvnieki [Mammals of Latvia]. Zvaigzne, Rīga. 256 p. (in Latvian)

Timm U., Pilāts V., Balčiauskas L. 1998. Mammals of the East Baltic. Proceedings of the Latvian Academy of Sciences. Section B, 52 (1/2): 1-9.

Von Ende R. 1982. Über Wölfe und Hunde. VEB Deutscher Landwirtschaftsverlag, Berlin, 280 S.

Ziediņš J. 1990. Medījamo savvaļas dzīvnieku skaits Latvijā [The number of game animals in Latvia]. – Mežsaimniecība un mežrūpniecība, 3: 26-30. (in Latvian)

Клевезаль Г.А. 1988. Регистрирующие структуры млекопитающих в зоологических исследованиях [Age-related structures in zoological studies of mammals]. Наука, Москва, 288 с.

Корытин С. 1990. О людоедстве волков [About men eating in wolves]. Охота и охотничье хозяйство, 7: 12-14. (in Russian)

Кудактин А. 1984. Волк в Кавказском заповеднике [The wolf in Kaukasus reserve]. - Охота и охотничье хозяйство, 6: 4-5. (in Russian)
Одум Ю. 1975. Основы экологии [Fandamentals of Ecology]. "Мир", Москва, 740 с. (in Russian)
Павлов М. П. 1990. Волк [The Wolf]. Агропромиздат, Москва, 349 с. (in Russian)
Рябов Л.С. 1988. Особенности размножения волков (*Canis lupus* L.) в Центральном Черноземье [Reproduction peculiarities in wolves (*Canis lupus* L.) from the Central Black Earth Region of Russia]. Экология, 6: 42-48. (in Russian)
Сабанеев Л. П. 1988. Охотничьи звери [Game mammals]. (Сост. Калганов Е. А.). Физкультура и спорт, Москва, 480 с. (in Russian)

Received 07 September 2001

СТАТУС ВОЛКА *CANIS LUPUS* L. И ПЕРСПЕКТИВЫ УПРАВЛЕНИЯ ЕГО ПОПУЛЯЦИЕЙ В ЛАТВИИ

Я. Озолиньш, Ж. Андерсоне, А. Пупила

Резюме

Волки в Латвии всегда считались вредителями, которых следует истреблять всеми возможными методами. С 1998 по 2000 гг. от добытых животных собирали образцы, чтобы изучить влияние неограниченного преследования на популяцию волка. Чтобы определить репродуктивное состояние самок, проводилось лабораторное изучение яичников и маток. В рогах матки подсчитывалось число плацентарных пятен или эмбрионов. Возраст зверей определяли по числу линий прироста в зубном цементе. Основные демографические показатели были следующими: соотношение между самцами и самками – 1 : 1,3 (n=84); среднее число эмбрионов на самку – 6,0 (n = 10; SD = 1,89). Доля сеголеток в взятой пробе меньше чем ожидалось, учитывая плодовитость самок. Высказано предположение, что неограниченная охота отражается в половозрастной структуре популяции волка. Приводятся предложения, касающиеся управления популяцией волка с предположительно меньшим негативным влиянием на ее структуру. Главными мероприятиями могли-бы служить запрет охоты на сезон размножения и система оперативного всеобщего прекращения охоты на волков после выполнения предусматриваемой нормы отстрела.

Ключевые слова: волк, охота, структура популяции, охрана видов

Paper III

1.2.3. Human-wolf conflicts in the East Baltic - past, present and future

1.1.

HUMAN – WOLF CONFLICTS IN THE EAST BALTIC – PAST, PRESENT, AND FUTURE

ZANETE ANDERSONE
Kemeri National Park, Kemeri - Jurmala, LV-2012, Latvia, zanete@kemeri.apollo.lv
LINAS BALCIAUSKAS
Institute of Ecology, Akademijos 2, 2600 Vilnius, Lithuania.
HARRI VALDMANN
Institute of Zoology and Hydrobiology, Tartu University, Vanemuise 46, 51014 Tartu, Estonia.

Abstract: Since the 19th century, major human – wolf (*Canis lupus*) conflicts in the Baltic States (Latvia, Lithuania, Estonia) have included livestock depredation, attacks on humans, competition for wild ungulates, and spreading of diseases. Damage to livestock varies by wolf population size and traditional livestock keeping techniques. Wolves impact wild ungulates and contribute to natural cycles of trichinosis and rabies. There is an urgent need for compromise from diverse interest groups to reduce human – wolf conflicts in the Baltic States.

Key words: *Canis lupus*, conflict, depredation, diseases, Estonia, human, Latvia, Lithuania, wolf

---

Historically, wolves have always been in opposition to human interests (Boitani 1995). The reasons for hatred of wolves are both secular and psychological, which has led to the worldwide focus on extermination of wolves (Lopez 1995). In the present territory of the Baltic States (Estonia, Latvia, and Lithuania), the wolf has coexisted as a part of theriofauna with humans since the last glaciation (Taurins 1982, Timm et al. 1998). In contrast to most western European countries, where the species was eradicated in the Middle Ages, the wolf has survived successfully in the East Baltic, although the species experienced considerable fluctuations from near eradication to > 1000 individuals per country (Fig. 1). This paper analyzes the major aspects of human - wolf conflicts in the East Baltic since the middle of the mid-19th century to the present.

WOLF – HUMAN CONFLICTS IN THE 19TH CENTURY

Although wolves have always inhabited the East Baltic, the first reliable information about their population and damage was available as late as the early 19th century. In 1839, the largest number of wolves hunted (523) was in northern Latvia (Ristals 1994). In only 2 provinces of Lithuania (Kaunas and Vilnius), about 3,300 wolves were exterminated between 1847-52 (Kontrimavicius 1988). Such a high hunting bag indirectly indicated one of the most significant increases in wolf population in the Baltic States. Consequently, wolves caused increased livestock depredation. In 1822-23, wolves killed 28,297 sheep, cows, horses, and other livestock (Greve 1909). In 1825, in the Livland province (northern Latvia and part of Estonia), livestock losses due to wolves increased to 29,625 individuals (Table 1).

Wolves also caused human deaths, mainly of children. The Livland region in the 19th century Russian Empire had the most wolf attacks on humans (Korytin 1990). The last documented case occurred in 1873 in Estonia (I. Rootsi, Institute of Forestry, Tartu, Estonia, personal communication) when a 7-year-old boy was killed. Those wolves may have been inflicted by rabies, but it is possible that even healthy animals could target people as easy food (Jhala and Sharma 1997).

STATUS IN THE 20TH CENTURY

As a result of intensive extermination in the mid-19th century, wolf numbers have decreased significantly. In 1860, only 60 wolves were hunted in Livland (Greve 1909). In 1923, 311 wolves existed in Latvia, but the number fell to 17 World War II (Kalnins 1943). The next peak in the wolf population was in 1948-50 (Fig.1); in 1948, there were 1,725 wolves in Lithuania (Giniunas 1988). This increase may have occurred because wolves are ignored during times of war and political instability (Jedrzejewska et al. 1996). Increases in wolf number together with decreases in wild prey species resulted in increased livestock depredation (Table 1). In Russia, wolf attacks on humans were also observed in the post-war period (Pavlov 1990). Data on livestock damage is incomplete, available only for livestock covered by insurance programs. For the same reason, damage to subadult livestock was also underestimated. No precise data exist on the level of wolf depredation in all 3 countries of the Baltic States because there are no compensation programs and no central database on insured animalsSurveys, carried out only in selected areas, reveal that sheep and dogs are preyed upon mainly (Table 1).

Damage to livestock is related not only to wolf numbers but also to changing animal husbandry techniques. Until the World War II 3 main methods were used: livestock was kept in large guarded herds, smaller unguarded herds, or a few animals near the farm. Combined herds, more widespread in Lithuania, were driven by a herdsman and several helpers. The herds were often guarded by dogs and for the night were led back to the village. In Russia, such helpers were sometimes attacked by wolves (Korytin 1990). Keeping livestock near a farm more typical in Latvia and Estonia. Also in these cases, livestock was kept inside at night. In the former Soviet Union, collective farms used the same

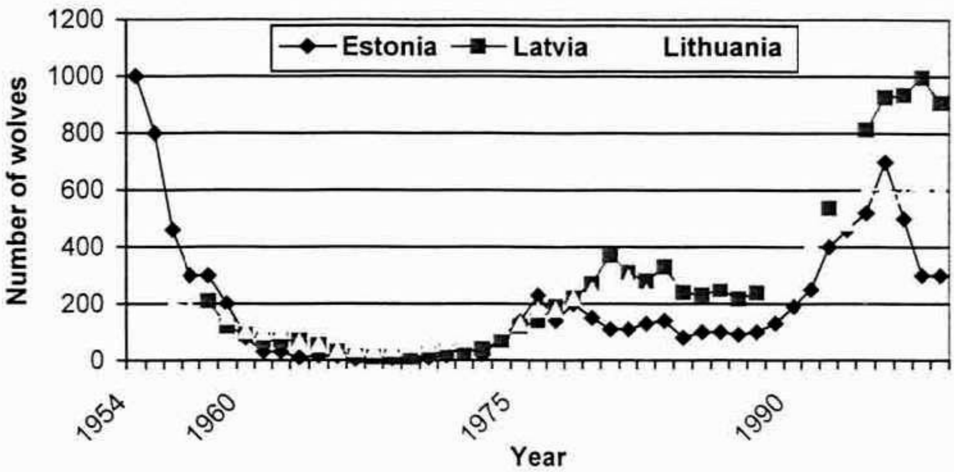


Fig. 1. Wolf population fluctuations in Estonia, Latvia, and Lithuania in 1954-98 (according to official inventory data from the national State Forest Services).

techniques of fences and herds driven by people, but with less care. Dead animals were not buried properly, thus attracting predators. Attracting wolves to food at garbage sites and hunters' baiting stations can explain the high proportion of domestic animals (about 30%) in the winter diet of wolves in Lithuania (Prusaite 1961).

Most livestock are preyed upon in late summer or autumn when adult wolves start teaching their young to hunt. Surplus killing is typical for this period. In August 1997 in eastern Latvia, 13 sheep were killed in one night, and only 2 of those sheep were used. In Estonia, according to a farmer who documented losses since 1995, maximum damage occurred in September 1997. Opposite is true for depredation on dogs, which are attacked more often in winter when wolves take chained guard dogs directly from yards.

Since the early 1990s, reprivatization of land caused livestock to be more exposed to large predators. Some of the land that people reclaimed was far from their farms, and therefore, livestock were not driven back to farms at night, thus leaving them guarded. Hiring a herdsman for a small herd was not economically feasible, so wolves could obtain an easy source of food. Livestock on private farms are attacked by wolves when left outside at night near a forest. However, in Latvia, an analysis of 8 attacks showed that 5 happened during the day and only 3 at night. In another analysis, 9 attacks happened in a yard or in a fenced area while 10 attacks occurred at ≥100 m from the home. Larger samples are needed to draw conclusions. Stray dogs are partly responsible for the depredation, but their contribution is not known in these data.

After an anti-wolf campaign in the 1950s, wolf numbers decreased to an all-time low (Fig.1). Wolf numbers started increasing in the mid-1970s and reached another peak in the 1990s after political changes weakened wolf control. An important factor promoting an increase in wolf populations was abandoning former agricultural lands. As the land became overgrown with shrubs, they provided additional refuge for wolves.

Another human - wolf conflict has developed: competition for the game mammals. Hunters have blamed wolves for decreases in wild ungulates since the early 1990s. However, poaching has occurred at a high level since the early 1990s, even with high bag limits. Thus, depression in wild ungulates may have been the result of cumulative impacts.

Roe deer is the species most vulnerable to wolf predation in Latvia and Lithuania (Prusaite 1961; Andersone 1998a,b). In Latvia, the proportion of roe deer in the summer diet of wolves was 65%, of which fawns constituted 31% (Andersone 1998a). In Estonia and Latvia, wild boar is a preferred prey (Andersone 1998b; Valdmann et al. 1998). High wolf numbers can reduce population growth of wild boar to 15% per year (H. Ling, University of Tartu, Estonia, personal communication). The influence of wolf predation on moose is insignificant in both Latvia and Lithuania (Prusaite 1961; Andersone 1998b), but in some parts of Estonia moose are important prey for wolves (Valdmann et al. 1998). In Lithuania, wolf predation is one of the factors preventing successful introduction of mouflon (*Ovis ammon*).

The third reason for human - wolf conflict is potential danger to public health. Wolves are vectors of trichinosis and rabies. In Latvia during the last 10 years, an average of one rabid wolf/year was found. In southeastern Lithuania, there have been

Table 1. Species composition (percent) of livestock attacked by wolves in Latvia and Estonia in 19th and 20th century. "*n*" refers to the number of wolf attacks.

Species	Latvia[a], 1825 n = 29,625	Latvia[b], 1997 – 1999 n = 188	Estonia, 1953 – 1962 n = 6,864
Horses	10.4	0.5	6.9
- foals	4.2		
- adults	6.2		
Cattle	8.6	19.7	19.3
- calves	2.5		
- adults	6.1		
Sheep	53.7	55.3	73.8
- lambs	2.5		
- adults	51.2		
Goats	8.5	0	0
- kids	0.6		
- adults	7.9		
Pigs	15.2	0	0
- piglets	14.1		
- adults	1.1		
Dogs	2.4	23.4	0
Poultry	0	1.1	0

[a] Data from Livland, which included northern Latvia and part of Estonia (Ristals 1994).
[b] Data from surveys in selected areas combined with data from Dundurs (1999).

documented cases of rabid wolves attacking humans (Giniunas 1988). Estonia seems to be free from rabid wolves, but in the neighboring Pskov Region of Russia, 11 people were bitten by rabid wolves in 1997. Wolves can also suffer from the sarcoptic mange (Pavlov 1990). However, of 348 wolves investigated in Latvia from 1997-99, only 2.9% had signs of mange (Z.Andersone and J.Ozolins, State Forest Inventory Institute, unpublished data).

FUTURE PROSPECTS

The Baltic States are just beginning scientific research on large carnivores, and serious investigations have not been carried out for at least several decades. Wolves were (and still are) treated as pests. Long-term management of the population of a species as complex as the wolf cannot rely only on removal of animals; other factors, including public attitudes and interests, need to be addressed. In Latvia, bounties for hunted wolves have been paid since 1997. At present, wolf numbers have stabilized or are even decreasing following strong hunting pressure. Currently, human interests demand regulation of wolf densities, especially to protect wild ungulates at an economically acceptable level. However, control of wolves should occur with some restraints (cancellation of bounties, closed hunting seasons, and quotas). Management plans for large carnivores, including wolves, have been developed in Estonia and Latvia. These management plans should establish principles of sustainable population regulation for carnivores.

One method to protect wolves is to change public attitudes by making the species a valuable game animal, which has already happened in Estonia. In Latvia, skulls of wolves are traditionally regarded as precious trophies. In Lithuania, the latest trophy exhibition showed 9 wolf skulls, all hunted between 1996–98 (Anonymous 1998). Trophy exhibitions can be a good indicator of population status and can serve as a tool for public education regarding wolf management. Economic incentives can be used to encourage hunters to support wolves on their hunting lands. For example, hunting clubs, which own land used by wolves, could pay reduced rent for the land. These incentive could help lessen the negative attitude among hunters and heavy hunting pressure on wolves.

One important issue is compensation for livestock damage. Compensation must occur simultaneously with public education, which includes teaching farmers techniques for livestock protection (using fences, guarding dogs, and keeping livestock indoors at night). Education of the public is also essential to create balanced attitudes toward the wolf, free of fear and prejudice.

Because these conflicts with wolves are varied, several target groups need to be addressed in resolving them: the public, hunters, farmers, scientists, and nature conservationists. Each group has different attitudes toward wolves, ranging from extremely negative (farmers) to strongly protective (conservationists). To reduce conflicts between humans and wolves, there is an urgent need for compromise among the different groups, which requires a multifaceted approach and further scientific studies on the species.

Acknowledgements. We thank M. Bondars for data on livestock damage in the Livani forestry district (Latvia), and J. Naaber for depredation data from the Harjumaa County (Estonia). A. Klimavicius (Lithuania) kindly supplied us with an official survey from 1987-98.

LITERATURE CITED

Andersone, Z. 1998a. Summer Nutrition of Wolf (*Canis lupus*) in the Slitere Nature Reserve, Latvia. Proceedings of the Latvian Academy of Sciences, Section B. 52 (1/2): 79-80.

----------------. 1998b. Wolf - wild ungulate interactions in Latvia. Advances in Ethology 33, (Supplement to Ethology): 87.

Anonymous. 1998. [Catalogue of the hunting and fishing trophies]. Vilnius: 1–34. [In Lithuanian]

Boitani, L. 1995. Ecological and cultural diversities in the evolution of wolf - human relationship. Pages 3 –13 *in* L. N. Carbyn, S. H. Fritts and D. R. Seip, editors. Ecology and Conservation of Wolves in a Changing World. Canadian Circumpolar Institute,

Occasional Publication.
Dundurs, A. 1999. [Wolves of More - Nitaure will not kill livestock any more]. Medibas, Makskeresana, Daba. Riga, 1: 6-10. [In Latvian]
Giniunas, K. 1988. [Wolf]. Mokslas, Vilnius. [In Lithuanian]
Greve, K. 1909. Säugetiere Kur-, Liv-, Estlands. W. Mellin u. Co, Riga.
Jedrzejewska, B., Jedrzejewski, W., Bunevich, A. N., Milkowski, L., and H. Okarma. 1996. Population dynamics of wolves *Canis lupus* in Bialowieza Primeval Forest (Poland and Belarus) in relation to hunting by humans, 1847 - 1993.Mammal Review 26: 103-126.
Jhala, Y. V., and D. K. Sharma. 1997. Child-lifting by Wolves in Eastern Uttar Pradesh, India. Journal of Wildlife Research, 2(2): 94-101.
Kalnins, A. 1943. [Huntsmanship]. Latvju gramata. Riga. [In Latvian]
Kontrimavicius, V., editor. 1988. [Fauna of Lithuania. Mammals]. Mokslas, Vilnius. [In Lithuanian]
Korytin, S. 1990. [On wolf cannibalism]. Ochota i ochotnichje khozjaistvo, 7: 12-14. [In Russian]
Lopez, B. H. 1995. Of Wolves and Men. Simon & Schuster, A Touchstone book.
Pavlov, M. P. 1990. [Wolf]. Agropromizdat, Moscow. [In Russian]
Prusaite, J. 1961. [Wolf diet and reproduction in Lithuania]. Liet. TSR MA darbai, Ser. C, 1(24): 177-190. [In Lithuanian]
Ristals. 1994. [From the ancient times to 1918]. Medibas, Makskeresana, Daba. Riga, 9: 28-29. [In Latvian]
Taurins, E. 1982. [Mammals of Latvia]. Zvaigzne, Riga. [In Latvian]
Timm, U., Pilats, V., and L. Balciauskas. 1998. Mammals of the East Baltic. Proceedings of the Latvian Academy of Sciences. Section B, 52 (1/2): 1-9.
Valdmann, H., Looga, A., and O. Koppa. 1998. Diet and prey selectivity of wolf *Canis lupus* in middle and southeastern Estonia. Baltic Forestry, 4 (1): 42-47.

1.3. Discussion and conclusions

The population development of wolves observed in Latvia is similar to that from the other Baltic countries (Блузма 1990, Bluzma 1999, 2000, Valdmann 2000). Peak wolf numbers were reported from the middle of the 19th century (Kalniņš 1943), also from Russia and Norway (Elgmork 2000). Wolf density in Latvia is relatively low compared to other localities - about 4.6-7.7 ind./1000 km^2, while in an exploited population in Belarus it was 9-15, and in non-exploited population in Poland – up to 72 inividuals, averaging 20-26 ind./1000 km^2 (Jędrzejewska et al. 1996a, Smietana and Wajda 1997, Okarma et al. 1998). Northern regions with poor productivity usually support much lower densities of wolves (Bibikov 1985). Wolves' present distribution in Latvia covers nearly the whole country (see chapter 1.2.2.), although in the depression phases of the population their distribution was significantly more limited (Appendix 1).

Data on the pack size in Latvia are insufficient and based on a few observations of relatively large packs (n = 15, average 5.8 ind./pack), while small packs seem to be more common. Fragmentation of packs is caused by the heavy hunting pressure (Haber 1996, Okarma et al. 1998), low wolf density resulting in a smaller pack size (Калецкая и Филонов 1987). The difference in pack size between harvested and non-exploited populations can be almost twofold (Okarma et al. 1998).

In addition to the hunting-caused mortality, indirect mortality is a consequence of the current all-year-round open season. Elimination of pregnant and lactating females from the population may add to wolf mortality, although some successful rearing cases by a single mate are known from areas with favourable feeding conditions (Boyd and Jimenez 1994).

Although data on litter size from Latvia were fragmentary (based on 7 known litters), they showed a great similarity to the data obtained from placental scars (number of embryos) – 6.6 and 6.0 accordingly, indicating that the latter method is a reliable estimate of the species fecundity. Litter size varies a lot depending on the local conditions and the population structure (Гептнер и Наумов 1967, Формозов и Голов 1975, Ватолин 1983, Danilov et al. 1985). Fecundity tends to increase when wolf density decreases (Рябов 1988). Unfortunately, the small sample size did not allow analysis of changes of fecundity in time or within the wolf range in Latvia but T-test so far showed no significant geographic difference between the east and west of the country in terms of the age composition. Further studies are needed to check the hypothesis about the difference in average age composition between wolves from the Kurland Peninsula and the rest of the country.

Also, there are indications that the female bias in sex ratio increases in heavily exploited populations (Smirnov and Korytin 1985), although normally male predominance is observed (Prusaite 1961a, Ватолин 1983, Smirnov and Korytin 1985, Jędrzejewska et al. 1996a). In Latvia, the proportion of females was higher among the wolves harvested in the last few years characterised by the exceptionally high hunting pressure. However, at the present stage, it is impossible to conclude whether it was a compensation for the increased mortality in the population or a result of potentially selective hunting. Further studies on the population demography are required before any final conclusions can be drawn.

Nowadays, human - wolf conflicts in the Baltic countries are mainly about competition for wild ungulates with hunters who blame wolves for the decline in ungulate populations (Gaross 1994). Livestock depredation problems are negligible compared to those elsewhere (Linnell et al. 1996). They are seasonal and / or local and the damage caused is relatively small due to the fact that animal farming is currently in depression. Most of the depredation cases could have been easily prevented by using certain preventive measures like night confinement and fences.

It can be concluded that:

- Wolves are currently widely distributed, relatively numerous and not threatened in Latvia;
- Several features are indicative of over-exploitation of Latvian wolves, i.e., recent numerical and distribution decline, high fecundity, prevalence of females and low proportion of old animals in the population;
- Damage to livestock is negligible and can be avoided by applying proper husbandry techniques;
- Rabies is relatively uncommon in wolves, and by controlling medium-sized predators, wolves may help to control rabies;
- The main wolf – human conflict nowadays is competition for prey (ungulates) with hunters;
- Management practices for wolves should be changed in order to ensure a sustainable harvest of the species rather than the maximum reduction of wolf numbers.

2. Morphometrics of wolves from Latvia

2.1. Introduction

Morphology of the wolf varies considerably within its distribution in terms of the pelt colour, body size and cranial characteristics (Sokolov and Rossolimo 1985, Mech 1995). As morphology is one of the criteria used in taxonomy (Sokolov and Rossolimo 1985), case studies are essential. In the Baltic countries, however, the only detailed study on the morphology of wolves was carried out in Lithuania in the late 1950s (Prusaite 1961b). The current study is the first attempt to obtain information on the current morphometrical parameters of wolves in Latvia.

Despite the fact that the wolf is regarded as a pest in the Baltic countries, it is a game species whose trophies (pelts and skulls) are very much valued by hunters (Prusaite et al. 1985). The high number of gold medal trophies from Latvia (Anonymous 1999) indirectly indicates to the presence of large wolves in the population. Exceptionally heavy wolves (up to 82 kg) were occasionally reported from the Baltics (Мятинг 1965 after Prusaite et al. 1985). Such a popularity of wolf trophies facilitated data collection. Wolf skulls from private collections (most from the 1990s, and a few from the 1980s) were used for craniometrical examination, while body parameters were measured according to a specially designed questionnaire for wolves harvested in 1997-2001.

The aim of the study was to investigate craniometrical and morphometrical parameters of wolves in Latvia, to determine whether they display any geographical variations within the country and to compare them with wolves from the neighbouring countries. Also, demographic structure and several non-parametrical morphological features of harvested wolves were analysed.

2.2. Results

Paper IV

2.2.1. Morphometrical characteristics of wolves from Latvia: experience of hunters' involvement in data collection

Morphometrical characteristics of wolves *Canis lupus* from Latvia: experience of hunters' involvement in data collection

Žanete Andersone, Jānis Ozoliņš

Ķemeri National Park, "Meža māja", Ķemeri – Jūrmala, LV-2012, Latvia, e-mail: zanete.a@delfi.lv; fax: +371-7765040 (ŽA); State Forest Service, 13.Janvāra Str. 15, Riga, LV-1932, Latvia (JO)

Abstract

In 1997 - 2001, a study of wolf *Canis lupus* Linnaeus, 1758 morphometrics (body metrical parameters and weight) has been carried out in Latvia by investigating harvested individuals. Hunters were involved in data collection, being obliged to precisely measure body size and weight and to note peculiar individual features of harvested wolves like injuries, signs of scabies etc. In total, 496 wolves were measured according to the questionnaire developed by the authors. Mean body length (without tail) of adult males was 117.7 cm, that of females - 109.8 cm. Mean body weight (whole carcass) of adult males was 41.2 kg, and 34 kg for females. Mean body height of males was 77.3 cm, females - 71 cm. Wolves were divided into three age classes - < 1 year, 1 - 2 years old, $\geq$ 3 years on the basis of tooth wear and the size of the individual. Age structure of the harvested wolves was biased towards adult animals, which constituted 71.7% in males and 53.9% in females. Sex ratio of harvested wolves was close to one with a slight

Table 1. Morphometrics of adult wolves hunted in Latvia in 1997-2001. Sample size (N), average value (X), minimum (Min) and maximum (Max) values, standard deviation (SD) and the ratio of sexual dimorphism are shown. Statistical difference between males and females is given (* - $p < 0.05$, ** - $p < 0.01$).

Parameters measured	Males					Females					Sexual dimorphism
	N	X	Min	Max	SD	N	X	Min	Max	SD	
Weight (kg)**	66	41.2	25.7	67	7.7	46	34	16	52	6.1	0.825
Body height (cm)**	173	77.3	62	108	9.5	134	71	54	85	5.9	0.918
Body length without tail (cm)**	173	117.7	148	78	11.5	131	109.8	71	140	12	0.933
Tail length (cm)	173	42.6	26	65	11.2	131	40.8	30	56	5.3	0.958
Total length (cm)**	173	159.2	119	201	11.7	132	150.5	112	180	13.2	0.945
Foot length (cm)**	171	27	17	36	11.2	127	24.3	10	34	3	0.900
Ear length - front edge (cm)	174	15.3	8	18	12.2	128	13.4	9	18	1.9	0.876
Ear length - rear edge (cm)	168	12.2	5	15	12.1	122	10.6	5	15	1.8	0.869

Table 2. Weight and body measurements of subadult wolves hunted in Latvia, 1997-2001. Sample size (N), average value (X), minimum (Min) and maximum (Max) values, standard deviation (SD) and ratio of sexual dimorphism are shown. Statistical difference between males and females is given (* - $p < 0.05$, ** - $p < 0.01$).

Parameters measured	Males					Females					Sexual dimorphism
	N	X	Min	Max	SD	N	X	Min	Max	SD	
< 1 yr. old											
Weight (kg)	10	26.5	18	37.1	6.2	7	23	16.4	34.5	7.2	0.868
Body height (cm)	36	61.4	48	80	8	41	63	40	78	8.7	1.026
Body length without tail (cm)	36	94	68	121	13	41	96.2	49	129	14.8	1.023
Tail length (cm)	36	35.8	24	46	5.1	41	35.4	22	55	6.6	0.989
Total length (cm)	36	129.9	97	166	16.1	41	130.9	94	170	17	1.008
Foot legth (cm)	35	22.8	15	29	2.7	41	22.6	11	29	3.2	0.991
Ear length – front edge (cm)	36	12.9	9	15	1.7	41	12.6	8	16	1.8	0.977
Ear length - rear edge (cm)	36	10.6	7	13.5	1.4	40	10.1	5	12.5	1.7	0.953
1-2 yrs. old											
Weight (kg)	9	28.8	22.7	39	5.7	25	29.7	16.4	52	6.3	1.031
Body height (cm)	32	69.9	54	82	6.3	75	68.7	50	81	5.7	0.983
Body length without tail (cm)	33	111.6	84	144	13.3	75	107.2	74	138	10.5	0.961
Tail length (cm)*	33	41.5	34	50	4.6	75	38.8	13	54	6.5	0.935
Total length (cm)*	33	153.1	121	185	13.6	74	146.2	107	192	12.3	0.955
Foot legth (cm)**	33	25.3	21	34	2.5	73	23	13	32	2.8	0.909
Ear length - front edge (cm)	33	13.5	11	17	1.5	72	12.9	6	16	2.3	0.956
Ear length - rear edge (cm)*	32	10.9	7	13.5	1.4	72	10	4	13	2	0.908

Table 3. Weight (kg) and the main body parameters (cm) of wolves from different countries. [1] - current study; [2] - Prusaite 1961; [3] - Valdmann et al. 1998; [4] - Sokolov and Rossolimo 1985; [5] - Geptner and Naumov 1967; [6] - Novikov 1956; [7] - Sokolov and Rossolimo 1985

Parameter	Sex	Latvia[1]	Lithuania[2]	Estonia[3]	Belarus[4]	Belarus (Bialowieza)[5]	Middle Russia[6]	Ukraine[7]
Body	♂♂	41.2	44.5		42	34.8	34-49	36
weight				46				
	♀♀	34.0	38.0		36	29.2	30-42	29
Body	♂♂	117.7	125.7	-	130	119	-	121
length	♀♀	109.8	120.5	-	128	111	-	115
Tail	♂♂	42.6	42.1	-	-	41	-	-
length	♀♀	40.8	40.5	-	-	40	-	-
Foot	♂♂	27.0	26.2	-	-	25	-	-
length	♀♀	24.3	23.6	-	-	23	-	-

Figure captions

Fig.1. Measurements scheme used by hunters to measure harvested wolves in Latvia. e-f: total body length; g-f: tail length; a-b: height; i-h: foot length; c-d: ear's front edge; c-k – ear's rear edge.

Fig.2. Age structure of hunted wolves based on age determination by hunters (N = 496).

Fig.1. Andersone and Ozolins

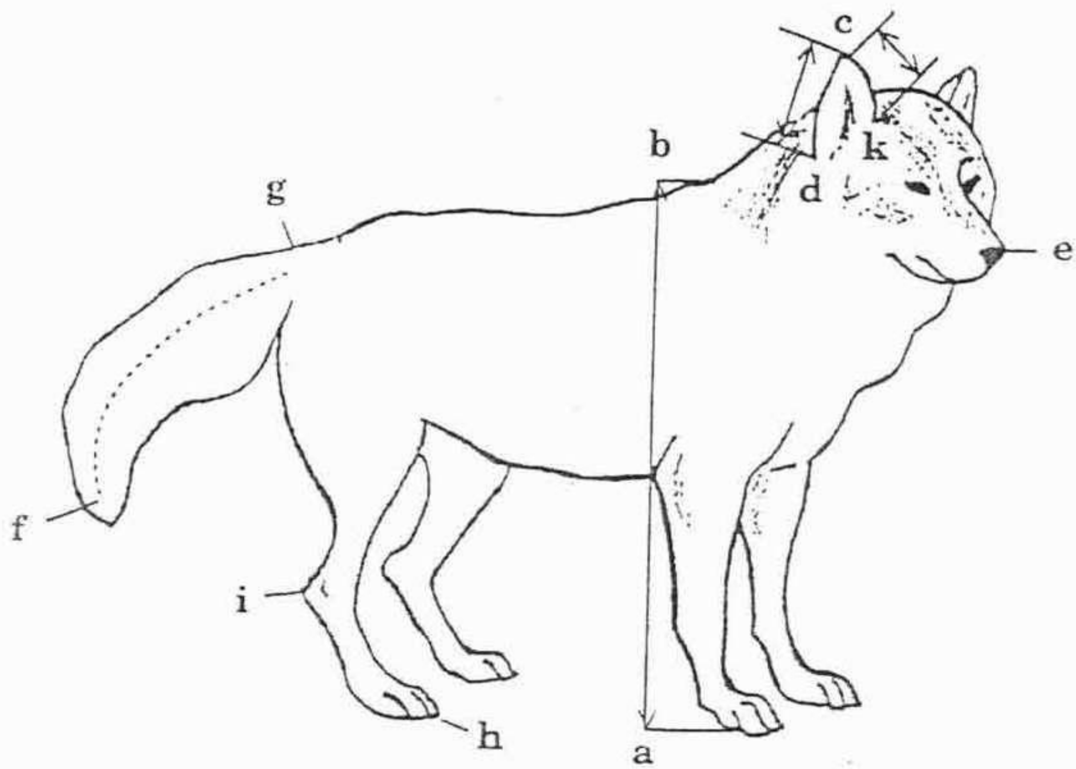
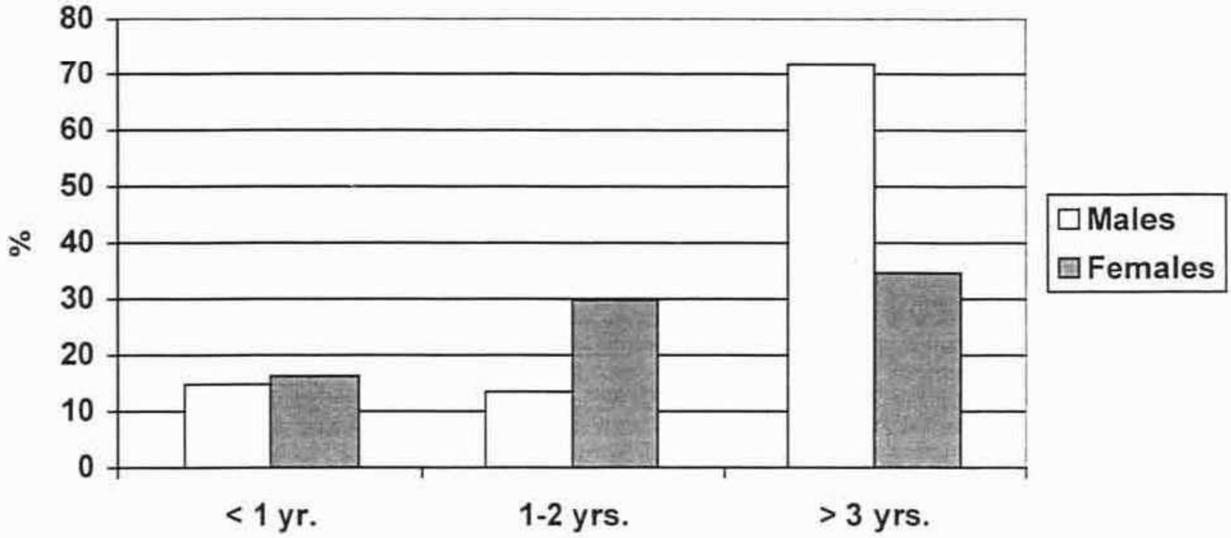


Fig. 2. Andersone and Ozolins



Paper V

2.2.2. Craniometrical characteristics and dental anomalies in wolves *Canis lupus* from Latvia

Acta Theriologica 45 (4): 549–558, 2000.
PL ISSN 0001-7051

Craniometrical characteristics and dental anomalies in wolves *Canis lupus* from Latvia

Žanete ANDERSONE and Jānis OZOLIŅŠ

Andersone Ž. and Ozoliņš J. 2000. Craniometrical characteristics and dental anomalies in wolves *Canis lupus* from Latvia. Acta Theriologica 45: 549–558.

A total of 187 skulls (115 adult males and 72 adult females) of the wolf *Canis lupus* Linnaeus, 1758 hunted in Latvia between 1975–1999 were measured, using 19 craniometrical parameters. General cranial characteristics were similar to those described from the wolf populations of Belarus and Poland (the difference was not statistically significant). Sexual dimorphism in skull size was determined. Most of the skull parameters from north and east Latvia appeared to be slightly larger than those from the Kurland Peninsula, being isolated by large cities, rivers and deforested lands. Also, anomalies in tooth formula were described. Deviations from the normal tooth pattern were found in 9.5% skulls. Congenital oligodonty and polydonty was found in 7.9% skulls. Polydonty was observed in 71.4% cases of tooth anomalies. Tooth anomalies were more common in males than in females.

Ķemeri National Park, "Meža māja", Ķemeri - Jūrmala, LV-2012, Latvia, e-mail: kemeri@vdc.lv (ŽA); State Forest Service, 13. Janvāra Str. 15, Riga, LV-1932, Latvia (JO)

Key words: *Canis lupus*, craniometry, dental anomalies, Latvia

Introduction

In Latvia, unlike many other European countries, the wolf *Canis lupus* Linnaeus, 1758 is still a very common large carnivore. According to the official inventory data, the population totals about 700 animals, with the highest density in the western and eastern parts of the country. Although double counting cannot be excluded and the actual number may be much lower, the population size certainly reaches several hundred animals. It is traditionally regarded by the public, especially by hunters and farmers, as a pest and is severely persecuted all year round. Despite its wide distribution, abundance and a remarkable yearly hunting bag exceeding 300 individuals since 1995, morphology of the Latvian wolf population has not been studied before. Only some body measurements of the Latvian wolves are represented in the national literature (Kalniņš 1943, Tauriņš 1982) while in the neighbouring countries numerous craniometrical studies on the species have been carried out (Novikov 1956, Geptner *et al.* 1967, Bibikov 1985, Okarma and Buchalczyk 1993).

The aim of this study was to give a basic craniometrical description of the wolf population in Latvia, to check the extent of sexual dimorphism of skull characteristics, and to compare craniometry of the Latvian wolves with those in the neighbouring territories.

Material and methods

Skulls of wolves hunted in Latvia in 1975–1999 were measured. The samples represented all the territory of Latvia (64 600 km^2), although most of the skulls originated from the eastern and western parts of the country, the regions of the highest wolf density. The River Daugava was chosen as a borderline between the Kurland Peninsula subpopulation (to the west from the river) and the northeastern subpopulation (from the region bordering with Estonia and Russia).

In total, 187 wolf skulls (115 males, 72 females) were measured. Thirty-two males and 21 female originated from the Kurland Peninsula. All the skulls studied were from hunters' private collections. In Latvia, wolf skulls are regarded as a valuable trophy. Male skulls predominate in the collections, since they are bigger and more impressive for exhibition than female skulls, which are often neglected. Only skulls of adult animals were measured since they present species specific characteristics. Sample size (*n*) differed for individual parameters as not all the measurements were available for every skull due to their different condition.

The following 18 parameters (Fig. 1) were measured according to Novikov (1956) as well as taking into account Okarma and Buchalczyk (1993), Ansorge (1994), Ansorge and Meinig (1996):

CbL – condylobasal length (aboral border of the occipital condyles – *Prosthion*),
ToL – total length (*Prosthion* – sagittal crest),
BaL – basal length (from posterior edge of alveolus of I^1 to *Foramen supramastoideum*),
FaL – facial length (Frontal midpoint – *Prosthion*),
NeL – upper neurocranium length (Frontal midpoint – *Opisthion*),
NaL – nasal length (length of joint between *Nasale*),
MNaL – maximum nasal length (from anterior edge of *Nasale* to its posterior edge),
PaL – palate length (from posterior edge of alveolus of I^1 to anterior edge of *Incisura palatina*),
IPaL – length of *incisura palatina* (from its anterior edge to the posterior edge of *Hamulus pterigoideus*),
C^1B – breadth of alveolus of the upper canine C^1 (measurement taken between exterior edges of canines),
ZyB – zygomatic breadth (*Zygion – Zygion*),
EntB – minimum breadth between the orbits (*Entorbitale – Entorbitale*),
LB – minimum breadth of skull (minimum aboral breadth of the supraorbital processes),
MB – maximum mastoid breadth (*Othion – Othion*),
SH – skull height,
MdL – total length of mandible (*Infradentale* – Condyle process),
TRL' – length of upper tooth row (from anterior edge of P^1 to posterior edge of alveola of M^2),
C_1Br – breadth between interior edges of alveoli of the lower canine C_1.

Measurements were taken with a caliper (30 cm) to an accuracy of 1 mm. Cranial characteristics underwent statistical analysis; the significance level was checked by the Student's *t*-test (Liepa 1974, Sokal and Rohlf 1981). For each parameter, standard deviation (SD) and coefficient of variation (CV) were calculated. Also, the Storer's index of sexual dimorphism was calculated (Okarma and Buchalczyk 1993). In addition, skull mass (SM) was measured. The skulls were weighed only when completely dry using an electronic balance (SC-3000) to 1 g preciseness.

Tooth formula was checked in all the skulls investigated in order to reveal possible deviations. We checked if the tooth formula of the skulls was in accordance with the normal tooth pattern of the wolf: I 3/3 C 1/1 P 4/4 M 2/3 (Görner and Hacketal 1987). Presence or absence of teeth was assessed externally by checking alveoli.

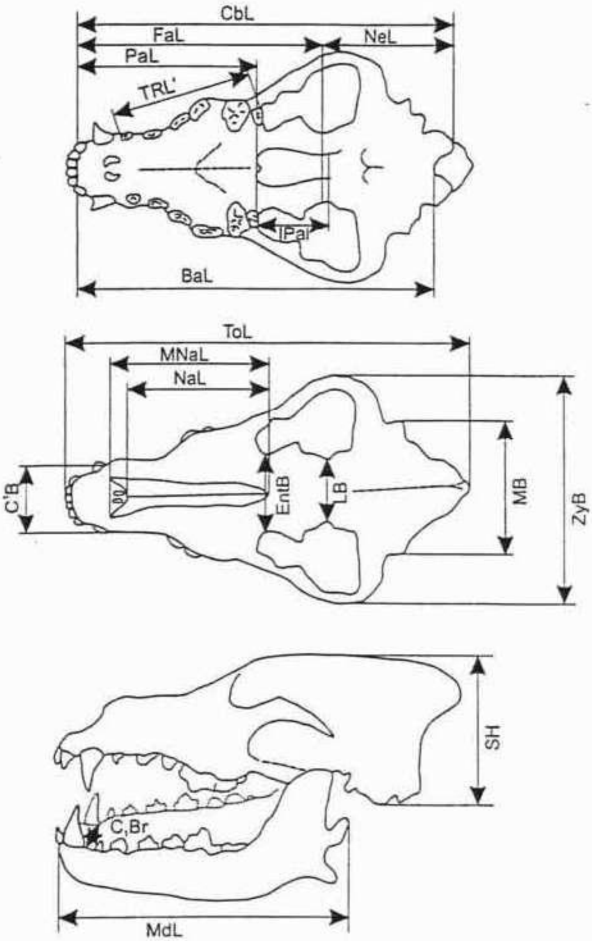


Fig. 1. Cranial parameters measured in wolf skulls. Explanations for each parameter are given in the text.

Results

Condylobasal length (CbL) of the wolf skulls measured varied from 20.0 to 25.9 cm (males: from 20.8 to 25.9 cm, females: from 20.0 to 24.4 cm). Zygomatic breadth (ZyB) ranged from 11.8 to 16.1 cm (males: 11.8–16.1 cm, females: 11.9–14.7 cm). All the craniometrical characteristics measured are shown in Table 1.

Male skulls were larger than those of females. The difference was statistically significant (t-test: t = 2.3 to 13.9, $p < 0.05$ to 0.001) for all the characteristics measured (Table 1). However, the Storer's index of sexual dimorphism was not high. It was more pronounced for the mass of skull (SM), minimum breadth between orbits (EntB) and for neurocranium length (NeL). The least difference

Table 1. Some linear skull parameters (cm) and skull mass (SM, g) of wolves from Latvia. Sample size (n), average value of character ($\bar{x}$), standard deviation (SD), minimum and maximum values of measurements, coefficient of variation (CV), and Storer's index of sexual dimorphism are displayed. Statistical difference between males and females is given (t-test: * $p < 0.05$, ** $p < 0.001$). n varies for different parameters because not all the measurements were available for every skull checked.

