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Population dynamics of large mammals in Latvia with an emphasis on prey-predator interactions

Key words: populations, ungulates, carnivores, numbers, linear regression, Latvia

Introduction

Knowledge of both population size and dynamics are essential for conservation and the use of wild animals. Game managers tend to maintain populations at the maximum growth rate yet under the maximal environmental capacity to avoid conflicts with other land users. For rare species, preserving the minimum size for demographically and genetically viable populations is a crucial target. Data on the population dynamics of the main game species in Latvia are available over different time periods since the beginning of the 20th century. They include the numbers of estimated and harvested animals in the entire country, while statistics on territorial subdivisions are scarcer and hardly comparable due to historical political, economic and administrative reforms.

The quality and reliability of population data is very important, especially when we consider long time series gathered by different executers according to different methods and sometimes even by different authorities. Nevertheless, game statistics have been used to assess the status of medium-sized and large mammals in Latvia (OZOLIŅŠ & PILĀTS 1995; ANDERSONE-LILLEY & OZOLINS 2005; ANDERSONE-LILLEY et al. 2010) as well as to seek for the correlates

with different environmental or social factors (MASSEI et al. 2014). The trends in population dynamics are tested for mutual relations between prey/predator species (KAWATA et al. 2008). Changes in population and harvest numbers in a limited area enable calculations of growth rates and carrying capacity (KAWATA et al. 2013; KAWATA & OZOLIŅŠ 2013).

Last but not least, the long-term time series of population size after statistical treatment can be used for a regional-scale transboundary management of large mobile mammals (e.g. KAWATA 2008). The studies mentioned above highlight the importance of documenting and publishing all available records about changes in animal abundance both of harvested and rare species.

In this article, we repeatedly summarize the numbers of estimated and hunted primary game species in Latvia and analyse the changes over a period of more than 30 years spanning from 1980 until the present day. Trends between estimates and the corresponding hunting bags, as well as population dynamics amongst species, are compared. The results are interpreted taking into consideration the ecology and socio-economic background of game management. Prey-predator interactions are particularly highlighted.

Material and methods

Study area

The study was conducted across the whole territory of Latvia (64,589 km²). The country is situated along the eastern coast of the Baltic Sea with a coastal border of 498 km. It has a terrestrial boundary of 1,370 km, which interfaces with Lithuania, Estonia, Russia and Belarus. The climate is temperate, with an average annual temperature of +5.9 °C and an annual precipitation of 550–850 mm. Snow cover lasts for 75–115 days mostly from the beginning of December until the end of March. The vegetation period begins at the end of April and lasts until late September. Approximately 50 % of the country is covered by woodland, consisting mostly of mixed boreal forests with Scotch pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and birch (*Betula* spp.). In 2015 the population of Latvia was 1,986,100. Registered hunters are typically around 22,000 and therefore compose only 1.1 % of the population.

Data source

Game animal census and number estimates in Latvia has always been a commitment of the state authorities supervising forestry and hunting. Since many state officials are members of hunter associations, there is highly likely some impact from the opinions of ordinary amateur hunters. Data are recorded at four administrative levels, with initial numbers reported by forest rangers.

These reports are summarised by the foresters at forestry management units, sent to a game management expert at head forestry and finally gathered by the supervising ministry department at the country level. In our study, we used the numbers of estimated and harvested individuals of nine mammal species found across the whole country: elk *Alces alces*, red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, wild boar *Sus scrofa*, lynx *Lynx lynx*, wolf *Canis lupus*, red fox *Vulpes vulpes*, raccoon dog *Nyctereutes procyonoides* and martens *Martes* sp. There are two marten species that inhabit Latvia – pine marten *Martes martes* and stone marten *Martes foina* (TIMM et al. 1998). The numbers of the

last two species are pooled in our statistics into one figure due to poor ability of hunters and forest rangers to distinguish between both martens. We also included one game bird – capercaillie *Tetrao urogallus* – in our study in order to examine its long-term interaction with large game and mammalian predators for the reasons suggested by SANIGA (2002) and SINKÄ et al. (2010).

We took all available data on number estimates and hunting bags from 1980 to 2015, thus each set is composed of 36 figures. Data on the hunting bags of medium-sized carnivores and lynx from 1989 are missing, likely because these data were not properly recorded due to the political turbulence at that time. A lack of number estimates for medium-sized carnivores around the year 2000 could be explained by administrative reforms in the forestry sector. The data on capercaillie are the scarcest with number estimates from as little as 24 years, and data on hunting bags only covering 23 years within our considered reference period. In capercaillie hunting, only the cocks were taken according to persisting regulation.

For territorial units smaller than the whole country, complete data sets were not available. Therefore, we selected three years with the most available animal numbers: 1990, 1995 and 2005 when the country was divided into 31, 36 and 26 management units (head forestry level) accordingly.

Analysing harvest results, we separated two groups of game animals. Small game such as red fox, raccoon dog and martens are taken by all hunters who exercise the right to hunt. They just must possess a hunting certificate, the hunter's seasonal card, a firearms permit in the case of using firearms or authorization of the use of other hunting gear if traps are used. For major game species such as elk, red deer, roe deer, wild boar and capercaillie a separate permit (licence) must be obtained for taking each animal and the annual quota is determined in each hunting ground by the supervising authority. Wolf and lynx were harvested as unlimited game until 2003 though restricted use with an annual quota was introduced in 2004.

Framework of analysis

To look for mutual quantitative relations we used a simple linear regression (FOWLER et al. 1998). We tested by regression analysis each pair of our two considered species, e.g. elk versus wolf or capercaillie versus lynx. Other interspecific ecological relations besides predation were included also, when we defined the numbers as independent or dependent variables. For instance, we tested relations among elk, red deer and roe deer numbers in order to reveal possible interspecific competition. If any mutual impact by our preliminary assessment unlikely occurred between two species, we ended the analysis. To compare at the regional scale, the same analysis was run using estimated and harvested numbers of animals for the forest management units for the three different years – 1990, 1995 and 2005.

For graphical evaluation of our data we divided our time series into to three sub-divisions: 1980–1990 was the time when socio-economic factors including the game management system was run under soviet rule (hereinafter referred to as the ‘soviet period’). 1991–2003 were the

years following when Latvia regained political independence (hereinafter referred to as ‘independence recovery’) and changes to national legislation meant that private ownership and the right to hunt became available to other social groups.

