Detection of density dependence and adequate representation of parameter uncertainty in population dynamics of Elk (*Alces alces*)

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Abstract

This project focuses on the study of the population dynamics of elk (*Alces alces*). Ricker model and exponential model are selected for the analysis. Firstly, the population dynamics are inferred from an abundance time series, the results of which show that density dependence is likely to exist in the population. Secondly, density dependence is detected with a modified model excluding external influences. Moreover, the impact of models is concluded that Ricker model makes better predictions than exponential model. Parameter uncertainty is also assessed by Ricker model, which leads to worse prediction quality but the trend in future population dynamics still remains the same. Finally, the requirement of further studies is discussed.

1 Introduction

Population dynamics of the elk (*Alces alces*) were analysed in the Bialowieza Primeval Forest, which is one of the best preserved forests of its size and where Europe´s largest community of ungulates, where *A. alces* belongs to, survived. According to Jędrzejewska et al. (1997), data containing information of a large time series is needed to make clear conclusions about the patterns and mechanisms of population change in ungulates. Furthermore, 16-38 year cycles of numbers can occur in nature populations of *A. alces* (Peterson et al. 1984). Here, population dynamics in ungulates were influenced by a combination of stochastic variation in the environment and in population density, leading to changes in their life history traits (Saethe 1997).

This project is based on a 48-year series of population data and consists of three main tasks:
1) inferring population dynamics from an abundance time series;
2) detecting density dependence;
3) assessing the impact of model as well as parameter uncertainty on the prediction of future population dynamics.

2 Materials and Methods

2.1 Materials

The data is an annual time series of the abundance of *A. alces* in Bialowieza Primeval Forest at the border of Poland and Belarus. The information about the *A. alces* population (see Figure 1) come from an experiment where factors influencing population dynamics of different ungulate species were analysed (Jędrzejewska et al. 1997). The data was collected from 1946 to 1993 by a combination of snow tracking, hunting, drive censuses, and counts at baiting sites. The recorded ranges of densities of elks are 0 - 0.6 inds/km^2. In the snow tracking method all tracks were counted and marked on a map and the number of individuals was measured by the difference between entering and leaving these tracks. During periods without snow the abundance was measured by counts at baiting sites or with drive censuses. During a drive census observers moved in an extended line through forest compartments and record the ungulates passing through the line of observers. Furthermore, hunting statistics and mortality data was used to assess the reliability of ungulates abundance (Jędrzejewska et al. 1997).