Parameter	Males						Females						Storer's index
	n	$\bar{x}$	Min	Max	SD	CV	n	$\bar{x}$	Min	Max	SD	CV	
CbL**	106	23.7	20.8	25.9	0.1	4.22	66	22.5	20.0	24.4	0.08	3.69	5.5
ToL**	115	26.5	23.0	28.8	0.11	4.15	71	24.8	22.2	26.5	0.09	3.78	6.4
BaL**	107	22.3	19.0	24.9	0.1	4.29	62	21.0	18.1	22.6	0.08	3.95	6.1
FaL**	114	15.7	11.1	19.0	0.12	7.37	69	15.0	12.8	17.8	0.1	7.68	4.3
NeL**	104	8.0	5.1	10.3	0.11	13.59	66	7.3	5.7	9.6	0.1	14.60	9.0
NaL**	115	8.5	6.5	9.6	0.06	7.12	71	8.0	6.7	9.1	0.05	6.69	6.7
MNaL**	115	9.7	7.4	11.4	0.06	6.60	72	9.1	7.6	10.1	0.06	6.02	6.5
PaL**	111	12.0	10.2	18.8	0.08	6.98	66	11.2	9.7	12.4	0.06	5.34	6.6
IPaL**	106	4.5	3.4	6.0	0.04	9.22	66	4.3	3.0	5.6	0.04	9.56	4.4
C^1B**	114	4.7	3.1	5.3	0.04	7.54	72	4.3	3.1	4.8	0.04	8.21	8.5
ZyB**	113	14.3	11.8	16.1	0.08	5.79	70	13.2	11.1	14.7	0.06	4.56	8.1
EntB**	114	4.7	3.7	6.0	0.05	9.84	72	4.3	3.1	5.1	0.04	9.10	9.4
LB**	114	4.2	3.1	5.5	0.04	9.32	71	4.0	3.0	5.0	0.04	9.50	4.2
MB**	105	7.9	5.6	9.2	0.1	13.13	67	7.3	5.7	8.9	0.09	12.18	8.4
SH**	112	8.8	7.5	10.4	0.07	7.53	69	8.3	7.1	9.6	0.05	6.47	6.4
MdL**	113	18.9	11.9	20.8	0.1	5.31	70	17.8	15.7	19.9	0.07	4.12	5.7
TRL'**	115	8.5	7.3	10.7	0.05	5.79	71	8.2	6.8	9.7	0.05	5.58	4.3
C_1Br*	100	1.5	0.9	1.9	0.02	15.83	68	1.4	0.9	1.9	0.02	15.41	4.9
SM**	97	565.3	381	749	79.2	14.01	63	459.6	301	600	60.2	13.09	20.6

between males and females was found for C_1Br but nevertheless it was statistically significant ($t = 2.3$, $p < 0.05$).

The SM, NeL, MB and C^1B parameters had the highest coefficients of variation. Males generally displayed slightly higher coefficients of variation than females. Coefficient of variation was higher in females only for the following parameters: FaL, NeL, IPaL, C^1B, and LB (Table 1).

Since the wolf range in Latvia is relatively continuous, significant geographical differences might not have been expected. However, the biggest trophies, evaluated by totaling CbL and ZyB, originated mainly from northern and eastern Latvia (Fig. 2). Comparison of the cranial parameters of wolves from the Kurland Peninsula, a relatively isolated population, and of wolves from northern and eastern Latvia revealed that most of the measurements were significantly bigger in wolves from northern and eastern Latvia, both in males and females (Table 2). For example, ToL in males from Kurland was 26.1 cm, that of males from the rest of the country – 26.6 cm ($t = 3.5$, $p < 0.001$). The only parameters that where significantly bigger

Fig. 2. Geographical distribution of 10 largest male and 10 largest female skulls in Latvia. Both males and females are ranked from 1 to 10 on the basis of the arithmetical sum of condylobasal length and zygomatic breadth. Solid lines are the borders of forestry districts.

Table 2. Differences in cranial parameters between wolves from western and northeastern Latvia. Statistical geographical difference in regard to sex is shown (t-test: * $p < 0.05$, ** $p < 0.001$). Asterisk corresponds to the region where the given measurement was significantly larger.

Parameter (cm)	Western Latvia			Northeastern Latvia		
	Males	Females	Storer's index	Males	Females	Storer's index
CbL	23.66	22.32	6.0	23.76	22.48	5.5
ToL	26.11	24.62	5.9	26.63**	24.79	7.2
BaL	21.93	20.73	5.6	22.38**	21.04**	6.2
FaL	16.28**	15.63**	4.1	15.29	14.63	4.4
NeL	7.14	6.46	10.0	8.49**	7.8**	8.5
NaL	8.40	7.90	6.1	8.59	8.02	6.9
MNaL	9.57	8.99	6.3	9.77*	9.15*	6.6
PaL	11.89	11.12	6.7	12.04	11.29*	6.4
IPaL	4.47	4.36**	2.5	4.45	4.21	5.5
C^1B	4.36	4.02	8.1	4.78**	4.41**	8.1
ZyB	13.81	12.87	7.0	14.50**	13.30**	8.6
EntB	4.43	4.08	8.2	4.80**	4.35**	9.8
LB	3.88	3.77	2.9	4.28**	4.10**	4.3
MB	6.76	6.69	1.0	8.43**	7.58**	10.6
SH	8.31	7.77	6.7	9.07**	8.52**	6.3
MdL	18.68	17.68	5.5	18.98**	17.88	6.0
TRL[1]	8.26	8.03	2.8	8.67**	8.25**	5.0
C_1Br	1.27	1.25	1.6	1.53**	1.46**	4.7
SM (g)	565.37	–	–	565.22	458.08	20.9

in the Kurland Peninsula were IPaL in females ($t = 3.8, p < 0.05$) and FaL both in females and males ($t = 5.9$ and 5.2 accordingly, $p < 0.001$).

Anomalous tooth formula were found in 18 skulls, which constituted 9.6% of all the skulls checked. Deviations from the normal tooth pattern were equally frequent in males and females. Congenital anomalies (oligodonty and polydonty) predominated (77.8% of all anomalies). Polydonty occurred more frequently than oligodonty (5.3% versus 2.1% of all skulls). The proportion of individuals with inherited or developmentally determined anomalies in tooth formula was higher in males than in females, both for oligodonty and polydonty ($t = 24$ and 4 accordingly, $p < 0.001$). All cases of oligodonty derived from the lack of M_3 (2.1% of all skulls). Twice M_3 was absent from both sides of the jaw, the total number of teeth equaling 40.

In most cases of polydonty (53.3%) additional minor molars and premolars were found both in upper and lower jaw. M^3 ($n = 1$) and M_4 ($n = 2$) were found as

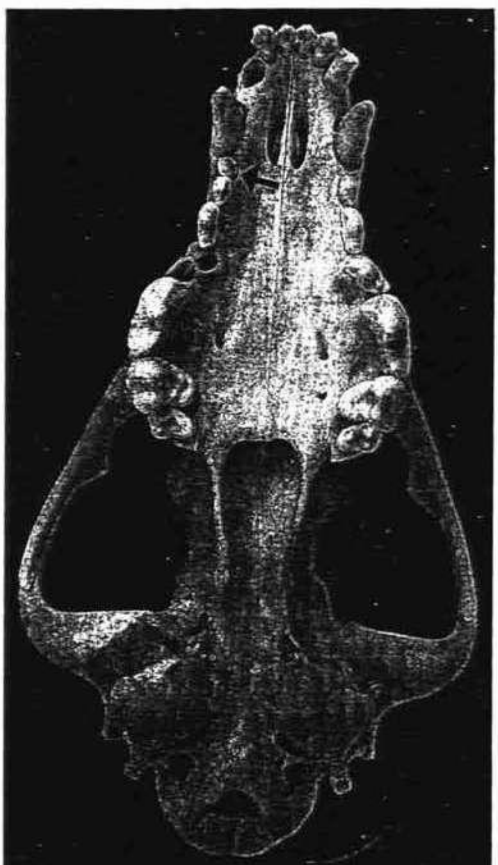


Fig. 3. Additional upper premolar (P^1) in a wolf skull from Latvia.

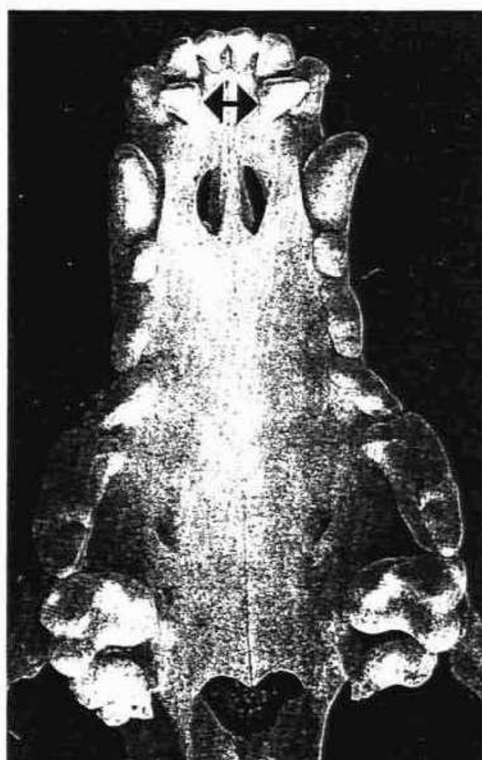


Fig. 4. Symmetric additional upper incisors in the female wolf from the Kurland Peninsula, Latvia.

additional molars. All the additional premolars were situated at P^1 (n = 3) or P_1 (n = 2) (Fig. 3). Usually additional molars and premolars were of irregular shape and smaller than the corresponding premolars. Twice additional incisors were found. One skull had a double I_1 just next to a canine. In another skull two additional symmetrical incisors (I^2I^2) of normal shape were found in the second tooth row (Fig. 4).

Also, traumatic anomalies were found in the wolf skulls checked. In two, broken teeth were found (a canine and two incisors); once P_1 and P^3 were lacking but their absence was obviously secondary. Alveoli were filled up with bone but still visible.

Discussion

Results of this study revealed the great similarity between the Latvian wolf population and the neighbouring populations of the species. For example, mean CbL in males from Latvia was 23.7 cm, in the Belarussian part of the Białowieża Forest it was the same, and in the Polish part it was 23.8 cm. Zygomatic breadth of males from Latvia was bigger than that of wolves from Białowieża Forest: 14.3 cm versus 14.1 (Polish part) and 13.9 cm (Belarussian part) (Geptner *et al.* 1967, Okarma and Buchalczyk 1993). However, condylobasal length of females from Latvia was smaller than that from the Białowieża population: 22.5 cm vs 22.9 and 22.7 cm accordingly (Geptner *et al.* 1967, Okarma and Buchalczyk 1993). Zygomatic breadth of females from Latvia was 13.2 cm vs 13.5 cm in females from the Polish part of the Białowieża Forest (Okarma and Buchalczyk 1993). Comparison of some selected skull indices of the Latvian wolves with those from the Białowieża population showed that skull proportions were fairly similar (Table 3).

Condylobasal length of the studied skulls varied from 20.0 to 25.9 cm, which exceeded the range 22.0 to 25.0 cm indicated previously for the wolves from Latvia by Tauriņš (1982). However, mean condylobasal length of 23.7 cm (males) and 22.5 cm (females) does not exceed the lower limit previously noted by Rossolimo and Dolgov (1965) for the forested zone of the former USSR.

Coefficients of variation of cranial parameters were generally higher in males with the exception for five characteristics (Table 1). The lowest variation was

Table 3. Comparison of some skull indices (%) of wolf skulls from Białowieża Forest and Latvia. [1] Polish part; Okarma and Buchalczyk 1993, [2] Belarussian part; Geptner *et al.* 1967.

Males				Females			
Index	Białowieża[1]	Białowieża[2]	Latvia	Index	Białowieża[1]	Białowieża[2]	Latvia
EntB/CbL	19.7	19.4	19.7	Zyb/CbL	54.6	58.1	58.6
LB/CbL	17.7	17.9	17.5	MdL/CbL	78.8	–	79.4
LB/EntB	89.9	92.4	88.5	ZyB/MdL	74.8	–	73.8

observed in ToL and CbL. Okarma and Buchalczyk (1993) obtained similar results from the Polish population.

Sexual dimorphism was statistically significant for all 19 parameters (Table 1). Skulls of females were smaller than those of males, similarly to the Polish population (Okarma and Buchalczyk 1993) and those from different regions of the former USSR (Geptner *et al.* 1967). The difference was the least pronounced in C_1Br: 1.5 cm in males and 1.4 cm in females ($t = 2.3$, $p < 0.05$).

A pronounced difference between the two parts of the Latvian wolf population – from the Kurland Peninsula and the rest of the country – was found. Eleven parameters were bigger in the northeastern population in both males and females, two in males only and one in females only (Table 2). This possibly indicates the impact of invaders from the neighbouring wolf populations in the north and the east. Although there are no geographical barriers between the two subpopulations, wolves of the Kurland Peninsula are separated from the eastern source population by the regions with low wolf density like deforested Zemgale lowland in the south of the country. Therefore, some divergence can not be excluded. Moreover, the difference can be heightened by more intensive hunting in Kurland, resulting in a lower average age of the animals there. It has been often reported in national press that hunters of Kurland have carried out wide wolf control measures while in eastern regions wolves are less intensively persecuted and are killed mostly by accident. Interestingly, facial length was significantly bigger in wolves from the Kurland Peninsula both in males and females. Another parameter – length of *incisura palatina* – was also significantly bigger in Kurland but in females only (Table 2).

Tooth formula in the Latvian wolf population is relatively conservative – anomalies occurred only in 9.6%. All deviations in tooth pattern belong to the second group of variations according to Wolsan (1984b) as the tooth set in wolves is rigid having no extreme variants as it is observed, for instance, in weasels (Wolsan 1983). In Ukraine, oligodonty and polydonty was found in 16.2% of skulls (Lihotop 1994). In wolves from the Western Carpathians, variations of dentition happened in 27.7% of animals (Hell and Duricka 1989) while in the Far East of Russia deviations from the normal tooth formula were found from 21.3 to 38.3% of the population (Yudin 1989). Such a high proportion of irregular tooth number was partly due to traumatic changes in tooth formula, though, natural causes played the main role (Yudin 1989). Congenital deviations in the teeth number may have two different causes – from an additional tooth germ and as a result of splitting of one germ due to a mutation or other factors affecting genetic control (Wolsan 1984c). Only the second type can be called true anomalies (Wolsan 1984b). In this case additional teeth are similar to the adjacent ones, which is corresponding to most of the deviations described from Latvia.

Traumatic deviations in the tooth formula of Latvian wolves also were rare (2.1% of all the skulls). Possibly, this is due to the fact that the animals with serious injuries are those most likely to be eliminated.

In Poland, the percentage of oligodonty and polydonty was similar to that in Latvia – 10.7% (Buchalczyk *et al.* 1981). The proportion of polydonty in the population was higher than that of oligodonty in the Carpathians and Poland (Buchalczyk *et al.* 1981, Hell and Duricka 1989) and lower in Ukraine and the Far East of Russia (Yudin 1989, Lihotop 1994). In different regions, certain types of dental anomalies are similar, eg oligodonty on M_3, polydonty on premolars (Buchalczyk *et al.* 1981, Hell and Duricka 1989, Yudin 1989, Lihotop 1994).

Congenital tooth anomalies (oligodonty and polydonty) were more often found in males, although the difference was not statistically significant. The same trend has been described from Poland (Buchalczyk *et al.* 1981) and Ukraine (Lihotop 1994).

Premolars and minor molars are less functional than other teeth and therefore they are subject to active evolutionary transformations resulting in deviations in teeth number (Yudin 1989). However, incisors also often show variation (Wolsan 1984a). Interestingly, the anomaly with two additional symmetrical incisors has also been described from Poland (Buchalczyk *et al.* 1981).

Thus, the similarity between the close populations of Latvia and Poland supports the idea expressed in previous studies that dental deviations might be used in phylogenetic studies and in studies on the population structure of the species (Buchalczyk *et al.* 1981, Hell and Duricka 1989, Yudin 1989). Further studies from the other Baltic States (Estonia and Lithuania) and the neighbouring territories in Russia and Belarus would add more information and would make a thorough comparative analysis possible.

Acknowledgements: We thank A. Strazds, M. Rantiņš, E. Doniks, J. Baumanis, J. Tauriņš for their help in data collection. We are very grateful to Dr H. Okarma and three anonymous reviewers for their invaluable help while reviewing and commenting on the paper. We express our cordial appreciation to N. Benvie for reviewing the English of the manuscript.

References

Ansorge H. 1994. Intrapopular skull variability in the red fox, *Vulpes vulpes* (Mammalia, Carnivora, Canidae). Zoologische Abhandlungen Staatliches Museum für Tierkunde Dresden 48(6): 103–123.

Ansorge H. and Meinig H. 1996. Craniological data and age structure of red foxes (*Vulpes vulpes arabica* Thomas, 1902) from Oman. Mammalia 12: 13–19.

Bibikov D. I. (ed) 1985. [The wolf. History, systematics, morphology, ecology]. Nauka Publishers, Moskva: 1-606. [In Russian]

Buchalczyk T., Dynowski J. and Szteyn S. 1981. Variations in number of teeth and asymmetry of the skull in the wolf. Acta Theriologica 26: 23–30.

Geptner V. G., Naumov N. P., Yurgenson P. B., Sludskii A. A., Chirkova A. F. and Bannikov A. G. 1967. [Mammals of the USSR]. Vol. 2. Vysshaja shkola Publishers, Moskva: 1-1004. [In Russian]

Görner M. and Hackethal H. 1987. Säugetiere Europas. Radebeul: Neumann Verlag, Leipzig: 1–372.

Hell P. and Duricka J. 1989. Anomalies of the dentition of the West Carpathian wolf (*Canis lupus*). Folia Venatoria 19: 339–347. [In Slovak with English summary]

Kalniņš A. 1943. [Huntsmanship]. Latvju Grāmata, Riga: 1-704. [In Latvian]

Liepa I. 1974. [Biometry]. Zvaigzne, Riga: 1-336. [In Latvian]

Lihotop R. I. 1994. Cranial and dentition anomalies in wolf of the Ukranian territory. Vestnik Zoologii 3: 45–50. [In Russian with English summary]

Novikov G. A. 1956. [Carnivorous mammals of the USSR fauna]. AN SSSR Publishers, Moskva – Leningrad: 1–293. [In Russian]

Okarma H. and Buchalczyk T. 1993. Craniometrical characteristics of wolves *Canis lupus* from Poland. Acta Theriologica 38: 253–262.

Rossolimo O. L. and Dolgov V. A. 1965. Variability of the skull in *Canis lupus* Linnaeus, 1758 from the USSR. Acta Theriologica 10: 195–207. [In Russian with English summary]

Sokal R. R. and Rohlf F. J. 1981. Biometry. W. H. Freeman and Co., New York: 1–859.

Tauriņš E. 1982. [Latvian mammals]. Zvaigzne, Riga: 1–256. [In Latvian]

Yudin V. G. 1989. The dental system of *Canis lupus* (Carnivora, Canidae) from the far east of the USSR. Zoologicheskiĭ Zhurnal 68(8): 115–123. [In Russian with English summary]

Wolsan M. 1983. Ancestral characters in the dentition of the weasel *Mustela nivalis* L. (Carnivora, Mustelidae). Annales Zoologici Fennici 20: 47–51.

Wolsan M. 1984a. Concerning the variation in the number, shape and size of incisors in fissiped carnivores. Acta Zoologica Cracoviensia 27: 107–120.

Wolsan M. 1984b. Two dental anomalies in the weasel (*Mustela nivalis* L.): a supernumerary premolar and reduced upper molar (Mammalia, Carnivora, Mustelidae). Zoologische Abhandlungen 40(5): 67–70.

Wolsan M. 1984c. The origin of extra teeth in mammals. Acta Theriologica 29: 128–133.

Received 13 October 1999, accepted 12 January 2000.

2.3. Discussion and conclusions

Body parameters and cranial characteristics were similar to those of wolves from the neighbouring countries (Prusaite 1961b, Гептнер и Наумов 1967, Buchalczyk 1981, Sokolov and Rossolimo 1985, Okarma and Buchalczyk 1993) confirming the population's integrity. However, the craniometrical data indicated some disruption between the western and eastern parts of the population within Latvia, although data from body parameters did not show any geographic difference. This requires further studies in combination with the research on wolves' demography, as such geographical dimorphism can also indicate the differences in the average age between the two sub-populations resulting from different hunting intensity.

Also, various anomalies in dental formula, which are frequent in carnivores (Wolsan 1984, Kvam 1985, Wolsan et al. 1985, Wolsan 1988, 1989, Federoff and Nowak 1998, Cerveny and Koubek 2000), were found in wolves from Latvia. Interestingly, such anomalies as duplicate upper incisors were found also in Poland and Russia (Buchalczyk et al. 1981, Vilà et al. 1993).

Most of the harvested wolves from Latvia had similar pelt colours to those of wolves from other localities in the forest zone of Europe (Prusaite 1961b, Sokolov and Rossolimo 1985) – greyish brown with different colour intensity, unlike the North American wolves, which display much higher degree of variability, ranging from nearly white to black (Goldman 1937). Black wolves were sometimes reported from the Baltics (Prusaite 1961b, Сабанеев 1988) but during this study such cases were not found. Abnormal pelt colour may be an indication of hybridisation with dogs (see chapter 4).

The evidence of the high proportion of injuries of human origin among harvested wolves indicates a heavy hunting pressure. Taking into account data on the demographic structure and population development, it implies that the population is currently being over-exploited, and changes in the species management are required.

It can be concluded that:

- Body parameters of wolves from Latvia were similar to those of wolves from adjacent territories;

- The degree of sexual dimorphism typical for wolves from Latvia was found both in body characteristics and in cranial parameters, males being bigger than females;
- Craniometrical differences found between wolves from western and eastern Latvia suggest that some degree of disruption within the population has occurred, the reasons to be specified by further research;
- The proportion of polydonty (5.3%) and oligodonty (2.1%) was not higher than elsewhere within the Eurasian distribution range of wolves;
- Nearly 10% of harvested individuals had former injuries, half of which were of anthropogenic origin, which suggests that the population is subject to heavy hunting pressure;
- The age and sex structure of the hunting bag (prevalence of females and the low proportion of old animals) also reflects high harvest rates.

3. Trophic ecology of wolves in Latvia

3.1. Introduction

"What does the predator eat?" is the most basic question in studying the predator - prey relationships. One has to answer it first before going any further to predation rates, selectivity of prey and, ultimately, to the impact on the prey populations. Many dietary studies on wolves have been carried out both in Eurasia (Bibikov 1985, Железнов 1990, Meriggi et al. 1991, Okarma et al. 1995, Bobek and Nowicki 1996, Haibin and Fuller 1996, Olsson et al. 1997, Poulle et al. 1997, Jędrzejewska and Jędrzejewski 1998 etc.) and North America (Messier and Crête 1985, Milne et al. 1989, Huggard 1993, Weaver 1993, Boyd et al. 1994, Mech 1995, Boertje et al. 1996, Spaulding et al. 1997, Hayes and Harestad 2000, Mech et al. 2001 etc.), while in the Baltic countries only a few case studies are known (Prusaite 1961a; Valdmann et al. 1998, Andersone 1998, 1999).

Usually the most abundant ungulate species is dominating in the wolf diet – red deer in Poland (Jędrzejewska et al. 1991, Jędrzejewski et al. 1992, Lesniewicz and Perzanowski 1993, Smietana and Klimek 1993, Jędrzejewska et al. 1994, Okarma 1995, Okarma and Jędrzejewski 1996 etc.), roe deer – in some parts of the former USSR, also in Estonia and Lithuania (Prusaite 1961a, Филонов 1982, Bibikov 1985, Valdmann et al. 1998), wild boar – in Italy, Slovakia (Brtek and Voskar 1987, Matteucci 1992, Mattioli et al. 1995, Meriggi et al. 1996), moose – in Scandinavia, parts of Russia and high latitudes of North America (Peterson and Page 1983, Peterson et al. 1984, Mech 1995, Olsson et al. 1997, Козловский 1997, Gade-Jørgensen and Stagegaard 2000), muskox – in Greenland (Marquard-Petersen 1998), wild reindeer - in Siberian tundra habitat (Линейцев 1983, Железнов 1990, 1992).

Wolf is a very plastic generalist species, easily adapting to particular conditions, which causes its highly variable diet. Moreover, diet composition can change with time depending on the dynamics of the prey populations (Boyd et al. 1994, Mattioli et al. 1995). Therefore, regional case studies are essential not only from the scientific, but also from the management point of view, as it is difficult to extrapolate data obtained in other localities (and to base management decisions on them) without a high risk of error.

The objective of this study was to investigate wolf diet in Latvia, its seasonal, geographical and sexual variation as well as to compare it with the diet of another sympatric large carnivore species – lynx *Lynx lynx* Linnaeus, 1758.

3.2. Results

Paper VI

3.2.1. Winter diets of wolf and lynx in Estonia and Latvia – implications for predator-prey management

Winter diets of wolf and lynx in Estonia and Latvia - implications for predator-prey management

Harri Valdmann, Zanete Andersone, Ott Koppa, Janis Ozolins, Guna Bagrade

Abstract

From 1997 to 2000, winter diets of wolf *Canis lupus* and lynx *Lynx lynx* in Latvia and Estonia were investigated. Stomach contents of hunted animals and scats (Estonia = 127 stomach contents with prey remains and of 28 lynx scats; wolf data was from previous study; Latvia - stomach contents; wolf = 99, lynx n = 49) were analysed. Cervids appeared to be the staple food for both predator species. Lynx diet to a high extent consisted of cervids (Estonia = 52%, Latvia = 88%), roe deer presumably predominating. The ratio of cervids in the lynx diet (Latvia) was significantly higher than in the diet of wolves ($t = 4.2$, $p < 0.01$). Mountain hare *Lepus timidus* made up from 9% (Latvia) to 31% (Estonia) of the lynx diet, red fox (*Vulpes vulpes*) - to 7.1% in Estonian sample. Wolf diet was more diverse and apart from cervids (44.1% in Latvia; 63% in Estonia) included wild boar *Sus scrofa* (32.3% in Latvia; 17% in Estonia), carrion (10.3%; Latvia), small rodents (10%; Estonia) and other food items. Proportion of empty stomachs was high both in wolves (37%) and lynxes (35%) in Latvia. Range of stomach content weights varied from zero to more than 4kg in wolves and almost 1.5kg in lynx.

Department of Animal Development and Systematics, University of Tartu, 46 Vanemuise Street, 51014, Tartu, Estonia, e-mail: harriva@ut.ee; (HV; OK);
Ķemeri National Park, "Meža māja", Ķemeri - Jūrmala, LV-2012, Latvia, e-mail: zanete.a@delfi.lv; fax: +371-7765040 (ŽA)[1];
State Forest Service, 13.Janvāra Str. 15, Riga, LV-1932, Latvia (JO);
Latvian Museum of Natural History, K. Barona Str. 4, Riga, LV-1050, Latvia (GB)
[1] - postal address till March 2002: Norwegian Institute for Nature Research (NINA), Tungasletta-2, 7485 Trondheim, Norway

Key words: *Canis lupus*, Latvia, Estonia, *Lynx lynx*, winter diet

RH: Winter diets of wolf and lynx in Latvia and Estonia

Introduction

Both the wolf *Canis lupus* Linnaeus, 1758 and the lynx *Lynx lynx* Linnaeus, 1758 have been severely persecuted in Europe, for centuries being regarded either as pests or human competitors for wild prey (Boitani 2000; Breitenmoser *et al.* 2000). As a result, their populations have been reduced considerably and nowadays the species play their natural ecological role in very few localities. Latvia and Estonia are one of the last strongholds of large carnivores where sympatric populations still exist. As both of these predators are harvested in Latvia and Estonia, as are their ungulate prey, it is very important to develop guidelines for sustainable management of both predators and prey.

Management of large carnivores can only be successful if it is based on a scientific background. Hunting success and food choice may be the two most basic factors determining the fitness of carnivores (Sunde and Kvam 1997), the study of their feeding ecology can provide valuable basic information and can be considered a logical first step in a regional large carnivore research programme. It is also important to assess the predators' impact on prey populations for planning ungulate management (Geptner and Sludsky 1972; Danilov and Rusakov 1979; Bibikov 1985).

Unfortunately, there is little data available from the Baltic region. Lynx diet has been studied briefly in neighbouring Leningrad oblast (Novikov 1970) and in Lithuania (Kazlauskas and Matuzevicius 1981), while the first studies on large carnivore ecology in Estonia and Latvia started in 1990s only (Andersone 1998, Valdmann *et al.* 1998, Andersone 1999, Ozoliņš 2000, Ozoliņš and Andersone 2000).

Of special interest is the degree of diet overlap between wolves and lynx, and regional differences in the diet between Estonia and Latvia. The current paper is aimed to sum the results of dietary studies of wolf and lynx in Estonia and Latvia and to draw some preliminary management guidelines.

Study area

Estonia and Latvia are situated in a transition zone of temperate climate between the coniferous Euro-Siberian taiga and European deciduous forests, 47.6% of the territory of Estonia and 44% of Latvia being covered by forest and woodlands. Permanent snow cover becomes established at the beginning of December, at the earliest; and by the end of March, the snow can be more than half a metre deep. In mild winters, however, Estonia and Latvia may not have lasting snow cover at all.

Being relatively small countries (Estonia occupies 45 215.4 km^2, Latvia - 64,500 km^2), Estonia and Latvia together host a population of about 600 wolves (about 300-400 in Latvia) and 1200 lynxes (about 400 in Latvia). In total, 64 species of mammals have been recorded in Estonia and Latvia, three of them have been introduced: the racoon dog *Nyctereutes procyonoides*, the American mink *Mustela vison,* and the muskrat *Ondatra zibethica*. The European beaver *Castor fiber*, hunted to extinction during 19th century, was reintroduced to Latvia in 1927 and to Estonia in the 1950s. Red deer *Cervus elaphus*, which was also re-introduced, is more common in Latvia than in Estonia, where it inhabits only western islands and southern parts of the republic. Other common ungulates in both countries are wild boar *Sus scrofa*, roe deer *Capreolus capreolus* and moose *Alces alces*.

Material and methods

Data from Estonia were collected during winters of 1998/99 and 1999/2000 and consist of 127 lynx stomachs and 28 lynx scats. Lynx carcasses were collected from hunters. The hunting season for lynx starts from 1 November and lasts till 28 February. Data on wolf diet is from a previous study (Valdmann *et al.* 1998).

Scats were collected in the process of snow-tracking lynx and belonged to several different animals, thus probably containing little bias. Snow-tracking was conducted in Soomaa National Park in south-western Estonia, approximately 250 km^2.

Carcasses found while snow-tracking were divided by weight to young animals (<15 kg; < 1.5 yrs.) and adults (> 15 kg; > 1.5 yrs.) (Schmidt *et al.* 1997) and sexed. Data was collected during four winter months (Nov - Feb). For analysis of seasonal differences in the diet, data was pooled up to two periods - late autumn (Nov-Dec) and late winter (Jan-Feb).

Material for the studies of the winter diet of wolf and lynx from Latvia was collected from 1 October to 31 March, in 1997 - 2001. Stomachs of wolves and lynx legally hunted in different parts of Latvia were collected and examined. In total, 98 stomachs of wolves and 49 stomachs of lynx were collected from hunters. Samples from both species were distributed unevenly over Latvia, mostly from northeastern and western parts, probably because of the presence of active hunters.

Stomach contents were either analysed fresh or kept in a freezer and analysed after thawing. Stomach contents were freshly weighted (Latvian sample only) using an electronic balance (SC-3000) to 1 g precision and then a sample was taken in order to determine the prey species.

Preparation of hair samples followed the standard procedures (Goszczynski 1974, Reynolds and Aebischer 1991). Identification of prey species was based on hair microstructure according to the key by (Day 1966; Teerink 1991) and our own reference collections. However, due to the great similarity in hair structure of cervids, and therefore, a high probability of bias, separate species within this family were not determined and were combined into one category in the Latvian sample unless the presence of other body parts or hair length allowed roe deer to be separated from red deer and moose.

Frequency of occurrence was used to assess the importance of food items in the diet (Ciucci *et al.* 1996).

The homogeneity in the overall ratio of roe deer and small game in the diet of lynx and wolf between sexes, age groups and study period was tested using one-way ANOVA. Differences in frequencies of occurrence were checked by t-test (Liepa 1974, Sokal and Rohlf 1997).

Standard error was calculated according to the formula:

$$SE = \sqrt{\frac{pq}{n}}$$

p is proportion of prey item in diet

q is 100 - p

n is number of prey items in diet

Food niche overlap between wolf and lynx winter diets was calculated using the index of Pianka (Krebs 1999).

Food niche breadths (B) were calculated after Levins (1968) using percent occurrence of a particular prey group and except for the Estonian lynx sample after relative prey biomass. It was calculated for 4 main food groups (ungulates, hares, rodents and other carnivores):

$$B = 1/\sum p_i^2,$$

where p_i - percent occurrence of a particular prey group.
For wolf in the Estonian sample biomass of ungulates was used, in the Latvian sample three more prey categories (beaver, other carnivores (mainly dog) and carrion) were added.

Results

A total of 11 prey species and taxas were identified in Estonia and Latvia (Table 1). Roe deer, hares (brown *Lepus* *europaeus* and mountain *Lepus timidus*) and red fox (*Vulpes vulpes*) were the most frequent components of lynx diet. One stomach of an adult male from the Estonian sample was filled with dry hay, this specimen was also heavily infested with roundworms *Toxocaria sp.*

One-way ANOVA test within each prey category revealed no indication of any association with sex or age group of local lynx diets. Males and females foraged equally ($F = 0.12$; $p = 0.73$). Neither were there any differences in the roe deer - other preys ratio between late autumn (Nov-Dec) and late winter (Jan-Feb) ($F = 2.17$; $p = 0.14$). Diet of juveniles did not differ from diet of adults ($F = 0.69$; $p = 0.40$). But some prey items from the Estonian sample, like wild boar, red deer and raccoon dog were found only in the diet of adult males. Remains of domestic pig (carcasses of dead domestic animals are sometimes used for hunting bait) were found only in the diet of the young individuals (two cases, Estonian sample). Weasel *Mustela nivalis* was found in Latvian sample.

Wolf diet during winter was much more diverse than that of lynx (Table 2). Apart from the cervids, it included also wild boar, beaver, raccoon dog, carrion (often used as bait by hunters), birds and in one case a stomach was filled with grass.

In general, ungulates largely dominated in winter diets of local lynx (Fig.1) and wolf (Fig.2) in both countries.

Due to the relatively large proportion of hares (31%) and red fox *Vulpes vulpes* (7.1%) in the lynx winter diet in Estonia, the ratio of cervids was lower than that in Latvia (Fig.1.).

Wolves exhibited different predation patterns, consuming wild boar in relative large proportions (Fig.2).

One-way ANOVA test within each prey category of Latvian wolf sample revealed no indication of any association with sex or location with diets ($F = 1.91$; $p = 0.16$).

The ratio of cervids in the lynx diet was significantly higher than that of the wolf ($t = 4.2$, $p < 0.01$) - minor prey and carrion was more often found in female wolf stomachs ($t = 2.12$, $p < 0.05$) while beavers were more often found in males ($t = 2.14$, $p < 0.05$).

A large proportion of the wolf stomachs from the Latvian sample were empty. Feeding on bait (or leftovers from the slaughter-houses) was more typical for female wolves while in males it was found only once. Among the wolf stomachs, 36.7% were empty - respectively 40.4% in females and 31.2% in males. However, the difference between females and males was not statistically significant. In lynx, 34.7% of stomachs investigated were empty. In females, 39.1% of stomachs were empty while in males - 28.6%, but the difference was not statistically significant.

The average weight of the fresh stomach contents in wolves from Latvia was 990.3 ± 849.3 g, ranging from zero to 4350 g. In lynx from the Latvian sample, stomach content's average weight was 440.5 ± 258.7 g, with the maximum weight 1370 g. The average weight of lynx female stomachs was slightly smaller than that of males - 431.1 ± 215.0 g versus 445.4 ± 323.9 g. In wolf, the opposite was observed - female stomachs were fuller, 1070.7 ± 938.0 g versus 850.6 ± 668.3 g in males.

Local diets of wolves (Valdmann *et al.* 1998) and lynx in Estonia coincided significantly (index of Pianka 0.8) and contained seven common diet items. Diets of wolf and lynx in Latvia coincided to a lesser extent (index of Pianka 0.44) and contained only three common diet items.

Levin's niche breadths, calculated using percent occurrence of a particular prey group for lynx in Estonia and Latvia were respectively 2.7 and 1.3; for wolf respectively 1.55 and 1.3. Niche breadths by relative prey biomass for wolf were respectively 2.2 and 2.5.

Discussion

The main prey of wolves in Europe are ungulates (Okarma 1995), with the proportion of each species in the diet depending on the ungulate community of the region. Wild ungulates are often preferred over livestock (Poulle *et al.* 1997). Moose dominates in the wolf diet in Finland (Gade-Jorgensen and Stagegaard

2000), red deer - in Poland (Lesniewicz and Perzanowski 1989; Okarma *et al.* 1995; Jedrzejewski *et al.* 2000; Smietana and Klimek 1993), wild boar - in some parts of Italy (Mattioli *et al.* 1995, Meriggi *et al.* 1996), Belarus (Rukovsky 1985), roe deer - in the European part of the former USSR (Rukovsky 1985), some parts of Poland (Suminski and Filipiak 1977) and Spain (Cuesta *et al.* 1991).

Lynx tend to specialise on small or medium sized ungulates - roe deer, chamois (*Rupicapra rupicapra*) and, locally, semidomestic reindeer (*Rangifer tarandus*) (Pulliainen 1981, Aanes *et al.* 1998, Pedersen *et al.* 1999, Weber and Weissbrodt 1999, Koubek *et al.* 2001).

Roe deer, where it's abundant, is the staple food for lynx, e.g., in Poland (Reig and Jedrzejewski 1988; Okarma *et al.* 1995, 1997, 2000), in the Alps (Jobin *et al.* 2000), Swiss Jura Mountains (Weber and Weissbrodt 1999), in some parts of Norway (Aanes *et al.* 1998).

Studies on lynx diet in Palearctic (Jedrzejewski *et al.* 1993) have demonstrated strong dependance of ungulate/lagomorphs ratio in the lynx diet on the latitude.

The proportion of lagomorphs in the diet is relatively large in the north (Pulliainen and Hyypia 1975) and decreases with latitude; south of 52 °-54 ° ungulates dominating lynx diets (Jedrzejewska and Jedrzejewski 1998). Concerning eastwardwestward trends, the percentage of lagomorphs in the lynx diet is higher in eastern populations (Pulliainen *et al.* 1995).

Diets of lynx in Estonia and Latvia seem to represent the middle of these trends - both lagomorphs and roe deer form a relatively large part of it. As roe deer dominate in the local lynx diet, the above-mentioned "borderline" of Jedrzejewska and Jedrzejewski (1998) must be moved - wild ungulates can dominate at significantly higher latitudes than 52 ° - 54 °, and in Estonia and Latvia roe deer clearly sustains the lynx population. This probably reflects the general ungulates oriented game management in these countries.

As Estonia is north of Latvia, it predictably possesses higher proportion of lagomorphs in the lynx diet in accordance with the above-mentioned north-south trend (Jedrzejewska and Jedrzejewski 1998). The higher proportion of roe deer in the Latvian sample can also be explained by better availability of roe deer as prey in Latvia - densities of roe deer in Latvia and Estonia are 1.06 and 0.66 ind./km^2 accordingly (official census data). As found, the proportion of roe deer in the lynx diet rapidly increases as the roe deer numbers grow (Okarma *et al.* 1997).

Studies in Bialowieza, where roe deer density is low, show that lynxes preyed on red deer disproportionately to their share in the ungulate community (Jedrzejewski *et al.* 1993). It is unlikely that this is the case in Latvia as roe deer is the most common ungulate species all over the country. Unfortunately, reliable distinction between roe deer and red deer hairs in the study was impossible therefore, a certain proportion of cervids remained undetermined. However, 82.7% of cervids in the lynx diet were precisely identified as roe deer due to the hair length or the presence of some other body parts indicating the size of the animal. Therefore, it is clear that roe deer constitute the bulk of lynx diet in wintertime, although some cases of depredation on red deer (mainly yearlings) were documented locally (Gaross 1997).

As generally recognised, hare densities tend to decline everywhere in Europe and thus probably the time lag between the lynx diet study in Lithuania (Kazlauskas and Matuzevicius 1981) and the current study explains the high proportion of hares (60%) in the Lithuanian study. This is probably also true for the study in neighbouring Leningrad district (Novikov 1970). In Latvia, hare densities have considerably declined since early 20th century (Taurins 1975), which can possibly explain the low percentage of hares in the lynx diet.

According to studies from Europe, intra-guild predation on foxes is widespread (Adlerberg 1935, Haglund 1966, Novikov, 1970, Pulliainen 1981, Sunde and Kvam 1997, Linnell *et al.* 1998, Sunde *et al.* 1999, 2000). The consumption of killed carnivores is not universal among cases of intra-guild predation (Peterson 1996), but fox is clearly regarded as prey and if lynx are not disturbed, most of the available meat on carcasses is consumed (Linnell *et al.* 1998). Sometimes a whole litter of foxes can be killed (Novikov 1970).

Unlike the studies in the Alps (Liberek (1992); ref: Weber & Weissbrot 1999), where predation on foxes may result from an individual specialisation to this prey, in the Estonian sample fox was clearly the most consumed alternative prey (7.1 %). Intraguild predation, though, was not typical for Latvian lynx - a small mustelid predator (weasel) was found in the stomach of lynx only once; larger sample size would have probably increased the proportion of fox in it as fox densities in Latvia are generally recognised as high (Ozolins and Pilats 1995).

Potential trade-off of intraguild predation on foxes and other carnivores is transmission of certain diseases in the process. Lynx have been recorded to die of sarcoptic mange (Linnell *et al.* 1998) and rabies (whole lynx family was found to be rabid in Estonia in winter 2001). In Estonia, scabies and rabies are widespread in foxes (Viltrop *et al.* 2000), thus, intraguild predation on them can create a potential transmission link for spreading these diseases to lynx.

The data on wolf diet and prey selectivity in Estonia have been analysed earlier (Valdmann *et al.* 1998; Table 2) and found to consist mainly of ungulate prey. Despite the domination (F%) of roe deer in diet, wild boar was found to be a preferred prey. Although slightly avoided, moose predictably dominated in relative biomass of ungulate prey. Avoidance of moose was explained by fragmentation of wolf packs as a result of wolf hunting, which can also be the case in Latvia where hunting pressure on wolves is high (Ozolins *et al.* in press). The later studies in Estonia have confirmed the role of wild boar as preferred prey - wolves quite regularly check the places, where supplementary feeding has been provided to wild boar. In general, wolves' diet in both countries seem to be similar as cervids and wild boar predominate in both cases, wild boar being more common in the diet of wolves in Latvia (Table 2).

High proportion of empty stomachs of both wolves and lynx can be explained by harsh feeding conditions during winter season. Also, the hunting method can influence the ratio of empty stomachs - distressed animals may empty their stomachs (Korytin 1986). Wolves kept in "fladry" for a couple of days digest the food present in the stomachs, which can give a biased result.

Although the analysis of stomach contents cannot answer the question of what the numerical and functional response relationships are, they can nevertheless give a hint of the predators' impact on the prey populations (Jobin *et al.* 2000). The results of the study demonstrate that species dominating in the prey community (roe deer, wild boar, moose and red deer) also dominate in the large predators' diet. However, more detailed research is needed in order to determine the predation rates and impact on the prey populations.

As shown, the diets of wolves and lynx in Estonia and Latvia overlap significantly, roe deer obviously being exposed to the highest degree of predation. Therefore, a proper management of this species is essential for both large carnivores but especially for lynx, which seems to be strongly dependent on the availability of this ungulate species. Consuming the alternative prey - fox - in relative large proportions in Estonia may already indicate a shortage of the main prey - roe deer and hares for sustaining it's relatively large population. Reduction of the hunting quotas and better law enforcement to reduce poaching on roe deer could be suggested in order to reduce the pressure on the species. Another recognised local problem in roe deer management is stray dogs chasing and killing roe deer. Equally important for wolf is the proper management of wild boar populations in both countries.

Acknowledgements

We sincerely thank A. Strazds, J. Baumanis, V. Rēders, A.Dundurs and numerous anonymous hunters and State Forest Service's employees for helping with material collection. We also thank A. Pupila, A. Ornicāns and M.Pihlak for their practical help. We thank Dr. J. Linnel for valuable comments on the manuscript. The manuscript was prepared during the stay of Zanete Andersone at the Norwegian Institute for Nature

Research funded by The Research Council of Norway (scholarship IS OE01-51).

References

Aanes R., Linnell J.D.C., Perzanowski K., Karlsen J. and Odden J. 1998. Roe deer as prey. [In: The European Roe Deer: The Biology of Success. Andersen R., Duncan P. and J.D.C. Linnell, eds]. Scandinavian University Press, Oslo: 139-159.

