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Progress of a Bioenergetic Simulator  
of Pine Vole Populations

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The pine vole research effort under way at VPI & SU has involved 4 parts: an investigation of nutrition and energetics, a study of habitat and behavior, an evaluation of chemical control, and the development of a computer simulation model of population dynamics. Coyle et al. (1981) reported on the results of a preliminary model developed by Coyle (1980), and outlined a second stage model to incorporate his (1980) recommendations and the continually expanding base of field and laboratory data. The preliminary model was a demographic simulator mechanistically driven by bioenergetic equations developed chiefly from laboratory studies at Virginia Tech. The second stage model was proposed to include 4 submodels, one each dealing with the biological and spatial aspects of pine vole populations, and with the control procedures and economic aspects of orchard management for pine voles. To date, the majority of work has been on the extensive refinement of the biological and spatial components, and only those refinements are discussed here.

To distinguish the second stage model from Coyle's (1980) model, called MICROTUS, the biological-spatial component of the newer version is named PITYMYS. It has been written in programming language PL/I for ease of programming and documentation, and may be executed at any reasonably-sized computer facility equipped with a PL/I compiler. The basic design is inspired by that of MICROTUS, and is shown in Figures 1 and 2. The design is highly modular, and makes liberal use of subroutines for identifiably separable biological and computational events. Figures 1 and 2 show the names of the principal subroutines of PITYMYS, and their associated functions.

Forages are divided into the same 5 classes (grasses, forbs, bulbs and roots, vine leaves, and apple fruit) as in MICROTUS, according to the classification of Lochmiller (1980). Female pine voles are divided into the same 6 energetic classes: sucklings, juveniles, non-reproductive adults, pregnant adults, lactating adults, and pregnant-and-lactating adults. And males are divided into the same 3 energetic classes: sucklings, juveniles, and adults. A major modification in PITYMYS is that animals are classified also by the additional criterion of age in weeks. Thus the population may be sectioned and summed along either dimension, according to the desired form of population appraisal. As MICROTUS, PITYMYS operates on a weekly time step, and is limited to a maximum simulation period of 52 weeks.

PITYMYS

Set up.	INPIT
Simulate by block or	BLOKMODL
Simulate by tree.	TREEMODL

Fig 1a. Design and subroutines of PITYMYS.

BLOKMODL

Initialize.	BLOKPRIM
Prepare.	BLOKPREP
Scale variables.	BLOKSCAL
Iterate by week.	BOUTPIT
Simulate bioenergetics.	BBIODRIV

Fig 1b. Design and subroutines of BLOKMODL.

BBIODRIV

Determine:

Daily energy budgets.

BDEBDRIVE

Energy acquisition.

BEATDRIVE

Growth.

BGROW

Stress.

BSTRESS

New population structure.

BSHIFT

Forage change rates.

BGRAZE

Energy availability.

BENERGY

Fig 2. Design and subroutines of BBIODRIV.

Subroutine INPIT prompts the user for the type (maintained or abandoned) and size of the orchard to be simulated, and the simulation time. In addition the user specifies the type of model to be used: BLOKMODL and TREEMODL are alternative subroutines driving 2 different population simulators. BLOKMODL drives BBIODRIV to treat the voles on a standardized orchard block as a single breeding population, whereas TREEMODL drives TBIODRIV to treat the voles at each tree as a separate subpopulation. Whichever model is chosen, the user is given a choice of whether or not to specify the initial forage structure, but must specify the initial population structure (by orchard or by tree). Except for computational expedients, the subroutines of BBIODRIV and TBIODRIV are identical, so only those of BBIODRIV are discussed here in detail.

BBEBDRIV computes the daily energy budget (DEB) of a representative animal of each energy class as the sum of its maintenance energy, growth energy, and reproductive energy needs. DEB's are simulated as functions of surface temperature, subsurface temperature, photoperiod, activity period, and activity level, and are computed using the data of Lochmiller (1980). This algorithm may be more precise than that of MICROTUS, where the effects of temperature and photoperiod are simulated only indirectly, via the assumption of an annually sinusoid basal metabolic rate.