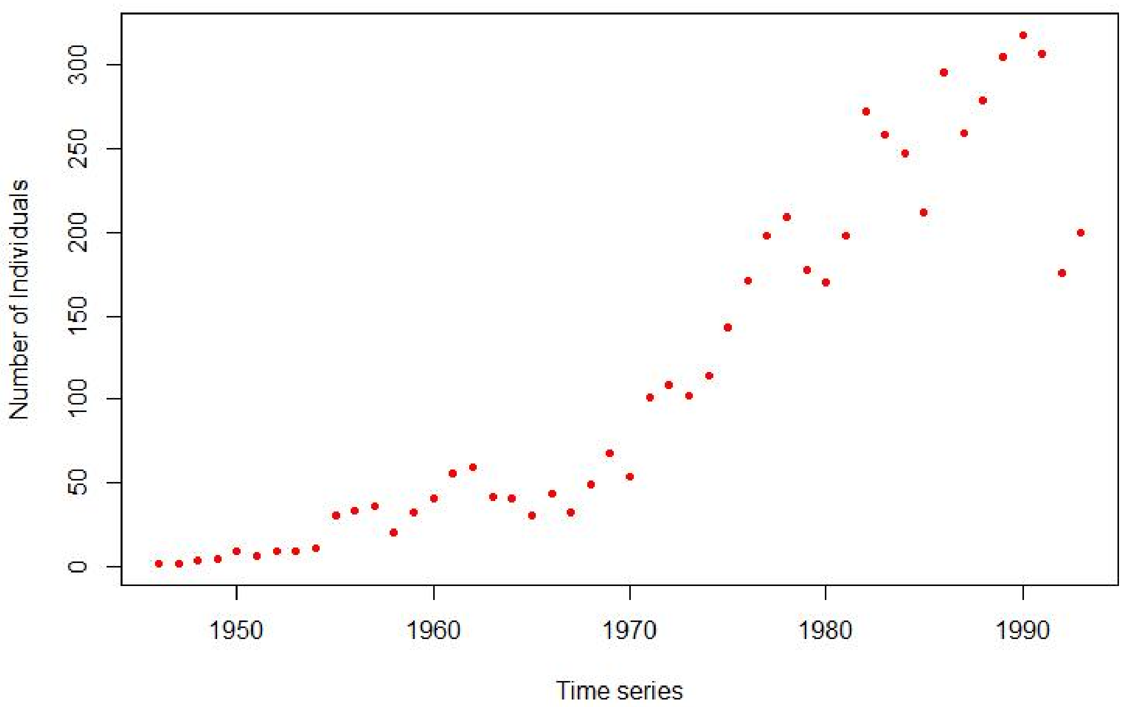

Figure 1: Annual time series from 1946 to 1993 of the abundance of *A. alces*.

2.2 Methods

The Ricker model (II) is the time-discrete equivalent of the logistic growth model (Pagel 2018). By formulating a likelihood function according to the stochastic Ricker model (I & II) as well as a Maximum-Likelihood approach, the parameters (r, K, s) of the model are estimated from the abundance time series. Additionally, a second model is formulated that does not include density dependence, to be specified, the exponential growth model (III) and the parameters (r, s) are estimated as well with a Maximum-Likelihood approach.

Stochastic Ricker model:

$$N_{t+1} \sim NegBinom\ (\tilde{N}_{t+1},\ s) \qquad (I)$$

$$\tilde{N}_{t+1} \sim N_t * (exp\ [r_t\ (1- \frac{Nt}{K})] \qquad (II)$$

Exponential growth model:

$$\tilde{N}_{t+1} \sim N_t * exp\ (r) \qquad (III)$$

The performance of both models is compared by Akaike's Information Criterion (AIC). Furthermore, the dynamics of the Elk population are simulated from year 1933 to 2013 with the Maximum-Likelihood parameters of both models separately. Here, the simulation is repeated 1000 times to quantify the predictive uncertainty that result from model stochasticity. The bootstrapping approach is then used to estimate the standard errors as well as the 95 % confidence intervals for the parameters of the Ricker model. Finally, the same deterministic simulation is performed for each bootstrapped parameter sample and the variation in the predicted abundances is compared to the results from the population simulation for the years 1994 to 2013. The analysis of the data was done with the statistic software R (R Core Team 2013), version 3.4.2.

3 Results

The abundance of *A. alces* from 1946 to 1933 can be seen in Figure 1. At the beginning of the observation only 2 individuals were recorded, but over time the population reached a maximum of 318 individuals in the year 1990 and decreased to 200 individuals in 1993.

3.1 Maximum-Likelihood Estimation

Firstly, the parameters of both models are estimated using a Maximum-Likelihood approach and the performances of both models are compared with the help of the Akaike´s Information Criterion (AIC) values.

The estimated parameters are shown in Table 1. For the Ricker model, the population has a growth rate of 0.22 individuals per time unit and reaches its carrying capacity at 242 individuals. For the exponential model, the population has a growth rate of 0.097 individuals per time unit.

Table 1: Maximum-Likelihood estimation parameters of the stochastic Ricker model and exponential model. r = intrinsic population growth rate, K = carrying capacity, s = size parameter of the negative binomial distribution

	r	***K***	***s***
Ricker model	0.2238823	241.9626011	22.7287586
Exponential model	0.09683957	-	19.29568433

In Table 2 the Akaike´s Information Criterion values of both models are recorded. The AIC value of the Ricker model is lower compared to the AIC value of the exponential model.

Table 2: Comparison of the Akaike´s Information Criterion (AIC) values of both models.

	Akaike's Information Criterion (AIC)
Ricker model	408.9202
Exponential model	412.9516

3.2 Predictions using different models

In the next step, the dynamics of the Elk population are simulated with both models from 1994 to 2013 by using the respective Maximum-Likelihood parameters. The simulations were repeated 1000 times and from the predictions of all replicates the mean, the 25 % as well as the 75 % quantiles and the variance were calculated.

Ricker model

The predicted mean population size ranges from 205 individuals in 1994 to 218 individuals in 2013, see Figure 2. The 25 % quantile has it´s minimum at 156 individuals and the 75 % quantile has it´s maximum at 268 individuals.

