Acta Biol. Univ. Daugavp. 13 (2) 2013
ISSN 1407 - 8953

ESTIMATING THE UPPER LIMIT OF THE GROWTH RATE OF THE EURASIAN BEAVER, *CASTOR FIBER* (LINNAEUS, 1758), IN LATVIA

Yukichika Kawata, Jānis Ozoliņš

Kawata Y., Ozoliņš J. 2013. Estimating the upper limit of the growth rate of the Eurasian beaver, *Castor fiber* (Linnaeus, 1758), in Latvia. *Acta Biol. Univ. Daugavp., 13 (2): 59 – 73.*

The purpose of this paper is to provide basic information on the growth of the beaver population in Latvia. We built a generalised logistic model and used time series data on beavers from 1927–2008 to estimate the upper limit of the population's growth rate. The main findings are as follows: (1) The upper limit of the annual growth rate was 0.121–0.270/year. The growth rates estimated in the literature were mostly lower than the upper growth rate limits estimated in this study. (2) Our results suggest that the growth curve is not well described by a logistic curve. However, the shape of the growth function around the end of the 1980s and early 1990s might be similar to a logistic curve, which implies that the results of previous studies are valid. (3) Our results suggest that the annual growth rate was relatively high around the end of the 1980s and early 1990s, which coincides with intensive beaver hunting. This result is interesting because we removed hunt data from estimations since it was appropriate. This might imply that our method and estimation results are appropriate.

Key words: beaver, growth rate, conservation, estimation, Latvia.

Yukichika Kawata. Obihiro University of Agriculture and Veterinary Medicine, Inada-cho, Obihiro, Hokkaido 080-8555, Japan, e-mail: ykawata@obihiro.ac.jp

Jānis Ozoliņš. Latvian State Forest Research Institute 'Silava', Rigas iela 111, Salaspils, LV-2169, Latvia, e-mail: janis.ozolins@silava.lv

INTRODUCTION

In Latvia, the beaver, *Castor fiber* (Linnaeus, 1758), was reintroduced for the first time in 1927. Supplementary reintroductions followed in 1935 and 1952. Natural dispersal from Belarus started between the late 1950s and the early 1960s (Balodis 1990). The number of beavers increased because of this successful re-acclimatisation; consequently, beaver hunting was reinitiated in 1981. Beavers have traditionally been a profitable game animal because of their expensive furs. The beaver population size has been monitored and/or estimated fairly regularly, and basic studies (e.g. on the distribution and growth rate) have been conducted.

However, the sale of beaver products in foreign markets stopped, especially after the 1990s; thereafter, the cull limits of the beaver in Latvia have not been met for many years. Furthermore, many other attractive, larger hunting animals such as moose, *Alces alces*, and red deer, *Cervus elaphus*, are considered more desirable trophies. Therefore, a substantial annual increase in the population has continued. Worse, the wolf, *Canis lupus*, is the only scientifically confirmed (Campbell et al. 2005) predator that preys on the beaver as one of its main foodstuffs, especially in the summer (Novak 1987, Andersone 1999, 2003, Ueda et al. 2004). However, the impact of the wolf on the beaver population appears to be too weak to control population growth. Consequently, the beaver's distribution has expanded, and the number of conflicts between beavers and humans has increased. Basic information is crucial for appropriate management of the beaver population. The Latvian State Forest Service has been monitoring the beaver population size continuously, but basic studies have not been performed since that of Balodis (1990, 1998).

The purpose of this paper is to estimate basic biological parameters, which are necessary in the conservation of the beaver. In this paper, we used the estimated population size and annual number of hunts to estimate the growth rate and carrying capacity of the beaver population. Unfortunately, we were unable to estimate the carrying capacity. However, if we assumed that the current population size is lower than the carrying capacity, we could estimate the upper limit of the growth rate. Moreover, by changing the range of estimation period, we could estimate the above parameters for different periods.

Some existing studies have estimated the growth rate of the beaver population in Latvia (Balodis 1990, 1998). The mathematical model used and/or mentioned as a growth function in these studies is the logistic curve.[1] However, there is no guarantee that the logistic curve best fits the growth function of the beaver in Latvia. One of the contributions of this paper is to adopt a generalised model of the logistic curve. As shown below, the best functional form is not necessarily a logistic curve.

[1] However, these studies basically use the following function for the estimation of the growth rate: $r = \sqrt[t]{N_t / N_0}$, where N_t and N_0 are the population size of the year t and initial year, respectively.

MATERIAL AND METHODS

Data

We used official data of the estimated population sizes provided by the Latvian State Forest Service; they are also available from the compilation of statistics by Vanags (2010). The beaver population size in Latvia has been estimated from 1928, with some gaps until 1953; thereafter, continuous estimated values are available. Cull limits are available from 1995 onwards; cull limits were also imposed during the Soviet era and were fully satisfied because fur was a quite profitable material at that time. Hunting started in 1981, and the continuous data of the number of hunts were available afterwards, although we did not use them. We used the estimated population size from 1954–2008 for estimations in this paper; this is because continuous data are required for estimation.

