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Research article

MODELLING BANK VOLE POPULATION DYNAMICS AS A FUNCTION OF CLIMATE VARIABLES

Sara Amirpour Haredasht[1], Piet Maes[2], Jan Clement[2], Willem W.Verstraeten[3,4], Marc Van Ranst[2],
Pol Coppin[5], Daniel Berckmans[1] and Jean-Marie. Aerts[1]

[1]Division Animal & Human Health Engineering, Department of Biosystems, KU Leuven, Kasteelpark Arenberg 30, B-3001 Leuven, Belgium
[2]Laboratory of Clinical Virology, Rega Institute, KU Leuven, Minderbroedersstraat 10, B-3000 Leuven, Belgium
[3]Royal Netherlands Meteorological Institute (KNMI), Climate Observations, PO Box 201, NL-3730 AE, De Bilt, the Netherlands
[4]Eindhoven University of Technology, Applied Physics, PO Box 513, 5600 MB, Eindhoven, the Netherlands
[5]Division of Crop Biotechnics, Department of Biosystems, KU Leuven, Willem de Croylaan 34, B-3001 Leuven, Belgium

ABSTRACT: Wildlife-originated zoonotic diseases are a major contributor to emerging infectious diseases. Understanding the role of climate factors in shaping the dynamics of the natural host population is a central challenge within the field of population ecology. Bank voles (*Myodes glareolus*) are reservoirs of the *Puumala hantavirus* (*PUUV*), which can cause the disease nephropathia epidemica (NE) in human.

In this study we model the bank vole population dynamics in Belgium and Finland using a multiple–input, single-output (MISO) transfer function. The output of the MISO models was the number of bank vole and the inputs were monthly North Atlantics Oscillation (NAO), average monthly precipitation (mm), and temperature (°C).

In a first step, the bank vole populations in Belgium were modelled based on data from 1976 till 1982 with a R_T^2 of 0.66. For Finland the modelled bank vole density dynamics using data from 1995-2001 resulted in a R_T^2 of 0.78. In a next step, the MISO models were validated using bank vole populations time series from 2009 to 2011 (R_T^2 of 0.68) for Belgium and from 2002 till 2008 (R_T^2 of 0.66) for Finland.

Despite the difference in bank vole population dynamics between the Western European temperate zone (such as Belgium) and boreal zones (such as Finland), the MISO model managed to describe the temporal characteristics of the two time series and their different dynamic mechanisms.

Such modelling approach might be used as a step towards the development of new tools for the prediction of future NE outbreaks.

Key words: Bank voles, Myodes glareolus, nephropathia epidemica, hantaviruses, rodent born diseases, population dynamics, model, climate change, zoonosis.

*Corresponding author: Jean-Marie. Aerts, Division Animal & Human Health Engineering, Department of Biosystems, KU Leuven, Kasteelpark Arenberg 30, B-3001 Leuven, Belgium E-mail: Jean-Marie.Aerts@biw.kuleuven.be +32 16 321434 or +32 16 321436

INTRODUCTION

Hanta viruses are rodent or insectivore borne viruses, some of which are recognized as a cause of hemorrhagic fever with renal syndrome (HFRS) in humans [1]. In Europe, one of the most important hantavirus is the *Puumala virus* (PUUV), which is transmitted to humans by infected bank voles (*Myodes glareolus*) [2]. PUUV causes a general mild form of HFRS called nephropathia epidemica (NE) [3]. Fifteen emerging zoonotic or vector-borne infections with increasing impact on humans in Europe were identified during the period 2000-2006. Rodent-borne Hantaviruses are part of this list [4]. Global climate change might be a major contributor to the spread of these vector-borne diseases [4, 5].

Rodent population dynamics in temperate zones (such as Belgium) and boreal zones (such as Finland) are very different. Climate change is known to be able to drive animal population dynamics between stable and cyclic phases [4,5]. For example, large scale climate fluctuations, such as the North Atlantic Oscillation (NAO) has been suggested to cause the recent changes in cyclic dynamics of bank voles and their predators in boreal zones [6]. However, although predator–rodent interactions are commonly argued to be the cause of the bank vole cycles [7,8,9], in boreal zones (such as Finland) the role of the environment in the modulation of such dynamics is often poorly understood in natural systems. In temperate zones (such as Belgium) high summer temperature induces the formation of flower buds of deciduous forest trees (oak and beech), resulting the next year in an abundance of seed production. Acorn and beech mast fall down in autumn, contributing to the high winter survival and early breeding of voles in a mast year (bottom-up regulation). This leads to high rodent densities and more human NE cases in summer [10]. In the boreal zone, like in Finland, the primarily coniferous forests do not provide significant mast production, so the vole cycles are determined predominantly by interactions between voles and their specialist mammalian predators (top-down regulation) and winter food resources [7, 8,9]. However, there is a trade-off between top-down and bottom-up regulation of summer population growth: shallow snow cover may reduce the densities of the specialist predators but cold temperatures may expose food plants to frost and desiccation damage and reduce their productivity during the following summer [11,12, 13]. Quantitative links (models) between climate-driven processes and rodent dynamics have so far been lacking**.**

Mechanistic models play an important role in analysing the spread and control of infectious diseases. Many attempts have been made to build mathematical models describing the dynamics of the bank voles' population and spread and survival of PUUV [14,15]. These models are typically based on components such as an epidemiological compartment structure, the nature of the incidence, a demographical structure of the population, and the interaction between the demographical structure and the epidemiological incidence of the disease.

Although these mechanistic models have important scientific merits, they also have limitations. Often, these models just show the demographic variability of the population without considering the environment and its impact on the target population.

Taking into account the role of the climate conditions, knowledge of these conditions can assist in (i) a better understanding the characteristics of the bank vole population dynamics, (ii) making forecasts about the bank vole population based on expected trends in future climatological conditions and (iii) analysing crucial data that influence the population of bank voles. Therefore, models that consider the dynamics of climate conditions may play an important role in improving modelling and predicting the voles population and therefore the NE cases.