Adlerberg G. P. 1935. [Lynx.] [In: Animals of Arctic. N.A. Smirnov, ed.]. Leningrad: 439-450. [In Russian]

Andersone Z. 1998. Summer Nutrition of the Wolf (*Canis lupus*) in the Slītere Nature Reserve, Latvia. Proceedings of the Latvian Academy of Sciences. Section B, 52 (1/2): 79-80.

Andersone Z. 1999. Beaver: A new prey of wolves in Latvia? Comparison of winter and summer diet of *Canis lupus* Linnaeus, 1758. [In: Beaver Protection, Management, and Utilization in Europe and North America. P. Busher and R. Dzieciolowski, eds]. Cluwer Academic / Plenum Publishers, New York: 103-108.

Andersone Z., Balciauskas L. and Valdmann H. Human-Wolf Conflicts in the East Baltic - past, present and future. Proceedings of the 2nd International Wildlife Management Congress. [In press]

Bibikov D.I., ed. 1985. [The Wolf. History, Systematics, Morphology, Ecology]. Nauka Publishers, Moscow: 1-606. [In Russian]

Boitani L. 2000. Action Plan for the conservation of wolves

(Canis lupus) in Europe. Council of Europe Publishing, Nature and environment, No.13: 1-86.

Breitenmoser U., Breitenmoser-Würsten C., Okarma H., Kaphegyi T., Kaphygyi-Wallman U. and Müller U. M. 2000. Action Plan for the conservation of the Eurasian lynx (*Lynx lynx*) in Europe. Nature and Environment, No. 112, Council of Europe Publishing: 1-69.

Ciucci P., Boitani L., Pelliccioni E. R., Rocco M. and Guy I. 1996. A comparison of scat-analisys methods to assess the diet of the wolf *Canis lupus*. Wildlife Biology 2: 37-48.

Cuesta L., Barcena F., Palacios F. and Reig S. 1991. The trophic ecology of the Iberian Wolf (*Canis lupus signatus* Cabrera, 1907). A new analysis of stomach data. Mammalia 55 (2): 239-254.

Danilov P. I. and Rusakov O.S. 1979. [Predatory animals of the North-West of the USSR]. Nauka, Leningrad: 132-148. [In Russian]

Day M. G. 1966. Identification of hair and feather remains in the gut and faeces of stoats and weasels. Journal of Zoology 148: 201-217.

Gade-Jorgensen I. and Stagegaard R. 2000. Diet composition of wolves Canis lupus in east-central Finland. Acta Theriologica 45 (4): 537-547.

Gaross V. 1997. [The impact of ecological, biological and other factors on the population of Cervidae, wolf and lynx]. Mezzinatne 7 (40): 108-123. [In Latvian with English summary]

Geptner V. G. and Sludsky A. A., eds. 1972. [Mammals of the

Soviet Union]. V.2 (II), Vyshaja shkola, Moskva: 385-457. [In Russian]

Goszczynski J. 1974. Sudies on the food of foxes. Acta Teriologica 19 (1): 1-18.

Haglund B. 1966. Winter habits of the lynx (*Lynx lynx* L.) and wolverine (*Gulo gulo* L.) as revealed by tracking in the snow. Viltrevy 4: 81-299. [In Swedish with English summary]

Jędrzejewski W., Schmidt K., Miłkowski L., Jędrzejewska B. and Okarma H. 1993. Foraging by lynx and its role in ungulate mortality: the local (Bialowieża Forest) and the Palaeartic viewpoints. Acta Theriologica 38 (4): 385-403.

Jędrzejewski W., Jedrzejewska B., Okarma H., Schmidt, K., Zub K. and Musiani M. 2000. Prey selection and predation by wolves in Bialowieza Primeval Forest, Poland. Journal of Mammology 81 (1): 197-212.

Jędrzejewska B. and Jędrzejewski W. 1998. Predation in vertebrate communities. The Białowieża Primeval Forest as a case study. Springer Verlang, Berlin: 1-450.

Jobin A., Molinari P. and Breitenmoser U. 2000. Prey spectrum, prey preference and consumption rates of Eurasian lynx in the Swiss Jura Mountains. Acta Theriologica 45 (2): 243-252.

Kazlauskas J. and Matuzevicius A. 1981. On the helminth fauna and ecology of lynxes in Lithuania. Acta Parasitologica Lituanica 19: 8-11.

Korytin S.A. 1986. [Habits of wild animals]. Agropromizdat, Moskva: 1-318 pp. [In Russian]

Koubek P., Cerveny J. and Bufka L. 2001. How is the lynx (Lynx lynx) hunting strategy of ungulates in the Sumava Mountains (Czech Republic). Abstracts of the 25th International Congress of IUGB, Lemesos, Cyprus: p.32.

Krebs C. J. 1999. Ecological methodology. 2nd ed. Benjamin / Cummings, CA: 468-471.

Lesniewicz K. and Perzanowski K. 1989. The Winter Diet of Wolves in Bieszczady Mountains. Acta Theriologica 34 (27): 373-380.

Levins R. 1968. Evolution in changing environment. Princeton University Press, Princeton: 1-120.

Liepa I. 1974. [Biometry]. Zvaigzne, Riga: 1-336. [In Latvian]

Linnell J.D.C., Odden J., Pedersen V. and Andersen R. 1998. 1998. Records of intra-guild predation by Eurasian Lynx *Lynx lynx*. The Canadian Field-Naturalist 112: 707-708.

Mattioli L., Apollonio M., Mazzarone V. and Centofanti E. 1995. Wolf food habits and wild ungulate availability in the Foreste Casentinesi National Park, Italy. Acta Theriologica 40(4): 387-402.

Meriggi A., Brangi A., Matteucci C. and Sacchi O. 1996. The feeding habits of wolves in relation to large prey availability in northern Italy. Ecography 19 (3): 287-295.

Novikov G.A., ed. 1970. [Lynx.] [In: Animals of Leningrad oblast]. Leningrad: 258-265. [In Russian]

Okarma H., Jedrzejewska B., Jedrzejewski W., Krasinski Z.A. and Milkowski, L. 1995. The roles of predation, snow cover, acorn crop, and man-related factors on ungulate mortality in Bialowieza Primeval Forest, Poland. Acta Theriologica 40 (2): 197-217.

Okarma H., Jędrzejewski W., Schmidt K., Kowalczyk R. and Jędrzejewska B. 1997. Predation of Eurasian lynx on roe deer and red deer in Białowieża Primeval Forest, Poland. Acta Theriologica 42 (2): 203-224.

Okarma H. 2000. [Lynx]. Oficyjna Edytorska "Wydawnictwo Świat": 1-80. [In Polish]

Ozoliņš J. 2000. Action plan for Lynx (*Lynx lynx*) conservation in Latvia. Latvijas mežu ierīcība, Salaspils: 1-32.

Ozoliņš J. and Andersone Ž. 2000. Action plan for Wolf (*Canis lupus*) conservation in Latvia. Latvijas mežu ierīcība, Salaspils: 1-38.

Ozolins J., Anderzone Z. and Pupila A. Status and Management Prospects of the Wolf *Canis lupus L.* in Latvia. Baltic Forestry [In press]

Ozolins J. and Pilats V. 1995. Distribution and status of small and medium-sized carnivores in Latvia. Annales Zoologica Fennici 32: 21 - 29.

Pedersen V.A., Linnell J.D.C., Andersen R., Andren H., Linden M. and Segerstrom P. 1999. Winter lynx *Lynx lynx* predation on semi-domestic reindeer *Rangifer tarandus* in northern Sweden. Wildlife Biology 5(4): 203-250.

Peterson R.O. 1996. Wolves as interspecific competitors in canid ecology. [In: Ecology and Conservation of Wolves in a Changing World. L.N. Carbyn, S.H. Fritts and D. R. Seip, eds]. Canadian Circumpolar Institute, Occasional Publication 35: 315-324.

Pulliainen E. and Hyypia V. 1975. [Winter food and feeding habits of lynxes(Lynx lynx) in southeastern Finland]. Suomen Riista 26: 60-6. [In Finnish with English summary]

Pulliainen E. 1981. Winter diet of *Felis lynx* in SE Finland as compared with the nutrition of other northern lynxes. Zeitschrift für Säugetierkunde 46: 249-259.

Pulliainen E., Lindgren E. and Tunkkari P.S. 1995. Influence of food availability and reproductive status on the body condition of the European lynx in Finland. Acta Theriologica 40: 181-196.

Reig S. and Jedrzejewski W. 1988. Winter and Early Spring Food of Some Carnivores in the Bialowieza National Park, Eastern Poland. Acta Theriologica 33 (5): 57-65.

Reynolds J. C. and Aebischer N. J. 1991. Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the Fox *Vulpes vulpes*. Mammal Review 21 (3): 97 - 122.

Rukovsky N.N. 1985. [Feeding]. [In: The Wolf. History, Systematics, Morphology, Ecology. Bibikov D.I., ed.]. Nauka Publishers, Moscow: 325-336. [In Russian]

Smietana W. and Klimek A. 1993. Diet of wolves in the Bieszczady Mountains, Poland. Acta Theriologica 38 (3): 245 - 251.

Sokal R. R. and Rohlf F. J. 1981. Biometry. W. H. Freeman and Co., New York: 1-859.

Suminski P. and Filipiak W. 1977. Beitrag zur Nahrungsuntersuchung des Wolfes (Canis lupus L.). Zeitschrieft für Jagdwissenschaft 23: 1-5.

Sunde P. and Kvam T. 1997. Diet patterns of Eurasian lynx *Lynx lynx*: what causes sexually determined prey size segregation? Acta Theriologica 42 (2): 189-201.

Sunde P., Overskaug K. and Kvam T. 1999. Intraguild predation of lynxes on foxes: evidence of interference competition? ECOGRAPHY 22: 521-523.

Sunde P., Kvam T., Bolstad J. P. and Bronndal M. 2000. Foraging of lynxes in a managed boreal-alpine environment. Ecography 23: 291-298.

Taurins E. 1975. [Game fauna in Latvian USSR and its rational use in future]. Ochrana i vosproizvodstvo prirodnyh resursov (Trudy LSHA) 83:18-28. [In Russian with English summary]

Teerink B.J. 1991. Hair of West-European Mammals. Cambridge University Press, Cambridge: 1-224.

Valdmann H., Koppa O. and Looga A. 1998. Diet and prey selectivity of wolf *Canis lupus* in middle- and south-eastern Estonia. Baltic Forestry 4 (1): 42-46.

Viltrop A., Lõhmus K., Must K., Jauram A., Viigipuu M. and Rander L. 2000. [Results of study of infectious diseases of mammals]. Eesti Loomaarstlik Ringvaade 3:100-114. [In Estonian]

Weber J.-M. and Weissbrodt M. 1999. Feeding habits of the Eurasian lynx in the Swiss Jura Mountains determined by faecal analysis. Acta Theriologica 44 (3): 333-336.

Table 1. Diet composition of lynx in Estonia and Latvia; F%- frequency of occurrence; B% - relative biomass eaten; B - food niche breadth. Food niche breadth by relative prey biomass is added for the Latvian sample. For Estonia, scats and stomachs have been combined.

Taxa	**Estonia**			**Latvia**			
	N	F%	SE	N	F%	SE	B%
Roe deer	76	49.0	± 5.7	24	72.7	± 7.8	86.5
Undet.cervids	-	-	-	5	15.2	± 6.2	4
Red deer	3	1.9	± 7.8	-	-	-	
Wild boar	1	0.6	± 7.7	-	-	-	
Hares	48	31.0	± 6.7	3	9.1	± 5.0	9.5
Fox	11	7.1	± 7.7	-	-	-	
Weasel	-	-	-	1	3.0	± 3.0	
Raccoon dog	1	0.6	± 7.7	-	-	-	
Gallinaceous	7	4.5	± 7.8	-	-	-	
Rodents	6	3.9	± 7.9	-	-	-	
Carrion	2	1.3	± 8.0	-	-	-	
Food niche breadth		**2.7**			**1.3**		
Food niche breadth by relative prey biomass							1.3
	155	100		33	100		

Table 2. Diet composition of wolf in Estonia and Latvia; F%- frequency of occurrence; B% - relative ungulate biomass eaten; B - food niche breadth (Estonian wolf data is from Valdmann *et al.*1998). Food niche breadth by relative prey biomass is added. (* - all other predators together form 4% in the Estonian sample)

Taxa	Estonia				Latvia			
	N Scats	F%	SE	B %	n	F%	SE	B %
Roe deer	264	51	±2.2	18.4	10	14.7	±3.3	20
Undet.cervids	-	-	-		20	29.4	±5.5	48
Wild boar	87	17	±1.6	19.3	22	32.3	±5.7	32
Undet.ungulates	-	-	-		1	1.5	±1.5	
Moose	61	12	±1.5	62.3	-	-	-	
Hares	30	6	±1.0		-	-	-	
Beaver	1	-	-		3	4.4	±2.5	
Small rodents	53	10	±1.5		-	-		
Wolf	4	*			-	-	-	
Raccoon dog	3	4	±0.9		1	1.5	±1.5	
Fox	2	*			-	-	-	
Dog	8	*			2	2.9	±2.0	
Reptiles	2	-			-	-	-	
Birds	2	-			1	1.5	±1.5	
Squirrel	1	-			-	-	-	
Carrion	-	-			7	10.3	±3.4	
Food niche breadth (B)		**2.7**				**1.30**		
Food niche breadth by relative ungulate prey biomass				**2.2**				**2.6**
	518	100		100	68	100		100

Captions to figures

Fig.1. Proportions of cervids and hares in diets of lynx in Estonia and Latvia

Fig.2. Proportions of cervids and wild boar in diets of wolf in Estonia and Latvia

Fig.1. Valdmann et al.

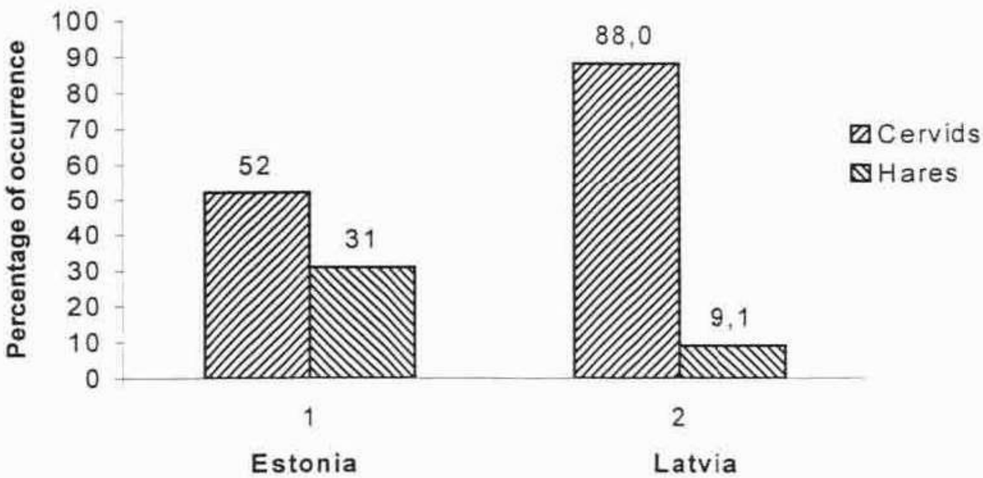
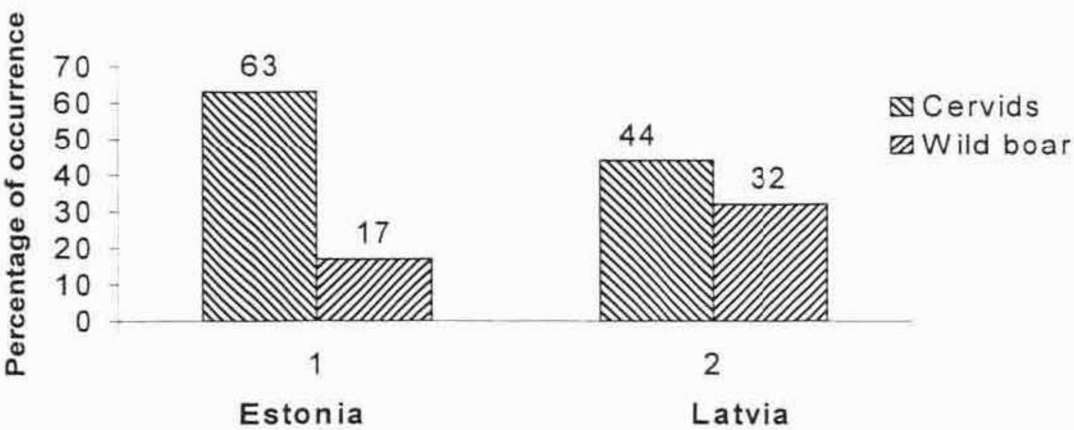


Fig.2. Valdmann et al.



Paper VII

3.2.2. Seasonal, geographical and sexual variations of the diet of wolves (*Canis lupus*) in Latvia

Seasonal, geographic and sexual variation in the diet of wolves (*Canis lupus*) in Latvia

Zanete Andersone, Janis Ozolins

Ķemeri National Park, "Meža māja", Ķemeri - Jūrmala, LV-2012, Latvia, e-mail: zanete.a@delfi.lv; phone: +371-7765386; fax: +371-7765040 (ZA)[1]

State Forest Service, 13.Janvāra Str. 15, Riga, LV-1932, Latvia, phone: +371-77212776, e-mail: janiso@vmd.gov.lv (JO)

[1] - corresponding author, postal address till March 2002: Norwegian Institute for Nature Research (NINA), Tungasletta-2, 7485 Trondheim, Norway, phone: +47-73801465; e-mail: zanete.andersone@ninatrd.ninaniku.no

Key words: beaver, diet, Latvia, ungulates, wolf

Abstract

Diet of wolves has been studied in Latvia from 1997 to 2001. In total, 302 scats and 107 stomachs of wolves were analysed. Wild ungulates (cervids and wild boar *Sus scrofa*) and beaver *Castor fiber* were found to be the staple food for wolves in Latvia. Cervids were found in 50% of samples (62% biomass), wild boar - 24.7% (21% biomass), beavers - 13.7% (11.5 biomass). Wild boar was positively selected, especially in winter when its ratio in the diet increased to 33.9% from 20% in summer. It was more a common prey in the east of the country. The ratio of beavers, small rodents and plant food was higher in summer, which resulted in a broader food niche in summer than winter (B = 2.53 versus B = 1.81). The role of domestic animals in the wolf diet was insignificant except for winter when they were consumed as carrion (13.1%). Minor sexual differences in the diet were found - males consumed beavers considerably more. 35.5% stomachs investigated were empty, the average weight of full stomachs being 972.8 ± 850.7g. The importance of the beaver as an alternative prey is discussed. It is conlcluded that wolves in Latvia prey generally on wild animals and conflicts with livestock owners are only local.

Introduction

Wolves *Canis lupus* Linnaeus, 1758 have traditionally been regarded as pests and suffered from extensive persecution all over Europe

(Boitani 2000). Also in Latvia, population dynamics of the species greatly depended on the intensity of hunting and varied from near extinction to more than 1000 animals, currently estimated at a few hundred individuals (Ozolins et al. in press). At the moment, the main conflict with human interests is competition for game species, especially ungulates.

The feeding habits of wolves have been widely studied all over the world (Bibikov 1985, Mech 1995, Jedrzejewska & Jedrzejewski 1998). Numerous case studies have shown that at northern latitudes, ungulates are the staple food for wolves (Bibikov 1985, Mech 1995, Okarma 1995). And yet, being an opportunistic predator, wolves take advantage of the most available prey, which causes a great diversity of their diet in different regions. Where wild ungulates are available, wolves prefer them to other items, even to livestock (Rukovsky 1985, Poulle, Carles & Lequette 1997), while in the absence of their natural prey they can switch to alternative prey - fruit in the south of the wolf's distribution range (Rukovsky 1985, Meriggi, Rosa, Brangi & Matteucci 1991, Brangi, Rosa & Meriggi 1994, Meriggi, Brangi, Matteucci & Sacchi 1996), garbage (Salvador and Abad 1987) or livestock (Lukarevsky 1988, Papageorgiou, Vlachos, Sfougaris & Tsachalidis 1994, Gao, Ma, Zhang, Gao & Zhao 1996). Therefore, the results from one area cannot be directly extrapolated to another region without a high risk of bias. As knowledge of wolf diet has very important practical implications, regional case studies are essential.

In the Baltic States, wolf diet has previously only been studied in Lithuania (Prusaite 1961). In Latvia and Estonia, where ecological conditions are slightly different than in Lithuania (due to a higher percentage of forest cover), the first studies on the wolf diet started in mid 1990s, when the first results on summer and winter diet of wolves were obtained (Andersone 1998, 1999; Valdmann, Koppa & Looga 1998; Valdmann, Andersone, Koppa, Ozolins & Bagrade in prep.). No data on the wolf diet in Latvia exist from earlier periods except for a very limited data from western Latvia (Gaross 1997).

The aim of this study was to carry out a thorough analysis of the wolf diet and to compare the variations in the predator's diet in relation to season, locality and sex of the animal.

Study area

Latvia is situated in a transition zone between the coniferous taiga and European deciduous forests. Its climate is mild in the coastal areas (west) and more continental in the east. Permanent snow cover becomes established in the beginning of December, but sometimes the first snow can be as early as October. Snow cover can stay till the end of March. However, due to the influence of the sea, mild winters, characteristic of the last decade, may have no lasting snow cover.

Almost a half (44%) of the area of Latvia (64,500 km^2 in total) is covered by forest, and some 10% of the area is covered by bogs. The wolf population comprises 300-400 individuals. The prey base is represented by four ungulate species - moose *Alces alces*, red deer *Cervus elaphus*, roe deer *Capreolus capreolus* and wild boar *Sus scrofa*. Beavers *Castor fiber* have also significantly increased in abundance and distribution (Balodis 1994, Balodis, Laanetu & Ulevicius 1999). Numerical trends of the four main prey species are shown in Fig.1.

Material and methods

The study was carried out in Latvia from winter 1997 till autumn 2001. The study period was divided into winter (October - March) and summer (April- September) seasons. In total, 302 wolf scats were collected (64 from winter, 238 from summer) and 107 stomachs of hunted wolves (99 from winter and 8 from summer). Distribution of sampling locations is shown in Fig.2. Data on 98 winter stomachs have been analysed earlier in comparison to lynx diet in Latvia and Estonia (Valdmann et al. in prep.).

Data on livestock depredation were obtained from the State Forest Service, which started registration of wolf attacks on livestock in 2001. In total, 21 wolf attack were reported. Killed and injured livestock were pooled to obtain the total number of wolf kills from which the frequency of occurrence of each species was calculated.

Laboratory analysis followed standard procedures (Lockie 1959, Goszczynski 1974; Litvaitis, Titus & Anderson 1996). Scats were washed through a sieve (1 mm mesh) in order to separate undigested parts (hairs, bones etc.) and dried at room temperature to constant weight. Stomach contents were either analysed fresh or kept in a freezer and analysed after thawing. Both fresh stomach contents and dried scats were weighted using an electronic balance (SC-3000) to 1 g precision. The microscopic slides of hairs were prepared in order to identify the prey species according to the keys by Day (1966) and Teerink (1991) as well as our own reference collection.

Data from scats and stomachs were pooled for the analysis of seasonal variations in wolf diet, otherwise, scats and stomachs were analysed separately. Absolute frequency of occurrence (F%) (from the number of samples analysed) and percentage of food biomass ingested (B%) was used to assess the importance of food items in the diet (Ciucci et al. 1996). Conversion coefficients to calculate the biomass ingested from the scat weight were taken from Goszczynski (1974), Lockie (1959), Floyd, Mech & Jordan

(1978) and Jedrzejewska & Jedrzejewski (1998). Although the plant material (including berries) has a low nutritional value (Jedrzejewska & Jedrzejewski 1998) it was also included in the analysis.

Sexual differences in stomach content weights, as well as the results obtained from stomach and scat analysis were checked by Mann-Whitney U-test while the Kruskal-Wallis test was used to analyse for geographic differences in occurrence of different prey categories and biomass ingested (SPSS 10.0 for Windows). Frequencies of occurrence of different prey categories were compared using t-test (Liepa 1974, Sokal & Rohlf 1995).

Food niche breadth (B) was calculated according to Levins' (1968) formula (using F%):

$$B = 1/\sum p_i^2,$$

p_i = percent occurrence of a particular prey group in the diet

Ivlev's selectivity index modified by Jacobs (1974) was calculated according to the formula:

$$D = (r - p)/(r + p) - 2\ rp$$

r = a fraction of a given prey in the wolf's diet

p = the fraction of the same prey in the environment (according to the official census data)

Standard error (SE) was calculated according to the formula:

$$SE = \sqrt{\frac{pq}{n}}$$

p = proportion of prey item in diet

q = 100 - p

n = number of prey items in diet

Results

At least 22 food categories were found in wolf diet, ungulates and beavers being the most common ones (Table 1). On average, cervids were found in 50% of samples, wild boar - in 24.7%, beaver - 13.7%. According to the relative biomass (B%), cervids constitute the bulk of the wolf's diet - 62%, wild boar add 21% and beaver - 11.5%.

In summer, wolves consumed considerably more beavers compared to the winter season ($t = 3.92$, $p < 0.01$) while the opposite was true for wild boar in the wolf diet ($t = 3.39$, $p < 0.01$). Similarly, livestock consumption was higher in winter, presumably as carrion ($t = 2.71$, $p < 0.01$) while the percentage of small rodents and berries and other plant material was higher in summer ($t = 2.83$, $p < 0.01$) (Table 1).

Selectivity indices showed a positive selection towards wild boar both in summer and winter, the selection being stronger in winter season (D = 0.49 versus D = 0.18 in summer).

Wild prey dominated in the wolf diet in both seasons, while domestic animals were more common food items in winter when they were mainly consumed as carrion. This pattern was especially pronounced in the results of the analysis of stomach contents in winter - livestock was found in 13.1% stomachs, which is due to the feeding at the dumpsites of the slaughter-houses and at baits put out by hunters.

The analysis of the livestock depredation data shows that sheep are most often preyed upon (70.8%). Calves (21.9%), dogs (5.2%) and goats (2.1%) made up the rest of the total depredation on domestic animals in 2001.

There were general geographic differences between west and east of the country in the consumption of cervids (Kruskal-Wallis test, $\chi^2 = 6.52$, $p < 0.01$) and livestock ($\chi^2 = 4.94$, $p < 0.05$; for B% $\chi^2 = 4.89$, $p < 0.05$), which were consumed more in the west.

More specific analysis of the summer diet of wolves was carried out in three protected areas - Slitere National Park from the north-west of Latvia (N = 105), in Teici Nature Reserve from the east ($N = 32$) and in Kemeri National Park which is situated in between them ($N = 33$) (Table 2). Consumption of wild boar in Slitere was significantly lower than in Teici ($t = 3.58$, $p < 0.01$) and in Kemeri ($t = 2.18$, $p < 0.05$). The ratio of beavers in the diet was also higher in the east both in summer and winter season but the difference wasn't statistically significant.

Diet composition compared for summers 1997-2001 varied considerably, however, cervids and wild boar remained the staple food for the whole study period, ranging from 64 to 84% of the diet (Fig.3).

Niche breadth (calculated for five food categories: cervids, wild boar, beaver, other animals, fruit) had some seasonal difference - it was higher in summer ($B = 2.53$) and lower in winter ($B = 1.81$).

When comparing the diet of male and females wolves (based on stomach contents), statistically significant difference was found neither in the prey composition nor in the stomach weight. Only when comparing winter diet, a significant difference in the beaver ratio was found between male and female wolves ($t = 2.22$, $p < 0.05$), males consuming more beavers than females. Neither were there any geographical differences in the diet among wolves of the same sex.

35.5% of all stomachs investigated were empty (39% in females and 31.2% in males). The distribution of stomach weights is shown in Fig.4. Average stomach weight was 972.8 ± 850.7g, stomach contents of males being lighter than those of females - 850.6 ± 668.3g and 1041.1 ± 939.8g accordingly. However, the difference was not statistically significant.

Discussion

As elsewhere, where the natural prey base is rich (Bibikov 1985, Mattioli, Apollonio, Mazzarone & Centofanti 1995, Jedrzejewska & Jedrzejewski 1998), Latvian wolves preyed mainly upon wild animals (Table 1). Cervids were the most common prey items but wild boar was preferred, similarly to some other localities where both species occur together (Mattioli et al. 1995, Meriggi et al. 1996, Valdmann et al. 1998), though in some areas wild boar is generally avoided by wolves (Jedrzejewska, Okarma, Jedrzejewski & Milkowski 1994, Okarma 1995). The negative relationships between wolf and wild boar densities can be found, indicating that wolves can possibly severely limit wild boar populations (Jedrzejewska, Jedrzejewski, Bunevich, Milkowski & Krasinski 1997, Kanzaki & Perzanowski 1997). However, adult boar are not an easy prey (Reig 1993), therefore, selective hunting for piglets is more common (Smietana & Klimek 1993, Mattioli et al. 1995, Jedrzejewski, Jedrzejewska, Okarma, Schmidt, Zub & Musiani 2000). The ratio of wild boar in the diet of wolves in Latvia was similar to that from lowland Poland (Reig & Jedrzejewski 1988), though in Bialowieza selection was negative toward wild boar (Jedrzejewska et al. 1994, Jedrzejewski et al. 2000). The lower proportion of wild boar in the diet of wolf in NW Latvia can be explained by different ecological conditions. There are mainly coastal dry pine woods in that area, which cannot support a large wild boar population.

In this study, we did not distinguish between different species of Cervidae in order to avoid bias due to similar hair structure but we suggest that roe deer constitute the bulk of it, which is indicated by the results from the pilot study in mid 1990s (Andersone 1998). The most common, which in most cases means the most available, ungulate species usually constitutes the majority of wolf diet (Zheleznov 1990, Mech 1995), and roe deer is undoubtedly the most numerous ungulate in Latvia (Andersone & Ozolins 2000). Latvian forests are patchy and interspersed by agricultural lands, both used and abandoned (Prusaite, Kaal & Volf 1985), and in such human dominated landscapes roe deer is the most common prey (Aanes, Linnell, Perzanowski, Karlsen & Odden 1998). If several large prey species occur in the region, wolves choose the smallest one (Gordiyuk 1991, Mech 1995), therefore, we suppose predation on moose in Latvia is light compared with predation on other ungulates. Besides, small pack size (due to intensive persecution by man) (Ozolins & Andersone 2000) might have contributed to the lower predation on moose, although there are indications that the pack size is not a principal factor influencing hunting success on moose (Thurber & Peterson 1993).

Wolves were blamed by hunters in Latvia for the decrease in the ungulate numbers during the 1990s (Gaross 1994), but as shown in other areas, even roe deer populations are not influenced by wolves if conditions are favourable (Olsson, Wirtberg, Andersson & Wirtberg 1997). As demonstrated in Poland, wolves can hardly influence the game resources if ungulate density is high (Jedrzejewska et al. 1994, Okarma, Jedrzejewska, Jedrzejewski, Krasinski & Milkowski 1995, Glowacinski & Profus 1997) while they can have a negative effect on ungulate populations in poor habitats where both human hunters and predators compete for the scarce prey (Mech & Nelson 2000). More probably, in Latvia we deal with the cumulative effect of increased predator numbers (both wolves and lynx) and hunting pressure from humans in the early 1990s.

Niche breadth for wolves in Latvia was found to be greater than that for wolves from Poland (Jedrzejewska & Jedrzejewski 1998) but lower than that from Italy (Mattioli et al. 1995), which only partly coincides with the geographic gradient of the wolf diet from north to the south (Rukovsky 1985). Similarly to other areas (Meriggi & Lovari 1996), niche breadth was lower in winter, when the proportion of ungulates in wolf diet increased. In summer, wolf diet in Latvia was more diverse and included smaller mammals as well as other groups of animals. However, the relative biomass for these prey types is usually insignificant (Muszynska 1996). In Latvia, the beaver was the only important additional food item.

Livestock constitutes only an insignificant part of the wolf diet. Depredation on livestock occurs locally and seasonally (Meriggi et al. 1996) and does not have a regular character in Latvia. A single wolf pack from northern Latvia (Valmiera district) was responsible for 28.6% of the depredation cases during the summer season of 2001. Feeding on livestock is secondary for wolves, which prefer wild prey whenever available (Rukovsky 1985, Meriggi & Lovari 1996). Depredation on livestock depends not only on availability of natural prey but also on acceptability of it (Meriggi & Lovari 1996), which is linked to the lack of proper husbandry techniques (Linnell, Odden, Smith, Aanes & Swenson 1999). It is typical for Latvia, that livestock is unguarded and often left at night in pastures, which can facilitate a wolf pack's specialisation on this type of food, as it seems to be the case with the pack in Valmiera district. 33% cases of depredation occurred in eastern Latvia, where the percentage of the area with forest cover is lower, thus possibly resulting in lower densities of the wolves' natural prey. Sheep are most vulnerable to wolf depredation (Formozov & Golov 1975, Sabanejev 1988, Genov 1992, Ciucci & Boitani 1998) and previous studies from the Baltic

(Andersone, Balciauskas & Valdmann in press) have also shown that sheep are the most popular target of wolves when livestock are attacked. However, the lack of big flocks of sheep and the richness of the natural prey base prevents high damages to the farmers.

Carrion can be an important food source for wolves in winter, constituting up to a third of the diet in some areas (Smietana & Klimek 1993, Lesniewicz & Perzanowski 1989). Carrion seems to be a food item extensively used by wolves in Latvia as well but to a lesser extent than in the latter studies.

Intra-guild predation is common among mammalian carnivores but consumption of a kill depends on the availability of other food items (Palomares & Caro 1999). Six different species of carnivores (including domestic dog *Canis familiaris*) featured on the wolf's diet in our study. Raccoon dogs *Nyctereutes procyonoides*, red foxes *Vulpes vulpes*, domestic dogs and badgers *Meles meles* are known to be often preyed upon by wolves (Matjushkin 1985, Prusaite et al. 1985; Brtek & Voskar 1987, Jedrzejewska & Jedrzejewski 1998, Olsson et al. 1997, Palomares & Caro 1999 etc.). Depredation on mustelids is not so common, however, it is known from Belarus (Sidorovich 1997) and North America (Kohira & Rexstad 1997, Route & Peterson 1991). Interestingly, river otter *Lutra canadensis* and small mustelids seem to be important prey items for wolves in

Alaska, especially in logged areas (Kohira & Rexstad 1997). In Latvia, otter and weasel remains were found in wolf scats only twice.

Beaver is an alternative prey, which appears to be important to wolves (Ballard, Whitman & Gardner 1987, Mech 1995), particularly when ungulate density is low (Milne, Harestad & Atkinson 1989, Shelton & Peterson 1983). In Latvia, the increase of beaver in wolf diet could have been caused by a depression of ungulate populations in the first half of the 1990s, which coincided with the rapid growth of the beaver population (Balodis et al. 1999). To our knowledge, this is the first study in Europe that shows such a high beaver percentage in the wolf's diet, which seasonally and locally can represent one third of the predator's diet (Andersone 1999). In most other European studies, beaver consumption ranged between 1% and 3.9% (Kozlo & Banad 1985, Olsson et al. 1997, Valdmann et al. 1998, Gade-Jørgensen & Stagegaard 2000, Jedrzejewski et al. 2000), while it could constitute more than a half of the wolf's diet in North America (Shelton & Peterson 1983, Mech 1995). In our study, the proportion of beaver in wolf diet was higher in summer while the opposite was shown from North America (Milne et al. 1989). It was shown that wolf presence in the area could help to significantly decrease beaver colonies (Potvin, Breton, Pilon & Macquart 1992) provided that both reach high levels (Shelton & Peterson 1983). However, in

Latvia, wolves seem to have no effect on the steadily increasing beaver population.

Data on stomach content weights obtained in Latvia are similar with data obtained elsewhere (Geptner & Naumov 1967, Rukovsky 1985). Average weight was bigger than that found in SE Poland (Lesniewicz & Perzanowski 1989) and lower than from most localities in the territory of the former USSR (Rukovsky 1985) and North America (Mech 1995). The lack of sexual differences in the stomach contents can be explained by the social organisation of the wolves. They live in packs, therefore, the kill made by the pack is likely to be consumed by all members of the pack, thus resulting in no differences in the prey composition between sexes.

Results obtained from the stomach and scat analysis did not differ considerably, thus suggesting that both methods are equally reliable when assessing the diet, therefore, the latter should be preferred whenever possible as the least invasive one.

To conclude, it can be pointed out that wolves in Latvia rely on wild animals as the main source of food, which should be regarded as the great advantage for the species conservation in the region. Beaver is an important alternative prey item, as it is widespread and reaches very high densities. Under these conditions, it can help to support the high densities of wolves even during depressions in ungulate populations. As there are no big conflicts between humans and wolves, apart from the competition for prey, it is essential to find a compromise with hunters based on scientifically correct information. Therefore, further studies on predation rates of wolves in Latvia are important.

Acknowledgements

We thank A. Strazds, J. Baumanis, V. Rēders, A. Dundurs and numerous anonymous hunters and State Forest Service's employees for helping with material collection, and appreciate A. Pupila's and A. Ornicāns' practical help. We express our cordial thanks to Dr. H. Okarma and J. Linnell for their valuable comments on the manuscript's draft, suggestions on the statistical analysis and linguistical corrections. The manuscript was prepared during a stay at the Norwegian Institute for Nature Research funded by The Research Council of Norway (scholarship IS OE01-51).

References

Aanes, R., Linnell, J.D.C., Perzanowski, K., Karlsen, J. & Odden, J. 1998: Roe deer as prey. - In: Andersen, R., Duncan, P. & Linnell, J.D.C. (Eds.); The European Roe Deer: The Biology of Success. Scandinavian University Press, Oslo, pp. 139-159.

Andersone, Z. 1998: Summer Nutrition of the Wolf (Canis lupus) in the Nature Reserve Slitere, Latvia. - Proceedings of the Latvian Academy of Sciences, Section B, 52 (1-2): 79-80.

Andersone, Z. 1999: Beaver: A new prey of wolves in Latvia? Comparison of winter and summer diet of Canis lupus Linnaeus, 1758. - In: Busher, P. & Dzieciolowski, R. (Eds.); Beaver Protection, Management, and Utilization in Europe and North America. Cluwer Academic / Plenum Publishers, New York, pp. 103 - 108.

Andersone, Z. & Ozolins, J. 2000: Big game and large carnivores in Latvia: present status and future prospects. - Journal of Wildlife Research. (In press).

Andersone, Z., Balciauskas, L. & Valdmann, H. Human-Wolf Conflicts in the East Baltic - past, present and future. - Proceedings of the 2nd International Wildlife Management Congress. (In press).

Ballard, W.B., Whitman, J.S. & Gardner, C.L. 1987: Ecology of an exploited wolf population in south-central Alaska. - Wildlife Monographs 98: 1-54.

Balodis, M. 1994: Beaver Population of Latvia: History, Development and Management. - Proceedings of the Latvian Academy of Sciences, Section B, 7/8 (564/565): 122 - 127.

Balodis, M., Laanetu, N. & Ulevicius, A. 1999: Beaver Management in the Baltic States. - In: Busher, P. & Dzieciolowski, R. (Eds.); Beaver Protection, Management, and Utilization in Europe and North America. Kluwer Academic / Plenum Publishers, New York, pp. 25-29.

Bibikov, D.I. (Ed.) 1985: (The wolf. History, Systematics, Morphology, Ecology.) - Nauka Publishers, Moscow, 606 pp. (In Russian).

Boitani, L. 2000: Action Plan for Conservation of Wolves in Europe (Canis lupus). - Nature and environment, Council of Europe Publishing, 113, 86 pp.

Brangi, A., Rosa, P. & Meriggi, A. 1994: Predation by Wolves (Canis lupus L.) on wild and domestic ungulates in Northern Italy. -Ongules / Ungulates 91: 541-543.

Brtek, L. & Voskar, J. 1987: Potravna biologia vlka v podmienkach Slovenskych Karpat. (In Czech with English summary: Food biology of the wolf in Slovak Carpathians.) - Biologia (CSSR) 42 (10): 985 - 990.

Ciucci, P. & Boitani, L. 1998: Wolf and dog depredation on livestock in Central Italy. - Wildlife Society Bulletin 26 (3): 504-514.

Ciucci, P., Boitani, L., Pelliccioni, E. R., Rocco, M. & Guy, I. 1996: A comparison of scat-analisys methods to assess the diet of the wolf Canis lupus. - Wildlife Biology 2: 37 - 48.

Day, M. G. 1966: Identification of hair and feather remains in the gut and faeces of stoats and weasels. - Journal of Zoology 148: 201 - 217.

Floyd, T. J., Mech, L. D. & Jordan, P. A. 1978: Relating wolf scat content to prey consumed. - Journal of Wildlife Management 42 (3): 528 - 532.

Formozov, A.N. & Golov, B.A. 1975: (On the wolf as a livestock pest in the Ural and Guryev oblast.) - Bull. Mosk. o-va ispytatelej prirody 50 (1): 108 - 116. (In Russian with English summary).

Gade-Jørgensen, I. & Stagegaard, R. 2000: Diet composition of wolves Canis lupus in east-central Finland. - Acta Theriologica 45 (4): 537 - 547.

Gao, Z., Ma, J., Zhang, H., Gao, Y. & Zhao, G. 1996: Preliminary studies on the food habits of the wolves in eastern Mongolia. - Acta Theriologica Sinica 16 (2): 95-99.

Gaross, V. 1994: Vilku un lusu ietekme uz briezveidigajiem dzivniekiem Kurzeme. - Meza Dzive, 3 (208): 10-15. (In Latvian).

Gaross, V. 1997: Ekologisko, biologisko, antropogeno u.c. faktoru ietekme uz Latvijas briezveidigo dzivnieku un pleseju populacijam. (In Latvian with English summary: The impact of economical, biological and other factors on the population of Cervidae, wolf and lynx.) - Mezzinatne 7 (40): 108-123.

Genov, P. 1992: The wolf Canis lupus L. in southwestern Bulgaria. - In: Bobek, B., Perzanowski, K. & Regelin, W.L. (Eds.); Global Trends in Wildlife Management. Swiat Press, Krakow-Warszawa, pp. 359 - 362.

Geptner, V.G. & Naumov, N.P. 1967: (The mammals of the USSR.) Vol. 2 (1). - Vysshaja shkola, Moskva, pp. 123-193. (In Russian).

Glowacinski, Z. & Profus, P. 1997: Potential impact of wolves

Canis lupus on prey populations in eastern Poland. - Biological Conservation 80 (1): 99-106.

Gordiyuk, N.M. 1991: (Interrelations between wolves and ungulates as registered by observation of the marked wolf pack in the southern Urals) - Bull. Mosk. o-va ispytatelej prirody 96 (1): 3-10. (In Russian with English summary).

Goszczynski, J. 1974: Studies on the Food of Foxes. - Acta Theriologica 19(1): 1 - 18.

Jacobs, J. 1974: Quantitative Measurement of Food Selection. A Modification of the Forage Ratio and Ivlev's Electivity Index. -Oecologia (Berl.) 14: 413 - 417.

Jedrzejewska, B. & Jedrzejewski, W. 1998: Predation in Vertebrate Communities: The Bialowieza Primeval Forest as a Case Study. - Springer Verlag, Berlin, 450 pp.

Jedrzejewska, B., Okarma, H., Jedrzejewski, W., Milkowski, L. 1994: Effects of exploitation and protection on forest structure, ungulate density and wolf predation in Bialowieza Primeval Forest, Poland. - Journal of Applied Ecology 31: 664 - 676.

Jedrzejewska, B., Jedrzejewski, W., Bunevich, A. N., Milkowski L. & Krasinski, Z. 1997: Factors shaping population densities and increase rates of ungulates in Bialowieza Primeval Forest (Poland and Belarus) in the 19th and 20th centuries. - Acta Theriologica 42: 399 - 451.

Jedrzejewski, W., Jedrzejewska, B., Okarma, H., Schmidt, K., Zub,

K. & Musiani, M. 2000: Prey selection and predation by wolves in Bialowieza Primeval Forest, Poland. - Journal of Mammology 81 (1): 197-212.

Kanzaki, N. & Perzanowski, K. 1997: The potential role of wolf predation in regulating wild boar population in Bieszczady, Poland. - Wildlife Conservation Japan 2 (4): 205-212.

Kohira, M. & Rexstad, E.A. 1997: Diets of wolves, Canis lupus, in logged and unlogged forests of southeastern Alaska. - Canadian Field-Naturalist 111 (3): 429-435.

Kozlo, P.G. & Banad, E.B. 1985: (Byelorussia.) - In: Bibikov, D.I. (Ed.); The wolf. History, Systematics, Morphology, Ecology. Nauka Publishers, Moscow, pp. 483-487. (In Russian).

Lesniewicz, K. & Perzanowski, K. 1989: The winter diet of wolves in Bieszczady Mountains. - Acta Theriologica 34 (27): 373 - 380.

