Summer 1973

A Simulation Model of *Peromyscus Leucopus* in an Area of the Great Dismal Swamp

James E. Paschal Jr.
Old Dominion University

Recommended Citation

Paschal, James E.. "A Simulation Model of *Peromyscus Leucopus* in an Area of the Great Dismal Swamp" (1973). Master of Science (MS), Thesis, Biological Sciences, Old Dominion University, DOI: 10.25777/342j-vw89
https://digitalcommons.odu.edu/biology_etds/240

A SIMULATION MODEL OF <u>PEROMYSCUS</u> <u>LEUCOPUS</u> IN AN AREA OF THE GREAT DISMAL SWAMP

by

JAMES E. PASCHAL, JR.

Submitted in partial fulfillment of the
requirements for the Degree of Master of Science

Department of Biology
OLD DOMINION UNIVERSITY
July, 1973

OLD DOMINION UNIVERSITY

DEPARTMENT OF BIOLOGY

We hereby approve the thesis of

JAMES E. PASCHAL, JR.

candidate for the Master of Science degree

SIGNED: Daniel E. Sonenshine

Daniel E. Sonenshine, Ph.D., Co-Chairman
Professor of Biology

John H. Richardson

John H. Richardson, Ph.D., Co-Chairman
Associate Professor of Biology

Ray S. Birdsong

Ray S. Birdsong, Ph.D.
Associate Professor of Biology

Date: 26 July 1973

A SIMULATION MODEL OF *PEROMYSCUS LEUCOPUS* IN AN AREA OF THE GREAT DISMAL SWAMP. James E. Paschal, Jr. Dept. of Biology, Old Dominion University, Norfolk, Va. 23508.

A computer simulation model was developed to explain the population dynamics of the white-footed mouse (*Peromyscus leucopus*) in an area of the Great Dismal Swamp. The model was designed to provide an experimental base for future studies. The model indicates relationships between food availability, home range size, competition with *Peromyscus nuttali*, habitat selection and reproduction.

White-footed mice were trapped in the Old Dismal Town site during each season from April, 1972 through March, 1973. The age-sex structure of the population was determined, and was compared with the simulated structure. Although there were significant discrepancies between the comparisons, the differences were explained, and so the model was accepted as representing the population dynamics in the study area.

The model constants were evaluated, and it was determined that the mortality rate of the young and food availability were the primary factors affecting population change. Other factors such as home range size and habitat selection might be of more relative importance at higher population densities.

ACKNOWLEDGMENTS

I wish to extend my appreciation to several people who have assisted and supported me in my research efforts. I thank the many teachers and counselors who have guided me during my years of schooling. To Dr. Daniel E. Sonenshine of the Department of Biology, Old Dominion University, I extend thanks for assistance and critical evaluation of my research. I am grateful for his example of excellence in research. To Dr. John H. Richardson, I extend my thanks for a close friendship, and the many hours of counsel and discussion. I will not forget his kindness, nor the close association with his family. I also wish to thank Mary Keith Garrett and Pat Gammon for their assistance in repairing traps, and for their encouragement. I wish to thank those people whom I have worked closely with in the Norfolk area for their friendship and kindness, particularly Mrs. Virginia Bagley and the Sanderlin family. I wish to extend much gratitude to my parents for their encouragement and support. Although they did not understand my work nor my goals, they have supported me in every way they could.

TABLE OF CONTENTS

APPENDIX I

APPENDIX II

LIST OF TABLES

LIST OF ILLUSTRATIONS

INTRODUCTION

Traditionally, experimental work in the physical and biological sciences emphasized the analysis of specific components of natural systems. Although investigators have realized that systems, rather than being sums of independent components, are products of interaction and interdependence between components, the technology to deal with systems studies was not previously available. With the development of computer technology, many of the problems have been overcome, and techniques have been developed that permit analysis and representation of the complexity in natural systems. Ecology has long suffered from the inability to construct and test hypotheses because of the complexity of the systems studied. Rather than studying simpler systems, an alternative approach is to model the natural system.

Simulation is a promising approach for developing models. The interactions of selected components of a natural system are expressed in computer language; the consequences of the interactions are solved numerically, and quantitatively expressed; then, by executing the program repetitively, the dynamics of the system (changes with respect to time) are expressed. The computer program and output, i.e., the simulated system, is then the model of the study system. If the simulated system is used to explain and predict properties of the natural system, it becomes a complex hypothesis.

Patten (1971) commented on this type of approach in ecology:

> "Systems ecology ... differs from statistical ecology in its greater emphasis on the explanatory criterion of truth as applied to holistic behavior. It accepts as an operating principle that no complex system can be fully known in all its interactive details, and accordingly seeks to elucidate global properties that characterize 'core' dynamics, the broad set of possibilities from which actual behavior is generated according to environmental inputs."

The computer simulation can be an "electronically assisted thought experiment" (Barton, 1970). Once the model "identifies" the natural system, the values of the variables can be changed and the consequent changes of the natural system can be assessed. The relative importance of each variable can be evaluated, and future experimental design proposed.

The purpose of this study was to observe a population of white-footed mice (Peromyscus leucopus) in an area of the Great Dismal Swamp, and based on these observations, develop a computer model to simulate changes of population structure (density, age and sex ratios). The basic philosophy underlying this study was that modelling could be a useful tool at all stages of the study. The model was designed as a guide for further studies of Peromyscus leucopus in the swamp.

Two closely related species of mice were present on the study area, the white-footed mouse (Peromyscus leucopus) and the golden mouse (Peromyscus nuttali). Peromyscus leucopus usually inhabits upland-conifer-hardwood forests, particularly oak forests (Buell, Langfor, Davidson and Ohmann, 1966; McCarley, 1964). Peromyscus nuttali is restricted to woodland habitat, usually near rivers or streams (Golley, 1962). Trapping during the summer months of 1971 demonstrated that a significant number of both species were present on the study area, however, it was not assumed at that time that either species was established in the study area. The status of the two species in the whole of the Great Dismal Swamp is unknown. The model was designed to explain only the population dynamics of P. leucopus, however, the data about P. nuttali was used to determine the area unavailable to P. leucopus.

The Great Dismal Swamp of North Carolina and Virginia is one of the largest remaining swamp forests of the southeastern coastal plain (Walker, 1972). Due to excessive inundation of water during several months of the year, the swamp was initially considered to be of minimum habitat value to small mammals. It was hoped that studies would indicate what adaptations permitted *Peromyscus leucopus* to colonize and maintain itself in the swamp.