Because of the dynamic nature of the bank vole populations, a dynamic systems approach might be a valuable alternative to mechanistic models for investigating the underlying mechanisms. The resulting dynamic data-based models of this type are often simple in structure, inherently stochastic in form and are characterised by the minimum number of parameters required to justify the dynamic information content of the available data [16].

We previously demonstrated that NE outbreaks can be predicted based on climate and vegetation data or bank vole dynamics by using dynamic data-based models [17]. Kalio et al., [18] were first to show that the human NE cases in Finland are predicted by bank vole dynamics, even without any knowledge about hantavirus dynamics in the host population. The time variation in NE outbreaks in Finland could be predicted three months ahead with a 34% mean relative prediction error (MRPE) by taking into account the measured population dynamics of the carrier species (bank voles) [17]. Time series analysis revealed that the vegetation index, changes in forest phenology (which can be derived from satellite images) and climate fluctuation, which are all considered as an effect of climate change, affect the mechanisms of NE transmission.

NE outbreaks in Belgium were predicted three months ahead with a 40% MRPE, based only on the climatological data and vegetation data, and without any knowledge of the bank vole population dynamics [17]. In another study, a multiple-input, single-output (MISO) model was developed, describing the NE cases as a function of three inputs: average measured monthly precipitation (mm), and temperature (°C), as well as the estimated carrying capacity (voles ha^{-1}) from the SIR (Susceptible, Infective and Remove with immunity) model of Sauvage et.al., [14,15] for Belgium over an 11 years study period (1996-2008) [19].

Since bank vole dynamics is a key factor in predicting and managing NE outbreaks on the one hand, but is very expensive and labour intensive to measure on the other hand, it would be a significant advantage if bank vole populations' dynamics could be modelled as a function of climatic drivers.

Therefore, the objective of this research was to build a multiple–input, single-output (MISO) transfer function to model the fluctuations of bank vole density dynamics. Because of the difference between the Western European temperate zone and boreal zones, we used time series data sets from Finland and Belgium. First, we modelled the bank vole population in Belgium from 1976 till 1982 as a function of measured average monthly air temperature (°C), monthly precipitation (mm) and NAO. We used the same approach to model the bank vole density in central Finland from 1995-2001. To validate the data based model we used the second part of the data set, namely the data derived from a bank voles trapping campaign in Belgium (from 2009-2011) and the dynamics of bank vole density in Finland from 2001-2008 and the average monthly air temperature (°C), monthly precipitation (mm) and NAO measured during these periods.

MATERIALS AND METHODS

Bank vole population data

Capture-mark-recapture data

Remotely sensed data and geographic information system (GIS) information were used to select two sites for trapping bank voles. The main selection criterion for field measurements was based on the preferred habitat of bank voles. Therefore, the search was directed to broad-leaved forests located in the neighbourhood of water streams and with presence of an understorey. The selection was done after field visits which were preceded by a GIS-based pre-selection phase. The forest stand where measurements were taking place was located in the municipality of Gierle (Antwerp, Belgium, 51.288 N, 4.885311 E). The trapping site had a dense understorey layer under an open canopy of beech (*Fagus sylvatica*) and native oak species (*Quercus robur, Quercus petraea*). Common understorey species belong to the *genus Rubus*, *Corylus*, *Rhamnus*, *Ilex* and *Equisetum*.

In 2009, these trappings were organized monthly (12 times a year), and in the years thereafter the trappings were organized once every season (4 times a year). During the years 2009-2011, Capture-Mark-Recapture (CMR) studies enabled monitoring of vole population dynamics.

In order to estimate the bank vole population density based on the CMR method we used the POPAN formulation (Schwarz & Arnason 1996) [20] of Jolly-Seber models [21] as implemented in the program Mark (version 4.10). Assumption of equal chances to capture-mark and recapture animals was made.

In the Jolly-Seber model, the parameter ρ is the probability of recapture marked and unmarked animals that are alive at occasion *i*, *Φ* is the survival probabilities of both marked and unmarked animals between occasion i and i+1 and the parameters b_i are referred to as the probability of entrance from the super population (*N*) between occasion *i* and *i*+1.

We started by fitting a fully-time dependent model {$\rho'\emptyset'b'$} (where the *apostrophe* represents the time dependency of the parameter).

Since the original sampling experience has approximately equal effort at all sampling occasions, a model with constant catchability over time might be suitable (i.e. model {$\rho\emptyset'b'$}. But also another sub model can be fit where both the catchability and the apparent survival rate (per unit of time) are constant over all intervals (i.e. model {$\rho\phi b'$}). This resulted in three possible candidate models: {$\rho'\emptyset'b'$}, {$\rho\emptyset'b''$} and [$\rho\phi b'$].

Selection among candidate models was carried out using Akaike's information criterion corrected for small sample sizes (hereafter AICc) (Burnham and Anderson, 1998). The smaller AICc, the better the model is relative to the other models in the set. We calculated the difference in AICc from the model with the lowest AICc score (noted ΔAICc). Models with 0≤ΔAICc≤2 were considered as substantially supported by the data. Models with larger ΔAICc scores 4≤ΔAICc≤7 were regarded as less supported or essentially not supported (ΔAICc≥10) by the data (Burnham and Anderson, 1998). Models with ΔAICc≤2 are not statistically distinguishable; when this occurs the model with the smallest number of parameters is preferred [22].

Existing bank vole population time series

Bank vole population data in Belgium were derived from Verhagen et al. [23]. Bank voles were trapped every three or four weeks from May 1976 to August 1982 in the military domain in Zevendonck, one kilometre away from our bank voles trapping site in Gierle.

Bank vole trapping index data in Finland were derived from Kallio et al. [18]. Trapping index (%), is equal to total number of rodents trapped/(total number of traps×total number of nights−1/2 of traps sprung not containing a rodent)×100 [24]. Bank voles were trapped in the Konnevesi area in Central Finland (628379 N, 268209 E) four times per year. They used the bank vole trapping index data of the captured bank voles from July 1995 to October 2008. The trapping plots were situated in coniferous forest dominated by Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and various shrubs (e.g. *Calluna sp*., *Vaccinium spp*).

