An Analysis of the Game Animal Population Data from Latvia

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Abstract

Large carnivores such as the wolf (*Canis lupus*) and the lynx (*Lynx lynx)* have never been eradicated in Latvia and their numbers particularly increased from the early 1970s onwards, which brought some conflict between the large carnivores and human interests. Therefore, it has always been a challenge for both gamekeepers and conservationists to reveal relationships between ungulates and large carnivores as well as to figure out relevant implications for their management.

The purpose of this paper is to reveal the above-mentioned relationships using statistical data. Fortunately, statistics on the abundance and hunting bag size of some game species in Latvia have been collected since the early 20th century. The study uses these data to examine four types of relationship within the period 1958 - 2005: (1) prey-prey relationships between the population estimates of moose *(Alces alces)*, red deer *(Cervus elaphus)*, roe deer *(Capreolus capreolus)*, wild boar *(Sus scrofa)*, (2) predator-prey relationships in the above four ungulate species, wolf and lynx; (3) relationships between the estimated numbers of wolf and lynx; (4) relationships among hunting bags in some of the species listed above. We applied unit root test to check if our statistical results suffered from the spurious correlation. We used regression analysis (dynamic OLS and generalized least square) to reveal statistical findings and examine them from the ecological point of view in order to check the validity of our results.

Our statistical results suggest that (1) For the red deer, roe deer is a competitor and vice versa. For the roe deer, moose is also a competitor in addition to the red deer. For the moose, red deer is a competitor. (2) For the wolf, red deer, roe deer and moose are prey whereas for the lynx, only roe deer is prey. (3) For lynx, wolf is a competitor, but for the wolf, lynx is not. (4) The elasticity of hunting with respect to population size is 2.55%, 0.91%, 2.14, 0.42% and 0.82%, for roe deer, red deer, moose, wolf and lynx, respectively. Most of the results are consistent with empirical findings from the field.

Key words: population dynamics; game statistics; game animals, spurious correlation

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Introduction

In Latvia, long stream of statistics on the abundance and hunting bag size of game species have been collected since the early 20th century. These statistics were used by the wildlife managers to decide the target number of the population size (Siliņš 1984). However, these data were not necessarily used for revealing the relationship between game animals and hunters. In sound ecology, cyclic changes in numbers of herbivores followed by delayed cycles in predator dynamics are known for game species too, *e.g.* the well known example on snow hare *Lepus americanus* and lynx *Lynx canadensis* (Begon *et al.* 1996).

It has always been a challenge for both gamekeepers and conservationists to reveal true relationships between ungulates and large carnivores as well as to figure out relevant implications for the species management. In addition, especially before and after the accession to the EU in 2004, the hunting policy of Latvia had to be changed and monitoring of large carnivores was required (Andersone 2001).

This paper, therefore, examines the relationship between large carnivores and ungulates as well as hunting activities so as to give a statistical background for beneficial the scientifically-based management of game animals. Specifically, we put stress on the following aspects. **Analysis 1:** to examine the relationship between prey species (roe deer *Capreolus capreolus*, red deer *Cervus elaphus*, wild boar *Sus scrofa* and moose *Alces alces*). **Analysis 2:** to examine the relationship between predators (lynx *Lynx lynx* and wolf *Canis lupus*) and prey. **Analysis 3:** to examine the relationship between predators. **Analysis 4:** to examine the relationship between human and game animals (the prey and predator species).

Here we should bring attention to the fact that the data used in this paper must have suffered from several kinds of biases. We will discuss possible biases in the later section in more detail, and we just would like to state here that even if some bias exists, our study is still useful at least in threefold; Firstly, one of the main contribution of the paper is to illustrate how to avoid spurious correlation issue, which have not been well known in the biology. Secondly, although bias might be crucial issues for some time period for some animals, it is not necessarily for other time and animals. In a related matter, this paper aims to test if game statistics from Latvia are in conformity with ecological knowledge. For this purpose, our data appear still valid. Thirdly, statistical analysis can give us objective results and may confirm the existing ecological knowledge even if some bias exists. It can even make us realise something that we could not have found by the existing methods and lead to the reexamination of ecological research. Ecological and statistical studies comprise a 'sort of both wheels' of the game management research. Our statistical findings should be checked by the ecological knowledge so as to avoid wrong conclusions which is done in the discussion section.

Materials and,methods

Data

We use estimates of the population size and data on the hunting bag of roe deer, red deer, moose, wild boar, lynx and wolf from 1958 to 2005. The estimates have been done annually in numerous spatial units by local foresters and hunters. Since the borders and size of the units were changed by political reforms with the lapse of time, we are able to use only total number of animals in entire country for our analysis. All of these data are official statistics of the Latvian State Forest Service either published (Andersone-Lilley, Ozoliņš 2005) or available from the internet on most recent years (www.vmd.gov.lv). Hereinafter, we denote these data as follows.

N^{roe} : the estimated population size of roe deer
N^{red} : the estimated population size of red deer
N^{moose} : the estimated population size of moose
N^{boar} : the estimated population size of wild boar
N^{wolf} : the estimated population size of wolf
N^{lynx} : the estimated population size of lynx
H^{roe} : hunting bag for roe deer
H^{red} : hunting bag for red deer
H^{moose} : hunting bag for moose
H^{boar} : hunting bag for wild boar
H^{wolf} : hunting bag for wolves
H^{lynx} : hunting bag for lynx

The hunting data for 1989 are not available and we calculated the data for the whole hunting data of 1989 as the arithmetic means of 1988 and 1990. We selected these game species not only because the available time series data are limited to these species, but also because these four ungulates seem to be the most important prey items for at least the wolf (Andersone and Ozoliņš 2004, p. 359).