MATERIALS AND METHODS

Description of the Study Area

The Great Dismal Swamp covers approximately 104,000 ha. of the North Carolina and Virginia coastal plain. The swamp area is steadily decreasing due to drainage and reclamation (Henry, 1970; Ramsey, Hinkle and Benander, 1970). Although the main swamp is considered to be the area surrounding Lake Drummond in Virginia, the swamp also extends into the North Carolina counties of Currituck, Camden, Perquimans, Gates and Pasquotank (deRageot, 1965). The Virginia portion includes eastern Nansemond County southeast of Suffolk, and a large area within the city limits of Chesapeake. The boundaries of the swamp are indefinite, except for the Suffolk Escarpment along its western edge (Henry, 1970; Ramsey et.al., 1970).

The Dismal Swamp is on a low, poorly-drained, flat marine terrace (Wingo, 1949), with heights ranging from approximately 4.5 to 7.5 meters above sea level (Henry, Chudoba and Porter, 1959). The soils of the swamp are highly organic and acidic (Kearny, 1901).

Kearny (1901) distinguished between two hydrophilic forest formations in the Dismal Swamp; the dark swamp, a dense deciduous virgin forest; and the light swamp, almost pure stands of southern white cedar which invaded when the virgin formation was disturbed. Meanly (1968) defined several community types including cypress-tupelo gum; swamp black gum; the mixed swamp, composed of red maple and swamp black gum or tupelo gum; the pocosin or evergreen shrub bog; the Atlantic white cedar, switch cane; and the upland border community composed of oaks, ash, elm and loblolly pine. Dean (1969) combined several of Meanly's community types. He claimed that gum swamps composed of maple, bays, cypress and gums existed along natural drainage. A pine zone, composed of loblolly and pond pine, occurred along ditch and canal banks where they could survive fires. Dean proposed other communities including "lights" composed of reeds and water grass, and white cedar stands on acidic peat overlying a sandy subsoil.

The study area was a 4 ha. wooded area at the site of Old Dismal Town immediately inside the southwest boundary of the Great Dismal Swamp.

Formulation of the Model

The approach used in the study was that formally stated by Platt (1964) as "strong inference". Simply, the approach is to ask precise questions about the study system, and then to formulate propositions that can be tested. Precise questions limit the number of simultaneous hypotheses the model is required to answer (K. W. Bridges, unpublished). The model was constructed after the format outlined by Kowal (1970): (1) the selection of variables of interest; (2) the construction of flow diagrams; (3) the classification of variables, operational definitions of the variables, and specification of the variable units; (4) the specification of the equations; and (5) the evaluation of constants.

Initially, factors known to affect small mammal populations were chosen, and a generalized flow diagram was drawn (see Figure 2). When selecting variables of interest, the "ideal" approach was used (Babbel, personal communication). The approach is to determine the goal, then to determine the least amount of information needed to explain a study system, and then to define existing constraints. Only that information required to achieve the goal is sought. Initially, an

FIGURE 1. Map of the Dismal Swamp. Composite of aerial photographs. Taken from S. W. Walker, 1972. Plant Succession in the Great Dismal Swamp. M.S. Thesis. Old Dominion University, Norfolk, Va.

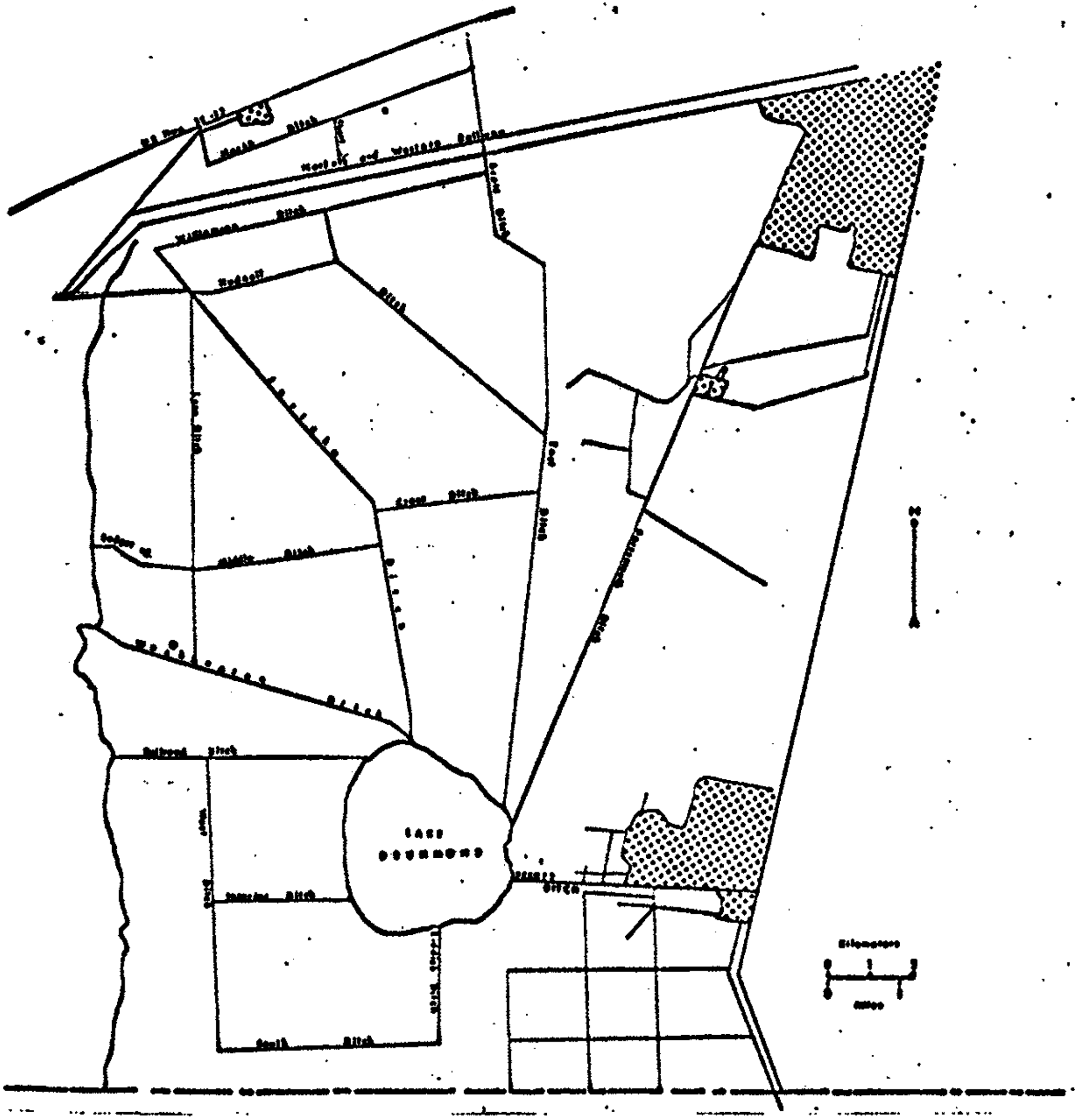
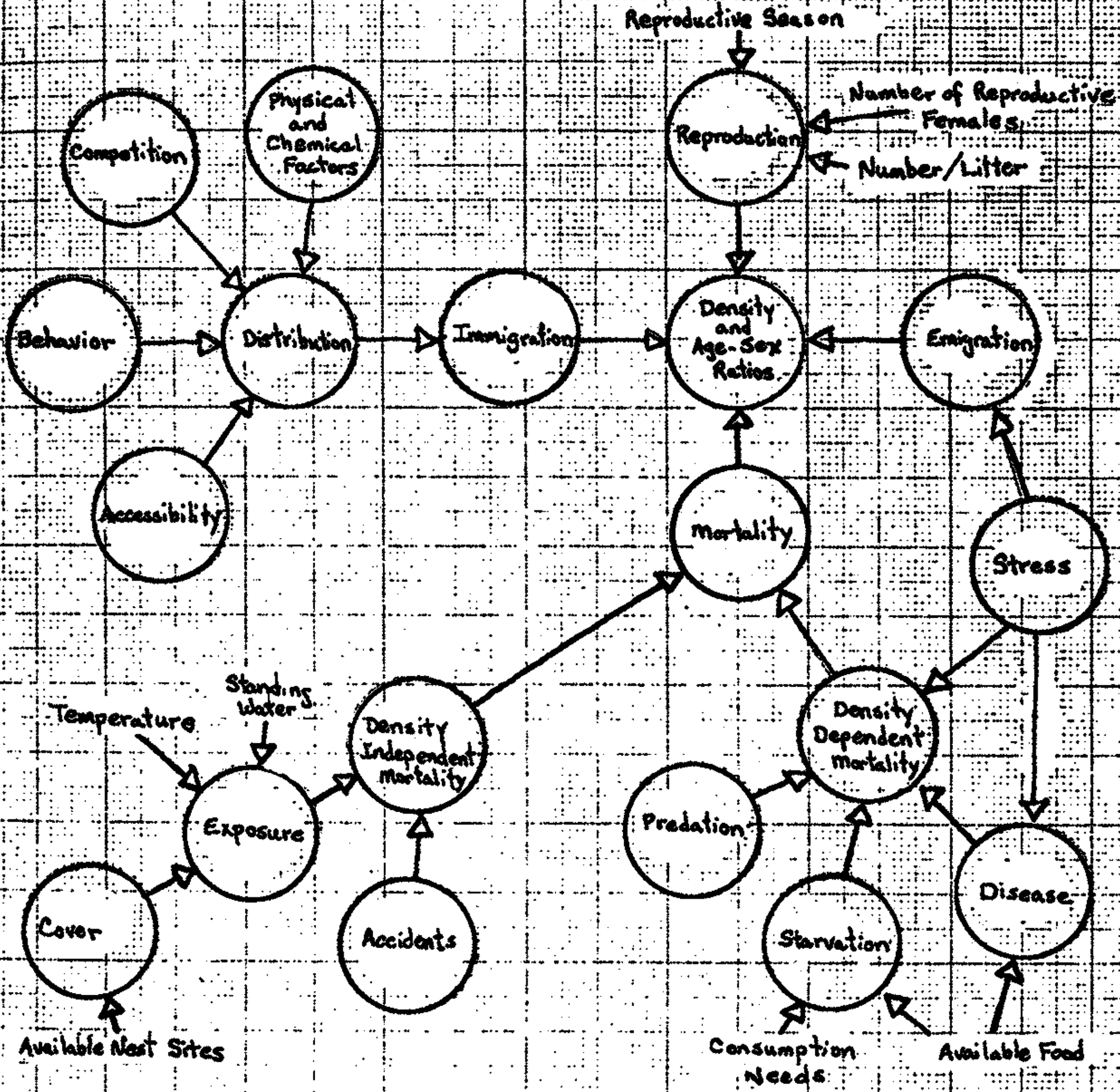