The population size of year *t* is denoted as $N(t)$, which is currently evaluated on April 1 every year. In fact, the beaver population census is conducted around this date.[2] Usually, beaver delivery occurs from late April to early May. For nearly a decade, hunting season started in August and continued until the end of the year, while mating season takes place from late January to February. As hunting season was extended after 2009 to include mating season, we used data until 2008 for analyses. For the sake of simplicity, we assumed all beavers reach maturity at 2 years of age.

[2] Currently, population censuses are conducted on April 1 every year. However, before 2003, they were conducted on March 1 every year. In fact, population estimates were made on March 1 for most of the beaver-harvesting period, but hunting season spanned October 1 until March 31. Therefore, this assumption might not be appropriate before 2003. However, the error might not be serious and we adopted this assumption for the sake of simplicity.

Mathematical models and methods

The mathematical model used in this paper is the generalised logistic curve (Richards 1959) with lag, which is as follows:

$$N(t+1)-N(t)=r\left[1-\frac{N(t-\tau)^{\theta}}{K}\right]N(t) \quad (1),$$

where $N(t)$, r, K, τ, and θ are the beaver population size in year t, growth rate, carrying capacity, time lag, and unspecified power, respectively. The value of τ is set at 2. If the values of θ and τ are set at 1 and 0, respectively, eq. (1) is reduced to the Verhulst-Pearl logistic curve; if they are set at 0 and 0, respectively, eq. (1) is reduced to the Gompertz curve (Gompertz 1825, Winsor 1932).

For the estimation, we modified eq. (1) as follows:

$$Y=rX-\frac{r}{K}Z+\varepsilon \quad (2),$$

where $Y=N(t+1)-N(T)$, $X=N(t)$, $Z=N(t-\tau)^{\theta}N(t)$, and ε is residual term.

The number of hunted beavers is often added as one of the factors in mathematical models. That is, we should use $Y=N(t+1)-N(t)+h(t)$ instead of $Y=N(t+1)-N(T)$. However, in our study, we did not include these values because the number of hunted beavers is somewhat in line with the declining reproduction in beaver families. However, the number of mating pairs does not decrease proportionally with culls in the population. Beavers usually share their nest with their family. If they have no offspring and a mate is killed, a new single partner living in a less favourable habitat from the surrounding area might join them and build a new family; this function can be referred to as 'mate substitution'. If a beaver pair has offspring and some of the offspring are killed, this does not directly influence the reproduction for that year. There might be a small possibility that parents are killed and only offspring are left at the nest. Therefore, although the number of reproducing pairs might be reduced due to hunting, the number of mating pairs will be maintained relative to the number of hunted beavers. Consequently, it follows that it is more appropriate to use $Y=N(t+1)-N(T)$ than $Y=N(t+1)-N(t)+h(t)$. In fact, when we used $Y=N(t+1)-N(t)+h(t)$ for estimation, the performance of the results was unfavourable since the t values were smaller, the sign of the parameter was not satisfied, and the estimated vales of the carrying capacity were negative.

We applied both simple ordinary least squares (OLS) and OLS with the Cochrane-Orcutt methods (OLSwCO). High or low Durbin-Watson statistics suggested the results suffered from serial correlation. One of the most widely used methods for avoiding correlations is the application of the OLSwCO (Wooldridge 2006).

As mentioned in the Results section, we cannot select the best model among candidates based on statistical criteria alone. Therefore, we estimated the upper limit of the growth rate assuming that the current population size is lower than the carrying capacity. This assumption is appropriate because the estimated population size increased until 2008. If the current population size is larger than the carrying capacity, the estimated population size is expected to decrease. We estimated the upper limit of the growth rate for 6 time ranges: 1956–1983, 1956–1988, 1956–1993, 1956–1998, 1956–2003, and 1956–2008.

RESULTS

The results are listed in Tables 1–6. As shown in each table, the performance of both $adj.R^2$ and the Akaike Information Criterion (AIC) improve as the value of θ increases. However, we cannot select the best model for the following reason. The AIC is usually used as a criterion for selecting the best model. If the difference in the AIC values of 2 models is <1, we cannot determine which one is better. As the differences in the AIC values were <1 in all tables (e.g. in Table 5, the AIC values are between 14.910 and 14.838 for the OLSwCO), we cannot select the best model (or the value of θ) from the 6 candidates. It follows that we cannot estimate the unique carrying capacity (K) or the

Table 1. Estimation results for 1956–2008 ($\tau = 2$)

