

## Using Density-Dependent Birth-Death Migration Models for Analyzing Muskrat Spread in the Netherlands

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### SUMMARY

The feasibility of using density-dependent birth-death-migration (BDM) models is demonstrated to analyse data specifically the spread of muskrats in the Netherlands over the past 35 years. Both single as well as multiple populations are dealt with. It is shown that density dependent BDM models are also available to investigate the properties of metapopulations, such as the variances, which are not available from deterministic models. The BDM models are found to be valuable tools for evaluating pest control strategies which might increase the death rate, decrease the birth rate or slow the migration rate.

*Key words* : Density independent models, Logistic models, Cumulant functions, Single and multiple populations.

### 1. Introduction

Spatio-temporal models of biological spread may be classified into three broad categories. A common category consists of the spatial statistical models [2]. These are empirical models, which are relatively easy to analyze statistically but which have little or no mechanistic basis. Another common category consists of the biological simulation models, which typically incorporate as much of the underlying biological and ecological theory as possible. Thus these are mechanistic models, usually with numerous parameters, and hence they are difficult to validate statistically due to their complexity. A third, less common category consists of low-order tractable mathematical models, which contain a few parameters describing some features of the underlying ecological mechanism but yet are amenable to statistical analysis. Diffusion models belong to this third category ([10], [12]) as do also the BDM models [11].

In light of the conceptual appeal of the BDM models for understanding and managing biological invasions ([5], [6]), it seems surprising that they have not been widely used in the past for this purpose. There has been a general feeling among modelers that net reproduction and migration could not be

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estimated simultaneously, hence population growth models have usually been fitted to abundance data from individual locations separately and the BDM models have been largely ignored. Indeed, we are not aware of any research that fitted BDM models to the present type of spatio-temporal data prior to [7], even though there is a long history in compartmental analysis of using the more restricted migration-death models for this purpose [4].

This paper should be regarded as a progress report in using BDM models for the analysis of data. Section 2 describes the data, basic assumptions and notation of the paper. Sections 3 and 5 review some density-independent models previously developed and fitted to the present data in [7]. Sections 4 and 6 develop and apply the new density-dependent models for the analysis. Concluding remarks including suggestions for future research are given in Section 7.

## 2. Description of Data Set, Notation, and Basic Assumptions

Data on the annual catch of muskrats in 11 Dutch provinces between 1968 and 1991 are described in Hengeveld [3] and the complete data set is listed in [7]. Figure 1 illustrates the observed muskrat harvests in the eleven provinces

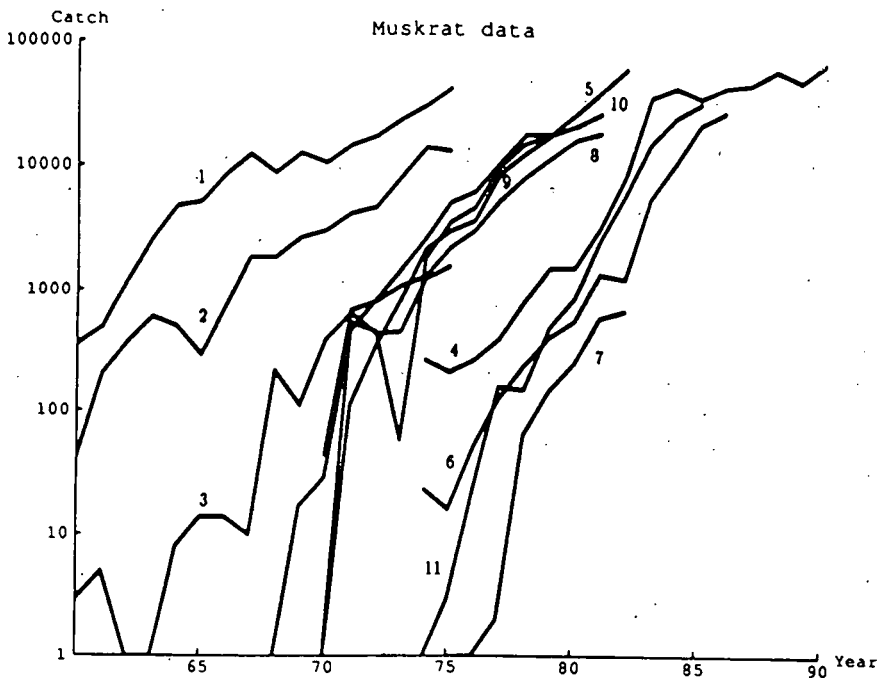


Figure 1. Data on muskrat harvest in 11 provinces in the Netherlands during their initial population growth periods from 1960-1991

during their respective growth periods. For simplicity, we regard the observed harvest values as representing actual population sizes.

The model will be developed for only up to two populations linked by migration, but the generalization to any arbitrary number of populations follows easily. Let

1.  $X_i(t)$ ,  $i = 1, 2$ ; denote muskrat abundance in province  $i$  at elapsed time  $t$ ,
2.  $\mathbf{X}(t) = [X_1(t), X_2(t)]'$  be the random vector of abundances at time  $t$ ,
3.  $\kappa_{v_1, v_2}(t)$  denote a joint cumulant of  $\mathbf{X}(t)$ , and
4.  $K_x(\theta, t)$  be the cumulant generating function (cgf) of  $\mathbf{X}(t)$ .

The cgf is defined as the logarithm of the moment generating function, and the cumulants are the coefficients in the Taylor series expansion

$$K_x(\theta, t) = \sum_{v_1, v_2 \geq 0} \kappa_{v_1, v_2}(t) \theta_1^{v_1} \theta_2^{v_2} / v_1! v_2! \quad (2.1)$$

In the standard BDM models, there are four possible types of changes over time, namely immigration, birth, death and migration, in a population size,  $X_i(t)$ . The "instantaneous" probabilities of these possible changes in small intervals of time from  $t$  to  $t + \Delta t$  are assumed to be independent with :

- a. Prob  $\{ X_i \text{ will increase by 1 due to immigration} \} = I_i \Delta t$ ,
- b. Prob  $\{ X_i \text{ will increase by 1 due to birth} \} = \lambda_i(X_i) \Delta t$ , (2.2)
- c. Prob  $\{ X_i \text{ will decrease by 1 due to death} \} = \mu_i(X_i) \Delta t$ ,
- d. Prob  $\{ X_i \text{ will increase by 1 and } X_j \text{ will decrease by 1 due to migration} \} = v_{ij} X_j \Delta t \text{ for } i \neq j$ .