The energy acquisition routine has been extensively revised. Under the single assumption that animals do not ingest more gross energy than they need for maintenance, growth, and reproduction, a dietary gross energy need is computed using steady-state flow equations, from the DEB, the mean daily mass of stomach contents (in terms of gross energy), the diet digestibility, and the food passage rate of each vole class. These 4 quantities are known with good precision, and their use in this algorithm (BEATDRIV) obviates the need for estimates of stomach size, the volume of food ingested per feeding, and the number of feeding times per day, as in MICROTUS. The act of feeding is simulated using a linear programming routine that calls an IMSL (International Mathematics and Statistics Library) version of the simplex algorithm (ZX3LP) to allocate limited forage energy among competing vole classes. The algorithm assumes no foraging hierarchy, as needed in MICROTUS, and weights the allocations by the number of voles in each class. The algorithm is iterated by forage class, in order of feeding preference, until all DEBs are met or until each forage class has been reduced to a level equal to the product of its availability and palatability. If any vole class DEB is not met, an energy restriction coefficient is computed for a representative of that class.

If a DEB is met, the body weight of a representative animal is increased according to the growth rate data of Derting and Cranford (pers. comm.), and the body fat level is increased according to the body composition analyses of Lochmiller (1980), Noffsinger (1976), and Servello (1981). Derting and Cranford (pers. comm.) have found juvenile growth patterns to differ among 3 photoperiods, and that effect is simulated by using linear regression to derive the body weight increase at the existing photoperiod from the 3 increases computed for the 3 known photoperiods. If a DEB is not met, the

body weight and fat levels are determined according to the severity of the energy restriction. Equations used to determine growth on restriction are derived from the data of Merson (1979).

Probabilities of transition between age and energy classes are computed, for representatives of the age-by-energy classes, as functions of body weight and fat levels. Nondietary effects on survivorship (predation, parasitism, disease, injury, old age) are not treated mechanistically, but are simulated by setting the maximum possible survivorship value for an age-by-energy class ( $p_{max}$ ) equal to the maximum observed in a natural population. Actual survivorship is then determined bioenergetically on the range (0.0,  $p_{max}$ ), so that there is always some mortality operating independently of energy acquisition. Natality is a function of maternal age and energy balance, and the number of breeding-age adults in the population.

The simulation of fractional animals is avoided by providing the user with a choice of vole class transition algorithms. In the deterministic algorithm the size of one class is multiplied by a probability of transition into a second class, and the product rounded to the nearest whole number. In the stochastic algorithm, the transition is simulated by independent Bernoulli trial, wherein a number is drawn from a uniform distribution between 0.0 and 1.0, compared with the transition probability, and if the random number is less than or equal to the probability, one animal is advanced. This algorithm is iterated over all of the animals in an age-by-energy class, yielding similar results for large samples to those of the deterministic algorithm. The stochastic algorithm is therefore offered as an option for the sake of biological realism, but may not be convenient for simulation studies where repeatability and comparison of control strategies are desirable.

Availability of forages other than grasses, and seasonal changes in digestibility, palatability, and preference of all forages, are simulated in subroutine BENERGY by a series of equations developed by Coyle (1980) from the data of Lochmiller (1980). The effect of grazing by pine voles is simulated for grasses by subroutine BGRAZE. The grass growth rate is taken as the first derivative of a curve describing grass gross energy availability as a function of Julian day. The grass growth rate that week is decremented by the amount grazed that week to yield an energy availability change rate. That change is added to the amount available at the beginning of the week to yield a prediction of the amount available at the beginning of the next week.

In addition to performing all of the functions of BLOKMODL at the level of the individual tree, TREEMODL allows animals to travel to or from neighboring trees at the end of each week, according to directional movement probabilities computed from field live-trap data as functions of adjacent tree subpopulation densities. The orchard population is then taken as the sum of the subpopulations.

Validation of PITYMYS will be by statistical comparison of simulation output to field live trap data, as analyzed via the demographic software discussed by Hasbrouck et al. (1982). Once validated, the model will be used to simulate, at low cost, experiments with management options on pine vole populations, and may provide some theoretical knowledge of small mammal population dynamics.

The control and economic submodels are being designed to operate about the biological-spatial submodel, but remain in need of 2 types of information: quantification of the relationship between pine vole population density and apple tree damage level, and quantification of the relationship between apple tree damage level and fruit yield reduction. Fruit yield reduction can be assessed at market value, and a population then can be assessed in dollar terms, at which point a tolerance level can be set as that at which the marginal cost of control equals its marginal gain. An optimization model can then be written to select the management option that minimizes total cost as the sum of cost due to control and cost due to damage. It should be noted that the cost of damage should include the current costs of crop reduction and tree replacement, and the cost and interest on crop reduction during the lag time to production by new trees.

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