θ	**0.2**		**0.4**		**0.6**		**0.8**		**1.0**		**1.2**	
OLS												
K	14.117		165.754		1,797.063		18,679.003		189,279.935		1,883,417.085	
r	0.220	***	0.156	***	0.135	***	0.124	***	0.117	***	0.112	***
Z	-0.016	**	-9.42×0^{-4}	**	-7.49×10^{-5}	**	-6.62×10^{-6}	**	-6.18×10^{-7}	**	-5.97×10^{-8}	**
$adj.R^2$	0.798		0.797		0.796		0.795		0.794		0.793	
$D.W.$	2.704		2.688		2.673		2.661		2.649		2.639	
AIC	16.559		16.565		16.570		16.575		16.580		16.584	
OLS-wCO												
K	13.717		158.447		1,699.681		17,477.961		175,405.564		1,925,000.000	
r	0.229	***	0.161	***	0.139	***	0.127	***	0.120	***	0.112	***
Z	-0.017	***	-1.02×10^{-3}	***	-8.15×10^{-5}	***	-7.26×10^{-6}	***	-6.83×10^{-7}	***	-5.84×10^{-8}	**
$AR(1)$	-0.308	***	-0.374	***	-0.369	***	-0.364	**	-0.360	**	3.33×10^{-4}	

θ	**0.2**		**0.4**		**0.6**		**0.8**		**1.0**		**1.2**	
$adj.R^2$	0.820		0.818		0.816		0.815		0.813		0.786	
$D.W.$	1.961		1.951		1.942		1.935		1.929		2.639	
AIC	16.469		16.480		16.490		16.499		16.508		16.644	

*** Significant at the 1% level, ** 5% level, * 10% level.

θ, K, r, $D.W.$, and AIC are the unspecified power, carrying capacity, growth rate, Durbin–Watson statistics, and Akaike Information Criterion, respectively. $Z = N(t-\tau)^{\theta} N(t)$.

Table 2. Estimation results for 1956–2003 ($\tau = 2$)

θ	**0.2**		**0.4**		**0.6**		**0.8**		**1.0**		**1.2**	
OLS												
K	16.878		212.004		2,397.205		25,697.609		268,144.208		2,755,150.000	
r	0.187	**	0.142	***	0.126	***	0.118	***	0.113	***	0.110	
Z	-0.011		-6.68×10^{-4}		-5.26×10^{-5}		-4.60×10^{-6}		-4.23×10^{-7}		-4.00×10^{-8}	
$adj.R^2$	0.703		0.701		0.700		0.699		0.698		0.698	
$D.W.$	2.529		2.515		2.504		2.495		2.488		2.482	
AIC	16.595		16.600		16.604		16.608		16.610		16.612	
OLS-wCO												

θ	0.2		0.4		0.6		0.8		1.0		1.2	
K	14.318		165.051		1,739.306		17,482.716		170,733.803		1,632,510.460	
r	0.218	***	0.158	***	0.138	***	0.127	***	0.121	***	0.117	***
Z	-0.015	**	-9.58×10^{-4}	*	-7.92×10^{-5}	*	-7.29×10^{-6}		-7.10×10^{-7}		-7.17×10^{-8}	
$AR(1)$	-0.413	**	-0.403	**	-0.394	**	-0.386	**	-0.380	**	-0.374	**
$adj.R^2$	0.734		0.731		0.728		0.726		0.724		0.722	
$D.W.$	1.857		1.851		1.847		1.844		1.843		1.842	
AIC	16.513		16.526		16.536		16.545		16.552		16.558	

*** Significant at the 1% level, ** 5% level, * 10% level.

θ, K, r, $D.W.$, and AIC are the unspecified power, carrying capacity, growth rate, Durbin–Watson statistics, and Akaike Information Criterion, respectively. $Z = N(t-\tau)^{\theta} N(t)$.

Table 3. Estimation results for 1956–1998 ($\tau = 2$)

θ	0.2		0.4		0.6		0.8		1.0		1.2	
OLS												
K	11.921		119.853		1,123.356		10,054.765		88,266.250		757,033.520	
r	0.274	***	0.192	***	0.164	***	0.150	***	0.141	***	0.136	
Z	-0.023	*	-1.60×10^{-3}	*	-1.46×10^{-4}		-1.49×10^{-5}		-1.60×10^{-6}		-1.79×10^{-7}	
$adj.R^2$	0.729		0.726		0.724		0.722		0.721		0.720	

θ	**0.2**		**0.4**		**0.6**		**0.8**		**1.0**		**1.2**	
$D.W.$	1.728		1.708		1.691		1.677		1.665		1.655	
AIC	15.772		15.781		15.789		15.796		15.801		15.805	
OLSwCO												
K	12.075		122.266		1,150.686		10,308.423		90,939.869		777,069.767	
r	0.267	**	0.188	***	0.161	***	0.147	***	0.139	***	0.134	
Z	-0.022		-1.54×10^{-4}		-1.40×10^{-4}		-1.42×10^{-5}		-1.53×10^{-6}		-1.72×10^{-7}	
$AR(1)$	0.137		0.147		0.156		0.163		0.169		0.713	
$adj.R^2$	0.723		0.721		0.720		0.718		0.718		0.717	
$D.W.$	1.971		1.971		1.972		1.973		1.974		1.957	
AIC	15.827		15.833		15.838		15.843		15.846		15.849	

*** Significant at the 1% level, ** 5% level, * 10% level.

θ, K, r, $D.W.$, and AIC are the unspecified power, carrying capacity, growth rate, Durbin–Watson statistics, and Akaike Information Criterion, respectively. $Z = N(t-\tau)^{\theta} N(t)$.

