

# ODD protocol for vole-mustelid IBM with phenomenological predator submodule

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## 1.1 Purpose

The purpose of the model is to assess which factors (or factor combinations) are needed for the generation of the cyclic pattern observed in natural vole populations. This goal is achieved by contrasting the alternative model versions by “switching off” some of the submodels in order to reflect the four combinations of the factors hypothesized to be driving vole cycles. The model is constructed as a theoretical extension of an empirical model system in an environment with boreal seasonality to explore long-term population dynamics in this system given the observed vole life-histories within the system combined with mustelid predation. So, the scope of the model is *Microtus* species living in productive habitats characterized by boreal seasonality. The complex life history of *Microtus* species could not be represented with the stage-based approach (as, for example, the fate of the weanlings depends on whether their mom is alive or not), and necessitate the use of individual-based approach.

## 1.2 Entities, state variables and scales

The model represents a typical enclosure used in experimental vole studies: an enclosure of 0.5 ha consisting of 6 habitat patches (225 m<sup>2</sup> each) separated by the hostile matrix (Andreassen et al. 1998, Ims and Andreassen 1999, 2000, Andreassen and Ims 2001, Huitu et al. 2003). So, our model directly replicates the experimental design usually used in the empirical model system (i.e. Evenstad Research Station). The landscape consists of grid cells (quadratic units) characterized by the nominal variable *habitat* that has two levels: habitat and matrix.

One time step in the model corresponds to one week, a year consists of 52 weeks, and the time horizon of the model is 35 years.

The entities in the model are (Table B 1):

- Spatial: grid cells (quadratic units) composing the landscape and characterized by nominal variable *habitat* with two levels: habitat and matrix. Grid cells compose six habitat patches (characterized by an ID), separated by hostile matrix. Such a system

represents a typical enclosure used in experimental vole studies (total area of 0.5 ha with six habitat patches of 225 m<sup>2</sup> each; Andreassen and Ims 2001).

- Biological: individuals characterized by the following state variables: *stage* (weanling, subadult, adult), *age* (weeks), *sex* (female or male), *family* (ID of the family an individual belongs to), a Boolean maturation indicator of adults (*mature*), and Boolean *reproductive* indicating whether the mature individual is reproducing or not. Reproductive females are additionally characterized by the ID of their dominant male, variable indicating weeks since the last reproduction, and the number of litters to be produced. The sex ratio at birth is assumed to be 1.

Table B 1. List of entities, their corresponding state variables and possible statuses or units in the individual-based model

Entities	State variables (code notation)	Status / units
Voles	Stage (stat)	Weanling (< 3 weeks old); subadult (4 <= weeks old >= 3), adult (> 4 weeks old)
	Age ( <i>age</i> )	Numeric (weeks)
	Sex ( <i>sex</i> )	0 (female), 1 (male)
	Family ID ( <i>family</i> )	Numeric
	Maturation indicator ( <i>mature</i> )	Boolean
	Reproductive indicator ( <i>reprod</i> )	Boolean
	Dominant ID ( <i>mydom</i> )	Numeric (ID of the dominant male, for females only)
	Weeks since last reproduction ( <i>weeks_since_rep</i> )	Numeric
Cell	Number of litters ( <i>numlitters</i> )	Numeric
	Habitat ( <i>hab</i> )	Matrix (0), habitat (numeric 1-6 for the patch ID)

### 1.3 Process overview and scheduling

Seasonality plays an important role in the life cycle of the voles (Gliwicz 1990, Korpimäki et al. 2004), with some processes occurring only during the summer. We therefore distinguish two seasons: summer (S, weeks 17-43) and winter (W, weeks 1-16 and 44-52). The model includes

the following processes with the period during which they occur indicated in the brackets: reproduction (S), survival (S, W), dispersal (S), predation (week 44), and ageing (S, W). Every time step the processes occur in the following order: survival, dispersal, reproduction and ageing. Predation occurs only on the 44<sup>th</sup> week of each year and is scheduled after survival. Individuals perform all the processes but survival in a random order. For survival, first reproductive females and their weanlings (in random order) are processed, and then the survival is estimated for all other individuals in a random order.

