LYNX (*LYNX LYNX*) AND WOLF (*CANIS LUPUS*) IN THE BALTIC REGION: DIETS, HELMINTH PARASITES AND GENETIC VARIATION

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is a summary of the following papers, referred to in the text by the Roman numerals:

I   Valdmann, H., Andersone-Lilley, Z., Koppa, O., Ozolins, J.& Bagrade,G. 2005. Winter diets of wolf *Canis lupus* and lynx *Lynx lynx* in Estonia and Latvia. *Acta Theriologica* 50 (4): 521–527.

II Valdmann, H., Moks, E. & Talvik, H. 2004. Helminth fauna of Eurasian lynx (*Lynx lynx*) in Estonia. *Journal of Wildlife Diseases*, 40(2), 356–360.

III Moks, E., Jõgisalu, I., Saarma, U., Talvik, H., Järvis, T. & Valdmann, H. 2006. Helminthologic survey of the wolf (*Canis lupus*) in Estonia, with an emphasis on *Echinococcus granulosus*. *Journal of Wildlife Diseases*, 42, 359–365.

IV Valdmann, H., Laanetu, N. & Korsten, M. 2004.Group size changes and age/sex composition in harvested wolves (*Canis lupus*) in Estonia. *Baltic Forestry*, 10 (2) 83–86.

V   Hellborg, L., Walker, C. W., Rueness, E. K., Stacy, J. E., Kojola, I., Valdmann, H., Vila, C., Zimmermann, B., Jacobsen, K. S & Ellegren, H. 2002. Differentiation and levels of genetic variation in northern European lynx (*Lynx lynx)* populations revealed by microsatellites and mitochondrical DNA analysis. *Conservation Genetics* 3(2):97–111.

Contributions

In papers I, II, III and IV, I initiated the study, participated in fieldwork, data collection and analysis, excluding PCR-RFLP analysis in paper IV. I also was responsible for writing papers I, II, IV and participated in writing papers III and V. In paper V, I was responsible for local data collection.

1. INTRODUCTION

Wolf and lynx (super-predators after J. Lepiksaar (1986)), migrated into the territory of Estonia after their potential prey species , moose *Alces alces* and mountain hare *Lepus timidus,* inhabited the paraglacial dense forest of the Early Preboreal period (Lõugas & Maldre 2000). Their other prey species – roe deer *Capreolus capreolus* and wild boar *Sus scrofa* – which are currently dominant in their diet (I), migrated into the area in Late Preboreal, when the climate was already warmer and broadleaf tree species formed food sources for them (Lepiksaar 1986, Lõugas 1997).

Lynx have generally been regarded as a game species and still are in Estonia and Latvia, although Lithuania and Poland introduced protection in 1975 and 1995, respectively. In Estonia and Latvia lynx appear to have increased in numbers since the 1950's and are now abundant throughout both countries. In contrast, the lynx populations in Lithuania and Poland have been stable, or slowly declining and occur at low levels (Bieniek *et al.* 1998, Bluzma 2000, Ozolins 2001).

Throughout history, wolves have always been heavily persecuted in the region. The standard management practice for most of the 20th century was open harvest, often with bounty incentives, all intended to exterminate wolves, or at least seriously reduce their numbers. This situation persisted until the 1990's, when restrictions on their harvest were gradually put into place in all countries. They are currently protected in Poland, but harvested in the 3 Baltic States. The trend throughout the region appears to have been very consistent. At the start of the 20th century populations were reduced, but still widely present; these increased during and after World War I. In the period between the wars, populations were greatly reduced again, but recovered to peak levels during and after World War II, only to be heavily persecuted in the 1950's, again reaching very low levels in the 1960's and early 1970's. They increased again, peaking in the early 1990's, but their ranks were again depleted in the late 1990's (Bluzma 2000, Jedrzejewska *et al.* 1996, Okarma 1989, Okarma 1993, Ozolins & Andersone 2001, Suminski 1975, Valdmann 2001).

In Europe, the populations of large carnivores found in the Baltic States are of great importance, both because of their size and potential to connect European populations with those in Russia and Belarus. Unfortunately, the knowledge base for their management in the Baltic States is generally poor.

Both species, as well as ungulates, are game animals in these countries, therefore it is important to develop local guidelines for sustainable management of both predators and prey.

As Estonian wolf and lynx populations were practically unscrutinised, I had to start with basic studies – diets, helminth fauna and genetic variability.

The study of their feeding ecology can provide valuable basic information, as hunting success and food choice may be the two most basic factors determining the fitness of carnivores (Sunde & Kvam 1997).

The main prey of wolf and lynx in Europe are ungulates, with lynx specialising in smaller and medium size ungulates, the proportion of each species in the diets depending on the ungulate community of the region (Pulliainen 1981, Okarma 1995, Aanes *et al*. 1998, Pedersen *et al*. 1999, Weber & Weissbrodt 1999, Koubek *et al*. 2001, Bluzma 2003, Kozlo 2003, Matjushkin 2003).

Wolf diet is highly variable throughout the world (Peterson & Ciucci 2003). In Eurasia, many native prey species were been extirpated, and native prey diversity has declined from five or six species to just two or three (Okarma 1995).

The predation of wolf in multiple-prey ecosystems is poorly understood and raises many questions. Do wolves prefer certain species and why? Does disintegration of groups resulting from wolf control affect prey choice?

Lynx has specialised in smaller and medium size ungulates with the proportion of each species in the diets depending on the ungulate community of the region (Pulliainen 1981, Okarma 1995, Aanes *et al*. 1998, Pedersen *et al*. 1999, Weber & Weissbrodt 1999, Koubek *et al*. 2001). Diet studies conducted in Europe reveal that where it is abundant, roe deer is the staple food for lynx, *e.g*., in Poland (Reig & Jedrzejewski 1988, Okarma *et al*. 1995, 1997, 2000), in the Alps (Jobin *et al*. 2000), Swiss Jura Mountains (Weber & Weissbrodt 1999), and in some parts of Norway (Aanes *et al*. 1998). Roe deer were also dominant in neighbouring parts of Russia-Pskov and Novgorod oblasts (Danilov *et al.* 2003).

The lynx diet has been studied briefly in neighbouring Leningrad oblast (Novikov 1970) and in Lithuania (Kazlauskas & Matuzevicius 1981), while the first studies on large carnivore ecology in Estonia and Latvia were initiated only in the 1990's (Andersone 1998, Valdmann *et al.* 1998, Andersone 1999, Ozoliņš 2000, Ozoliņš & Andersone 2001).