Specification of Regression Models

In this section, we specify the regression models.

Analysis 1 to 3

To find out the relationships between game animals, we employ a statistical method. We build the extended discrete version of Lotka-Volterra models (Begon *et al.*, 1996) as follows:

$$N^{roe}(t+1) - N^{roe}(t) + H^{roe}(t) = \left[\beta_{10}^{roe} + \beta_{12}^{roe\cdot red} N^{red}(t) + \beta_{13}^{roe\cdot moose} N^{moose}(t) + \beta_{14}^{roe\cdot boar} N^{boar}(t) + \beta_{15}^{roe\cdot wolf} N^{wolf}(t) + \beta_{16}^{roe\cdot lynx} N^{lynx}(t)\right] N^{roe}(t) + \varepsilon_1$$

$$N^{red}(t+1) - N^{red}(t) + H^{red}(t) = \left[\beta_{20}^{red} + \beta_{21}^{red\cdot roe} N^{roe}(t) + \beta_{23}^{red\cdot moose} N^{moose}(t) + \beta_{24}^{red\cdot boar} N^{boar}(t) + \beta_{25}^{red\cdot wolf} N^{wolf}(t) + \beta_{26}^{red\cdot lynx} N^{lynx}(t)\right] N^{red}(t) + \varepsilon_2$$

$$N^{moose}(t+1) - N^{moose}(t) + H^{moose}(t) = \left[\beta_{30}^{moose} + \beta_{31}^{moose\cdot roe} N^{roe}(t) + \beta_{32}^{moose\cdot red} N^{moose}(t) + \beta_{34}^{moose\cdot boar} N^{boar}(t) + \beta_{35}^{moose\cdot wolf} N^{wolf}(t) + \beta_{36}^{moose\cdot lynx} N^{lynx}(t)\right] N^{moose}(t) + \varepsilon_3$$

$$N^{boar}(t+1)-N^{boar}(t)+H^{boar}(t)=\left[\beta_{40}^{boar}+\beta_{41}^{boar\cdot roe}N^{roe}(t)+\beta_{42}^{boar\cdot red}N^{red}(t)+\beta_{43}^{boar\cdot moose}N^{moose}(t)+\beta_{45}^{boar\cdot wolf}N^{wolf}(t)+\beta_{46}^{boar\cdot lynx}N^{lynx}(t)\right]N^{boar}(t)+\varepsilon_4$$

$$N^{wolf}(t+1)-N^{wolf}(t)+H^{wolf}(t)=\left[\beta_{50}^{wolf}+\beta_{51}^{wolf\cdot roe}N^{roe}(t)+\beta_{52}^{wolf\cdot red}N^{red}(t)+\beta_{53}^{wolf\cdot moose}N^{moose}(t)+\beta_{54}^{wolf\cdot boar}N^{boar}(t)+\beta_{56}^{wolf\cdot lynx}N^{lynx}(t)\right]N^{wolf}(t)+\varepsilon_5$$

$$N^{lynx}(t+1)-N^{lynx}(t)+H^{lynx}(t)=\left[\beta_{60}^{lynx}+\beta_{61}^{lynx\cdot roe}N^{roe}(t)+\beta_{62}^{lynx\cdot red}N^{red}(t)+\beta_{63}^{lynx\cdot moose}N^{moose}(t)+\beta_{64}^{lynx\cdot boar}N^{boar}(t)+\beta_{65}^{lynx\cdot wolf}N^{wolf}(t)\right]N^{lynx}(t)+\varepsilon_6$$

where β and ε_k denote parameters and unobserved errors, respectively.

The sign of the parameters convey meanings, which depend on the combination of the variables of each parameter. For the first four equations, β_{ij}, j = 1,...4 means the relationship with other ungulates. If it is negative, it suggests that there is competition between them (main topic in **Analysis 1**).β_{ij}, j = 5.6, means the relationship with predators. If it is negative, it suggests that this ungulate is a prey to this predator (one of the main topic in **Analysis 2**).

On the other hand, for the last two equations, β_{ij}, j = 1,...4, means the relationship with prey species. If it is positive, it suggests that they prey on this ungulate (this is also one of the main topic in **Analysis 2**). β_{ij}, j = 5.6 means the relationship with the other predator. If it is negative, it suggests that it competes with the other predator (main topic in **Analysis 3**).

Analysis 4

To investigate the relationship between humans and prey/predator species, we build estimation equations as follows:

$$LnH^{roe}=\gamma_{10}^{0}+\gamma_{11}LnN^{roe}+\varepsilon_1^{roe}$$

$$LnH^{red}=\gamma_{20}^{0}+\gamma_{21}LnN^{red}+\varepsilon_2^{red}$$

$$LnH^{moose}=\gamma_{30}^{0}+\gamma_{31}LnN^{moose}+\varepsilon_3^{moose}$$

$$LnH^{boar}=\gamma_{40}^{0}+\gamma_{41}LnN^{boar}+\varepsilon_4^{boar}$$

$$LnH^{wolf}=\gamma_{50}^{0}+\gamma_{51}LnN^{wolf}+\varepsilon_5^{wolf}$$

$$LnH^{\mathrm{lynx}}=\gamma_{60}^{0}+\gamma_{61}LnN^{\mathrm{lynx}}+\varepsilon_6^{lynx}$$

where γ_i^0, γ_j and ε_k denote intercepts, slopes and unobserved errors, respectively.