Levins, R. 1968: Evolution in changing environment. - Princeton University Press, Princeton, 120 pp.

Liepa, I. 1974: Biometrija. Zvaigzne, Riga, 336 pp. (In Latvian).

Linnell, J.D.C., Odden, J., Smith, M.E., Aanes, R. & Swenson, J.E. 1999: Large carnivores that kill livestock: do "problem individuals" really exist? - Wildlife Society Bulletin 27 (3): 698-705.

Litvaitis, J.A., Titus, K. & Anderson, E. M. 1996: Measuring Vertebrate Use of Terrestrial Habitats and Foods. - In: Bookhout, T.A. (Ed.); Research and Management Techniques for

Wildlife and Habitats. The Wildlife Society, Bethesda, Maryland, pp. 254-274.

Lockie, J. D. 1959: The estimation of the food of foxes. - Journal of Wildlife Management 23 (2): 224 - 227.

Lukarevsky, V.S. 1988: (Diet of the leopard, striped hyena and wolf in south-western Kopetdag) - Zoologicheskij zhurnal 67 (2): 310-315. (In Russian with English summary).

Matjushkin, E. N. 1985: (Relationships with other predatory mammals) - In: Bibikov, D.I. (Ed.); The Wolf. History, Systematics, Morphology, Ecology. Nauka Publishers, Mocow, pp. 355 - 370. (In Russian).

Mattioli, L., Apollonio, M., Mazzarone, V. & Centofanti, E. 1995: Wolf food habits and wild ungulate availability in the Foreste Casentinesi National Park, Italy. - Acta Theriologica 40 (4): 387-402.

Mech, L.D. 1995: The Wolf. The Ecology and Behaviour of an Endangered Species. 8th ed. - University of Minnesota Press, Minneapolis, 384 pp.

Mech, L.D. & Nelson, M.E. 2000: Do wolves affect white-tailed buck harvest in northeastern Minnesota? - Journal of Wildlife Management 64 (1): 129-136.

Meriggi, A., Brangi, A., Matteucci, C. & Sacchi, O. 1996: The feeding habits of wolves in relation to large prey availability in northern Italy. - Ecography 19 (3): 287-295.

Meriggi, A. & Lovari, S. 1996: A review of wolf predation in southern Europe: Does wolf prefer wild prey to livestock? - Journal of Applied Ecology 33 (6): 1561-1571.

Meriggi, A., Rosa, P., Brangi, A. & Matteucci, C. 1991: Habitat use and diet of the wolf in northern Italy. - Acta Theriologica 36 (1-2): 141 - 151.

Milne, D.G., Harestad, A.S. & Atkinson, K. 1989: Diets of wolves on northern Vancouver Island. - Northwest Science 63 (3): 83-86.

Muszynska, M. 1996: Comparison of the spring and summer diet of the wolf and the red fox in the Bieszczady Moutains. - Journal of Wildlife Research 1 (2): 182 - 185.

Okarma, H. 1995: The trophic ecology of wolves and their predatory role in ungulate communities of forest ecosystems in Europe. - Acta Theriologica 40 (4): 335 - 386.

Okarma, H., Jedrzejewska, B., Jedrzejewski, W., Krasinski, Z.A. & Milkowski, L. 1995: The roles of predation, snow cover, acorn crop on ungulate mortality in Bialowieza Primeval Forest, Poland. - Acta Theriologica 40 (2): 197-217.

Olsson, O., Wirtberg, J., Andersson, M. & Wirtberg, I. 1997: Wolf Canis lupus predation on moose Alces alces and roe deer Capreolus capreolus in south-central Scandinavia. - Wildlife Biology 3 (1): 13-23.

Ozoliņš, J., Andersone, Ž. & Pupila, A. Status and Management Prospects of the Wolf Canis lupus L. in Latvia. - Baltic Forestry (In press).

Palomares, E. & Caro, T.M. 1999: Interspecific killing among mammalian carnivores. - American Naturalist 153 (5): 492-508.

Papageorgiou, N., Vlachos, C., Sfougaris, A. & Tsachalidis, E. 1994: Status and diet of wolves in Greece. - Acta Theriologica 39 (4): 411 - 416.

Potvin, F., Breton, L., Pilon, C. & Macquart, M. 1992: Impact of an experimental wolf reduction on beaver in Papineau-Labelle Reserve, Quebec. - Canadian Journal of Zoology 70 (1): 180-183.

Poulle, M.-L., Carles, L. & Lequette, B. 1997: Significance of ungulates in the diet of recently settled wolves in the Mercantour Mountains (southeastern France). - Rev. Ecol. (Terre Vie) 52: 357-368.

Prusaite, J. 1961: Lietuvos vilku mityba is veisimasis. - LTSR MS Darbai, Serija C 1 (24): 177-191. (In Lithuanian).

Prusaite, A. Ya., Kaal, M. & Volf, A. 1985: (Baltic republics.) - In: Bibikov, D.I. (Ed.); The Wolf. History, Systematics, Morphology, Ecology. Nauka Publishers, Moscow, pp. 476-478. (In Russian).

Reig, S. 1993: Non aggressive encounter between a wolf pack and a wild boar. - Mammalia 57 (3): 451-453.

Reig, S. & Jedrzejewski, W. 1988: Winter and early spring food of some carnivores in the Bialowieza National Park, Eastern Poland. - Acta Theriologica 33 (5): 57 - 65.

Route, W.T. & Peterson, R.O. 1991: An incident of wolf, Canis lupus, predation on a river otter, Lutra canadensis, in Minnesota. - Canadian Field-Naturalist 105 (4): 567-568.

Rukovsky, N. N. 1985: (Feeding.) - In: Bibikov, D.I. (Ed.); The Wolf. History, Systematics, Morphology, Ecology. Nauka Publishers, Moscow, pp. 325-336. (In Russian).

Sabanejev, L.P. 1988: (Game animals.) - Fizkultura i sport, Moskva, 480 pp. (In Russian).

Salvador, A. & Abad, P. L. 1987: Food habits of the wolf population (Canis lupus) in Leon province, Spain. - Mammalia 5 (1): 45 - 52.

Shelton, P. C. & Peterson, R. O. 1983: Beaver, wolf and moose interactions in Isle Royale National Park, USA. - Acta Zoologica Fennica 174: 265 - 266.

Sidorovich, V.E. (Ed.). 1997: Mustelids in Belarus. Evolutionary Ecology, Demography and Interspecific Relationships. - Zolotoy uley, Minsk, 263 pp. (In Russian with English summary).

Smietana, W. & Klimek, A. 1993: Diet of wolves in the Bieszczady Mountains, Poland. - Acta Theriologica 38 (3): 245 - 251.

Sokal, R.R. & Rohlf, F.J. 1995: Biometry. 3rd ed. - W.H.Freeman and Company, New York, 887 pp.

Teerink, B. J. 1991: Hairs of West European Mammals. - Cambridge University Press, Great Britain, 224 pp.

Thurber, J.M. & Peterson, R.O. 1993: Effects of population-density and pack size on the foraging ecology of gray wolves. -

Journal of Mammology 74 (4): 879-889.

Valdmann, H., Koppa, O. and Looga, A. 1998: Diet and prey selectivity of wolf Canis lupus in middle- and south-eastern Estonia. - Baltic Forestry 4 (1): 42-46.

Zheleznov, N.K. 1990: (Wild ungulates of the USSR North-East.) - Far Eastern Branch of the Academy of Sciences, Vladivostok, 480 pp. (In Russian with English summary).

Table 1. Diet composition of wolves in Latvia, 1997-2001, in summer (April - September) and winter (October - March). Data from stomach and scat analysis combined for calculating the absolute frequency of occurrence (F%). For calculating percentage of food biomass (B%), only scat data were used (N = 302). ** - significant difference ($p < 0.01$) between the seasons is shown.

Item	Spring-summer			Autumn-winter		
	F%	SE	B%	F%	SE	B%
Cervidae	49.4	± 8.2	62.2	51.2	± 4.2	56.8
Wild boar** (*Sus scrofa*)	20	± 2.3	19.3	33.9	± 4.0	32.1
Livestock**	2.9	± 1.0	2.3	9.4	± 2.5	4.4
Undetermined ungulate	0.4	± 0.4	0.3	1.6	± 1.1	-
Ungulates total	**72.7**		**84.1**	**96.1**		**93.3**
Beaver** (*Castor fiber*)	18.8	± 2.2	12.6	3.9	± 1.6	3.1
Domestic dog (*Canis familiaris*)	-	-	-	2.4	± 1.3	0.7
Raccoon dog (*Nyctereutes procyonoides*)	1.2	± 0.6	0.4	1.6	± 1.1	1.8
Fox (*Vulpes vulpes*)	1.6	± 0.7	0.3	-	-	-
Badger (*Meles meles*)	0.4	± 0.4	-	-	-	-
Otter (*Lutra lutra*)	0.4	± 0.4	< 0.1	-	-	-
Weasel (*Mustela nivalis*)	0.4	± 0.4	< 0.1	-	-	-
Brown hare (*Lepus europaeus*)	0.4	± 0.4	0.1	-	-	-
Mountain hare (*L. timidus*)	-	-	-	0.8	± 0.8	-
Mole (*Talpa europaea*)	0.4	± 0.4	< 0.1	-	-	-
Undetermined shrew (*Sorex* sp.)	0.4	± 0.4	< 0.1	-	-	-
Yellow-necked mouse (*Apodemus flavicollis*)	0.4	± 0.4	< 0.1	0.8	± 0.8	0.4
Undetermined vole (*Microtus* sp.)	3.3	± 1.0	0.2	1.6	± 1.1	0.3

Table 1 (continued).

Bank vole (*Clethrionomys glareolus*)	3.3	± 1.0	0.2	-	-	-
Water vole (*Arvicola terrestris*)	0.8	± 0.5	0.4	-	-	-
Undet.rodents	2.8	± 0.9	0.2	0.8	± 0.8	0.4
Small rodents total**	**10.6**		**2.0**	**3.2**		**1.1**
Undetermined birds	4.1	± 1.1	0.2	0.8	± 0.8	-
Undetermined reptiles	0.8	± 0.5	< 0.1	-	-	-
Beetles	1.6	± 0.7	< 0.1	-	-	-
Berries and plants**	10.6	± 1.8	0.2	2.4	± 1.3	0.1
N	**245**			**127**		

Table 2. Geographic differences in wolf diet (F%). Slitere National Park = NW, Teici Nature Reserve = E, Kemeri National Park = central Latvia. Significant differences between Slitere NP and two other areas are shown (* - $p < 0.05$, ** - $p < 0.01$).

	Slitere	Kemeri	Teici
Cervidae	57.1	54.5	37.5
Wild boar	9.5	24.2*	37.5**
Beaver	18.1	18.2	28.1
Rodents	7.6	9.1	6.3
Berries	12.4	6.1	9.4
Other items	18.1	9.1	9.4
N scats	**105**	**33**	**32**

Fig.1. Population dynamics of the main prey species of wolves in Latvia, 1995-2001 (according to the data from the State Forest Service).

Fig.2. Locations of collected stomachs and scats containing identifiable prey items:


< 10 samples collected;


10-20 samples collected;


> 20 samples collected.

Fig.3. Yearly variation of wolf summer diet in Latvia (N = 238), 1997-2001.

Fig.4. The range of stomach content weights in male (N = 20) and female (N = 35) wolves from Latvia (only stomachs with contents were considered).

Fig.1. Andersone and Ozolins

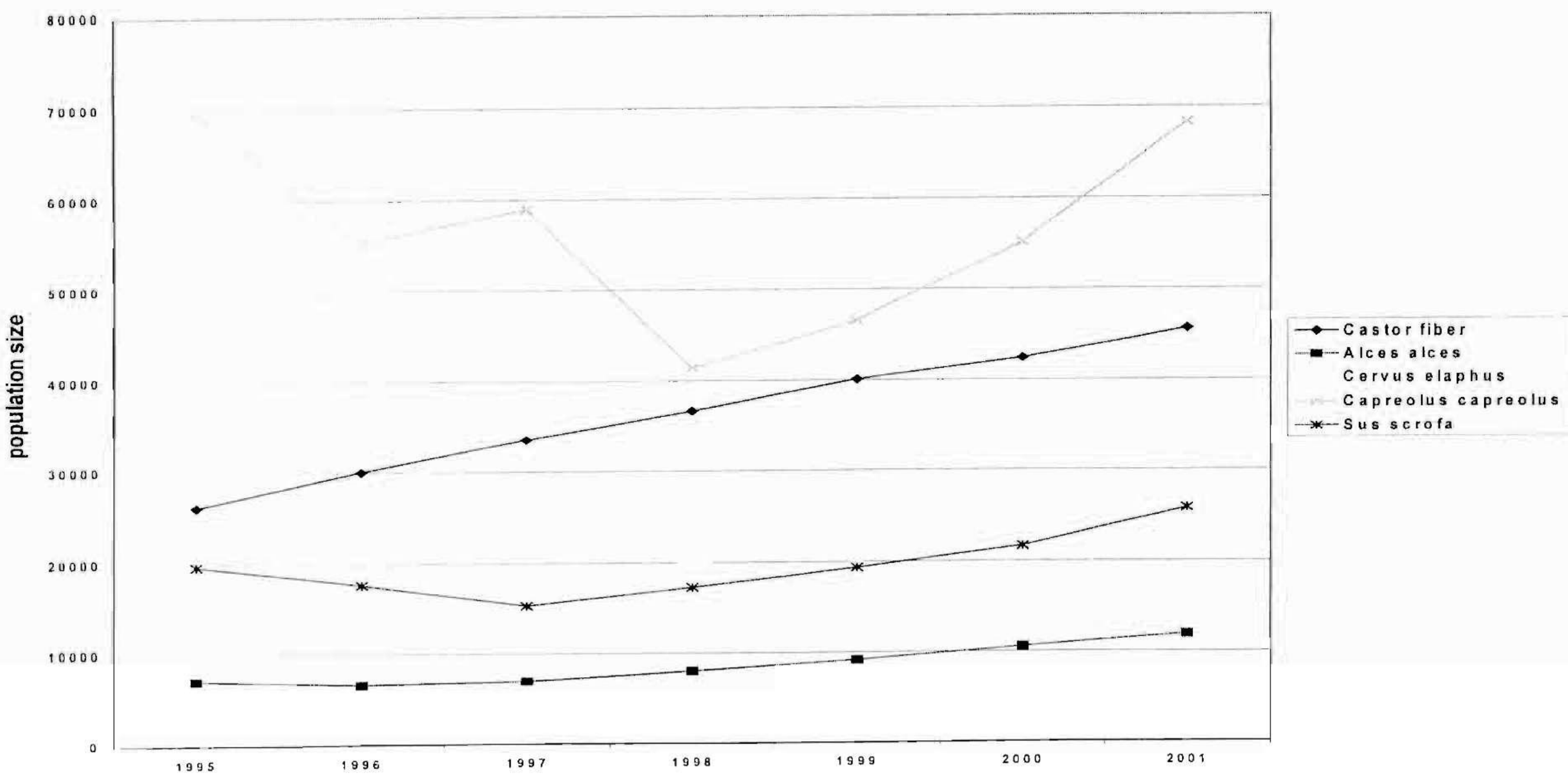


Fig.2. Andersone and Ozolins

Fig. 3. Andersone and Ozolins

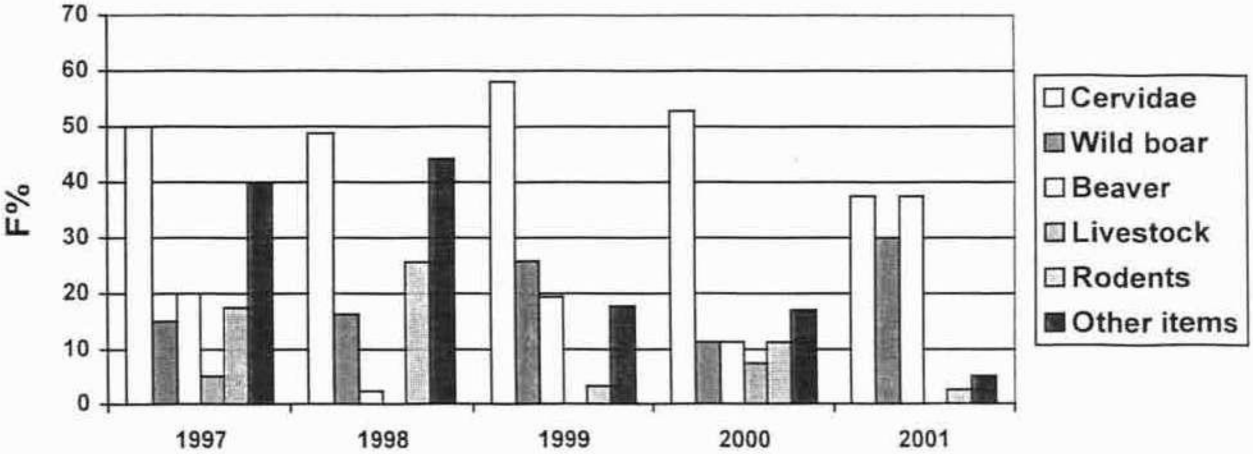
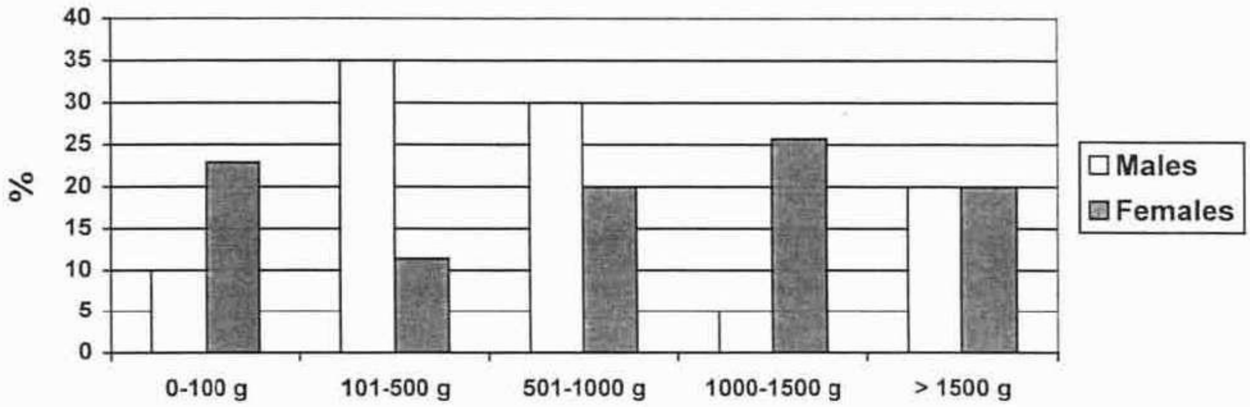


Fig.4. Andersone and Ozolins



3.3. Discussion and conclusions

Wolves usually selectively prey on certain age and sex groups – mainly old and / or young animals (Okarma 1984, Peterson et al. 1984, Гордиюк 1991, Bobek et al. 1992, Smietana and Klimek 1993, Boyd et al. 1994, Adams et al. 1995, Linnell et al. 1995, Kanzaki and Perzanowski 1997, Kunkel and Pletscher 1999, Mech et al. 2001). Often these are females (Okarma 1991, Гордиюк 1991, Mech et al. 2001), however, selective predation on males is also known (Bobek et al. 1992, Huggard 1993). The fact that wolves prey on different age classes than human hunters do (Bobek et al. 1992, Boyd et al. 1994) means that hunting by humans in no ways can be a substitute for a natural predation. Moreover, ungulate populations can deteriorate after removal of predators (Филонов 1982). Prey selection by human hunters is directed toward adult individuals, which can affect the ungulate population dynamics more than wolf-induced calf mortality (Linnell et al. 1995). The most precise method to assess age of prey is studying the diet by investigating carcasses of killed animals, which was not possible during the present study. Therefore, to avoid possible bias, age determination from scats was not carried out, although results of the pilot study (Andersone 1998a) indicated a high proportion of roe deer fawns in the summer diet of wolves. Further studies are needed in order to investigate selectivity of prey by wolves and their predation rates.

The current study revealed that cervids (presumably roe deer) are the most common prey items for wolves in Latvia, however, wild boar was a preferred species (Andersone 1998b) similarly to the results from Estonia (Valdmann et al. 1998). Significance of an alternative prey, which in our case was the beaver, usually increases when the principal food resource is scarce (Messier and Crête 1985, Gauthier and Theberge 1987). Beavers were relatively uncommon in Latvia before the 1980s, when the beaver population started rapid expansion all over the country (Балодис 1990, Balodis 1994), and, therefore, could have been a new type of prey, which wolves had to adjust to. The increase of its proportion in wolf diet could have started in the early 1990s after the collapse of ungulate populations caused by combination of various factors (over-hunting, poaching, collapse of collective farms, relieved control of the predators etc.). It is mainly a seasonal prey, though, as in wintertime its availability is limited due to ice and beaver activity patterns (Peterson 2001, Sharpe et al. 2001).

Local and seasonal variations in the wolf diet demonstrated that predator feeding ecology is dynamic, and even within such a small country as Latvia geographic differences in the predator's diet can be found. They are determined by the variations in the local habitat conditions, which in their turn shape the prey community of a particular area. Seasonal variations are caused by the availability of various food items in different seasons – berries and small vertebrates are mainly available in summertime, consequently, they feature on the wolf's menu during that period. However, their relative biomass consumed was insignificant compared to that of ungulates and beavers.

Competition for prey with other carnivore species was not very high for wolves in Latvia. They can seasonally compete for prey with brown bear (Завацкий 1990, Вайсфельд и Честин 1993) but as bears are so rare in Latvia it can hardly affect the population of wolves. Competition with lynx, as shown in the study, was relatively low, as food niche overlaped only partially. However, as the percentage of roe deer could have been higher in the wolf diet should other study methods have been used, it is probable that further studies will reveal a higher degree of competition between wolf and lynx. Yet lynx often is a victim of intra-guild predation by wolves (Pulliainen 1965, Matjushkin 1985, Завацкий 1990), thus likely to be a more vulnerable species to suffer from food competition. Especially, lynx have a narrower food niche, and depend on roe deer as the main prey in winter, even if roe deer are at low densities (Jędrzejewski et al. 1993, Okarma et al. 1997), while wolf as a typical generalist prey also on other species available. Scavengers (foxes, raccoon dogs, wild boar etc.) can consume a big part of wolves' kill, thus indirectly forcing predators to increase kill rates (Filonov and Kaletskaya 1985, Matjushkin 1985, Haber 1996). The only significant competitor for the wolf in Latvia is the man, hunting the same ungulate species.

It can be concluded that:

- Ungulates (cervids and wild boar) were shown to be the staple food for wolves in Latvia, in both seasons, ranging from 55.7% in summer to 76.6% in winter, wild boar being a preferred prey;
- Beaver was an important alternative prey, its proportion in wolf diet (18.8% of summer diet) being considerably higher than elsewhere in Europe;
- The food niche of wolves was broader in summer (B = 2.53), but ungulates nevertheless made up the bulk of the biomass consumed (89%);

- Some geographic and sexual differences were found - wolves preyed on wild boar considerably more in the east of the country, and male wolves hunted considerably more beavers than did females;
- Livestock was only an occasional food source for wolves in Latvia but the carrion could be seasonally important (13.1% in winter);
- Trophic competition with lynx was moderate, however, further studies are required to make the final conclusions about interrelations of these species.

4. Hybridisation between wolves and free-ranging dogs in Latvia

4.1. Introduction

Hybridisation is a natural part of evolution, therefore, it is anthropogenic hybridisation which is of concern from the conservationist's point of view (Allendorf et al. 2001). Hybridisation with domestic forms has been a hot issue in conservation of such species as the European wildcat and Australian dingo (McOrist and Kitchener 1994, Wilton et al. 1999, Beaumont et al. 2001, Daniels et al. 2001). Despite the controversy surrounding the origin of domestic dogs (Bibikov 1985), recent studies demonstrate the relatively recent divergence of wolves and dogs (Vilà et al. 1997) indicating that they are closely related forms (Lorenzini and Fico 1995). However, nowadays both species occupy so different environments, and dogs have undergone such considerable artificial selection that we can speak of hybridisation if both ecological forms interbreed.

Wolf - dog hybridisation is known from studies in the former USSR (Галака 1969, Кронит 1971, Ryabov 1985), Italy (Boitani 1983) and few other localities (Vilà and Wayne 1999, Randi et al. 2000). It usually occurs under certain circumstances such as the lack of intraspecific mates due to a disturbed demographic and spatial structure given the presence of free-ranging dogs in the area (Boitani 1983, Ryabov 1985, Blanco et al. 1992). In Latvia, no data on hybridisation was available except for a single case morphologically described from the early 1970s (Кронит 1971). However, the severe hunting pressure during the mid-1990s facilitated by a state financed bounty system must have influenced the wolf population in Latvia. It has declined both numerically and spatially (see chapter 1.2.), which suggested that hybridisation might have happened locally, where the wolf densities were low, as there is no shortage of potential mates - free-ranging dogs. This was supported by occasional reports from hunters of abnormally coloured wolves in some parts of Latvia. That was the impetus to start the current study.

Genetic samples were collected from wolves harvested in different parts of Latvia and analysed in Italy (National Institute of Wildlife Research) and Sweden (Uppsala University).

The aim of this study was to look for the occurrence of wolf – dog hybrids in Latvia as well as to compare different methods of the genetic analysis used for detecting hybridisation.

4.2. Results

Paper VIII

4.2.1. Combined use of maternal, paternal and bi-parental genetic markers for the identification of wolf-dog hybrids

Combined use of maternal, paternal and bi-parental genetic markers for the identification of wolf-dog hybrids

C. Vilà*†, C. Walker†, A.-K. Sundqvist†, Ø. Flagstad†, Z. Andersone‡, A. Casulli§, I. Kojola¶, H. Valdmann°, J. Halverson¦, H. Ellegren†

† *Department of Evolutionary Biology, Uppsala University, Norbyvägen 18D, S-75236 Uppsala, Sweden,* ‡ *Kemeri National Park, "Meza maja", Kemeri – Jurmala, LV-2012, Latvia,* § *Laboratory of Parasitology, Istituto Superiore di Sanità, Viale Regina Elena 299, 00161, Rome, Italy,* ¶ *Finnish Game and Fisheries Research Institute, Oulu Game and Fisheries Research, Tutkijantic 2A, FIN-90570 Oulu. Finland,* ° *Institute of Zoology and Hydrobiology, Tartu University, EE2400, Vanemuise 46, Estonia and* ¦ *PE AgGen Inc, Davis, CA 95616 USA.*

*Correspondence: Carles Vilà, Department of Evolutionary Biology, Uppsala University, Norbyvägen 18D, S-75236 Uppsala (Sweden).
Tel. +46-18-471 6464; Fax. +46-18-471 6310; Email. Carles.vila@ebc.uu.se

Keywords: *Canis lupus*, *Canis familiaris*, hybridization, Y chromosome, mtDNA, Microsatellites.

Running title: Wolf-dog hybridization in Scandinavia

SUMMARY

The identification of hybrids is often a subject of primary concern for the development of conservation and management strategies, but can be difficult when the hybridizing species are closely related and do not posses diagnostic genetic markers. However, the combined use of mitochondrial DNA (mtDNA), autosomal and Y chromosome genetic markers may allow the identification of hybrids and of the direction of hybridization. We used these three types of markers to genetically characterize a possible wolf-dog hybrid in the endangered Scandinavian wolf population. We first characterized the variability of mtDNA and Y chromosome markers in Scandinavian wolves as well as in neighboring wolf populations and in dogs. While the mtDNA data suggested that the target sample could correspond to a wolf, its Y chromosome type had not been observed before in Scandinavian wolves. We compared the genotype of the target sample at 18 autosomal microsatellite markers with those expected in pure specimens and in hybrids using assignment tests. The combined results led to the conclusion that the animal was a hybrid between a Scandinavian female wolf and a male dog. This finding confirms that inter-specific hybridization between wolves and dogs occurs in natural wolf populations. The incidence of such hybridization may be negatively correlated with wolf population density.

INTRODUCTION

Hybridization is a natural process that can lead to speciation but also an undesirable issue threatening the genetic integrity of endangered species (Arnold, 1997). Detecting the degree or extent of hybridization between species is thus important for evolutionary studies of speciation processes, as well as for conservation biology studies of species potentially in genetic peril. Moreover, being able to detect individual cases of hybridization events may be important from a management perspective. Studies on hybridizing species and populations have increasingly sought to use genetic markers that are unique for each taxon (Saetre et al., 2001), in some cases combined with morphological characters (Beaumont et al., 2001). Also, hybrid populations have been compared to pure populations to infer the degree of gene flow (Reich et al., 1999; Madrigal et al., 2001). However, given that hybridization is most likely between closely related taxa, in many cases differentiation between hybridizing populations may be primarily in the form of allele frequency differences rather than the frequent occurrence of private alleles. Identifying individual hybrids in such cases may be particularly problematic. The issue of potential hybridization between wolves (*Canis lupus*) and dogs (*C. familiaris*) represents an example of this situation.

Hybridization can occur between many species of the canid family (Gray, 1954; Lehman et al., 1991; Mercure et al., 1993; Roy et al., 1996;

Wayne and Brown 2001) and sometimes threatens the survival of endangered canid species or populations (Nowak, 1979; Wayne and Jenks, 1991; Gottelli et al., 1994; Roy et al., 1994). The close relationship between wolves and dogs, a consequence of their recent divergence (Vilà et al. 1997), suggests that hybridization between these species could be especially common since reproductive isolation may be not completely developed. Wolves coexist with dogs across most of their range.

Wolf populations in Eurasia have become increasingly fragmented during the last centuries (Mech, 1970; Wayne et al., 1992). Their numbers have dramatically decreased and in most areas of Europe only small populations survive in close contact with increasing numbers of humans and domestic dogs (Promberger and Schröder, 1992). It is under these conditions that hybridization between wolves and dogs is most likely to occur (Boitani, 1983; Bibikov, 1988; Blanco et al., 1992). Boitani (1984) hypothesized that the recovery of wolf populations in Italy could have been the result of hybridization with dogs and Butler (1994) suggested that European wolf populations could be composed mainly of hybrids.

Despite these concerns, a recent review of genetic evidence has suggested that wolf-dog hybridization may not be a threat even in small, endangered wolf populations near human settlements (Vilà and Wayne, 1999). Specifically, the analysis of mitochondrial DNA (mtDNA) suggests that hybridization between wolves and dogs is uncommon, i.e. there is no clear evidence of introgression of dog mtDNA into wolf populations, except a few cases in an east European wolf population (Randi et al., 2000). However, this infrequent presence of dog mtDNA haplotypes in wolves only implies that offspring of crosses between female dogs and male wolves are uncommon or do not back-cross into wolf populations. The use of mtDNA cannot provide any information about introgression of hybrids of crosses between male dog and female wolf. The scarce genetic information available on genetic markers corresponding to nuclear DNA suggests that this type of cross could also be uncommon, but the evidence is only circumstantial (Vilà and Wayne, 1999). In fact, pairs composed of a female wolf and a male dog have been observed in Russia, Israel, Italy and Spain (Ryabov, 1985; Randi et al., 1993; Vilà and Wayne, 1999; however, see Randi et al., 2000). More detailed genetic studies using a variety of genetic markers and in different populations are thus necessary to conclusively address the issue of wolf-dog hybridization and, if it occurs, to understand its directionality.

Hybridization with dogs could potentially be expected for Scandinavian (Swedish+Norwegian) wolves. This wolf population, presumed extinct during the 1970s, was founded by a very small number of individuals in the early 1980s (Wabakken et al., 2001), and by the winter 2000-2001 was about 87-97 animals (Terje Bø, pers. comm.). In 1999, a presumed juvenile wolf was found road-killed in southern Norway, close to

Oslo. The uncommon morphology of the animal gave rise to questions about its possible hybrid origin. In this study we combined the use of mtDNA, autosomal and Y chromosome markers to analyze the identity of this juvenile canid and we attempt to genetically characterize it as either a pure Scandinavian wolf, a migrant from Finland or Russia, a domestic dog, or a first generation hybrid between any of these groups.

MATERIAL AND METHODS

Samples

The study focused on two samples from the county of Østfold in southern Norway: sample *A* was blood from a juvenile individual killed by a car in October 1999 and sample *B* constituted snow with urine and blood collected in March 1999. Sample *A* is derived from the suspected hybrid, while sample *B* was assumed to correspond to the alpha female in oestrus from a wolf pack close to the site where sample *A* was killed. As far as is known, this female bred for the first time in 1999 (Terje Bø, pers. com.). In the winter of 1998/99 she was in oestrus but snow tracking suggested she was not yet paired to a male. However, during spring 1999 she was sighted with a male wolf and in the summer a litter of at least four pups was detected (Terje Bø, pers. com.).

Samples *A* and *B* were analyzed together with DNA samples extracted from muscular tissue of wolves from Scandinavia collected after

1980 (n= 25), Finland (n= 23), northwest Russia (n= 24), Estonia (n= 23) and Latvia (n =8), as well as of 44 domestic dogs. The dog samples correspond to pure-bred Huskies, Eskimo dogs, Akita, Elkhound, Wolfspitz, Great Pyrenees, Kuvasz and German Shepherd dogs. Although the dog samples originated from the USA, we assume that members of the same breeds in different continents will still be more similar to each other than to different populations of wolves. A separate set of 38 male pure bred Scandinavian dogs from diverse breeds was also genotyped for Y chromosome markers.

Laboratory procedures

DNA was isolated using variations on phenol-chloroform extraction methods (Sambrook et al., 1989). For sample *B*, snow containing urine and blood was centrifuged for over 30 minutes to concentrate cells before attempting DNA isolation.

Amplification of a 350 base pairs (bp) fragment of the mtDNA control region I was performed via the polymerase chain reaction (PCR) using primers Thr-L 15926 and DL-H 16340 (modified from Kocher et al., 1989). PCR conditions and profile were as described in Vilà et al. (1999). PCR products were sequenced using Big Dye Terminator cycle sequencing chemistry on an ABI 377 instrument (Perkin Elmer), following protocols provided by the manufacturer. Sequences were aligned using the program

CLUSTAL W (Higgins et al., 1992) and checked by eye. All sequences were compared to each other and to sequences available in GenBank and databases previously developed (based on Ellegren et al., 1996; Okumura et al., 1996; Taberlet et al., 1996; Tsuda et al., 1997; Vilà et al., 1997; Pilgrim et al., 1998; Vilà et al., 1999; Randi et al., 2000), using the program PAUP*4.0b8 (Swofford, 1998).

Eighteen autosomal microsatellites developed for dogs were selected for this study: c2001, c2010, c2017, c2054, c2079, c2088 and c2096 (Francisco et al., 1996), vWF (Shibuya et al., 1994), u213, u250 and u253 (Ostrander et al., 1993), and PEZ01, PEZ03, PEZ05, PEZ06, PEZ08, PEZ12 and PEZ20 (Perkin Elmer, Zoogen; see dog genome map at http://www.fhcrc.org/science/dog_genome/dog.html). In addition, one highly polymorphic Y chromosome microsatellite, MS41B (Sundqvist et al., 2001), was analyzed. This marker was only genotyped in the additional set of 38 pure bred male dogs and the target samples. PCR products, including one fluorescently labeled primer, were run on an ABI 377 instrument (Perkin Elmer) following protocols provided by the manufacturer. PCR primers, conditions and profile, were essentially as in the original reports. The alleles observed for each microsatellite were sized and scored using the software Genescan 3.1 and Genotyper 2.1 (Perkin Elmer). Due to the small amount of DNA extracted from sample *B* only a limited number of microsatellite amplifications could be successfully performed for this individual.

Data analysis

To study the likelihood of finding one of the observed autosomal genotypes in each one of the reference populations we used an assignment test (Paetkau et al., 1995, 1998; Waser and Strobeck, 1998). This calculates the log-likelihood of finding a certain genotype combination in each population and assigns the individual to the population for which it has the highest likelihood. From the moderate number of genotypes gathered from each population (n= 23-44) we cannot expect the samples to represent most of the variability in the populations, although the allele frequencies should be well represented. To characterize how well an individual genotype did fit into the distribution of genotypes expected from each population, we generated 1000 synthetic genotypes taking random alleles for each locus according to their frequency. Similarly, we generated populations of 1000 synthetic genotypes of hybrids between dogs and Scandinavian wolves, and between dogs and wolves from neighboring populations (see Thulin, 2000). In these cases the synthetic genotypes contained one allele derived from each of the two parent populations at each locus. We then calculated the likelihood of assignment to the Scandinavian wolf population. If the likelihood of the assignment of a target sample was outside the range observed for the 1000 synthetic genotype combinations we assumed that the sample did not belong to this population. To standardize the likelihood estimates, the log likelihood of assignment of the target sample to the wolf population was subtracted from the log likelihoods of the synthetic genotypes. After standardizing, the likelihood for the target sample becomes zero. If the value zero lies outside the distribution of assignment likelihoods for the synthetic population (or inside the 2.5% margins at each side of the distribution), the hypothesis that the target sample belongs to that population should be rejected. Since the number of microsatellites successfully scored was different for each target sample, the analyses were redone for each of the target samples including only the loci successfully amplified.

As a complement to the assignment test we also used a model-based genetic mixture analysis developed by Pritchard et al. (2000) which is implemented in the program Structure (available at http://www.stats.ox.ac.uk/~pritch/software.html). This program is based on a Bayesian approach and we used it to identify two groups (K= 2) in a sample composed of Scandinavian wolves and domestic dogs. Besides this initial classification of each individual sample, we used Structure to estimate the probability that each sample represented an immigrant or had a parent or grandparent that was an immigrant.

Assuming that the female of sample *B* is the mother of sample *A* (see below), we deduced the composition of paternally contributed alleles. We constructed a synthetic genotype homozygous for those alleles and calculated its assignment likelihood to different populations. Thus, the likelihood for the paternal haplotype is the square root of the likelihood for the synthetic homozygous individual.

RESULTS

Mitochondrial DNA sequences

The Scandinavian wolf population is fixed for a mtDNA haplotype H1 (Ellegren et al. 1996). This variant is also the most common in neighboring populations, present in about 65% of north European wolves, although it is not fixed in any of them (Table 1). Four different haplotypes were observed in Estonia and Finland, and five in Russia. Haplotype H1 has not been reported in domestic dogs (Okumura et al., 1996; Tsuda et al., 1997; Vilà et al., 1997; and complete GenBank searches). Both sample *A* and *B* were found to carry the H1 mtDNA haplotype. We thus conclude that the suspected hybrid was either a pure wolf or represented a hybrid with wolf ancestry in the maternal line. However, the geographical origin of this ancestry cannot be revealed by the mtDNA data.

Y chromosome microsatellite

Table 2 shows the alleles observed in one Y chromosome microsatellite (MS41-B) in male wolves from northern Europe and in 38 male dogs. Nine alleles have been observed in wolves: eight of them in the Baltic States (Estonia and Latvia), six in Russia and four in Finland. A total of eight alleles were observed in our sample of domestic dogs, including the two alleles found in Scandinavian wolves and almost all of the alleles observed in other wolf populations.

Among the two target samples the Y chromosome microsatellite was successfully amplified in sample *A* only, confirming that this came from a male and indicating that sample *B* was a female. The allele identified (*222*) was not found in Scandinavian wolves, but has been seen in other North European wolf populations and in dogs. Thus, this result does not discriminate between a wolf or a dog as the father of sample *A*. However, it suggests that the father was not a Scandinavian wolf.

Autosomal microsatellites

An assignment test comparing wolves from the Scandinavian population and dogs clearly shows that the allelic distributions allow for distinguishing between them (Fig. 1, all dogs are located above the diagonal, indicating a higher likelihood of being dogs than wolves, whereas all wolves are below the diagonal). Figure 1 also includes the target samples. Sample *A* lies between the distributions of dogs and wolves, a position that would be expected for a wolf-dog hybrid. Sample *B* appears at the limit of the distribution of wolves. This sample has the highest likelihood, among all animals, of assignment to the Scandinavian wolf population; this extreme position is likely to be a consequence of the low number of microsatellites successfully scored for this individual (11). Its likelihood of being a wolf is clearly higher than the likelihood of being a dog.

To analyze if the target samples differed significantly from the distribution of expected haplotypes for either Scandinavian wolves, dogs or F_1 hybrids, we analysed the distribution of the log likelihood of assignment to the Scandinavian wolf population of three groups: 1000 synthetic hybrids, 1000 synthetic dogs and 1000 synthetic Scandinavian wolves. Figure 2 (left) shows that the genotype combination of sample *A* is significantly different from that expected for pure dogs or wolves, but is inside the distribution for F_1 hybrids. Figure 2 (right) indicates that the genotype of sample *B* is outside the expected distribution for hybrids or dogs, but inside the distribution expected for Scandinavian wolves. A similar analysis shows that none of the target samples can be identified as a wolf immigrant from Finland or Russia (Table 3). We also tested if the assignment likelihoods of sample *A* and *B* were outside the expected distribution for a F_1 hybrid between a dog and an immigrant. The target samples were outside the distributions in both cases and thus this possibility could be excluded as well (analyses not shown).

The allelic composition of the two target samples is indicated in Table 4. For 10 out of 11 loci for which genotyping was successful for both sample *A* and *B*, sample *B* is compatible with being the parent of sample *A*. However, one locus (c2079) excludes this possibility: sample *A* is heterozygote for alleles 275 and 283, whereas *B* is homozygote for allele 271. We consider a technical artifact to be the most likely explanation for this non-congruence and that sample *B* is indeed parent to sample *A*. The quality and quantity of the DNA extracted from the thawed snow (sample *B*) might have been so low that allelic dropout has occurred. Allelic dropout, the accidental lack of amplification of one allele, is more common in samples of poor quality (Taberlet et al., 1999). This idea lends support from the fact that seven loci failed to amplify for sample *B* and possibly also from the fact that 10 out of 11 (91%) of the amplifying loci appeared homozygous. The average observed heterozygosity for all Scandinavian wolves for the 18 microsatellite markers was 0.65 (S.D.= 0.16) and, consequently, for 11 loci typed for sample *B* we would expect to have around 7 heterozygous loci. Unfortunately, the small amount of DNA obtained for sample *B* did not allow for further amplifications that may have detected allelic dropout.

Making the tentative assumption that sample *B* represents the mother of sample *A*, we determined the paternally contributed allele at 13 loci (Table 4). As above, the origin of the paternal haplotype was assessed by comparison to synthetic genotypes (Table 3). The likelihood of obtaining this haplotype from the Scandinavian, Finnish or Russian wolf population is extremely low and outside their expected distribution expected. Also, this haplotype is not expected from a hybrid between a Scandinavian wolf and a domestic dog. However, the likelihood for the paternal haplotype falls inside the distribution for pure dogs.

Additional support for these results was provided by the model-based method of Pritchard et al. (2000). All Scandinavian wolves had a probability of at least 0.95 of being classified as pure wolves (the probability was higher than 0.99 for 92% of the wolves). Similarly, all dogs but one had a probability higher than 0.95 of being genetically identified as pure dogs. The target sample *B*, in spite of its incomplete genotype, had a probability of 0.998 of corresponding to a pure Scandinavian wolf. On the other hand, the corresponding probability for sample *A* was only 0.264. For this sample, the probability of having one dog as parent was 0.402 and the probability of having it as a grand parent was 0.334. The probability of assignment to the dog population was 0.000. Consequently, sample *A* was likely to have a hybrid origin (probability= 0.402+0.334= 0.736).

DISCUSSION

The absence of species-specific genetic markers seemingly makes the identification of hybrids difficult, but the recent development of methods aimed at identifying inter-population migrants based on the initial characterization of allelic distributions in the parent populations (species) offer new means for hybrid identification (Paetkau et al., 1995; Pritchard et al., 2000). In addition, the combined use of autosomal markers and both paternally and maternally inherited markers may allow the direction of hybridization events to be determined. However, such precise knowledge on hybridization has so far not been possible to derive due to a general lack of polymorphic Y chromosome markers. This study therefore represents one of the first applications of Y chromosome polymorphisms, together with mtDNA and autosomal markers, to study hybridization in nature (c.f. Evans et al., 2001). The combined use of the markers allowed us to conclude that a hybridization event between dog and wolf had occurred in the endangered Scandinavian wolf population. The direction of hybridization was a male dog paired with a female wolf, the latter coming from the Scandinavian wolf population. Indeed, Vilà and Wayne (1999) suggested that if wolves and dogs would hybridize, the most likely direction is male dog crossing with female wolf. However, the lack of observable effects on the wolf populations led these authors to suggest that survival of hybrid pups could be difficult because dog fathers are less likely to help to raise the offspring and because their integration in wolf packs could be difficult.