## 1.4 Design Concepts

*Basic Principles:* This model is built to be able to discriminate alternative hypotheses suggested for the factors causing the vole population cycles. The question of what mechanisms underlie the formation of a regular cyclic pattern in voles intrigued scientists for decades, yet an unambiguous answer was not yet found. The main hypotheses supported in literature concern the impact of extrinsic (predation) and intrinsic (sociality, and dispersal) factors (Krebs 1996, Stenseth et al. 1996, Boonstra et al. 1998, Andreassen et al. 2013). Moreover, multi-factorial hypothesis was formulated stating that one factor is not sufficient for cycle formation; rather an interaction of several factors is needed (Krebs 1996, Stenseth et al. 1996). An individual-based model incorporating the mechanistic description of vole life-history processes offers a unique opportunity for testing a set of alternative hypotheses. This is achieved by contrasting the alternative model formulations representative of different hypotheses with a set of empirical patterns that describe vole cycles observed in the field. Thus, the use of individual based modelling (IBM) together with pattern-oriented modelling (POM) provides favourable settings for answering the question of what drives vole population cycles.

*Emergence:* Individual-based rules lead to the emergence of the spatial distribution of individuals (occupancy of different patches) and temporal population dynamics, resulting in multi-annual cycles of amplitude and period that differ as a function of processes assumed according to each tested hypothesis.

*Sensing*: Individual voles can sense the sex and stage of other individuals, their dominant status and family ID, and the number of other voles in the same patch.

*Interaction*: Interactions between individuals are indirect, modelled by: suppressing the reproduction of other females when the maximum number of reproductive females per patch is reached; male infanticide via decreased weanling survival rates in case of male turnover; and decrease in female survival due to male turnover. Also in winter the interactions between individuals are mediated via intraspecific competition for resources, which is modelled using density-dependent survival.

*Stochasticity*: Demographic stochasticity is incorporated via Bernoulli trials to assess the survival of individuals, emigration propensity, and their maturation; and via Poisson distribution to assess the number of litters. Inter-individual variation is incorporated via uniform distribution adding a random number for each individual when estimating emigration propensity and the number of weanlings to be produced.

*Collectives*: individuals belong to families, each family has an ID. A family ID is assigned according to the ID of the mother.

*Observation*: Each simulation was run for 35 years (or until the population went extinct) and first 5 years were discarded since predation affects the vole population from the year 5 and on. For the model analysis we recorded vole population size in the whole system and in each patch each week for each of 1000 model runs. For contrasting the model with field patterns only the population size in week 44 (1<sup>st</sup> of November) was used for calculation of 1) the mean (and SD) autumn population size across 1000 runs; 2) the cycle period using acf; 3) the amplitude defined as ratio of maximum to minimum autumn population size observed during each run; 4) and the natural logarithm of the yearly population growth rates calculated on the autumn population sizes.

## **1.5 Initialization**

The model is initialized to reflect as close as possible the setup of the vole enclosure experiments (Andreassen and Ims 2001): simulations start on the week 25 with four families “released” in the system, each family consists of a mature reproductive female and the number of her weanlings drawn from Poisson distribution with mean = 4.37 (H. P. Andreassen, unpublished data). Each family is randomly assigned to one of the patches. The age of the females is drawn randomly from the uniform distribution ([39, 52] weeks), number of litters is drawn from the Poisson distribution (mean = 3.12), and weeks since reproduction is set to 4. The age of weanlings is set to 2 weeks, their family ID is set to their mother’s ID, and sex is assigned to either a male or a female with even probability. The predator population size ( $P$ ) is initialized in the 5<sup>th</sup> year of the simulation by dividing the vole population size in the system ( $N$ ) by the equilibrium prey-predator ratio ( $Q$ ).

## **1.6 Input data**

The model does not use input data.

## **1.7 Submodels**

The values of the parameters, their description and sources from which they were derived are given in Table B 2. All parameter estimates are coming from the literature and own experimental data.

### **1.7.1 Reproduction**

Reproduction takes place in summer. Only mature reproductive females can reproduce given there is a mature dominant male present in the same patch. There is a limit for the number of reproductive females that can be located in the same patch, set to 2; the reproduction of other mature females is suppressed. When a female becomes reproductive, it first draws the number of litters to be produced from the Poisson distribution with mean of 3.12 (truncated at 1 and 5 individuals). Then every three weeks a female produces a litter until the maximum number of

litters is reached. The number of weanlings in each litter ( $Num_{wean}$ ) is a function of the number of reproductive females in the same patch, reflecting kinship effect (Lambin and Yoccoz 1998) on reproductive output (the number of reproductive females is used as a proxy to the higher female densities and associated higher female range overlap in the “clumped” food treatment, which resulted in the higher female reproductive output, as found by Rémy 2011, Chapter III, Eq. B.1):

$$Num_{wean} = \exp(\alpha_{rep} + \beta_{rep} * overlap + U[0, b_{rep}]) \quad (\text{Eq. B.1})$$

where  $\alpha_{rep}$  and  $\beta_{rep}$  are an intercept and slope,  $U[0, b_{rep}]$  is a uniform distribution with parameters 0 and  $b_{rep}$ , which is used to incorporate the variation between females (Table B 2), and  $overlap$  is the percentage of home range overlap for reproductive females, which is set to 50% if 2 reproductive females are present in the patch and 0% if 1 female is present or not sociality in reproduction is included (for testing the hypothesis of no sociality effect). The value  $Num_{wean}$  obtained with eq. B.1 is rounded to the integer. If the estimated number of weanlings exceeds 6, it is set to 6.