Wolf and lynx usually are infested with helminth parasites, which cause no harm. However, when factors such as malnutrition or viral or bacterial disease weaken the animal, the effects of parasites may become more serious or even fatal (Mech 1977). Depending on prey species diversity and even their relative population densities, helminth parasite fauna may vary markedly in hosts (Guberti *et al.* 1993).

Little is known about lynx parasites in the Baltics and neighbouring areas. They have been studied in Lithuania (Kazlauskas & Prusaite 1976, Kazlauskas & Matuzevicius 1981) and are currently being investigated in Latvia (Bagrade *et al*. 2002).

Mange, described in Eurasian lynx, is the most common disease affecting lynx and is an important cause of death especially in northern Europe (Ryser-Degiorgis 2001). Intestinal worms (especially roundworms) are very common,

Toxocara sp. apparently being the most prevalent, pathogenic, and sometimes fatal, especially for juvenile hosts (Schmidt-Posthaus *et al.* 2002). Infections with Toxoplasma and Trichinella also occur frequently in North America and Europe, but seldom cause disease symptoms (Ryser-Degiorgis 2001). Lungworms from *genus Capillaria* have been found occasionally in Sweden (Ryser-Degiorgis 2001) and *Aelurostrongylus abstrusus* was found to cause lung inflammation in one lynx in Switzerland (Schmidt-Posthaus *et al.* 2002).

Data about wolf helminths in Northern and Eastern Europe are relatively scarce. Helminth fauna of wolves was described for the European part of Russia (Jushkov 1995), Lithuania (Kazlauskas & Prusaite, 1976), Poland (Soltys 1964) and Belorussia (Shimalov & Shimalov 2002).

In the northern latitudes of Eurasia, the wolf is considered the principal definitive host for *Echinococcus granulosus*, which can cause the life-threatening disease cystic echinococcosis (CE). Distribution of the tapeworm *Echinococcus granulosus* (Hirvelä-Koski *et al.* 2003, Lavikainen *et al.* 2006) and nematodes of the genus *Trichinella* among wolves were studied in Finland (Oivanen *et al.* 2002) and Estonia (Järvis et *al.* 2001, Miller 2003). In addition, the infection of wolves with *E. granulosus* was reported in adjacent countries: Russia (Jushkov 1995) and Lithuania (Kazlauskas & Prusaite 1976). However, the sylvatic cycle of *E. granulosus* was described only in Finland, identifying wolf as a definitive host and reindeer (*Rangifer tarandus*) as an intermediate host (Hirvelä-Koski *et al.* 2003).

E. granulosus is characterised as the most diverse species in the genus. To date, ten different genotypes (G1-G10) have been identified and categorised according to their host and geographic range (McManus 2002, Lavikainen *et al.* 2003). Several of the seven strains found in humans (G1, G2, G5, G6, G7, G8 and G9) are dangerous to the humans population, it is of great importance to use genetic methods for correct species and strain identification.

Both these predator species were greatly reduced during the 19th century in the Baltic States, being almost exterminated from Lithuania, confined to the extreme northwest and east of Latvia, and were generally rare throughout Estonia (Bluzma 2000, Ozolins 2001, Valdmann 2001). Therefore a proper management of these populations may require detailed knowledge of the effects of possible historic bottlenecks in genetic variability and structure (Westmeier *et al.*1998).

The goals of my thesis were the following:
1. To analyse the diet of two large carnivores – wolf and lynx in Estonia and Latvia.
2. To accurately determine the species of helminths, infecting lynx and wolf in Estonia.
3. To estimate prevalence and intensity of helminth infections in relation to their sex and age.

4. To evaluate the possible relationships between helminth fauna and diets of lynx and wolf.
5. To analyse the genetic variability, population structure and history of lynx in Northern Europe.

2. MATERIAL AND METHODS

2.1. 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 usually establishes 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 Estonia and Latvia may not have lasting snow cover at all.

In total, 64 species of mammals are recorded in Estonia and Latvia, some having been introduced or reintroduced. Among ungulates, wild boar, roe deer and moose are widespread, red deer *Cervus elaphus* is more common in Latvia.

2.2. Material and methods

In Estonia, data on lynx diet were collected during the winters of 1998–1999 and 1999–2000. A total of 127 lynx stomachs were obtained from hunters. Lynx carcasses were separated to young animals (< 15 kg, <1.5 yrs.) and adults (>15 kg, >1.5 yrs.) (Schmidt *et al.* 1997) and their sex was determined. Diet composition was analysed in two periods – late autumn (November-December) and winter (January-February) – as well as in the whole season. Wolf scats (n = 518) were collected in central and southeastern Estonia in April, 1996–1997. Preliminary analysis of the wolf data was presented by Valdmann *et al.* (1998).

In Latvia, stomachs of wolves (n = 98) and lynxes (n = 49) were collected in October-March 1997–2001. Animals of both species were legally hunted in various parts of Latvia, mostly the northeastern and western regions. (For additional details, see I.)

For helminth parasite study, lynx carcasses were obtained from hunters from 12 of 15 Estonian counties. The lynxes were sexed and divided into two groups:1) young animals (body weight less than 15 kg and age under 1.5 years) and 2) adults (body weight over 15 kg and age over 1.5 years) according to Schmidt *et al.* (1997). The groups contained 10/11 and 9/6 females/males animals respectively.

Thorough necropsies were performed on 37 lynx. In addition, 61 faecal samples, collected from the wild during snow tracking of 9 lynx, were examined for parasite eggs, and muscle samples from 27 carcasses were examined for *Trichinella* larvae. (For more details, see II.)

Twenty six (26) wolf carcasses were collected from 9 of 15 Estonian counties during the hunting seasons 2000/2001 and 2003/2004. Carcasses were

sexed and aged into two classes, according to Aul *et al.* (1957): young (less than two years old, body weight < 40 kg) and adult (more than two years old, weight > 40 kg).

Two mature specimens of *E. granulosus*, isolated from a single wolf, were subjected to DNA extraction, PCR (polymerase chain reaction), PCR-RFLP (restriction fragment length polymorphism) and sequencing analysis. One mature *E. multilocularis*, isolated from the red fox *Vulpes vulpes* (Moks *et al.* 2005), was analysed for comparison. (For more details, see III.)