The assumption of independent unit changes is not realistic for these large populations of muskrats. The mean value function is not affected by these assumptions, however the variances derived for the population size must be regarded with caution.

The birth and death rate functions are defined as polynomials of the form :

$$\lambda_i(X_i) = a_{i1} X_i - b_{i1} X_i^{s+1} \text{ and } \mu_i(X_i) = a_{i2} X_i + b_{i2} X_i^{s+1} \quad (2.3)$$

where the  $a_{ij} \geq 0$  denote the "intrinsic" (per capita) rates and the  $b_{ij} \geq 0$  are the "crowding" effects. We review in Sections 3 and 5 density independent models with  $b_{ij} \equiv 0$  for all  $i$  and  $j$  in (2.3). We then present in Sections 4

and 6 the logistic models with  $b_{ij} > 0$  and integer  $s \geq 1$ . The migration in all of these models is assumed to be simple, linear (donor-controlled) migration.

### 3. Density Independent Models of Growth for a Single Population

#### 3.1 Assumptions

Consider the single model population with

$$\lambda(X) = a_1 X \text{ and } \mu(X) = a_2 X \quad (3.1)$$

Such density-independent models could hold only for periods of initial growth.

#### 3.2 Deterministic model

The corresponding deterministic model is

$$\dot{X}(t) = (a_1 - a_2) X + I \quad (3.2)$$

which has solution

$$X(t) = X_0 e_t + I(e_t - 1) / (a_1 - a_2) \quad (3.3)$$

$$\text{where } e_t = \exp \{ (a_1 - a_2) t \} \quad (3.4)$$

#### 3.3 Equations for cumulant functions

The pde for the cgf is, from [6] :

$$\frac{\partial K}{\partial t} = \{ a_1 (e^\theta - 1) + a_2 (e^{-\theta} - 1) \} \frac{\partial K}{\partial \theta} + I (e^\theta - 1) \quad (3.5)$$

The equations for the first two cumulants, i.e. mean and variance, are

$$\dot{\kappa}_1(t) = (a_1 - a_2) \kappa_1 + I \quad (3.6)$$

$$\dot{\kappa}_2(t) = (a_1 + a_2) \kappa_1 + 2(a_1 - a_2) \kappa_2 + I \quad (3.7)$$

#### 3.4 Solutions for cumulant functions

Equation (3.6) has the same form as (3.2), hence the mean value function  $\kappa_1(t)$  has the same solution as (3.3). The analytical solution to (3.7) is given in [5].

#### 3.5 Application to muskrat population dynamics

Model (3.3) fits the data from each province well, as given in [7]. For subsequent comparisons, detailed results will be given for four adjacent provinces, gelderl, overijl, dr, and gron. The estimated net birth rates,

$a_n = a_1 - a_2$ , with standard errors in parentheses, are 0.365 (0.016), 0.296 (0.035), 0.421 (0.055) and 0.258 (0.023)/yr, respectively, with corresponding estimated immigration rates of 92 (16), 173 (49), 115 (46) and 342 (60) muskrats/yr. The life expectancy of muskrat is about four years, hence we assume that  $a_2 = 0.25/\text{yr}$  and  $a_1 = (a_n + 0.25)/\text{yr}$ . From these, one could solve for the variance function in (3.7).

#### 4. Power Law Logistic Models of Growth for a Single Population

##### 4.1 Assumption

Consider now a generalized model with population rates

$$\lambda(X) = \begin{cases} a_1 X - b_1 X^{s+1} & \text{for } X < (a_1/b_1)^{1/s} \\ 0 & \text{otherwise} \end{cases} \quad (4.1)$$

$$\mu(X) = a_2 X + b_2 X^{s+1} \quad \text{for integer } s \geq 1 \quad (4.2)$$

##### 4.2 Deterministic model

The analogous deterministic model is

$$\dot{X}(t) = (a_1 - a_2)X - (b_1 + b_2)X^{s+1} \quad (4.3)$$

The model is reviewed in [1] which gives the solution

$$X(t) = \frac{K}{[1 + m \exp(-ast)]^{1/s}} \quad (4.4)$$

where  $a = (a_1 - a_2)$ ,  $b = (b_1 + b_2)$ ,  $K = (a/b)^{1/s}$  and  $m = (K/X_0)^s - 1$ , (4.5)

and where  $K$  denotes the asymptotic size, or "carrying capacity". The point of inflection for the model occurs at time  $t_i = [\log_e(m/s)]/as$  with population size

$$X(t_i) = K/(1+s)^{1/s} \quad (4.6)$$

The special case of  $s=1$  in (4.3) gives the well-known Verhulst-Pearl model. Its classic solution in (4.4) is the ordinary logistic equation, with point of inflection at size  $K/2$ .

##### 4.3 Equations for cumulant functions

Consider slightly modifying the birth assumption from (4.1) to

$$\lambda(X) = a_1 X - b_1 X^{s+1} \quad (4.7)$$

for all  $X > 0$ , which has little effect on most practical applications. The pde for the moment generating function of the process defined by (4.2) and (4.7) is, from [8] :

$$\begin{aligned} \frac{\partial M}{\partial t} = & [(e^\theta - 1) a_1 + (e^{-\theta} - 1) a_2] \frac{\partial M}{\partial \theta} \\ & + [(e^\theta - 1) (-b_1) + (e^{-\theta} - 1) b_2] \frac{\partial^{s+1} M}{\partial \theta^{s+1}} \end{aligned} \quad (4.8)$$

Differential equations for the cumulant functions may be obtained by substituting  $K = \log M$  into (4.8), and expanding using (2.1). Some equations for  $\kappa_1(t)$  are :

$$\text{for } s = 1; \dot{\kappa}_1(t) = (a - b\kappa_1) \kappa_1 - b\kappa_2 \quad (4.9)$$

$$\text{for } s = 2; \dot{\kappa}_1(t) = (a - b\kappa_1^2) \kappa_1 - b(\kappa_3 + 3\kappa_1 \kappa_2) \quad (4.10)$$

$$\begin{aligned} \text{for } s = 3; \dot{\kappa}_1(t) = & (a - b\kappa_1^3) \kappa_1 - b(\kappa_4 + 4\kappa_3\kappa_1 + 3\kappa_2^2 + 6\kappa_2\kappa_1^2) \\ & \quad \quad \quad (4.11) \end{aligned}$$