Because we take logarithm of both explanatory and explained valuables, they are constant elasticity models and the value of γ_{i1} (i =1,…, 6) suggests the elasticity of hunting with respect to population size. Therefore, 1% increase of population size will bring γ_{i1}% increase in hunting. The concept of elasticity has its origin in the microeconomics, and sometimes applied to the Ecology (for example, see Vandermeer and Goldberg 2003).

Unit Root Test

Recently, more and more attention has been paid to the stationary of the time series data, where stationary means that the mean and autocovariances of the time series data do not depend on time. If time series data are non-stationary, the data should be transformed. Otherwise, the estimation result may suffer from spurious correlation (Granger-Newbold 1974), which means that even if explained variable and explanatory variable(s) do not statistically correlate, it may result in a higher coefficient of determination and significant t values. As a result, it can be mistakenly decided that there is a statistically significant correlation.

To avoid this misidentification, we have conducted the unit root tests on the data described above. This method as well as the Co-integration test mentioned below, are often used in the field of econometrics, and they were started to be used in the field of ecology (for example, Ewing *et al.* 2007, Kawata 2008). In this paper, we use the Kwiatkowski, Phillips, Schmidt and Shin (KPSS) test. The reasons why we used this test is that, 1) some of the previous studies in this field selected them (for example, Ewing *et al.* 2007, Kawata 2008) and 2) although the augmented Dickey-Fuller (ADF) test seems to be used most often, the power of the ADF test is relatively weak, and sometimes null hypothesis (time series has a unit root) is not rejected when unit root is almost 1 (Matsuura and McKenzie 2001, p. 247). To relieve such a problem we select the KPSS test, whose null hypothesis is different from the ADF test; the time series does not have a unit root.

Even if two or more time series data are non-stationary, linear combination of them can be stationary as long as they are $I(1)$ (hereinafter we denote $I(1)$ when crude time series data are non-stationary but their first differences are stationary. In addition, we denote $I(0)$ when crude time series are stationary) and cointegration exists. We will conduct the Co-integration test to check if cointegration exists. Such a co-integrating equation can be interpreted in a way that it represents long-term relationship among the variables.

Unit Root Test Results for Data of Analysis 1 to 3 data

Spurious correlation may happen when an explained variable and at least one explanatory variable are non-stationary (in more detail, see Wooldrige 2006, p. 647). Therefore, we check whether each equation presented in the above subsections contains $I(1)$ explained variable and $I(1)$ explanatory variable(s).

Firstly, we examine the data of Analysis 1 to 3. As for the explained variable $N(t+1)-N(t)-H(t)$, the KPSS test reject the null hypothesis (the time series does not have a unit root) concerning the wild boar at 10% level (Table 1). As for the explanatory variable $N(t)^i N(t)^j$, the KPSS test reject the null hypothesis in case of roe deer - wolf, red deer - lynx and moose - lynx. As for the other explanatory variables, *N(t)* the null hypothesis cannot be rejected at 10% level. As a whole, there is no case where spurious correlation should be concerned as for the Analysis 1 to 3.

Unit Root Test Results for the Analysis 4 data

As for the data of Analysis 4, based on the results of the KPSS test, the usual regression can be applied for roe deer, moose, wolf and lynx (Table 1). On the other hand, for red deer and wild boar, both explained variable and explanatory variables are non-stationary. Therefore, 1st difference is taken to check if they are $I(1)$, and as Table 2 shows, both variables are $I(1)$ based on the KPSS test.

As shown in the above subsection, because both *LnH* and *LnN* of the roe deer and the wolf as well as either *LnH* or *LnN* of the moose and the lynx are $I(0)$, the usual OLS or advanced method such as generalized least square (GLS) can be applied. However, both *LnH* and *LnN* of the red deer and the wild boar are $I(1)$, we need to check whether they have co-integration. If co-integration exists, some modified OLS such as dynamic OLS (DOLS) can be applicable, and the results give us long-term relationship.

The results are shown in Table 3. We applied third type of deterministic trend cases presented by Johansen (1995). Based on the Trace test and the Max-eigenvalue test, the red deer has co-integration whereas the wild boar has no co-integration. Therefore, we will exclude the wild boar from Analysis 4.

Table 1. Results of the Unit Root Tests (*level*)

	LM stat.	bandwidth	type
N(t+1)-N(t)+H(t) : 1958-2004			
Roe deer	0.07	4	T & I
Red deer	0.09	4	T & I
Moose	0.26	5	I
Wild boar	0.45 *	5	I
Wolf	0.06	4	T & I
Lynx	0.08	4	T & I
$N(t)^i N(t)^j$: 1958-2004			
Roe deer : Red deer	0.07	4	T & I
Roe deer : Moose	0.09	5	T & I
Roe deer : Wild boar	0.05	4	T & I
Roe deer : Wolf	0.13 *	4	T & I
Roe deer : Lynx	0.1	3	T & I
Red deer : Moose	0.08	5	T & I
Red deer : Wild boar	0.07	4	T & I
Red deer : Wolf	0.12	5	T & I
Red deer : Lynx	0.17 **	4	T & I
Moose : Wild boar	0.09	5	T & I
Moose : Wolf	0.09	4	T & I
Moose : Lynx	0.13 *	5	T & I
Wild boar : Wolf	0.81	5	I
Wild boar : Lynx	0.1	3	T & I
Wolf : Lynx	0.13	5	T & I
N : 1958-2004			
Roe deer	0.07	4	T & I
Red deer	0.09	5	T & I
Moose	0.15	5	I
Wild boar	0.07	4	T & I
Wolf	0.1	5	T & I
Lynx	0.06	5	T & I
Ln(H) : 1958-2005			
Roe deer	0.09	4	T & I
Red deer	0.23 ***	5	T & I
Moose	0.37 *	5	I
Wild boar	0.21 **	5	T & I
Wolf	0.11	5	T & I
Lynx	0.08	4	T & I
Ln(N) : 1958-2005			
Roe deer	0.07	5	T & I
Red deer	0.21 **	5	T & I
Moose	0.2	5	I
Wild boar	0.2 **	5	T & I
Wolf	0.08	5	T & I
Lynx	0.14 *	5	T & I