An important consequence from our results is the confirmation, with compelling genetic evidence, that hybridization between wolves and dogs does occasionally occur in the wild and that hybrids can be successfully raised. However, as all 25 Scandinavian wolves included in the study are clearly differentiated from domestic dogs, i.e. do not show signs of recent hybridization, this indicates that hybridization may be an uncommon event.

The generation of synthetic genotypes for both pure specimens and hybrids allowed an intuitive representation of the variability that can be expected in each population group. This method allowed us to infer that the genotype of the target sample *A* would be very uncommon for pure dogs or Scandinavian wolves. The generation of synthetic genotypes is dependent on a fairly accurate knowledge of the allelic frequencies. The low genetic variability of Scandinavian wolves (Ellegren et al., 1996; Ellegren, 1999) simplifies the estimation of the allele frequencies, but this can be a harder task for dogs. The strong genetic fragmentation of dogs into breeds may limit the power of hybridization tests like the one we present here. Modern breeding practices imply the almost complete reproductive isolation between breeds, each of them with a small effective population size, leading to fast inter-breed differentiation due to genetic drift (Lingaas et al., 1996; Zajc et al., 1997; Wilton et al., 1999). The selection of local dogs belonging to the breeds that could be most likely to hybridize could increase the resolution of the test, allowing for an increase in power that could enhance the likelihood of detecting F_2 hybrids and backcrosses.

The birth of a litter had been detected in the area where the individual corresponding to sample *A* was killed. During autumn 1999 five cubs were observed. The killed animal was assumed to be one of these pups. Direct observation of the litter had suggested that these animals could be of hybrid origin. The determination of the hybrid status of sample *A* confirmed the suspicion and led to the management decision to remove its presumed siblings. As a result of the management efforts, two of them were killed by government officials. Another one is believed to have been illegally killed, and the last one is unaccounted for (Terje Bø, pers. comm.). This action should have reduced the chances of dog genes introgressing into the wolf population.

Further research is necessary in order to confirm if fragmented and low density wolf populations that coexist with larger number of domestic dogs are at high risk of hybridization, as suggested (Boitani, 1983; Blanco et al., 1992). If this is shown to be the case, management strategies that could result in the decrease of the density of already threatened wolf populations, or in the disruption of social groups, should be avoided.

ACKNOWLEDGEMENTS

The collection of samples in Russia was supported by the Swiss National Science Foundation SNF31-46691.96 and the Institutional Partnership Programme SNF 7IP051224, and was carried out with the help of Vladimir Bologov from the Central Natural Reserve Zapoviednik. Janis Ozolins, Agris Strazds, Janis Baumanis and other employees of the Latvian Forest Service and volunteer hunters assisted in the collection of Latvian wolves. Jonathan Stone developed the program used to generate synthetic genotypes. Jennifer Seddon and Frank Hailer provided valuable comments to the manuscript. This research has been supported by Direktoratet for Naturforvaltning (Norway), Swedish Environmental Protection Agency, the Swedish Research Council for Agriculture and Forestry, the Swedish Hunting Association, the Nordic Arctic Research Program, and by the Olle Engkvist, Carl Trygger, Oscar and Lili Lamms, and the Sven and Lilly Lawski's foundations. H.E. is a Royal Swedish Academy of Sciences Research fellow supported by a grant from the Knut and Alice Wallenberg foundation.

REFERENCES

ARNOLD, M.L. 1997. *Natural Hybridization and Evolution.* Oxford Series in Ecology and Evolution. Oxford University Press, New York.

BEAUMONT, M., BARRATT, E.M., GOTTELLI, D., KITCHENER, A.C., DANIELS, M.J., PRITCHARD, J.K. AND BRUFORD, M.W. 2001. Genetic diversity and introgression in the Scottish wildcat. *Mol. Ecol.*, **10**, 319-336.

BIBIKOV, D.I. 1988. *Der Wolf.* Die Neue Brehm-Bucherei. A. Ziemsen, Wittenberg Lutherstadt.

BLANCO, J.C., REIG, S. AND DE LA CUESTA, L. 1992. Distribution, status and conservation problems of the wolf *Canis lupus* in Spain. *Biol. Conserv.*, **60**, 73-80.

BOITANI, L. 1983. Wolf and dog competition in Italy. *Acta Zoologica Fennici,* **174**, 259-264.

BOITANI, L. 1984. Genetic considerations on wolf conservation in Italy. *Boll. Zool.*, **51**: 367-373.

BUTLER, D. 1994. Bid to protect wolves from genetic pollution. *Nature,* **370**, 497.

ELLEGREN, H., SAVOLAINEN, P. AND ROSÉN, B. 1996. The genetical history of an isolated population of the endangered gray wolf *Canis lupus*: a study of nuclear and mitochondrial polymorphisms. *Philos. T. Roy. Soc. B,* **351**, 1661-1669.

ELLEGREN, H. 1999. Inbreeding and relatedness in Scandinavian grey wolves *Canis lupus*. *Hereditas,* **130**, 239-244.

EVANS, B.J., SUPRIATNA, J. AND MELNICK, D.J. 2001. Hybridization and population genetics of two macaque species in Sulawesi, Indonesia. *Evolution,* **55**, 1686-1702.

FRANCISCO, L.V., LANGSTON, A.A., MELLERSH, C.S., NEAL, C.L. AND OSTRANDER, E.A. 1996. A class of highly polymorphic tetranucleotide repeats for canine genetic mapping. *Mamm. Genome,* **7**, 359-362.

GOTTELLI, D., SILLERO-ZUBIRI, C., APPLEBAUM, G.D., ROY, M.S., GIRMAN, D.J., GARCÍA-MORENO, J., OSTRANDER, E.A. AND WAYNE, R.K. 1994. Molecular genetics of the most endangered canid: the Ethiopian wolf *Canis simensis. Mol. Ecol.,* **3**, 301-312.

GRAY, A.P. 1954. *Mammalian hybrids; a check-list with bibliography.* Commonwealth Agricultural Bureau, Famham Royal, Bucks, United Kingdom.

HIGGINS, D.G., BLEASBY, A.J. AND FUCHS, R. 1992. CLUSTAL V: improved software for multiple sequence alignment. *Computer Applications in Biosciences,* **8**, 189-191.

KOCHER, T.D., THOMAS, W.K., MEYER, A., EDWARDS, S.V., PÄÄBO, S., VILABLANCA, F.X. AND WILSON, A.C. 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. *P. Natl. Acad. Sci. USA,* **86**, 6196-6200.

LEHMAN, N., EISENHAWER, A., HANSEN, K., MECH, D.L., PETERSON, R.O. AND WAYNE, R.K. 1991. Introgression of coyote mitochondrial DNA into sympatric North American gray wolf populations. *Evolution,* **45**, 104-119.

LINGAAS, F., AARSKAUG, T., SORENSEN, A., MOE, L. AND SUNDGREEN, P.-E. 1996. Estimates of genetic variation in dogs based on microsatellite polymorphism. *Anim. Genet.,* **27**, 29.

MADRIGAL, L., WARE, B., MILLER, R., SAENZ, G., CHAVEZ, M. AND DYKES, D. 2001. Ethnicity, gene flow, and population subdivision in Limon, Costa Rica. *Am. J. Phys. Anthropol.,* **114**, 99-108.

MECH, L.D. 1970. *The wolf. The Ecology and Behavior of an Endangered Species.* Doubleday, New York.

MERCURE, A., RALLS, K., KOEPFLI, K.P. AND WAYNE, R.K. 1993. Genetic subdivisions among small canids: mitochondrial DNA differentiation of swift, kit and arctic foxes. *Evolution,* **47**, 1313-1328.

NOWAK, R.M. 1979. *North American Quaternary Canis.* No. 6. Museum of Natural History, University of Kansas, Lawrence.

OKUMURA, N., ISHIGURO, N., NAKANO, M., MATSUI, A. AND SAHARA, M. 1996. Intra- and interbreed genetic variations of mitochondrial DNA major non-coding regions in Japanese native dog breeds (*Canis familiaris*). *Anim. Genet.,* **27**, 397-405.

OSTRANDER, E.A., SPRAGUE JR., G.F. AND RINE, J. 1993. Identification and characterization of dinucleotide repeat $(CA)_n$ markers for genetic mapping in the dog. *Genomics,* **16**, 207-332.

PAETKAU, D., CALBERT, W., STIRLING, I. AND STROBECK, C. 1995. Microsatellite analysis of population structure in Canadian polar bears. *Mol. Ecol.,* **4**, 347-354.

PAETKAU, D., SHIELDS, G.F. AND STROBECK, C. 1998. Gene flow between insular, coastal and interior populations of brown bears in Alaska. *Mol. Ecol.* **7**: 1283-1292.

PILGRIM, K.L., BOYD, D.K. AND FORBES, S.H. 1998. Testing for wolf-coyote hybridization in the Rocky Mountains using mitochondrial DNA. *J. Wildlife Manage.,* **62**, 683-689.

PRITCHARD, J.K., STEPHENS, M. AND DONNELLY, P. 2000. Inference of population structure using multilocus genotype data. *Genetics,* **155**, 945-959.

PROMBERGER, C. AND SCHRÖDER, W. (eds.). 1992. *Wolves in Europe. Status and Perspectives.* Wildbiologische Gesellschaft München e.V., Munich.

RANDI, E., LUCCHINI, V. AND FRANCISCI, F. 1993. Allozyme variability in the Italian wolf (*Canis lupus*) population. *Heredity,* **71**, 516-522.

RANDI, E., LUCCHINI, V., CHRISTENSEN, M.F., MUCCI, N., FUNK, S.M., DOLF, G. AND LOESCHCKE, V. 2000. Mitochondrial DNA variability in Italian and East European wolves: detecting the consequences of small population size and hybridization. *Conserv. Biol.,* **14**, 464-473.

REICH D.E., WAYNE, R.K. AND GOLDSTEIN, D.B. 1999. Genetic evidence for a recent origin by hybridization of red wolves. *Mol. Ecol.,* **8**, 139-144.

ROY, M.S., GEFFEN, E., SMITH, D., OTSRANDER, E.A. AND WAYNE, R.K. 1994. Patterns of differentiation and hybridization in North American wolflike canids, revealed by analysis of microsatellite loci. *Mol. Biol. Evol.*, **11**, 553-570.

ROY, M.S., GEFFEN, E., SMITH, D. AND WAYNE, R.K. 1996. Molecular genetics of pre-1940 red wolves. *Conserv. Biol.,* **10**, 1413-1424.

RYABOV, L.S. 1985. Results of wolf population disturbances. In: Bibikov, D. I. (ed.) *Wolf. History, Systematics, Morphology, Ecology,* pp. 431-446. Nauka Publishers, Moscow. [In Russian]

SAETRE G.P., BORGE, T., LINDELL, J., MOUM, T., PRIMMER, C.R., SHELDON, B.C., HAAVIE, J., JOHNSEN, A. AND ELLEGREN, H. 2001. Speciation, introgressive hybridization and nonlinear rate of molecular evolution in flycatchers. *Mol. Ecol.*, **10**, 737-749.

SAMBROOK, E., FRITSCH, F. AND MANIATIS, T. 1989. *Molecular Cloning*. Cold Spring Harbor Press, Cold Spring Harbor, New York.

SHIBUYA, H., COLLINS, B.K., HUANG, T.H-M. AND JOHNSON, G.S. 1994. A polymorphic (AGGAAT)n tandem repeat in an intron of the canine von Willebrand factor gene. *Anim. Genet.* **25**: 122.

SUNDQVIST, A.-K., ELLEGREN, H., OLIVIER, M. AND VILÀ, C. 2001. Y chromosome haplotyping in Scandinavian wolves (*Canis lupus*) based on microsatellite markers. *Mol. Ecol.*, **10**, 1959-1966.

SWOFFORD, D.L. 1998. *PAUP* Phylogenetic analysis using parsimony and other methods*. Sinauer Associates, Sunderland, Massachussets.

TABERLET, P., GIELLY, L. AND BOUVET, J. 1996. *Etude génétique sur les loups du Mercantour.* Rapport pour la Direction de la Nature et des Paysages, Ministère de l'Environnement (unpub.), 8pp.

TABERLET, P., WAITS, L. AND LUIKART, G. 1999. Noninvasive genetic sampling: look before you leap. *Trends Ecol. Evol.*, **14**, 323-327.

THULIN, C.-G. 2000. *Hybridisation between introduced brown hares and native mountain hares in Sweden*. Ph.D. thesis. Uppsala University.

TSUDA, K., KIKKAWA, Y., YONEKAWA, H. AND TANABE, Y. 1997. Extensive interbeeding occurred among multiple matriarchal ancestors during the domestication of dogs: evidence from inter- and intraspecies polymorphisms in the D-loop region of mitochondrial DNA between dogs and wolves. *Genes Genet. Syst.*, **72**, 229-238.

VILÀ, C., SAVOLAINEN, P., MALDONADO, J.E., AMORIM, I.R., RICE, J.E., HONEYCUTT, R.L., CRANDALL, K.A., LUNDEBERG, J. AND WAYNE, R.K. 1997. Multiple and ancient origins of the domestic dog. *Science,* **276**, 1687-1689.

VILÀ, C., AMORIM, I.R., LEONARD, J.A., POSADA, D., CASTROVIEJO, J., PETRUCCI-FONSECA, F., CRANDALL, K.A., ELLEGREN, H. AND WAYNE, R.K. 1999. Mitochondrial DNA phylogeography and population history of the gray wolf *Canis lupus*. *Mol. Ecol.,* **8**, 2089-2103.

VILÀ, C. AND WAYNE, R.K. 1999. Hybridization between wolves and dogs. *Conserv. Biol.* **13**: 195-198.

WABAKKEN, P., SAND, H., LIBERG, O. AND BJÄRVALL, A. 2001. The recovery, distribution, and population dynamics of wolves on the Scandinavian Peninsula, 1978-1998. *Can. J. Zool.,* **79**, 710-725.

WASER, P.M. AND STROBECK, C. 1998. Genetic signatures of interpopulation dispersal. *Trends Ecol. Evol.,* **13**, 43-44.

WAYNE, R.K. AND JENKS, S.M. 1991. Mitochondrial DNA analysis implying extensive hybridization of the endangered red wolf, *Canis rufus*. *Nature,* **351**, 565-568.

WAYNE, R.K., LEHMAN, N., ALLARD, N.W. AND HONEYCUTT, R.L. 1992. Mitochondrial DNA variability of the gray wolf: genetic consequences of population decline and habitat fragmentation. *Conserv. Biol.*, **6**, 559-569.

WAYNE, R.K. AND BROWN, D.M. 2001. Hybridization and conservation of carnivores. In Gittleman, J.L., Funk, S.M., Macdonald, D. and Wayne, R.K. (eds.) *Carnivore Conservation*, pp. 145-162. Cambridge University Press, Cambridge, U.K.

WILTON, A.N., STEWARD, D.J. AND ZAFIRIS, K. 1999. Microsatellite variation in the Australian dingo. *J. Hered.*, **90**, 108-111.

ZAJC, I., MELLERSH, C.S. AND SAMPSON, J. 1997. Variability of canine microsatellites within and between different dog breeds. *Mamm. Genome*, **8**, 182-185.

Table 1. Mitochondrial DNA haplotypes in wolves from Northern Europe and in the target samples.

	Populations					
	Scand.	Finland	Russia	Estonia	Sample *A*	Sample *B*
H1	25	10	6	19	X	X
H2		2				
H3			3			
H4		10	12	1		
H5			2	1		
H6		1				
H7			1	2		

Table 2. Y chromosome microsatellite alleles (locus MS41-B) observed in male wolves from Northern Europe (data from Sundqvist et al. 2001), pure-bred dogs, and in the target sample *A*.

MS41-B alleles (bp):	*212*	*214*	*216*	*218*	*220*	*222*	*224*	*226*	*228*
Scandinavia		3			9				
Finland			6	5		2			3
Russia			8	13	1	1	1		2
Baltic States (Estonia+Latvia)	1	5	5	5		5	4	3	3
Dogs		6	2	8	7	3	5	3	4
Sample *A*						X			

Table 3. Proportion (P) of 1000 synthetic genotypes in which the likelihood of assignment to the respective wolf population is lower than the likelihood of assignment observed for the target samples (*A*, *B* and for the synthetic father, see text). Figures shown in bold indicate those tests where the sample could not be excluded from the simulated distribution. *N* is the number of microsatellite loci considered for the analysis.

		Sample *A*		Sample *B*		Synthetic father	
Synthetic population:	Assigned to:	P	*N*	P	*N*	P	*N*
1000 Scand. wolves	Scand. wolf pop.	0.000	18	**0.917**	11	0.000	13
1000 dogs	Scand. wolf pop.	1.000	14	1.000	8	**0.256**	10
1000 F_1 Hybrids*	Scand. wolf pop.	**0.648**	14	1.000	8	0.000	10
1000 Finnish wolves	Finnish wolf pop.	0.000	18	0.000	11	0.000	13
1000 Russian wolves	Russian wolf pop.	0.000	18	0.002	11	0.000	13

*F_1 Hybrid: Dog X Scandinavian wolf

Synthetic Population	Assignment to:	Sample *A*		Sample *B*		Synthetic father	
		P	*N*	P	*N*	P	*N*
1000 Scand. Wolves	Scand. Wolf	0.000 (-3.79)	18	**0.917** (N/A)	**11**	0.000 (-11.3)	13
1000 Dogs		1.000 (+1.2)	14	1.000 (+4.10)	8	**0.256** (N/A)	**10**
1000 F_1 Hybrids [Dog X Scand. Wolves]		**0.648** (N/A)	**14**	1.000 (+1.70)	8	0.000 (-2.08)	10
1000 Finnish Wolves		0.000 (-1.19)	18	0.000 (-0.70)	11	0.000 (-3.31)	13
1000 Russian Wolves		0.000 (-2.89)	18	0.002 (N/A)	11	(-4.27)	13

Table 4. Microsatellite alleles identified for each target sample. The last column indicates alleles that could be identified as coming from the father of *A* assuming that *B* is the mother.

Locus	Sample *A*	Sample *B*	Paternal allele for sample A
c2001	149/153	153/153	149
c2010	225/237		
c2017	258/266		
c2054	148/152	148/148	152
c2079	275/283	271/271	
c2088	131/135	127/135	131
c2096	95/103	95/95	103
PEZ01	112/120	120/120	112
PEZ03	132/138	138/138	132
PEZ05	96/104	96/96	104
PEZ06	174/174	174/174	174
PEZ08	238/238		238
PEZ12	272/272		272
PEZ20	177/177	177/177	177
u213	159/162		
u250	126/138		
u253	106/112	106/106	112
VWF	157/157		157

FIGURE LEGENDS

Figure 1. Log likelihood of assignment for dogs (open triangles) and Scandinavian wolves (black circles). The log likelihoods for the two target samples (*A, B*) are also indicated.

Figure 2. Distribution of the log likelihood of assignment to the Scandinavian wolf population of 1000 synthetic genotypes corresponding to dogs, Scandinavian wolves and F_1 hybrids between dogs and wolves. Values are standardized by subtracting the log likelihood calculated for each target sample. If the value 0 (corresponding to the target sample) is outside the distribution, we can conclude that the genotype of the target sample is unlikely to occur in the dog, wolf or hybrid population.

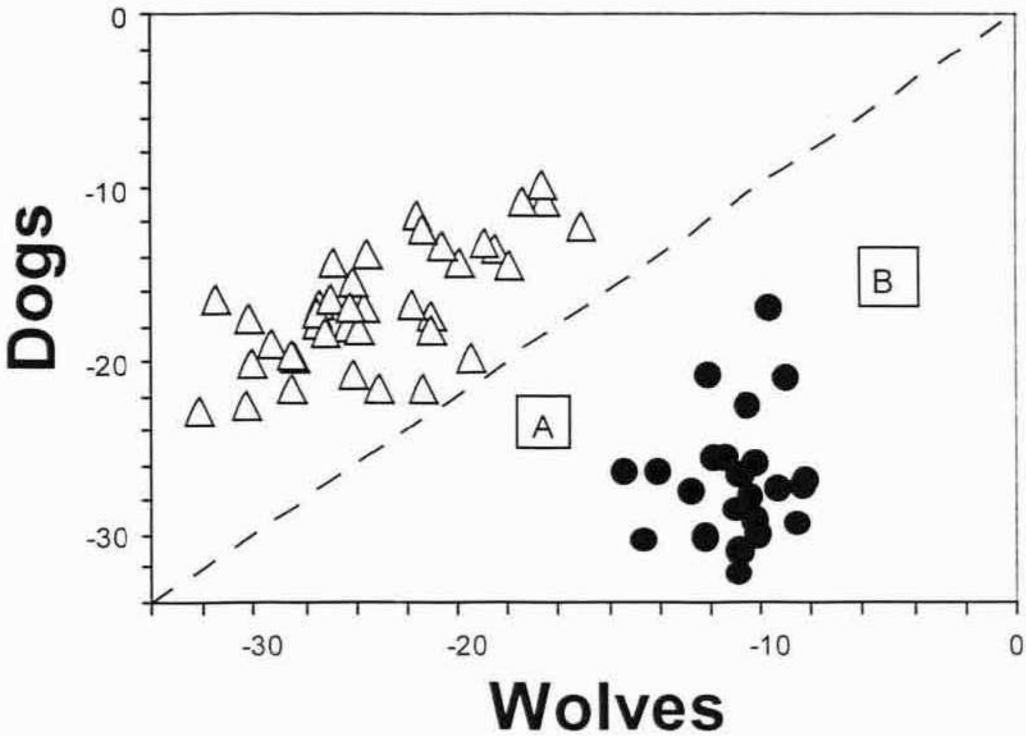


Fig. 1

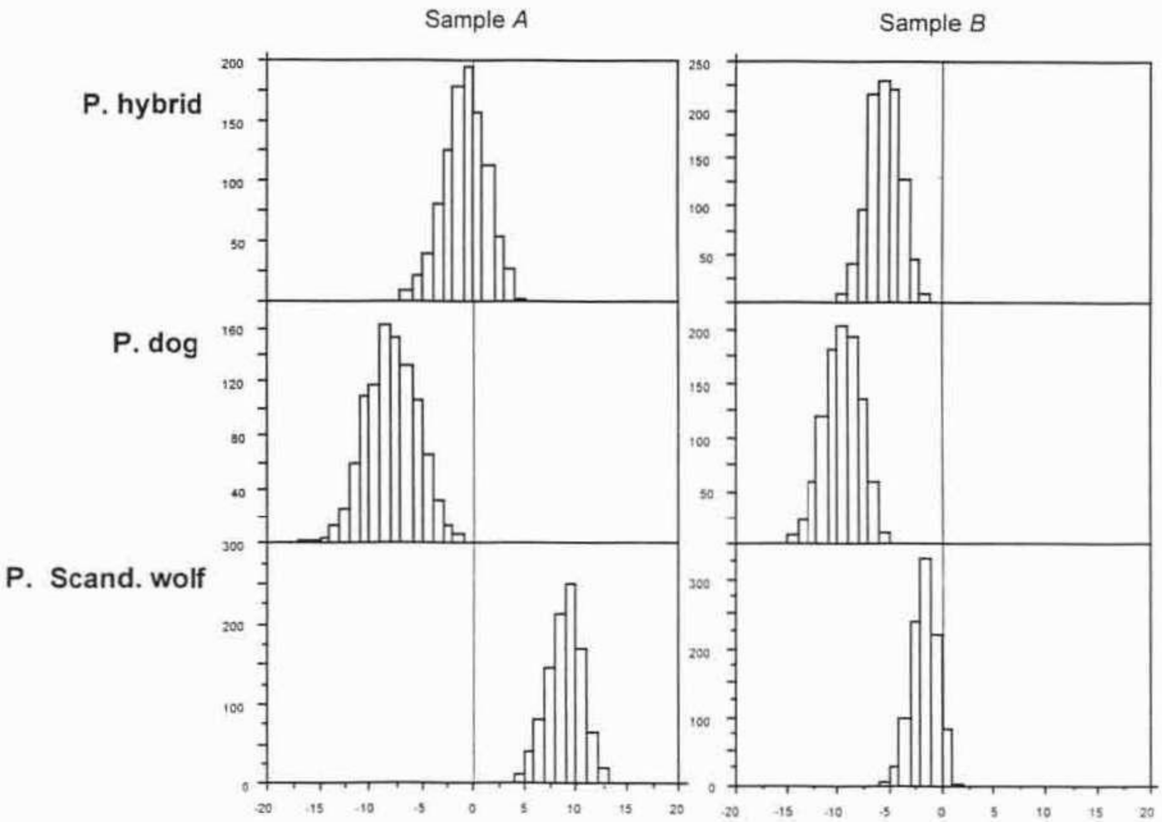


Fig. 2

Paper IX

4.2.2. Hybridisation between wolves and dogs in Latvia as documented using mitochondrial and microsatellite DNA markers

Mamm. biol. 67 (2002) 79–90
© Urban & Fischer Verlag
http://www.urbanfischer.de/journals/mammbiol

Mammalian Biology
Zeitschrift für Säugetierkunde

Original investigation

Hybridisation between wolves and dogs in Latvia as documented using mitochondrial and microsatellite DNA markers

By Žanete Andersone, V. Lucchini, E. Randi, and J. Ozoliņš

Ķemeri National Park, Jūrmala, Latvia; Istituto Nazionale per la Fauna Selvatica, Ozzano dell'Emilia, Italy; State Forest Service, Rīga, Latvia

Receipt of Ms. 11. 09. 2000
Acceptance of Ms. 24. 07. 2001

Abstract

Crossbreeding between wolves and dogs in the wild has been sometimes reported, but always poorly documented in scientific literature. However, documenting frequency of hybridisation and introgression is important for conservation of wild living wolf populations and for the management of free ranging dogs. Here we report the results of molecular genetic analyses of 31 wolf samples collected in Latvia from 1997 to 1999, including six pups originated from a litter found in northern Latvia in March 1999, and six wolves showing morphological traits that suggested hybrid origin. Nucleotide sequencing of the hypervariable part of the mtDNA control-region and genotyping of 16 microsatellite loci suggested that both pups and the morphologically anomalous wolves might originate from crossbreeding with dogs. Causes of wolf-dog crossbreeding, as well as possible management effort to avoid further hybridisation in the wild, are discussed.

Key words: *Canis lupus*, feral dogs, hybridisation, Latvia

Introduction

Recent genetic findings (Tsuda et al. 1997; Vilà et al. 1997; Randi et al. 2000) indicated that, in agreement with morphological, ethological and chromosomal data (Herre and Röhrs 1990), wolves (*Canis lupus*) and dogs are closely related, wolves being the only ancestors of domestic dogs (Geptner and Naumov 1967; Herre and Röhrs 1990). Wolves and dogs have identical karyotypes, can hybridise and produce fertile offspring in captivity and, eventually, also in nature where they meet (Mengel 1971; Vilà and Wayne 1999). Often wolves and free-ranging or feral dogs use different ecological niches (Boitani et al. 1995), but their interactions are variable and may range from a sort of predator–prey relationship to coexistence, which ultimately may lead to crossbreeding and hybridisation (Vilà and Wayne 1999). Risk of hybridisation in the wild could be higher in areas where wolves are rare and in contact with free-ranging dogs, as it was documented for the Ethiopian wolf *Canis simensis* (Gottelli et al. 1994), and feared for some wolf populations in Europe (Butler 1994). Hybridisation has the potential to produce morphological, physiological and behav-

1616-5047/02/67/02-079 $ 15.00/0.

ioural changes in captive and wild-living canids (MENGEL 1971; THURBER and PETERSON 1991; LARIVIERE and CRETE 1993). Therefore, the introgression of domestic genes may threaten the integrity of the gene pool of wild canids (BOITANI 1984; GOTTELLI et al. 1994). Moreover, hybridisation between wolves and free-ranging dogs deserves serious attention because of its ecological and management consequences. For example, wolf – dog hybrids tend to have synanthropic behaviour and are more difficult to control than wolves (BIBIKOV 1985).
Occasional crossbreeding between wolves and dogs in the wild were observed in Italy (BOITANI 1983), Russia (BIBIKOV 1985), Ukraine (GALAKA 1969; GURSKY 1975), Belarus (V. SIDOROVICH, pers. comm.), and in other European countries as well. However, field observations and genetic studies (BOITANI 1983; VILÀ and WAYNE 1999; RANDI and LUCCHINI 2001) suggest that crossbreeding might be very limited in west European wolf populations, while it might be more frequent in some parts of eastern Europe (BIBIKOV 1985; RANDI et al. 2000).
VILÀ et al. (1997) and RANDI et al. (2000) showed that nucleotide sequences from the hypervariable part of the mitochondrial DNA control-region (mtDNA CR) define haplotypes that are different in most of the European wolf populations, and not shared with any of the dog breeds studied so far. Thus, mtDNA CR haplotypes can be used as maternal genetic markers to detect wolf-dog hybridisation. Moreover, RANDI and LUCCHINI (2001) used a panel of canine microsatellite loci (NEFF et al. 1999; DOLF et al. 2000), hypervariable biparental genetic markers, which can be used to identify individual wolf and dog genotypes, and to detect cases of hybridisation and gene introgression.
A putative case of wolf-dog hybridisation in the wild was described in 1971 in eastern Latvia, based only on morphological observations (KRONIT 1971). In the 1990s, hunters periodically reported the presence of eventual wolf – dog hybrids in Latvia (I. JAUNPUJĒNS, pers. comm.). Therefore, within the wolf research project carried out from 1997 to 1999 by the State Forest Inventory Institute, collection of wolf tissue samples for genetic analyses started.
The aim of this study was to describe the genetic status of Latvian wolves and, using genetic markers to document occurrence of wolf – dog hybridisation.

Material and methods

Wolf hunting in Latvia is permanently allowed as the means of population control. In 1997–1999, about 800 wolves were shot. Hunters were obliged to report hunted wolves, and a portion of the carcasses was used for investigations. For this study, 31 well-preserved muscle samples were collected in 1997–1998, directly by hunters or by ourselves, when visiting the local forestry districts.
In March 1999, a litter of seven two-weeks-old pups was found in the wild in northern Latvia. These pups showed variable coat colours, suggesting hybridisation. Six pups were grey, one was black with white spots on the paws and breast. Most of the pups had pendant ears; four of them had five digits on at least one hind paw, and one pup had six digits (the fifth was divided into two). Blood samples were collected from six pups. Samples were also collected from their potential mother, a wolf-like female with the signs of recent lactation, and the potential father, a male with abnormal coat colour indicating hybridisation. Both were shot in the same area where the hybrid pups were found. The female also showed dog-like skull traits, which were determined using criteria of SUMINSKI (1975). These two animals were supposed to be the potential parents of the hybrids, because both were regularly observed (directly and by snow-tracking) in the area where the pups were later found. Other six wolves, collected in Latvia, were identified as potential hybrids because of abnormal morphological traits, such as coat colour or dog-like skull traits (SUMINSKI 1975).
Tissues and blood samples were preserved in 100% ethanol, and in a Tris/SDS storage buffer (LONGMIRE et al. 1988) at −20 °C. Total DNA was extracted from about 30–50 mg of each muscle tissue sample using a guanidinium-silica protocol (GERLOFF et al. 1995). A standard CHELEX boiling procedure (WALSH et al. 1991) was used to extract DNA from 100 microliters from each blood sample.
The entire (mtDNA CR) was PCR-amplified in all samples using primers L-Pro and H-Phe, which were originally designed from mammalian con-

sensus sequences of the tRNA-Pro and tRNA-Phe genes, respectively (DOUZERY and RANDI 1997; RANDI et al. 2000). PCRs were carried out on a Perkin Elmer 9600 thermocycler, using the following steps: initial denaturation at 94 °C for 2 minutes, 30 cycles at 94 °C for 15 seconds, 55 °C for 15 seconds, 72 °C for 1 minute, and a final extension at 72 °C for 5 minutes. Amplification products were purified from low-melting agarose gels using Gene Clean II (Bio101, La Jolla, CA). Double-strand cycle sequencing was performed using the PRISM Dye Terminator Kit (ABI), according to manufacturer's instructions, with the external primer L-Pro and the internal primers H350 (5'-GGG CCT GAA GTA AGA ACC AGA TGC C-3').

Electrophoresis of the purified sequencing products was carried out using an ABI 373A automatic sequencer. Sequences were aligned to a set of available mtDNA CR haplotypes from European wolves (RANDI et al. 2000), using the software CLUSTAL W (THOMPSON et al. 1994). Sequence divergence and phylogenetic relationships among the haplotypes were estimated by neighbor-joining analysis (NJ; SAITOU and NEI 1987) of pairwise Tamura-Nei genetic distances (TN; TAMURA and NEI 1993), using the computer program PAUP* 4.0 (SWOFFORD 1998).

Individual genotypes were determined using a set of 16 microsatellites (RANDI and LUCCHINI 2001), originally derived from dogs (NEFF et al. 1999), which are polymorphic in wolf populations (ROY et al. 1994; ELLEGREN et al. 1996; DOLF et al. 2000). These microsatellites were PCR-amplified in volumes of 10 microliters (containing 50 ng of DNA solution, 10 mM Tris-HCl, pH 8.3, 50 mM KCl, 1.5 $MgCl_2$, 0.1 µg BSA, 2 nmol of each dNTP, 0.25 units of Taq polymerase and 1–5 pmol of fluorescently labelled primers) using a Perkin Elmer 9600 thermal cycler. The microsatellites were analysed using an ABI 373A automatic sequencer and the software GENOTYPER 2.1. Inter-individual relationships and assignment tests of microsatellite genotypes were performed using the programmes KINSHIP 1.2 (GOODNIGHT and QUELLER 1999), and STRUCTURE (PRITCHARD et al. 2000), respectively.

Results

Mitochondrial DNA CR haplotypes in the Latvian samples

We extracted 31 DNA samples from Latvian wolves listed in table 1. Based on phenotypes, individuals W448 to W468 (n = 19) were identified as pure wolves, individuals W452 and W526 to W530 (n = 6) were identified as putative hybrids, and W513 to W518 (n = 6) were the hybrid pups. From these samples we sequenced about 294 nucleotides from the hypervariable part of the mtDNA CR, which were aligned and added to an extensive collection of canine mtDNA CR sequences (RANDI et al. 2000). The NJ tree depicting phylogenetic relationships among these sequences (Fig. 1) showed that sequences from the 19 Latvian wolves joined into two distinct groups of wolf haplotypes. The first one (including samples W449, W455, and W456) joined into a basal wolf clade (supported by BP = 59%) related to other wolf and dog sequences. All the other Latvian sequences joined more derived clades (one supported by BP = 70%, plus closely related haplotypes W450 and W458) including only those wolf haplotypes, which are distinct from any other known dog haplotype.

The six hybrid pups (W513 to W518) showed a unique mtDNA CR sequence, which was identical to other Latvian wolf haplotypes (Fig. 1), thus suggesting that their mother was a wolf. In fact, female W529, which was indicated as the putative hybrid mother of the pups, showed the same mtDNA CR haplotype of the pups. Male W452, which was indicated as the putative hybrid father of the pups, showed a unique haplotype, not shared with any other wolf, which was related to the Latvian wolves joining the basal clade (Fig. 1). The other four putative hybrids showed two distinct mtDNA haplotypes: the first one (in samples W526, W527, and W528) was identical with the haplotype of the hybrid pups, the second one (W530) joined a clade including only dog haplotypes. Thus, we suggest that sample W530 had a mtDNA of domestic origin.

Microsatellite variability and identification of pup genotypes

The distributions of allele frequencies at 16 microsatellite loci (Fig. 2) in the studied

Table 1. List of the Latvian wolf samples studied.

Sample label	Sampling locality	Phenotype
W448	Latvia	Wolf
W449	Latvia	Wolf
W450	Latvia	Wolf
W451	Latvia	Wolf
W453	Latvia	Wolf
W454	Latvia	Wolf
W455	Latvia	Wolf
W456	Latvia	Wolf
W457	Latvia	Wolf
W458	Latvia	Wolf
W459	Latvia	Wolf
W460	Latvia	Wolf
W461	Latvia	Wolf
W462	Kostantinova	Wolf
W463	Kostantinova	Wolf
W464	Kostantinova	Wolf
W467	Latvia	Wolf
W468	Latvia	Wolf
W469	Latvia	Wolf
W529	Dikļi (North Latvia)	Putative hybrid mother
W452	Aloja (North Latvia)	Putative hybrid father
W513	Aloja (North Latvia)	Hybrid pup
W514	Aloja (North Latvia)	Hybrid pup
W515	Aloja (North Latvia)	Hybrid pup
W516	Aloja (North Latvia)	Hybrid pup
W517	Aloja (North Latvia)	Hybrid pup
W518	Aloja (North Latvia)	Hybrid pup
W526	Padure (West Latvia)	Putative hybrid wolf
W527	Aloja (North Latvia)	Putative hybrid wolf
W528	Padure (West Latvia)	Putative hybrid wolf
W530	Kuldīga (West Latvia)	Putative hybrid wolf

Latvian wolves and in the putative hybrids were compared to a sample of 95 dogs (data from RANDI and LUCCHINI 2001). The hybrid pups showed several alleles that were present only in the dog sample and that were absent from the Latvian wolves. For example, alleles 97 and 107 at locus CPH2 of hybrid pups were absent in the Latvian wolf sample, while they were present at relatively high frequency in dogs. Also, alleles 173 at locus CPH7, 152 at locus CPH9, 129 and 149 at locus C09.250, and 158 at locus vWF.X of hybrid pups were shared only with dogs. On the other hand, alleles 203 at bocus CPH12 and 134 at locus vWF, which were shared between the pups and the Latvian wolves, were absent in the dog sample (Fig. 2). These results, therefore, suggest a hybrid origin of the pups.

The assignment test, performed with STRUCTURE, showed that all dogs and all the Latvian wolf samples were assigned to two distinct clusters (cluster I and II, respectively) with individual probability values $q \geq 0.93$ (Tab. 2). Using the dogs and Latvian wolf samples as population reference we performed an assignment test on all pups and putative hybrids. All of them showed a mixed ancestry in both dog and wolf clusters, except wolf W528 that was assigned to the Latvian wolf population (cluster II) with $q = 0.90$. Wolves W526 and W527 were also assigned to the wolf cluster but with a $q < 0.90$. Sample W530, the one

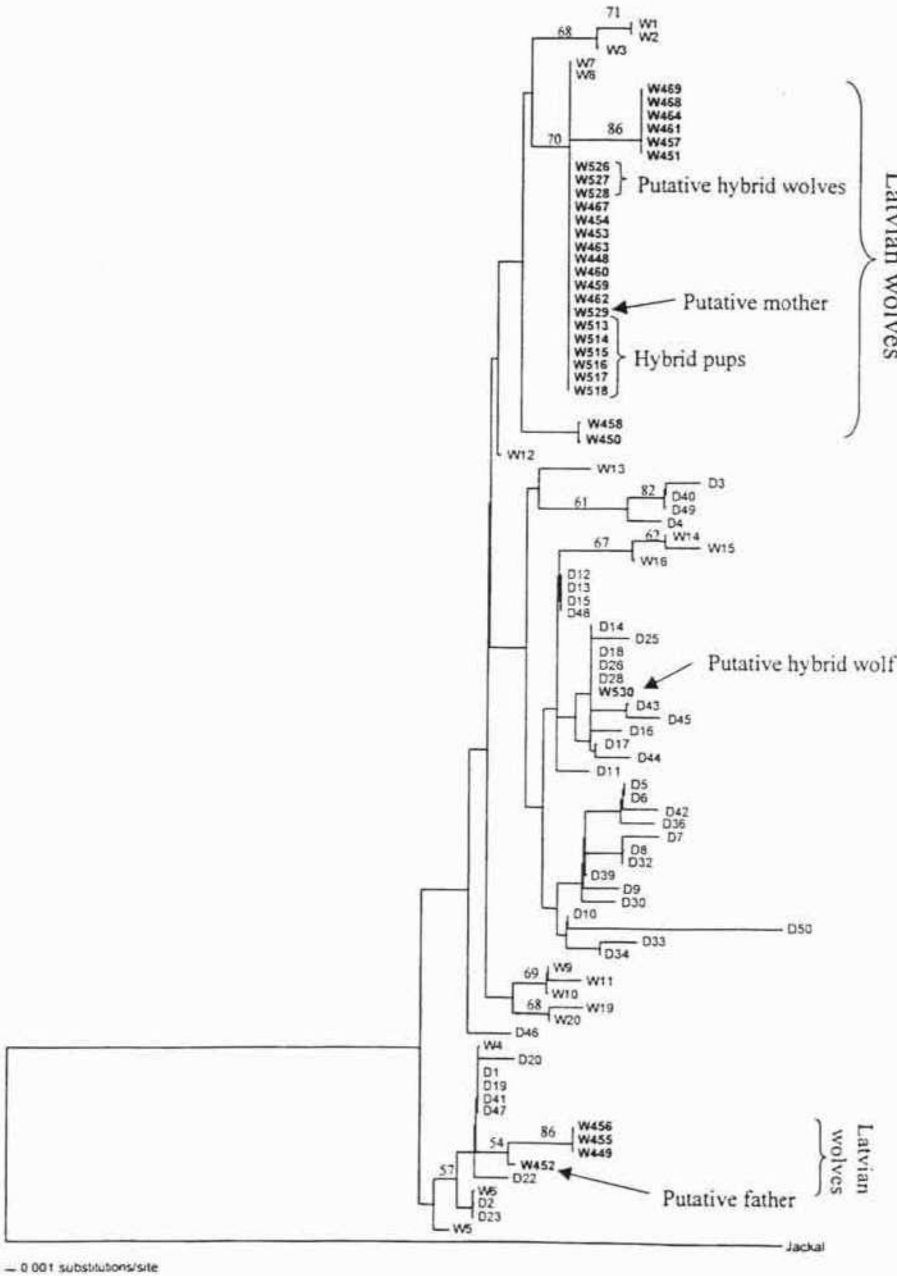


Fig. 1. Neighbour-joining tree, computed using Tamura-Nei DNA distances, showing the phylogenetic relationships among wolf and dog mtDNA CR haplotypes. Bootstrap values obtained after 1 000 resamplings are indicated only for those branches supported by values higher than 50%. Latvian wolves and putative hybrids are indicated in bold. Wolf and dog haplotypes are indicated with W and D, respectively, and the same numbers used in RANDI et al. (2000). The geographical origin of the wolves' haplotypes are as follows: Bulgaria = W1, W2, W5, W6, W9, W15, W16; Croatia = W3, W10; Greece = W4; Finland = W7, W8, W13; Turkey = W9; Israel = W11, W12; Italy = W14; Spain W19, W20.

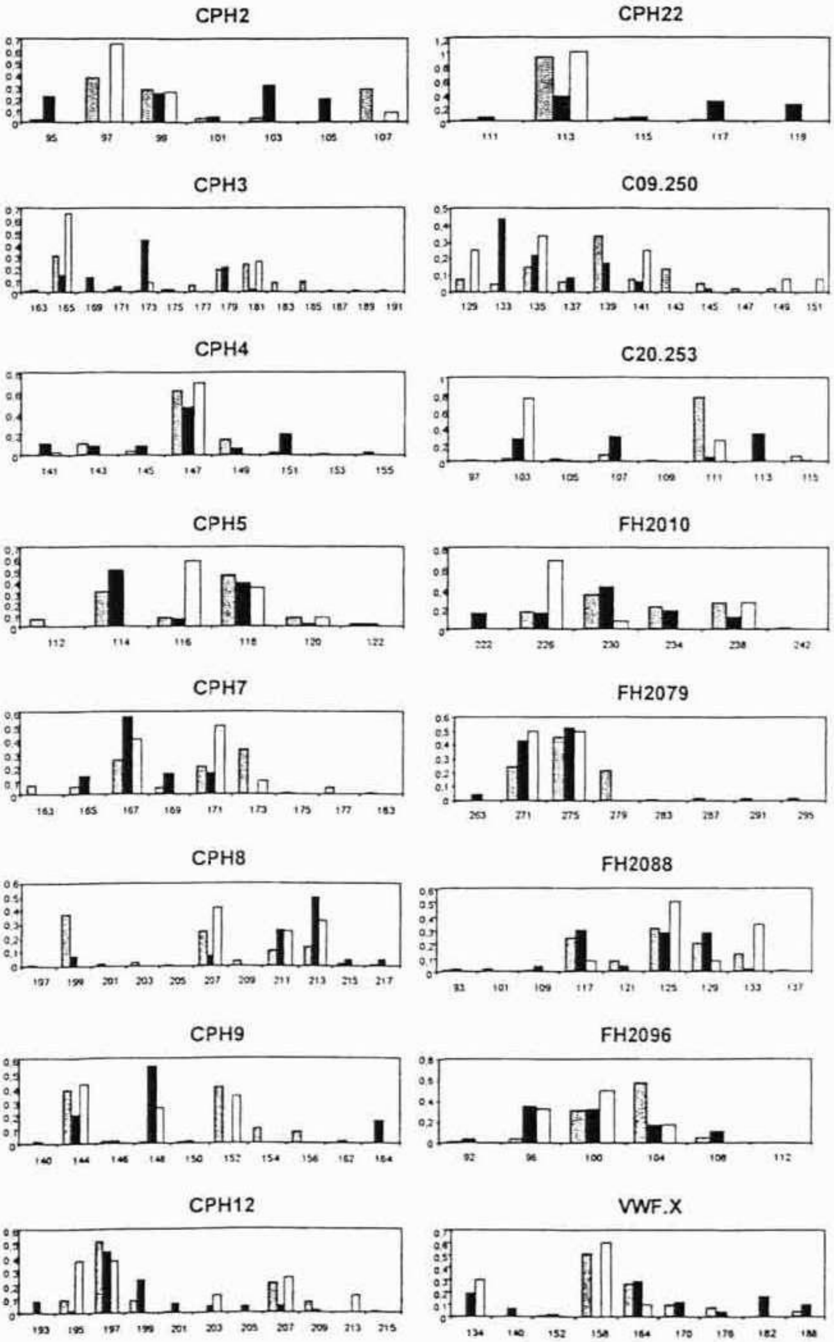


Fig 2. Distributions of the allele frequencies at 16 microsatellite loci in 95 dogs (grey bars; data from RANDI and LUCCHINI, 2001), in the 19 Latvian wolves studied (black bars) and in the putatively hybrid wolves (white bars). The horizontal scales indicate the molecular weights (in base pair length) of the different alleles; the vertical scales indicate the relative allele frequencies.