In 2004, Latvia became an EU member state (hereinafter referred to as the ‘EU period’) and several conservation measures were introduced to wildlife management, particularly regarding large carnivores (OZOLIŅŠ et al. 2014).

Results

Changes in population size

There have been fairly gradual population changes for the four ungulate species in Latvia (Fig. 1–4), with their overall dynamics showing a generally growing trend over the whole 35 year period. In none of the graphs were any sharp fluctuations apparent, bearing in mind that empiric values were used without any mathematical treatment. A slight increase in the numbers of all species was observed during the

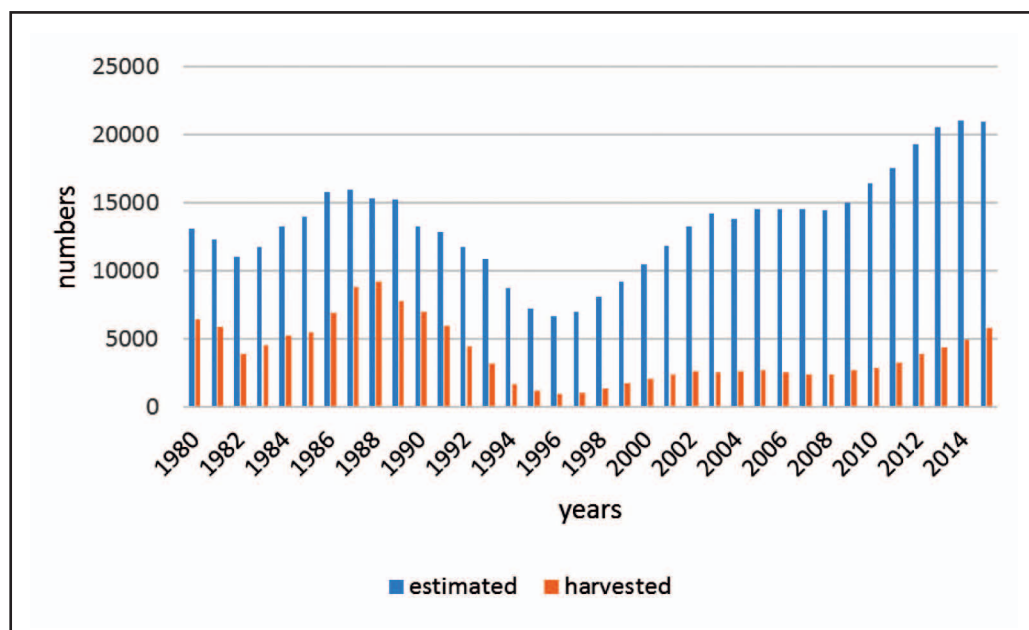


Fig. 1 Dynamics of elk *Alces alces* population

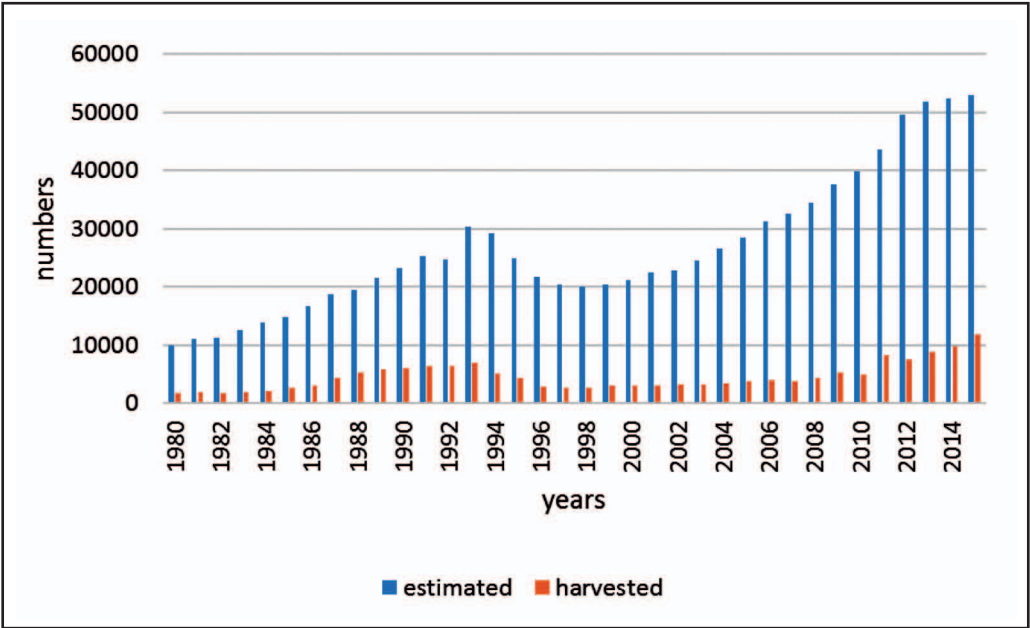


Fig. 2 Dynamics of red deer *Cervus elaphus* population

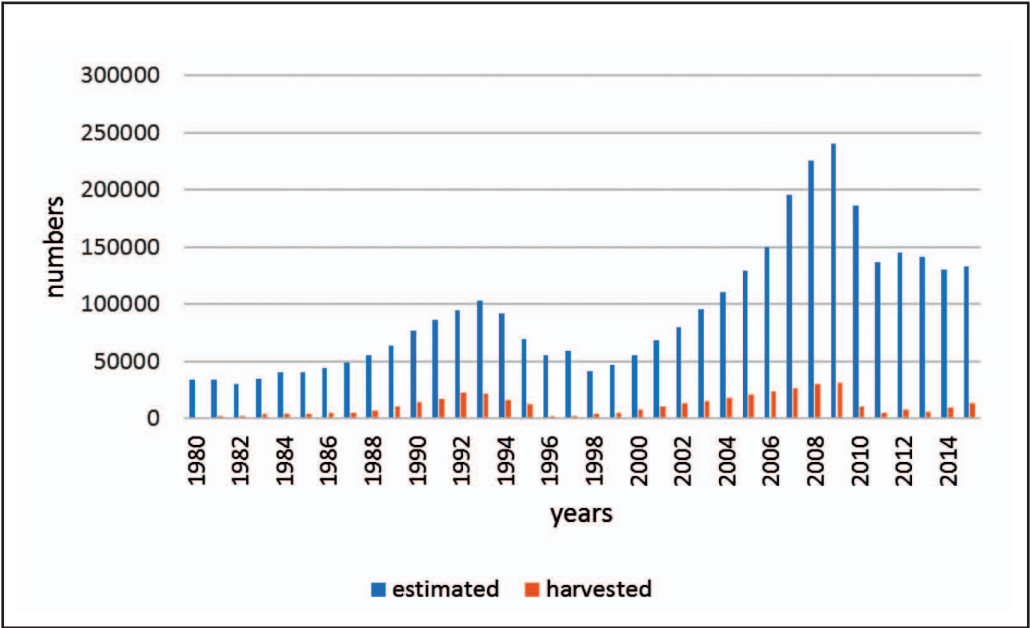


Fig. 3 Dynamics of roe deer *Capreolus capreolus* population

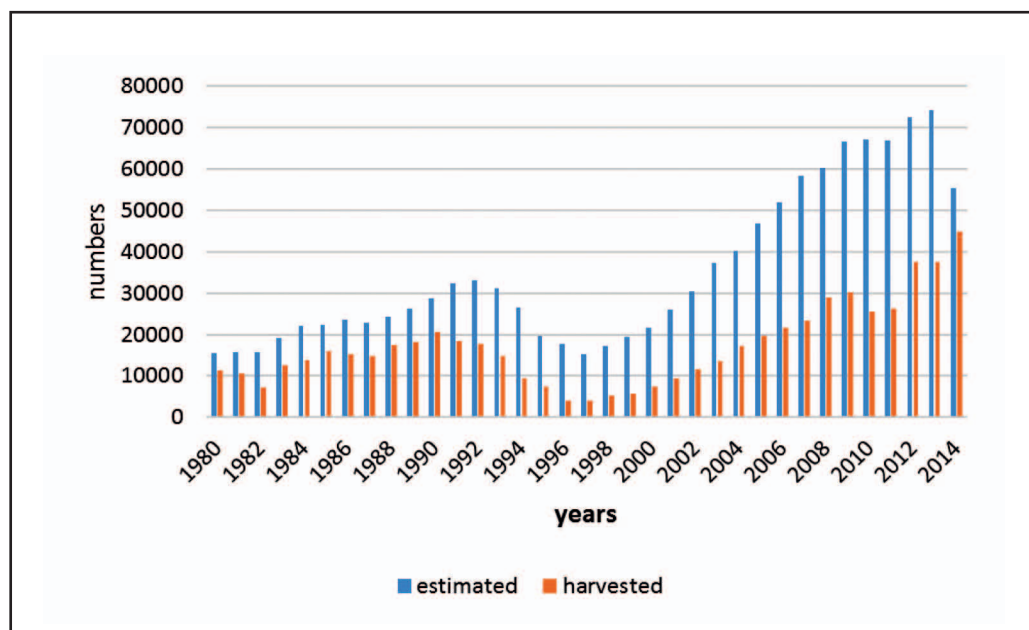


Fig. 4 Dynamics of wild boar *Sus scrofa* population

soviet period. During the independence recovery period, species declined quite dramatically, however numbers started to recover again remarkably from the beginning of the 21st century. Recently, roe deer and wild boar populations are estimated to be below the maximal numbers they reached by the end of the first decade after the turn of the century. Elk and red deer continue to expand.

