International Congress on Environmental Modelling and Software

6th International Congress on Environmental Modelling and Software - Leipzig, Germany - July 2012

Jul 1st, 12:00 AM

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International Environmental Modelling and Software Society (iEMSs)
2012 International Congress on Environmental Modelling and Software
Managing Resources of a Limited Planet, Sixth Biennial Meeting, Leipzig, Germany
R. Seppelt, A.A. Voinov, S. Lange, D. Bankamp (Eds.)
http://www.iemss.org/society/index.php/iemss-2012-proceedings

Application of a Metapopulation Approach for Analysis of Space-Time Population Dynamics (case study using ungulates)

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Abstract: This paper is devoted to the analysis of basic regularities in spatial dynamics of the wild boar (*Sus scrofa ussuricus* Heude, 1888) and the red deer (*Cervus elaphus xanthopigus* Milne-Edwards, 1867) numbers in the Russian Middle Amur area, on the example of the Jewish Autonomous Region. We research a model of space-time metapopulation dynamics based on a coupled map lattice. We use the metapopulation approach for quantitative analysis of migration activity for the wild boar and the red deer populations. Using the model estimates of migration and reproductive parameters we described the main migration routes of these populations. It is shown that individuals of wild boar population migrate stronger than individuals of red deer population. It is demonstrated the maximum reproduction subpopulations of ungulates metapopulation were characterized by highest out-migration of individuals and stable non-zero number of the subpopulations with minimal reproduction rate were supported only immigrants.

***Keywords**:* Metapopulation, migration, coupled map lattices, Ricker model, space-time population dynamics.

1 INTRODUCTION

The Jewish Autonomous Region (JAR) territory, situated on the left bank of the Amur river in its middle section, has a high patchiness of different landscapes and habitats as result it manifested in inhomogeneous distribution of some food resources. It leads to spottiness of a spatial structure of animal communities consisting of the same species and related migration coupling. The dynamics of local population and biological community studied is well and described models in discrete and continuous time. The irregular and periodic changes in their dynamics numbers can be explained a density-dependent growth or a periodic nature of an external factors or an interspecific competition.

The habitat of the real biological populations and community generally is fragmented. They can be presented as the system of local populations coupled by migration. Such a system is called metapopulation [Hanski and Gaggiotti 2004]. In this case the population dynamics is more complicated than a single local population or biological community. A multistability, synchronization, intermittency and clustering are observed in models of such systems [Bezruchko et al. 2003, Wysham and Hastings 2008, Silva and Giordani 2006, Kaneko, 1990, Kulakov and Frisman 2010, Castro et al. 2006, Omelchenko et al. 2005].

In this paper we analyse a basic regularities in spatial dynamics of the wild boar (Sus scrofa ussuricus Heude, 1888) and the red deer (*Cervus elaphus xanthopigus Milne-Edwards*, 1867) numbers in the Russian Middle Amur area, on the example of the Jewish Autonomous Region. The paper objective is modeling space-time population dynamics of hunting species by coupled map lattices. The quantitative analysis of population dynamics and migration activity is made for case study ungulates.

2 MATHEMATICAL MODELS

We assume that on some territory there are the isolated local habitats which inhabit small local populations. The relationship between neighboring populations is only migration. The area of modeling metapopulation is divided into equal patches of $k+1$ nodes in lines and $n+1$ nodes in columns by a uniform lattice. For this patches we accept the adjacent to each other population monitoring zones.

Each of patches is labeled from 1 to $N = kn$. We suppose that individuals living in same patch (subpopulation) isolated from each other and related to season migration in conformity with individual activity range. Intensity of migration flow in each of these patches is determined by the population density of all adjacent patches. If there are discrete stages of individual development and migration resettlement is once per season then we can write the equations of the space-time metapopulation dynamics as follows:

$$x_{n+1}^{(i)} = \sum_{j=1}^{N} m_{i,j} f\left(x_n^{(j)}\right) \ (i = 1, 2, \ldots, N), \qquad (1)$$

where $x_n^{(i)}$ is population size of site i ($i = 1, 2, \ldots, N$) at discrete time n, $m_{i,j} \geq 0$ ($i \neq j$) is fraction of population size of patch j that will arrive in site i, $f(x)$ is stock-recruitment function. The matrix $M = \left(m_{i,j}\right)$ is called a migration matrix. Diagonal element of the matrix M is $m_{i,i} = 1 - \sum_{j=1}^{N} m_{j,i}$. It equals a fraction of the individuals that did not leave patch j before season migration.

As stock-recruitment function $f(x)$ we considered in the form of the Ricker model: $f(x) = a \cdot x \cdot \exp(-bx)$, where a is the reproductive potential, i.e. the maximum possible annual reproduction without density-dependent limiting, b is inverse value of population density, in which birth is maximum, i.e. it characterizes the density-dependent limitation for growth number of population.