Wolf group sizes in Estonia were registered from 1977–1999. Sightings were carried out in November–December and again in February.

Thirty-one (31) wolves, killed during sports hunting were sexed and aged. *Cementum annuli* counts in canines was selected as the most accurate method for aging killed animals (Klevezal & Kleinenberg 1967, Grue & Jensen 1979, Goodwin & Ballard 1985, Ozolinš *et al.* 2001). Due to the previous good results with ungulate teeth, we generally followed the method by G. Klevezal (1988). (For additonal details see IV.)

For genetic variation study, eighty nine samples from Sweden and 107 samples from Norway were collected from legally harvested lynxes during the 1996–1998 and 1993–1997 hunting seasons, respectively. Similarly, 48 lynx samples were collected from Finland in 1997–1998, 24 in Estonia in 1998–1999 and eight in Latvia in 1997–1998.

Populations were defined as Scandinavia (Sweden and Norway), Finland and the Baltic States (Estonia and Latvia). (For additional details, see V.)

3. RESULTS

3.1. Diets

In the winter diets of lynx, a total of 11 prey species or other taxa were identified in Estonia and Latvia. Roe deer and hares (brown hare *Lepus europaeus* and mountain hare) were the most important prey of lynx. In the Estonian sample, no age or sex-related differences in the diet composition of lynx were revealed Neither were there any differences in the roe deer – other prey ratios between late autumn and winter. However, it is noteworthy that some prey species (namely wild boar, red deer, and raccoon dog *Nuctereutes procyonoides*) were found only in the stomachs of adult males. In Latvia, 35% of stomachs were empty (39% of females and 29% in males). The mean weight of stomach content was 440.5 ± 258.7g (SE) with the maximum weight 1370 g. The average weight of female stomach content was 431 ± 215.0 g; of males 445 ± 323.9 g.

Niche breadths of the lynx in Estonia and Latvia were 2.68 and 1.28.

The winter diet of wolves was more diverse than that of lynx (I). Besides deer, it also included moose, wild boar, beaver, domestic dog, and carrion (often exposed as bait by hunters). One stomach (in Latvia) was filled with grass. No differences in prey composition were found between male and female wolves. In the Latvian sample, 37 of wolf stomachs were empty (40.4% in females and 31.2% in males). The average weight of the fresh stomach content was 990.3 ± 849.3 g, ranging from zero to 4350 g. Female stomachs were fuller, 1070.7 ± 938.0 g versus 850.6 ± 668.3 g in males.

Food niche breadths of wolves in Estonia and Latvia were 1.54 and 1.65.

Diets of these species overlapped highly between species and countries (Table 1) (details in I).

Table 1. Food niche overlaps (Pianka's index α calculated for four prey groups – ungulates, hares, rodents and carnivorous prey) among predator species and countries.

Species	Lynx Estonia	Lynx Latvia	Wolf Estonia	Wolf Latvia
Lynx Estonia	*	0.89	0.90	0.85
Lynx Latvia		*	0.99	0.99
Wolf Estonia			*	0.99

3.2. Helminth faunas

All 37 intestinal tracts of analyzed lynx contained *Taenia pisiformis,* and at least one helminth species. Eight different helminth species were found, with the number of species per lynx varying from 1 to 5. *T. pisiformis* and *Toxocara cati* were the most prevalent helminths and also had the highest mean intensities of infection. *T. cati* and *Trichinella* sp. were recovered at necropsy but, despite the recovery of eggs of *Capillaria* from 8 fecal samples collected from free-ranging lynx, *Capillaria* spp. worms were not found. There were no statistically significant differences in the intensity of infection of helminths among sex or age groups, except where young male lynx had fewer *Taenia pisiformis* and *Taenia laticollis* than did older lynx.

A significant correlation between host age and the number of species of parasite per individual was observed only in males, with old males having more species per host than young males.

All analyzed wolves were infected with parasites. Thirteen species of helminths (one trematode, seven cestode and five nematode species) were identified. The most prevalent species were *Alaria alata* and *Uncinaria stenocephala,* which also showed the highest mean intensity, 303 and 11.6 respectively. The average number of gastrointestinal helminths per host was 325, ranging from 2 to 1571. Both *Trichinella nativa* and *T. britovi* larvae were detected from muscle samples. Eggs of *Capillaria spp*. were found from three faecal samples. No *Capillaria* worms were found at necropsy. Eggs of *U. stenocephala* and *Toxocara canis* were present in faecal samples. No differences in the intensity of infection were found among age and sex groups.

The examination of morphological characters following criteria given by Abuladze (1964) revealed the presence of *E. granulosus* in wolf in Estonia. To confirm the morphological identification of *E. granulosus* by means of genetic analysis, total genomic DNA was isolated from two specimens of *E. granulosus*. Initially, the PCR and PCR-RFLP analyses described by Gonzalez *et al.* (2002) were used. Fragments of the Eg9 and Eg16 loci were successfully PCR-amplified (Fig. 1). Sizes of the PCR products were similar to those obtained by Gonzalez *et al.* (2002). The Eg9 PCR product was cleaved with two restriction enzymes in separate reactions. Restriction enzyme Cfo I did not cut the Eg9 sequence for *E. granulosus*, while for *E. multilocularis*, Eg9 sequence was cut and gave exactly the same restriction pattern as described in Gonzalez *et al.* (2002). Rsa I had no recognition sequence within Eg9 locus for *E. granulosus* isolate 1, but for the isolate 2, Rsa I gave a fragment that was slightly over 400bp, demonstrating that the Eg9 sequence was somewhat different between two *E. granulosus* isolates. Rsa I did not cut *E. multilocularis* Eg9 sequence. Both PCR and PCR-RFLP confirmed that *E. granulosus* specimens were correctly identified using morphological characters.