Note: We use E-views 6 for unit root tests. Basically, we show the most preferable results, which is chosen from (1) without trend and intercept (N), (2) without trend and with trend (I) and (3) with trend and intercept (T & I). In the ADF test, lag is decided by the Schwarz info criterion, and in the KPSS test, spectral estimation method is default (Bartlett kernel) and bandwidth is automatically selected by Newey-West bandwidth

Results

Estimation Method Selection

Analysis 1 to 3: We apply the GLS for the crude time series data. We selected GLS because we use time series data and the error term may have suffered from autocorrelation.

Table 2. Results of the Unit Root Tests (*1st difference*)

	ADF		KPSS		
	t stat.		lag	LM stat.	bandwidth
Ln(H) **: 1958-2005**					
Red deer	-6.97	***	0	0.05	3
Wild boar	-5.89	***	0	0.11	2
Ln(N) **: 1958-2005**					
Red deer	-5.52	***	0	0.05	3
Wild boar	-3.43	*	0	0.12	4

Note: Same as Table 1.

Table 3. Results of cointegrated test

			Trace test		Max-eigenvalue test	
	Null	Eigenvalue	Trace Statistic	Prob.	Max-Eigen Statistic	Prob.
Red deer	r = 0	0.31	22.50	0.02	16.82	0.04
	r = 1	0.12	5.68	0.22	6.68	0.22
Wild boar	r = 0	0.13	11.64	0.48	6.65	0.71
	r = 1	0.10	5.00	0.28	5.00	0.28

Notes:
(1) Trend assumption is 2.
(2) Prob. is MacKinnon-Haug-Michelis (1999) p-values.

Analysis 4: We apply GLS for roe deer, moose, and wolf and lynx. Because both explained variable and explanatory variable of the red deer is $I(1)$, and they are co-integrated, we apply DOLS instead of the usual OLS. The reason is the following: although we will have consistent estimator of the coefficient by applying the usual OLS, Table 2. The relationship between selected key issues and weaknesses in this case ‘the OLS estimation has a non-normal distribution, and inferences based on its *t*-statistics can be misleading’ (See Stock and Watson 2002, p. 556). Therefore, we apply DOLS.

The estimation equation is modified as follows.

$$LnH_t^{red} = \varphi_{20}^0 + \varphi_{21} LnN_t^{red} + \sum_{l=-p}^{p} \delta_l^{red} \Delta LnN_{t-l}^{red} + \varepsilon_t^{redD}$$

where, φ^0 is intercept, φ and δ are slopes, ε_t is unobserved error and Δ is lag operator.

Results for Analysis 1 to 3

In Table 4, we summarize the estimation results of Analysis 1 to 3. The table is made based on the sign of parameter values. The explained variable is shown at the far left line and explanatory variables are at the front row. When the parameter value takes meaningful sign, we substitute the sign with its meaning. They are the following:

when the explained variable is a predator, and

explanatory variable is a predator: negative sign means competition

explanatory variable is a prey: positive sign means prey

when the explained variable is a prey, and

explanatory variable is a predator: negative sign means preyed

explanatory variable is a prey: negative sign means competition

	wolf	lynx	red deer	roe deer	moose	wild boar	R^2
wolf	–	+	prey	prey	–	prey	0.73
lynx	competition	–	–	prey	–	–	0.53
red deer	preyed	+	–	competition	+	competition	0.73
roe deer	preyed	+	competition	+	competition	+	0.47
moose	+	preyed	competition	+	–	+	0.63
wild boar	+	+	competition	+	competition	–	0.79

Notes:
(1) See App. Table 1 to 6 for greater detail.
(2) These results are the case when wild boar is included as explanatory variable.

Table 4. Summarize of the estimation results of Analysis 1 to 3

when the explained variable and explanatory variable are the same,

positive sign means that as the population of one year is bigger, the increment of the population gets to be higher,

and vice versa for each case.

Analysis 1 Results of prey – prey relationship analysis

Based on the above-mentioned definition of the relationship, the roe deer is a competitor for the red deer and vice versa, as is indicated in Table 4. For the red deer, the wild boar is a competitor and vice versa. For the roe deer, in addition to the red deer, the moose is also a competitor. For the moose, the red deer is a competitor. For the wild boar, the moose is also a competitor.

Analysis 2 Results of predator – prey relationship analysis

For the wolf, the red deer, the roe deer and the wild boar are prey whereas for the lynx, only the roe deer is prey. On the other hand, when we look at it from the prey side, the wolf is a predator to the red deer and the roe deer, for the moose, its predator is the lynx.

Analysis 3 Results of wolf – lynx relationship analysis

When the explained variable is the wolf, variable lynx is positive. It suggests that as the population of the lynx increases, the wolf population also increases. On the other hand, when the explained variable is the lynx, variable wolf is negative. It suggests that as the population of the wolf increases, the lynx population decreases. It seems to suggest that on the one hand, the wolf is not affected by the population of the lynx whereas the increase in the lynx population is limited by the wolf.