Table 4. Estimation results for 1956–1993 ($\tau = 2$)

θ	**0.2**		**0.4**		**0.6**		**0.8**		**1.0**		**1.2**	
OLS												
K	8.054		61.610		459.779		3,382.906		24,730.069		179,111.712	
r	0.549	***	0.344	***	0.274	***	0.237	***	0.215	***	0.199	***
Z	-0.068	***	-5.59×10^{-3}	***	-5.96×10^{-4}	***	-7.02×10^{-5}	***	-8.68×10^{-6}	***	-1.11×10^{-6}	***
$adj.R^2$	0.544		0.543		0.539		0.534		0.528		0.522	
$D.W.$	2.277		2.268		2.249		2.223		2.195		2.165	
AIC	15.524		15.528		15.536		15.547		15.560		15.573	
OLSwCO												
K	8.014		61.098		454.751		3,344.571		24,421.188		178,201.770	
r	0.562	***	0.352	***	0.279	***	0.241	***	0.218	***	0.201	***
Z	-0.070	***	-5.76×10^{-4}	***	-6.14×10^{-4}	***	-7.22×10^{-5}	***	-8.92×10^{-6}	***	-1.13×10^{-6}	***
$AR(1)$	-0.150		-0.148		-0.139		-0.126		-0.112		-0.097	
$adj.R^2$	0.534		0.532		0.527		0.520		0.512		0.504	
$D.W.$	2.063		2.058		2.049		2.039		2.028		2.019	
AIC	15.586		15.590		15.600		15.615		15.631		15.648	

*** Significant at the 1% level, ** 5% level, * 10% level.

θ, K, r, $D.W.$, and AIC are the unspecified power, carrying capacity, growth rate, Durbin–Watson statistics, and Akaike Information Criterion, respectively. $Z = N(t-\tau)^{\theta} N(t)$.

Table 5. Estimation results for 1956–1988 (τ = 2)

θ	**0.2**		**0.4**		**0.6**		**0.8**		**1.0**		**1.2**	
OLS												
K	8.357		61.577		429.122		2,905.585		19,355.580		128,456.566	
r	0.541	***	0.373	***	0.315	***	0.286	***	0.267	***	0.245	
Z	-0.065	**	-6.06×10^{-3}	**	-8.35×10^{-4}	**	-9.83×10^{-5}	**	-1.38×10^{-5}	***	-1.98×10^{-6}	
$adj.R^2$	0.691		0.695		0.699		0.702		0.704		0.705	
$D.W.$	2.513		2.551		2.579		2.601		2.617		2.628	
AIC	14.920		14.904		14.892		14.883		14.876		14.871	
OLSwCO												
K	8.589		63.741		445.746		3,024.809		20,147.143		133,232.292	
r	0.528	***	0.368	***	0.314	***	0.286	***	0.268	***	0.256	
Z	-0.062	***	-5.78×10^{-3}	***	-7.04×10^{-4}	***	-9.44×10^{-5}	***	-1.33×10^{-5}	***	-1.92×10^{-6}	
$AR(1)$	-0.342	*	-0.351	*	-0.375	*	-0.361	*	-0.363	*	-0.364	
$adj.R^2$	0.707		0.714		0.720		0.723		0.726		0.728	
$D.W.$	2.158		2.194		2.223		2.246		2.263		2.276	
AIC	14.910		14.887		14.868		14.855		14.845		14.838	

*** Significant at the 1% level, ** 5% level, * 10% level.

θ, K, r, $D.W.$, and AIC are the unspecified power, carrying capacity, growth rate, Durbin–Watson statistics, and Akaike Information Criterion, respectively. $Z = N(t-\tau)^{\theta} N(t)$.