Equations for the variance function for some small  $s$  are :

$$\text{for } s = 1; \dot{\kappa}_2(t) = (c - d\kappa_1) \kappa_1 + (2a - d - 4b\kappa_1) \kappa_2 - 2b\kappa_3 \quad (4.12)$$

$$\begin{aligned} \text{for } s = 2; \dot{\kappa}_2(t) = & (c - d\kappa_1^2) \kappa_1 + (2a - 3d\kappa_1 - 6b\kappa_1^2 - 6b\kappa_2) \kappa_2 \\ & - (d + 6b\kappa_1) \kappa_3 - 2b\kappa_4 \quad (4.13) \end{aligned}$$

$$\begin{aligned} \text{for } s = 3; \dot{\kappa}_2(t) = & (c - d\kappa_1^3) \kappa_1 + (2a + 6d\kappa_1^2 + 8b\kappa_1^3 + 3d\kappa_2 \\ & + 24b\kappa_1\kappa_2) \kappa_2 - 4(d\kappa_1 + 3b\kappa_1^2 + 5b\kappa_2) \kappa_3 \\ & - (d + 8b\kappa_1) \kappa_4 - 2b\kappa_5 \quad (4.14) \end{aligned}$$

where  $a = a_1 - a_2$ ,  $b = b_1 + b_2$ ,  $c = a_1 + a_2$ , and  $d = b_1 - b_2$ . In principle, one could derive directly such equations for any cumulant of any  $s$ -power model, but the algebra becomes tedious. We obtain such expressions for higher order cumulants and for larger  $s$  from (4.8) using the symbolic computer software package *Mathematica* [14].

#### 4.4 Solutions for cumulant functions

Equations (4.9)–(4.14) suggest, and it is easily proven, that the differential equation for the  $j^{\text{th}}$  cumulant function for an  $s$ -degree power law logistic model involves terms up to the  $(j + s)^{\text{th}}$  cumulant. Obviously this fact rules out exact

solutions to the equations. We propose approximating the cumulant functions of any specific order, say  $i$ , of an  $s$ -power law model by solving a system of up to the first  $(i + s)$  cumulant functions with all higher order cumulants set to 0. The accuracy of these approximate cumulant functions depends clearly on the specific parameter values. The mean value functions,  $\hat{\kappa}_1(t)$ , have been very accurate, with a maximum error rate of less than 0.5% over  $t$ , in our limited previous studies with parameter vectors that yield relatively small population sizes. We expect similar accuracy for the mean functions of larger populations. The approximate variance function,  $\hat{\kappa}_2(t)$ , has an error rate of less than 4% in our previous studies, and research is in progress to investigate its error rate for larger populations.

#### 4.5 Application to muskrat population dynamics

The populations in four provinces, limb, gelderl, overijl and dr, leveled off to some apparent quasi-equilibrium size. The deterministic model in (4.4) with various fixed, small integer  $s \geq 1$  was fitted to the data from each of the latter three provinces, which are adjacent eastern provinces in the Netherlands, using *Scientist* [9]. Research is in progress in fitting the mean value functions of the stochastic model to data. The best fitting curves for the three provinces has  $s$  values ranging from 2 to 5. Figure 2 illustrates the fitted curves with  $s = 1$  and  $s = 2$  for two adjacent provinces.

Table 1. Parameter estimates, with standard errors, and mean squared errors for power law logistic model (eq. 4.4) fitted to population data from three provinces.

Province	$K$	$se$	$a$	$se$	$b$	$MSE \times 10^{-6}$
for $s = 1$ :						
gelderl	48669	4104	0.408	0.125	$8.38 \times 10^{-5}$	72.7
overijl	17595	601	0.583	0.102	$3.31 \times 10^{-5}$	2.7
drente	13590	796	0.644	0.225	$4.74 \times 10^{-5}$	6.2
for $s = 2$ :						
gelderl	46216	2959	0.334	0.076	$1.56 \times 10^{-10}$	64.3
overijl	17388	483	0.429	0.066	$1.42 \times 10^{-9}$	2.1
drente	13503	695	0.483	0.163	$2.65 \times 10^{-9}$	5.4

Table 1 lists the parameter estimates with their standard errors and the mean squared error (MSE) from model (4.4) for  $s = 1$  and  $s = 2$  for each of the three eastern provinces. In each case, the standard errors are relatively small, indicating excellent precision. For each province, the model with  $s = 2$  had a better fit, i.e. lower MSE, a lower carrying capacity,  $K$ , and a lower net intrinsic rate,  $a$ .