Results of analysis of the Relationship between Human Impacts and Game Animals (Analysis 4)

The relationship between humans and prey are shown in Table 5. Lead and lag of the DOLS model is decided so that the Akaike information criteria (AIC) takes the least value. Based on this procedure, we select 3 period leads and lags where all leads and lags are included. Then the model is re-estimated based on the AIC and p-value so as to exclude insignificant variables. For the inference, we use heteroscedastic autoregression covariances (HAC). The above procedure is heavily dependent on the one used in Kristin and Frank (2005).

As a result, 1% increase in the population sizes of the roe deer, the red deer and the moose results in the increase of the hunting bag for each species by 2.55% (γ_{11}), 0.91% (φ_{21}) and 2.14% (γ_{31}), respectively.

The relationship between humans and predators are shown in Table 6. 1% increase in the population sizes of the wolf and the lynx results in the increase of the

Table 5. Human impacts on the preys (Analysis 4)

	Roe deer			Red deer			Moose	
γ_{10}^0	-19.49	***	φ_{20}^0	-25.27	***	γ_{30}^0	-12.23	***
	(-7.43)			(-14.37)			(-7.95)	
γ_{11}	2.55	***	φ_{21}	0.91	**	γ_{31}	2.14	***
	(10.57)			(2.40)			(12.97)	
R	0.70			0.998			0.78	
R^2	0.69			0.996			0.77	
	GLS			DOLS			GLS	

Notes:
(1) t-values are in parentheses.
(2) *** p-value is less than 0.01, **0.05, *0.1
(3) Data period is 1954-2005 for all game animals.

Table 6. Human impacts on the predators (Analysis 4)

	Wolf (1)		Wolf (2)		Wolf (3)		Wolf (4)			Lynx	
γ_{50}^0	2.75	***	2.22	***	-1.73		-3.41	*	γ_{60}^0	-1.29	
	(13.54)		(12.34)		(-1.13)		(-2.12)			(-0.78)	
γ_{51}	0.42	***	0.56	***	1.09	***	1.33	***	γ_{61}	0.82	***
	(10.99)		(14.54)		(4.70)		(5.39)			(2.77)	
R	0.72		0.86		0.71		0.66			0.14	
R^2	0.71		0.86		0.67		0.63			0.12	
	GLS		GLS		GLS		GLS			GLS	
period	58-05		58-90		91-99		91-05			58-05	

Notes:
(1) t-values are in parentheses.
(2) *** p-value is less than 0.01, **0.05, *0.1
(3) Note 2: Data of 1989 for all wildlife and of 1969 for lynx are not available and these years are omitted in the regressions.
(4) Data period is 1954-2005 for wolf (1) and lynx cases.

hunting bag for each predator by 0.42% (γ_{51} for the period 1958-2005) and 0.82% (γ_{61}), respectively.

Discussion and Conclusions

Examination of the Validity of Statistical Results

In what follows, we will discuss the cases where the statistic results (Table 7) are not consistent with the ecological knowledge or the cases where some remark should be provided.

Prey – Prey Relationship (Analysis 1)

Red deer and Wild boar: Statistical analysis suggests that the wild boar and the red deer compete with

Table 7-1. Predator-prey model for roe deer

		Full model		Modified model	
roe deer	β^0_{10}	0.20 (1.94)	*	0.13 (1.39)	
red deer : roe deer	β_{12}	-1.86*10^{-05} (-2.30)	**	-2.76*10^{-5} (-4.76)	***
moose : roe deer	β_{13}	-1.99*10-5 (-2.77)	***	-1.38*10^{-5} (-2.18)	**
wolf : roe deer	β_{15}	-4.55*10^{-4} (-1.71)	*		
lynx: roe deer	β_{16}	4.00*10-4 (1.46)			
wild boar : roe deer	β_{14}	1.34*10^{-5} (2.25)	**	1.98*10^{-5} (4.22)	***
R^2		0.47		0.44	

Notes:
(1) t-values are in parentheses.
(2) *** p-value is less than 0.01, **0.05, *0.1
(3) The data for the whole of 1989 is the arithmetic means of 1988 and 1990

Table 7 - 2. Predator-prey model for red deer

		Full mode l		Modified model	
red deer	β^0_{20}	-0.36 (-2.54)	**	-0.46 (-4.71)	***
roe deer : red deer	β_{21}	-1.07*10^{-6} (-0.79)		-1.70*10^{-6} (-3.13)	***
moose : red deer	β_{23}	1.44*10^{-5} (1.48)		2.27*10^{-5} (4.74)	***
wolf : red deer	β_{25}	-1.14*10^{-6} (-0.28)			
lynx: red deer	β_{26}	4.25*10^{-4} (2.15)	**	2.84*10^{-4} (2.79)	***
wild boar : red deer	β_{24}	-1.79*10^{-4} (-0.96)			
R^2		0.73		0.72	

Notes:
(1) Same as Table 7 - 1.