Climate data

Monthly indices of the NAO, defined as the difference of normalized sea level pressures (SLP) between Ponta Delgada, Azores and Stykkisholmur-Reykjavik, Iceland are available since 1865. These data were provided by the Climate Analysis Section, NCAR, Boulder, USA (Hurrell and Dickson, 2004).

The Royal Meteorological Institute of Belgium (Ukkel) provided daily data on air temperature (°C) and precipitation (mm) for the periods 1976-1982 and 1996-2008. For modelling the dynamics of the NE cases, we calculated monthly average precipitation (mm) and average temperatures (°C) based on the daily reported climate data of Turnhout (Belgium).

The Finnish Meteorological Institute provided climatological data of monthly values for the Konnevesi area in Central Finland (again, the most endemic region of the country). Mre specifically, for modelling the dynamics of the bank voles population, we obtained the sum of precipitation (mm) and average air temperature (°C) from 1996-2008.

METHODS

Dynamic data-based modelling

The objective of the next step was to quantify the dynamics of the bank voles population in North of Belgium and Central of Finland and to relate it with environmental data. Therefore, a multiple–input, single-output (MISO) transfer function (TF) was used to model the bank vole population from 1976 until 1982 as function of the climatological data of average measured temperature, precipitation and NAO. The used model structure could be described as follows:

$$\boldsymbol{R(t)} = \frac{B_T(z^{-1})}{A(z^{-1})}\boldsymbol{N(t - nt_N)} + \frac{B_N(z^{-1})}{A(z^{-1})}\boldsymbol{T(t - nt_T)} + \frac{B_N(z^{-1})}{A(z^{-1})}\boldsymbol{P(t - nt_P)} + \boldsymbol{\varepsilon(t)} \qquad \text{Equation 1}$$

Where $R(t)$ is the number of bank voles per hectare; t represents discrete-time instants with a measurement interval of one month, $N(t)$, $T(t)$ and $P(t)$ represent the three inputs of the model namely: monthly NAO, average monthly air temperature (°C) and monthly precipitation (mm) respectively. nt_i is the number of the time delays (expressed in month) between each input i and their first effects on the output; $A(z^{-1})$ is the denominator polynomial and equals to $1+a_1 z^{-1}+a_2 z^{-2}+\ldots+a_{na} z^{-na}$; $B_i(z^{-1})$ are the numerator polynomials linked with the inputs i and equals to $b_{0i}+b_{1i} z^{-1}+b_{2i} z^{-2}+\ldots+b_{nbi} z^{-nbi}$; a_j, b_i are the model parameters to be estimated; z^{-1} is the backward shift operator, defined as $z^{-1}\, y(t)=y(t-1)$; na, nb_i are the orders of the respective polynomials; $\varepsilon(t)$ is additive noise, a serially uncorrelated sequence of random variables with variance σ^2 that accounts for measurement noise, modelling errors and effects of unmeasured inputs to the process (assumed to be a zero mean).

In order to be able to use the estimated dynamics of bank vole density by the MISO model we had to interpolate the bank vole population data since the estimated numbers were not equidistant. The interpolation was performed using a dynamic harmonic regression model (DHR) which is fully described in Taylor et al. [25]. The same approach was used to interpolate the bank vole population in Finland [17].

The model parameters of the MISO model were estimated by means of a refined instrumental variable approach using the Captain toolbox in Matlab® [16, 25].

The dynamics of bank vole density in Belgium were modelled based on data from 1976 till 1982 and the dynamics of bank voles density in central Finland were modelled based on data from 1995-2001. In a next step, the MISO models were validated using bank vole population time series in Belgium from 2009 to 2011 and bank vole trapping index in Finland from 2002 till 2008. For each data set, the model parameters of Equation 1 were estimated. The resulting models were evaluated by the coefficient of determination (R_T^2; Young & Lees, 1993).

The ability to estimate the parameters of a transfer function model represents only one side of the model identification problem. Equally important is the problem of objective model order identification. This involves the identification of the best choice of orders of the polynomials $A(z^{-1})$ and $B_i(z^{-1})$. The process of model order identification can be assisted by the use of well-chosen statistical measures that indicate the presence of over parameterisation. A good identification procedure used to select the most appropriate model order [na, nb_i] is based on the minimisation of the Young Identification Criterion [26].

The YIC is a heuristic statistical criterion that consists of two terms. The first term provides a normalised measure of how well the model fits the data. The smaller the variance of the model residuals in relation to the variance of the measured output, the more negative this term becomes. The second term is a normalised measure of how well the model parameter estimates are defined. This term tends to become less negative when the model is over parameterised (more complex) and the parameter estimates are poorly defined. Consequently, the model that minimises the YIC provides a good compromise between goodness of fit and parametric efficiency (which is equivalent to complexity).

Next to the YIC, the standard errors on the parameter estimates were calculated as the root of the diagonal elements of the covariance matrix. Based on the standard errors the 95% confidence interval ($CI_{95\%}$) for each parameter estimated ($\hat{\theta}$) could be calculated as:

$$CI_{95\%} = \hat{\theta} \pm t_{0.025N-np} SE(\hat{\theta}) \qquad \text{Equation 2}$$

Where $t_{0.025,N-np}$ is the value given by the two tailed student t distribution with N the number of data used to estimate the parameters and np the number of the parameters. In this study, the value for the $t_{0.05,N-np}$ was approximately two. This means that the parameter estimation was considered to be reliable when the observed value of the parameter estimate was at least twice the value of its standard error (meaning that the parameters value was significantly different from zero) [16].

Finally, the model stability was calculated for the selected TF models as part of the model evaluation. Stability was determined by quantifying the poles (roots of the $A(Z^{-1})$ polynomial) of the models. The model is considered stable when all the poles lie within the unity circle in the complex plane or z plane [27].