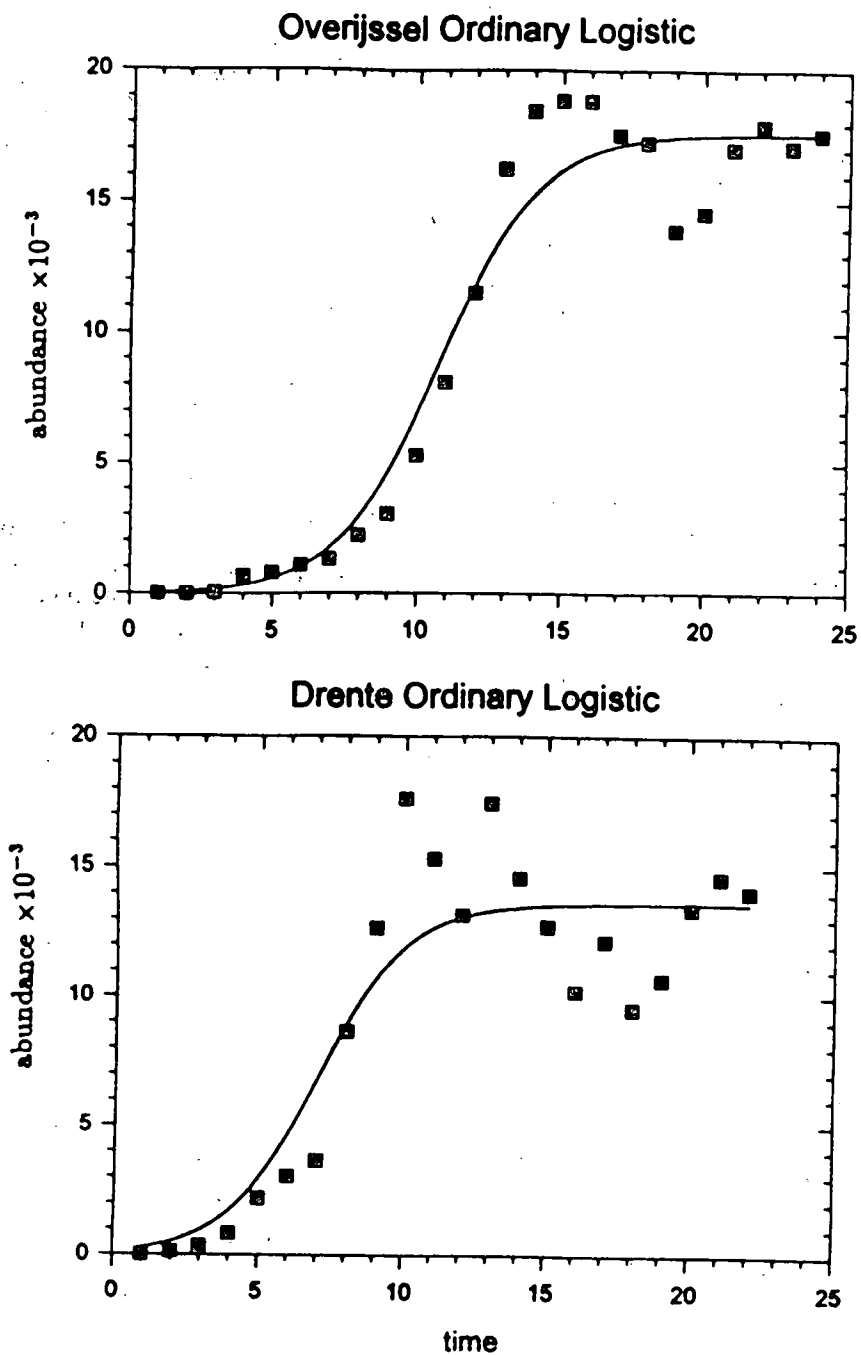


Figure 2 (a) Logistic models with  $s = 1$  fitted to data on muskrat harvests in Overijssel and Drente



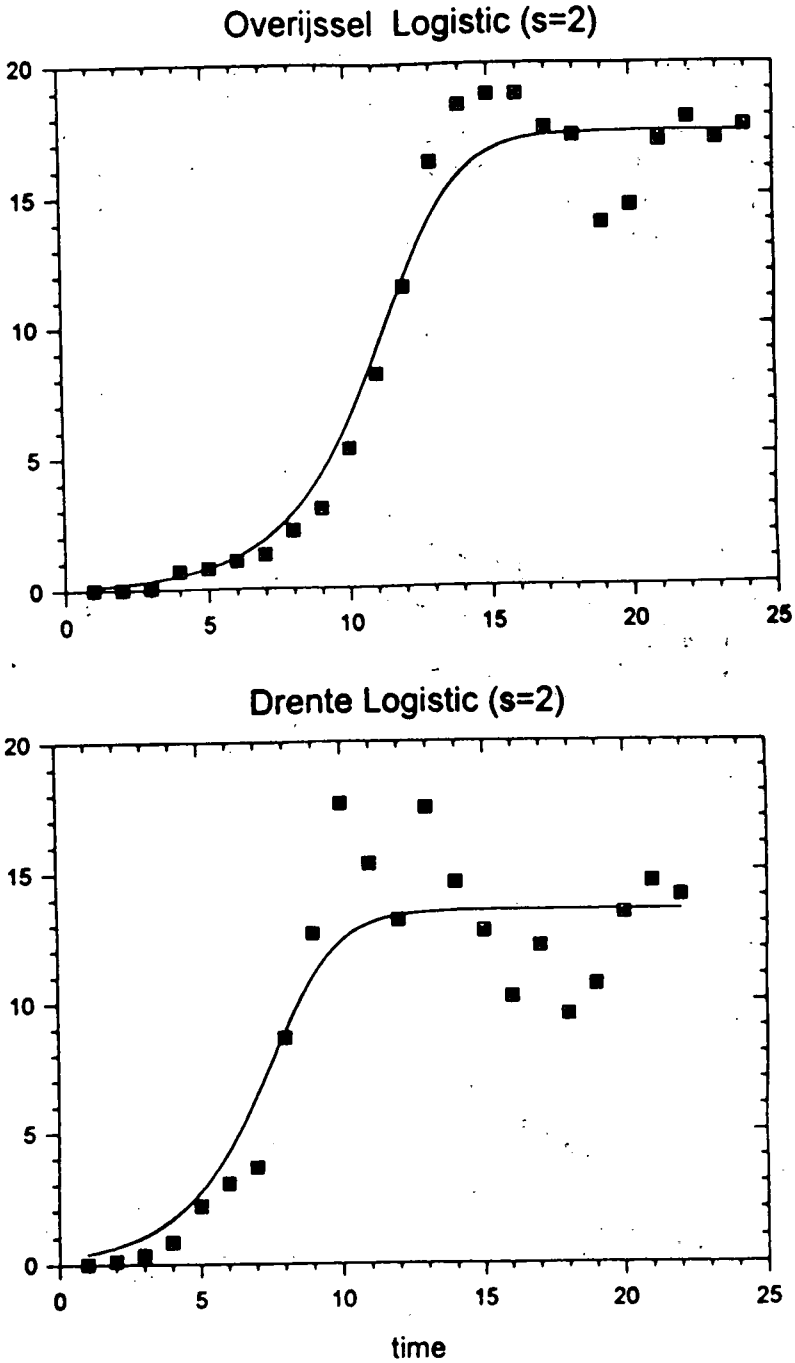


Figure 2. (b) Logistic models with  $s = 2$  fitted to data on muskrat harvests in Overijssel and Drente

For comparative purposes, we assume again a density independent death rate function with parameters  $a_2 = 0.25$  and  $b_2 = 0$  for each province. This implies that the birth rate function is density dependent with resulting parameters  $a_1 = a + 0.25$  and  $b_1 = b$ . The assumed death rate function and the estimated birth rate functions for three models, (3.2) and (4.4) with  $s = 1$  and  $s = 2$ , are illustrated in Figure 3 for overijl and dr provinces.