Table 7 - 3. Predator-prey model for moose

		Full model		Modified model	
moose	β^0_{30}	-0.15 (-1.36)		-0.18 (-1.70)	*
roe deer : moose	β_{31}	2.79*10^{-6} (1.26)		3.46*10^{-6} (2.07)	**
red : moose	β_{32}	-3.54*10^{-5} (-2.46)	**	-2.95*10^{-5} (-4.28)	***
wolf : moose	β_{35}	1.23*10^{-3} (2.99)	***	1.08*10^{-3} (4.33)	***
lynx: moose	β_{36}	-7.34*10^{-4} (-1.55)		-5.60*10^{-4} (-1.93)	*
wild boar : moose	β_{34}	6.47*10^{-6} (0.47)			
R^2		0.63		0.63	

Notes:
(1) Same as Table 7 - 1.

Table 7 - 4. Predator-prey model for wild boar

		Full model		Modified model	
wild boar	β^0_{40}	-0.63 (-2.75)	***	-0.73 (-9.20)	***
roe deer : wild boar	β_{41}	3.29*10^{-6} (1.88)	*	2.80*10^{-6} (2.01)	*
red : wild boar	β_{42}	-2.30*10^{-5} (-3.41)	***	-2.08*10^{-5} (-3.53)	***
moose : wild boar	β_{43}	-5.67*10^{-6} (-0.37)			
wolf : wild boar	β_{45}	2.02*10^{-5} (0.07)			
lynx : wild boar	β_{46}	8.99*10^{-4} (3.54)	***	9.46*10^{-4} (5.76)	***
R^2		0.79		0.78	

Notes:
(1) Same as Table 7 - 1.

Table 7 - 5. Predator-prey model for wolf

		Full model		Modified model	
wolf	β^0_{50}	-1.23 (-5.38)	***	-1.27 (-13.10)	***
roe deer : wolf	β_{51}	1.32*10^{-6} (0.48)			
red : wolf	β_{52}	2.40*10^{-5} (2.36)	**	4.02*10^{-5} (9.40)	***
moose : wolf	β_{53}	-1.23*10^{-5} (-0.71)			
lynx : wolf	β_{56}	2.11*10^{-4} (0.87)			
wild boar : wolf	β_{54}	9.20*10^{-6} (0.86)			
R^2		0.73		0.71	

Notes:
(1) Same as Table 7 - 1.

Table 7 - 6. Predator-prey model for lynx

		Full model		Modified model	
lynx	β_{60}^{0}	-0.14 (-0.69)		-0.23 (-4.19)	***
roe deer : lynx	β_{61}	6.99*10-6 (4.39)	***	6.66*10-6 (4.74)	***
red deer : lynx	β_{62}	-7.61*10-6 (-1.04)		-8.17*10-6 (-2.08)	**
moose : lynx	β_{63}	-5.44*10-6 (-0.40)			
wolf : lynx	β_{65}	-8.06*10-5 (-0.53)			
wild boar : lynx	β_{64}	-6.62*10-6 (-1.35)		-6.24*10-6 (-1.70)	*
R^2		0.53		0.52	

Notes:
(1) Same as Table 7 - 1.

one another. It is known from empirical knowledge that remains of various mammals are found in faeces (Baubet *et al.* 2004) or stomachs (Herrero *et al.* 2004) of the wild boar. In theory, they might consume a helpless calf of the red deer in breeding season or a cadaver in sever winter. However, while predation of the wild boar on large mammals unlikely happens, the red deer and the wild boar can be rather competitors for food resource or habitat.

Roe deer and Moose: For the roe deer, the moose does not seem to be a competitor based on the ecological knowledge. Our statistical results may reflect the fact that the population fluctuations coincided for the roe deer and the moose. Further investigation is required.

Wolf - Prey (Analysis 2)

Wolf and Red deer: Statistical analysis suggests that for the wolf, the red deer is prey and vice versa. However, the red deer is unevenly distributed over the territory of the wolf range, *e.g.* it is abundant in the central part of Latvia where wolves are scarce or absent. Our statistical analysis seems to contradict this empirical fact.

Wolf and Wild boar: Statistical analysis suggests that for the wolf, the wild boar is a prey, but for the wild boar, the wolf is not a predator. One possible reason could be the following. The population size of the wild boar is far greater than that of the wolf. Therefore, the population size of the wolf is affected by that of the wild boar, but not the other way around - the predation by the wolf does not affect the wild boar population that much.

Lynx - Prey (Analysis 2)

Lynx and Roe deer: Existing ecological studies have shown that both the wolf and the lynx prey on the roe deer. However, our statistical results suggest that for the roe deer, the wolf can be a predator but the lynx is not. The reason we have such results may be the following. The wolf can change the prey easily and the amount of the roe deer in its diet depends on the population of the roe deer. However, the lynx heavily depends on the roe deer as the staple diet, and the amount of the roe deer in its diet can be relatively stable regardless of the population size of the roe deer. Therefore, the fluctuation of the wolf and the roe deer can be reversely correlated while that of the lynx and the roe deer cannot. In addition, the wolf can also prey on bigger roe deer than the lynx. With this explanation in mind our statistical results are valid.

Lynx and Moose: In reality, it is not easy for the lynx to feed on the moose. Therefore, there can not be a definite predator-prey relationship. Statistical analysis also supports that the lynx and the moose do not have predator-prey relationship when the explained variable is the lynx.

However when the explained variable is the moose, the lynx is predator for the moose. The reason we have this result may be that populations of the lynx and the moose fluctuate reversely. However, it is a coincidence and could not be a true relationship.

Wolf - Lynx (Analysis 3)

Previous ecological studies revealed that while food spectrum of the lynx is rather limited (Jedrzejewska and Jedrzejewski 1998; Breitenmoser *et al.* 2001, Ozoliņš 2002), the wolf tends to feed on the most abundant prey (Jedrzejewska and Jedrzejewski 1998; Ozoliņš and Andersone 2003, Andersone and Ozoliņš 2004, Valdmann *et al.* 2005). Our statistical results also support this fact: for the wolf, the roe deer, the red deer and the moose are prey whereas for the lynx, only the roe deer is prey.