There was no pronounced growth for carnivore populations during soviet period (Fig. 5–7) and lynx and wolf numbers even declined slightly (Fig. 8 and 9). Carnivore harvest increased for the medium-sized species (Fig. 5–7). During the independence recovery period, the numbers of all carnivore species increased, with a particularly strong increase in the estimated numbers of wolf (Fig. 8). As there was no increase in harvest intensity during this time of population growth, carnivores were not harvested with a corresponding intensity hence their populations continued to increase.

Capercaillie population changes developed differently. It was recorded as comparatively small but stable during the soviet period. Some growth was recognized during the independ-

ence recovery period, however this was followed by a rapid decline during the EU period (Fig. 10).

Dynamics of harvest rate

We found a positive significant interrelation (at $P=0.05$) between numbers of estimated and harvested individuals for elk ($R=0.467$), red deer ($R=0.832$), roe deer ($R=0.754$), wild boar ($R=0.871$) and red fox ($R=0.869$). Elk had the least tight relationship due to an obvious differentiation between the periods before and after the population minimum during the middle 1990s (Fig. 11).

Harvest rates of wild boar developed in accordance with actual abundance (Fig. 12). The same pattern was observed for red fox harvest rates (Fig. 13). Martens were only harvested intensively during the soviet period and the general trend in harvest rate over the whole reference period appears to be negative (Fig. 14). Positive though insignificant correlation was observed between estimated and harvested numbers for raccoon dog, wolf and lynx ($R=0.402$; 0.349 and 0.449 respectively).