Table 6. Estimation results for 1956–1983 ($\tau = 2$)

θ	**0.2**		**0.4**		**0.6**		**0.8**		**1.0**		**1.2**	
OLS												
K	18.269		148.895		1,015.324		6,425.964		39,107.276		232,361.392	
r	0.264		0.231	*	0.219	**	0.213	***	0.210	***	0.207	***
Z	-0.014		-1.55×10^{-3}		-2.16×10^{-4}		-3.32×10^{-5}		-5.36×10^{-6}		-8.91×10^{-7}	
$adj.R^2$	0.632		0.632		0.632		0.632		0.632		0.632	
$D.W.$	1.893		1.893		1.891		1.889		1.887		1.885	
AIC	13.769		13.769		13.769		13.770		13.770		13.770	
OLSwCO												
K	20.184		168.304		1,165.092		7,494.229		46,139.013		277,323.970	
r	0.254		0.025		0.214	**	0.209	**	0.206	***	0.203	***
Z	-0.013		-1.33×10^{-3}		-1.84×10^{-4}		-2.79×10^{-5}		-4.46×10^{-6}		-7.34×10^{-7}	
$AR(1)$	0.051		0.051		0.052		0.053		0.054		0.055	
$adj.R^2$	0.610		0.610		0.610		0.610		0.610		0.610	
$D.W.$	1.925		1.924		1.924		1.922		1.921		1.920	
AIC	13.882		13.882		13.882		13.882		13.882		13.883	

*** Significant at the 1% level, ** 5% level, * 10% level.

θ, K, r, $D.W.$, and AIC are the unspecified power, carrying capacity, growth rate, Durbin–Watson statistics, and Akaike Information Criterion, respectively. $Z = N(t-\tau)^{\theta} N(t)$.

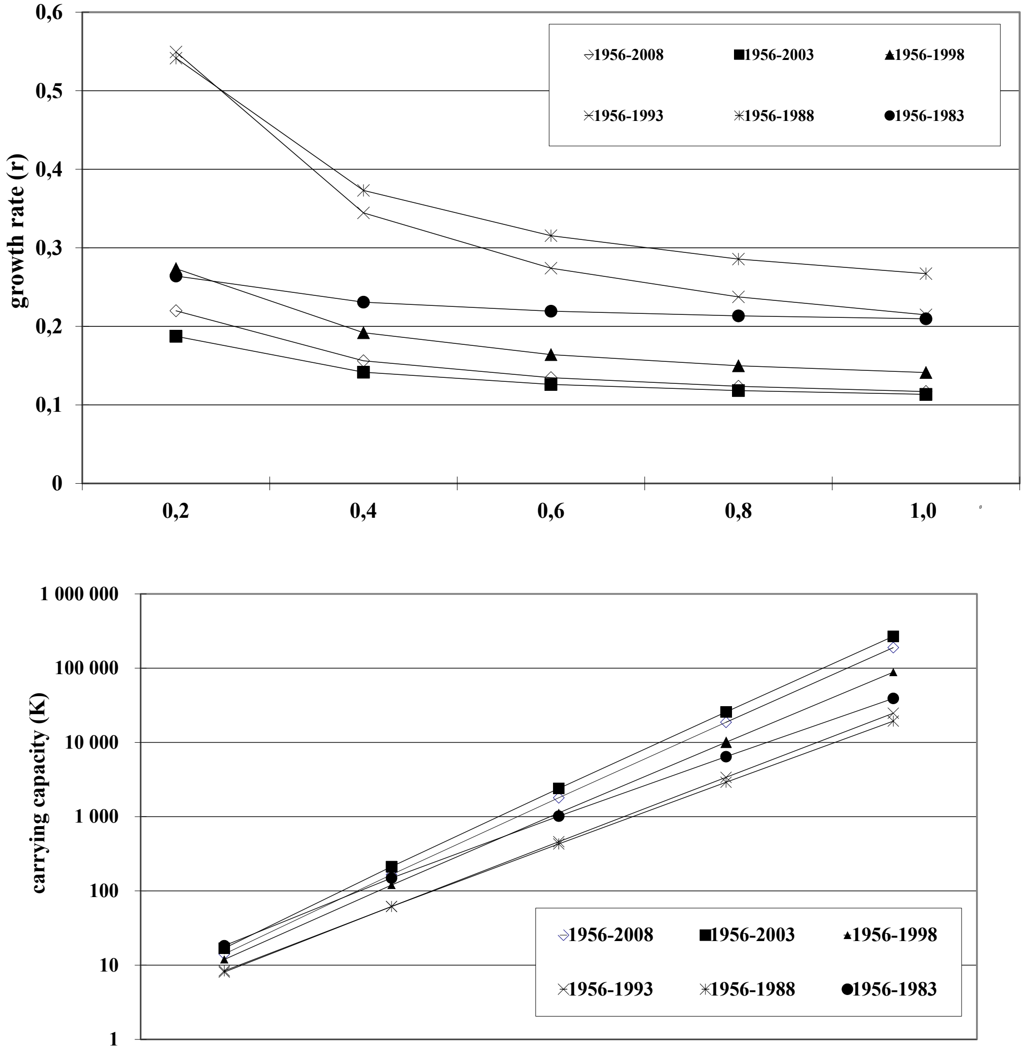

Fig. 1. Relationships between θ and the estimated growth rate (above), and between θ and the estimated carrying capacity (below) when applying the OLS.

growth rate (r) from our data.[3]

However, as suggested above, it is possible to estimate the upper limit of the growth rate if we assume that the current population size is less than the carrying capacity. The relationships among θ , K , and r , whose values are provided in Tables 1–6, are plotted in Fig.1 (OLS) and Fig. 2 (OLSwCO). We applied two functions to calculate the value of the upper limit of r . For example, calculations were performed as follows in the case of the OLS from 1956–2008. First, we applied the exponential function for the graph plotted in Fig. 1.