Additional molecular characterization and phylogenetic analyses were conducted by amplification and sequencing of a fragment of the mitochondrial ND1 gene together with the ND1 sequences of *E. multilocularis* and other *E. granulosus* available in the GenBank. As a positive control, the sequence of the same ND1 locus of *E. multilocularis* that was obtained during another study (Moks *et al*. 2005) preparation) was included. Both *E. granulosus* isolates gave identical sequences of 426bp in length. The sequence was submitted to GenBank (AY842287). When aligned with sequences from the GenBank, the *E. granulosus* sequence from Estonia was found to be identical with AF525297 (genotype G10), a ND1 sequence of *E. granulosus*, isolated from reindeer and moose in Finland (Lavikainen et al., 2003). MODELTEST selected the TrN+I+G model of DNA substitutions that best fitted the data. On an ML phylogenetic tree, *E. granulosus* ND1 sequence from Estonia clustered with other *E. granulosus* sequences and were clearly distinguished from sequences of all other species, including *E. multilocularis* (data not shown). Topology of the phylogenetic tree was essentially the same as described in Lavikainen *et al*. (2003). The most remarkable feature of the phylogram is that geographically distant genotypes G10 (from Finland and Estonia) and G8 (from the USA) group together. Their closest neighbours are genotypes G6 and G7. The genotype G10 differs from G8 and G6 by 12 mutations and from G7 by 14 mutations. A more distant genotype G5 is separated from G10 by 28 mutations.

Sorensen's binary coefficient of helminth fauna similarity between local wolf and lynx was 0.42. (details in II and III).

3.3. Wolf groups and age composition

Wolf group sizes in Nov–Dec (mean 4.58) and in February (mean 2.07) differed significantly. In Nov–Dec, wolf groups were regular and consisted usually of 4–5 animals. In February, groups were mostly fragmented, singles and pairs dominated. From a sample of 31 killed wolves 16±6.6% were pups; 10±5.6% were sub-adults and 74±7.9% adults. The overall male:female ratio of all animals was 2:1, but obviously due to the small sample, it did not differ significantly from 1:1 (Corrected *chi*-square 1.1, df = 1, $p > 0.05$). The mean age of adults was 5.3±0.4 yrs. (5.4±1 for males and 4.8±0.5 for females). The oldest animal in the sample was a ten (10) years old male (details in IV).

3.4. Mitochondrial DNA

The overall level of genetic variability was very low, only one haplotype was found in Scandinavia. This variant (type 1) was also the most common in Finland and the Baltic States. In addition, two other variants were found in both areas, and a fourth type was unique to the Baltic population

3.5. Genetic variability of microsatellite loci

Levels of genetic variability at 11 feline di- and tetra- nucleotide microsatellite loci genotyped in all 276 animals corresponded to what might be considered as moderate for microsatellites, i.e. mean heterozygosities between 0.51–0.62 for the three defined populations (Scandinavia N = 196, Finland N = 48 and Baltic N = 32). Mean heterozygosity and mean number of alleles were lower in all of the 100 simulated data sets of Scandinavian individuals of equal sample size to Finland+Baltic. Mean heterozygosity in the 100 re-samples was 0.51, ranging from 0.50 to 0.53, compared to 0.63 for Finland+Baltic. The mean number of alleles in the 100 Scandinavian re-samples(4.2 with a range from 3.8 to 4.5) was significantly lower compared to Finland+Baltic. A significant support for a recent bottleneck in Scandinavia (p = 0.006) was observed in our data. Twenty alleles that were observed in the Finnish and Baltic populations were not observed in the much larger Scandinavian sample, whereas the reverse was true for only seven alleles (details in V).

4. DISCUSSION

Wolves in both countries mostly prey upon on three species of ungulates. Roe deer, wild boar and red deer form the staple food of wolf in Latvia. In Estonia red deer, being relatively rare, is partly replaced by moose.The dominant species (F%) was roe deer, followed by wild boar. The dominant (F%) prey species of wolf in Latvia was wild boar and in Estonia, compared to its availability as prey, it was preferred over other ungulate species, as moose was avoided (Valdmann *et al.*1998, Valdmann 1998.).

The preference of ungulate prey by wolves is well documented, but prey selection in a multiple-prey system is not. Early predator-prey theory predicted that per capita kill rates depend exclusively on changes in prey density (Lotka 1925, Volterra 1926). Later it was recognised that other factors, including behaviour of predators and prey are important determinants of the per capita kill rate (Taylor 1984). Hunting success of predators may be affected by prey-related factors, such as species, age and sex structure of the prey population and prey group size (Fuller & Kat 1993, Stander & Albon 1993, Mech & Peterson 2003). Environmental factors such as season, habitat type and weather have also proved to be important as individual traits of predators (Holekamp *et al.*1997 , Hebblewhite *et al*. 2002, Mech & Peterson 2003).

What factors may be the most important determinants of prey species composition in the wolf diet in Estonian and Latvian multiple-prey ecosystems?

The latest studies in Scandinavia showed, that the age of males, but not female breeding wolves, was a significant predictor of hunting success of moose, and that hunting success increased in packs after breeding males had attained maximum body size (1,5–2,5 years), reaching maximum values at 4,5–5,5 years of age (Sand *et al*. in press).

In our study, the mean age of hunted wolves in Estonia was 5,4 years for males and 4,8 for females (IV). But, despite these relatively high values moose was avoided in the study area. Obviously, proportions of wild ungulate species in wolf diet in study area are determined by other factors.

Concerning high densities of wild boar and roe deer in Estonia and Latvia, I suggest that high consumption of these species by wolf can be explained by preferable predator:prey ratios. It is also possible that aggregations of wild boar, especially piglets, form a cost-effective prey for disrupted packs, pairs or even single animals, resulted from wolf hunting (Ozolins *et al*. 2001, IV). This conclusion is supported by O. V. Bakin, (2002), and by P. I. Danilov (2005) in Volgo-Kamsk Nature Reserve and Karelia (Russia), where wolf diet strictly depended on group size. Single wolves mostly relied on smaller prey, one wolf even regularly visited so called "badger towns", preying on foxes and raccoon dogs, moose was successfully hunted only by larger family groups. It is also probable that positive selection of wild boar is due to the habit of wolves in the study area regularly visiting areas of supplementary feeding of boars, where

they can directly ambush incoming animals or follow their tracks from there, thus minimizing efforts for locating prey animals.

Lynx. In our study areas roe deer clearly constituted the most important lynx food source, especially in Latvia. As found, the proportion of roe deer in the lynx diet rapidly increases as the roe deer numbers grow (Okarma *et al.* 1997) and the availability of roe deer as prey in study area is high: densities of roe deer in Latvia and Estonia are 1.06 and 0.66 ind./km^2 accordingly (official census data, but obviously even more).

Concerning the ungulate/lagomorphs ratio in the lynx diet, it strongly depends on latitude (Jedrzejewski *et al.* 1993).