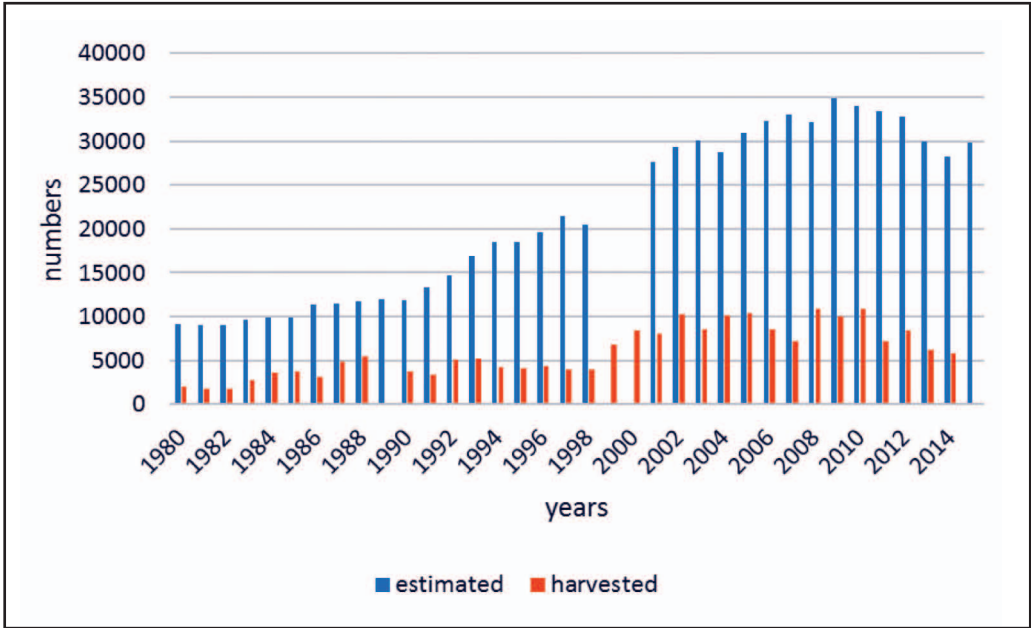


Fig. 5 Dynamics of red fox *Vulpes vulpes* population

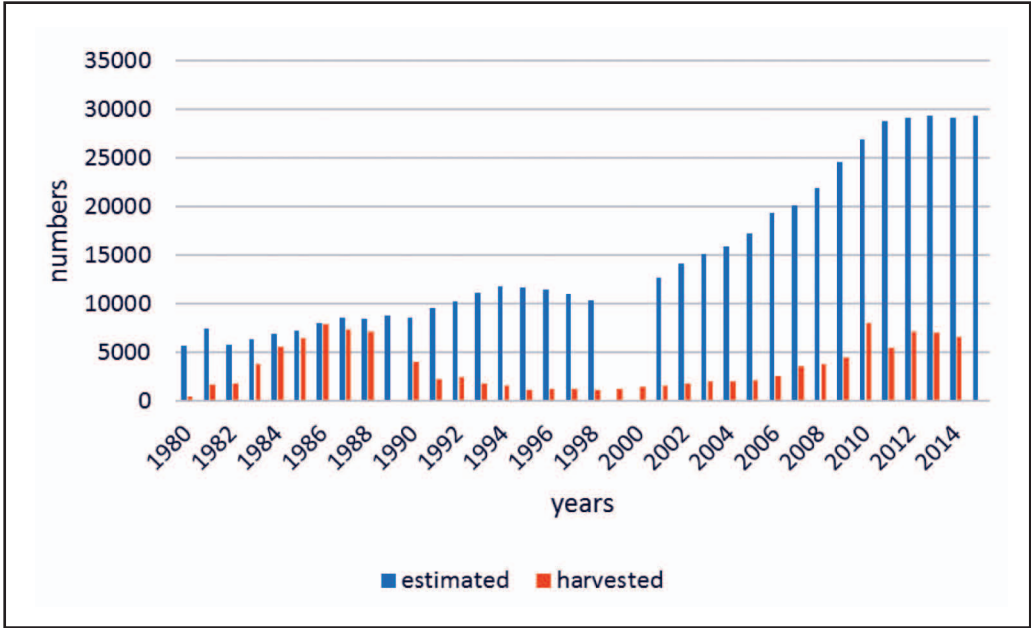


Fig. 6 Dynamics of raccoon dog *Nyctereutes procyonoides* population

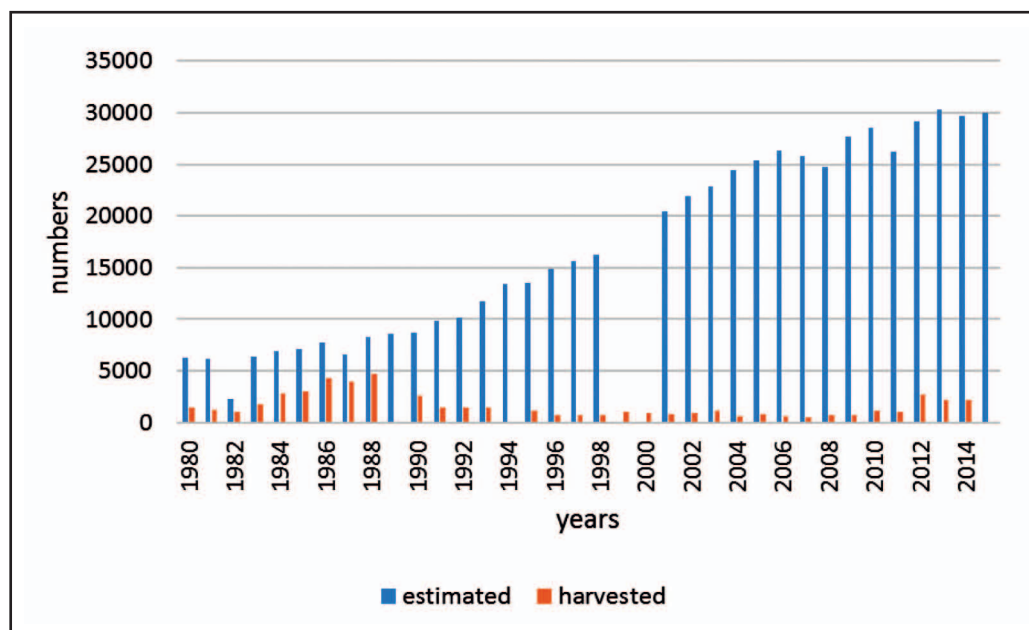


Fig. 7 Dynamics of pooled *Martes* sp. populations

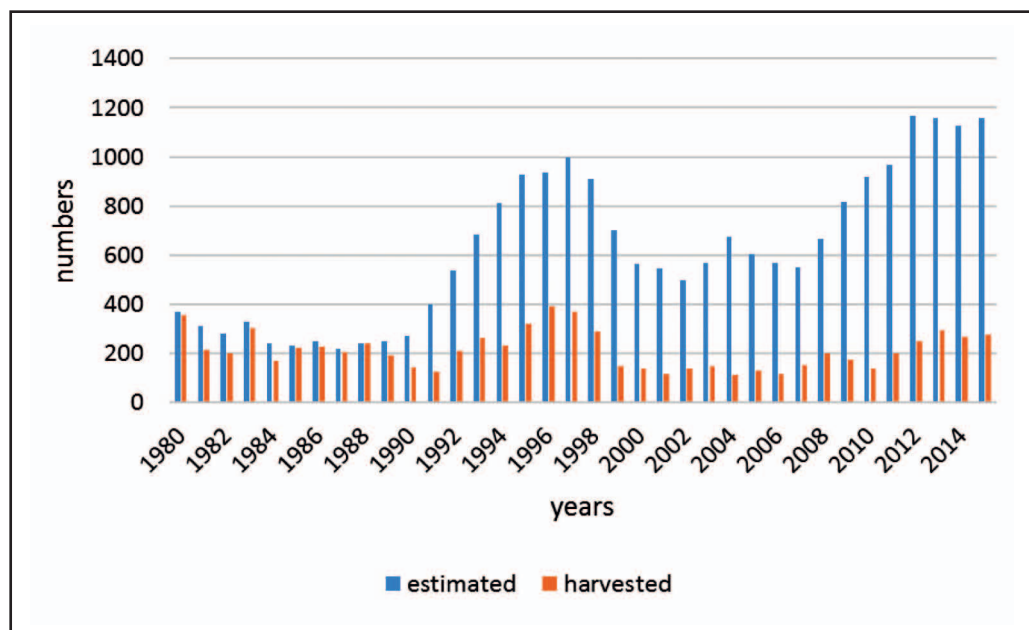


Fig. 8 Dynamics of wolf *Canis lupus* population

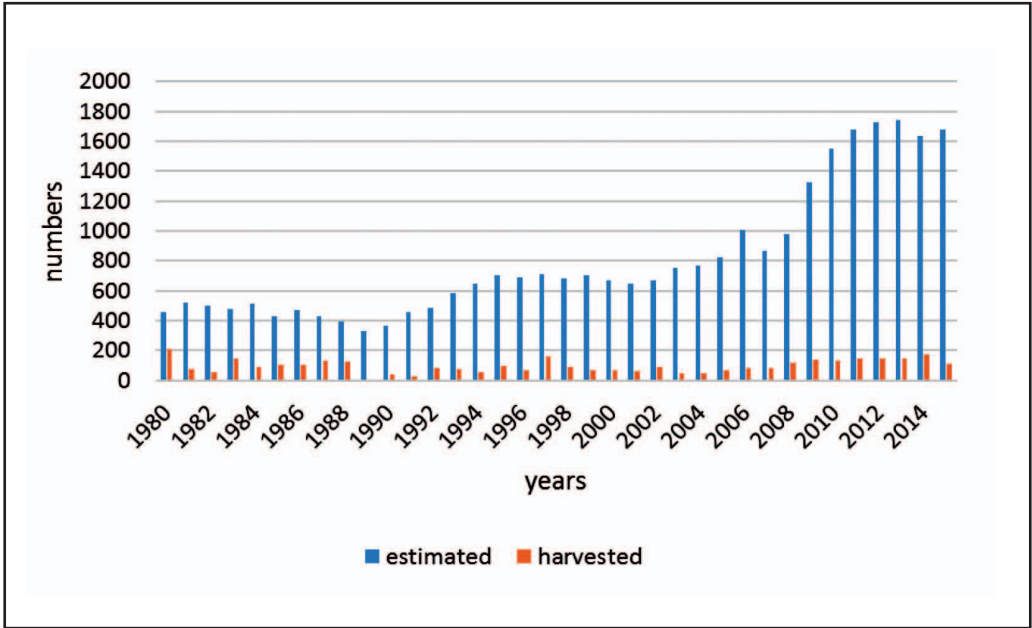