North Ditch
Norfolk and Western Railroad
Williamson Ditch
Hudnell Ditch
Jericho Ditch
Cross Ditch
Middle Ditch
Washington Ditch
Railroad Ditch
LAKE
DRUMMOND
Interior Ditch
Feeder Ditch
South Ditch
N
Kilometers
0
1
2
0
1
Miles

FIGURE 2. A general model of factors affecting population density.


Reproductive Season
Physical and Chemical Factors
Competition
Reproduction
Number of Reproductive Females
Number/Litter
Behavior
Distribution
Immigration
Density and Age-Sex Ratios
Emigration
Accessibility
Mortality
Stress
Standing Water
Temperature
Density Independent Mortality
Density Dependent Mortality
Exposure
Predation
Disease
Cover
Accidents
Starvation
Available Nest Sites
Consumption Needs
Available Food

"ideal" state with unlimited resources, time, money and data was assumed. Each factor was then evaluated, and a realistic experiment was designed; the ideal conditions were modified until they represented what could actually be done. Forrester (1968) stated a similar approach: "formulating a model of a system should start from the question: 'where is the boundary, that encompasses the smallest number of components, within which the dynamic behavior under study is generated?'" During the modelling process, other variables were incorporated, and some of the initial variables were deleted.

It was initially assumed that standing water, nest-site availability, food availability, reproduction and home range (assuming the home ranges were exclusive) would account for the greatest change of population density in the study area. Later, emigration, competition with Peromyscus nuttali and habitat selection were included, nest-site availability was changed to available habitat sites.

Flow diagrams were drawn to indicate paths of cause and effect; the diagram components were drawn as suggested by Forrester (1968). (Figures 3 and 4).

Although living systems are open, the simulated system is closed because of its defined boundary; i.e., it is not dependent on inputs from outside. The simulated system is inter-linked by a negative feedback loop, i.e., its state is a function of its previous states. The operation of the system was determined by input variables, state variables (variables dependent on previous values) and rate variables (variables not dependent on previous values). Explicit operational definitions were assigned each variable, and the units were stated (Table 1).

FIGURE 3. The systems model of the study population with selected variables.