The proportion of lagomorphs in the diet is relatively large in the north (Pulliainen & Hyypia 1975) and decreases with latitude, south of 52–54° ungulates dominate in lynx diets (Jedrzejewska & Jedrzejewski 1998). Concerning eastward-westward 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 also the general ungulates- oriented game management in these countries or very favourable predator: prey ratios.

As Estonia is north of Latvia, it predictably possesses a higher proportion of lagomorphs in the lynx diet in accordance with the abovementioned north-south trend (Jedrzejewska & Jedrzejewski 1998).

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 throughout the country. Unfortunately, reliable distinction between roe deer and red deer hair 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).

Hare densities tend to decline everywhere in Europe, and lately European brown hare syndrom (EBHS), increasing hare mortality, was identified in neighbouring Finland (Syrjälä *et al.* 2005). The existence of EBHS in Estonia is thus quite likely and can considered a serious mortality- increasing factor.

Thus the time lag between the lynx diet study in Lithuania (Kazlauskas and Matuzevicius 1981) and the current study can probably explain high proportion of hares (60%) in the Lithuanian study. This may be also true for the study in

neighbouring Leningrad district by Novikov (1970), as currently lynx there preys mostly on roe deer and wild boar (Danilov *et al.* 2003).

In Latvia, hare densities also have considerably declined since the early 20th century (Taurins 1975), possibly explaining the low proportion of hares in local lynx diet.

According to studies from Europe, intraguild predation on foxes is widespread (Adlerberg 1935, Haglund 1966, Novikov 1970, Pulliainen 1981, Sunde & Kvam 1997, Linnell *et al.* 1998, Sunde *et al*. 1999, 2000, Danilov *et al.* 2003, Kozlo 2003, Kozlovski 2003).

The consumption of killed carnivores is not universal among cases of intraguild 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 (F%) 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, a larger sample size probably would have increased the proportion of fox, as fox densities in Latvia are generally recognised as high (Ozolins & Pilats 1995).

A trade-off of intraguild predation on foxes and other carnivores could be the transmission of certain diseases in the process. Lynx have been recorded to die of sarcoptic mange (Linnell *et al.* 1998) and rabies (one 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.

Food niche breadths of wolf were similar in both countries reflecting consumption of 1–2 major food types. Higher food niche breadth of lynx in Estonia (2.68) results from more even consumption of 1–3 main food types, namely roe deer and hares. But the Latvian lynx sample was relatively small; a larger sample probably would have lessened the difference.

High and very high Pianka's food niche overlap indexes (0,90 and 0,99) in Estonia and Latvia reflect the heavy dependence of both predator species on roe deer as a major food source.

From management standpoint it is important to manage roedeer very carefully as this small ungulate forms a prey base for both these large predators and is also heavily hunted by human hunters.

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.

Helminth fauna of predators reflects their food habits. A total of 7 lynx helminth species were recorded in our study (II). In Latvia 6 helminth species were recorded *Taenia pisiformis*, *Toxocara mystax* (most common) *Thominx aerophilus, Capillaria felis-cati, Trichinella* sp. and one species not identified (Bagrade *et al.* 2002). Six from 10 helminth species reported from lynx in Lithuania (Kazlauskas & Prusaite 1976, Kazlauskas & Matuzevicius 1981) were also recovered in the present study. In addition, 3 of the 6 species of helminths reported from lynx in neighbouring northwestern Russia (Geptner & Sludski 1972, Jushkov 1995) were found in Estonian lynx.

Accordingly, lynx helminth biodiversity for our particular region is quite similar and is obviously caused by feeding on the same species of prey; namely roe deer (*Capreolus capreolus*) and mountain hare (*Lepus timidus*).

Roe deer is one of the intermediate hosts of *Taenia hydatigena* in Estonia, although the proportion of infected animals in population was low (7%), (Järvis 1993). Roe deer is the predominating item in lynx diets in Estonia and Latvia (I) and may act as a transmission link of *Taenia hydatigena* for lynx. *T. hydatigena* was only identified from one animal, indicating that our roe deer is probably not very often infected with this particular cestode. Similar results were obtained in Belorussia, of 16 analysed roe deer, only one was infected with *Taenia hydatigena* (Shimalov & Shimalov 2003). It is also possible, that seasonal variation of prey animals in the diet might lead to seasonal variation in the helminth fauna of the lynx, perhaps with fewer adult *T. hydatigena* occuring in the intestines of lynx in winter than in summer.

Mountain hare is probably the most important intermediate host of *T. pisiformis* and *T. laticollis* (Abuladse 1964, Zyll de Yong 1966, Smith *et al.* 1985 Jushkov 1995), accordingly, leading to a high prevalence of these helminth species in our study. *Taenia pisiformis* was also very common in Latvian lynx (Bagrade *et al.* 2002).

Toxocara cati is the most frequent ubiquitous nematode infecting domestic cats (Eckert 2000), and was both very prevalent and had the highest intensity of infection in the present study. This is consistent with other studies where *Toxocara cati* had the highest intensity of infection among lynx in Lithuania (Kazlauskas & Prusaite 1976, Kazlauskas & Matusevicius 1981) and *Toxocara sp.* most prevalent in lynx in Switzerland (Schmidt-Posthaus *et al.* 2002).

Helminths not only reflect food habits of predators but, to some extent, also reflect the extent of niche overlap among predators. In Belorussia *Taenia pisiformis, Taenia hydatigena* and *Spirometra larvae* were the most common helminths in lynx and also in wolf (*Canis lupus*), fox (*Vulpes vulpes*) and raccoon dog (*Nyctereutes procyonoides*) (Karasev 1975, Shimalov & Shimalov 2002, 2002a, 2002b). Similarly, Estonian wolf and lynx share 3 cestodes (*Diphyllobothrium latum, Taenia pisiformis, Taenia hydatigena*) (III) and 7 common food items (I).

European fox serves as a source of *Trichinella* infection (Kutzer 1994, Pozio *et al.* 2001). Since lynx kill and consume fox in relatively large quantities in Estonia (frequency of occurrence 7%), (I), fox may be a main reservoir of *Trichinella* for lynx in Estonia. The prevalence of *Trichinella* in lynx in the present study (29,6%) is comparable to the results of earlier studies of *Trichinella* sp., in Estonian wildlife that reported both *T. nativa* and *T. britovi* in lynx with a prevalence of 38.5% (Järvis & Miller 1999). Studies from other European countries have also reported a high prevalence of *Trichinella* in lynx, with almost 50% in Slovenia and Ex-Jugoslavia (Brglez 1989), 40% in Finland (Oksanen *et.al.* 1998) and 50% in Switzerland (Ryser-Degiorgis 2001). *Trichinella* also infects lynx (*L. l. canadensis*) in North America (Zarnke *et al.* 1995).