Figure 3 shows the predicted variance of the simulated *A. alces* population. In the first 6 years the variance increases significantly from 2120 in 1994 to 6540 in year 2000. Afterwards, the variance ranges around 6200 and reaches in 2008, after 14 years, its maximum at 6993.

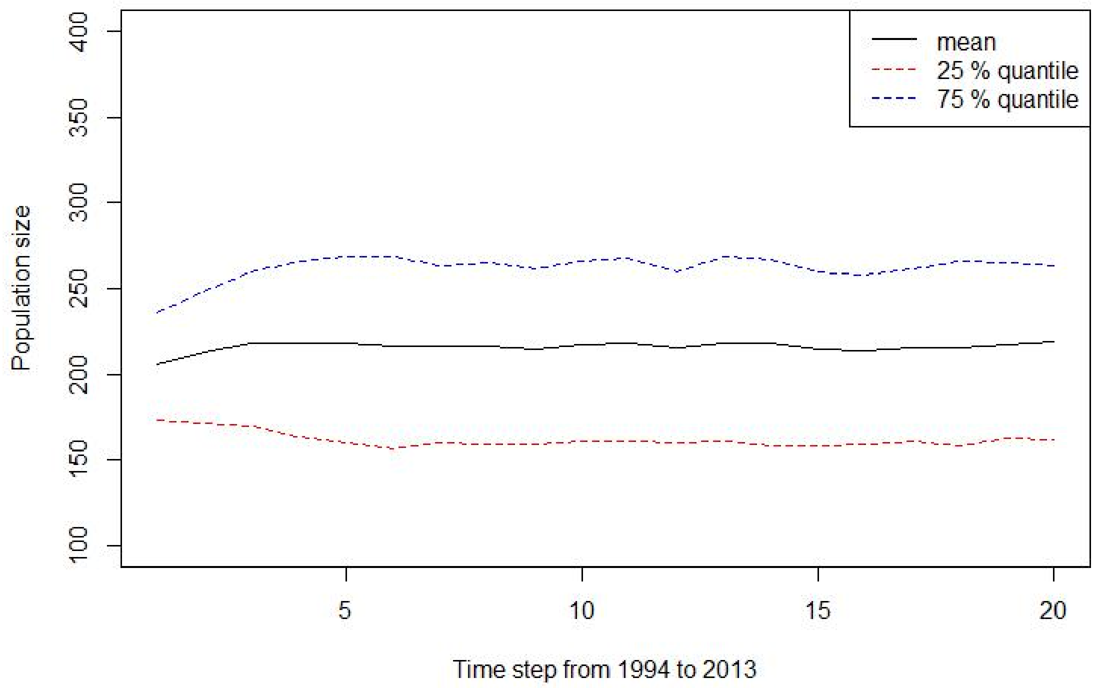

Figure 2: Predicted mean and 25 % quantile as well as 75 % quantile of the simulated *A. alces* population from 1994 to 2013.