Fig. 9 Dynamics of lynx *Lynx lynx* population

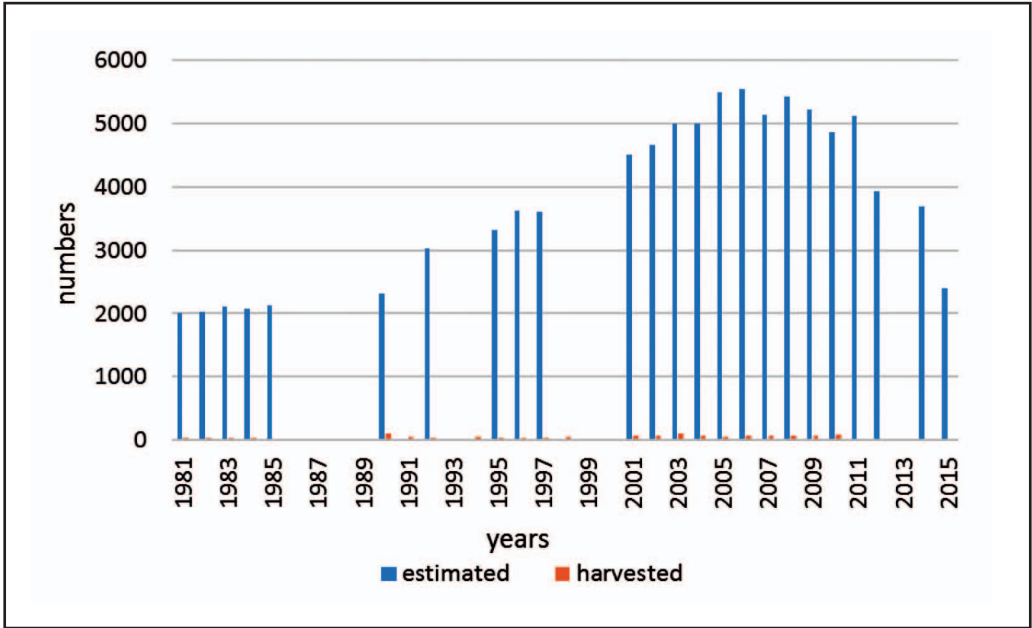


Fig. 10 Dynamics of capercaillie *Tetrao urogallus* population

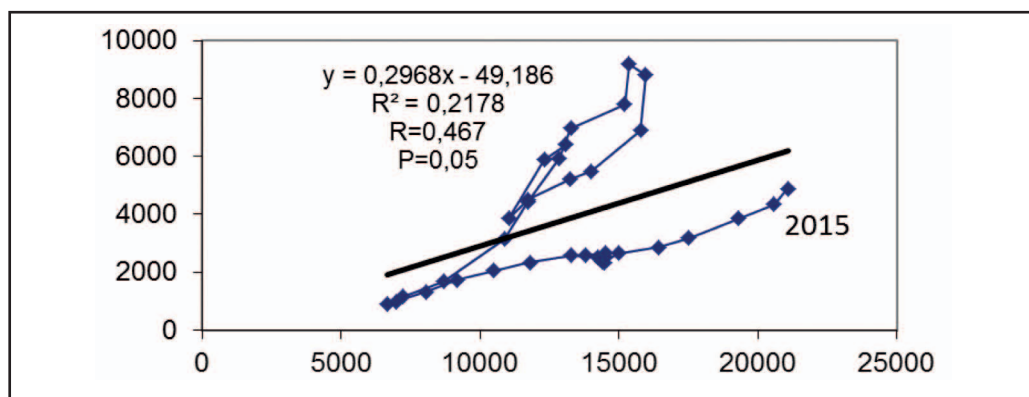


Fig. 11 Relationship between numbers of estimated (X) and hunted (Y) animals for the elk *Alces alces* population. Label '2015' in the plot area indicates the variables in the last year of the reference period.