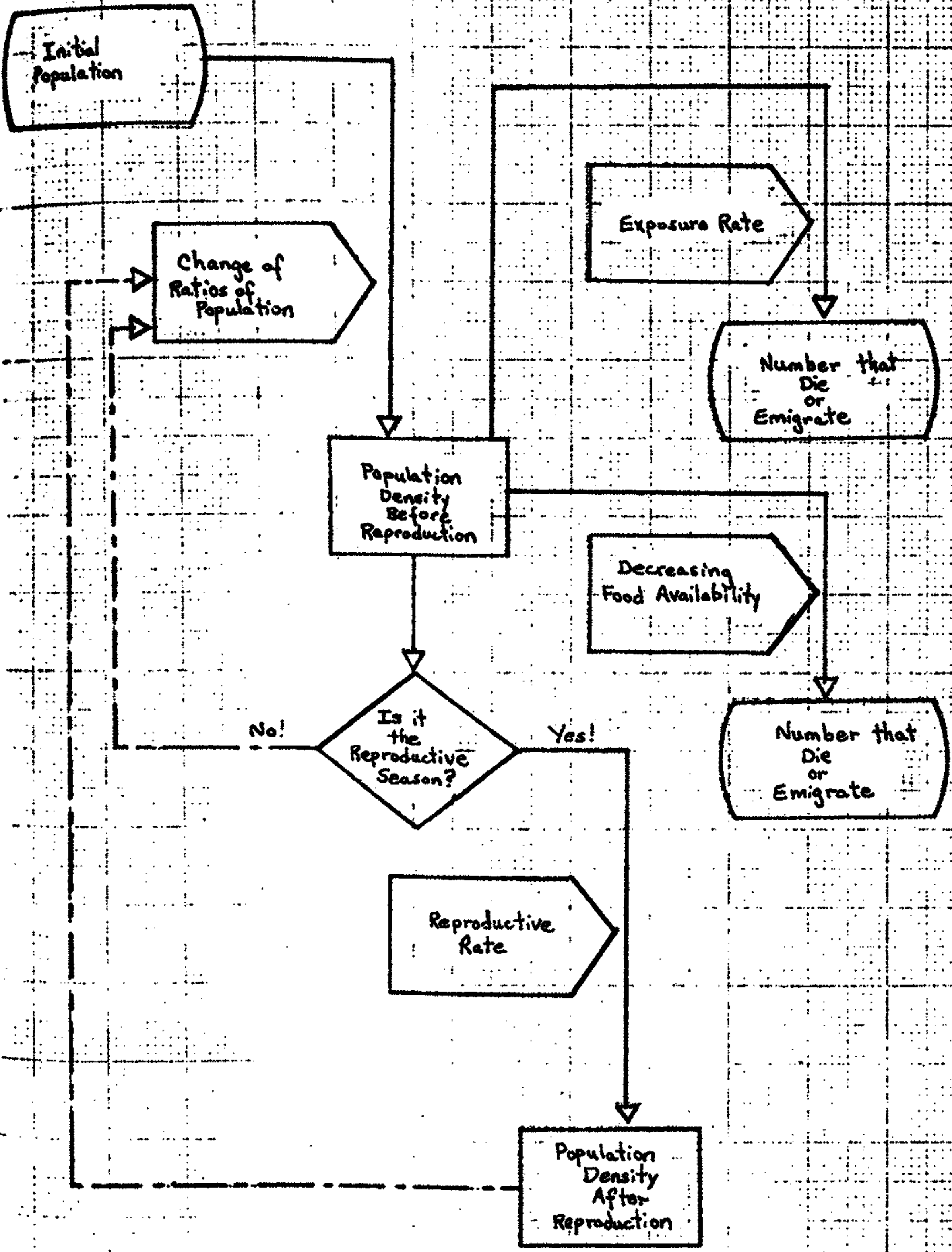

Initial Population
Change of Ratios of Population
Exposure Rate
Number that Die or Emigrate
Population Density Before Reproduction
Decreasing Food Availability
Number that Die or Emigrate
No!
Is it the Reproductive Season?
Yes!
Reproductive Rate
Population Density After Reproduction

FIGURE 4. The detailed systems model indicating data input and the conditions of the decision statements.