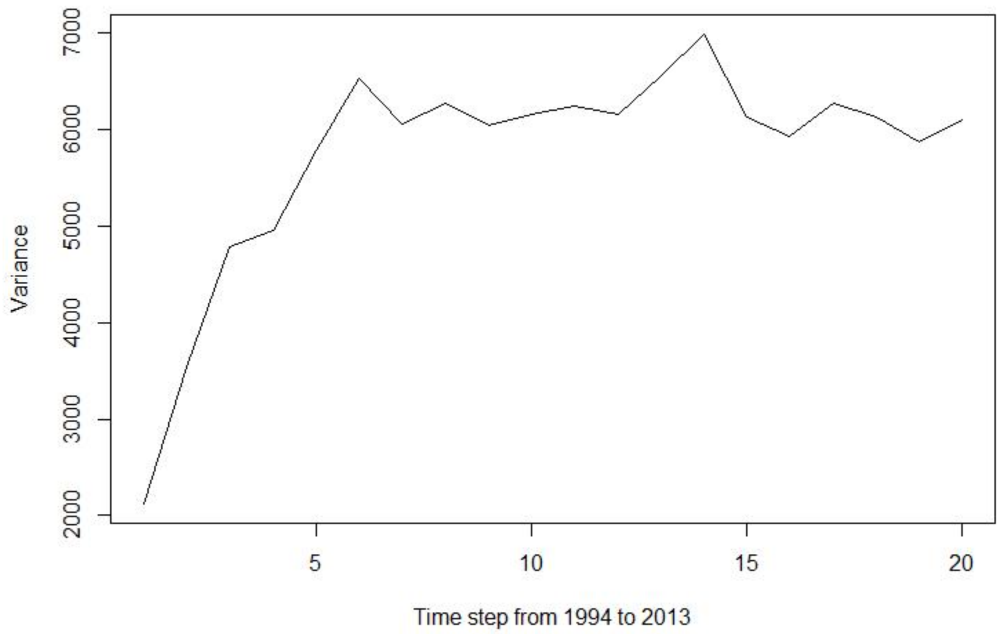

Figure 3: Predicted variance of the simulated *A. alces* population from 1994 to 2013.

Exponential model

The predicted mean population size increases from 223 individuals in 1994 to 1470 individuals in 2013, see Figure 4. The 75 % quantile also increases with time from 255 individuals in the beginning to 1850 in 2013, whereas the 25 % quantile reaches a maximum of 410 individuals.

Figure 5 shows the predicted variance of the simulated *A. alces* population. The variance increases exponential from 2700 in 1994 to 3 652 000 in the year 2013.

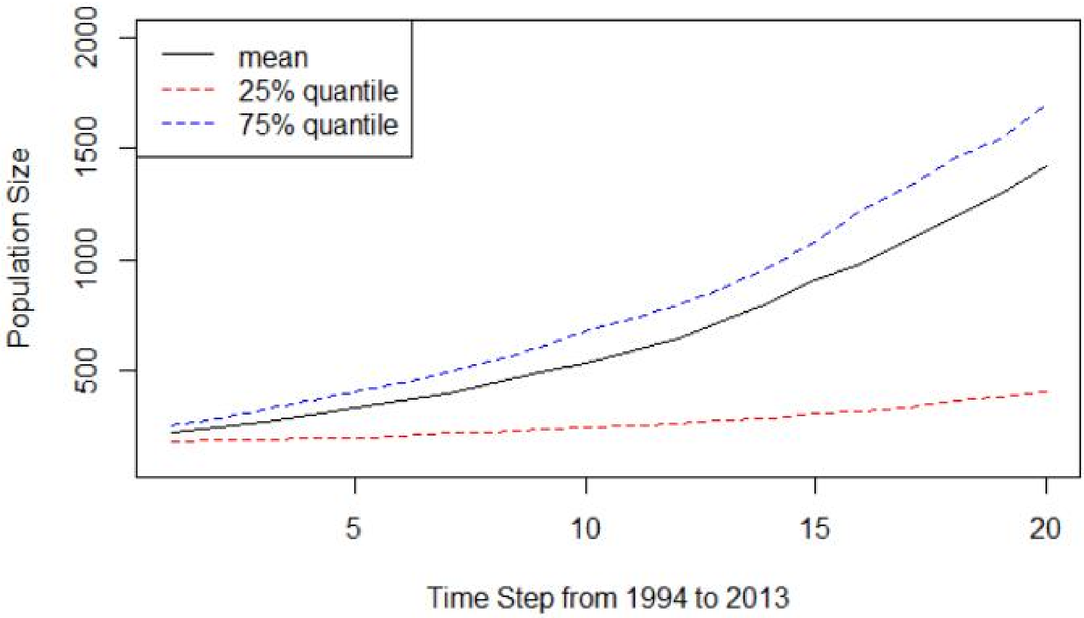

Figure 4: Predicted mean and 25 % quantile as well as 75 % quantile of the simulated *A. alces* population from 1994 to 2013.