Table 2. Results of the assignment of individual microsatellite genotype to distinct cluster I and II, performed with STRUCTURE ($K = 2$; Usepopinfo = 1). The q values reported indicate the probability of individual genotypes to have ancestry in one or two genetic clusters. For sample identification see Tab. 1.

Sample	Cluster I (dogs)	Cluster II (wolves)
Dogs	≥0.93	<0.07
Latvian wolves	<0.07	≥0.93
W452 putative father	0.37	0.63
W529 putative mother	0.52	0.48
W513 pup	0.82	0.18
W514 pup	0.72	0.28
W515 pup	0.73	0.27
W516 pup	0.46	0.56
W517 pup	0.65	0.35
W518 pup	0.77	0.23
W526 putative hybrid	0.12	0.88
W527 putative hybrid	0.12	0.88
W528 putative hybrid	0.10	0.90
W530 putative hybrid	0.86	0.14

which showed a dog mtDNA haplotype, was assigned to the dog cluster with a high probability ($q = 0.86$), thus suggesting it could be a hybrid back-crossed into the dog population or simply a stray dog. The putative hybrids W529 and W452 presented the more evident ancestry in the dog population with a probability to be assigned to the dog population of $q = 0.52$ and $q = 0.37$, respectively.

Analyses of relatedness performed using KINSHIP allowed estimating the likelihood of two hypothetical pedigree relationships, a primary versus a null hypothesis, for each individual pair. Likelihood ratios of primary/null hypotheses >1 suggest that the primary hypothesis is the most probable, with confidence levels computed by simulating 10000 dyads sampled from the allele frequencies of the reference population. In this study, we tested a primary hypothesis of first-order relationships (e.g., dyads represent full sibs or parental-offspring with expected relatedness $r = 0.5$) versus a null hypothesis of no relationships ($r = 0.0$) in all the genotypes found in the study areas. When ratios between primary and null hypothesis are statistically significant, we can reject the null hypothesis and avoid a type II error (that siblings are incorrectly classified as unrelated) at a given level of significance. Results showed that the putative mother W529 had a highly significant $p < 0.001$) parental relationship with the pups. Thus, both mtDNA and microsatellite data suggested that the six pups are hybrids, and that female wolf W529 might be their (hybrid) mother. Wolf W452 resulted not significantly related to the pups, indicating that probably it was not the father.

Discussion

Recent studies (Vilà et al. 1997; Randi et al. 2000) indicated that nucleotide sequences from the hypervariable part of the mtDNA CR define haplotypes that are different in most of the European wolf populations, and not shared with any of the dog breeds studied so far. Thus, mtDNA CR haplotypes can be used as maternal genetic markers to detect wolf–dog hybridisation. Moreover, Dolf et al. (2000) and Randi and Lucchini (2001), using canine microsatellites to identify individual Italian wolf and dog genotypes, showed that these loci can be used to detect wolf–dog hybridisation and introgression of domestic genes into wild-living wolf populations.

Extensive molecular analyses of wolves in Spain (VILÀ et al. 1999) and Italy (RANDI et al. 2000; RANDI and LUCCHINI 2001) suggested that crossbreeding with dogs and introgression of domestic genes into wild populations is rare in western Europe. However, mtDNA data documented some putative cases of hybridisation in east European countries (RANDI et al. 2000). Results from this study confirm that crossbreeding of wolves and dogs might occur more frequently in eastern Europe than elsewhere. Rates of hybridisation and introgression might vary due to variable local ecological conditions or due to the relative density of wild living wolves and free ranging dogs.

Field observations and genetic analyses presented in this study document the occurrence of wolf–dog crossbreeding in Latvia. A litter of wolf pups found in March 1999 in northern Latvia showed a mtDNA CR haplotype that was previously found in wolves from Finland (haplotypes W7 and W8 in RANDI et al. 2000). These wolf haplotypes are distinct from the dog haplotypes described so far. However, results of assignment tests based on microsatellite allelic variability, and external morphological features concordantly indicate a hybrid origin of the litter. Morphologically all six pups resembled mongrels, having coat colour unusual for wolves. Such kind of coat colour variability of wolf–dog hybrids, which frequently show white spots or are darkly coloured, has been reported in the literature (BIBIKOV 1985; ZIMEN 1997). Moreover, the observed period of delivery, which occurred at the end of February, was not typical for wolves in Latvia, where pups usually are born in late April–May.

About 44% of the Latvian territory is still forested, the proportion of forested areas ranging from 25% in southern Latvia, the region with the most intensive agriculture, up to more than 70% in western and northern Latvia. These habitat conditions are very favourable for wolves. Prey species, including moose *Alces alces*, red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, wild boar *Sus scrofa*, European beaver *Castor fiber*, mountain and brown hare *Lepus timidus* and *L. europaeus*, and many small prey species are also abundant. In the area, where the hybrid pups were found, all these prey species are present and the forest coverage is high (about 50%). Nevertheless, the potential mother of the hybrid pups was observed to feed regularly at garbage sites. The limited available data do not allow estimating the extent and rate of wolf–dog crossbreeding in Latvia. However, the documented cases of crossbreeding suggest that hybridisation may be a threat to wild living wolves, at least in some areas of Latvia.

Hybridisation might be sustained by several factors. First, the number of free-ranging dogs is very high in Latvia (Fig. 3). In 1971, there were 174 000 stray dogs in the countryside (TAURINSH and YANSON 1975). Only some of these dogs were truly feral, and most of the others were free ranging dogs owned by farmers. Dog owners in the countryside are still not aware or simply do not care about the possible consequences of keeping free-ranging dogs. It is a common practice in the rural areas of Latvia for owners to let dogs roam freely nearby their farms. Free ranging dogs differ from small to large sized breeds, but German shepherd dogs and similar morphotypes are common and can be appropriate partners for dispersing solitary wolves.

The intensive wolf hunting that occurred during the last years could also favour crossbreeding with dogs. Wolf density in Latvia fluctuated widely depending on hunting activity. In the 20th century, the number of wolves in the country ranged from almost zero up to more than 1 000 (ANDERSONE and OZOLINS 2000 a). Now wolf hunting in Latvia is allowed throughout the year. The annual hunting bag in the middle of the 1990s exceeded 300 individuals (Fig. 3). Such a severe hunting pressure caused a sharp population decline, and both wolf population size and range decreased in the last few years across the country. Currently, the western and eastern parts of the Latvian wolf population are, at best, only weakly connected (Fig. 4). Genetic drift due to population isolation and decline could have already produced some morphological divergence

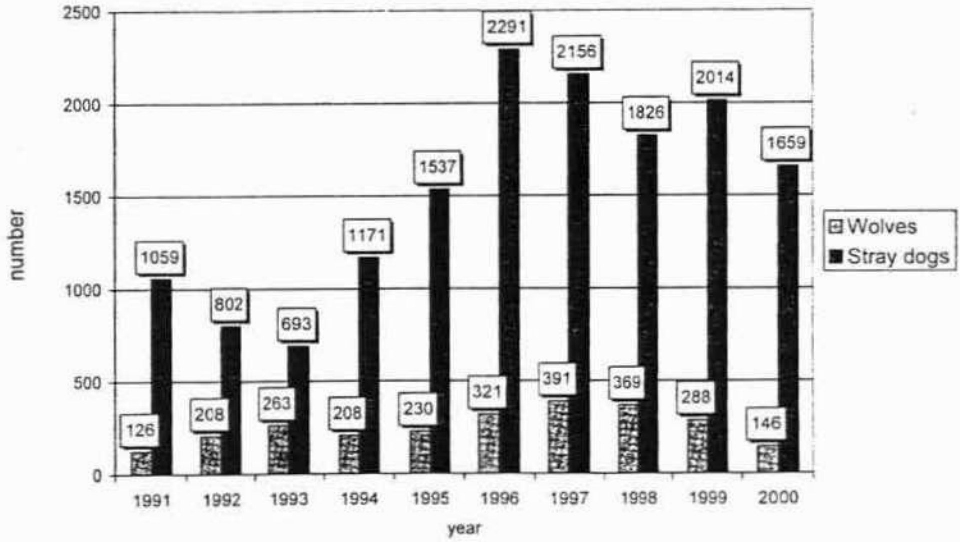


Fig. 3. Number of wolves and stray dogs hunted in Latvia, 1991–2000 (according to data of the State Forest Service).

Fig. 4. Distribution of counted and shot wolves in Latvia, 2000. The grey shading indicates forest distribution. Altogether, 144 wolves were shot from 1 April 1999 till 31 March 2000 (according to data of the State Forest Service). ● more than one specimen shot in a local forestry district (ca 150–200 km^2 area); • one specimen shot in a local forestry district; ○ no specimen shot but occurrence recorded

(ANDERSONE and OZOLINS 2000 b) and may reduce genetic diversity and raise rates of inbreeding in the future (RANDI 1993).

Rates of crossbreeding could be higher in wolf populations surviving at low density (Randi and Lucchini 2001). All reported cases of hybridisation in Latvia, the present one from northern Latvia, one in the 1970s (KRONIT 1970) and one from western Latvia (I. JAUNPUJĒNS, pers. comm.) occurred in areas of low population density, where few wolves are present, according to the annual census data of the State Forest Service (Fig. 4). These areas are forested, and can provide predators with prey and den sites, thus allowing stray dogs to survive in the wild.

Wolves often prey on dogs (BIBIKOV 1985; SABANEJEV 1988), which constitute 22% of all domestic animals attacked by wolves in Latvia (ANDERSONE et al. 2001). However, when wolf population density is low and their social structure is disrupted, wolves can interbreed with widespread free-ranging dogs (BIBIKOV 1985). It is obvious that dogs' keeping regulations are crucially important for forested areas where feral dogs can find excellent habitat and crossbreed with the few wolves present or with migrating wolves invading the area.

This study suggests that, locally in Latvia, the social structure of wolf populations may have been disrupted, thus leading to increasing hybridisation.

Acknowledgements

We thank A. STRAZDS and the Riga Zoo staff (P. PETROVS, B. DRAPČA, R. SIERIŅA, and others) for their help in keeping hybrid pups and taking the genetic samples. We express our cordial gratitude to the Gauja National Park in the persons of J. STRAUTNIEKS, and J. RUPMEJS and especially V. VĪTOLA who has devoted and is still devoting so much of her time to the captive hybrids. Thanks go also to V. SIDOROVICH for information about hybrids in Belarus. Special thanks for fruitful co-operation to all officers of the Latvian State Forest Service who found time for their contribution to this study and to those who provided additional information, e.g., I. JAUNPUJĒNS from Andumi forestry. We express our deepest appreciation to N. BENVIE for reviewing the English of the manuscript and Dr. ANDREAS KRANZ for translating the German summary.

Zusammenfassung

Hybridisation von Wölfen und Hunden in Lettland, dokumentiert über mitrochondriale und Mikrosatelliten-DNA-Marker

Über die Kreuzungen von Wölfen und Hunden in freier Wildbahn wurde manchmal berichtet, aber wenig oder gar nicht in der wissenschaftlichen Literatur dokumentiert. Es erscheint aber von Bedeutung, Vorstellungen über die Häufigkeit derartiger Bastardierungen zu erhalten, da Introgressionen von Hundegenen in das Wolfgenom von unmittelbarer Relevanz für den Schutz der Wölfe und das Management von frei laufenden Hunden ist. In dieser Studie wurden von 31 Wölfen molekulargenetische Analysen durchgeführt, darunter waren auch sechs Welpen eines Wurfes aus dem Norden von Lettland. Sechs dieser Wölfe wiesen morphologische Kennzeichen auf, die auf Hybridisation mit Hunden hindeuteten. Die nukleotide Sequenz des hypervariablen Teils der mtDNA und der Genotyp von 16 Microsatellit-Loci deuteten darauf hin, daß sowohl die Welpen als auch die morphologisch verdächtigen erwachsene Wölfe Hybriden waren. Die Ursache derartiger Kreuzungen und auch mögliche Managementmaßnahmen zur Vermeidung derartiger Vorkommnisse werden diskutiert.

References

ANDERSONE, Z.; BALCIAUSKAS, L.; VALDMANN, H. (2001): Human – Wolf Conflicts in the East Baltic. Proc. 2nd Internat. Wildlife Management Congress (in press).

ANDERSONE, Z.; OZOLINS, J. (2000 a): Big game and large carnivores in Latvia: present status and future prospects. J. Wildlife Res. (in press).

ANDERSONE, Z.; OZOLINS, J. (2000 b): Craniometrical characteristics and dental anomalies in wolves *Canis lupus* from Latvia. Acta Theriol. **45**, 549–558.

BIBIKOV, D. I. (ed.) (1985): The Wolf. History, Systematics, Morphology, Ecology. Moskva: Nauka Publishers (in Russian).

BOITANI, L. (1983): Wolf and dog competition in Italy. Acta Zool. Fennica **174**, 259–264.

BOITANI, L. (1984): Genetic considerations on wolf conservation in Italy. Boll. Zool. **51**, 367–373.

DOLF, G.; SCHLAPFER, J.; GAILLARD, C.; RANDI, E.; LUCCHINI, V.; BREITENMOSER, U.; STAHLBERGER SAITBECOVA, N. (2000): Differentiation between Italian wolf and domestic dog based on microsatellite analysis. Genet. Sel. Evol. **32**, 533–541.

DOUZERY, E.; RANDI, E. (1997): The mitochondrial control region of Cervidae: Evolutionary patterns and phylogenetic content. Mol. Biol. Evol. **14**, 1154–1166.

ELLEGREN, H.; SAVOLAINEN, P.; ROSEN, B. (1996): The genetical history of an isolated population of the endangered grey wolf *Canis lupus*: A study of nuclear and mitochondrial polymorphisms. Phil. Trans. R. Soc. Lond. B **351**, 1661–1669.

GALAKA, B. O. (1969): Hybrid wolves in the Vinnitsa region. Zbirnik prac zoologichnogo muzeju **33**, 113–114 (in Ukrainian).

GEPTNER, V. G.; NAUMOV, N. P. (eds.) (1967): Mammals of the Soviet Union. Moskva: Vysshaya shkola. Vol. 2/I, 123–193 (in Russian).

GERLOFF, U.; SCHLOTTERER, C.; RASSMANN, K.; RAMBOLD, I.; HOHMANN, G.; FRUTTH, B.; TAUTZ, D. (1995): Amplification of hypervariable simple sequence repeats (microsatellites) from excremental DNA of wild living bonobos (*Pan paniscus*). Mol. Ecol. **4**, 515–518.

GOODNIGHT, K. F.; QUELLER, D. C. (1999): Computer software for performing likelihood tests of pedigree relationship using genetic markers. Mol. Ecol. **8**, 1231–1234.

GOTTELLI, D.; SILLERO-ZUBIRI, C.; APPELBAUM, G. D.; ROY, M. S.; GIRMAN, D. J.; GARCIA-MORENO, J.; OSTRANDER, E. A.; WAYNE, R. K. (1994): Molecular genetics of the most endangered canid – the Ethiopian wolf *Canis simensis*. Mol. Ecol. **3**, 301–312.

GURSKY, I. G. (1975): Hybridization between wolves and dogs in nature. Bull. Mosk. obshchestva ispytatelej prirody, Otd. Biol. **50**, 131–136 (in Russian).

HERRE, W.; RÖHRS, M. (1990): Haustiere – zoologisch gesehen. 2. Aufl. Stuttgart, New York: Gustav Fischer.

KRONIT, J. (1971): Hybrids of wolf and dog. Ochota i ochotnichje khozyastvo **11**, p. 46 (in Russian).

LARIVIERE, S.; CRETE, M. (1993): The size of eastern coyotes (*Canis latrans*): A comment. J. Mammalogy **74**, 1072–1074.

LONGMIRE, J. L.; LEWIS, A. K.; BROWN, N. C.; BUCKINGHAM, J. M.; CLARCK, L. M.; JONES, D. M.; MEINCKE, L. J.; MEYNE, J.; RATLIFF, R. L.; RAY, F. A.; WAGNER, R. P.; MOYZIS, R. K. (1988): Isolation and molecular characterization of a highly polymorphic centromeric tandem repeat in the family Falconidae. Genomics **2**, 14–24.

MENGEL, R. M. (1971): A study of dog-coyote hybrids and implications concerning hybridization in *Canis*. J. Mammalogy **52**, 316–336.

NEFF, M. W.; BROMAN, K. W.; MELLERSH, C. S.; RAY, K.; ACLAND, G. M.; AGUIRRE, G. D.; ZIEGLE, J. S.; OSTRANDER, E. A.; RINE, J. (1999): A second-generation linkage map of the domestic dog, *Canis familiaris*. Genetics **151**, 803–820.

PRITCHARD, J. K.; STEPHENS, M.; DONNELLY, P. J. (2000): Inference of population structure using multilocus genotypes data. Genetics **155**, 945–959.

RANDI, E. (1993): Effects of fragmentation and isolation on genetic variability of the Italian populations of wolf *Canis lupus* and brown bear *Ursus arctos*. Acta Theriol. **38**, Suppl. 2, 113–120.

RANDI, E.; LUCCHINI, V. (2001): Detecting rare introgression of domestic dog genes into wild wolf (*Canis lupus*) populations by Bayesian admixture analyses of microsatellite variation. Cons. Gen. (in press).

RANDI, E.; LUCCHINI, V.; CHRISTENSEN, M. F.; MUCCI, N.; FUNK, S.; DOLF, G.; LOESCHCKE, V. (2000): Mitochondrial DNA analysis indicates low genetic variability and no hybridization in the Italian wolf but high variability and sporadic hybridisation in east European wolves. Cons. Biol. **14**, 1–11.

ROY, M. S.; GEFFEN, E.; SMITH, D.; OSTRANDER, E. A.; WAYNE, R. K. (1994): Pattern of differentiation and hybridization in North America wolf-like canids, revealed by analysis of microsatellite loci. Mol. Biol. Evol. **11**, 553–570.

SAITOU, N.; NEI, M. (1987): The neighbor-joining method: A new method for reconstructing phylogenetic trees. Mol. Biol. Evol. **4**, 406–425.

SABANEJEV, L. P. (1988): Game animals. Moskva: Fizkultura i sport (in Russian).

SUMINSKI, P. (1975): Morphologische Unterscheidungsmerkmale zwischen Wolfs- (*Canis lupus* L.) und Hundeschädeln (*Canis familiaris* L.). Z. Jagdwiss. **21**, 227–232.

SWOFFORD, D. L. (1998): PAUP*: Phylogenetic analysis using parsimony (and other methods), version 4.0b2a. Sunderland, Massachusetts: Sinauer Associates.

TAMURA, K.; NEI, M. (1993): Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. Mol. Biol. Evol. **10**, 512–526.

TAURINSH, E.; YANSON, J. (1975): The problem of stray dogs and cats should be solved. Proc. Latvian Agriculture Academy **83**, 82–87 (in Russian with English summary).

THOMPSON, J. D.; HIGGINS, D. G.; GIBSON, T. J. (1994): CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. N. A. R. **22**, 4673–4680.

THURBER, J. M.; PETERSON, R. O. (1991): Changes in body size associated with range expansion in the coyote (*Canis latrans*). J. Mammology **72**, 750–755.

TSUDA, K.; KIKKAWA, Y.; YONEKAWA, H.; TANABE, Y. (1997): Extensive interbreeding occurred among multiple matriarchal ancestors during the domestication of dogs: Evidence from inter- and intraspecies polymorphisms in the D-loop region of mitochondrial DNA between dogs and wolves. Genes Genet. Syst. **72**, 229–238.

VILA, C.; SAVOLAINEN, P.; MALDONADO, J. E.; AMORIM, I. R.; RICE, J. HONEYCUTT, R. L.; CRANDALL, K. A.; LUNDEBERG, J.; WAYNE, R. K. (1997): Multiple and ancient origins of the domestic dog. Science **276**, 1687–1689.

VILA, C.; WAYNE, R. K. (1999): Hybridization between wolves and dogs. Cons. Biol. **13**, 195–198.

WALSH, P. S.; METZGER, D. A.; HIGUCHI, R. (1991): Chelex 100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. BioTechniques **10**, 506–513.

ZIMEN, E. (1997): Der Wolf: Verhalten, Ökologie und Mythos. München: Knesebeck.

Authors' addresses: ŽANETE ANDERSONE, Ķemeri National Park, "Meža māja", Ķemeri–Jūrmala, LV-2012, Latvia (e-mail: zanete@kemeri.apollo.lv); VITTORIO LUCCHINI and ETTORE RANDI, Istituto Nazionale per la Fauna Selvatica, Via Ca'Fornacetta 9, 40064 Ozzano dell'Emilia (BO), Italy; JĀNIS OZOLIŅŠ, State Forest Service, 13. Janvāra Str. 15, LV-1932, Rīga, Latvia.

4.3. Discussion and conclusions

Traditionally, hybridisation between wolves and dogs was detected by morphological features (Галака 1969, Кронит 1971, Ryabov 1985, Stubbe, 1989, Zimen 1997), which is not a reliable method as hybrids can be morphologically very similar to wolves (Ryabov 1985). Unusual pelt colour and pup delivery times were the most common indications of hybridisation (Ryabov 1985). Some attempts to distinguish between metrical parameters of wolves and dogs or hybrids appeared to be unsuccessful (Suminski 1975b, Гурский 1975), although some allometrical dissimilarities can be indicative of hybridisation (Clutton-Brock et al. 1994). When genetic methods developed, it became possible to study the relationships between individuals on the DNA level, which has so far been the most precise technique for studying species evolution (Wayne et al. 1992, Vilà et al. 1997, Wilson et al. 2000) and isolation effects (Randi 1993, Randi et al. 2001). Some methods such as using mtDNA markers have limitations, as they can track only maternal lines and introgresson of female dog genomes is a rare event (Randi et al. 1995), while the combination of mtDNA, autosomal, and Y-chromosome markers gives the best results (see chapter 4.2.1.).

When checking Y-chromosome haplotypes, the Latvian wolf population showed a high genetic diversity compared to the isolated population of Scandinavia (Sundqvist et al. 2001). Also, the mtDNA variability was higher in non-isolated populations (Randi et al. 2000). However, genetic diversity is not necessarily a sign of a stable population structure – over-hunted wolf populations can have a high rate of individuals' turnover resulting in higher genetic diversity on the pack level (Jędrzejewski et al. 2000). Interestingly, Scandinavian wolves share one Y-chromosome haplotype with the Baltic wolves (Sundqvist et al. 2001), which is obviously an indication of a common origin of these populations, although recent exchange between the populations seems to be very unlikely due to the geographic isolation.

Documented cases of hybridisation in Latvia were found in the area where wolf density was low, which conforms to the generally accepted theory of hybridisation reasons (Boitani 1983, Lehman et al. 1991). Most of the analysed samples (61%) from Latvia showed no signs of previous hybridisation events, which can be partly explained by the fact that the majority of samples was checked using mtDNA analysis revealing only maternal line. The proportion of pureblood wolves would be even higher if samples were collected from "normal" wolves, while we were more interested in confirming the origin of doubtful cases having unusual morphological features. A few hybridisation cases found cannot seriously threaten the population provided that it is not isolated from the main population eastwards from Latvia (Andersone et al. 2001). However, such cases are an indication of the population's over-exploitation, and wildlife managers should take it into account when planning wolf harvest in the future.

It can be concluded that:

- Hybridisation between wolves and dogs in Latvia has been documented by genetic methods for the first time;
- Hybridisation was a relatively rare event, however, presumably more common than found in other localities in Europe;
- The combined use of mtDNA, autosomal and Y-chromosome markers could be recommended for better identification of wolf – dog hybrids;
- Hybridisation cases were found in localities with low wolf densities, being in conformity with the known preconditions for wolf - dog hybridisation;
- All but one hybrid originated from a particular area in northern Latvia, suggesting that hybridisation was rather a local problem;
- Hybridisation was likely to be the consequence of improper wildlife management – over-exploitation of wolves and an abundance of stray dogs, therefore, more flexible wolf management principles and reduction of hunting pressure on the species (especially in areas with low wolf density) as well as dog control could be recommended.

5. Practical implications

Before setting any management goals, census issues should be resolved (Linnell et al. 1998). At the moment, over-estimation of large carnivore numbers is widespread – each forestry unit counts wolves separately, therefore, the sum exceeds the real number of wolves. There are a wide variety of methods and approaches to carnivore monitoring and abundance estimation (Seber 1982, Cavallini 1994, Becker et al. 1998, Linnell et al. 1998) but most of them are time- and resource-consuming and, therefore, require co-ordination. For large carnivore management, co-operation between neighbouring jurisdictions is crucially important (Fritts and Carbyn 1995). For a better wolf monitoring, it can be recommended to continue monitoring of harvested animals and to introduce simultaneous sessions of extensive snow-tracking in order to avoid double-counting. However, as the snow conditions are unstable in the recent years, radio-telemetry is of vital importance.

It was proposed in the Latvian Wolf Action Plan (Ozoliņš and Andersone 2000) that hunting quotas be set for the whole country, and the hunting season would be closed as soon as the quota is reached. The Action Plan does not have legal implications yet, and it is unlikely to happen in the near future. Legislative issues are one of the most complicated to deal with (Vraka 1997), but this is also the most important issue because available habitat alone is not a guarantee for a successful carnivore conservation (Linnell et al. 2001). In the Soviet times, the Baltic countries were included in the zone of medium wolf control, allowing no more than 2 ind./ 1000 km^2 (Bibikov et al. 1985b). The current number is about three times higher, which can be regarded as a compromise between hunters and conservationists. About 30% of the early winter population is the maximum harvest tolerated by wolves (Pulliainen 1985, Anonymous 1997), 30-40% harvest often causing the decline of wolf populations (Peterson et al. 1984, Ballard et al. 1987). This threshold was obviously exceeded in the anti-wolf campaign of the mid-1990s in Latvia. The wolf is a species with a highly organised social structure (Mech 1999, 2000). Therefore, however quickly wolf populations can recover following heavy hunting pressure (Bibikov et al. 1983), numerical recovery does not ensure a population's stability as over-exploitation can adversely affect wolves' behaviour, social structure, genetic variations etc. (Haber 1996). Heavy hunting pressure is known to reduce pack size (Peterson et al. 1984, Okarma et al. 1998), while the home range size increases with population reduction (Bibikov et al. 1983). There are indications of that in Latvia but more research is required. Studies on home range size are essential as it varies a lot depending on the local conditions (Bibikov et al. 1985a, Ballard et al. 1998, Findo 1998, Jedrzejewski et al. 2001). Knowing the size of the home range also helps to assess the total population size (Linnell et al. 1998).

Wolves are very mobile animals (Musiani et al. 1998, Jędrzejewski et al. 2001), being effective at dispersal and re-colonisation (Pulliainen 1980, Bjärvall 1983, Pulliainen 1985). There is a constant exchange between wolf populations in the Baltic countries and Russia (Ozoliņš and Andersone 2000, Andersone et al. 2001) where wolf density is higher (V.Fedotov, State Informational – analytical centre of game animals and the environment, Russia, pers. comm.). Being strictly territorial animals, wolves are guarding the boundaries of their home range from strange wolves (Harrington and Mech 1983, Mech 1994, Бологов 1984), while over-hunting destroys the social structure of local packs (Haber 1996) attracting new animals from the adjacent areas (Bibikov and Filimonov 1985). However, from the conservation point of view, relying on immigration has its ecological drawbacks, as there is a time lag, while re-colonising wolves adapt to local conditions (Кудактин 1984). Therefore, it can be suggested that only a surplus production should be harvested (especially in the areas bordering Russia and Belarus) in order to ensure the stable social and spatial structure of local wolves. Also, cross-border and internal ecological corridors should be maintained in the future to provide free genetic exchange. The link between the Kurland Peninsula and the eastern part of Latvia is especially important in the view of the results of the craniometrical analysis (see chapter 2.2.2.). Therefore, hunting limitations on wolves and lynx should be introduced in the Ķemeri National Park and adjacent areas in southern Latvia, which is the main link between the west and east of the country. Data on migration via Lithuania are absent but the high degree of habitat fragmentation in that country (Bluzma 1999) makes it unlikely.

The strict wolf control in Latvia is justified by the hunters' interests of maintaining high ungulate densities (Gaross 1997). However, reducing predation as one mortality factor for ungulates does not mean that the overall mortality will decrease as the significance of other mortality factors may increase (Филонов 1980), which makes the logic of wolf control campaigns very questionable. Besides, predators alone can rarely cause a decline in prey populations, which is usually caused by a combination of several factors (Gauthier and Theberge 1987, Peterson 2001). However, wolves can severely limit ungulate populations once the low-density phase has been established (Skoog 1983, Gasaway et al. 1992, Hayes and Harestad 2000b). Effects of predation and harvest can be cumulative and are likely to cause ungulate population decline (Gauthier and Theberge 1987, Jędrzejewski et al. 2000). That was the situation in the early 1990s in Latvia. To halt the ungulate decline, it can be necessary to reduce both wolf numbers and hunting (Gauthier and Theberge 1987), while in Latvia the main emphasis was put on the wolf control only. Now, when wolf numbers have been significantly reduced, sustainable harvest of wolves can be recommended, providing a stable wolf population is conserved. To avoid additive effect of predation and harvest on ungulate populations in the future, it is important to take into account the carnivores' impact when setting the hunting quotas for ungulate species. An alternative, somewhat more effective method of controlling harvest would be regulation of the harvesting effort (e.g., by means of a flexible hunting season depending on particular conditions), which is regarded as a safer and more efficient means of population management (Caughley and Sinclair 1994). However, due to the lack of preventive measures to avoid damage to sylvi- and agriculture by game animals, high densities of ungulates are unlikely to be tolerated, which is another drawback for carnivore conservation in Latvia.

Wolves can effectively control beaver populations (Potvin et al. 1992, Peterson 2001), provided that both species reach high levels (Shelton and Peterson 1983). From this viewpoint it can be recommended to ensure stable wolf numbers in areas with significant beaver damage. There was also an attempt to use predators' smell as a repellent to reduce damage by beavers (Rosell and Czech 2000), which could be worth trying under Latvian conditions.

At the moment, farmers do not use any protection measures to prevent livestock damage, which is, however, negligible compared to some other European countries (Fourli 1999) due to the overall agricultural depression in the country. Very simple measures like fladry (Musiani and Visalberghi 2001), fences or night-time enclosure of livestock (Linnell et al. 1996, Nowak and Myslajek 1999b) could help to protect domestic animals. Livestock tends to be only seasonally available to predators (Pulliainen 1963, 1965), therefore, it is only a temporary prey for wolves, which otherwise rely on wild animals as a food resource wherever available (Priklonsky 1985, Vos 2000). Provided that effective protection measures are taken, and garbage (especially leftovers from slaughter-houses) is disposed of properly, positive conditioning of wolves to livestock as a source of food is unlikely. Also, proper wolf management is essential. E.g., hunting wolves in summer time should be banned as elimination of one adult partner of a wolf-pair raising pups may cause increased depredation on livestock. Therefore, in the wolf areas, farmers should be informed about the most cost-effective protection methods and obtain financial support from the state for installation of the necessary devices (e.g., fences) when necessary.

It should be noted that large carnivore management cannot be separated from socio-economics, which is a matter of a recently developed human dimensions research (Kellert 1985, Bath and Buchagan 1989, Bath 1994, Bath 1996, Kellert et al. 1996). It includes investigation of public opinion and, consequently, educational activities to increase the level of public awareness and changing the attitudes. The best conservation efforts will be fruitless if the public opinion about large carnivores is negative (Breitenmoser 1998). A pilot human dimensions study was also carried in Latvia in 2001 (Andersone and Ozoliņš unpubl.), revealing that the general public is more in favour of large carnivores than hunters. It is an unstable situation and more efforts should be put into education of different interest groups, especially of those involved in nature-related activities.

Wolf hybridisation with dogs has important practical implications (Ryabov 1985) for wildlife management as it is very likely to have negative consequences for game fauna and livestock owners, and should be avoided by all means possible. As there is a negative correlation between wolf and dog abundance (Blanco et al. 1992, Ovsyanikov and Poyarkov 1996), it is crucial to control stray dogs in areas with low wolf densities. At the same time it is necessary to manage the wolf population in a sustainable way ensuring a stable social structure at a certain numerical level. Monitoring the demographic structure of harvested wolves will help to detect any dangerous trends and allow reaction by changing management practices.

The future priorities in regard to wolf research and management are as follows:

- Establish a reliable system for large carnivore monitoring;
- Change the wolf's legal status by extending the closed season and, possibly, by introducing hunting quotas;
- Monitor the demographic structure of harvested wolves in order to detect undesirable trends and adequately change management practices;
- Carry out a field research using radio-telemetry techniques in order to study predation rates and wolf impact on ungulate populations, homes range size and spatial structure in Latvia;

- Set hunting quotas for ungulates, taking into account predation by wolves and lynx, or alternatively, provide a flexible hunting season in order to regulate hunting effort;
- Control stray dogs and ensure that wolf management in Latvia provides a stable social and spatial structure of the predator's population;
- Develop international co-operation to continuously monitor movements of large carnivores in cross-border areas;
- Ensure maintenance of ecological corridors in cross-border areas and within the country by applying regional hunting bans for a particular species or during a certain period;
- Raise public awareness, especially in such nature-oriented target groups as farmers and hunters;
- Ensure state support for preventive measures against livestock depredation whenever necessary.

Conclusions

- Wolves are currently widely distributed and relatively numerous in Latvia, occurring in all forestry units and numbering 300-500 individuals.

- Morphologically, Latvian wolves are similar to the wolves from other areas of European forest zone. The degree of sexual dimorphism typical for Latvian wolves was determined both for body size and weight and for cranial parameters, males being bigger than females. The occurrence of polydonty and oligodonty was not higher than elsewhere within the Eurasian distribution of wolves.

- Craniometrical differences in wolves from western and eastern Latvia suggest some disruption of the population has occurred, probably due to different hunting intensity in eastern and western parts of the country, however, further morphometrical and demographic studies are necessary to clarify this phenomenon.

- Ungulates (cervids and wild boar) are the staple food for wolves in both seasons but wild boar is a preferred prey. Wolf diet is more diverse in summer but ungulates made up the bulk of the biomass consumed in both seasons. Some geographic and sexual differences in the diet were found - wolves preyed on wild boar considerably more in the east of the country, and males hunted considerably more beavers than did females. Carrion can be an important food item in winter, therefore, proper garbage disposal is essential in order to prevent undesirable food conditioning of wolves.

- Beavers were found to be an important alternative prey making up to a third of the wolf summer diet. Their proportion in the wolf diet in Latvia was considerably higher than elsewhere in Europe.

- Trophic competition with lynx was moderate, however, more studies are required to further analyse the relationships between these species.

- Wolf - dog hybrids were found in the localities where wolf densities were low due to over-hunting by humans. Hybridisation between Latvian wolves and stray dogs is a relatively rare event, which cannot pose a serious threat to the Latvian wolf population, however, it was relatively more common than elsewhere in Europe. Further management based on the principles of sustainable harvest should prevent favourable conditions for such cases in the future.

- The main wolf – human conflict is competition for prey with hunters. Depredation on livestock is not widespread nowadays and can be easily prevented by proper husbandry techniques.

- The pattern of the sex and age structure of the harvest bag, i.e., low proportion of old animals, female predominance and their high fecundity (6 embryos on average), all points towards the current over-exploitation of the population. A relatively low ratio of juveniles (20%) is an indication of additional pre- and neonatal mortality factors, possibly elimination through hunting of pregnant and lactating females. The high proportion of animals with human-caused injuries (3.8%) is another evidence of the strong hunting pressure.

- Although wolves are currently widely distributed and relatively numerous in Latvia, several features are indicative of high human-caused mortality rate, i.e., recent numerical and distributional decline, high fecundity, prevalence of females in the harvest bag. In order to avoid further numerical decline caused by the current over-exploitation of the wolf population, the legal status of the species and management practice should be changed from the present policy of maximum reduction of wolf numbers to a sustainable use, ensuring a longer closed season in summer and / or hunting quotas in order o provide stable spatial and social structure of the population.

References

Aanes, R., Linnell, J.D.C., Perzanowski, K., Karlsen, J., Odden, J. 1998. Roe deer as prey. [In: *The European Roe Deer: The Biology of Success*. Andersen R., Duncan P. and Linnell J.D.C., eds]. Scandinavian University Press, Oslo: 139-159.

Adamic, M. 1996. An expanding brown bear population in Slovenia: Current Management Problems. *Journal of Wildlife Research* 1 (3): 297-300.

Adamic, M., Kobler, A., Berce, M. 1998. The return of the wolf (*Canis lupus*) into its historic range in Slovenia – is there any place left and how to reach it? *Zbornik gozdarstva in lesarstva* 57: 235-254.

Adams, L.G., Singer, F.J., Dale, B.W. 1995. Caribou calf mortality in Denali National Park, Alaska. *Journal of Wildlife Management* 59 (3): 584-594.

Adlerberg G. P. 1935. [Lynx.] [In: *Animals of Arctic. Smir nov*, N.A., ed.]. Leningrad: 439-450. [In Russian]

Allendorf, F.W., Leary, R.F., Spruell, P., Wenburg, J.K. 2001. The problems with hybrids: setting conservation guidelines. *TRENDS in Ecology & Evolution* 16 (11): 613-620.

Anderson, R.M. 1943. Summary of the large wolves of Canada, with description of three new Arctic races. *Journal of Mammology* 24: 386-393.

Andersone, Ž. 1998a. Summer Nutrition of the Wolf (*Canis lupus*) in the Nature Reserve Slītere, Latvia. *Proceedings of the Latvian Academy of Sciences,* Section B, 52 (1-2): 79-80.

Andersone, Ž. 1998b. Wolf – wild ungulate interactions in Latvia. *Advances in Ethology* (Supplement to Ethology) 33: 87.

Andersone, Ž. 1999. Beaver: A new prey of wolves in Latvia? Comparison of winter and summer diet of *Canis lupus* Linnaeus, 1758. [In: *Beaver Protection, Management, and Utilization in Europe and North America.* Busher, P. and Dzieciolowski, R., eds.]. Cluwer Academic / Plenum Publishers, New York: 103-108.

Andersone, Ž., Ozolins, J. 2000a. Big game and large carnivores in Latvia: present status and future prospects. *Journal of Wildlife Research.* [In press]

Andersone, Ž., Ozolins, J. 2000b. Craniometrical characteristics and dental anomalies in wolves *Canis lupus* from Latvia. *Acta Theriologica* 45 (4): 549-558.

Andersone, Ž., Ozolins, J. 2000c. First results of public involvement into wolf research in Latvia. *Folia Theriologica Estonica* 5: 5-12.

Andersone, Ž., Laanetu, N., Oetjen, R., Ozolins, J. 2001. Transboundary movements of wolves in Latvia and Estonia: results of a pilot study. *Programme and Abstracts of the Canid Biology and Conservation Conference*, 17-21 September – 2001, Oxford: 35.

Andersone, Ž., Balciauskas, L., Valdmann, H. 2002. Human-Wolf Conflicts in the East Baltic – past, present and future. *Proceedings of the 2nd International Wildlife Management Congress*. [In press]

Anonymous. 1994. Seminar on the management of small populations of threatened mammals. *Environ. Encounters* 17: 1-128.

Anonymous. 1997. *Wolves, Bears, and Their Prey in Alaska. Biological and Social Challenges in Wildlife Management*. National Academy Press. National Research Council Committee on Management of Wolf and Bear Populations in Alaska, National Academy Press, Washington, D.C.: 1-207.

Anonymous. 1998. [*Catalogue of the hunting and fishing trophies*]. Vilnius: 1-34. [In Lithuanian]

Anonymous. 1999. Katalogs. *Medības, Makšķerēšana, Daba,* Nr. 11, Rīga: p. 17. [In

Latvian]
Ansorge, H. 1994. Intrapopular skull variability in the red fox, *Vulpes vulpes* (Mammalia, Carnivora, Canidae). *Zoologische Abhandlungen Staatliches Museum für Tierkunde Dresden* 48 (6): 103-123.
Ansorge, H., Meinig, H. 1996. Craniological data and age structure of red foxes (*Vulpes vulpes arabica* Thomas, 1902) from Oman. *Mammalia* 12: 13-19.
Arnold, M.L. 1997. *Natural Hybridization and Evolution. Oxford Series in Ecology and Evolution.* Oxford University Press, New York.
Ballard, W.B., Whitman, J.S., Gardner, C.L. 1987. Ecology of an exploited wolf population in south-central Alaska. *Wildlife Monographs* 98: 1-54.
Ballard, W.B., Edwards, M., Fancy, S.G., Boe, S., Krausman, P.R. 1998. Comparison of VHS and satellite telemetry for estimating sizes of wolf territories in northwest Alaska. *Wildlife Society Bulletin* 26 (4): 823-829.
Balodis, M. 1994. Beaver Population of Latvia: History, Development and Management. *Proceedings of the Latvian Academy of Sciences,* Section B, No. 7/8: 122-127.
Balodis, M., Laanetu, N., Ulevicius, A. 1999. Beaver Management in the Baltic States. [In: *Beaver Protection, Management, and Utilization in Europe and North America.* P.Busher and Dzieciolowski, R., eds.]. Kluwer Academic / Plenum Publishers, New York: 25-29.
Barcena, F., Hermida, R. 2001. On biometry and sexual dimorphism in wolf. *Programme and Abstracts of the Canid Biology and Conservation Conference*, 17-21 September – 2001, Oxford: 37.
Bath, A.J. 1994. Public attitudes toward polar bears: An application of human dimensions in wildlife resources research. [In: *Proceedings of International Union of Game Biologists' XXI Congress.* Thompson, I., ed.]. Vol.1. Can.For.Ser., Halifax, Canada: 168-174.
Bath, A.J. 1996. Increasing the applicability of human dimensions research to large predators. *Journal of Wildlife Research* 1 (2): 215-220.
Bath, A.J., Buchagan, T. 1989. Attitudes of interest groups in Wyoming toward wolf restoration in Yellowstone National Park. *Wildlife Society Bulletin* 17: 519-525.
Beaumont, M., Barratt, E.M., Gottelli, D., Kitchener, A.C., Daniels, M.J., Pritchard, J.K., Bruford, M.W. 2001. Genetic diversity and introgression in the Scottish wildcat. *Molecular Ecology* 10: 319-336.
Becker, E.F., Spindler, M.A., Osborne, T.O. 1998. A population estimator based on network sampling of tracks in the snow. *Journal of Wildlife Management* 62 (3): 968-977.
Begon, M., Harper, J.L., Townsend, C.R. 1986. *Ecology. Individuals, Populations and Communities.* Blackwell Scientific Publications, Oxford: 1-876.
Berger, J. 1999. Anthropogenic extinction of top carnivores and interspecific animal behaviour: implications of the rapid decoupling of a web involving wolves, bears, moose and ravens. *Proc. R. Soc. Lond.* B 266: 2261-2267.
Bergmanis, U. 2000. Klinšu ērgļa *Aquila chrysaetos* atgriešanās Teiču purvā. [Return of the Golden Eagle *Aquila chrysaetos* to Teiči bog]. *Putni dabā* 10 (4): 6-11. [In Latvian with English summary]
Bibikov, D. I. (ed.) 1985. *The Wolf. History, Systematics, Morphology, Ecology.* Nauka Publishers, Moscow: 1-606. [In Russian]
Bibikov, D.I. 1988. Der Wolf. Die Neue Brehm-Bucherei. A. Ziemsen, Wittenberg Lutherstadt.
Bibikov, D.I., Filimonov, A.N., Kudaktin, A.N. 1983. Territoriality and migration of the wolf in the USSR. *Acta Zoologica Fennica* 174: 267-268.