In addition to model (1) for analysis of space-time metapopulation dynamics we used the modified version of the Malthus model (with migration):

$$x_{n+1}^{(i)} = s^{(i)} \cdot x_n^{(i)} + m^{(i)}, \qquad (2)$$

where $s^{(i)} = e^{\varepsilon_i}$ is parameter characterizing the annual reproduction of subpopulation, $m^{(i)}$ is a conditional annual immigration flow. Its intensity compensates for a small reproduction of the individuals that caused by ecological limitations. For model (2) the equilibrium value is:

$$\bar{x}^{(i)} = m^{(i)} / (1 - s^{(i)}). \qquad (3)$$

3 DATA AND PARAMETERS ESTIMATION OF MODELS

We estimated the parameters of models (1)-(2) using the annual reports of winter track surveys for population the wild boar and the red deer. The factual size of the hunting populations in the Obluchensky, Birobidzhansky, Octyabrsky and Leninsky districts of the JAR was analyzed. The patch centers of the lattice model (1)-(2) were located through the administrative units as shown in figure 1.

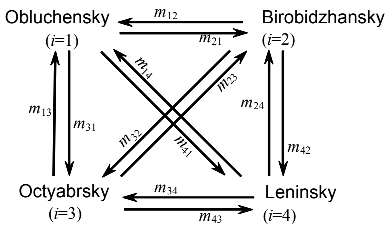

Figure 1. The general scheme for season migration of ungulates between the JAR administrative districts. Arrows indicate the direction animal resettlement

The estimates of population ($a^{(i)}$, $b^{(i)}$ and $s^{(i)}$) and migration ($m^{(i)}$) parameters and equilibrium values $\bar{x}^{(i)}$ for ungulates populations are shown in Table 1. For model (2) the values $\bar{x}^{(i)}$ equal (3) and for models (1) they are result of numerical calculations.

Table 1. Parameters estimation

Population monitoring zones	Model (1)			Model (2)		
	The wild boar population					
	$a^{(i)}$	$b^{(i)}$	$\bar{x}^{(i)}$	$s^{(i)}$	$m^{(i)}$	$\bar{x}^{(i)}$
Obluchensky	16.6468	0.0052	993	0.04	1069	1114
Octyabrsky	17.9732	0.0039	896	0.18	727	883
Birobidzhansky	4.3297	0.0002	314	0.41	214	362
Leninsky	36.2462	0.0200	109	0.12	1197	2352
–	The red deer population					
Obluchensky	12.0846	0.0070	965	0.5	678	1361
Octyabrsky	17.8087	0.0041	672	0.39	462	757
Birobidzhansky	2.7850	0.0188	407	0.05	363	380
Leninsky	24.1558	0.00004	54	0.56	51	114

The estimates of the migration matrices of model (1) for the wild boar (M_1) and the red deer (M_2) populations are written as:

$$M_1 = \begin{pmatrix} 0.03141 & 0.4642 & 0.8131 & 0.0044 \\ 0.2767 & 0.1566 & 0.1748 & 0.0043 \\ 0.1198 & 0.3438 & 0.000001 & 0.9845 \\ 0.5721 & 0.0353 & 0.0121 & 0.0068 \end{pmatrix},$$

$$M_2 = \begin{pmatrix} 0.0000003 & 0.00005 & 0.0064 & 0.7396 \\ 0.0531 & 0.9976 & 0.4323 & 0.0486 \\ 0.0004 & 0.0023 & 0.5613 & 0.1802 \\ 0.9465 & 0.00004 & 0.00004 & 0.0316 \end{pmatrix}.$$

The actual and model numbers of population dynamics of these species living in monitoring zones are shown in figure 2.