The correlation between host age and the number of parasites was observed only in male lynx. Cestodes *Taenia pisiformis* and *T. laticollis* were more numerous in adult males. Similarly low numbers of both cestodes were found in young and adult females as in young males. In various parts of Europe, male lynx have significantly larger bodies than females, weighing 2.8–7.2 kg more (Pulliainen 1981). The larger males presumably consume more roe deer and mountain hare (harbouring *Taenia pisiformis* and *Taenia laticollis*) and thus have higher probability for acquiring these tapeworms. Smith et *al.* (1985) reported a positive correlation between numbers of helminths and condition indices of lynx. It is possible that males, who probably invest less into parental care, are generally in better condition, eat more and acquire more parasites. Similarly, male sex and increasing age were also found to be associated with trichinellosis infection of lynx in Finland (Oksanen *et al.* 1998).

No correlation between prevalence of *Toxocara cati* and age/sex was found, although, predominant lactogenic infection (Eckert 2000) could account for a higher prevalence of *T. cati* in younger lynx.

The number of gastrointestinal parasite species per individual was significantly higher in adult than in young Iberian lynx and other wild carnivores from Central Spain (Rodriguez & Carbonell, 1998), but in our study it holds true only in males. This is consistent with our observation of more diverse food of old males (I).

All attempts to find *Capillaria* spp. from intestinal tract, lungs, liver or bladder failed. Shedding of adult worms or unidentified *Capillaria* eggs by feces has often been observed in domestic cats (Raschka *et. al*. 1994). Egg shedding may be partially caused when a cat eats intestinal passers-by. Mice, rats and lagomorphs are often infected with *Capillaria hepatica*, and when eaten by a cat, parasite eggs get free from the liver during digestion and are shed by feces to the environment where they develop into infective stage (Anderson 1992, Cross 1998). Because hare is a frequent prey of Estonian lynx (I), *Capillaria hepatica* infection from consumed hare could cause egg shedding in lynx feces after digestion.

As a rule, carnivorous hosts do not suffer markedly from infection with either adult cestodes or nematodes. In addition, reports of clinical disease from

helminth infections are rare in lynx populations (Ryser-Degiorgis 2001). Only *Toxocara cati* may threaten kittens under certain additional unfavourable conditions. In contrast to other wild carnivores like fox and badger (*Meles meles*), lynx is seemingly not an important distributor of infections. As a predator, lynxes acquire infections through their prey. However, due to their relatively solitary lifestyle, they have limited opportunities for transmission of helminths.

 According to our survey the helminth burden of lynx in Estonia is not high enough to affect the health of the population. Nevertheless, older and bigger animals did have more worms.

All helminth species of wolves characterised in Estonia during this study have also been found in adjacent countries: Russia, Lithuania and Poland (Jushkov 1995, Kozlov 1977, Kazlauskas & Prusaite 1976, Soltys 1964). Moreover, the number and species composition of helminths of the wolf in Estonia and neighbouring areas is comparable as well. Similarity in helminth fauna is obviously determined by a similar diet.

The PCR-RFLP analysis of two specimens of *E. granulosus* (obtained from a single wolf) revealed different genotypes at the Eg9 locus in the specimens, implying that the wolf most likely acquired infection of *E. granulosus* from more than one source.

The strain of *E. granulosus* from the wolf in Estonia carries an identical mtDNA ND1 sequence with the strain G10, identified from cervids (moose and reindeer) in Finland (Lavikainen *et al.* 2003). In addition to G10, another cervid strain, G8 from the USA (Minnesota and Alaska), has been isolated from moose, but also from humans (Bowles & McManus 1993, McManus *et al.* 2002). Interestingly, *E. granulosus* genotype G8 from the USA (Minnesota) was the closest taxon to the genotype G10 from Finland and Estonia and these haplotypes, together with genotypes G6 and G7, form a cluster on a phylogenetic tree (Lavikainen *et al*. 2003). Specificity of G8 and G10 to cervids is a likely explanation to their proximity on the phylogenetic tree. Moreover, taking into account the close phylogenetic position of mtDNA genotypes G6, G7, G8, and G10 and the fact that G6, G7 and G8 have been found also in humans, it is likely that the G10 strain has a potential to become a threat to the human population.

Two subspecies of *E. granulosus*, described by Sweatman & Williams (1963), occur in North America: *E. granulosus borealis* (North American origin) and *E. granulosus canadensis* (Scandinavian origin). Cervid genotype G10 is supposed to be related to *E. g. canadensis* (Lavikainen *et al.* 2003). Surprisingly, morphological features (the number of segments and the length of the gravid proglottid) of *E. granulosus* G10 in Estonia were more similar to the *E. g. borealis*. However, the incomplete set of morphological characters and limited number of *E. granulosus* did not allow closer examination of subspecies status nor analysation of the correlation between morphology and the mtDNA genotype (the particular wolf infected with *E. granulosus* was in a rather bad

condition – all specimens of *E. granulosus* were without hooks). As there is large variation in morphological characters within the *E. granulosus* (Thompson & McManus, 2001), subspecies identification and correlation of fenotypes with genotypes requires an analysis of large numbers of specimens sampled all over the world.

Populations of *E. granulosus*-infected wildlife can act as an important reservoir in promoting the transmission of the parasite to both domestic animals and humans. Considering the fact that cysts of *E. granulosus* have been found from moose in Estonia (I. Jõgisalu & T. Järvis, unpublished results), it is conceivable that the wolf obtained the *E. granulosus* by consuming moose. Therefore, further studies are required to evaluate different cycles responsible for spreading echinococcosis in Estonia.

The general domestic life cycle of *E. granulosus* involves the dog as the definitive host and livestock animals as intermediate hosts (Eckert *et al*. 2001). Among domestic animals in Estonia, *E. granulosus* larvae were found only from pigs (Lešins, 1955). No infected dogs have been reported (Talvik 1998, Jõgisalu 2003).