In order to identify the models for the whole period 1976-1982 for Belgium, different combinations for na, nb_N, nb_T, nb_P, nt_N, nt_T and nt_P were calculated. More specifically for the MISO model with three inputs, na, nb_T, nb_P and nb_N ranged from1 up to 2, nt_N, nt_T and nt_P ranged from 0 up to 6. Therefore, to identify the first MISO model of three inputs and one output in total 5488 ($2 \times 2 \times 2 \times 2 \times 7 \times 7 \times 7$) possible TF models were calculated.

All these models were ranked based on the YIC (from low to high values). Only the first 20 best models as indicated by the YIC were selected for further evaluation. Using the resulting 20 models, the TF order identification was made on the basis of the goodness of fit, expressed as the coefficient of determination R_T^2, the confidence interval of the estimated model parameters and the stability of the resulting model. This approach was used to identify one final model (i.e. model structure with specific model parameters) for the whole period from 1976 until 1982. The identified model structure was validated by applying the same model structure (i.e. using the same model order but different time delays) to input-output data from 2009-2011. Validation can be defined as the process that determines the accuracy of with which a model represents a real system [26].

The same approach was used to model the dynamics of bank vole density in Finland for the period 1995-2001. More specifically for the MISO model with three inputs, na, nb_T and nb_N ranged from1 up to 2, nt_N, nt_T and nt_P ranged from 0 up to 12. Therefore, to identify the first MISO model of three inputs and one output in total 35152 ($2 \times 2 \times 2 \times 2 \times 13 \times 13 \times 13$) possible TF models were calculated. The identified model was validated by applying the same model structure to input-output data of Finland from 2002-2008.

RESULTS

According to ΔAICc we selected the model $\{\rho\phi b'\}$ (Table1). The bank vole abundance estimated by POPAN formulation in Mark together with the resulting interpolated series using the DHR model is demonstrated in Figure 1.

Table 1. Selection summary of three models examine by MARK to estimate the bank voles population in Belgium based on the capture-mark-recapture in Gierle from 2009 till 2011.

models	AICc	ΔAICc
$\rho\phi b'$	336.5520	0.0000
$\rho\phi' b'$	343.7631	7.2111
$\rho'\phi' b'$	352.8824	16.3304

The apostrophe represents the time dependent parameter.

The aim of this study was to quantify the dynamics of the bank vole density in Belgium and Finland and to relate it with climatological data (average monthly temperature, precipitation and NAO) only. When applying the modelling approach to the period from, 1976 until 1982, YIC selected models that were predominantly second order (na = 2, equation 1). There was one model structure that (i) was selected by YIC as being one of the 20 best models, and (ii) was stable (all poles within the unit-circle in the z-plane). This model structure was described by na =2, nb_T =1, nb_P =1, nt_N = 5, nt_T= 4 and nt_P= 5. The resulting TF model structure is represented in Equation (3, 4):

$$R(t) = \frac{b_T z^{-1}}{1+a_1 z^{-1}+a_2 z^{-2}} N(t-nt_N) + \frac{b_P z^{-1}}{1+a_1 z^{-1}+a_2 z^{-2}} T(t-nt_T) + \frac{b_N z^{-1}}{1+a_1 z^{-1}-a_2 z^{-2}} P(t-nt_P) \quad \text{Equation 3}$$

or written in time series notation as:

$$R(t) = -a_1 R(t-1) - a_2 R(t-2) + b_N N(t-5) + b_T T(t-4) + b_p P(t-5) \quad \text{Equation 4}$$

From the modelling results in Figure 2, it is clear that the model was able to describe the dynamics of bank vole density quite well (with R_T^2 of 0.66). The specific values for the model parameters and their standard errors are presented in Table 2.

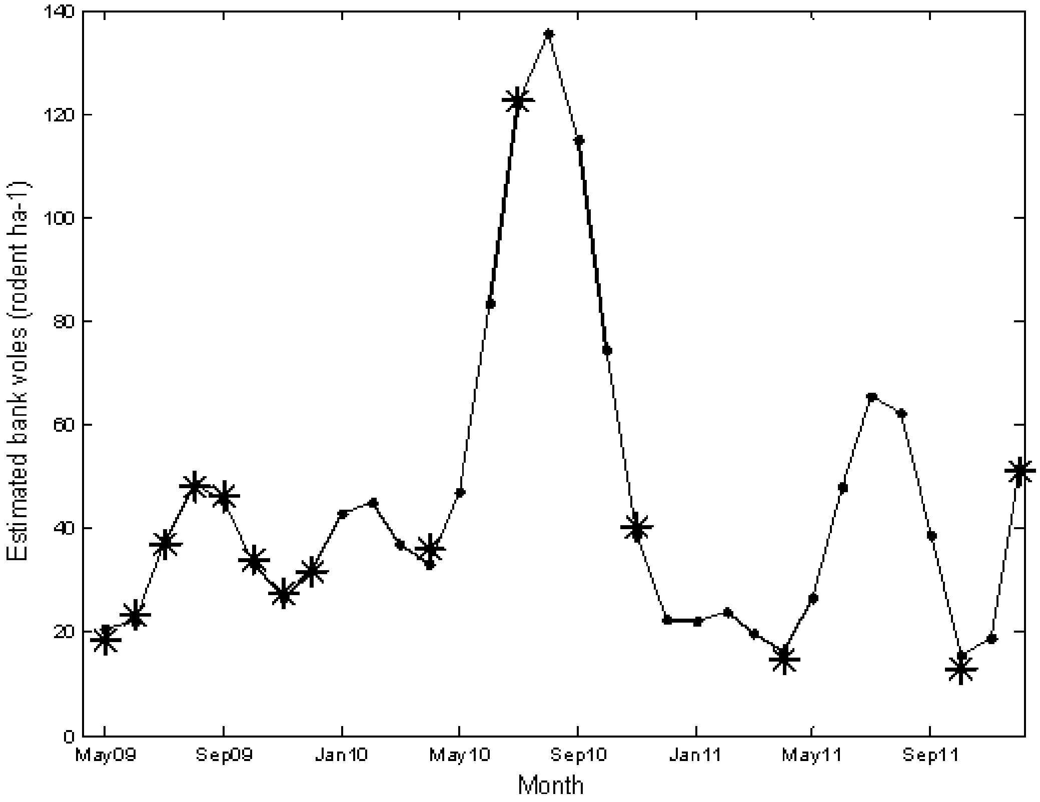


Figure 1. Bank voles population estimated by POPAN formulation in MARK (*) and interpolated bank voles population by DHR model (--•-----).