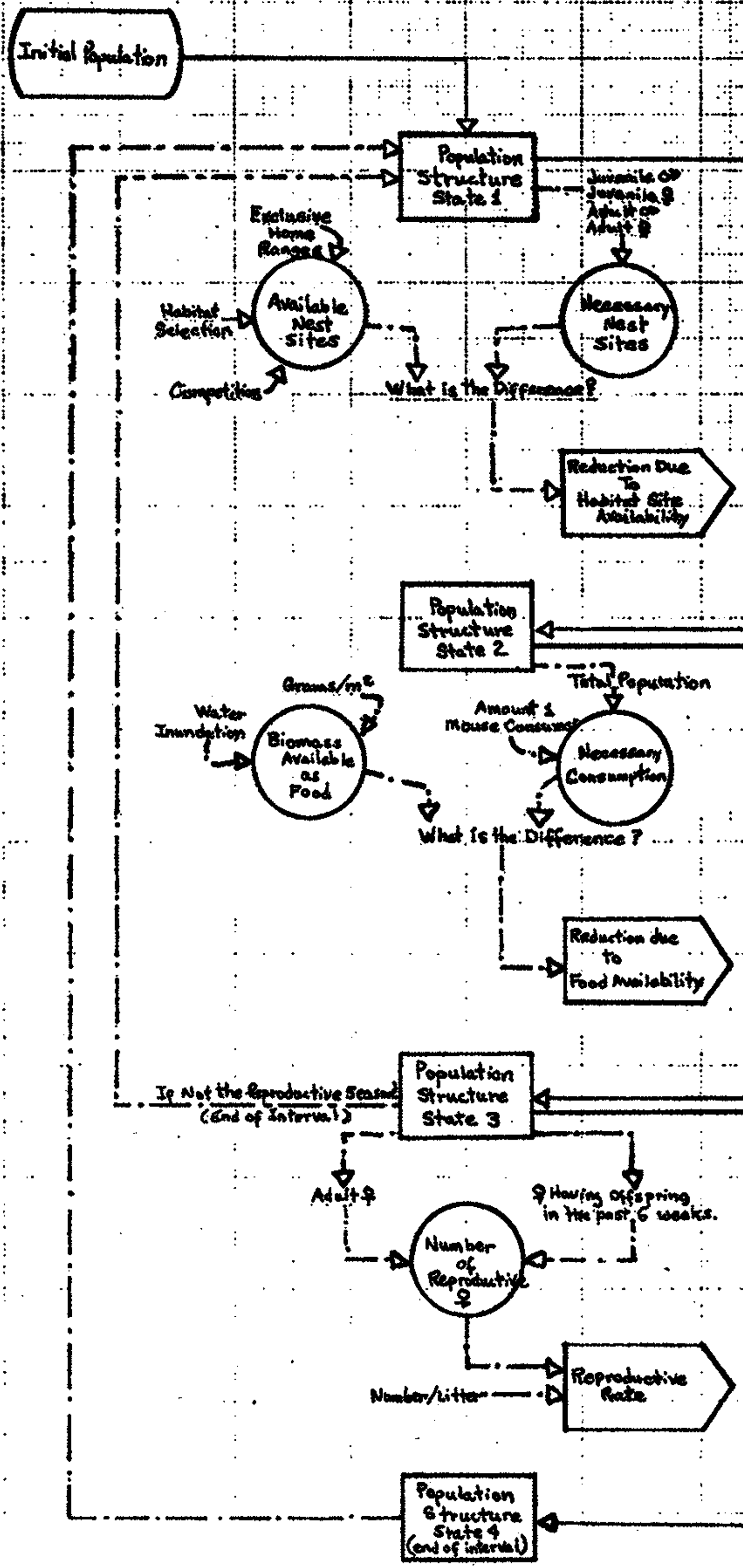

Initial Population
Population Structure State 1
Juvenile ♂
Juvenile ♀
Adult ♂
Adult ♀
Exclusive Home Ranges
Habitat Selection
Available Nest Sites
Competition
Necessary Nest Sites
What is the Difference?
Reduction Due To Habitat Site Availability
Population Structure State 2
Total Population
Grams/m²
Water Inundation
Biomass Available as Food
Amount 1 Mouse Consumes
Necessary Consumption
What Is the Difference ?
Reduction due to Food Availability
If Not the Reproductive Season (End of Interval)
Population Structure State 3
Adult ♀
♀ Having Offspring in the past 6 weeks.
Number of Reproductive ♀
Number/Litter
Reproductive Rate
Population Structure State 4 (end of interval)

TABLE 1. Population Model Variables*

Symbol	Description	Units
Input Variables		
AMNTI(I)	The amount of food one mouse consumes during a two-week period.	grams
BIOSM(I)	The amount of food present.	grams/m^2
STH2O(I)	Standing water at the surface for the total area (the fraction of the total area).	pure no.
Rate Variables (the variables utilized in decision statements)		
AMNS	The number of habitat sites available to adult males.	pure no.
XJMNS	The number of habitat sites available to juvenile males.	pure no.
AFNS	The number of habitat sites available to adult females.	pure no.
XJFNS	The number of habitat sites available to juvenile females.	pure no.
TBIOA	The total amount of food available to the population.	grams
CONSN	The total amount of food required by the population.	grams
REPRO	The total reproduction for the time period.	pure no.
DYNG	The number of young that die (exclusive of juveniles).	pure no.
State Variables (the variables that define the condition of the system)		
SPLT(IND,ITIME)	Age-sex structure of population	pure no's.
SPLT(I,ITIME)	Number of juveniles.	
SPLT(2,ITIME)	Number of adults.	
SPLT(3,ITIME)	Number of females.	
SPLT(4,ITIME)	Number of males.	
SPLT(5,ITIME)	Number of juvenile males.	
SPLT(6,ITIME)	Number of juvenile females.	
SPLT(7,ITIME)	Number of adult males.	
SPLT(8,ITIME)	Number of adult females.	
SPLT(9,ITIME)	Total number of population.	
SPLT(10,ITIME)	Number reproduced.	
SPLT(11,ITIME)	Number of reproductive females.	

*All variables are for the given simulation period, and are based on the total area of 40,000 m^2.

State variables, called levels by Forrester (1968) or dynamic state variables by Kowal (1970), accumulate material in the system and are conserved unless material flows across the system boundary. Flow rates are more generally termed decision statements (Forrester, 1968), and include a goal or limiting condition, an actual state condition, an expression of the difference between the goal and the actual condition and an expression for determining action based upon the difference. Rate variables are also called nondynamic state variables by Kowal (1970). Information variables are unconserved, i.e., they are not exhausted, nor do they accumulate flow; and they are the input to the rate equations.

The model equations expressed the state variables as functions of the input variables and other state variables. The equations were the axioms of the mathematical structure of the model, and the arguments of each function were the causes or controls of system behavior. The set of equations was the complex hypothesis, and each equation was a sub-hypothesis subject to testing and modification.

The set of equations was programmed in FORTRAN IV and run on the IBM 360 computer. Starting with a set of estimated or observed values for the population structure, the program simulated the population change every two weeks for a period of one year (Appendix I).

Finally, the constants of the equations were evaluated. The constants were: (1) formulated hypotheses, (2) values from the literature or (3) actual measurements (Table II). By changing the values one at a time, and determining the effect of the change on the simulated population structure, a heirarchy for experimentation in the study area was determined.

TABLE II. Population Model Constants

	Symbol	Physical Description	Units	Value	Referenc
1.	TOTAR	The total area of the study site.	m^2	$4x10^4$	measured
2.	HRMALE	The mean home range size of males.	m^2	1,100	Jameson, 1952
3.	HRFEM	The mean home range size of females.	m^2	850	Jameson, 1952
4.	PNUTT	The area inhabited by *Peromyscus nuttali*.	m^2	6,400	measured
5.	HSELN	The area that *P. leucopus* did not inhabit (other than that because of competition).	m^2	4,800	measured
6.	ISSN	The reproductive season (February to October).	pure no.	5-20	Stickel Worbach 1960
7.	XNL	The modal number of young per litter.	pure no.	4	Asdell, 1952
8.	BENDL	The fraction of young that die.	pure no.	.96	Bendell, 1959
9.		The mean number of litters born per month per female during the breeding season.*	no./month	.6	Jackson, 1952

* It is therefore assumed that adult females have one litter per six weeks during the breeding season.

> "It is in the evaluation of model constants that mathematical modeling has great value in guiding activities of the researcher. The model indicates what kinds of measurements are important, and what kinds are not. It provides a definite goal for the researcher, leading him toward the most useful observations to be made in order to accomplish his objectives." (Kowal, 1970)

Trapping

White-footed mice and golden mice were trapped live with "Sherman" traps, 7.6 x 7.6 x 25.4 cm. The traps were distributed at 20-meter intervals on an area 100 meters by 400 meters. Two traps were placed at each 20-meter interval except for the line nearest the road where only one trap/interval was placed. Due to a limited number of traps, and the presumption that the road acted as a natural barrier, the arrangement was considered to be the most acceptable. The trapping was done during each of the four seasonal periods from April, 1972 through March, 1973. Data collected during two nights of one week served as capture data, and data collected during two nights of the following week served as recapture data. The population density was estimated by using the Lincoln Index.

RESULTS

Identification of the System

The comparisons of the simulated population structure, the observed population structure and the estimated population structure are outlined in Table III and Figure 5.

Chi-square tests were used to test for significant differences between frequency distributions at each season (X^2=3.815, 3 d.f., .05P). No significant difference between the frequencies of the observed, estimated and simulated population structures was indicated except for the fall period. The X^2 values for the observed population structure and the simulated population structure based on the observed values of the first trapping period were: .36, .28, 7.12 and 2.28 for the spring, summer, fall and winter periods respectively. The X^2 values for the estimated population structure and the simulated population structure based on the estimated values for the first trapping period were: .00, 2.22, 15.00 and .31 for the spring, summer, fall and winter periods respectively. It was assumed that the discrepancy during the fall period was due to the unexpectedly high number of juvenile males caught. By assuming that three of the juvenile males caught were adult males, the chi-square comparison showed no significant difference between the observed and simulated population (X^2=2.78). However, the discrepancy between the estimated population and the simulated population was not removed by assuming that three of the juvenile males were adult males (X^2=11.14). This was probably due to the high number of adult females expected from the simulation based on estimated values.