The value of the calculated binary similarity coefficient of Sorensen (0.42) for wolf and lynx presumably reflects the presence of common prey species. Indeed, high local wolf and lynx food niche overlap of their winter diets (I) most certainly provides a good ground for wolf and lynx to have similar helminth faunas. On the other hand, one would expect to have higher overlap in helminths, as the food niche overlap was remarkable. Relatively modest overlap in helminth faunas can be explained by different susceptibility of hosts to certain helminth species. Moreover, different summer diets of these predators may also impact their helminth faunas.

It can be concluded, that overall helminth burden of wolf is probably not high enough to affect the health of the population of this predator.

The study of **genetic variability** and structure provides strong evidence for population structuring among northern European lynx populations. Two important patterns were seen: distinct differentiation between Scandinavian and adjacent eastern populations, and structuring consistent with isolation by distance inducing a differentiation along a north-south gradient along Scandinavia. At least two scenarios can be postulated to explain the strong differentiation between Scandinavia and Finland/Baltics. First, similar to data documented for several other mammals (brown bear *Ursus arctos,* Taberlet *et al*. 1995, European shrew *Sorex araneus*, Fredga & Nawrin 1977, field vole *Microtus agrestis*, Jaarola & Tegelström 1995, bank vole *Clethrionomys glareolus*, Tegelström 1987), the postglacial recolonization of Scandinavia by lynxes may have been through two different routes: one from the south through a land bridge from Denmark and another one from the east through Finland. The unique mtDNA haplotypes seen in Finland and the Baltic States could, in this perspective, be taken as indicators of a separate origin. However, the close similarity between haplotypes, and the fact that the haplotype fixed in

Scandinavia was also very common in Finland and the Baltics argues against this idea. Moreover, in the case of contrasting evolutionary histories, a significant number of microsatellite alleles being unique to the different groups of animals should have been reciprocally expected. A large number of alleles found in Finland and the Baltic States were indeed not observed in Scandinavia, but only a few alleles observed in Scandinavia were lacking in the more eastern populations. Since the degree of variability differed between the populations, and since a differentiation with distance exists even inside Scandinavia, it is not apparent that a contrasting evolutionary history can be invoked. Firmly addressing phylogeographic patterns of lynxes in Europe will therefore require analysis of historical samples and/or samples from other geographical regions.

An alternative explanation to the differentiation between Scandinavia and Finland/Baltics is that, although populations are geographically very close, gene flow through the north of the Scandinavian peninsula is severely restricted. The vegetation in the far north of Finland and Scandinavia is dominated by tundra, whereas forest, the preferred habitat of the lynx, is scarce. The occurrence of carnivores in this area may also be in conflict with reindeer husbandry. Indeed, lynxes have been rare in the very north of Scandinavia and Finland until only recently (O. J. Sikku pers. comm.). It is also possible, that strong genetic drift during the documented bottlenecks in Scandinavia in recent centuries may have contributed to genetic differentiation.

The overall level of genetic variability observed for northern European lynx populations was low (mtDNA) to moderate (microsatellites). A single mtDNA control region haplotype was fixed in the Scandinavian population and this population also displayed a lower mean heterozygosity (0.51) at microsatellite loci than the Finnish and Baltic populations (0.60–0.62). In the latter, a limited number of mtDNA haplotypes were seen, but the nucleotide diversity was low (0.00066 and 0.00215, respectively). It might be argued that the moderate variability indicated from the set of 11 feline microsatellite markers we applied is at least partly a consequence of using heterologous markers (cf. Ellegren *et al.* 1995). However, eight out of these 11 markers have been used in cross-species amplification of leopard Panthera pardus (Spong et al. 2000) and lion Panthera leo (G. Spong pers. comm.) populations, and have revealed high genetic variability in these species (He = 0.80 and 0.76, respectively). We therefore speculate that northern European lynx populations have lower levels of genetic variability than what is seen for other felids.

It may be argued that the low variability seen in northern European lynx populations, in particular in Scandinavia, is a consequence of the heavy hunting pressure during the last two centuries, translating into recorded population decreases across all of Europe (Breitrenmoser & Breitenmoser-Würsten 1990). Genetic drift, especially during bottlenecks, may thus have led to reduced levels of genetic variability. Although hunting is likely to have been intense also in Finland and the Baltic States, the contact with the larger Russian lynx population may have prevented loss of genetic variability to the same extent as

hypothesised for Scandinavia. This scenario lends support to the bottleneck test. Alternatively, moderate variability may have been characteristic to all lynxes in Europe, resulting from their survival in a single glacial refugium. The very low sequence divergence between mtDNA haplotypes observed in this study supports this idea. A similar interpretation, expansion from a single glacial refugium, has been used to explain the low mtDNA sequence diversity seen in otters (Lutra lutra) across Europe (Cassens *et al.* 2000). In theory, the low variability of Eurasian lynxes could be a species-specific trait due to either a recent origin or a slow mutation rate. However, the fossil record indicates that the lynx was present in Eurasia over one million years ago (Werdelin 1981), and substitution rates do not seem lower in lynxes than in other felids (Johnson & O'Brien 1997, Pecon & O'Brien 1998). Four large carnivores inhabit the Scandinavian peninsula: the wolf, the wolverine *Gulo gulo*, the brown bear and the lynx. With this study, basic population genetic parameters of Scandinavian populations of all four species have now been addressed using molecular genetic approaches (Ellegren *et al.* 1996, Ellegren 1999, Waits *et al.* 2000, Walker *et al.* 2001). Interestingly, three of these species (wolf, wolverine and lynx) show very similar patterns, i.e. little or no mtDNA variability and low to moderate microsatellite variability. A common denominator for the three species is that due to persecution and overhunting, all have gone through severe bottlenecks in recent times. This might suggest that their reduced levels of genetic variability can commonly be explained by these bottlenecks.

SUMMARY

The present thesis focuses on aspects of the biology of wolf and lynx in the Baltic region. Using different methods, I explored diets and helminth fauna of lynx and wolf, group size changes and age composition of wolf samples in Estonia, and genetic differentiation and variation of lynx populations in the Baltic region and in Scandinavia. All of these studies are the first conducted in Estonia.

Ungulates dominated in the preys of lynx and wolf, roe deer and wild boar being the main ungulate prey species. Predator: prey relationships and likely effects of wolf hunting were considered as main predictors of diet composition in the study area. Food niche overlaps between species were very high, indicating the use of roe deer as a main resource in both countries.