The second part of the Belgium data set (from 2009 till 2011) was used for validation, more specifically to test whether the model structure (na =2, nb_N = 1, nb_T = 1 and nb_P = 1) described in equation 3 was adequate for describing the recently generated field data. The selected models, based on the YIC, had time delays of nt_N = 6 , nt_T = 3 and nt_P = 4 respectively (Table 2). From figure 3, it is clear that the second order model (equation 5) allowed describing the bank vole density dynamics as well (with R_T^2 of 0.68) as on the original training data.

$$R(t) = -a_1 R(t-1) - a_2 R(t-2) + b_N N(t-6) + b_T T(t-3) + b_p P(t-4) \quad \text{Equation 5}$$

The same approach was used to model the dynamic of bank vole density in Finland. The selected model for the training data set (from 1995 till 2001) was described by na =2, nb_T = 1, nb_P = 1, nt_N = 9 , nt_T = 6 and nt_P = 4 with R_T^2 of 0.78 (Figure 4). The resulting model structure is represented in Equation (6). The specific values for the model parameters are presented in Table 2.

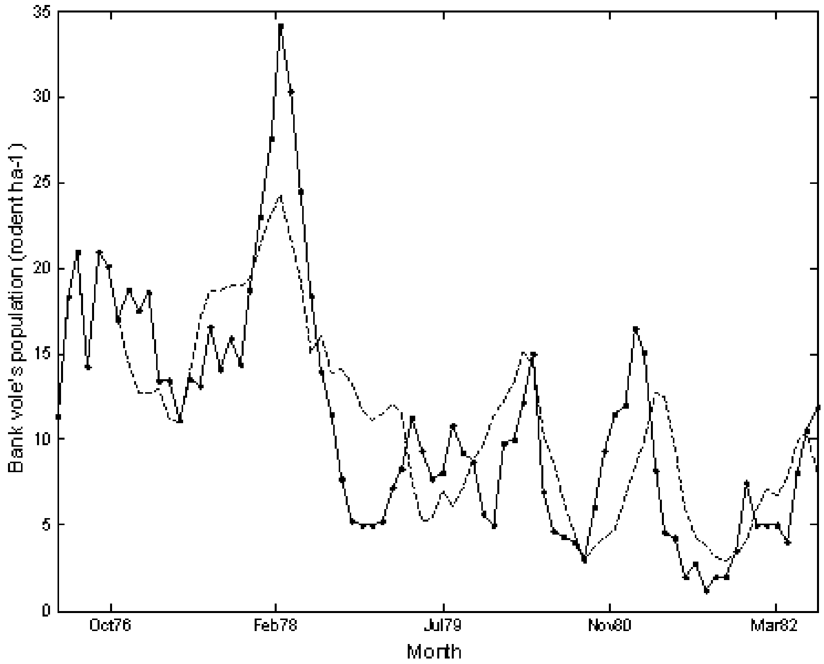
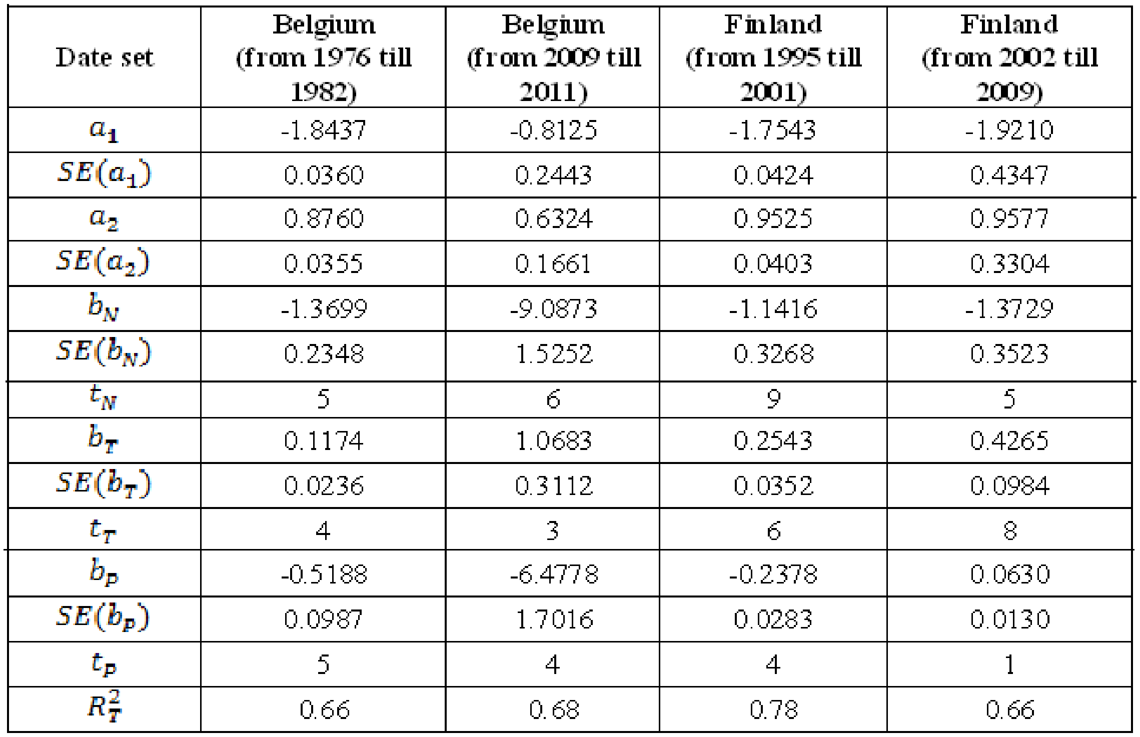


Figure 2. The resulting model simulation (- - - - -) of the data-based MISO model with 3 inputs (average monthly temperature, precipitation and NAO) versus measured (-•-) bank voles population in Belgium for the training data from 1976 till 1982 (R_T^2 of 0.66). The first data and model points fall together because of the time delay between the inputs (climate variables) and the output (bank vole density) we assumed at the beginning of the time series that the model simulation is equal to the data.

