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As reported previously (Coyle and Tipton 1980), we have been engaged in the development of a computerized system which outlines the basic demographic features of a pine vole population. The system, when complete, will hopefully contain four subsystems (biological, spatial, control, and economic). This paper will discuss the biological submodel, its development and validity, and prospects for its future.

A mathematical model of pine vole population dynamics was constructed using bioenergetic information supplied by Cengel et al. (1978) and Lochmiller (1980) to describe the biological relationships (Coyle 1980). Interactions within the population were described using energetic stages (i.e. a group of animals with similar daily energy requirements) instead of age classes because pine voles are very difficult to accurately age and age-specific data were scarce. Matrices of transition probabilities for transfer between the energetic stages were generated each week during the simulations.

Relative energy balance, as simulated from energy transfers, was used as the driving force in the model. Functions for weekly energy availability and digestibility of forages were derived from field data. The processes of energy requirements, energy acquisition, energy deposition, and energy mobilization were simulated based on available energy. Algorithms for these processes were developed using field and laboratory data, and personal opinion where data were lacking. The degree of weekly energy restriction was used as input for routines calculating survival, reproduction, and transfer of individuals between stages. We originally intended to use body fat level as an indicator of energy restriction, but inconsistencies between field and laboratory data required re-evaluation of its use.

Validation of the model was conducted using population data collected from the 2 apple orchards used by Lochmiller (1980) and Kukila (unpublished data). Simulations were conducted from 1 December to 1 March using vole population densities of 75 and 70 animals per 1/2 ha for the maintained and abandoned orchards, respectively. The densities, age distributions, proportions of females reproductively active were taken from data (unpublished) collected in the same orchards that Lochmiller (1980) used to determine the energy availability values. Discrepancies between simulated and observed values were attributed to several factors, including the incomplete data sets, and inaccurate program algorithms.

Sensitivity analysis, the process of varying parameter values to determine their relative importance to model output, revealed that estimates of daily energy budget, number of feeding times per day, and the degree of forage utilization were important components of the model. Further refinements of the mathematical representations of these processes, as well as additional collection of data, are needed. Simulation results indicated also that juvenile growth rates are not expressed accurately in the model, and that further refinement of that algorithm is needed. Nineteen recommendations for further study are included in Coyle's (1980) thesis.

In addition to the sensitivity simulations, two simulation experiments of a year in length (from 8 September to 1 September of the following year) were conducted. The original population level consisted of 98 animals (50 males [13 juveniles, 37 adults] and 48 females [13 juveniles, 6 nonreproductive adults, 29 pregnant adults], values from unpublished field data) on a 1/2 ha grid in an apple orchard.

During the reference simulation, population levels increased by 16 percent during the year (to 114 voles). Cohorts in spring and summer contributed significantly to the over-wintering population. Although these population levels could not be accurately verified with existing field and laboratory data, the general trend of the population dynamics appeared to be reasonable.

A second simulation was conducted (with the above-mentioned initial population levels) to examine the effect of a pesticide application in mid-October. The effect of the application was to remove 80 percent of the individuals in all stages of voles. The population level decreased by 47 percent (to 60 voles) from the previous simulation. Most over-wintering reproductively inactive females conceived and bore young during April. After sexual maturity, this strong cohort contributed to an equally strong August cohort. Although the population was reduced by 80 percent at the outset of the simulation, results indicated the potential for the population to increase prior to the following winter due to strengths of the April and August cohorts. This hypothesis confirms prior observations that pine vole populations can and do recover within 1 year after a pesticide application.

The next phase of model construction will refine the algorithms representing bioenergetic regulation of survivorship, growth, and reproduction. The biological submodel will then be nested in a larger model of intra-orchard spatial movement. This larger model will itself be nested within a control optimization routine intended to recommend optimum treatment regimes for controlling pine vole populations in individual orchards.

Possible refinements of the bioenergetic model involve determining:

1.) seasonal digestibilities and palatibilities of forages,

2.) the effects of population density and forage abundances, digestibilities, and palatibilities on utilization rates,

3.) the effects of utilization rates on the subsequent abundances of forages,

4.) how survivorship varies as a function of age, energy balance, body weight, and body fat level,

5.) how growth and body fat level vary as functions of age, energy balance, and litter size,

6.) how litter size varies as a function of maternal age, energy balance, body weight, and body fat level,

7.) how energy intake, and thus utilization, vary as functions of energy balance, with stomach size limiting only when digestibility is so low that food bulk, rather than energy balance, limits energy intake,

8.) how ambient temperature, light/dark cycle of illumination, fossorial behavior, and social strife affect survivorship, growth, and reproduction,

9.) the effects of a positive or negative energy blance achieved gradually, rather than suddenly, on survivorship, growth, and reproduction.

Evidence that pine voles live and reproduce in tree-specific demes (Stehn et al. 1977) suggests that the orchard can be treated as a matrix of subpopulations, rather than as a single population. Since some limited movement has been shown to occur between trees and rows, a corresponding matrix of movement probabilities might be computed for density differences between adjacent tree subpopulations. Both the population matrix and the spatial distribution matrix could be stacked in a third dimension to represent the different energetic stages. The total orchard population size, as simulated from the bioenergetic and spatial distribution submodels, could be computed as the three dimensional sum of the subpopulations.

The control optimization routine would operate bioenergetically at the tree subpopulation level, with effects summed to yield commercial impact at the orchard level, the level of concern to the orchardist. Control options would consider the following parameters:

1.) type of control substance,

2.) purchase cost per unit mass,

3.) cost of application,

4.) effectiveness on populations of different sizes and age structures at different times of the year under different forage conditions.

Control options would be evaluated in terms of total cost to the orchardist, with recommendations made to minimize the sum of the cost of control and of pine vole damage to current and future apple crops via apple consumption and tree damage. Benefits and costs of each control option would be present-discounted at the specified market rate to yield practical benefit-cost analysis.

Current work at VPI & SU, both in the field and in the lab will provide important information in achieving the refinements mentioned above. The present state of the model embodies the results of extensive research into pine vole population demography and nutritional needs. This knowledge has been unified in a bioenergetic format that resolves populations into the energetic stages traversed in a single male or female life history. The future effort will address what happens when those nutritional needs are not met, the importance of other environmental and social variables on population demography, the impact of voles on orchards, and the recommendation of orchard control practices. These refinements, along with additional data, may eventually be incorporated in a system that will prove useful as a management tool for pine voles.

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