This result is also consistent with the relationship between the wolf and the lynx. For the wolf, the lynx is not a competitor but for the lynx, the wolf is a competitor. The prey for the lynx is limited to the roe deer and when the population of the roe deer is abundant, the wolf competes with the lynx. The wolf can change between different prey types and before there is too much competition with the lynx over the roe deer, wolves can switch to the red deer and the moose. Therefore, for the wolf, the lynx is not necessarily a competitor.

Human Impacts and Game Animals (Analysis 4)

We calculated the elasticity of hunting in relation to population size. That is, γ_{11}, φ_{21}, γ_{31}, γ_{51} and γ_{61}. When they take the value more than 1 and less than 1, we call it elastic hunting and inelastic hunting, respectively. We summarize the results in Table 8.

Table 8. Elasticity of hunting in relation to population size

	notation	elasticity	
Roe deer	γ_{11}	2.55	elastic
Red deer	φ_{21}	0.91	inelastic
Moose	γ_{31}	2.14	
Wolf	γ_{51}	0.42 (1958-2005) 0.56 (1958-1990) 1.33 (1991-2005)	inelastic inelastic elastic
Lynx	γ_{61}	0.82	inelastic

Elastic hunting suggests that the number of hunts varies considerably when the population size varies while inelastic hunting suggests the rigidity of the number of hunts. There may be many reasons for the hunting to be elastic and inelastic. One argument is that if that game species is considered to be beneficial, hunters are more conservative and the number of hunts is more dependent on the population size, resulting in elastic hunting. On the other hand, if the species is considered to be a pest, hunters try to keep population size at a lower level, and as a result, the number of hunts is less dependent on the population size.

Although the elasticity of the red deer is a little less than 1, that of the other two ungulates is more than 1. As a whole, ungulates seem to be seen as beneficial game animals. In case of predators, it is interesting to divide data periods. During the Soviet era (until the 1990s), it was an official policy to control the wolf population (Andersone 2003a, Andersone and Ozolins 2005). At that time wolves were under a high hunting pressure and the population size was maintained at a low level. In short, the wolf was totally seen as pest.

From 1991 (after the independence was restored) to 1999 (before joining the EU), the wolf population size increased. Because wolves competed with hunters for the prey species, wolves were sometimes under strong hunting pressure within that period, especially during the anti-predatory campaign with a reward of 75 LVL (106.23 EUR) per head (Andersone and Ozolins 2005, Ozoliņš *et al.* 2005). Therefore, the wolf could be pest and managed. After 2000, the hunting policy gradually started to follow the EU regulations, which decreased the number of wolves harvested. It suggests that the wolf get to be a protected animal.

These tendencies are consistent not only with the elasticity (see, Table 8), but also with the population-hunting relationship shown in Figure 1, which depicts the relationship between the number of the wolf hunts and the wolf population size. When separated as above, 1% increase in the population size of the wolf may result in the increase in the number of hunts by 0.56% (γ_{51} for the period 1958-1990), 1.10% (γ_{51} for the period 1991-1999) and 1.33% (γ_{51} for the period 1991-2005), respectively.

In case of the lynx, the tendency is not as clear as for the wolf. Elasticity of hunting is 0.82 (inelasticity), suggesting that the lynx is rather seen as a pest. As shown in Figure 2, it can be separated into three periods: until 1984 when there was no closed hunting season, and after 2002 when the lynx management plan was introduced. The unclear tendency may be attributed to the fact that the lynx has been considered as a valuable fur-bearing animal too, and the hunting bag was at least limited by a closed season.

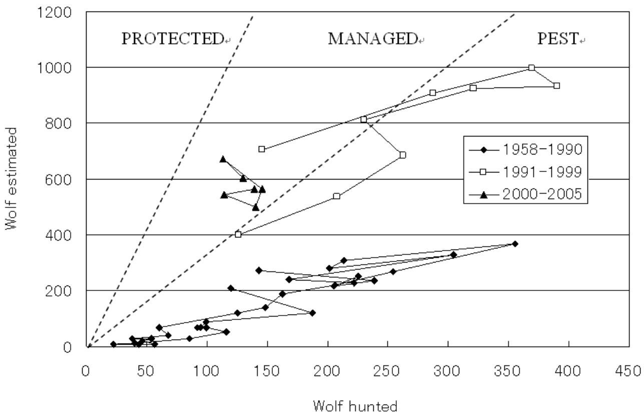

Figure 1. The relationship between number of wolf estimated and hunted

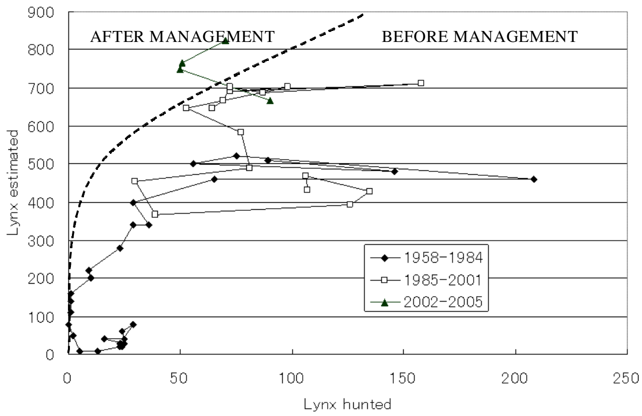

Figure 2. The relationship between number of lynx estimated and hunted

In Figure 1, we also drew lines to depict the difference in the policy, which we have already suggested above. These lines are arbitrary and each area corresponds to the policies when large carnivores were regarded as a pest, were managed or protected. Here again, the tendency is less clear in case of the lynx (Figure 2). Because the lynx is not necessarily seen as a pest, we divided the graph into two periods - before and after the management.