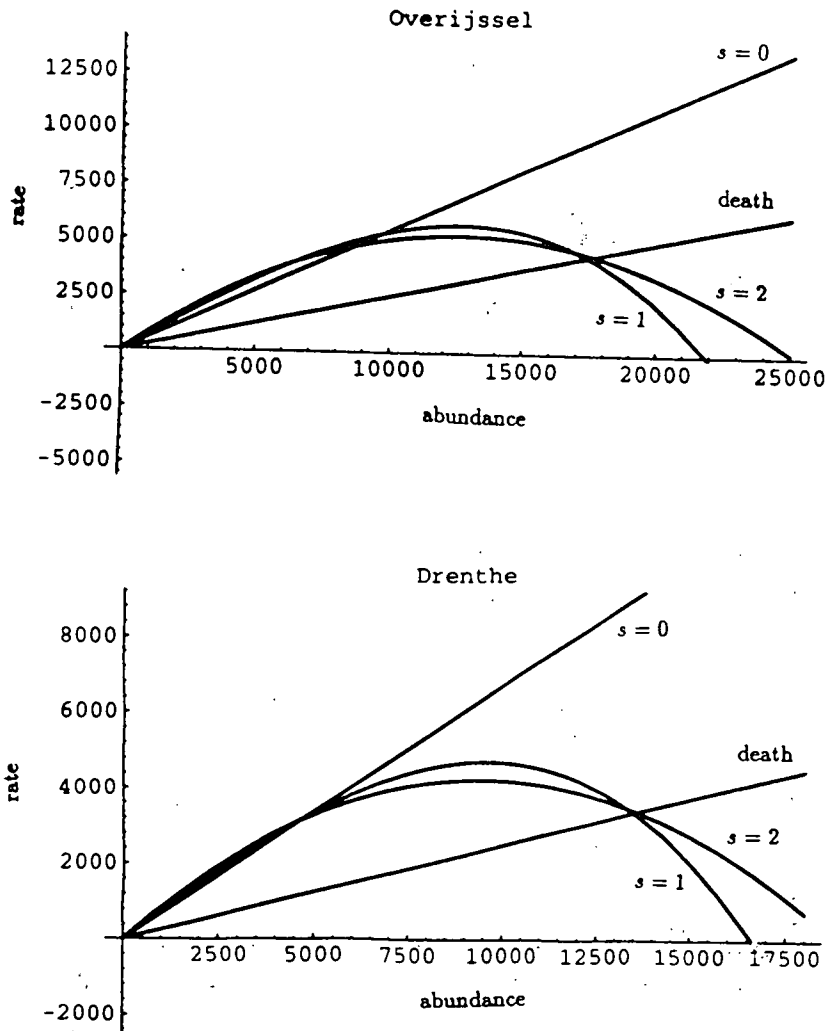


Figure 3. Assumed death rate and estimated birth rate functions for logistic models with  $s = 0, 1$  and  $2$ . A. Overijssel B. Drenthe

These parameter estimates may be substituted into (4.9)–(4.14) to obtain approximate mean and variance functions. As an illustration, Figure 4 illustrates the mean and variance functions for the model with  $s = 1$  and  $s = 2$  for overijl.

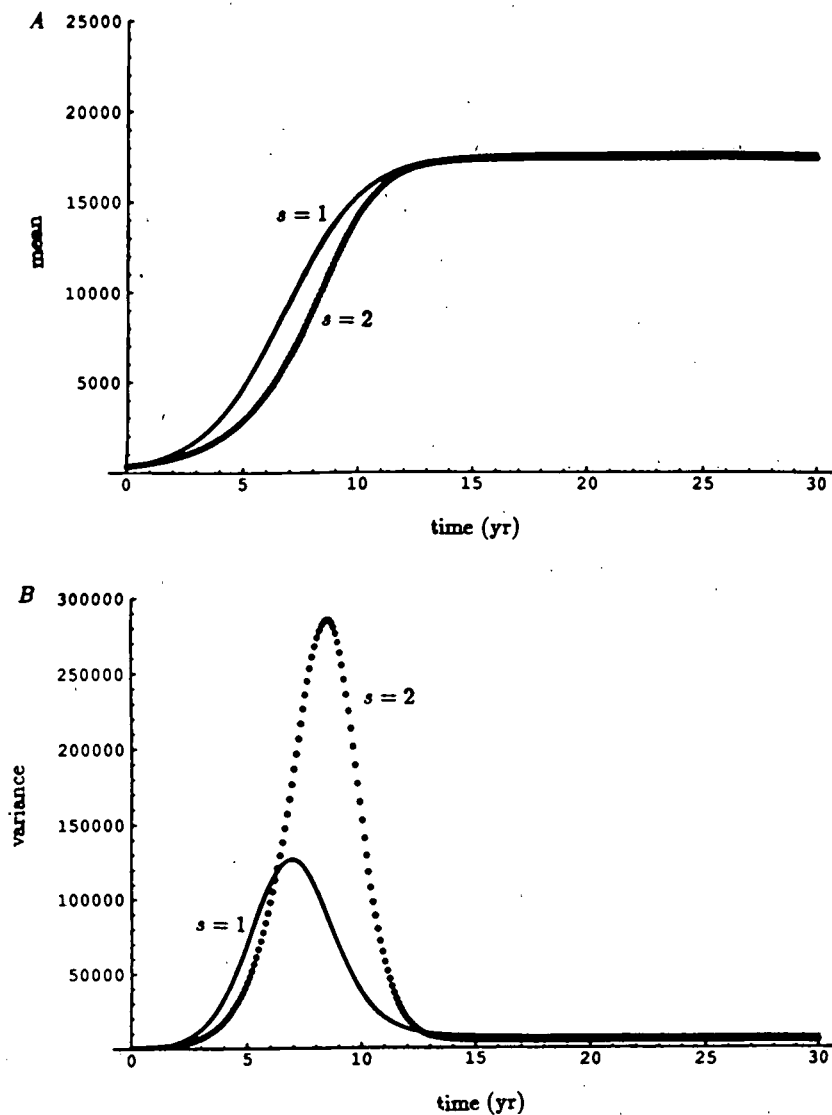


Figure 4. Cumulant functions for logistic model with  $s = 1$  and  $s = 2$  for Overijssel  
A. Means, B. Variances