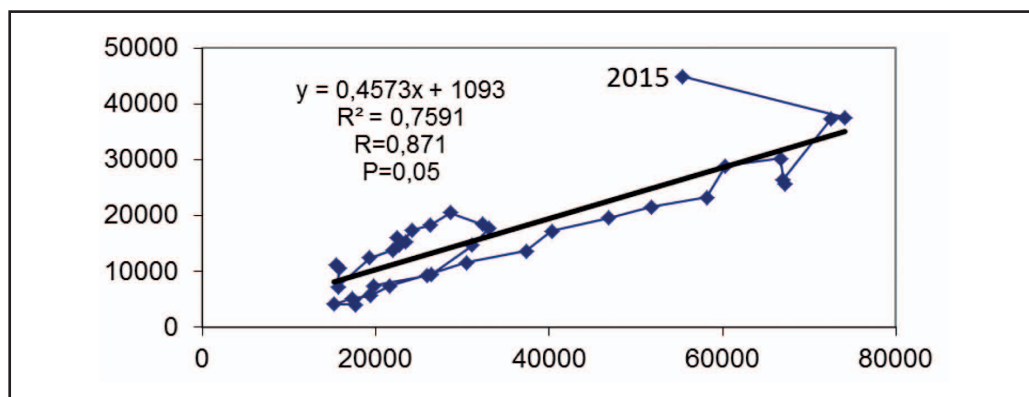


Fig. 12 Relationship between numbers of estimated (X) and hunted (Y) animals for the wild boar *Sus scrofa* population. Label '2015' in the plot area indicates the variables in the last year of the reference period.

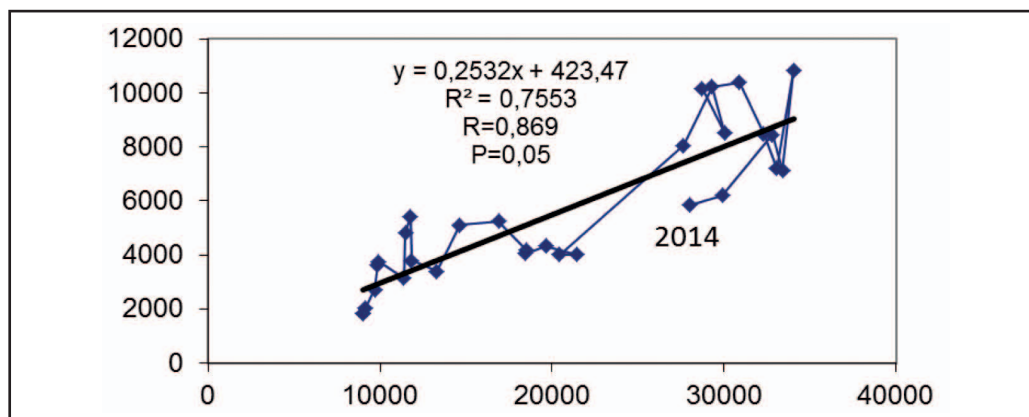


Fig. 13 Relationship between numbers of estimated (X) and hunted (Y) animals in the red fox *Vulpes vulpes* population. Label '2014' in plot area indicates the variables in the last year of the reference period.

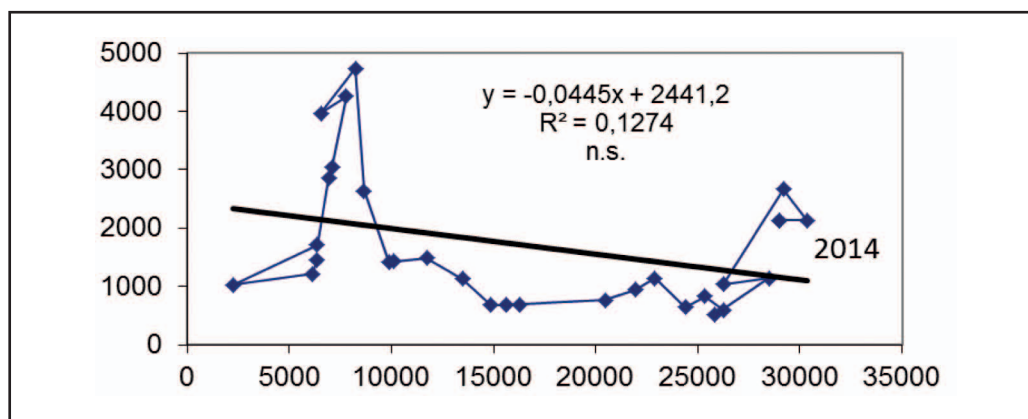


Fig. 14 Relationship between numbers of estimated (X) and hunted (Y) animals in pooled pine and stone marten *Martes sp.* population. Label '2014' in plot area indicates the variables in the last year of the reference period.

Dynamics of interspecific relations

We tested the interactions between estimated numbers in 27 pairs of species out of 45 theoretically possible combinations (Table 1). Eighteen pairs of species were disregarded for the analysis as they were deemed less relevant to our study aim. As little as two pairs showed insignificant mutual interactions but 25 pairs had positive and statistically significant correlation at $P=0.05$.

One of the tightest relationships was confirmed between lynx and raccoon dog numbers. As seen from the distribution of the first 10 dots at the beginning of the trend line in Figure 15, there is little or no correlation between both carnivores during soviet period. The general trend over the whole period, however, is explicitly positive.

The capercaillie population shows a trend confirming its long-term positive relation with theoretical predators – martens and red fox (Fig. 16). Capercaillie also positively correlates with the estimated numbers of lynx (Fig. 17), however, a negative trait begins during the EU period. Lynx is a species whose numbers are significantly related with the maximum of other game species in terms of total population dynamics during the whole reference period (Table 1), and also at the scale of territorial management units in all three of the examined years (Tables 2–4). Meanwhile, we found comparatively few significant mutual interactions

between species at the territorial scale. In 1990 there were five but in 1995 and 2005 there were only two out of 21 theoretically expected possibilities. Among them, lynx was involved in seven correlations out of nine.