Table 2. Parameter estimation results with bank voles population as the output and monthly NAO, average monthly temperature (°C) and average monthly precipitation (mm) as inputs. Note: for each model the parameters ($a_{1\ and\ 2}$, b_N, b_T, b_p) with corresponding standard error (SE), the time delay (t_T, t_p, t_N) and the coefficient of determination (R_T^2) are shown.



Date set	Belgium (from 1976 till 1982)	Belgium (from 2009 till 2011)	Finland (from 1995 till 2001)	Finland (from 2002 till 2009)
a_1	-1.8437	-0.8125	-1.7543	-1.9210
$SE(a_1)$	0.0360	0.2443	0.0424	0.4347
a_2	0.8760	0.6324	0.9525	0.9577
$SE(a_2)$	0.0355	0.1661	0.0403	0.3304
b_N	-1.3699	-9.0873	-1.1416	-1.3729
$SE(b_N)$	0.2348	1.5252	0.3268	0.3523
t_N	5	6	9	5
b_T	0.1174	1.0683	0.2543	0.4265
$SE(b_T)$	0.0236	0.3112	0.0352	0.0984
t_T	4	3	6	8
b_p	-0.5188	-6.4778	-0.2378	0.0630
$SE(b_p)$	0.0987	1.7016	0.0283	0.0130
t_p	5	4	4	1
R_T^2	0.66	0.68	0.78	0.66

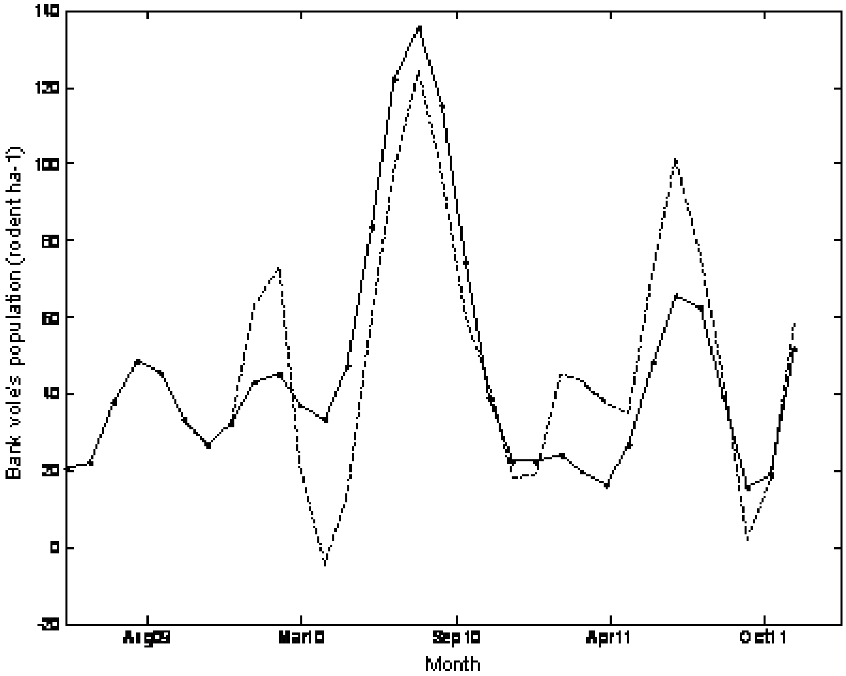


Figure 3. The resulting model simulation (- - - - -) of the data-based MISO model with 3 inputs (average monthly temperature, precipitation and NAO) versus measured (-•-) bank voles population in Belgium for the evaluation data from 2009 till 2011. The model described the data with the R_T^2 of 0.68. The first data and model points fall together because of the time delay between the inputs (climate variables) and the output (bank vole density) we assumed at the beginning of the time series that the model simulation is equal to the data.