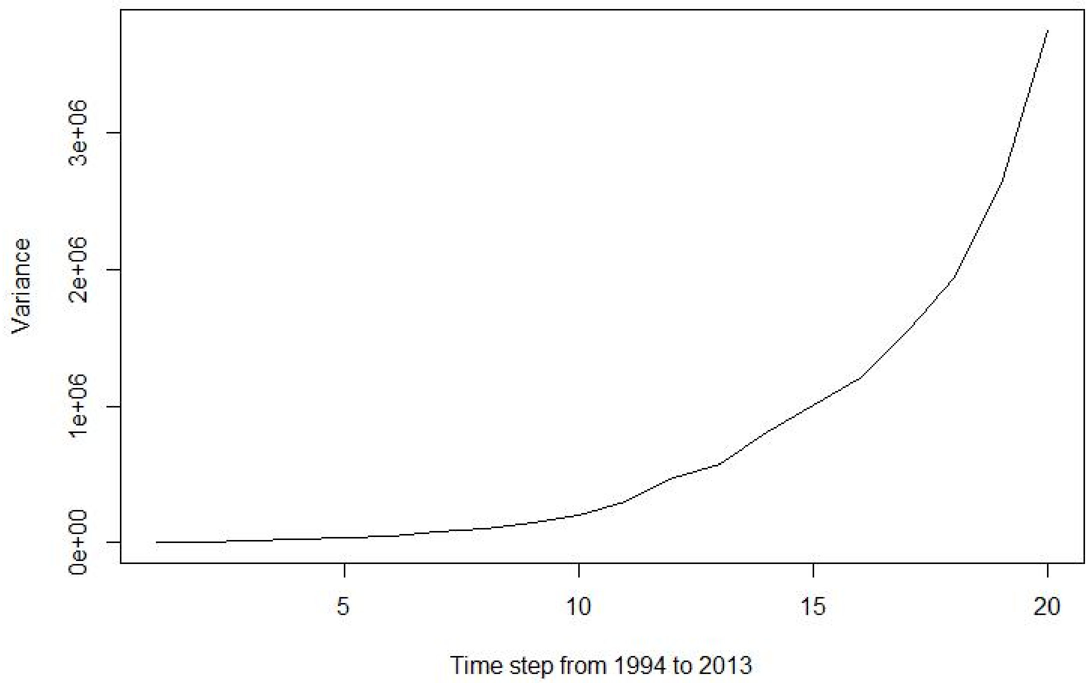

Figure 5: Predicted variance of the simulated *A. alces* population from 1994 to 2013.

3.3 Bootstrapping

Furthermore, the bootstrapping approach is used to estimate the standard errors as well as the 95 % confidence intervals for the parameters of the Ricker model.

The standard error of the parameter r of the Ricker model is 0.079, of parameter K is 290600 and of parameter s is 17.56, see Table 3.

Table 3: Estimated standard errors as well as the mean values for the parameter of the Ricker model. r = intrinsic population growth rate, K = carrying capacity, s = size parameter of the negative binomial distribution

	r	***K***	***s***
Mean	0.2238599	55373.36	28.60074
Standard error	0.0789525	290616.9	17.5621

The histograms for the bootstrap samples of all parameters of the Ricker model can be seen in Figure 6. The confidence intervals of r, K and s lie between 0.066 and 0.370, 156.31 and 667.64, 13.86 and 61.72 separately.