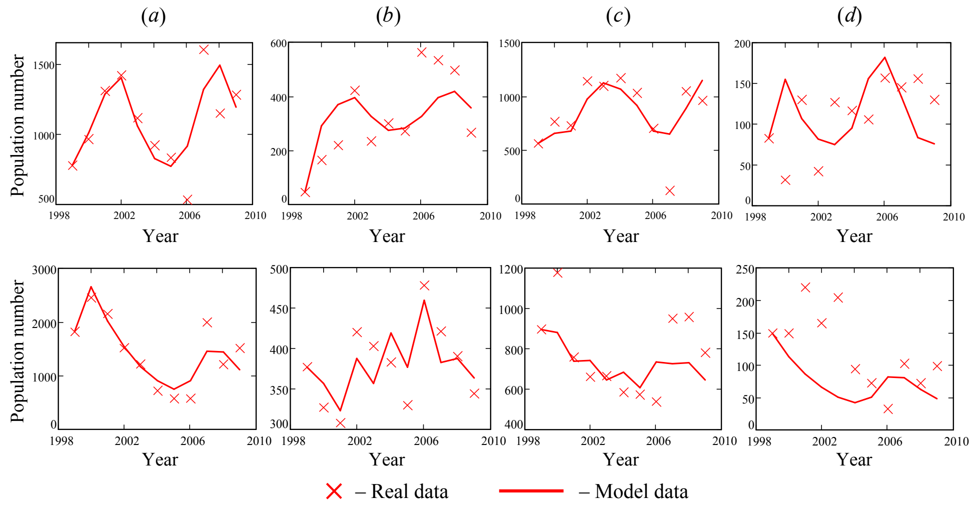

Figure 2. The number dynamics of the local populations of the wild boar (top row) and the red deer (bottom row) living in the Obluchensky (a), Birobidzhansky (b), Octyabrsky (c) and Leninsky (d) districts of the Jewish Autonomous Region

4 RESULTS AND DISCUSSION

For subpopulation of the wild boar in Obluchensky districts was obtained the highest rate of the migration component in population dynamics. According to estimation of the modified version of Malthus model (2) a conditional rate of individuals immigrating is close to 96 % (an average of 1070 individuals).

By estimation of model (1) the fraction of wild boar individuals not involved in long-distance migrations in Obluchensky districts amounts to 3 % of all population (see M_1). In this case this area is mostly replenished by migrants from Octyabrsky districts – about 81 % of the average number of population or 720 individuals. Also this population increases its density by migrants from Birobidzhansky districts – about 46 % of average number of wild boar's population in Birobidzhansky districts or 144 individuals.

By estimation of model (2) the conditional rate of individuals immigrating in Octyabrsky districts is around 730 individuals or 82 % of the equilibrium value. But according to estimation of model (1) the fraction of wild boar not left this site is close to zero. On this area the main flow of migrants is emanated from the Obluchensky districts (12 % or an average of 120 individuals), Birobidzhansky districts (34% or 130 individuals) and Leninsky districts (98 % or 106 individuals) (see M_1). Perhaps in Octyabrsky districts individuals of wild boar migrate from neighboring area to JAR.

Proportion the local wild boar population making small movements in the Birobidzhansky forest land is 16 % of the total population. On average the annual immigration flow to the area is about 60 % of the equilibrium value (214 individuals).

According to simulation results we can assume that most of migrants follow from Obluchensky districts. Also in this area the wild boar migrates from the Obluchensky districts.

A comparison of the estimates by population and migration parameters for models (1) and (2) is shown the local Leninsky's population characterized by a maximum reproduction and the highest out-migration of individuals in comparison to other areas. As we can see, the migration matrix M_1 indicates this area is mostly replenished by migrants from Obluchensky districts.

For red deer population we shown the maximum reproduction areas are Leninsky and Obluchensky districts. These areas are characterized by highest out-migration of individuals (see M_2 and Table 1). At the same time the individuals from the forest land of Leninsky districts principally migrate to the area of Obluchensky districts. On the other hand individuals from the site of Obluchensky districts migrate to the Leninsky districts. So there is the constant interchange of seasonal migrations between these territories. In addition individuals from Leninsky districts made small movements to Birobidzhansky (4 %) and Octyabrsky districts (18 %).

As well we found the Birobidzhansky's population of red deer is a minimal reproduction rate site. Its stable number of population is supported only by small birth and the immigrants from Obluchensky (5 %) and Leninsky districts (5 %). By estimations of model (1) 99 % individuals of local population make movements within its local area.

5 CONCLUSIONS

Using the metapopulation approach the quantitative analysis of space-time dynamics has been made for some commercial species of ungulates in JAR. It is shown in particular the individuals of wild boar populations migrate with more intensity than the individuals of red deer populations.

A comparison of parameter estimates for the model based on coupled map lattice (1) and the migration modified version of the Malthus model (2) was shown the maximum reproduction subpopulations of ungulates metapopulation were characterized by highest out-migration of individuals and stable non-zero number of the subpopulations with minimal reproduction rate were supported only immigrants.

It is shown the equilibrium values estimates of number population by model (1) and (2) for the subpopulations wild boar and red deer are comparable and close to their values in spite of the various estimates of population parameters. This fact indicates the adequacy of using model approach for analysis of space-time dynamics of ungulates.

ACKNOWLEDGMENTS

This work is in part supported by the Russian Foundation for the Fundamental Research (no. 11-01-98512-r_vostok_a) and the Far Eastern Branch of the Russian Academy of Sciences (no 12-I-OBN-05).

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