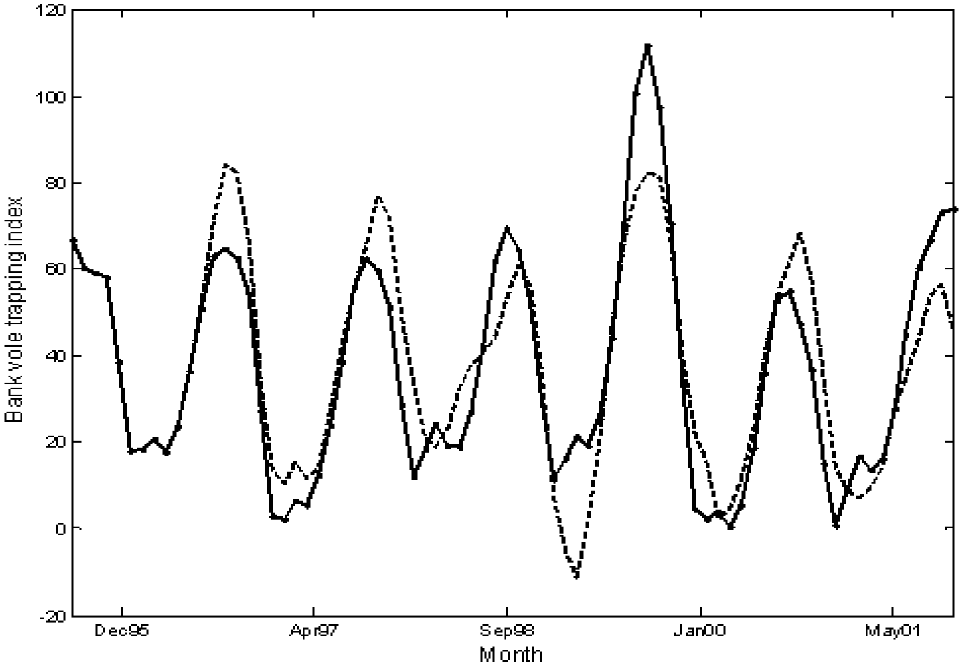


Figure 4. The resulting model simulation (- - - - -) of the data-based MISO model with 3 inputs (average monthly temperature, precipitation and NAO) versus measured (-•-) bank voles population in Finland for the training data from 1995 till 2001. The model described the data with the R_T^2 of 0.78. The first data and model points fall together because of the time delay between the inputs (climate variables) and the output (bank vole density) we assumed at the beginning of the time series that the model simulation is equal to the data.

$$R(t) = -a_1R(t-1) - a_2R(t-2) + b_NN(t-9) + b_TT(t-6) + b_PP(t-4) \quad \text{Equation 6}$$

The second part of the data set (from 2002 till 2008) was used for validation, namely to determine whether the model structure ($na = 2$, $nb_N = 1$, $nb_T = 1$ and $nb_P = 1$) described in equation 3 was adequate for describing the second data set. The selected model had a time delays of $nt_N = 5$, $nt_T = 8$ and $nt_P = 1$ respectively (Table 2, equation 7). From figure 5, it is clear that the model was able to describe the bank vole density dynamics quite well (with R_T^2 of 0.66).

$$R(t) = -a_1R(t-1) - a_2R(t-2) + b_NN(t-5) + b_TT(t-8) + b_PP(t-1) \quad \text{Equation 7}$$

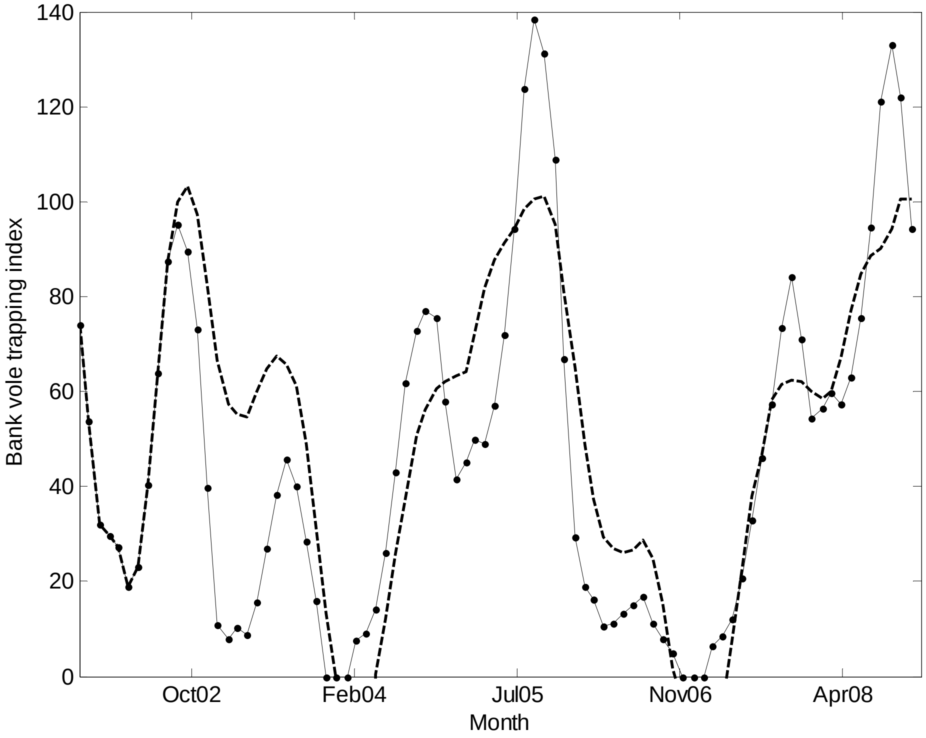


Figure 5. The resulting model simulation (- - - - -) of the data-based MISO model with 3 inputs (average monthly temperature, precipitation and NAO) versus measured (-•-) bank voles population in Finland for the training data from 2002 till 2008. The model described the data with the R_T^2 of 0.78. The first data and model points fall together because of the time delay between the inputs (climate variables) and the output (bank vole density) we assumed at the beginning of the time series that the model simulation is equal to the data.

DISCUSSION

Our analysis suggests that there is a delay of around half a year between the bank vole density and the NAO index. This, and the negative value of the parameter b_{0N} (Table 2), is in agreement with the study of Post and Forchhammer (2002) in which it was concluded that a low NAO index (corresponding to cold winters) half a year previously corresponds to high current vole density. This result was also in agreement with the work of Palo [6], showing a significant negative correlation between the NAO and the bank vole population in Sweden. Palo [6] and Amirpour Haredasht et al. [17] showed that the NAO index does not have a significant effect on the human NE cases in both Belgium and Finland. Therefore, we can conclude that colder winters (low NAO) will not increase the likelihood of the higher transfer of virus from bank voles to man.

The value of the parameter in the data-based model related with average monthly temperature (b_{0T}) (°C) is positive (Table 2). Weather condition affects bank vole number both directly and indirectly, through food supply. In the Western European temperate zone (Belgium in our study) the high bank vole abundance has been related to mast years which are mainly induced by summer temperature, especially by elevated average temperature [28]. In boreal zones, such as Finland, there is a positive correlation between the spruce seed production and the mean summer temperature which leads to increases in the bank vole's population [29].

However, the bank vole number is lagged with one year relative to the seed crop, i.e. if seeds of forest trees are important, there should be two year time lag between summer temperature and bank voles number. In the areas where bilberry plants are important winter food, there may rather be a negative 1-2 years delay relationship between summer temperatures and bank vole number [29, 30]. Because our data time series covers a short period, we could not analyse the mast phenomena and our results showed the direct effect of the temperature on bank voles. In this regard, we can refer to the paper of Tersago et al. [30] that indicated that higher temperatures mean a lower use of resources to maintain the high metabolic rate of bank voles. Furthermore, reduced autumn snow cover and mild winter temperatures benefit vole populations during the summer [31].