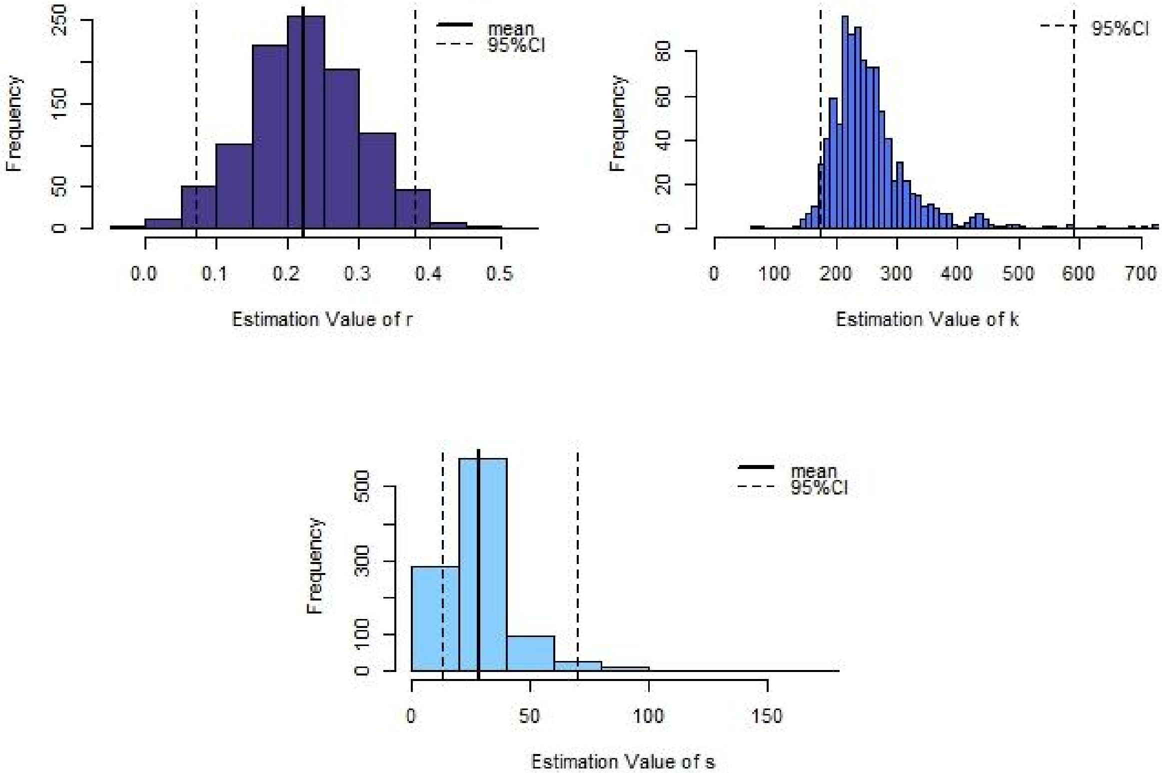

Figure 6: Histogram of the bootstrap sample for parameter r, K and s.

It is worthy to mention that, there are some very large estimations of parameter K, which are far beyond the 95% confidence interval and make the mean very large and standard error very high. It is possible that when the resampled data of bootstrapping are mostly from the early years, when the population stays in a small size, the trend of the population dynamics will be close to an exponential growth. But since the large K estimations are all beyond 95% confidence interval, Ricker model is still considered as more fitted to the time series data.

3.4 Parameter uncertainty

Finally, the same deterministic simulation is performed for each bootstrapped parameter sample and the variation in the predicted abundances is compared to the results from the population simulation for the years 1994 to 2013.

As shown in Figure 7, the predicted mean population size increases from 1994 with 208 individuals to 265 individuals in 2013, due to several very large values of parameter K. In order to represent the data better, the median of the predictions is also calculated. The 25 % quantile keeps stable at about 210 individuals, whereas the 75 % quantile increases from 213 individuals in the beginning to 283 individuals in 2013.

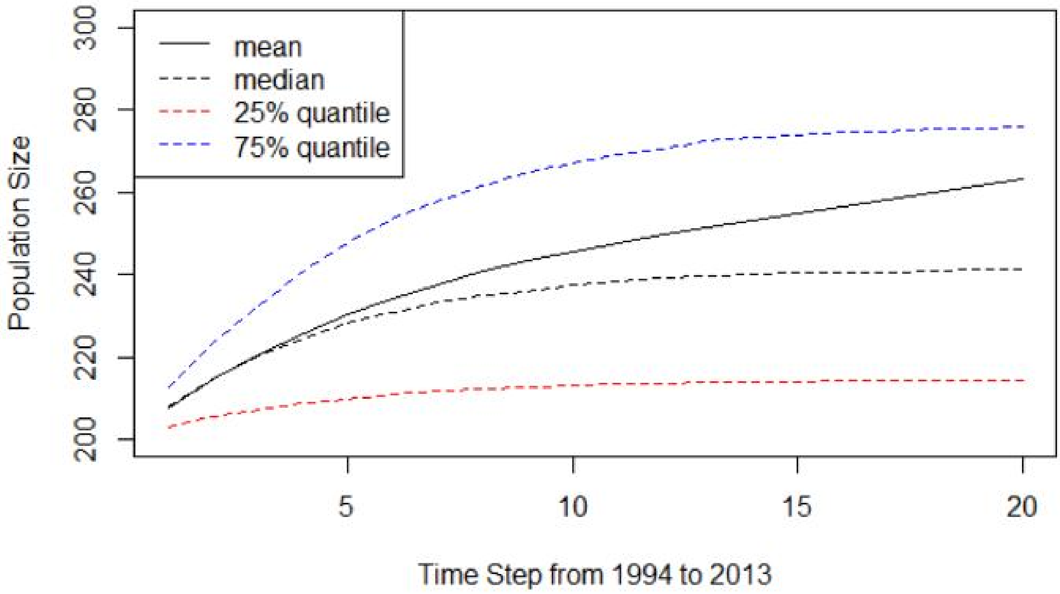

Figure 7: Predicted mean and 25 % quantile as well as 75 % quantile of the deterministic simulated *A. alces* population from 1994 to 2013.