Remaining issues

There are some remaining issues. Firstly, we discuss about possible bias. As we have mentioned in the introduction, our data might have suffered from some biases. The source of the bias can be varied. Because sampling place, time and counting methods for population estimation are fixed through time in case of this study, it might not bring serious bias: at least trend of population fluctuation has been captured with some accuracy. Therefore, here we concentrate on the bias concerning hunting bag, which is estimated through the licensing system.

There are three things that we should point out. Firstly, this bias does not concern the carnivores because they were not under quota system until 2004. Secondly, for other game animals, this bias concerns only the period before the 1990s. This is because afterwards most quotas were not fulfilled despite the low price of hunting licenses. Lastly, we should confess that bag of some ungulates might not be counted correctly for some time before. For example, the moose was rather underestimated in the 1970-1980s because a considerable amount of venison had to be delivered for export and the hunters and the game keepers were not paid for their work. Consequently, they were not motivated to receive proper amount of shooting permits and did falsify count data. It is true that especially the last one can be problematic, and we leave it as one of the remaining issues.

Secondly, we discuss the explanatory variables. We need to add other explanation variables in the estimation. We should be careful about the fact that visually the red deer and the wild boar declined only once (middle of the 1990s) while the abundance of the roe deer, the moose, and predators changed several times. Some decreases seem to depend on socio-economic reasons, and not on natural predator-prey relationships, *e.g.* they coincide with the decline of agriculture, outbreak of illegal hunting or changes in forestry policy. One way to consider the socio-economic changes is to include new parameters such as gross agricultural production, and the area of clear-cut forest. However, we did not include those parameters because of the lack of data.

Concluding Remarks

For the scientific adaptive management of game animals, there are some issues to be examined: 1) treatment of biases, 2) building of models with some accuracy and 3) learning by doing in the real management. In this paper, we focus our attention to building models, which is beneficial because it enables us to predict the population dynamics in the future by assuming the future population size based on the trend of the previous years. As we mentioned in the introduction, in sound ecology, cyclic changes of the predator and prey populations are observed, and we have successfully showed using statistical methods that it is also the case in Latvia. In other words, we showed the possibility of proceeding with adaptive management based on the statistical analysis applied to the Latvian game animals.

One more main contribution that we represent in this paper is that the view towards game animals is influenced by the social, political and management changes. We employed elasticity concept, and successfully explained these changes using this concept. We also utilize this concept to determine whether each game animal is regarded as a pest or as a beneficial species. Insofar as we know, these analyses are the first attempt of this kind. Although there is a room for improvement of the method, elasticity can be used to classify game animals and used when preparing management plans.

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АНАЛИЗ ПОПУЛЯЦИОННЫХ ДАННЫХ ОХОТНИЧЬИХ ВИДОВ В ЛАТВИИ

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Резюме

Крупные хищники, такие как волк (*Canis lupus*) и рысь (*Lynx lynx*) постоянно населяли территорию Латвии. Их численность особенно увеличилась с начала 1970-х годов, что вызвало ряд конфликтов между крупными хищниками и интересами человека. Поэтому для охотоведов и биологов всегда нелегкой задачей было раскрыть взаимоотношения между копытными и крупными хищниками, а также разработать соответствующие рекомендации для управления популяциями.

Целью настоящей статьи является раскрытие вышеупомянутых взаимоотношений при помощи статистических данных. К счастью, данные о численности и размере добычи ряда охотничьих видов в Латвии доступны за период с начала 20-го века. Эти данные были использованы нами для исследования четырех типов взаимоотношений за период 1958-2005 годов: (1) взаимоотношения в системе «жертва-жертва» между популяциями лося (*Alces alces*), благородного оленя (*Cervus elaphus*), косули (*Capreolus capreolus*), кабана (*Sus scrofa*), (2) взаимоотношения в системе «хищник-жертва» между популяциями вышеупомянутых видов копытных, волком и рысью; (3) взаимооотношения между популяциями волка и рыси; (4) взаимоотношения между данными добычи ряда вышеупомянутых видов. Чтобы проверить, не страдают ли наши статистические результаты от ложной корреляции, мы применили тест единичного корня. Чтобы раскрыть статистические результаты и изучить их с экологической точки зрения для проверки их достоверности, мы использовали анализ регрессии (динамический ОЛС и обобщенный метод наименьших квадратов).

Результаты нашего анализа указывают на то, что (1) для благородного оленя косуля является конкурентом и наоборот. Для косули, в дополнение к оленю, лось также является конкурентом. Для лося конкурентом является олень. (2) Для волка жертвами являются олень, косуля и лось, в то время как для рыси жертвой является только косуля. (3) Для рыси волк является конкурентом, но для волка рысь таковым не является. (4) Эластичность охоты по отношению к величине популяции равна 2.55%, 0.91%, 2.14%, 0.42% и 0.82%, для косули, благородного оленя, лося, волка и рыси соответственно. Большинство результатов хорошо согласуются с эмпирическими данными.

Ключевые слова: динамика популяции, охотничья статистика, охотничьи животные, ложная корреляция