### 1.7.2 Survival

#### Winter

Winter survival probability ( $s_{win}$ ) is negative density-dependent so as to yield the population rate of change during winter estimated by Aars and Ims (2002). Aars and Ims (2002) ascribed the negative density dependent winter population growth rate to winter recruitment, however since we do not model reproduction during the winter period (due to the lack of data and knowledge to parameterize it, Krebs 2013), we assume that this negative density dependence lies in the winter survival. Therefore, the survival in winter is modeled according to Beverton and Holt population model, using the following equation:

$$s_{win} = \frac{1}{1 + (e^{R_{max}} - 1) \cdot N_t / K_{win}}; \quad (\text{Eq. B.2})$$

where  $R_{max}$  is the maximum winter population growth rate,  $N_t$  is the vole population size in a given patch at time  $t$ ,  $K_{win}$  is the carrying capacity in individuals for this patch (Table B 2). We then each week calculate the all-winter survival probability based on the current number of individuals in the patch and re-calculate it to the weekly survival probability as:  $Weekwinsurv = (s_{win})^{\frac{1}{26}}$ ; because winter consists of 26 weeks.

## Summer

First each reproductive female checks if its dominant male is present. If it is absent or has been replaced by another male (“male turnover”, Andreassen and Gundersen 2006), the two sociality-related processes can happen: decrease in weanlings survival due to male infanticide and decrease in female survival. If sociality submodel is activated, then the female survival is set to  $s_f$  (Table B 2, 0.87) and her weanlings survive with probability  $s_w$  (0.38). If mother of weanlings die, they all die irrespective of the presence of a dominant male in the patch. In case sociality submodel is not activated or a dominant male is present, the survival probability for all individuals (females, males, subadults and weanlings) is determined by a Bernoulli trial with a probability  $s_{sum}$  (0.98).

### 1.7.3 Dispersal

Only adults and subadults can disperse. First, emigration probability is determined for each individual as a function of its sex ( $sex$ ), stage ( $stage$ ), density of individuals in the same patch ( $dens$ ) and interaction between these parameters (Andreassen and Ims 2001).

$$y_{em} = \alpha_{em} + \beta_{sex} \cdot sex + \beta_{stage} \cdot stage + \beta_{dens} \cdot num + \beta_1 \cdot sex \cdot stage + \beta_2 \cdot dens \cdot stage + \beta_3 \cdot dens \cdot sex + U[0, b_{em}] \quad (\text{Eq. B.3})$$

$$Prob_{em} = \frac{1}{(1 + \exp(-y_{em}))}; \quad (\text{Eq. B.4})$$



Where  $\alpha_{em}$ ,  $\beta_{sex}$ ,  $\beta_{stage}$ ,  $\beta_{dens}$ ,  $\beta_1$ ,  $\beta_2$ , and  $\beta_3$  are the coefficients as estimated by Andreassen and Ims (2001),  $y_{em}$  is emigration probability on the logit scale, and  $U[0, b_{em}]$  is a uniform distribution with parameters 0 and  $b_{em}$ , which is used to incorporate the inter-individual variation and variation in emigration propensity along the summer (Table B 2). A Bernoulli trial with  $Prob_{em}$  is used to decide whether an individual will disperse. If an individual leaves its patch, it is first confronted with the dispersal mortality with the survival probability  $s_{disp}$  (Table B 2, 0.94). If it survives, it checks five other patches in a random order, and settles in one of them given the patch does not contain an adult of the same sex as a disperser, a disperser then becomes dominant (if it is a male) or reproductive (if it is a female). If no such patch is present, a disperser comes back to its patch of departure.

#### 1.7.4 Ageing and maturation

Each week individuals update their age and, if required, their stage corresponding to their age. Only adults can become mature. Maturation probability is decreasing as a function of the week number, with all adult individuals becoming mature in the week 17, and none of them getting mature from week 39 and on (Table B 3).