Figure 8 shows the predicted variance of the deterministic simulated *A. alces* population. The variance increases from 52 in 1994 to 15053 in the year 2013.

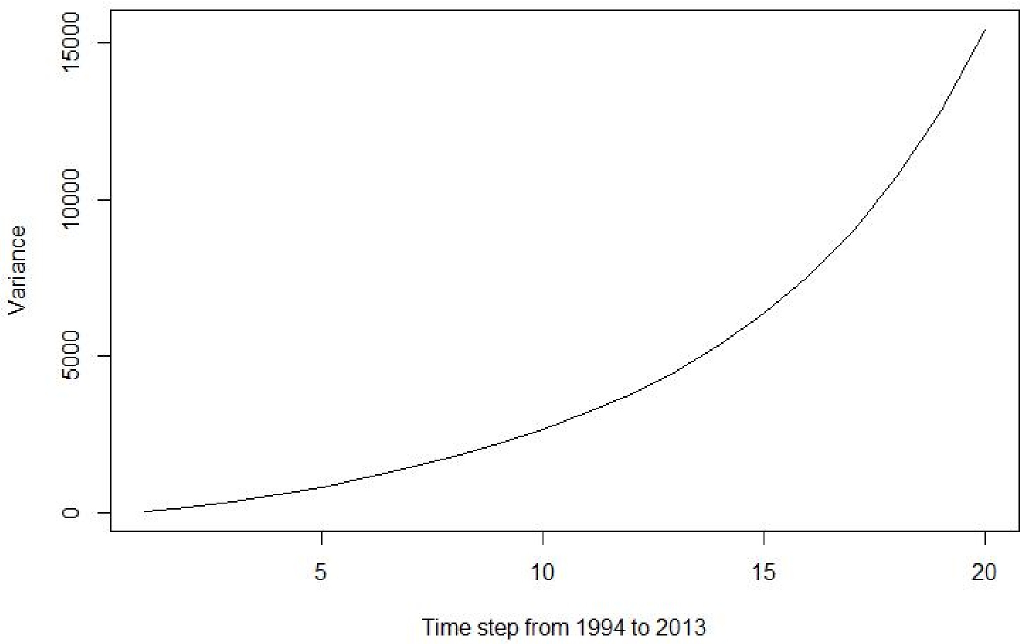

Figure 8: Predicted variance of the deterministic simulated *A. alces* population from 1994 to 2013.

4 Discussion

4.1 Population dynamics and density dependence

The inference of population dynamics from year 1946 to 1993 is attempted by two models: stochastic Ricker model (I & II) and exponential model (III). As AIC (Table 2) of Ricker model is lower, it appears to describe the dynamics better, which indicates the possible existence of density dependence as an intrinsic characteristic in this population. The prediction conducted with stochastic Ricker model (Figure 2) shows a carrying capacity around 220.

In order to detect the density dependence more clearly, another prediction by deterministic Ricker model was conducted which excludes the external influences. The results (Figure 7) show that the population growth will slow down even if external influences are removed from the model.

The conclusion can be made that Elk's population is likely to have density dependence. And the hypothesis is made that the carrying capacity might be around 220 as shown in this study.

4.2 Impact of model and parameter uncertainty

The impacts of models are assessed by making predictions with stochastic Ricker model and exponential model. The variance curves (Figure 3 & 5) are compared. The Ricker model has a less variance growth, which indicates a more accurate prediction.

Parameter uncertainty is also assessed with stochastic and deterministic Ricker model. A certain parameter set is used for the prediction with the former model and an "uncertain" group of parameter sets from bootstrapping approach are used for the latter. The median of predictions (Figure 7) shows the same trend of reaching a carrying capacity. As the variance increases in the latter case (Figure 8), a conclusion can be drawn that parameter uncertainty leads to worse accuracy in prediction but the trend in future population dynamics still remains the same.

4.3 Requirement of further studies

When the data were checked again, however, there's evidence that appears to oppose the hypothesis made in 4.1. The population declines suddenly in the last two years, the reason of which is indicated by Jędrzejewska et al. (1997) to be elevated hunting plans. This external influence leads to a wrong estimation of the carrying capacity. In order to get a more convincing result, further studies are required.

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