Bibikov, D. I., Ovsyannikov, N. G., Filimonov, A. N. 1983. The status and management of the wolf population in the USSR. *Acta Zoologica Fennica* 174: 269-271.
Bibikov, D. I., Filimonov, A. N. 1985. Spacial structure. [In: *The Wolf. History, Systematics, Morphology, Ecology*. Bibikov, D. I., ed.]. Nauka Publishers, Moscow: 408–415. [In Russian]
Bibikov, D. I., Kudaktin, A. N., Filimonov, A. N. 1985a. Territoriality, movements. [In: *The Wolf. History, Systematics, Morphology, Ecology*. Bibikov, D. I., ed.]. Nauka Publishers, Moscow: 415-431. [In Russian]
Bibikov, D. I., Priklonsky, S. G., Filimonov, A. N. 1985b. Population management. [In: *The Wolf. History, Systematics, Morphology, Ecology*. Bibikov, D. I., ed.]. Nauka Publishers, Moscow: 562-571. [In Russian]
Bienek, M., Wolsan, M., Okarma, H. 1998. Historical biogeography of the lynx in Poland. *Acta zool.cracov*. 41 (1): 143-167.
Bjärvall, A. 1983. Scandinavia's response to a natural repopulation of wolves. *Acta Zoologica Fennica* 174: 273 - 275.
Blanco, J. C., Reig, S., Cuesta, L. 1992. Distribution, status and conservation problems of the wolf *Canis lupus* in Spain. *Biological Conservation* 60: 73 - 80.
Bluzma, P. 1999. Estimation of the state of lynx and wolf populations in Lithuania. *Acta Zoologica Lituanica* 9 (1): 35-41.
Bluzma, P. 2000. Large predatory mammals in Lithuania: Abundance dynamics, distribution, population density. *Folia Theriologica Estonica* 5: 35-41.
Bobek, B., Perzanowski, K., Smietana, W. 1992. The influence of the snow cover on wolf *Canis lupus* and red deer *Cervus elaphus* relationships in Bieszczady Mountains. [In: *Global Trends in Wildlife Management*. Bobek, B., Perzanowski, K. and Regelin, W. L., eds.]. Swiat Press, Krakow-Warszawa: 341-348.
Bobek, B., Nowicki, P. 1996. Food intake and digestibility of various natural diets in wolves. *Journal of Wildlife Research* 1 (2): 148-154.
Boertje, R. D., Valkenburg, P., McNay, M. E. 1996. Increases in moose, caribou, and wolves following wolf control in Alaska. *Journal of Wildlife Management* 60 (3): 474-489.
Boitani, L. 1983. Wolf and dog competition in Italy. *Acta Zoologica Fennica* 174: 259-264.
Boitani, L. 1984. Genetic considerations on wolf conservation in Italy. *Boll. Zool.* 51: 367-373.
Boitani, L. 1992. Wolf research and conservation in Italy. *Biological Conservation* 61: 125-132.
Boitani, L. 1995. Ecological and cultural diversities in the evolution of wolf-human relationship. [In: *Ecology and Conservation of Wolves in a Cahnging World*. Carbyn, L.N., Fritts, S.H. and Seip, D.R., eds.]. Canadian Circumpolar Institute, Occasional Publication: 3-13.
Boitani, L. 2000. *Action Plan for Conservation of Wolves in Europe* (*Canis lupus*). Nature and environment, No.113. Council of Europe Publishing: 1-86.
Boles, B.K. 1977. Predation by wolves on wolverines. *Canadian Field Naturalist* 19 (1): 68-69.
Boman, M. 1995. Estimating costs and Genetic Benefits of Various Sizes of Predator Populations: The case of Bear, Wolf, Wolverine and Lynx in Sweden. *Journal of Environmental Management* 43: 349-357.
Boman, M., Bostedt, G. 1994. A bioeconomic approach to wolf population management. *Scandinavian forest economics* 35: 250-263.
Bookhout, T.A. (ed.) 1996. *Research and Management Techniques for Wildlife and*

Habitats. 5th ed. The Wildlife Society, Bethesda: 1-740.
Boyd, D.K., Jimenez, M.D. 1994. Successful rearing of young by wild wolves without mates. *Journal of Mammology* 75 (1): 14-17.
Boyd, D.K., Ream, R.R., Pletscher, D.H., Fairchild, M.W. 1994. Prey taken by colonizing wolves and hunters in the Glacier National Park area. *Journal of Wildlife Management* 58 (2): 289-295.
Brangi, A., Rosa, P., Meriggi, A. 1994. Predation by Wolves (*Canis lupus* L.) on Wild and Domestic Ungulates in Northern Italy. *Ongules / Ungulates* 91: 541-543.
Breitenmoser, U. 1998. Large predators in the Alps: The fall and rise of man's competitors. *Biological Conservation* 83 (3): 279-289.
Breitenmoser, U., Breitenmoser-Würsten, C., Okarma, H., Kaphegyi, T., Kaphygyi-Wallman, U., Müller, U.M. 2000. *Action Plan for the Conservation of the Eurasian Lynx in Europe (Lynx lynx).* Nature and environment, No.112, Council of Europe Publishing: 1-69.
Brtek, L., Voskar, J. 1987. Food biology of the wolf in Slovak Carpathians. *Biologia (ČSSR)* 42 (10): 985-990. [In Slovak with English summary]
Buchalzcyk, T. 1981. Order: Carnivores - *Carnivora*. [In: *Keys to vertebrates of Poland Mammals*. Pucek, Z., ed.]. PWN - Polish Scientific Publishers, Warsaw: 260-306.
Buchalczyk, T., Dynowski, J., Szteyn, S. 1981. Variations in number of teeth and asymmetry of the skull in the wolf. *Acta Theriologica* 26: 23-30.
Burns, T.P. 1989. Lindeman's contradiction and the trophic structure of ecosystems. *Ecology* 70 (5): 1355-1362.
Butler, D. 1994. Bid to protect wolves from genetic pollution. *Nature* 370: 497.
Butzeck, S. 1993. Wolfsland Brandenburg - die wildökologische Brücke zum Osten. *Natur und Landschaft in der Niederlausitz* 14: 27-30.
Carbyn, L. 1983. Management of non-endangered wolf populations in Canada. *Acta Zoologica Fennica* 174: 239-243.
Carbyn, L.N., Fritts, S.H., Seip, D.R. (eds.).1995. *Ecology and Conservation of Wolves in a Changing World.* Canadian Circumpolar Institute, Occasional Publication 35: 1-620.
Caughley, G., Sinclair, A.R.E. 1994. *Wildlife Ecology and Management*. Blackwell Science, Oxford: 1-334.
Cavallini, P. 1994. Faeces count as an index of fox abundance. *Acta Theriologica* 39 (4): 417 – 424.
Cerveny, J., Koubek, P. 2000. Variability of body and skull dimensions of the lynx (*Lynx lynx*) in the Czech Republic. *Lynx (Praha)* 31: 5-12.
Cerveny, J., Koubek, P., Bufka, L. 2000. [*Large carnivores in our nature*]. Korsach: 1-32. [In Czech]
Ciucci, P., Boitani, L. 1998. Wolf and dog depredation on livestock in Central Italy. *Wildlife Society Bulletin* 26 (3): 504-514.
Ciucci, P., Boitani, L., Pelliccioni, E. R., Rocco, M., Guy, I. 1996. A comparison of scat-analysis methods to assess the diet of the wolf *Canis lupus*. *Wildlife Biology* 2: 37-48.
Clutton-Brock, J., Kitchener, A.C., Lynch, J.M. 1994. Changes in the skull morphology of the Arctic wolf, *Canis lupus arctos*, during the twentieth century. *Journal of Zoology* 233 (1): 19-36.
Cozza, K., Fico, R., Battistini, M.L., Rogers, E. 1996. The damage-conservation interface illustrated by predation on domestic livestock in central Italy. *Biological Conservation* 78 (3): 329-336.
Cuesta, L., Barcena, F., Palacios, F. Reig, S. 1991. The trophic ecology of the Iberian

Wolf (*Canis lupus signatus* Cabrera, 1907). A new analysis of stomach's data. *Mammalia* 55 (2): 239-254.
Daniels, M.J., Beaumont, M.A., Johnson, P.J., Balharry, D., MacDonald, D.W., Barrat, E. 2001. Ecology and genetics of wild-living cats in the north-east of Scotland and the implications for the conservation of the wildcat. *Journal of Applied Ecology* 38 (1): 146-161.
Danilov, P. I., Gursky, I. G., Kudaktin, A. N. 1985. Reproduction. [In: *The Wolf. History, Systematics, Morphology, Ecology*. Bibikov, D. I., ed.]. Nauka Publishers, Moscow, 378–389. [In Russian]
Day, M. G. 1966. Identification of hair and feather remains in the gut and faeces of stoats and weasels. *Journal of Zoology* 148: 201 - 217.
Delibes, M. 2000. *Status and conservation needs of the wolf (Canis lupus) in the Council of Europe Member States*. Council of Europe Publishing, Nature and Environment 47: 5-46.
Dimmick, R.W., Pelton, M.R. 1996. Criteria of Sex and Age. [In: *Research and Management Techniques for wildlife and Habitats*. Bookhout, T. A., ed.]. The Wildlife Society, Bethesda, Maryland: 169-214.
Dolf, G., Schlapfer, J., Gaillard, C., Randi, E., Lucchini, V., Breitnemoser, U., Stahlberger Saitbecova, N. 2000. Differentiation between Italian wolf and domestic dog based on microsatellite analysis. *Genet. Sel. Evol*. 32: 533-541.
Douzery, E., Randi, E. 1997. The mitochondrial control region of Cervidae: Evolutionary patterns and phylogenetic content. *Mol. Biol. Evol*. 14: 1154-1166.
Dundurs, A. 1999. [Wolves of More-Nitaure will not kill livestock anymore.]. *Medības, Makšķerēšana, Daba,* Nr.1, Riga: 6-10. [In Latvian]
Elgmork, K. 2000. Abundance of brown bears and wolves in central south Norway after 1733 as revealed by bounty records. *Fauna Norvegica* 20: 1-8.
Ellegren, H. 1999. Inbreeding and relatedness in Scandinavian grey wolves *Canis lupus*. *Hereditas* 130: 239-244.
Ellegren, H., Savolainen, P., Rosen, B. 1996. The genetical history of an isolated population of the endangered grey wolf *Canis lupus*: A study of nuclear and mitochondrial polymorphisms. *Phil. Trans. R. Soc. Lond.* B. 351: 1661–1669.
Evans, B.J., Supriatna, J., Melnick, D.J. 2001. Hybridization and population genetics of two macaque species in Sulawesi, Indonesia. *Evolution* 55: 1686-1702.
Federoff, N.E., Nowak, R.M. 1998. Cranial and dental abnormalities of endangered red wolf Canis rufus. *Acta Theriologica* 43 (3): 293-300.
Filonov, C. 1980. Predator-prey problems in nature reserves of the European part of the RSFSR. *Journal of Wildlife Management* 44 (2): 389-396.
Filonov, K. P., Kaletskaya, M. L. 1985. Influence of wolf predation on wild ungulates. [In: *The Wolf. History, Systematics, Morphology, Ecology*. Bibikov, D. I., ed.]. Nauka Publishers, Moscow: 336-354. [In Russian]
Findo, S. 1995. Present situation and perspectives on conservation of the gray wolf (*Canis lupus*) in Slovakia. *Vyskum a ochrana cicavcov na Slovensku* 2: 37-46. [In Slovak with English summary]
Findo, S. 1998. Wolf (*Canis lupus*) movements and home ranges in the Slovak Carpathians. *Vyskum a ochrana cicavcov na Slovensku* 3: 25-30. [In Slovak with English summary]
Floyd, T. J., Mech, L. D., Jordan, P. A. 1978. Relating wolf scat content to prey consumed. *Journal of Wildlife Management* 42 (3): 528-532.
Fourli, M. 1999. *Compensation for damage caused by bears and wolves in the European Union.* European Commission DG XI, Environment, Nuclear Security and Civil

Protection: 1-68.
Francisco, L.V., Langston, A.A., Mellersh, C.S., Neal, C.L., Ostrander, E.A. 1996. A class of highly polymorphic tetranucleotide repeats for canine genetic mapping. *Mamm. Genome* 7: 359-362.
Fritts, S.H., Carbyn, L.N. 1995. Population viability, nature reserves, and the outlook for gray wolf conservation in North America. *Restoration Ecology* 3 (1): 26-38.
Frkovic, A., Ruff, R. L., Cicnjak, L., Huber, D. 1992. Wolf mortality during 1945-86 in Gorski Kotar of Croatia, Yugoslavia. [In: *Global Trends in Wildlife Management.* Bobek, B., Perzanowski, K. and Regelin, W. L., eds.]. Swiat Press, Krakow-Warszawa: 353-357.
Gade-Jørgensen, I., Stagegaard, R. 2000. Diet composition of wolves *Canis lupus* in east-central Finland. *Acta Theriologica* 45 (4): 537–547.
Gao, Z., Ma, J., Zhang, H., Gao, Y., Z., G. 1996. Preliminary studies on the food habits of the wolves in eastern Mongolia. *Acta Theriologica Sinica* 16 (2): 95-99.
Gaross, V. 1994. Vilku un lūšu ietekme uz briežveidīgajiem dzīvniekiem Kurzemē. [Impacts of wolves and lynxes on cervids in Kurzeme.]. Meža Dzīve, 3 (208): 10 – 15. [In Latvian]
Gaross, V. 1997. Ekoloģisko, bioloģisko, antropogēno u.c. faktoru ietekme uz Latvijas briežveidīgo dzīvnieku un plēsēju populācijām. [The impact of economical, biological and other factors on the population of Cervidae, wolf and lynx.]. Mežzinātne 7 (40): 108-123. [In Latvian with English summary]
Gasaway, W.C., Boertje, R.D., Kelleyhouse, D.G., Stephenson, R.O., Larsen, D.G. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. *Wildlife Monographs* 120: 1-59.
Gauthier, D.A., Theberge, J.B. 1987. Wolf predation. [In: *Wild furbearer management and conservation in North America.* Novak, M., Baker, J.A., Obbard, M.E. and Malloch, D., eds.]. Ministry of Natural Resources, Ontario: 119-127.
Genov, P. 1992. The wolf *Canis lupus L.* in southwestern Bulgaria. [In: *Global Trends in Wildlife Management.* Bobek, B., Perzanowski, K. and Regelin, W. L., eds.]. Swiat Press, Krakow-Warszawa: 359-362.
Gerloff, U., Schlotterer, C., Rassmann, K., Rambold, I., Hohmann, G., Frutth, B., Tautz, D. 1995. Amplification of hypervariable simple sequence repeats (microsatellites) from excremental DNA of wild living bonobos (*Pan paniscus*). *Mol. Ecol.* 4: 515-518.
Giniunas, K. 1988. [*The wolf*]. Mokslas, Vilnius: 1-78. [In Lithuanian]
Gipson, P.S., Ballard, W.B., Nowak, R.M., Mech, L.D. 2000. Accuracy and precision of estimating age of grey wolves by tooth wear. *Journal of Wildlife Management* 64 (3): 752-758.
Glowacinski, Z., Profus, P. 1997. Potential impact of wolves Canis lupus on prey populations in eastern Poland. *Biological Conservation* 80 (1): 99-106.
Goldman, E.A. 1937. The wolves of North America. *Journal of Mammology* 18: 37-45.
Goodnight, K.F., Queller, D.C. 1999. Computer software for performing likelihood tests of pedigree relationship using genetic markers. *Mol. Ecol.* 8: 1231-1234.
Goszczynski, J. 1974. Studies on the Food of Foxes. *Acta Theriologica* 19 (1): 1 - 18.
Görner, M., Hackethal, H. 1987. *Säugetiere Europas.* Radebeul: Neumann Verlag, Leipzig: 1-372.
Gottelli, D., Sillero-Zubiri, C., Applebaum, G.D., Roy, M.S., Girman, D.J., Garcia-Moreno, J., Ostrander, E. A., Wayne, R. K. 1994. Molecular genetics of the most endangered canid- the Ethiopian wolf *Canis simensis. Mol. Ecol.* 3: 301-312.

Gray, A.P. 1954. *Mammalian hybrids; a check-list with bibliography*. Commonwealth Agricultural Bureau, Famham Royal, Bucks, United Kingdom.

Greve, K. 1909. *Säugetiere Kur-, Liv-, Estlands*. W. Mellin u.Co, Riga: 1-183.

Haber, G.C. 1996. Biological conservation and ethical implications of exploiting and controlling wolves. *Conservation Biology* 10 (4): 1068-1081.

Haglund, B. 1966. Winter habits of the lynx (*Lynx lynx* L.) and wolverine (*Gulo gulo* L.) as revealed by tracking in the snow. *Viltrevy* 4: 81-299. [In Swedish with English summary]

Haibin, W., Fuller, T.K. 1996. Food habits of large canids in southeast China. *Journal of Wildlife Reseacrh* 1 (2): 155-157.

Halaj, J., Wise, D.H. 2001. Terrestrial Trophic Cascades: How Much Dp They Trickle? *American Naturalist* 157 (3): 262-281.

Harrington, F. H., Mech, L. D. 1983. Wolf Pack Spacing: Howling As a Territory-Independent Spacing Mechanism In a Territorial Population. *Behav. Ecol. Sociobiol.* 12:161 - 168.

Hayes, R.D., Baer, A. 1992. Brown Bear, *Ursus arctos*, Preying Upon Gray Wolf, *Canis lupus*, Pups at a Wolf Den. *The Canadian Field Naturalist* 106: 381-382.

Hayes, R.D., Harestad, A.S. 2000. Demography of a recovering wolf population in the Yukon. *Canadian Journal of Zoology* 78: 36-48.

Hayes, R.D., Harestad, A.S. 2000. Wolf functional response and regulation of moose in the Yukon. *Canadian Journal of Zoology* 78: 60-66.

Hector, A., Joshi, J., Lawler, S.P., Spehn, E.M., Wilby, A. 2001. Conservation implications of the link between biodiversity and ecosystem functioning. *Oecologia* 129: 624-628.

Hell, P., Duricka, J. 1989. Anomalies of the dentition of the West Carpathian wolf (*Canis lupus*). *Folia Venatoria* 19: 339-347. [In Slovak with English summary]

Herre, W., Röhrs, M. 1990. *Haustiere – zoologisch gesehen*. 2. Aufl. Stuttgart, New York: Gustav Fischer.

Higgins, D.G., Bleasby, A.J., Fuchs, R. 1992. CLUSTAL V: improved software for multiple sequence alignment. *Computer Applications in Biosciences* 8: 189-191.

Huggard, D.J. 1993. Prey selectivity of wolves in Banff National Aprk. II. Age, sex, and condition of elk. *Canadian Journal of Zoology* 71 (1): 140-147.

Ingelog, T., Andersson, R., Tjernberg, M. (eds.). 1993. *Red Data Book of the Baltic* Region. Part 1. Lists of threatened vascular plants and vertebrates. Swedish Threat. Species Unit, Uppsala: 1-95.

Jacobs, J. 1974. Quantitative Measurement of Food Selection. A Modification of the Forage Ratio and Ivlev's Electivity Index. *Oecologia (Berl.)* 14: 413-417.

Jędrzejewska, B., Jędrzejewski, W., Okarma, H. 1991. Wilk jest dziki, wilk jest zly? [Wolf is wild, wolf is bad?]. Parki Narodowe 1: 7-9. [In Polish]

Jędrzejewska, B., Okarma, H., Jędrzejewski, W., Milkowski, L. 1994. Effects of exploitation and protection on forest structure, ungulate density and wolf predation in Bialowieza Primeval Forest, Poland. *Journal of Applied Ecology* 31: 664-676.

Jędrzejewska, B., Jędrzejewski, W., Bunevich, A. N., Milkowski, L., Okarma, H. 1996a. Population dynamics of wolves *Canis lupus* in Bialowieza Primeval Forest (Poland and Belarus) in relation to hunting by humans, 1847 - 1993. *Mammal Review* 26 (2–3): 103-126.

Jędrzejewska, B., Milkowski, L., Jędrzejewski, W., Okarma, H., Buniewich, A. N. 1996b. Z plachta na... wilka, czyli dawne polowania w Puszczy Bialowieskiej. Lowiec Polski 2: 26-27. [In Polish]

Jędrzejewska, B., Jędrzejewski, W., Bunevich, A. N., Milkowski, L., Krasinski, Z. 1997.

Factors shaping population densities and increase rates of ungulates in Bialowieza Primeval Forest (Poland and Belarus) in the 19th and 20th centuries. *Acta Theriologica* 42: 399-451.

Jędrzejewska, B., Jędrzejewski, W. 1998. *Predation in Vertebrate Communities: The Bialowieza Primeval Forest as a Case Study*. Springer Verlag, Berlin: 1-450.

Jędrzejewski, W., Jędrzejewska, B., Okarma, H., Ruprecht, A. L. 1992. Wolf predation and snow cover as mortality factors in the ungulate community of the Bialowieza National Park, Poland. *Oecologia* 90: 27 - 36.

Jędrzejewski, W., Schmidt, K., Miłkowski, L., Jędrzejewska, B. and Okarma, H. 1993. Foraging by lynx and its role in ungulate mortality: the local (Bialowieža Forest) and the Palaeartic viewpoints. *Acta Theriologica* 38 (4): 385-403.

Jędrzejewski, W., Jędrzejewska, B., Okarma, H., Schmidt, K., Zub, K., Musiani, M. 2000. Prey selection and predation by wolves in Bialowieza Primeval Forest, Poland. *Journal of Mammology* 81 (1): 197-212.

Jędrzejewski, W., Veit, C., Branicki, W., Bunevich, A.N., Jędrzejewska, B., Schmidt, K., Theerkauf, J., Okarma, H., Gula, R., Szymura, L. 2000. [Genetic and social structure of the wolf Canis lupus population in Bialowieza Forest]. [*Abstracts of the VIII All-Polish Theriological Conference*]. Lublin: 56-57. [In Polish]

Jędrzejewski, W., Schmidt, K., Theurkauf, J., Jędrzejewska, B., Okarma, H. 2001. Daily movements and territory use by radio-collared wolves (Canis lupus) in Bialowieza Primeval Forest in Poland. *Canadian Journal of Zoology* 79: 1993-2004.

Jhala, Y.V., Sharma, D.K., 1997. Child-lifting by wolves in eastern Uttar Pradesh, India. *Journal of Wildlife Research* 2 (2): 94-101.

Jobin, A., Molinari, P., Breitenmoser, U. 2000. Prey spectrum, prey preference and consumption rates of Eurasian lynx in the Swiss Jura Mountains. *Acta Theriologica* 45 (2): 243–252.

Kalniņš, A. 1943. *Medniecība*. [*The Huntsmanship*]. Latvju grāmata, Rīga: 1-704. [In Latvian]

Kanzaki, N., Perzanowski, K. 1997. The potential role of wolf predation in regulating wild boar population in Bieszczady, Poland. *Wildlife Conservation Japan* 2 (4): 205-212.

Kazlauskas, J., Matuzevicius, A. 1981. On the helminth fauna and ecology of lynxes in Lithuania. *Acta Parasitologica Lituanica* 19: 8-11.

Kehoe, N.M. 1995. Grizzly Bear, *Ursus arctos*, - Wolf, *Canis lupus*, Interaction in Glacier National Park, Montana. *The Canadian Field-Naturalist* 109: 117-118.

Kellert, S.R. 1985. Public perceptions of predators, particularly the wolf and coyote. *Biological Conservation* 31 (2): 167-189.

Kellert, S.R., Black, M., Reid Rush, C., Bath, A.J. 1996. Human Culture and Large Carnivore Conservation in North America. *Conservation Biology* 10 (4): 977-990.

Kirkpatrick, L. 1980. Physiological indices in wildlife management. [In: Wildlife Management Techniques Manual. S.D. Schemnitz, ed.]. The Wildlife Society, Washington: 99-112.

Kocher, T.D., Thomas, W.K., Meyer, A., Edwards, S.V., Pääbo, S., Vilablanca, F.X., Wilson, A.C. 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. *P. Natl. Acad. Sci. USA* 86: 6196-6200.

Kohira, M., Rexstad, E.A. 1997. Diets of wolves, *Canis lupus*, in logged and unlogged forests of southeastern Alaska. *The Canadian Field-Naturalist* 111 (3): 429-435.

Kontrimavicius, V. (ed.) 1988. [*Fauna of Lithuania. Mammals*]. Mokslas, Vilnius: 1-259. [In Lithuanian]

Koubek, P., Cerveny, J., Bufka, L. 2001. How is the lynx (*Lynx lynx*) hunting strategy of ungulates in the Sumava Mountains (Czech Republic). *Abstracts of the 25th International Congress of IUGB*, Lemesos, Cyprus: 32.
Kozlo, P.G., Banad, E.B. 1985. Byelorussia. [In: The Wolf. History, Systematics, Morphology, Ecology. Bibikov, D. I., ed.]. Nauka Publishers, Moscow: 483-487. [In Russian]
Krebs, C. J. 1999. *Ecological methodology*. 2nd ed. Benjamin / Cummings, CA: 468-471.
Kunkel, K., Pletscher, D.H. 1999. Species-specific population dynamics of cervids in a multipredator ecosystem. *Journal of Wildlife Management* 63 (4): 1082-1093.
Kunz, T.H., Wemmer, C., Hayssen, V. 1996. Sex, age, and reproductive condition of mammals. [In: *Measuring and Monitoring Biological Diversity: Standard Methods for Mammals.* Wilson, D.E., Cole, F.R., Nichols, J.D., Rudran, R., Foster, M.S., eds.]. Smithsonian Inst. Press, Washington and London: 279-290.
Kvam, T. 1985. Supernumerary teeth in the European lynx, *Lynx lynx lynx*, and their evolutionary significance. *Journal of Zoology, London* (A) 206: 17-22.
Landon, D.B., Waite, C.A., Peterson, R.O., Mech, L.D. 1998. Evaluation of age determination techniques for gray wolves. *Journal of Wildlife Management* 62 (2): 674-682.
Lange, W.L. 1970. *Wild und Jagd in Lettland.* Harro von Hirschedt Vrlg., Hannover-Dohren: 1-280.
Lariviere, S., Crête, M. 1993. The size of eastern coyotes (*Canis latrans*): A comment. *Journal of Mammalogy* 74: 1072-1074.
Lehman, N., Eisenhawer, A., Hansen, K., Mech, D.L., Peterson, R.O., Wayne, R.K. 1991. Introgression of coyote mitochondrial DNA into sympatric North American gray wolf populations. *Evolution* 45: 104-119.
Lesniewicz, K., Perzanowski, K. 1989. The winter diet of wolves in Bieszczady Mountains. *Acta Theriologica* 34 (27): 373 - 380.
Levins, R. 1968. *Evolution in changing environment*. Princeton University Press, Princeton: 1-120.
Li, W., Fuller, T.K., Garshelis, D.L., Quigley, H.B. 1996. The status of large carnivores in China. *Journal of Wildlife Research* 1 (2): 202-209.
Liepa, I. 1974. *Biometrija. [Biometry*]. Zvaigzne, Rīga: 1-336. [In Latvian]
Lingaas, F., Aarskaug, T., Sorensen, A., Moe, L., Sundgreen, P.-E. 1996. Estimates of genetic variation in dogs based on microsatellite polymorphism. *Anim. Genet.* 27: 29.
Linnell, J.D.C., Aanes, R., Andersen, R. 1995. Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. *Wildlife Biology* 1 (4): 209-223.
Linnell, J.D.C., Smith, M.E., Odden, J., Kaczensky, P., Swenson, J.E. 1996. *Strategies for the reduction of carnivore – livestock conflicts: a review*. NINA, Trondheim 443: 1-118.
Linnell, J.D.C., Odden, J., Pedersen, V., Andersen, R. 1998. Records of Intra-guild Predation by Eurasian Lynx, *Lynx lynx*. *The Canadian Field-Naturalist* 112: 707-708.
Linnell, J.D.C., Swenson, J.E., Landa, A., Kvam, T. 1998. *Methods for monitoring European large carnivores – A worldwide review of relevant experience*. NINA, Trondheim 549: 1-38.
Linnell, J.D.C., Odden, J., Smith, M.E., Aanes, R., Swenson. J.E. 1999. Large carnivores that kill livestock: do ""problem individuals" really exist? *Wildlife Societ Bulletin* 27 (3): 698-705.
Linnel, J.D.C., Swenson, J.E., Andersen, R. 2000. Conservation of biodiversity in

Scandinavian boreal forests: Large carnivores as flagships, umbrellas, indicators, or keystones? *Biodiversity and Conservation* 9: 857-868.
Linnell, J.D.C., Swenson, J.E., Andersen, R. 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. *Animal Conservation* 4: 345-349.
Linnell, J.D.C., Andersen, R., Andersone, Z., Balciauskas, L., Blanco, J.C., Boitani, L., Brainerd, S., Breitenmoser, U., Kojola, I., Liberg, O., Løe, J., Okarma, H., Pedersen, H.C., Promberger, C., Sand, H., Solberg, E.J., Vadlmann, H., Wabakken, P. 2002. *The fear of wolves: A review of wolf attacks on humans*. NINA Oppdragsmelding 731: 1-65.
Litvaitis, J.A., Titus, K., Anderson, E. M. 1996. Measuring Vertebrate Use of Terrestrial Habitats and Foods. [In: *Research and Management Techniques for wildlife and Habitats*. Bookhout, T. A., ed.]. The Wildlife Society, Bethesda, Maryland: 254-274.
Lockie, J. D. 1959. The estimation of the food of foxes. *Journal of Wildlife Management* 23 (2): 224-227.
Longmire, J. L., Lewis, A. K., Brown, N. C., Buckingham, J. M., Clarck, L. M., Jones, D. M., Meincke, L. J., Meyne, J., Ratliff, R. L., Ray, F. A., Wagner, R. P., Moyzis, R. K. 1988. Isolation and molecular characterization of a highly polymorphic centromeric tandem repeat in the family Falconidae. *Genomics* 2: 14-24.
Lopez, B. H. 1995. *Of wolves and men*. Simon & Schuster, A Touchstone book: 1-309.
Lorenzini, R., Fico, R. 1995. A genetic investigation of enzyme polymorphisms shared by wolf and dog – suggestions for conservation of the wolf in Italy. *Acta Theriologica* S3: 101-110.
Madrigal, L., Ware, B., Miller, R., Saenz, G., Chavez, M., Dykes, D. 2001. Ethnicity, gene flow, and population subdivision in Limon, Costa Rica. *Am. J. Phys. Anthropol*. 114: 99-108.
Marquard-Petersen, U. 1998. Food habits of arctic wolves in Greenland. *Journal of Mammalogy* 79 (1): 236-244.
Matjushkin, E. N. 1985. Relationships with other predatory mammals. [In: *The Wolf. History, Systematics, Morphology, Ecology*. Bibikov, D. I., ed.]. Nauka Publishers, Moscow: 355–370. [In Russian]
Matteucci, C. 1992. Preliminary data on the ecology of a wolf *Canis lupus L.* population in northern Italy. [In: *Global Trends in Wildlife Management*. Bobek, B., Perzanowski, K. and Regelin, W. L., eds.]. Swiat Press, Krakow-Warszawa: 367-370.
Mattioli, L., Apollonio, M., Mazzarone, V., Centofanti, E. 1995. Wolf food habits and wild ungulate availability in the Foreste Casentinesi National Park, Italy. *Acta Theriologica* 40 (4): 387-402.
McOrist, S., Kitchener, A.C. 1994. Current threats to the European wildcat, *Felis silvestris*, in Scotland. *AMBIO* 23 (4-5): 243-245.
Mech, L.D. 1970. *The Wolf. The Ecology and Behavior of an Endangered Species*. Doubleday, New York.
Mech, L. D. 1994. Buffer zones of territories of grey wolves as regions of intraspecific strife. *Journal of Mammalogy* 75 (1): 199-202.
Mech, L.D. 1995. *The Wolf. The Ecology and Behaviour of an Endangered Species*. 8th ed. University of Minnesota Press, Minneapolis: 1-384.
Mech, L.D. 1999. Alpha status, dominance, and division of labor in wolf packs. *Canadian Journal of Zoology* 77: 1196-1203.
Mech, L.D. 2000. A Record Large Wolf, Canis lupus, Pack in Minnesota. *The Canadian*

Field-Naturalist 114 (3): 504-505.
Mech, L. D., Hertel, H. H. 1983. An eight-year demography of a Minnesota wolf pack. *Acta Zoologica Fennica* 174: 249 - 250.
Mech, L.D., Nelson, M.E. 1990. Evidence of prey-caused mortality in three wolves. *American Midland Naturalist* 123 (1): 207-298.
Mech, L. D., Fritts, S. H., Nelson, M. E. 1996. Wolf management in the 21st century: from public input to sterilization. *Journal of Wildlife Research* 1 (2): 195 - 198.
Mech, L.D., Nelson, M.E. 2000. Do wolves affect white-tailed buck harvest in northeastern Minnesota? *Journal of Wildlife Management* 64 (1): 129-136.
Mech, D.L., Smith, D.W., Murphy, K.M., MacNulty, D.R. 2001. Winter severity and wolf predation on a formerly wolf-free elk herd. *Journal of Wildlife Management* 65 (4): 998-1003.
Mengel, R. M. 1971. A study of dog-coyote hybrids and implications concerning hybridization in *Canis*. *Journal of Mammalogy* 52: 316-336.
Mercure, A., Ralls, K., Koepfli, K.P., Wayne, R.K. 1993. Genetic subdivisions among small canids: mitochondrial DNA differentiation of swift, kit and arctic foxes. *Evolution* 47: 1313-1328.
Meriggi, A., Rosa, P., Brangi, A., Matteucci, C. 1991. Habitat use and diet of the wolf in northern Italy. *Acta Theriologica* 36 (1 - 2): 141 - 151.
Meriggi, A., Brangi, A., Matteucci, C., Sacchi, O. 1996. The feeding habits of wolves in relation to large prey availability in northern Italy. *Ecography* 19 (3): 287-295.
Meriggi, A., Lovari, S. 1996. A review of wolf predation in southern Europe: Does wolf prefer wild prey to livestock? *Journal of Applied Ecology* 33 (6): 1561-1571.
Messier, F., Crête, M. 1985. Moose-wolf dynamics and the natural regulation of moose populations. *Oecologia (Berlin)* 65: 503-512.
Mills, S. 1987. Does Sweden have room for its wolves? *Oryx* 21 (2): 69-92.
Milne, D.G., Harestad, A.S., Atkinson, K. 1989. Diets of wolves on northern Vancouver Island. *Northwest Science* 63 (3): 83-86.
Mitchell-Jones, A.J., Amori, G., Bogdanowicz, W., Krystufek, B., Reijnders, P.J.H., Spitzenberger, F., Stubbe, M., Thissen, J.B.M., Vohralik, V., Zima, J. (eds.) 1999. *The Atlas of European Mammals*. Academic Press, London: 1-484.
Musiani, M., Okarma, H., Jędrzejewski, W. 1998. Speed and actual distances travelled by radiocollared wolves in Bialowieza Primeval Forest (Poland). *Acta Theriologica* 43 (4): 409-416.
Musiani, M., Visalberghi, E. 2001. Effectiveness of fladry on wolves in captivity. *Wildlife Society Bulletin* 29 (1): 91-98.
Muszynska, M. 1996. Comparison of the spring and summer diet of the wolf and the red fox in the Bieszczady Moutains. *Journal of Wildlife Research* 1 (2): 182-185.
Naess, A., Musterud, I. 1987. Philosophy of Wolf Policies I: General Principles and Preliminary Exploitation of Selected Norms. *Conservation Biology* 1 (1): 22-34.
Nader, I.A. 1996. Distribution and status of five species of predators in Saudi Arabia. *Journal of Wildlife Research* 1 (2): 210-214.
Neff, M. W., Broman, K. W., Mellersh, C. S., Ray, K., Acland, G. M., Aguirre, G.D., Ziegle, J. S., Ostrander, E.A., Rine, J. 1999. A second-generation linkage map of the domestic dog, *Canis familiaris*. *Genetics* 151: 803-820.
Nelson, M.E., Mech, L.D. 1985. Observation of a wolf willed by a deer. *Journal of Mammalogy* 66 (1): 187—188.
Nitsche, K.-A. 1996. Status und Schutz des Wolfes (*Canis lupus L., 1758*) in Europa. *Lounais-Hameen luonto* 83: 90-103.
Nowak, S., Myslajek, R. 1999a. [Conservation problems of the wolf *Canis lupus* in

Poland]. *Przeglad Przyrodniczy* 10 (3/4): 163-172. [In Polish]
Nowak, S., Myslajek, R. 1999b. [*Livestock protection from wolves*]. Stowarzyszenie dla Natury "Wilk", Godziszka: 1-40. [In Polish]
Nowak, R.M. 1979. *North American Quaternary Canis*. No. 6. Museum of Natural History, University of Kansas, Lawrence.
Odum, E.P. 1959. *Fundamentals of ecology*. 2nd edition. W.B. Saunders Company, Philadelphia and London: 1-546.
Okarma, H. 1984. The physical condition of red deer falling a prey to the wolf and lynx and harvested in the Carpathian Mountains. *Acta Theriologica* 29 (23): 283-290.
Okarma, H. 1989. Distribution and numbers of wolves in Poland. *Acta Theriologica* 34: 35: 497–503.
Okarma, H. 1991. Marrow fat content, sex and age of red deer killed by wolves in winter in the Carpathian Mountains. *Holarctic Ecology (Copenhagen)* 14: 169-172.
Okarma, H. 1993. Status and management of the wolf in Poland. *Biological Conservation* 66: 153–158.
Okarma, H. 1994. Protection and management of large carnivores (wolf, lynx) in Bialowieza Primeval Forest, Poland. Seminar on the management of small populations of threatened mammals. *Environment encounters* 17: 56-59.
Okarma, H. 1995. The trophic ecology of wolves and their predatory role in ungulate communities of forest ecosystems in Europe. *Acta Theriologica* 40 (4): 335-386.
Okarma, H. 1996. Man and wolf in Poland – a delicate balance. *Anthropozoologica* 22: 69-75.
Okarma, H. 2000. [*Lynx*]. Wydawnictwo Swiat, Warszawa: 1-80. [In Polish]
Okarma, H., Buchalczyk, T. 1993. Craniometrical characteristics of wolves *Canis lupus* from Poland. *Acta Theriologica* 38 (3): 253-262.
Okarma, H., Jędrzejewska, B., Jędrzejewski, W., Krasinski, Z. A., Milkowski, L. 1995. The roles of predation, snow cover, acorn crop, and man-related factors on ungulate mortality in Bialowieza Primeval Forest, Poland. *Acta Theriologica* 40 (2): 197-217.
Okarma, H., Jędrzejewski, W. 1996. Wilk *Canis lupus* w Puszczy Bialowieskiej – ekologia i problemy ochrony. [Wolf Canis lupus in Bialowieza Forest – ecology and conservation prblems]. *Przyroda Chronimy Ojcrysta* 52: 16-30. [In Polish]
Okarma, H., Jędrzejewski, W., Schmidt, K., Kowalczyk, R., Jędrzejewska, B. 1997. Predation of Eurasian lynx on roe deer and red deer in Białowieża Primeval Forest, Poland. *Acta Theriologica* 42 (2): 203–224.
Okarma, H., Jędrzejewski, W., Schmidt, K., Sniezko, S., Bunevich, A.N., Jędrzejewska, B. 1998. Home ranges of wolves in Bialowieza Primeval Forest, Poland, compared with other Eurasian populations. *Journal of Mammalogy* 79 (3): 842-852.
Oksanen, L., Fretwell, S.D., Arruda, J., Niemela, P. 1981. Exploitation Ecosystems in Gradients of Primary Productivity. *American Naturalist* 118 (2): 240-261.
Okumura, N., Ishiguro, N., Nakano, M., Matsui, A., Sahara, M. 1996. Intra- and interbreed genetic variations of mitochondrial DNA major non-coding regions in Japanese native dog breeds (*Canis familiaris*). *Anim. Genet.* 27: 397-405.
Olsson, O., Wirtberg, J., Andersson, M., Wirtberg, I. 1997. Wolf Canis lupus predation on moose Alces alces and roe deer Capreolus capreolus in south-central Scandinavia. *Wildlife Biology* 3 (1): 13-23.
Ostrander, E.A., Spague JR, G.F., Rine, J. 1993. Identification and characterization of dinucleotide repeat $(CA)_n$ markers for genetic mapping in the dog. *Genomics* 16: 207-332.

Ovsyanikov, N.G., Poyarkov, A.D. 1996. Wolves and feral dogs in the Ecosystems of Russian Nature Reserves. *Journal of Wildlife Research* 1 (3): 240-244.

Ozoliņš, J. 2000. *Action plan for the conservation of Eurasian lynx (Lynx lynx) in Latvia.* Latvian Forest Inventory Ltd., Salaspils: 1-31.

Ozoliņš, J., Pilāts, V. 1995. Distribution and status of small and medium-sized carnivores in Latvia. *Ann. Zool. Fennici* 32: 21 - 29.

Ozoliņš, J., Rantiņš, M. 1995. The data on otter *Lutra lutra* population provided by beaver trapping in Latvia. *Ekologija (Vilnius)* 2: 64-69.

Ozolins, J., Andersone, Ž. 2000. *Action Plan or the Conservation of Wolf (Canis lupus) in Latvia.* Latvian Forest Inventory Ltd., Salaspils: 1-38.

Ozoliņš, J., Andersone, Ž., Pupila, A. Status and Management Prospects of the Wolf *Canis lupus L.* in Latvia *Baltic Forestry* 7, No. 2(13): 63-69.

Pace, M.L., Cole, J.J., Carpenter, S.R., Kitchell, J.F. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution* 14 (12): 483-488.

Paetkau, D., Calbert, W., Stirling, I., Strobeck, C. 1995. Microsatellite analysis of population structure in Canadian polar bears. *Mol. Ecol.* 4: 347-354.

Paetkau, D., Shields, G.F., Strobeck, C. 1998. Gene flow between insular, coastal and interior populations of brown bears in Alaska. *Mol. Ecol.* 7: 1283-1292.

Palomares, E., Caro, T.M. 1999. Interspecific killing among mammalian carnivores. *American Naturalist* 153 (5): 492-508.

Papageorgiou, N., Vlachos, C., Sfougaris, A., Tsachalidis, E. 1994. Status and diet of wolves in Greece. *Acta Theriologica* 39 (4): 411 - 416.

Paquet, P.C., Carbyn, L.N. 1986. Wolves, *Canis lupus*, Killing Denning Black Bears, *Ursus americanus*, in the Riding Mountain National Park Area. *The Canadian Field-Naturalist* 100: 371-372.

Pedersen, V.A., Linnell, J.D.C., Andersen, R., Andren, H., Linden, M., Segerstrom, P. 1999. Winter lynx *Lynx lynx* predation on semi-domestic reindeer *Rangifer tarandus* in northern Sweden. *Wildlife Biology* 5(4): 203-250.

Peterson, R.L. 1947. A record of a timber wolf attacking a man. *Journal of Mammology* 28 (3): 294-295.

Peterson, R.O. 1995. Wolves as Interspecific Competitors in Canid Ecology. [In: *Ecology and Conservation of Wolves in a Changing World.* Carbyn, L.N., Fritts, S.H. and Seip, D.R., eds.]. Canadian Circumpolar Institute, University of Alberta, Edmonton, Alberta, Canada: 315-323.

Peterson, R.O. 1996. Wolves as interspecific competitors in canid ecology. [In: *Ecology and Conservation of Wolves in a Changing World.* Carbyn, L.N., Fritts, S.H., Seip, D.R., eds.]. Canadian Circumpolar Institute, Occasional Publication 35: 315-324.

Peterson, R.O. 2001. Wolves as Top Carnivores: New Faces in New Places. [In: *Wolves and Human Communities. Biology, Politics, and Ethics.* Sharpe, V.A., Norton, B. and Donnelley, S., eds.]. Island Press, Washington, D.C.: 151-160.

Peterson, R. O., Page, R. E. 1983. Wolf-moose fluctuations at Isle Royale National Park, Michigan, U.S.A. *Acta Zoologica Fennica* 174: 251–253.

Peterson, R.O., Woolington, J.D., Bailey, T.N. 1984. Wolves of the Kenai Peninsula, Alaska. *Wildlife Monographs* 88: 1-52.

Pilgrim, K.L., Boyd, D.K., Forbes, S.H. 1998. Testing for wolf-coyote hybridization in the Rocky Mountains using mitochondrial DNA. *Journal of Wildlife Management* 62: 683-689.

Polis, G.A., Strong, D.R. 1996. Food web complexity and community dynamics. The *American Naturalist* 147 (5): 813-846.