The negative value of the parameter in the data-based model derived for average monthly precipitation (b_{1P}) (mm) (Table 2) indicates a negative correlation between the bank vole density and monthly precipitation. This is in agreement with the studies of Linard et al. [32] in which it was concluded that the bank voles are negatively influenced by high winter and spring precipitations. In east central part of Finland (e.g. Konnevesi area), the increasing autumn temperatures and decreasing snow depth are expected to increase summer and winter population growth rates as well as cycle amplitude. The increasingly warm and long growing seasons may contribute to weaker direct and stronger delayed density dependence during summers [31].

The bank vole population time series in Finland covered a period of 14 years, during which bank vole populations did not fluctuate in a multiannual manner (1995-2001) as well as years when bank vole population fluctuate in full three-year cycles (2002-2008). The positive gain value (parameters b_P) derived for the average monthly precipitation in the period 2002-2008 could be an indicator of the effect of climate variation in the mechanism which affects the fluctuations of the bank voles. In order to take into account disturbances, such as climate fluctuations, time varying parameter models could be suitable tools in future to monitor and predict the bank vole population [17].

Andreo et al. [33] performed a non-linear logistic population model to model yearly population dynamics of two rodent species (*Calomys. venustus & Akodon azarae*) in agro-ecosystems of central Argentina using climate factors (monthly temperature -minimum, average, and maximum- and precipitation) as well as normalized vegetation index (NDVI) as inputs. They generated several models to model the population dynamics of the two mentioned rodents with different combinations of inputs. In their models, they assumed a positive constant representing the maximum finite reproductive rate, a constant representing competition and resource depletion. They modelled the yearly population of *C. venustus* (from 1990-2007) with a R^2 of 0.63 using the spring mean temperature as an input. Their selected model indicated that the dynamics of *A. azarae* seems to be mainly affected by the annual minimum NDVI (R^2 of 0.76). Although Andreo et al. [33] used a dynamic data-based model, called R-function (Berryman 1999), their analyses were based on some assumptions. In our study we used data-based mathematical procedures, where the model parameters were directly estimated from experimental data using more objective statistically based methods.

Although the modelling results look promising compared to the available literature, several limitations can be identified which are related to the applied modelling methodology. The first limitation we faced when identifying the data-based model was that the used recent bank voles' time series in Belgium cover a period of only three years (from 2009 till 2011) with a caption intervals of four month. In order to be able to use the dataset in our analysis the bank vole data had to be interpolated. The interpolation smoothed the data and therefore influenced the estimation of the model parameters.

The second limitation in identifying the data-based model was that the available bank vole series in Belgium covering a periods of only three years (from 2009 till 2011) and six years (1978-1982) in Belgium. Although the number of samples was theoretically sufficient in order to estimate the model parameters of the used model structure, as indicated by the acceptable standard errors on the parameter estimates (Table 2), a dataset covering a longer period might improve the modelling results.

It is also known that bank voles populations fluctuate regionally, but the frequency and timing of these fluctuations vary in different regions, due to latitudinal and longitudinal variation in the environment [31]. Because of nonlinearities and thresholds in ecological responses to climate change [34], the short term, potentially even transient [35], impacts of climate may be different from those observed in the long term. Therefore, neither geographic gradients in climate nor local temporal variation in weather are alone directly applicable to predict the effects of climate change; both sources of variation should be considered. Combining data on a latitudinal, climatic gradient with long-term local temporal variation will allow a robust analysis of how animal populations respond to climate change [31].

Another limitation is that in this study we only analysed the effect of climate factors in relation to the dynamics of the bank voles. However, also other processes such as the availability of food and space have an important role in regulation of the bank vole population.

Therefore, determining a dynamic data-based model for bank vole density which includes factors such as vegetation coverage and abundance of food for bank voles' may provide us with an expert tool to monitor and predict the fluctuations in bank voles population by making use of remote sensing tools for measuring broad leaves forest phenology and monitoring the vegetation dynamics together with climatological data.

We managed to quantify the dynamics of the bank vole density as a function of climate data. Previous studies (Amirpour Haredasht et al., 2011, 2012) quantified the NE cases based on the climate and vegetation data. In order to monitor the NE incidence it is necessary to understand the effect of climate and vegetation on the bank vole population. This approach can be used to predict the dynamics of the bank vole population under different climate scenarios and hence to predict the NE incidence.

We showed that the dynamic data-based modelling approach is a useful tool for monitoring and predicting the dynamics of bank vole population in different ecosystems. The results of our study might be used as a tool in future to predict the temporal dynamics of bank vole population and thus the NE occurrence, and to evaluate strategies to control the epidemics.

CONCLUSION

Estimating the bank vole population dynamic is a key in predicting the NE outbreaks. However, trapping bank vole is an expensive and time consuming activity and therefore there is a need for less demanding methods for estimating the bank vole population.

In this study the bank voles population in the North of Belgium were modelled based on data from 1976 till 1982 with a R_T^2 of 0.66 and the bank voles density in Central Finland from 1995-2001 with a R_T^2 of 0.78. In the next step the MISO model was validated for bank vole density in Belgium from 2009 to 2011 (R_T^2 of 0.68) and bank vole density in Central Finland from 2002 till 2008 (R_T^2 of 0.66).

Despite the difference in bank vole population dynamics and NE cases between the Western European temperate zone (i.e. Belgium) and boreal zones (i.e. Finland) the MISO model managed to describe temporal characteristic of the two time series and their different dynamic mechanisms.

Such a modelling approach might be used as a step towards the development of new tools for the prevention of future NE outbreaks by making use of satellite remote sensing tools for forest phenology and monitoring the vegetation dynamics together with climatological data.

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