Table B 3. Probability to become mature for adults as a function of week

Weeks		Probability
From	Till (inclusive)	
17	21	1
22	25	0.8
26	29	0.6
30	34	0.4
35	38	0.2
39	Next year (week 16)	0

### 1.7.5 Predation

Predation is modelled using the predator-prey model commonly used for voles incorporating the effect of specialist predator with Type 2 functional response (Hanski et al. 1991, Hanski and Korpimaki 1995, Turchin and Hanski 1997, for detailed discussion of different predator-prey models used for voles see Hanski et al. 2001). We used the estimates of parameters available for these models (Hanski and Korpimaki 1995, Turchin and Hanski 1997) and for the sake of simplicity and computational efficiency modelled predation only once a year in week 44 starting from the 5<sup>th</sup> year of the simulation. In a first step the predator population density is updated using the predator growth rate. The predator growth rate is calculated in one of the ways depending on the vole population density as compared to the critical prey density below which the predator cannot reproduce ( $N_{crit}$ ):

$$R_{pred} = \exp\left(S_{max} \cdot \left(1 - \frac{Q \cdot P}{N}\right)\right) \text{ if } N > N_{crit}; \quad (\text{Eq. B.5})$$

$$R_{pred} = \exp(d_{low}) \text{ if } N \leq N_{crit}; \quad (\text{Eq. B.6})$$

where  $S_{max}$  is predator intrinsic rate of increase,  $P$  and  $N$  are the predator and vole population densities respectively, and  $Q$  is equilibrium prey-predator ratio (Table B 2). If vole population density is below  $N_{crit}$  there is no reproduction and the predator population density declines exponentially with the predator growth rate  $d_{low}$  (Hanski and Korpimaki 1995, Table B 2). We included the possibility for predators to prey on alternative prey by setting the fixed lower limit for a predator population density,  $P_{min} = 0.005$  ind/ha, modelling the refuge for predator *sensu* Hanski and Korpimaki (1995).

In the second step the number of prey to be killed by predator is determined only if the vole population density is higher than  $N_{crit}$ , as following:

$$nkill = \exp\left(\frac{c \cdot P}{(N+D)}\right) \quad (\text{Eq. B.7})$$

where  $nkill$  is the number of voles to be preyed on,  $c$  is the maximum per capita predation rate,  $P$  and  $N$  are the predator and vole population densities respectively, and  $D$  is predation half-

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saturation constant (Table B 2). If an estimated number of voles to be preyed on ( $n_{kill}$ ) is lower than the vole population density ( $N$ ), then  $n_{kill}$  number of voles are killed, otherwise the number of voles to be killed is defined as a difference between the vole population density ( $N$ ) and critical prey density ( $N_{crit}$ ).

## 2 DATA FOR MODEL PARAMETERIZATION

The life history and behavioral data used to parameterize the vole demographic submodule is collected mostly on *M. oeconomus* in the experiments conducted at the Evenstad Research Station (for detailed data sources see Table B3). The only exception is the data on the increased reproductive output as a result of female sociality, which is parameterized with the data collected on another species, *Myodes glareolus*, yet with the experiments conducted in the same settings at Evenstad Research Station. Availability of the data collected on the same species in the same settings is advantageous as it ensures the consistency of the data and saves the time needed to bring the parameter estimates collected under different environmental conditions / different biological systems in agreement. Still, some care had to be taken when using those data to parameterize the model. Thus, double-accounting of mortality may occur if survival estimates are based on the apparent survival (as is often the case with Capture-Mark-Recapture studies), and therefore implicitly also incorporate the mortality due to dispersal. In our case the survival probability were obtained from the live-trapping of individuals (as described in Andreassen and Ims 2001) that did not change the patch they inhabited from one week to the next one. Alternatively, the dispersal mortality was estimated using the survival estimates obtained for the individuals that shifted from one patch to the other between trapping sessions, when accounting for the survival as estimated for individuals that did not move.

The parameters describing weasel demography and its effect on the vole population dynamics were taken from the previous predator-prey models developed for this system (Hanski and Korpimäki 1995, Turchin and Hanski 1997). We had to slightly adjust the values for critical prey density ( $N_{crit}$ ) and predator mortality when prey is scarce ( $d_{low}$ ; for details see Table B1), however these parameters did not have much effect on the model output as later revealed with the sensitivity analysis (Figure 5, Figure C1 and Figure C2). We are aware of the critics regarding the values used in the models on vole-mustelid population dynamics (Xavier Lambin, *pers. comm*) and therefore conducted a) sensitivity analysis to assess the effect of each parameter

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on the model output; and b) developed a second model version where the weasel demography was implemented in a mechanistic way (Appendix A).

