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PROGRESS AND PROSPECT OF A BIOENERGETIC SIMULATION
MODEL OF PINE VOLE POPULATIONS

by

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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the model was conducted using population data collected from the 2 apple orchards used by Lochmiller (1980) and Kukila (unpublished data).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 The densities, age distributions, proportions of females reproductively active were taken from data (unpublished) collected in the same orchards that Lochmiller (1980) used to determine the energy availability values.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 determin-
ing:

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 abund-
ances 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 balance
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 com-
mmercial 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.

LITERATURE CITED