### 5. Density Independent Models of Growth for Multiple Populations

#### 5.1 Assumptions

Consider now a multiple population density-independent model, with immigration, migration, and assumed birth and death rates :

$$\lambda_i(X_i) = a_{i1} X_i \text{ and } \mu_i(X_i) = a_{i2} X_i \quad (5.1)$$

#### 5.2 Deterministic model

The deterministic model for  $k = 2$  populations is

$$\dot{X}_1(t) = a_{1n} X_1 + v_{12} X_2 + I_1 \quad (5.2)$$

$$\dot{X}_2(t) = v_{21} X_1 + a_{2n} X_2 + I_2 \quad (5.3)$$

where  $v_{ij}$  is the assumed migration rate and  $a_{in}$  is the net rate

$$a_{in} = a_{i1} - a_{i2} - \sum_{j \neq i} v_{ji} \quad (5.4)$$

#### 5.3 Equations for cumulant functions

The pde for the cgf is, from [7] :

$$\begin{aligned} \frac{\partial K(\theta, t)}{\partial t} &= [(e^{\theta_1} - 1) a_{11} + (e^{-\theta_1} - 1) a_{12} + (e^{-\theta_1 + \theta_2} - 1) v_{21}] \frac{\partial K}{\partial \theta_1} \\ &+ [(e^{\theta_2} - 1) a_{21} + (e^{-\theta_2} - 1) a_{22} + (e^{\theta_1 - \theta_2} - 1) v_{12}] \frac{\partial K}{\partial \theta_2} \\ &+ \sum_{i=1}^2 (e^{\theta_i} - 1) I_i \end{aligned} \quad (5.5)$$

The differential equations for the means,  $\kappa_{10}(t)$  and  $\kappa_{01}(t)$ , are identical to (5.2) and (5.3). The equations for the second order cumulants are,

$$\dot{\kappa}_{20}(t) = (a_{11} + a_{12} + v_{21}) \kappa_{10} + v_{12} \kappa_{01} + 2a_{1n} \kappa_{20} + 2v_{12} \kappa_{11} + I_1 \quad (5.6)$$

$$\dot{\kappa}_{11}(t) = -v_{21} \kappa_{10} - v_{12} \kappa_{01} + v_{21} \kappa_{20} + (a_{1n} + a_{2n}) \kappa_{11} + v_{12} \kappa_{02} \quad (5.7)$$

$$\dot{\kappa}_{01}(t) = v_{21} \kappa_{10} + (a_{21} + a_{22} + v_{12}) \kappa_{01} + 2v_{21} \kappa_{11} + 2a_{2n} \kappa_{02} + I_2 \quad (5.8)$$

#### 5.4 Solutions for cumulant functions

Explicit solutions for the first and second order cumulants are given in [11]. We consider for subsequent application only models with one-way

migration, i.e. with  $v_{21} = 0$ , for which the individual differential equations may be solved recursively.

### 5.5 Application to muskrat population dynamics

Models of the form in (5.2) and (5.3) with migration were fitted to the data in [7]. With migration, the net birth-rates in adjacent provinces are not usually significantly different, for example the net rates for overijl, dr and gron are not significantly different, and the common net rate is estimated to be 0.328/yr. The absence of migration in (3.3) thus tends to underestimate the intrinsic birth rate in a donor province and overestimate it in a recipient province. The models with migration included typically fit the data better [7].

## 6. Ordinary Logistic Models of Growth for Multiple Populations

### 6.1 Assumptions

Consider multiple ordinary logistic populations linked with migration. The birth and death rate assumptions are

$$\lambda_i(X_i) = \begin{cases} a_{i1} X_i - b_{i1} X_i^2 & \text{for } X_i < (a_{i1} / b_{i1}) \\ 0 & \text{otherwise} \end{cases} \quad (6.1)$$

$$\mu_i(X_i) = a_{i2} X_i + b_{i2} X_i^2 \quad (6.2)$$

It is assumed also that the populations are linked by one-way migration from population 1 to population 2 at rate  $v_{21}X_1$ .

### 6.2 Deterministic model

The analogous deterministic model for this system is

$$\dot{X}_1(t) = a_{1n} X_1 - b_{1n} X_1^2 \quad (6.3)$$

$$\dot{X}_2(t) = v_{21} X_1 + a_{2n} X_2 - b_{2n} X_2^2 \quad (6.4)$$

where  $a_{in}$  are given in (5.4) and  $b_{in} = b_{i1} + b_{i2}$

Equation (6.3) is identical in form to (3.3), hence it has the logistic solution in (4.4) with equilibrium value  $K_1 = a_{1n}/b_{1n}$ . Equation (6.4) is a Riccati equation [1] with equilibrium value

$$K_2 = [a_{2n} + (a_{2n}^2 + 4b_{2n}v_{21}K_1)^{1/2}] / 2b_{2n} \quad (6.5)$$

### 6.3 Equations for cumulant functions

We again define a modified BDM process in which the birth rates are defined as a quadratic function of  $X$ , i.e.

$$\lambda_i(X) = a_{i1} X - b_{i1} X^2 \quad (6.6)$$

The effect of this change is usually negligible on the first population as previously observed, but may be substantial on the second population. The pde for the cgf is :

$$\begin{aligned} \frac{\partial K}{\partial t} = & \sum_{i=1}^2 [(e^{\theta_i} - 1) a_{i1} + (e^{-\theta_i} - 1) a_{i2}] \frac{\partial K}{\partial \theta_i} \\ & + \sum_{i=1}^2 [(e^{\theta_i} - 1) (-b_{i1}) + (e^{-\theta_i} - 1) b_{i2}] \left[ \frac{\partial^2 K}{\partial \theta_i^2} + \left( \frac{\partial K}{\partial \theta_i} \right)^2 \right] \\ & + (e^{-\theta_1 + \theta_2} - 1) v_{21} \frac{\partial K}{\partial \theta_1} \end{aligned} \quad (6.7)$$