TABLE III. Comparisons of Simulated Values to the Observed and Estimated Values

Date[1]	Observed	Simulated[2]	Estimated	Simulated[3]
May 25, 1972				
Juvenile males	5	5	5	5
Juvenile females	1	1	1	1
Adult males	5	7	7	7
Adult females	3	3	6	6
Total	14	16	19	19
September 1, 1972				
Juvenile males	0	1	0	1
Juvenile females	0	0	0	1
Adult males	7	13	8	14
Adult females	2	4	2	8
Total	9	18	10	24
November 28, 1972				
Juvenile males	4	1	4	0
Juvenile females	1	1	1	0
Adult males	4	13	4	12
Adult females	1	5	1	8
Total	10	20	10	20
March 10, 1973				
Juvenile males	1	1	1	1
Juvenile females	1	0	1	1
Adult males	4	10	7	9
Adult females	3	4	3	5
Total	9	15	12	16

[1] The last trapping day of the seasonal period.

[2] Based on the observed values of the first period as the initial values.

[3] Based on the estimated values of the first period as the initial values.

FIGURE 5. The comparisons of the simulated population structure and the observed and estimated population structures. The X-axis represents one year of time (1972-1973), and the Y-axis represents the number of animals.

The solid lines represent the number of animals; the dashed lines represent the simulated values.

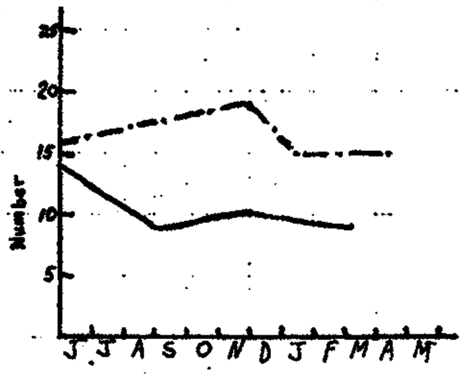


Fig. A. Total Observed Population.

Fig. B. Juvenile males Observed.

Fig. C. Juvenile Females Observed.

Fig. D. Adult males observed.

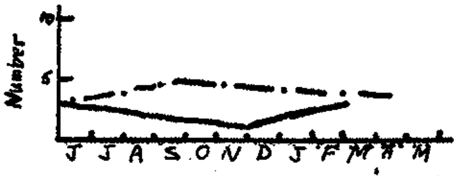


Fig. E. Adult Females Observed.

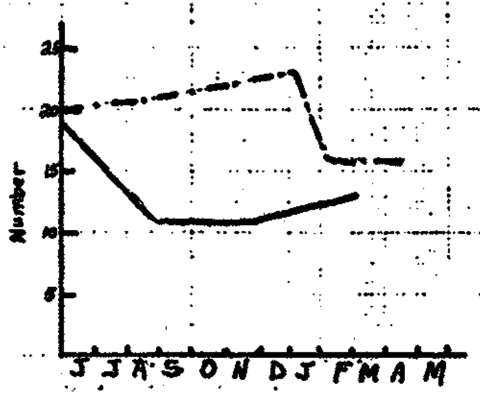


Fig. F Total Estimated Population.

Fig. G. Juvenile males Estimated.

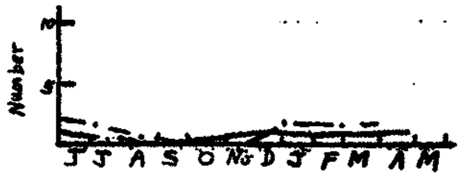


Fig. H. Juvenile Females Estimated.

Fig. I. Adult Males Estimated.

Fig. J. Adult Females Estimated.

——— Observed or Estimated

—·—·—· Simulated

Comparisons of the number of animals in each group indicated that the simulated populations were different from the observed and estimated populations. However, since the frequencies were not significantly different (or the discrepancies of frequency could be accounted for), and the discrepancies between the totals were expected (see the discussion), the model is assumed to explain the dynamics of the population when it is used as a first approximation.

Incrementation of Constants and Input Variables

The effects of incrementing the model constants and the input variable of food/m^2 are indicated in Figure 6.

The relative importance of each value to the simulation (in decreasing order of importance) was:

1. The mortality rate of the young.
2. The food/m^2.
3. The area that *Peromyscus leucopus* selects against.
   The area occupied by *Peromyscus nuttali*.
4. The home range of males.
5. The number of young per litter.
6. The breeding season.
7. The home range of females.

The apparent difference between the area selected against and the area occupied by *P. nuttali* was the result of the different valuse used for incrementation. The two constants affect the model in the same way.

FIGURE 6. The effects of incrementing constants and the input variable of food/m^2. The X-axis represents one year of time (1972-1973), and the Y-axis represents the total number of animals in the population.

The solid line represents the simulated population as standardized in the model. The dashed lines represent the population changes caused by incrementing the values. The dashed lines represent either the values showing high and low significance, or the extreme high and low values used when incrementing. The absence of a dashed line with a number indicates that there was no change from the standardized values.

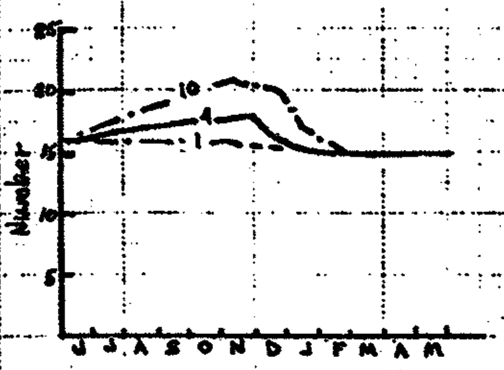


Fig. A. Number of Young/Litter.

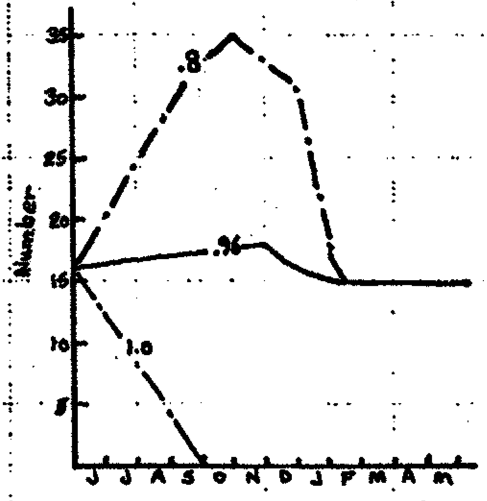


Fig. B. Mortality Rate of the Young.