The result was $K = 1.3882\exp(2.3732\theta)$ (Table 7). Next, we calculated the value of

[3] To be more precise, we must select the best value of θ that minimizes the AIC. However, in our case, the AIC monotonically increases or decreases within the range of $0.2 < \theta < 1.0$.

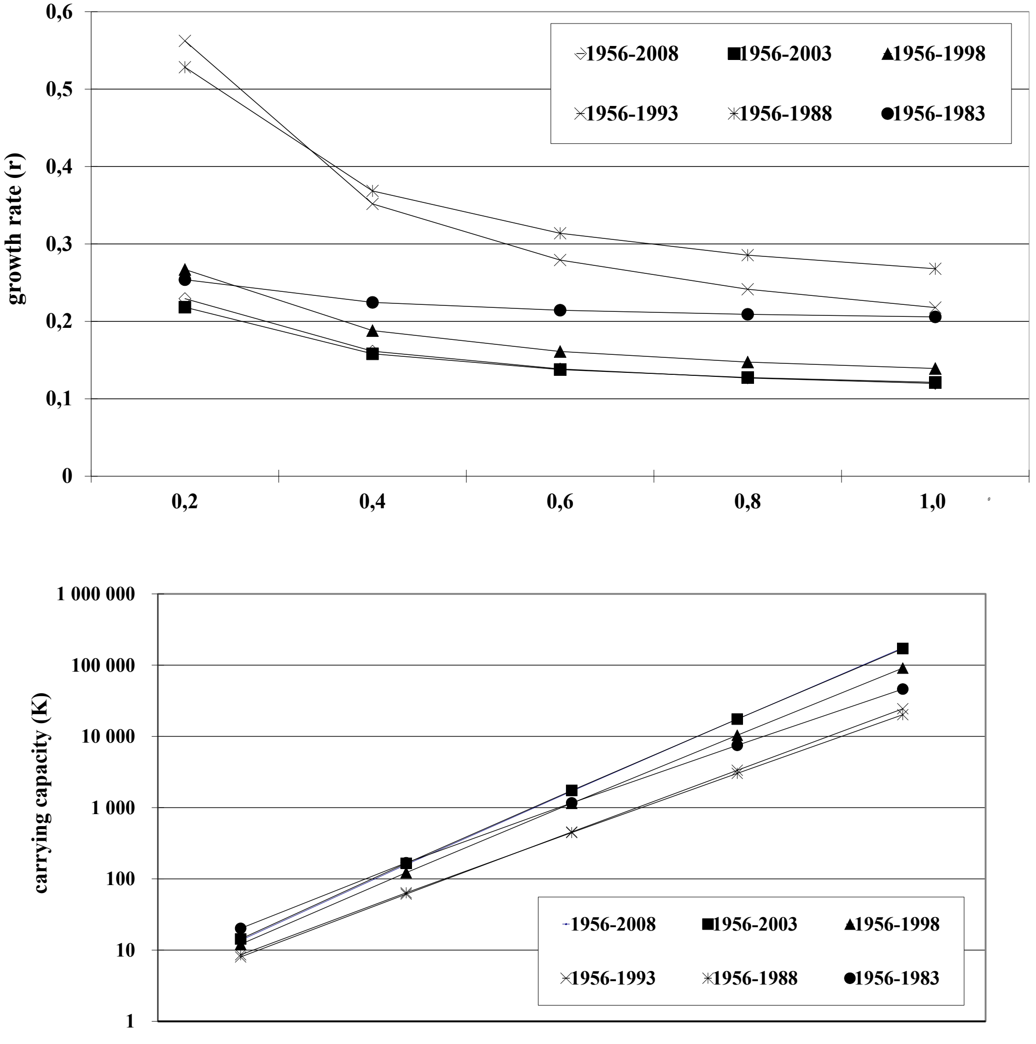

Fig. 2. Relationships between θ and the estimated growth rate (above), and between θ and the estimated carrying capacity (below) when applying the OLSwCO.