Probably due to hunting, wolf groups lost on average two members during winter; singles and pairs dominated in February.

Helminth fauna of wolf and lynx in study area was similar to that in neighbouring regions. A total of 7 helminth species were recorded for lynx and 13 species for wolf. *T. pisiformis* and *Toxocara cati* were the most prevalent helminths of lynx and *Alaria alata* and *Uncinaria stenocephala* of wolf. In lynx, older males had more species per host than young males.

The strain of *E. granulosus* from wolf was identified as G10, which can be a potential threat to local human population. *E. granulosus* belongs to the list of zoonoses to be monitored in the member states of the European Union, according to Directive 2003 99/ EC.

The northern lynx populations differed by their genetic diversity and population structure. The overall level of mtDNA variability was very low with only one haplotype found in Scandinavia, also most common in Finland and the Baltic States. Two other variants were found in Finland and the Baltic States, and a fourth type was unique to the Baltic population. Microsatellite variability was moderate for the three defined populations. Several explanations (different postglacial history, gene flow restrictions, recent bottlenecks) are brought out.

SUMMARY IN ESTONIAN

Käesolev töö keskendub hundi ja ilvese bioloogia mõningatele aspektidele Balti regioonis. Mitmesuguseid meetodeid rakendades selgitati nende toitumist ja anti ülevaade nende helmintofaunast. Vaadeldi ka hundigruppide suuruse ja koosseisu muutusi Eestis ja ilvese geneetilist diferentseerumist ja variatsiooni Balti regioonis ja Skandinaavias. Kõik need uurimused olid esimesteks taolisteks uuringuteks Eestis.

Mõlema suurkiskja toidus domineerisid sõralised saakliigid. Kiskja:saaklooma suhe ja võimalik küttimise mõju on ilmselt olulisemateks sõraliste saakliikide proportsioone hundi toidus määravateks teguriteks. Hundi ja ilvese toiduishide kattuvus oli väga suur, andes tunnistust metskitse kui peamise saakliigi olulisusest nendele suurkiskjatele. Ilmselt tänu küttimisele vähenes hundigrupi suurus talve jooksul keskmiselt kahe liikme võrra ja veebruaris domineerisid paarid või ka üksikud hundid.

Uuritud liikide helmintofauna oli sarnane ümbritsevates regioonides saadud tulemustele. Seitse helmindiliiki registreeriti ilvesel ja 13 helmindiliiki hundil.

T. pisiformis ja *Toxocara cati* domineerisid ilvesel ja *Alaria alata* ja *Uncinaria stenocephala* olid domineerivateks helmindiliikideks hundil. Hundil leitud *E. granulosus*'e tüvi identifitseeriti kui G10, mis on potentsiaalseks ohuks ka inimesele.

E. granulosus kuulub vastavalt EU Direktiivile 2003 /99/EC liikmesriikide poolt kohustuslikult seiratavate zoonooside hulka.

Põhjamaade ilvesepopulatsioonid eristusid uuringus variatsiooni ja populatsiooni struktuuri põhjal. Mitokondriaalse DNA üldine varieeruvus oli väga väike. Skandinaavias esines ainult üks haplotüüp, mis oli tavalisim ka Soomes ja Baltimaades. Lisaks leiti kaks haplotüüpi veel Soomes ja Baltimaades ning üks ainult Baltimaades esinev haplotüüp. Ka mikrosatelliitide varieeruvus oli vähene kõigis uuritud populatsioonides. Diskuteeriti mitmeid hüpoteese (erinev postglatsiaalne ajalugu, geenisiirde piiratus, hiljutised pudelikaelad).

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mustrite võrdlus ja dünaamika Venemaa Euroopa osas aastatel 1841–
1861".

Scientific publications

1. Saarma, U., Ho, S., Pybus, O., Kaljuste, M., Tumanov, I., Kojola, I., Vorobiev, A., Markov, N., Saveljev, A., Valdmann, H., Lyapunova, E., Abramov, A., Männil, P., Korsten, M., Vulla, E., Pazetnov, S., Pazetnov, V., Putchkovskiy, S., Rõkov, A. (2006).Mitogenetic structure of brown bears (*Ursus arctos* L.) in north-eastern Europe and a new time-frame for the formation of European brown bear lineages. *Molecular Ecology*, in press.

2. Moks, E., Jõgisalu, I., Saarma, U., Talvik, H., Järvis, T., Valdmann, H. (2006). Helminthological survey of wolf *Canis lupus* in Estonia, with an emphasis on the tapeworm *Echinococcus granulosus*. *Journal of Wildlife Diseases,* 42, 359–365.

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6. Hellborg, L., Walker,C.W., Rueness, E.K., Stacy, J.E., Kojola, I., Valdmann, H., Vila, C., Zimmermann, B., Jacobsen, K. S. and Ellegren, H. 2002. Differentiation and levels of genetic variation in northern European lynx (*Lynx lynx*) populations revealed by microsatellites and mitochondrical DNA analysis. – *Conservation Genetics* 3(2):97–111.

7. Vilà, C. Walker, A.-K. Sundqvist, Ø. Flagstad, A. Casulli, I. Kojola , H. Valdmann, J**.** Halverson, H. Ellegren. 2003 Combined use of maternal, paternal and bi-parental genetic markers for the identification of wolf-dog hybrids. *Heredity* 90, 17–24.

8. Valdmann, H., Laanetu, N., Korsten, M. 2004.Group size changes and age/sex composition of harvested wolves (*Canis lupus*) in Estonia. *Baltic Forestry*, 10 (2), pp. 83–86.

9. Valdmann, H. 2003. Rõs v Estonii. In: Ye. E. Matjushkin and M.A. Vaisfeld (eds.) Rõs (The Lynx). *Regionalnõe osobennosti ekologii, ispolzovanie i ohranõ.* Moskva, *Nauka* 91–104. (in Russian and English).

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12. Linnell, J., Andersen, R., Andersone, Z., Balciauskas, L.,Blancos, J-C., Boitani, L., Brainerd, S., Breitenmoser, U., Kojola, I., Liberg, O., Loe, J., Okarma, H., Pedersen H-C., Promberger, C., Sand, H., Solberg, E-J., Valdmann,

H**.** and Wabakken, P. 2002.The fear of wolves: A review of wolf attacks on humans. *Nina Norsk Institutt for naturforskning oppdragsmelding,* pp. 1–64.

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Teaduspublikatsioonid

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