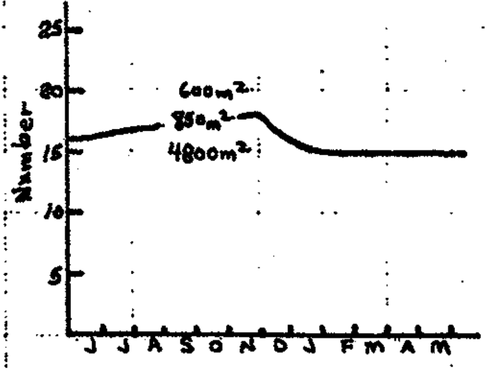


Fig. C. The Home Range of Females.

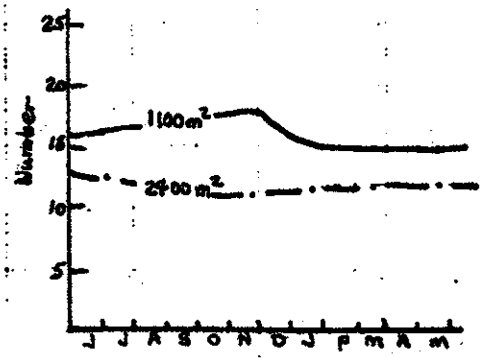


Fig. D. The Home Range of Males.

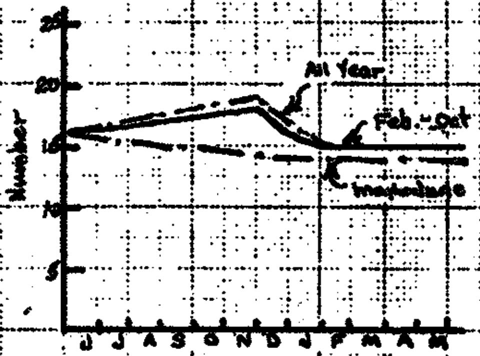


Fig. E. The Breeding Season.

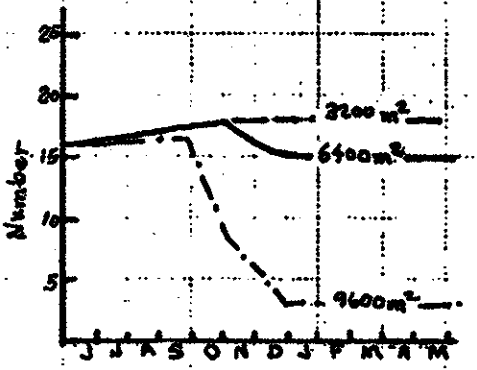


Fig. F. The Area Used by Peromyscus nuttali.

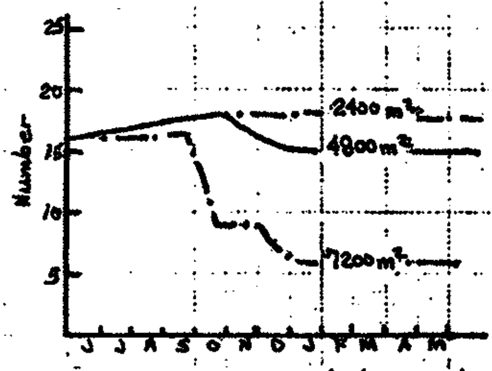


Fig. G. The area selected against.

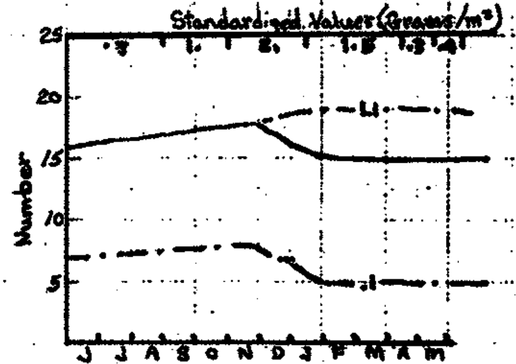


Fig. H Food/m².

DISCUSSION

The Format of the Model

The complete computer program of the model is shown in Appendix I. The following explains the logical format and the biological justification of the model.

The state of the system was described by the population structure variables and the indices of the limiting factors. The population was represented as a two-dimensional matrix [SPLT(IND,ITIME)], one dimension represented the age-sex groups of the population (IND), and the other dimension represented the simulation period (ITIME). The following represents the two-dimensional structure (See Table I for the complete structure):

SPLT(5,16), the number of juvenile males during the 16th time period.

SPLT(6,ITIME), the number of juvenile females during a given simulation period.

SPLT(7,ITIME), the number of adult males during a given simulation period.

SPLT(8,ITIME), the number of adult females present during a given simulation period.

The initial values of the population structure were input to the program, and the simulation, based on two-week intervals, was executed for the 26 time periods using a DO-loop based on the statements:

```
      DO 12 ITIME=2,27
          .
          .
          .
   12 CONTINUE
```

The two-week simulation interval was chosen because it was one-third of the shortest time delay in the system (six weeks). Forrester (1968) found that a simulation interval should be one-half or less of the shortest time delay in the system in order to reduce fluctuation produced as an artifact of the calculations.

The changes of adult males, juvenile males, adult females and juvenile females were calculated separately. Initially, the changes due to reproduction and maturation from the previous time period were calculated, then the change due to habitat and food availability during the existing time period were determined.

The number of juveniles was calculated as the number surviving from the previous time period, plus the number produced, minus the number that matured. The number of juvenile males was equal to .569 of reproduction; the number of juvenile females was equal to .431 of reproduction (Rood, 1966). Wild mice were considered sexually mature at 75 to 90 days of age (Clark, 1938). The number matured was the product of the survival factors from the previous two time periods and the number of juveniles from the period six weeks previous to the present period. The products of maturation of juvenile males and juvenile females were A5 and A6, respectively.

A5=SPLT(5,ITIME-3) X F53 X F52

A6=SPLT(6,ITIME-3) X F63 X F62

The equations for the change of juveniles were:

Juvenile males:
S5=SPLT(5,ITIME-1) + .569 X SPLT(10,ITIME-1) - A5

Juvenile females:
S6=SPLT(6,ITIME-1) + .431 X SPLT(10,ITIME-1) - A6

The number of adults was calculated as the number of adults surviving from the previous time period, plus the number of mice that matured.

The equations for the change of adults were:

Adult males:

```
     S7=SPLT(7,ITIME-1)+A5
```

Adult females:

```
     S8=SPLT(8,ITIME-1)+A6
```

After maturation was considered, the survival of each group was determined for the time period. The factors used were density-dependent, therefore, the number within each age-sex group was compared with the limiting conditions. If the density was greater than the carrying capacity, the population was reduced.