Substituting (2.1) and expanding in powers of  $\theta_1$  and  $\theta_2$ , one obtains the following differential equations for the first and second order cumulants :

$$\dot{\kappa}_{10} = (a_{1n} - b_{1n} \kappa_{10}) \kappa_{10} - b_{1n} \kappa_{20} \quad (6.8)$$

$$\dot{\kappa}_{01} = v_{21} \kappa_{10} + (a_{2n} - b_{2n} \kappa_{01}) \kappa_{01} - b_{2n} \kappa_{02} \quad (6.9)$$

$$\begin{aligned} \dot{\kappa}_{20} = & (c_{1n} - d_{1n} \kappa_{10}) \kappa_{10} + (2a_{1n} - d_{1n} - 4b_{1n} \kappa_{10}) \kappa_{20} \\ & - 2b_{1n} \kappa_{30} \end{aligned} \quad (6.10)$$

$$\begin{aligned} \dot{\kappa}_{02} = & (c_{2n} - d_{2n} \kappa_{01}) \kappa_{01} + (2a_{2n} - d_{2n} - 4b_{2n} \kappa_{01}) \kappa_{02} \\ & + v_{21} (\kappa_{01} + 2\kappa_{11}) - 2b_{2n} \kappa_{03} \end{aligned} \quad (6.11)$$

$$\begin{aligned} \dot{\kappa}_{11} = & (c_{1n} - 2b_{1n} \kappa_{10} + c_{2n} - 2b_{2n} \kappa_{01}) \kappa_{11} + v_{21} (\kappa_{20} - \kappa_{10}) \\ & - b_{1n} \kappa_{21} - b_{2n} \kappa_{12} \end{aligned} \quad (6.12)$$

with  $a_{in}$  and  $b_{in}$  as before, with

$$c_{in} = a_{i1} + a_{i2} + v_{ji} \text{ and } d_{in} = b_{i1} - b_{i2} \quad (6.13)$$

### 6.4 Solutions for cumulant functions

As proposed in Section 4.4, we recommend solving equations (6.8)—(6.13) by obtaining the four equations with third order cumulants from *Mathematica*,

and then solving the combined system of nine equations with all cumulants of fourth or higher order set to 0.

### 6.5 Application to muskrat population dynamics

In order to investigate the effect of migration in these density dependent growth models, consider two populations with identical birth and death rate functions. As observed in [7], adjacent provinces are likely to have such identical rate functions. To be specific, we assume that an identical logistic model with  $s = 1$  holds for both a donor (overijl) and a recipient (dr) province. The assumed common parameter estimates are the median values in Table 1, namely those estimated for overijl. If these provinces also have identical starting values, then in the absence of migration they clearly would also have identical cumulant functions.

Three levels of migration are investigated. The first is  $v_{21} = 0.10$ , as suggested by the results in [7]. In the second level, the rate is doubled to  $v_{21} = 0.20$ ; in the third it is halved to  $v_{21} = 0.05$ . To adjust for migration from the first population, the overall intrinsic death rate,  $a_2 = 0.25$ , is partitioned into the migration rate,  $v_{21}$ , and a new intrinsic mortality rate,  $a_{12} = a_2 - v_{21}$ . The common parameters are  $a_{11} = a_{21} = 0.833$ ,  $b_{11} = b_{21} = 3.31 \times 10^{-5}$ ,  $a_{22} = 0.25$ , and  $b_{11} = b_{21} = 0$ , with estimated initial values  $X_1(0) = X_2(0) = 340$ .

The mean and variance functions for the first population (overijl) were given in Figure 4. Figure 5 illustrates for the three levels of migration the comparative mean and variance functions for the second population (dr) and also the covariance functions. It is clear that the migration effect, even at the very low levels compared to the birth rate, has a substantial influence on the cumulant functions of the recipient province.

Consider first the mean value functions. The asymptotic mean value for overijl, the donor province with migration, is 17613; whereas the asymptotic means for the three levels of migration for dr, the recipient province, are 18317, 19133, and 20527 for  $v = 0.05, 0.10$ , and  $0.20$  respectively. The three proportional increases are 0.040, 0.086 and 0.165.

Though the absolute values of the variances are relatively small, due to the law of large numbers, there are striking effects of migration in the shape of the curves. For simplicity, we consider the standard deviation of population size. The peak standard deviation for the donor province in Figure 5 is 355.7; whereas the corresponding peaks for the three levels of migration in the recipient province are 312.8, 294.7 and 286.7 respectively, for proportional decreases of 0.121, 0.171 and 0.194. The asymptotic standard deviation for overijl is 86.9, and the corresponding values for dr with the three migration levels are 83.7,