Discussion

A period of 35 years seems to be a short time in the history of mutual relationships between large mammals. Nevertheless, our results confirm multiple changes in the rates of growth or decline in numbers. Such a large range between the lowest and highest numbers within this relatively short time frame can only be related to drastic corresponding human impacts. Attempts to explain the sharp decrease of large mammal populations due to the political and economic upheavals within a territory of Russia has been done in a study by BRAGINA et al. (2015). Historically, Latvia and bordering Russia have had periods of both similar and separated legislation and management systems (KALNIŅŠ 1943; LANGE 1970; SKRIBA 2011). Since regaining independence in 1991, Latvia can be regarded as managing its game resource differently, especially concerning requirements set by the directives and regulations of the European Community that became relevant in 2004. However, we cannot exclude the supplementation of large carnivore or elk populations in Latvia by animal

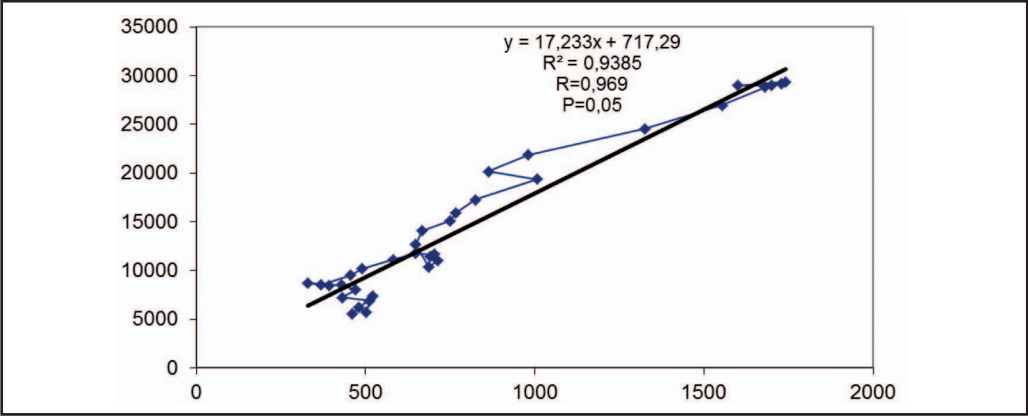


Fig. 15 Linear relationship between lynx (X) and raccoon dog (Y) numbers over 35 years

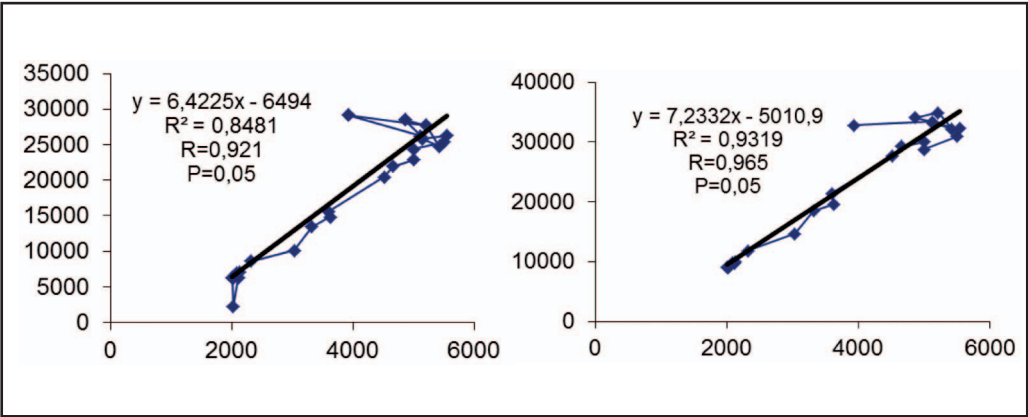


Fig. 16 Linear relationship between capercaillie(X)/marten (Y) numbers – left, and capercaillie (X)/red fox (Y) numbers – right over 35 years.

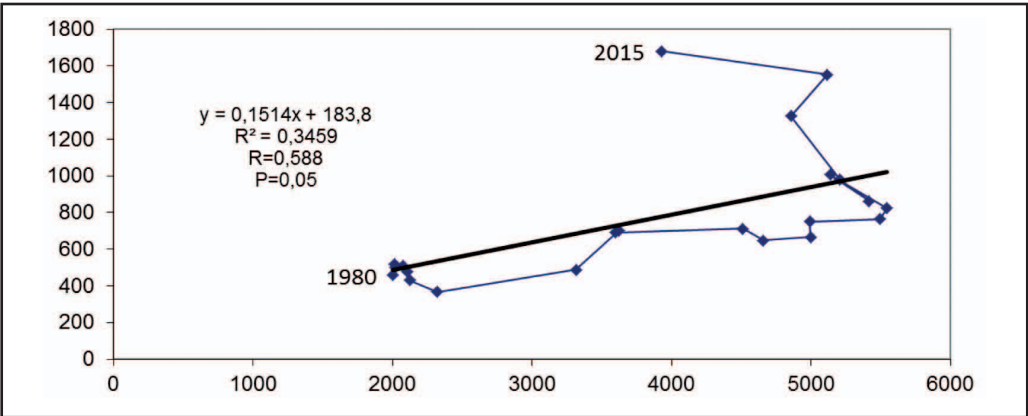


Fig. 17 Linear relationship between lynx (Y) and capercaillie (X) numbers over 35 years. Labels '1980' and '2015' in plot area point at the variables in the first and last years of the reference period.

Table 1 Simple linear regression between the estimated numbers of game populations for the entire country (1980 – 2015): R values are given for significant relationships; n.s. indicates an insignificant relationship; n.r. indicates that the relationship was not tested because the preliminary assessment was deemed as non-relevant

Species	Red deer	Roe deer	Wild boar	Wolf	Lynx	Red fox	Raccoon dog	Marten	Capercaillie
Elk	0.662	0.477	0.714	n.s.	0.635	n.r.	n.r.	n.r.	n.r.
Red deer	-	0.757	n.r.	0.789	0.916	n.r.	n.r.	n.r.	0.740
Roe deer	-	-	0.900	0.493	0.691	n.r.	n.r.	n.r.	n.r.
Wild boar	-	-	-	0.555	0.854	n.r.	n.r.	n.r.	n.s.
Wolf	-	-	-	-	0.820	0.688	0.777	0.755	0.550
Lynx	-	-	-	-	-	0.782	0.969	0.861	0.588
Red fox	-	-	-	-	-	-	n.r.	n.r.	0.965
Raccoon dog	-	-	-	-	-	-	-	n.r.	0.792
Martens	-	-	-	-	-	-	-	-	0.921

Table 2 Simple linear regression (R values) between numbers of game populations in 31 forestry management units as estimated for the year 1990

Species	Red deer	Roe deer	Wild boar	Wolf	Lynx	Capercaillie 1984
Elk	n.s.	n.s.	n.s.	n.s.	0.495	n.s.
Red deer	-	n.s.	n.s.	0.633	n.s.	n.s.
Roe deer	-	-	n.s.	n.s.	n.s.	n.s.
Wild boar	-	-	-	0.719	0.626	n.s.
Wolf	-	-	-	-	0.796	n.s.
Lynx	-	-	-	-	-	n.s.