Polis, G.A., Anderson, W.B., Holt, R.D. 1997. Toward an Integration of Landscape and

Food Web Ecology: The Dynamics of Spatially Subsidized Food Webs. *Annu. Rev. Ecol. Syst*. 28: 289-316.
Post, E., Peterson, R.O., Stenseth, N.C., McLaren, B.E. 1999. Ecosystem consequences of wolf behavioural response to climate. *Nature* 401: 905-907.
Potvin, F., Breton, L., Pilon, C., Macquart, M. 1992. Impact of an experimental wolf reduction on beaver in Papineau-Labelle Reserve, Quebec. *Canadian Journal of Zoology* 70 (1): 180-183.
Poulle, M.-L., Carles, L., Lequette, B. 1997. Significance of ungulates in the diet of recently settled wolves in the Mercantour Mountains (southeastern France). *Rev. Ecol. (Terre Vie)* 52: 357-368.
Priklonsky, S. G. 1985. [Relationships with domestic animals]. [In: *The Wolf. History, Systematics, Morphology, Ecology*. Bibikov, D. I., ed.]. Nauka Publishers, Moscow: 374–377. [In Russian]
Pritchard, J.K., Stephens, M., Donnelly, P. J. 2000. Inference of population structure using multilocus genotypes data. *Genetics* 155: 945-959.
Promberger, C., Schröder, W. (eds.) 1992. *Wolves in Europe. Status and Perspectives*. (Proceedings of the workshop "Wolves in Europe - current status and prospects"). Munich Wildlife Society: 1-136.
Prusaite, J. 1961a. Lietuvos vilku mityba is veisimasis. [Diet and breeding of wolves in Lithuania]. *LTSR MS Darbai*, Serija C 1 (24): 177-191. [In Lithuanian with Russian summary]
Prusaite, J. 1961b. Lietuvos vilku morfologine charakteristika ir ju paplitimas. [Morphological characteristics and distribution of wolves in Lithuania]. *LTSR MS Darbai*, Serija C 1 (24): 161-176. [In Lithuanian with Russian summary]
Prusaite, A. Ya., Kaal, M., Volf, A. 1985. Baltic republics. [In: *The Wolf. History, Systematics, Morphology, Ecology*. Bibikov, D. I., ed.]. Nauka Publishers, Moscow: 476 - 478. [In Russian]
Pulliainen, E. 1963. [Food and feeding habits of the wolf (*Canis lupus*) in Finland.] *Suomen Riista* 16: 136-150. [In Finnish with English summary]
Pulliainen, E. 1965. Studies on the wolf (*Canis lupus* L.) in Finland. *Annales Zoologici Fennici* 2: 215-259.
Pulliainen, E. 1980. The status, structure and behaviour of populations of the wolf (*Canis l. lupus* L.) along the Fenno-Soviet border. *Annales Zoologici Fennici* 17: 107 – 112.
Pulliainen, E. 1981. Winter diet of *Felis lynx* L. in SE Finland as compared with the nutrition of other northern lynxes. *Zeitschrieft für Säugetierkunde* 46 (4): 249-259.
Pulliainen, E. 1985. The expansion mechanism of the wolf (Canis lupus) in northern Europe. *Rev. Ecol. (Terre Vie)* 40: 157-162.
Pulliainen, E., Hyypiä, V. 1975. Winter food and feeding habits of lynxes (*Lynx lynx*) in southeastern Finland. Suomen Riista 26: 60-63. [In Finnish with English summary]
Pulliainen, E., Lindgren, E., Tunkkari, P.S. 1995. Influence of food availability and reproductive status on the diet and body condition of the European lynx in Finland. *Acta Theriologica* 40 (2): 181-196.
Randi, E. 1993. Effects of fragmentation and isolation on genetic variability of the Italian populations of wolf *Canis lupus* and brown bear *Ursus arctos*. *Acta Theriologica* 38, Suppl.2: 113-120.
Randi, E., Lucchini, V., Francisci, F. 1993. Allozyme variability in the Italian wolf (*Canis lupus*) population. *Heredity* 71: 516-522.

Randi, E., Francisci, F., Lucchini, V. 1995. Mitochondrial-DNA restriction fragment length monomorphism in the Italian wolf (*Canis lupus*) population. *Journal of Zoological Systematics and Evolutionary Research* 33 (3): 97-100.

Randi, E., Lucchini, V., Christensen, M.F., Mucci, N. Funk, S.M., Dolf, G., Loeschcke, V. 2000. Mitochondrial DNA Variability in Italian and East European Wolves: Detecting the Consequences of Small Population Size and Hybridization. *Conservation Biology* 14 (2): 464-473.

Randi, E., Lucchini, V. 2001. Detecting rare introgression of domestic dog genes into wild wolf (*Canis lupus*) populations by Bayesian admixture analyses of microsatellite variation. *Cons. Gen.* [In press]

Reich, D.E., Wayne, R.K., Goldstein, D.B. 1999. Genetic evidence for a recent origin by hybridization of red wolves. *Mol. Ecol.* 8: 139-144.

Reig, S. 1993. Non aggressive encounter between a wolf pack and a wild boar. *Mammalia* 57 (3): 451-453.

Reig, S., Jedrzejewski, W. 1988. Winter and early spring food of some carnivores in the Bialowieza National Park, Eastern Poland. *Acta Theriologica* 33 (5): 57-65.

Reig, S., Cuesta, L., Palacios, F., Barcena, F. 1992. Status of the wolf in Spain. [In: *Global Trends in Wildlife Management.* Bobek, B., Perzanowski, K. and Regelin, W. L., eds.]. Swiat Press, Krakow-Warszawa: 371-374.

Reynolds, J. C., Aebischer, N. J. 1991. Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the Fox *Vulpes vulpes*. *Mammal Review* 21 (3): 97 - 122.

Ripple, W.J., Larsen, E.J., Renkin, R.A., Smith, D.W. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological Conservation* 102: 227-234.

Ristāls. 1994. No tālās senatnes līdz 1918.gadam. [From the ancient times to 1918]. *Medības, Makšķerēšana, Daba*, Nr.9, Rīga: 28-29 [In Latvian]

Rosell, F., Czech, A. 2000. Responses of foraging Eurasian beavers Castor fiber to predator odours. *Wildlife Biology* 6 (1): 13-21.

Route, W.T., Peterson, R.O. 1991. An incident of wolf, *Canis lupus*, predation on a river otter, *Lutra canadensis*, in Minnesota. *The Canadian Field-Naturalist* 105 (4): 567-568.

Roy, M.S., Geffen, E., Smith, D., Otsrander, E.A., Wayne, R.K. 1994. Pattern of differentiation and hybridization in North America wolf-like canids, revealed by analysis of microsatellite loci. *Mol. Biol. Evol.* 11: 553-570.

Roy, M.S., Geffen, E., Smith, D., Wayne, R.K. 1996. Molecular genetics of pre-1940 red wolves. *Conservation Biology* 10: 1413-1424.

Rukovsky, N. N. 1985. Feeding. [In: The *Wolf. History, Systematics, Morphology, Ecology*. Bibikov, D. I., ed.] Nauka Publishers, Moscow: 325-336. [In Russian]

Ryabov, L. S. 1985. Results of wolf population disturbances. [In: *The Wolf. History, Systematics, Morphology, Ecology*. Bibikov, D. I., ed.]. Nauka Publishers, Moscow: 51-63. [In Russian]

Saetre, G.P., Borge, T., Lindell, J., Moum, T., Primmer, C.R., Sheldon, B.C., Haavie, J., Johnsen, A., Ellegren, H. 2001. Speciation, introgressive hybridization and nonlinear rate of molecular evolution in flycatchers. *Mol. Ecol.* 10: 737-749.

Saitou, N., Nei, M. 1987. The neighbor-joining method: A new method for reconstructing phylogenetic trees. *Mol. Biol. Evol.* 4: 406-425.

Salvador, A., Abad, P. L. 1987. Food habits of the wolf population (*Canis lupus*) in Leon province, Spain. *Mammalia* 5 (1): 45 - 52.

Sambrook, E., Fritsch, F., Maniatis, T. 1989. *Molecular Cloning*. Cold Spring Harbor Press, Cold Spring Harbor, New York.
Schmitz, O.J., Hambaeck, P.A., Beckerman, A.P. 2000. Trophic Cascades in Terrestrial Systems: A Review of the Effects of Carnivore Removals on Plants. *American Naturalist* 155 (2): 141-153.
Schwartz, M.W., Brigham, C.A., Hoeksema, J.D., Lyons, K.G., Mills, M.H., Mantgem, van P.J. 2000. Linking biodiversity to ecosystem function: implications for conseravtion ecology. *Oecologia* 122: 297-305.
Seber, G.A.F. 1982. *The estimation of animal abundance and related parameters*. 2nd ed. Charles Griffin & Company Ltd., London and High Wycombe: 1-654.
Sharpe, V.A., Norton, B., Donnelley, S. 2001. *Wolves and Human Communities. Biology, Politics, and Ethics.* Island Press, Washington, D.C.: 1-321.
Shelton, P. C., Peterson, R. O. 1983. Beaver, wolf and moose interactions in Isle Royale National Park, USA. *Acta Zoologica Fennica* 174: 265 - 266.
Shibuya, H., Collins, B.K., Huang, T.H.-M., Johnson, G.S. 1994. A polymorphic (AGGAAT)n tandem repeat in an intron of the canine von Willebrand factor gene. *Anim. Genet.* 25: 122.
Sidorovich, V.E. (ed.). 1997. Mustelids in Belarus. Evolutionary Ecology, Demography and Interspecific Relationships. Zolotoy uley, Minsk: 1-263. [In Russian with English summary]
Skogland, T. 1991. What are the effects of predators on large ungulate populations? *Oikos* 61: 401-411.
Skoog, R. O. 1983. Results of Alaska's attempts to increase prey by controlling wolves. *Acta Zoologica Fennica* 174: 245-247.
Smietana, W., Klimek, A. 1993. Diet of wolves in the Bieszczady Mountains, Poland. *Acta Theriologica* 38 (3): 245-251.
Smietana, W., Wajda, J. 1997. Wolf number changes in Bieszczady National Park, Poland. *Acta Theriologica* 42 (3): 241-252.
Smirnov, V. S., Korytin, N. S. 1985. Age structure and sex ratio. [In: *The Wolf. History, Systematics, Morphology, Ecology.* Bibikov, D. I., ed.]. Nauka Publishers, Moscow: 51-63. [In Russian]
Smith, D.W., Brewster, W.G., Bangs, E.E. 1999. Wolves in the Greater Yellowstone Ecosystem: Restoration of a Top Carnivore in a Complex Management Environment. [In: *Carnivores in Ecosystems. The Yellowstone Experience*. Clark, T.W., Curlee, A.P., Minta, S.C., Kareiva, P.M., eds.]. Yale University Press, New Haven and London: 103-125.
Sokal, R.R., Rohlf, F.J. 1995. *Biometry*. 3rd ed. W.H.Freeman and Company, New York: 1-887.
Sokolov, V. E., Rossolimo, O. L. 1985. Taxonomy and variability. [In: *The Wolf. History, Systematics, Morphology, Ecology.* Bibikov, D. I., ed.]. Nauka Publishers, Moscow: 21-50. [In Russian]
Spauding, R., L., Krausman, P.R., Ballard, W.B. 1997. Calculation of prey biomass consumed by wolves in northwest Alaska. *Journal of Wildlife Research* 2 (2): 128-132.
Spaulding, R. L., Krausman, P.R., Ballard, W.B. 2000. Observer bias and analysis of gray wolf diets from scats. *Wildlife Society Bulletin* 28 (4): 947-950.
Stephenson, T.R., Vanballenberge, V. 1995. Defense of one twin calf against wolves, Canis lupus, by a female moose, Alces alces. *The Canadian Field-Naturalist* 109 (2): 251-253.
Stubbe, M. 1989. Wolf *Canis lupus L.* [In: *Buch der Hege Haar Wild*]. VEB Deutscher

Landwirtschaftsverlag, Berlin: 383 - 400.
Suminski, P. 1975a. Morphologische Unterscheidungsmerkmale zwischen Wolfs- (*Canis* lupus L.) und Hundeschädel (Canis familiaris L.). Zeitschrieft für Jagdwissenschaft 21: 227-232.
Suminski, P. 1975b. Vergleichende Untersuchungen zwischen dem Wolfsschädel (*Canis lupus* L.) und dem Hundeschädel (*Canis familiaris* L.). *Zeitschrieft für Jagdwissenschaft* 21: 129-133.
Suminski, P., Filipiak, W. 1977. Beitrag zur Nahrungsuntersuchung des Wolfes (*Canis lupus* L.). *Zeitschrieft für Jagdwissenschaft* 23: 1-5.
Sunde, P., Kvam, T. 1997. Diet patterns of Eurasian lynx *Lynx lynx*: what causes sexually determined prey size segregation? *Acta Theriologica* 42 (2): 189-201.
Sunde, P., Overskaug, K., Kvam, T. 1999. Intraguild predation of lynxes on foxes: evidence of interference competition? *ECOGRAPHY* 22: 521-523.
Sunde, P., Kvam, T., Bolstad, J.P., Bronndal, M. 2000. Foraging of lynxes in a managed boreal-alpine environment. *ECOGRAPHY* 23: 291-298.
Sundqvist, A.-K., Ellegren, H., Olivier, M., Vila, C. 2001. Y chromosome haplotyping in Scandinavian wolves (Canis lupus) based on microsatellite markers. *Molecular Ecology* 10: 1959-1966.
Sutherland, W.J. 2000. *The conservation handbook. Research, management and policy.* University Press, Cambridge: 1-278.
Swofford, D.L. 1998. *PAUP*: Phylogenetic analysis using parsimony (and other methods), version 4.0b2a.* Sinauer Associates, Sunderland, Massachusetts.
Taberlet, P., Gielly, L., Bouvet, J. 1996. *Etude génétique sur les loups du Mercantour.* Rapport pour la Direction de la Nature et des Paysages, Ministère de l'Environnement (unpub.): 1-8.
Tamura, K., Nei, M. 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Mol. Biol. Evol.* 10: 512-526.
Tauriņš, E. 1982. *Latvijas zīdītājdzīvnieki. [Mammals of Latvia]*. Zvaigzne, Rīga: 1-256. [In Latvian]
Teerink, B. J. 1991. *Hairs of West European Mammals*. Cambridge University Press, Great Britain: 1-224.
Thompson, J.D., Higgins, D.G., Gibson, T.J. 1994. CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *N. A. R.* 22: 4673-4680.
Thulin, C.-G. 2000. *Hybridisation between introduced brown hares and native mountain hares in Sweden*. Ph.D. thesis. Uppsala University.
Thurber, J.M., Peterson, R.O. 1991. Changes in body size associated with range expansion in the coyote (*Canis latrans*). *Journal of Mammalogy* 72: 750-755.
Thurber, J.M., Peterson, R.O. 1993. Effects of population-density and pack size on the foraging ecology of gray wolves. *Journal of Mammology* 74 (4): 879-889.
Timm, U., Pilats, V., Balciauskas, L. 1998. Mammals of the East Baltic. *Proceedings of the Latvian Academy of Sciences*, section B 52 (1/2): 1-9.
Tsuda, K., Kikkawa, Y., Yonekawa, H., Tanabe, Y. 1997. Extensive interbreeding occurred among multiple matriarchal ancestors during the domestication of dogs: Evidence from inter- and intraspecies polymorphisms in the D-loop region of mitochondrial DNA between dogs and wolves. *Genes Genet. Syst.* 72: 229–238.
Valdmann, H. 2000. The status of large predators in Estonia. *Folia Theriologica Estonica* 5: 158-164.

Valdmann, H., Koppa, O., Looga, A. 1998. Diet and prey selectivity of wolf Canis lupus in middle- and south-eastern Estonia. *Baltic Forestry* 4 (1): 42-46.
Vanags, J. (ed.) Medību gads. [Hunting year]. Avots, Rīga: 173-175. [In Latvian]
Vilà, C., Urios, V., Castroviejo, J. 1993. Tooth losses and anomalies in the wolf (*Canis lupus*). *Canadian Journal of Zoology* 71 (5): 968-971.
Vilà, C., Savolainen, P., Maldonado, J. E., Amorim, I. R., Rice, J. E., Honeycutt, R. L., Crandall, K. A., Lundeberg, J., Wayne, R. K. 1997. Multiple and ancient origins of the domestic dog. *Science* 276: 1687–1689.
Vilà, C., Amorim, I.R., Leonard, J.A., Posada, D., Castroviejo, J., Petrucci-Fonseca, F., Crandall, K.A., Ellegren, H., Wayne, R.K. 1999. Mitochondrial DNA phylogeography and population history of the gray wolf *Canis lupus*. *Mol. Ecol.* 8: 2089-2103.
Vilà, C., Wayne, R.K. 1999. Hybridization between Wolves and Dogs. *Conservation Biology* 13 (1): 195-198.
Viltrop, A., Lõhmus, K., Must, K., Jauram, A., Viigipuu, M, Rander, L. 2000. [Results of study of infectious diseases of mammals]. *Eesti Loomaarstlik Ringvaade* 3:100-114. [In Estonian]
Von Ende, R. 1985. *Über Wölfe und Hunde*. VEB Deutscher Landwirtschaftsverlag, Berlin: 1-280.
Vos, J. 2000. Food habits and livestcok depredation of two Iberian wolf packs (*Canis lupus signatus*) in the north of Portugal. *J. Zool. Lond.* 251: 457-462.
Vraka, E. 1997. *Study of the legislation regarding the natural environment and the brown bear in the South Balkans*. ARCTUROS, Thessaloniki: 81-152.
Wabakken, P., Sand, H., Liberg, O., Bjärvall, A. 2001. The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978-1998. *Canadian Journal of Zoology* 79 (4): 710-725.
Wabakken, P., Sorensen, O. J., Kvam, T. 1983. Wolves (*Canis lupus*) in southeastern Norway. *Acta Zoologica Fennica* 174: 277 p.
Wabakken, P., Kvam, T., Sorensen, O. J. 1984. Wolves *Canis lupus* in southeastern Norway. *Fauna Norvegica* Ser.A: 50 - 52.
Walsh, P. S., Metzger, D. A., Higuchi, R. 1991. Chelex 100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. *BioTechniques* 10: 506-513.
Waser, P.M., Strobeck, C. 1998. Genetic signatures of interpopulation dispersal. *Trends Ecol. Evol.* 13: 43-44.
Wayne, R.K., Jenks, S.M. 1991. Mitochondrial DNA analysis implying extensive hybridization of the endangered red wolf, *Canis rufus*. *Nature* 351: 565-568.
Wayne, R.K., Lehman, N., Allard, M.W., Honeycutt, R.L. 1992. Mitochondrial DNA variability of the gray wolf: Genetic consequences of population decline and habitat fragmentation. *Conservation Biology* 6 (4): 559-569.
Wayne, R.K., Brown, D.M. 2001. Hybridization and conservation of carnivores. [In: *Carnivore Conservation*. Gittleman, J.L., Funk, S.M., Macdonald, D. and Wayne, R.K., eds.]. Cambridge University Press, Cambridge, U.K.: 145-162.
Weaver, J.L. 1993. Refining the equation for interpreting prey occurrence in gray wolf scats. *Journal of Wildlife Management* 57 (3): 534-538.
Weaver, J.L., Arvidson, C., Wood, P. 1992. 2 Wolves, Canis lupus, killed by a moose, Alces alces, in Jasper National Park, Alberta. *The Canadian Field-Naturalist* 106 (1): 126-127.
Weber, J.-M., Weissbrodt, M. 1999. Feeding habits of the Eurasian lynx in the Swiss Jura Mountains determined by faecal analysis. *Acta Theriologica* 44 (3): 333-336.

Wilson, P.J., Grewal, S., Lawford, I.D., Heal, J.N.M., Granacki, A.G., Pennock, D., Theberge, J.B., Theberge, M.T., Voigt, D.R., Waddell, W., Chambers, R.E., Paquet, P.C., Goulet, G., Cluff, D., White, B.N. 2000. DNA profiles of the eastern Canadian wolf and the red wolf provide evidence for a common evolutionary history independent of the gray wolf. *Canadian Journal of Zoology* 78: 2156-2166.

Wilton, A.N., Steward, D.J., Zafiris, K. 1999. Microsatellite variation in the Australian dingo. *Journal of Heredity* 90: 108-111.

Wobeser, G. 1992. Traumatic, degenerative, and developmental lesions in wolves and coyotes from Saskatchewan. *Journal of Wildlife Diseases* 28 (2): 268-275.

Wolsan, M. 1983. Ancestral characters in the dentition of the weasel *Mustela nivalis* L. (Carnivora, Mustelidae). *Annales Zoologici Fennici* 20: 47-51.

Wolsan, M. 1984a. An incisor with double crown in a Stoat (*Mustela erminea* L.). *Zeitschrieft für Säugetierkunde* 49 (1): 57.

Wolsan, M. 1984b. Concerning the variation in the number, shape and size of incisors in fissiped carnivores. *Acta Zoologica Cracovensia* 27: 107-120.

Wolsan, M. 1984c. Dental Abnormalities in the Pine Marten *Martes martes* (L.) (*Carnivora, Mustelidae*) from Poland. *Zool. Anz. (Jena)* 213 (1/2): 119-127.

Wolsan, M. 1984d. Two dental anomalies in the weasel (*Mustela nivalis* L.): a supernumerary premolar and reduced upper molar (Mammalia, Carnivora, Mustelidae). *Zoologische Abhandlungen* 40 (5): 67-70.

Wolsan, M. 1984e. The origin of extra teeth in mammals. *Acta Theriologica* 29: 128-133.

Wolsan, M. 1988. Morphological Variations of the First Upper Molar in the genus *Martes* (*Carnivora, Mustelidae*). [In: *Teeth Revisited: Proceedings of the VIIth International symposium on Dental Morphology*, Paris, 1986. Russell, D.E., Santoro, J.-P. and Sigogneau-Russell, D., eds.]. Mem. Mus. Natn. Hist. Nat., Paris, (serie C) 53: 241-254.

Wolsan, M. 1989. Dental Polymorphism in the Genus *Martes* (*Carnivora: Mustelidae*) and Its Evolutionary Significance. *Acta Theriologica* 34 (40): 545-593.

Wolsan, M., Ruprecht, A.L., Buchalczyk, T. 1985. Variation and Asymmetry in the Dentition of the Pine and Stone Martens (Martes martes and M.foina) from Poland. *Acta Theriologica* 30 (3): 79-114.

Wolsan, M., Bieniek, M., Buchaczyk, T. 1992. The history of distributional and numerical changes of the wolf *Canis lupus L.* in Poland. [In: *Global Trends in Wildlife Management.* Bobek, B., Perzanowski, K. and Regelin, W. L., eds.]. Swiat Press, Krakow-Warszawa: 375-380.

Zajc, I., Mellersh, C.S., Sampson, J. 1997. Variability of canine microsatellites within and between different dog breeds. *Mamm. Genome* 8: 182-185.

Zheleznov, N. 1992. Ecology of the grey wolf *Canis lupus L.* on Chukotka. [In: *Global Trends in Wildlife Management.* Bobek, B., Perzanowski, K. and Regelin, W. L., eds.]. Swiat Press, Krakow-Warszawa: 381-384.

Ziediņš, J. 1990. Medījamo savvaļas dzīvnieku skaits Latvijā. [The number of game animals in Latvia]. *Mežsaimniecība un mežrūpniecība* 3: 26-30. [In Latvian]

Zimen, E. 1997. *Der Wolf. Verhalten, Ökologie und Mythos*. Knesebeck, München: 1-448.

Балодис, М. 1990. Лесоэкологические аспекты бобрового хозяйства в антропогенном ландшафте. *Лесоведение* 1: 29-37. [In Russian with English summary]

Бибиков, Д.И., Караваева, В.И. 1989. Опыт мониторинга системы "Растительность – копытные – крупные хищники ". *Экология* 1: 20-27.

Блузма, П. (ред.) 1990. *Млекопитающие в культурном ландшафте Литвы.* Мокслас, Вильнюс: 1-152.
Бологов, В. 1984. Контроль за численностью волка. *Охота и охотничье хозяйство* 2: 4-5.
Вайсфельд, М.А., Честин, И.Е. (ред.) 1993. *Медведи.* Наука, Москва: 1-519. [In Russian with English summary]
Ватолин, В. 1983. Волки Брянской области. *Охота и охотничье хозяйство* 5: 7.
Галака, Б.О. 1969. Гібридні вовки у Вінницькій області. *Збірник праць зоологічного музею*, Наукова Думка 33: 113-114. [In Ukrainian with English summary]
Гептнер, В.Г., Наумов, Н.П. (ред.) 1967. *Млекопитающие Советского Союза.* 2 (1). Высшая школа, Москва: 123-193.
Гептнер, В.Г, Слудский, А.А. (ред.). 1972. *Млекопитающие Советского Союза.* 2(II). Высшая школа, Москва: 385-457.
Гордиюк, Н.М. 1991. Взаимоотношения волка и копытных по наблюдениям за меченой стаей волков на Южном Урале. *Бюлл. Моск. о-ва исп. природы, Отд.биологич.* 96 (1): 3-10. [In Russain with English summary]
Гурский, И.Г. 1970. Форма прикуса и стираемось зубов. *Вестник Зоологии*: 56-60. [In Russian with English summary]
Гурский, И.Г. 1975. Гибридизация волка с собакой в природе. *Бюлл. Моск. о-ва исп. природы, Отд.биологич.* 50 (1): 131-136. [In Russian with English summary]
Данилов, П.И., Русаков, О.С. 1979. *Хищные звери Северо-Запада СССР.* Наука, Ленинград: 132-148.
Железнов, Н.К. 1990. *Дикие копытные Северо-Востока СССР.* АН СССР, Дальневосточное отделение, Владивосток: 1-480.
Завацкий, Б.П. 1990. Взаимоотношения волка с другими крупными хищниками Западного Саяна. *Вопросы охотоведения Сибири*, Красноярск: 74-83.
Калецкая, М.Л., Филонов, К.П. 1987. Стайность волка (*Canis lupus*) в Дарвинском заповеднике. *Зоологический журнал* 58 (8): 1230-1238. [In Russian with English summary]
Клевезаль, Г.А. 1988. *Регистрирующие структуры млекопитающих в зоологических исследованиях.* Наука, Москва: 1-288.
Козловский, И. 1997. Волки – вечная проблема России. *Охота и охотничье хозяйство* 12: 12-14.
Корытин, С.А. 1986. *Повадки диких зверей.* Агропромиздат, Москва: 1-319.
Корытин, С.А. 1990. О людоедстве волков. *Охота и охотничье хозяйство* 6: 12-14.
Корытин, С.А. 1997. Половой и возрастной состав людей, подвергавшихся нападению волков в разные сезоны года. Вопросы прикладной экологии (природопользования), охотоведения и звероводства. *Материалы научной конференции, посвященной 75-летию ВНИИОЗ*, Киров: 143-146.
Кронит, Я. 1971. Гибриды волка и собаки. *Охота и охотничье хозяйство* 11: 46.
Кудактин, А. 1984. Волк в Кавказском заповеднике. *Охота и охотничье хозяйство* 11: 8-9.
Кучерук, В.В. (ред.) 1989. *Медицинская териология: Грызуны, хищные, рукокрылые.* Наука, Москва: 1-272.
Линейцев, С. 1983. Волки Путорана. *Охота и охотничье* хозяйство 6: 4-5.
Лихотоп, Р.И. 1994. Аномалии черепа и зубной системы волка с территории Украины. *Вестник Зоологии* 3: 45-50. [In Russian with English summary]
Лукаревский, В.С. 1988. Питание леопарда, полосатой гиены и волка на Юго-Западном Копетдаге. *Зоологический журнал* 67 (2): 310-315. [In Russian with English summary]

Новиков, Г.А. 1956. *Хищные млекопитающие фауны СССР*. Изд-во АН СССР, Москва-Ленинград: 1- 239.
Новиков, Г.А. (ред.) 1970. Рысь. [В: *Звери Ленинградской области*]. Ленинград: 258-265.
Одум, Э. 1975. *Основы экологии*. Мир, Москва: 1-740.
Осмоловская, В.И., Приклонский, С.Г. 1975. Среднерусский волк (распределение, численность и его взаимоотношения с человеком. *Бюлл. Моск. о-ва исп. природы, Отд.биологич.* 50 (1): 117-130. [In Russian with English summary]
Павлов, М.П. 1982. *Волк*. Лесная промышленность, Москва: 1-208.
Павлов, М.П. 1990. *Волк*. Агропромиздат, Москва: 1-349.
Россолимо, О.Л., Долгов, В.А. 1965. Изменчивость черепа волка *Canis lupus* Linnaeus, 1758 в СССР. *Acta Theriologica* 10: 195-207. [In Russian with English summary]
Рябов, Л.С. 1988. Особенности размножения волков (*Canis lupus* L.) в Центральном Черноземье. *Экология* 6: 42-48.
Сабанеев, Л.П. 1988. Охотничьи звери. Физкультура и спорт, Москва: 1-480.
Скриба, Г. 1975. История и результаты реакклиматизации благородного оленя (*Cervus elaphus* L.) в Латвийской ССР. *Охрана и воспроизводство природных ресурсов. (Труды ЛСХА)* 83: 2-40. [In Russian with English summary]
Тауриньш, Э. 1975. Характеристика охотничьей фауны Латвийской ССР и перспективы рационального ее использования. *Охрана и воспроизводство природных ресурсов. (Труды ЛСХА)* 83: 18-28. [In Russian with English summary]
Тауриньш, Э., Янсон, Я. 1975. Проблема бродячих собак и кошек. *Охрана и воспроизводство природных ресурсов. (Труды ЛСХА)* 83: 82-87. [In Russian with English summary]
Филонов, К.П. 1982. Влияние хищников на копытных в заповедниках. [В: *Вопросы териологии. Промысловая териология*]. Наука, Москва: 210-217.
Формозов, А.Н., Голов, Б.А. 1975. О волке как вредителе животноводства в Уральской и Гурьевской областях. *Бюлл. Моск. о-ва исп. природы, Отд.биологич.* 50 (1), 108 -116. [In Russian with English summary]
Юдин, В.Г. Зубная система волка Дальнего Востока СССР. *Зоологический журнал* 68

Appendices

Appendix 1. Occurrence of wolves in Latvia in 1940 and 1970 based on the official census data.

1940


1 wolf present;


2-5 wolves present;


6-10 wolves present.

Appendix 1 (continued)

1970

1 wolf present; 2-5 wolves present;

6-10 wolves present.

Appendix 2. Results of the statistical analysis of body parameters of wolves – comparison between males (2) and females (1) (all age classes pooled) and between different age classes (1 – juvenile wolves < 1 year old; 2 – subadult wolves from 1 to 2 years; 3 – adult wolves > 3 years old)

Sexual differences in morphometrical parameters between male and female wolves (all age classes pooled together).

Descriptives

		N	Mean	Std. Deviation	Std. Error
WEIGHT	1.00	78	31.6571	7.0402	.7971
	2.00	85	38.1882	9.2663	1.0051
	Total	163	35.0629	8.8764	.6953
HEIGHT	1.00	250	69.0200	6.9499	.4395
	2.00	241	73.9668	10.6501	.6860
	Total	491	71.4481	9.2859	.4191
TOTALL	1.00	248	145.9214	15.2611	.9691
	2.00	242	154.0269	16.3094	1.0484
	Total	490	149.9245	16.2847	.7357
TAIL	1.00	247	39.3263	6.2137	.3954
	2.00	242	41.4070	10.0705	.6474
	Total	489	40.3560	8.4043	.3801
BODYL	1.00	247	106.7769	13.0190	.8284
	2.00	242	113.3264	14.5498	.9353
	Total	489	110.0182	14.1681	.6407
FOOT	1.00	241	23.6286	3.0574	.1969
	2.00	239	26.1548	9.7252	.6291
	Total	480	24.8865	7.2990	.3332

Descriptives

		95% Confidence Interval for Mean			
		Lower Bound	Upper Bound	Minimum	Maximum
WEIGHT	1.00	30.0697	33.2444	16.00	52.00
	2.00	36.1895	40.1869	18.00	67.00
	Total	33.6900	35.4358	16.00	67.00
HEIGHT	1.00	68.1543	69.8857	40.00	85.00
	2.00	72.6154	75.3182	46.00	172.00
	Total	70.6247	72.2715	40.00	172.00
TOTALL	1.00	144.0127	147.8301	94.00	192.00
	2.00	151.9616	156.0921	97.00	201.00
	Total	148.4790	151.3699	94.00	201.00
TAIL	1.00	38.5476	40.1050	13.00	56.00
	2.00	40.1318	42.6822	24.00	172.00
	Total	39.6093	41.1028	13.00	172.00
BODYL	1.00	105.1453	108.4085	49.00	140.00
	2.00	111.4840	115.1689	68.00	172.00
	Total	108.7593	111.2771	49.00	172.00
FOOT	1.00	23.2407	24.0166	10.00	34.00
	2.00	24.9156	27.3941	15.00	170.00
	Total	24.2318	25.5411	10.00	170.00

ANOVA

		Sum of Squares	df	Mean Square	F	Sig.
WEIGHT	Between Groups	1735.041	1	1735.041	25.328	.000
	Within Groups	11029.087	161	68.504		
	Total	12764.128	162			
HEIGHT	Between Groups	3002.791	1	3002.791	37.412	.000
	Within Groups	39248.634	489	80.263		
	Total	42251.426	490			
TOTALL	Between Groups	8046.914	1	8046.914	32.285	.000
	Within Groups	121631.29	488	249.244		
	Total	129678.21	489			
TAIL	Between Groups	529.208	1	529.208	7.594	.006
	Within Groups	33939.117	487	69.690		
	Total	34468.325	488			
BODYL	Between Groups	5243.519	1	5243.519	27.543	.000
	Within Groups	92714.629	487	190.379		
	Total	97958.148	488			
FOOT	Between Groups	765.778	1	765.778	14.788	.000
	Within Groups	24753.284	478	51.785		
	Total	25519.062	479			

Differences in morphometrical parameters between different age classes of wolves

Descriptives

		N	Mean	Std. Deviation	Std. Error
WEIGHT	1.00	17	25.0441	6.6226	1.6062
	2.00	34	29.4529	6.0743	1.0417
	3.00	112	38.2866	7.8868	.7452
	Total	163	35.0629	8.8764	.6953
HEIGHT	1.00	77	62.2468	8.3495	.9515
	2.00	107	69.0561	5.8646	.5669
	3.00	307	74.5896	8.6972	.4964
	Total	491	71.4481	9.2859	.4191
TOTALL	1.00	77	130.4156	16.4759	1.8776
	2.00	108	148.2222	13.0063	1.2515
	3.00	305	155.4525	13.0797	.7489
	Total	490	149.9245	16.2647	.7357
TAIL	1.00	77	35.6234	5.9184	.6745
	2.00	108	39.6537	6.0655	.5837
	3.00	304	41.8043	9.1655	.5257
	Total	489	40.3560	8.4043	.3801
BODYL	1.00	77	95.1818	13.9725	1.5923
	2.00	108	108.5685	11.5711	1.1134
	3.00	304	114.2911	12.3304	.7072
	Total	489	110.0182	14.1681	.6407
FOOT	1.00	76	22.6974	2.9956	.3436
	2.00	106	23.7358	2.8696	.2787
	3.00	298	25.8540	8.8378	.5120
	Total	480	24.8865	7.2990	.3332

Descriptives

		95% Confidence Interval for Mean			
		Lower Bound	Upper Bound	Minimum	Maximum
WEIGHT	1.00	21.6391	28.4492	16.35	37.10
	2.00	27.3335	31.5724	16.40	52.00
	3.00	36.8099	39.7633	16.00	67.00
	Total	33.6900	36.4358	16.00	67.00
HEIGHT	1.00	60.3516	64.1419	40.00	80.00
	2.00	67.9320	70.1801	50.00	82.00
	3.00	73.6128	75.5663	54.00	172.00
	Total	70.6247	72.2715	40.00	172.00
TOTALL	1.00	126.6760	134.1552	94.00	170.00
	2.00	145.7412	150.7032	107.00	192.00
	3.00	153.9787	156.9262	112.00	201.00
	Total	148.4790	151.3699	94.00	201.00
TAIL	1.00	34.2801	36.9667	22.00	55.00
	2.00	38.4967	40.8107	13.00	54.00
	3.00	40.7698	42.8387	26.00	172.00
	Total	39.6093	41.1028	13.00	172.00
BODYL	1.00	92.0105	98.3532	49.00	129.00
	2.00	106.3613	110.7758	74.00	144.00
	3.00	112.8995	115.6828	71.00	172.00
	Total	108.7593	111.2771	49.00	172.00
FOOT	1.00	22.0128	23.3819	11.00	29.00
	2.00	23.1832	24.2885	13.00	34.00
	3.00	24.8465	26.8616	10.00	170.00
	Total	24.2318	25.5411	10.00	170.00

ANOVA

		Sum of Squares	df	Mean Square	F	Sig.
WEIGHT	Between Groups	3940.364	2	1970.182	35.725	.000
	Within Groups	8823.764	160	55.149		
	Total	12764.128	162			
HEIGHT	Between Groups	10161.164	2	5080.582	77.261	.000
	Within Groups	32090.262	488	65.759		
	Total	42251.426	490			
TOTALL	Between Groups	38939.278	2	19469.639	104.494	.000
	Within Groups	90738.929	487	186.322		
	Total	129678.21	489			
TAIL	Between Groups	2415.534	2	1207.767	18.313	.000
	Within Groups	32052.791	486	65.952		
	Total	34468.325	488			
BODYL	Between Groups	22726.454	2	11363.227	73.407	.000
	Within Groups	75231.694	486	154.798		
	Total	97958.148	488			
FOOT	Between Groups	783.519	2	391.759	7.555	.001
	Within Groups	24735.543	477	51.856		
	Total	25519.062	479			

Post Hoc Tests

Multiple Comparisons

Dunnett C

Dependent Variable	(I) AGE	(J) AGE	Mean Difference (I-J)	Std. Error	95% Confidence Interval Lower Bound	95% Confidence Interval Upper Bound
WEIGHT	1.00	2.00	-4.4088	2.2059	-9.2771	.4594
		3.00	-13.2425*	1.9330	-17.7472	-8.7377
	2.00	1.00	4.4088	2.2059	-.4594	9.2771
		3.00	-8.8337*	1.4541	-11.9427	-5.7246
	3.00	1.00	13.2425*	1.9330	8.7377	17.7472
		2.00	8.8337*	1.4541	5.7246	11.9427
HEIGHT	1.00	2.00	-6.8093*	1.2118	-9.4532	-4.1655
		3.00	-12.3428*	1.0335	-14.8976	-9.7881
	2.00	1.00	6.8093*	1.2118	4.1655	9.4532
		3.00	-5.5335*	.9104	-7.3138	-3.7532
	3.00	1.00	12.3428*	1.0335	9.7881	14.8976
		2.00	5.5335*	.9104	3.7532	7.3138
TOTALL	1.00	2.00	-17.8066*	2.0359	-23.1912	-12.4220
		3.00	-25.0369*	1.7409	-29.8562	-20.2176
	2.00	1.00	17.8066*	2.0359	12.4220	23.1912
		3.00	-7.2302*	1.5284	-10.6841	-3.7764
	3.00	1.00	25.0369*	1.7409	20.2176	29.8562
		2.00	7.2302*	1.5284	3.7764	10.6841
TAIL	1.00	2.00	-4.0303*	1.2113	-6.1573	-1.9034
		3.00	-6.1809*	1.0361	-8.2099	-4.1519
	2.00	1.00	4.0303*	1.2113	1.9034	6.1573
		3.00	-2.1506*	.9097	-4.0059	-.2953
	3.00	1.00	6.1809*	1.0361	4.1519	8.2099
		2.00	2.1506*	.9097	.2953	4.0059
BODYL	1.00	2.00	-13.3867*	1.8557	-18.0226	-8.7508
		3.00	-19.1093*	1.5873	-23.2608	-14.9578
	2.00	1.00	13.3867*	1.8557	8.7508	18.0226
		3.00	-5.7226*	1.3937	-8.8451	-2.6001
	3.00	1.00	19.1093*	1.5873	14.9578	23.2608
		2.00	5.7226*	1.3937	2.6001	8.8451
FOOT	1.00	2.00	-1.0385	1.0824	-2.0940	1.706E-02
		3.00	-3.1567*	.9254	-4.6108	-1.7025
	2.00	1.00	1.0385	1.0824	-1.7058E-02	2.0940
		3.00	-2.1182*	.8144	-3.4888	-.7475
	3.00	1.00	3.1567*	.9254	1.7025	4.6108
		2.00	2.1182*	.8144	.7475	3.4888

*. The mean difference is significant at the .05 level.

Appendix 3. The questionnaire used in the study on wolf morphometrics in Latvia.

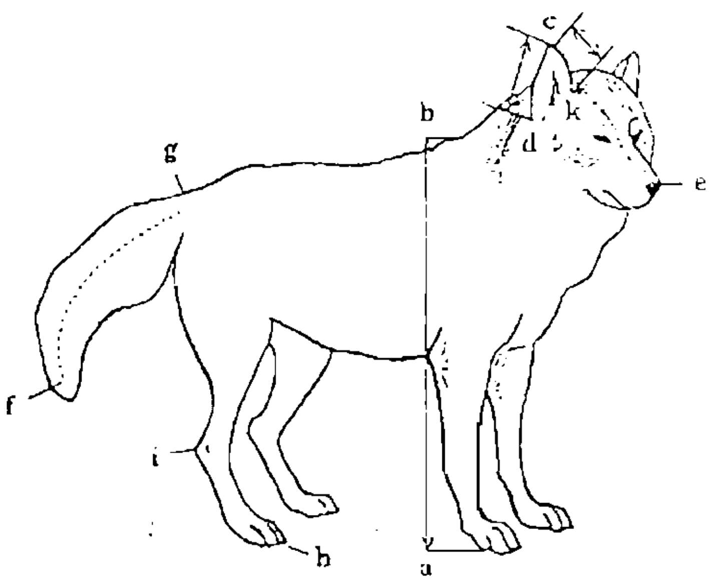
Valsts mežzinātnes institūts
Medību zinātnes sektors
Rīga, Kristapa iela 30, LV - 1046
Tālr. 7614808

Virsmežniecība LIEPĀJAS .... mežniecība VAIŅODES .... pagasts EMBŪTES .... | JW |

Nomedītā vilka vērtējums

Datums	Nomedīšanas vieta (kvartāla Nr., zemnieku saimniecība, u.c.)	Dzimums, aptuvens vecums	Svars (atzīmēt - mērījums veikts precīzi vai aptuveni)	Ķermeņa augstums, cm (a - b)	Ķermeņa garums, cm (e - f)	Astes garums, cm (g - f)	Pakaļpēdas garums, cm (h - i)	Auss garums, cm	
								(c - d)	(c - k)
21.02. 2001	z/s „Sirpi"	TĒVIŅŠ JAUNĀKS PAR GADU	≈ 20	54	122	36	22	14	11

ĪPAŠAS ATZĪMES (savainojumi un tml.) SADURSME AR TRANSPORTA LĪDZEKLI



PASKAIDROJUMI:
- ķermeņa augstums (a - b) tiek mērīts guļošam dzīvniekam no pēdas spilventiņa aizmugurējās malas (a) līdz muguras augstākajai vietai (b);
- ķermeņa garums (e - f) tiek mērīts guļošam dzīvniekam no deguna gala (e) pa muguras vidu līdz pēdējā astes skriemeļa galam (f);
astes garums (g - f) tiek mērīts pa astes apakšu no anālās atveres (g) līdz pēdējā astes skriemeļa galam (f);
pakaļpēdas garuma (h - i) mērījums tiek veikts labajai kājai no garākā pirksta gala neskaitot nagu (h) līdz locītavai (i);
auss augstums jāuzrāda kā divi mērījumi labajai ausij no auss gala pa iekšējo auss gliemežnīcas malu līdz pamatam (c - k) un pa ārējo auss gliemežnīcas malu līdz pamatam (c - d).

Lapu aizpildīja:
Mednieks CĪRULIS TREIJA ____ 2001. gada 29. AUGUSTĀ
vārds, uzvārds — paraksts
VMD darbinieks: MEŽSARGS EDGARS TREIJA ____ 2001. gada 29. AUGUSTĀ
amats, vārds, uzvārds — paraksts

Appendix 4

Fig.1. Wolf scats were used for the analysis of wolf diet.

Fig.2. Scats were collected in selected areas as well as during snow-tracking.

Appendix 4 (continued)

Fig.3. Wolf den on a mineral soil island in a raised bog.

Fig.4. Typical wolf habitat – raised bog in eastern Latvia.

Appendix 4 (continued)

Fig.5. Beaver ponds serve for wolves as a source of both water and food.

Fig.6. Hybrid pups found in northern Latvia in 1999.