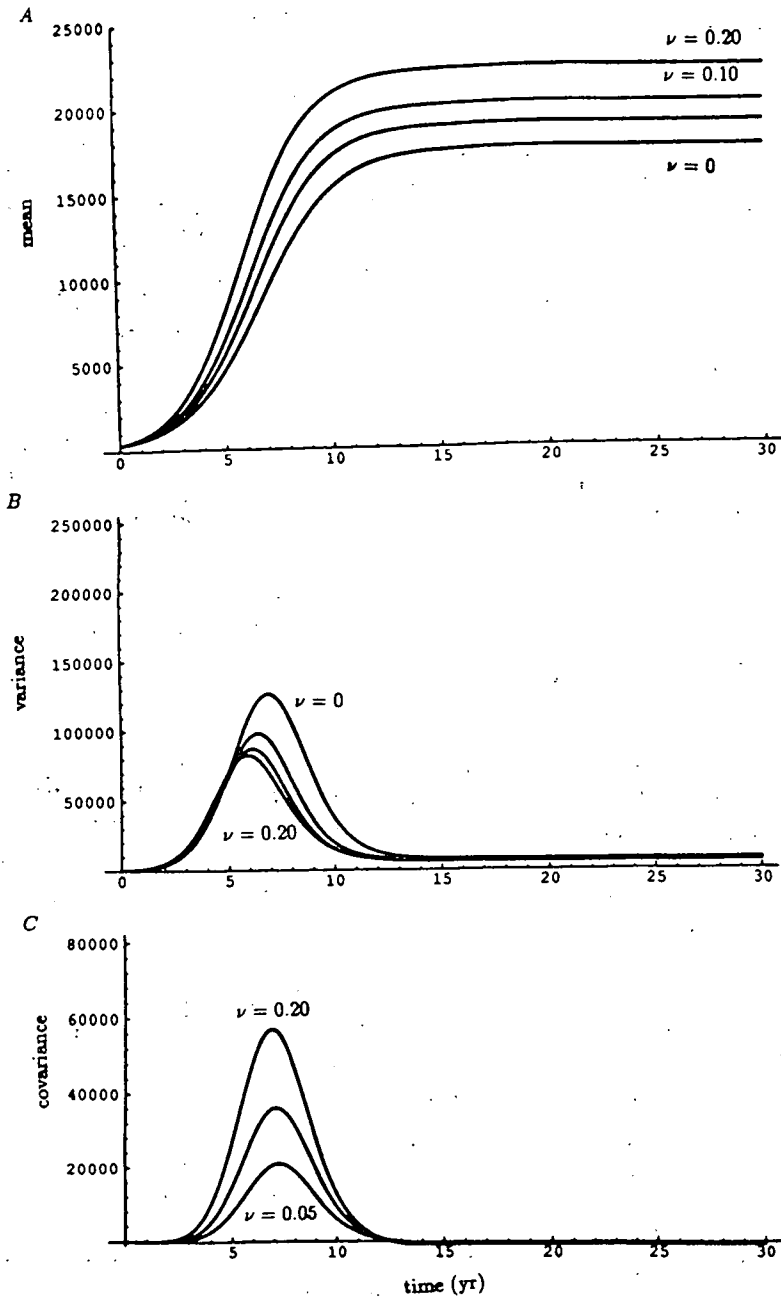


Figure 5. Comparative cumulant functions for  $s = 1$  logistic model for Drente with migration levels  $\nu = 0.05, 0.10$  and  $0.20$   
 A. Means, B. Variances, C. Covariances



81.1, and 77.0, respectively, which represent decreases. It is interesting that the lower migration rates which give the smaller mean values also yield the larger standard deviations. Because the asymptotic variances are small, it follows that the differences between the carrying capacities and the corresponding asymptotic values of the equilibrium distributions are also small.

### 7. Conclusions

Multiple populations linked by migration, called metapopulations, are of great interest in ecology and are widely studied using various deterministic and simulation models. This paper demonstrates two facts. Firstly, it shows that these density-dependent BDM models are also available to investigate the properties of metapopulations, such as the variances, which are not available from deterministic models. Secondly, the BDM models are valuable tools for evaluating pest control strategies which might increase the death rate, decrease the birth rate, or slow the migration rate. Migration is usually the most difficult of these to investigate, and this paper establishes the feasibility of using BDM models for this purpose.

This paper illustrates only one data set, and should be regarded as a progress report. Clearly many other data sets should be studied. For the present data, the derived variances are too low, which is due in part to a number of simplifying assumptions. The initial assumptions in Section 2 relating to unit changes and implicitly to exponentially distributed time intervals between events are not realistic biologically and in aggregate they damped the variance drastically. The model was generalized in [6], which yields much larger variances but a corresponding more difficult analysis. Also, we assumed in Sections 4 and 6 that all of the density-dependence is attributable to the birth rate function. This assumption also reduces the variances, and could be easily modified. Another major implicit assumption is the lack of so-called environmental stochasticity in the data. This additional component could be readily incorporated by adding some new constant to the differential equations for the variances, but is not pursued at present.

Research is also in progress to ascertain more precisely the accuracy of the cumulant approximations for the second population, and to develop approximating bivariate distributions by matching low-order cumulants, as in [13]. Though much work remains to develop these models fully, much has also been accomplished. In particular, this paper demonstrates the feasibility of using density-dependent BDM models for describing the spread of muskrats in the Netherlands, and in general it establishes the promise of these BDM models for successful use with similar data sets on spatial-temporal spread.

## REFERENCES

- [1] Banks, R. B., 1994. *Growth and Diffusion Phenomena*. Springer-Verlag, New York.
- [2] Cressie, N., 1993. *Statistics for Spatial Data*, 2nd ed. John Wiley and Sons, New York.
- [3] Hengeveld, R., 1989. *Dynamics of Biological Invasions*. Chapman and Hall, London.
- [4] Matis, J. H. and Wehrly, T. E., 1994. Compartmental models of ecological and environmental systems. In : *Handbook of Statistics, 12, Environmental Statistics* (G.P. Patil and C.R. Rao, eds.), Elsevier, New York.
- [5] Matis, J. H., Kiffe, T. R. and Otis, G. W., 1994. Use of birth-death-migration processes for describing the spread of insect populations. *Environ. Entomol.*, **23**, 18-28.
- [6] Matis, J. H., Zheng, Q. and Kiffe, T. R., 1995. Describing the spread of biological populations using stochastic compartmental models with births. *Math. Biosci.*, **126**, 215-247.
- [7] Matis, J. H., Kiffe, T. R. and Hengeveld, R., 1996. Estimating parameters for birth-death-migration models from spatio-temporal abundance data : Case of muskrat spread in the Netherlands. *J. Ag. Biol. Environ. Stat.*, **1**, 1-20.
- [8] Matis, J. H., Kiffe, T. R. and Parthasarathy, P. R., 1996. On the cumulants of population size for the stochastic power law logistic model. Manuscript.
- [9] Micromath, 1995. *Scientist, for Experimental Data Fitting*. MicroMath, Inc, Salt Lake City, UT.
- [10] Okubo, A., 1980. *Diffusion and Ecological Problems : Mathematical Models*. Springer-Verlag, New York.
- [11] Renshaw, E., 1991. *Modeling Biological Populations in Space and Time*. Cambridge University Press, New York.
- [12] Skellam, J. G., 1951. Random dispersal in theoretical populations. *Biometrika*, **38**, 196-218.
- [13] Wehrly, T. T., Matis, J. H. and Otis, G. W., 1993. Approximating multivariate distributions in stochastic models of insect population dynamics. In : *Multivariate Environmental Statistics* (G.P. Patil, C. R. Rao and N. P. Ross, eds.), Elsevier, New York.
- [14] Wolfram, S., 1991. *Mathematica, A System for Doing Mathematics by Computer*, 2nd ed. Addison-Wesley, Redwood City, CA.