Table 3 Simple linear regression (R values) between numbers of game populations in 36 forestry management units as estimated for the year 1995

Species	Red deer	Roe deer	Wild boar	Wolf	Lynx	Capercaillie
Elk	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Red deer	-	n.s.	n.s.	n.s.	n.s.	n.s.
Roe deer	-	-	n.s.	n.s.	n.s.	n.s.
Wild boar	-	-	-	n.s.	0.557	n.s.
Wolf	-	-	-	-	0.536	n.s.
Lynx	-	-	-	-	-	n.s.

Table 4 Simple linear regression (*R* values) between numbers of game species in 26 forestry management units as estimated for the year 2005

Species	Red deer	Roe deer	Wild boar	Wolf	Lynx	Capercaillie
Elk	n.s.	n.s.	n.s.	n.s.	0.633	n.s.
Red deer	-	n.s.	n.s.	n.s.	n.s.	n.s.
Roe deer	-	-	n.s.	n.s.	n.s.	n.s.
Wild boar	-	-	-	n.s.	n.s.	n.s.
Wolf	-	-	-	-	n.s.	n.s.
Lynx	-	-	-	-	-	0.725

immigration from the less intensively managed areas behind the border with Russia. Climate and meteorological factors may also shape population dynamics remarkably. Red deer cannot be considered as an autochthonous species in Latvia. It reached its population maximum five to six thousand years ago (the boreal - Atlantic period), however the native Latvian population of red deer went extinct by the 10th century. Re-introductions began in the 17th century. Initially the animals brought from Germany and Poland were kept in fenced areas. Since the very beginning of 19th century some of these individuals escaped and started to reproduce in the wild (KALNIŅŠ 1943; SKRIBA 2011). Later animals were intentionally released. They established several local micro-populations which were not connected with each other. Restocking was done in the 1980s, hence the recorded increase in numbers was comparatively slow and related to the rate of spatial expansion (SKRIBA 2011). Roe deer today is a common and numerous species and an important prey for large carnivores (ŽUNNA et al. 2009; 2011). Roe deer inhabits all woodlands as well as open patches of landscape (BURBAITE & CSANYI 2009). However, in the past it went extinct by the 17th–18th century. Extinction was explained as a natural process caused by climate cooling simultaneously with an increase in wolf density. Natural re-population started only in the 19th century and came gradually from the South (TAURINŠ 1982). German naturalist LANGE (1970) was of the opinion that population recovery had been considerably supported also by intentional release and occasional escape of introduced individuals. In the 20th century, the population of roe deer has

also suffered from harsh winters (PRIEDĪTIS & OZOLIŅŠ 2005). During the first decade of 21st century, the population showed a fast increase, however a decline occurred around 2010 and was due to a very snowy winter in 2009/2010. Correlating population dynamics between both ecologically closely related and likely unrelated species allows for a number of potential hypotheses. Prey-predator relations is one of the first to be considered, however results show that higher numbers of carnivores does not necessarily mean less ungulates and vice versa. Given that the theoretical interaction between prey and predator is typically not synchronic, it is unlikely that significant correlations can be found between numbers at the spatial scale as this only considers data from an individual year and the delay within predator – prey cycles may become apparent, i.e. by comparing number estimates in the forestry management units. We should also not forget about the significant role that hunter opinion could play if they recognise a decline in valuable game. Typically, the initial blame is placed on carnivores, thus overestimating their numbers unless a proper census is applied.

There is a particular discrepancy in opinions between bird conservationists and hunters about mitigation of predator impact on capercaillie. Capercaillie is a typical forest dweller and its reproduction success depends on a specific habitat – pine forest with open underbrush for good visibility and the presence of bilberry bush in the vicinity for foraging juveniles. Woodlands around large raised bogs are particularly suitable. Capercaillie is still a game species in Latvia however the open season for hunting male birds

exclusively has shifted from spring (10th April – 10th May) to autumn (1st Sept. – 31st Oct.). Hunters in Latvia are convinced that this change will not improve the species status because formerly only a restricted number of cocks were killed in the most abundant lek sites, while the hunters were involved in conservation of capercaillie habitats by reporting on the numbers and activity of mating birds, and the control of their predators. Our study testifies rather a long term coexistence of capercaillie and its main mammalian predators. Insignificant correlations in population dynamics between capercaillie and ungulates could possibly be explained by the supporting of large game through recent management practices.

The relationships revealed by our analysis between the sizes of two populations may not be as straightforward as it appears, despite some very tight positive regressions. Numerical relationships among species are dynamic and typically depend on the specific reference period. We often found examples when protracted and positively correlated dynamics between two species also indicated a negative interaction at some short reference period (5–10 years). Most likely the dynamics of all the species considered is shaped by a «third» unidentified factor or factors. Amongst those factors, an increase of environmental capacity due to deliberate and undeliberate human interference should be not underestimated. Nature conservation policy has also played an important role, especially in populations of large carnivores (CHAPRON et al. 2014).

Summary

The dynamics of estimated and harvested numbers in the populations of ten game species in Latvia were analysed using data gathered by the managing and supervising authorities from 1980 to 2015. A simple linear regression analysis is applied to examine the significance of possible relations between every two species, taking into consideration changes in population size over a considered reference period, as well as within certain reference territories after comparable time intervals. Results are represented graphically and include regression

equations calculating statistical significance for all functions. Long-term positive and significant correlations were found including pairs of both prey-predators and competitors for habitat. On the scale of short-term intervals or spatial distribution of populations, the numbers may change controversially, i.e. show mutually negative trends in growth even for the species with a tight long-term positive correlation. Thus, numerical relationships between ecologically related species are also dynamic and depend on the considered reference period. In conclusion, the dynamics of all considered species are likely shaped by a «third» unidentified factor or factors. Amongst those factors, an increase of environmental capacity caused by human activities and management politics appears to be a very important driving force.

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