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Table B 2. Parameters, their description, nominal values and sources from which they were obtained. Parameters are grouped under the processes they are acting on: survival, dispersal, reproduction and predation. For each parameter we report minimum and maximum values that were used for global sensitivity analysis.

Parameter	Description (units)	Value	Range		Source
Survival			Min	Max	
$s_w$	Survival rate of weanlings due to male turnover (week $^{-1}$ )	0.38	0.22	0.58	Andreassen and Gundersen 2006
$s_f$	Survival rate of reproductive females due to male turnover (week $^{-1}$ )	0.87	0.82	0.92	Andreassen and Gundersen 2006
$s_{sum}$	Baseline survival rate in summer (week $^{-1}$ )	0.98	0.96	1	H. P. Andreassen, unpublished data
$R_{max}$	Winter maximum population growth rate (week $^{-1}$ )	0.4	0.3	0.6	Aars and Ims 2002
$K_{win}$	Carrying capacity in winter (ind./patch)	6.5	4.5	8.5	Aars and Ims 2002
Dispersal					
$\alpha_{em}$	Intercept in the emigration equation	-1.247	-1.965	-0.529	Andreassen and Ims 2001
$\beta_{sex}$	Effect of sex in the emigration equation	-0.554	-1.004	-0.104	
$\beta_{stage}$	Effect of stage in the emigration equation	0.221	-0.256	0.698	
$\beta_{dens}$	Effect of density in the emigration equation	-0.846	-1.092	-0.601	
$\beta_1$	Coefficient for sex*stage interaction in the emigration equation	-1.502	-1.889	-1.114	
$\beta_2$	Coefficient for density*stage interaction in the emigration equation	0.493	0.234	0.753	
$\beta_3$	Coefficient for density*sex interaction in the emigration equation	0.287	0.039	0.536	
$b_{em}$	Maximum in the uniform distribution for the random effect in the emigration equation	0.814	`	`	H. P. Andreassen, unpublished data
$s_{disp}$	Dispersal survival rate (week $^{-1}$ )	0.94	0.9	0.96	
Reproduction					
$numlit_{Pois}$	Lambda for Poisson distribution used for the number of litters produced per female	3.12	2	5	H. P. Andreassen, unpublished data

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$Min_{numlit}$	Minimum number of litters	1	`-	`-	
$Max_{numlit}$	Maximum number of litters	5	`-	`-	
$Weeks$	Number of weeks between two reproduction events	3	`-	`-	Ims 1997
$\alpha_{rep}^1$	Intercept in the reproduction equation	0.775	0.492	1.058	Rémy 2011
$\beta_{rep}^1$	Effect of sociality in the reproduction equation	0.011	0.004	0.018	Rémy 2011
$b_{rep}^1$	Maximum in the uniform distribution for the random effect in the reproduction equation	0.45	`-	`-	Rémy 2011
$Max_{wean}$	Maximum number of weanlings	6	`-	`-	Ims 1997
<b>Predation</b>					
$S_{max}$	Predator intrinsic growth of increase ( $yr^{-1}$ )	2.8	2.4	3.2	Hanski and Korpimaki 1995
$Q$	Predator-prey ratio constant (voles*predator $^{-1}$ )	42	40	100	Turchin and Hanski 1997
$c$	Maximum consumption per predator (voles*year $^{-1}$ *predator $^{-1}$ )	200	150	300	Hanski and Korpimaki 1995 <sup>2</sup>
$d_{low}$	Predator mortality rate when prey is scarce ( $yr^{-1}$ )	-4	-5	-2	Hanski and Korpimaki 1995 <sup>3</sup>
$N_{crit}$	Critical prey density for predator reproduction (voles*ha $^{-1}$ )	30	20	80	Turchin and Hanski 1997 <sup>4</sup>
$D$	Predation half-saturation constant (voles*ha $^{-1}$ )	6	4	12	Turchin and Hanski 1997
$P_{min}$	Lower limit for a predator population density (predator*ha $^{-1}$ )	0.005	`-	`-	Hanski and Korpimaki 1995

<sup>1</sup>Demographic parameters parameterized with the data on *Myodes glareolus* (unlike the rest of the parameters that are derived for *M. oeconomus*)

<sup>2</sup>Maximum consumption per predator had to be adjusted since predation occurs only once a year

<sup>3</sup>Close to the  $d_{high}$  estimated by Hanski and Korpimaki (1995) to be -5

<sup>4</sup>Used critical prey density is slightly higher than estimated by Turchin and Hanski (1997): 14 voles\*ha $^{-1}$

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