θ assuming that the carrying capacity and the current population size were the same. Since the estimated current population size in 2008 was 82,277 heads, θ should be 4.63081.[4] Then, we applied a cubic function for the graph plotted in Fig. 2. The result was $r = -0.0032\theta^3 + 0.0373\theta^2 - 0.1517\theta + 0.337$ (Table 7). By inputting $\theta = 4.63081$, we obtained $r = 0.117$. If we apply the above procedure for all 12 cases (6 cases for OLS and OLSwCO each), we obtain the results shown in Tables 7 and 8.

[4] The values of θ = 0.2, 0.4, 0.6, 0.8, and 1.0 were automatically replaced by 1, 2, 3, 4, and 5 in graphs in Microsoft Excel. Therefore, θ = 4.631 was divided by 5 to calculate the true value of θ = 0.926 in Table 7.

DISCUSSION

Since there is a risk of serial correlation in many cases, we used the results that were based on the OLSwCO. However, since the estimated values

Table 7. Estimation results of the upper limit of r when applying the OLS

	N	Exponential function	Cubic functions	Upper limit of θ	r
1983	5974	$K = 3.0161\exp(1.9103\theta)$	$r = -0.0016\theta^3 + 0.0193\theta^2 - 0.0788\theta + 0.325$	0.795	0.216
1988	15052	$K = 1.2548\exp(1.9345\theta)$	$r = -0.0083\theta^3 + 0.098\theta^2 - 0.3996\theta + 0.8504$	0.971	0.270
1993	20867	$K = 1.1013\exp(2.0065\theta)$	$r = -0.0101\theta^3 + 0.119\theta^2 - 0.4857\theta + 0.925$	0.982	0.214
1998	36755	$K = 1.355\exp(2.2249\theta)$	$r = -0.004\theta^3 + 0.0475\theta^2 - 0.1938\theta + 0.4234$	0.918	0.148
2003	54684	$K = 1.6168\exp(2.4144\theta)$	$r = -0.0023\theta^3 + 0.0267\theta^2 - 0.1087\theta + 0.2713$	0.864	0.115
2008	82277	$K = 1.3882\exp(2.3732\theta)$	$r = -0.0032\theta^3 + 0.0373\theta^2 - 0.1517\theta + 0.337$	0.926	0.117

Table 8. Estimation results of the upper limit of r when applying the OLSwCO

	N	Exponential function	Cubic functions	Upper limit of θ	r
1983	5974	$K = 3.2902\exp(1.9265\theta)$	$r = -0.0014\theta^3 + 0.017\theta^2 - 0.0693\theta + 0.3075$	0.779	0.213
1988	15052	$K = 1.2865\exp(1.938\theta)$	$r = -0.0079\theta^3 + 0.0931\theta^2 - 0.3795\theta + 0.8217$	0.967	0.270
1993	20867	$K = 1.0967\exp(2.0047\theta)$	$r = -0.0103\theta^3 + 0.1221\theta^2 - 0.4988\theta + 0.9481$	0.983	0.223
1998	36755	$K = 1.3685\exp(2.2295\theta)$	$r = -0.0039\theta^3 + 0.046\theta^2 - 0.1876\theta + 0.4121$	0.915	0.143
2003	54684	$K = 1.4601\exp(2.3435\theta)$	$r = -0.003\theta^3 + 0.0352\theta^2 - 0.1432\theta + 0.3289$	0.899	0.124
2008	82277	$K = 1.3613\exp(2.3616\theta)$	$r = -0.0034\theta^3 + 0.0398\theta^2 - 0.1617\theta + 0.3543$	0.932	0.121

of the upper limits of r by both the OLS and OLSwCO are close, the conclusions for both cases will be the same.

First, let us compare our results with the estimated values in existing studies. Balodis (1990) provides values for several parts of Latvia in Table 3.34; the r values range 1.12–1.65. Balodis (1998) estimated the growth rate of beavers in Gauja National Park at 1.103/year. As our results are net growth rates and earlier studies estimated gross growth rates, some modification is necessary to enable comparisons.[5] As expected, some studies report larger values compared to the upper limit of our results; however, most of these values are close to or satisfy the upper limits.[6] Therefore, our results are concordant with those of previous studies.

Second, let us discuss the change in upper limits of r. As mentioned above, beaver hunting was reinitiated in 1981, and relatively intensive but well-controlled hunting continued until 1991. The upper limit of r achieves a maximum when estimating using data from 1956–1988. This result is consistent with intensive hunting during that time. It is quite interesting that although we did not include the number of hunted beavers in our estimation, the results suggest that the growth rate when hunting was intensive was substantially higher than that during other periods. Yet, this phenomenon might also be due to tendencies in number estimation procedures. The figures are possibly biased by the strict regulation of harvest quotas; i.e. during the period of high demand for beaver fur, population estimates pulled ahead of quota allowance.

Third, the upper limit of r decreases after the data range from 1956–1993 is used (Table 8). The possible reasons for this are that (1) hunting pressure was reduced, and (2) the population size increased, making it more difficult to support additional population.

Finally, let us determine if the application of a logistic curve as the growth function is appropriate in the case of beavers in Latvia. The values of θ range 0.795–0.982 and 0.779–0.983 for the OLS and OLSwCO cases, respectively. Our model was reduced to a logistic curve when $\theta = 1$. It is well known that if $\theta = 1$, the growth curve is a convex upward quadratic function. In our case, $\theta < 1$; therefore, the growth function was skewed towards the left, which implies that the peak of the population increment occurred in the first half stage of population growth. As the values of θ around 1956–1988 and 1956–1993 are near 1, the results of Balodis (1990, 1998) appear to be valid.

CONCLUSIONS

The number of hunted beavers has become progressively lower than the cull limits set by the Latvian State Forest Service for 2 decades. On the other hand, forestry damage caused by beavers is one of the most crucial human–wild animal conflicts. To obtain basic information for proper management, we estimated the upper limit of the growth rate of beavers in Latvia. Our results suggest that the growth rate was higher during the 1980s, when beaver fur was most expensive and hunting pressure was strongest. The high growth rate might imply a compensatory response of the beaver population; however, bias in number estimates caused by fur demand cannot be excluded. Although the growth rate decreased recently under weak hunting pressure, the beaver population might increase until it reaches the carrying capacity. In addition, when considering habitat quality, it might be favourable for beavers to limit their population size. The lower growth rate observed in recent years might reflect the fact that the population size was substantially large compared with the carrying capacity, also

[5] For comparisons, the net growth rate of 0.15 can be stated as 15% and the gross growth rate of 1.15 can be stated as 15%.

[6] Since we used data from all of Latvia, our results are average values for the entire beaver population in Latvia. This implies that when comparing results from a specific place, the growth rate in specific places is actually larger than that reported in our results.

reflecting the fact that hunting pressure was low. From both human (e.g. commercial forest preservation) and beaver perspectives (e.g. better habitat), some measure of beaver population control is necessary.

ACKNOWLEDGEMENTS

This paper was first presented at the 8th Baltic Theriological Conference held on 8–9 October 2011 in Lithuania under the title 'Status of the Eurasian Beaver (*Castor fiber* L.) in Latvia after 85 Years of Reintroduction: Emphasis on the Last Few Decades'. The authors are pleased to have had the opportunity to present and receive comments.

REFERENCES

Andersone Ž. 1999. Beaver: a new prey of wolves in Latvia? Comparison of winter and summer diet of *Canis lupus* Linnaeus, 1758. In: Busher P.E. and Dzieciolowski R.M. (eds.): Beaver Protection, Management and Utilization in Europe and North America. Kluwer Academic. Pp. 103 – 108.

Andersone Ž. 2003. Wolves in Latvia: Past and Present. *Wolf Print,* 16: 13 – 14.

Balodis M. 1990. The Beaver. Biology and Management in Latvia. Rīga. Zinātne Publishers (in Russian with English and Latvian summary).

Balodis M. 1998. Beavers in the Gauja National Park, Latvia. *Proc. Latv. Acad. Sci. Sec.* B, 52(1/2): 49 – 53.

Campbell R.D., Rosell F., Nolet B.A., Dijkstra V.A.A. 2005. Territory and group sizes in Eurasian beavers (*Castor fiber*): echoes of settlement and reproduction? *Behav. Ecol. Sociobiol.*, 58(6): 597 – 607.

Gompertz B. 1825. On the nature of the function expressive of the law of human mortality, and on a new method of determining the value of life contingencies. *Phil. Trans. Roy. Soc.*, 115: 513 – 583.

Novak M. 1987. Beaver. In: Novak M., Baker J.A., Obbard M.E., Malloch, B. (eds.): Wild Furbeaver Management and Conservation in North America. Ontario Ministry of Natural Resources: Toronto. Pp. 283 – 312.

Richards F.J. 1959. A flexible growth function for empirical use. *J. Exp. Bot.*, 10: 290 – 300.

Starikov V.P., Anchugov, S.A. 2009. The state of European beaver (*Castor fiber* L., 1758) Population in Kurgan Oblast. *Russ. J. Ecol.,* 40(5): 351 – 355.

Ueda S., Sasaki N., Sweda, T. 2004. Seasonal scatology of wolves along the Dempster Highway, Northwestern Canada: An introduction of pollen analysis for dating old scats. *Polar Biosci.,* 17: 95 – 105.

Vanags J. (ed.) 2010. Medības: Atziņas un Patiesības (Hunting: Cognition and Facts). Rīga. Author's Edition (In Latvian).

Winsor C.P. 1932. The Gompertz curve as a growth curve. *Proc. Natl. Acad. Sci. US A*, 18(1): 1 – 8.

Wooldridge J.M. 2006. Introductory Econometrics: A Modern Approach. Fourth Edition. South-Western.

Received:12.09.2013.
Accepted: 10.10.2013.