The number of sites available to P. leucopus was a function of the total area (calculated as 40,000 m^2), the area P. leucopus selected against (HSELN), the area competed for with P. nuttali (PNUTT) and the exclusive home ranges (HRMALE and HRFEM). The potential habitat of P. leucopus was the total area minus the area selected against, minus the area competed for with P. nuttali. Of the potential habitat, each mouse required 1100 m^2 (males) or 850 m^2 (females). A habitat site was operationally defined as the area of potential habitat necessary for one mouse. The number of available habitat sites was compared with the number in the age-sex group present during the time interval; if the number of available habitat sites was not sufficient, the number of the age-sex group was reduced to capacity. A "0" was output if the number of habitat sites was not limiting, a "1" was output if the number of habitat sites was limiting. The following part of the discussion shows the justification for the factors used to calculate the available habitat site, and then indicates how the calculation was performed.

Experiments have shown that members of the genus Peromyscus will select specific habitats (Wecker, 1964). No mice were captured within a certain portion of the study area during the entire year. It was assumed that this area was unused by P. leucopus, and was therefore selected against. This calculated area was 4800 m^2.

Peromyscus leucopus and Peromyscus nuttali were never captured together in the same immediate vicinity, therefore, it was assumed that if P. nuttali inhabited an area, it would exclude P. leucopus. The area that P. nuttali inhabited was 6400 m^2.

The average size of a male home range of P. leucopus is 1100 m^2, that of a female is 850 m^2 (Jameson, 1952). Male and female home ranges overlap, and the female's ranges are minimal during the breeding season (Sheppe, 1965). Metzgar (1971) found that mice of the same sex tended to occupy mutually exclusive home ranges. Also, he found that the home range sizes were stable, and that they remained exclusive at high population density. White-footed mice generally spend their entire life within the home range (Nicholson, 1941; and Snyder, 1956). In the model, the home ranges were assumed to be exclusive by sex, that is, males excluded other males, and females excluded other females; the sizes of the home ranges were assumed to remain constant throughout the year.

The number of available habitat sites was calculated as the total habitat area, minus the area utilized by the opposite age group (e.g., adult males cannot inhabit area already inhabited by juvenile males), divided by the home range size of the sex class. The adults were considered dominant; therefore, the available area for adults was calculated first, thus giving the adults of an increasing population the first opportunity to inhabit available area.

The calculations of the available habitat sites, and the decision statements (rates) were as follows:

Adult males:

```
     AMNS=(TOTAR-HSELN-PNUTT-(SPLT(5,ITIME-1)
    *X HRMALE))/HRMALE
```

If (AMNS-S7) is less than zero, the number of adult males will be reduced.

```
     IF(AMNS-S7) 1122,1,1   (decision statement)
   1 SPLT(7,ITIME)=S7   (the adult males are not
     reduced)
     IAM=0   (output factor)
     GO TO 3
1122 SPLT(7,ITIME)=AMNS   (the adult males are
     reduced)
     IAM=1
```

Juvenile males:

```
   3 XJMNS=(TOTAR-HSELN-PHUTT-(SPLT(7,ITIME)
    *X HRMALE))/HRMALE:
   4 SPLT(5,ITIME)=S5   (the juvenile males are not
     reduced)
     IJM=0
     GO TO 6
   5 SPLT(5,ITIME)=XJMNS   (the juvenile males are
     reduced)
     IJM=1
```

Adult females:

```
   6 AFNS=(TOTAR-HSELN-PNUTT-(SPLT(6,ITIME-1)
    *X HRFEM))/HRFEM
     IF(AFNS-S8) 8,7,7
   7 SPLT(8,ITIME)=S8   (the adult females are not
     reduced)
     IAF=0
     GO TO 9
   8 SPLT(8,ITIME)=AFNS   (the adult females are
     reduced)
     IAF=1
```

Juvenile females:

```
   9 XJFNS=(TOTAR-HSELN-PNUTT-(SPLT(6,ITIME-1) X
    *HRFEM))/HRFEM
     IF(XJFNS-S6) 11,10,10
  10 SPLT(6,ITIME)=S6   (juvenile females are not
     reduced)
     IJF=0
     GO TO 112
  11 SPLT(6,ITIME)=XJFNS   (juvenile females are
     reduced)
     IJF=1
```

Water inundation was not used as a function of the calculations to determine available habitat sites due to the high trapping success in inundated areas, and the observation that mice climbed and nested in the trees.

The next part of the model determined the food availability; if the food was limiting, the population was reduced to carrying capacity. If food was not limiting, a "0" was output; if food was limiting, a "1" was output. The food requirement was assumed to be the same for adults and juveniles, and for both sexes, therefore, the calculations were based on the total population.

Necessary consumption was calculated as the product of the amount one mouse consumes in a two-week period and the total number of animals of the population. The consumption by one mouse was based on Sealander (1952):

°C	Dry food consumed/day(gm)	Caloric intake/gm/day
8.5	6.26 - 6.85	.99 - 1.13
20.5	4.19 - 1.40	.67 - .74
30.5	2.79 - 2.94	.44 - .49

The food available to the population was calculated as the produc of food/m^2 and the ground area available to the population. The food/m^2 was hypothesized as having a seasonal range between .3 of a gram/m^2 and 2.0 grams/m^2. The ground area with available food was calculated as the total area, minus the area selected against, minus the area inhabited by Peromyscus nuttali, minus the area covered with water. Concurrent studies in the swamp indicated that there was about 60 percent inundation of water on the study area during four months of the year (Garrett, M. K., personal communication).

The equations used to determine the population change due to food availability were:

The available area with food:

AVAIL=TOTAR-HSELN-PNUTT-(STH20(I) X TOTAR)

The total food available:

```
TBIOA=BIOSM(I) X AVAIL
```

The amount of food required by the population:

```
CONSN=AMNT(I) X AVAIL
```

The determination of the change of the population:

```
   IF(CONSN=TBIOA) 13,13,14
13 If the difference is less than or equal to 0.,
   the population is not reduced.

   KSURV=0
14 If the difference is greater than 0., the popu-
   lation is reduced.

   TTPLT=TBIOA/AMNT1(I)
   KSURV=1
```

The age-sex groups were recalculated if the population was reduced by limiting food. It was assumed that the age and sex groups were affected alike.

The next portion of the program determined the effect of reproduction during the time period. If the simulated time period occurred during the reproductive season, the reproduction subroutine was called. The reproductive season was based on Stickel (1960). Stickel found the reproductive season in Maryland to be from February to October. This corresponds to the two-week periods in the model between three and 20. The decision statement used to call the reproduction subroutine was:

```
IF(ISSN.GE.3.AND.ISSN.LE.20) call reproduction.
```

ISSN was the variable representing the simulation period.

In southern Michigan, adult females averaged .6 of a litter per month (Jackson, 1952). It was assumed in the model that adult females had a litter every six weeks during the breeding season. The number of reproductive females of the time period was calculated as the number of adult females, minus the number of adult females producing litters in the previous two time periods. The survival of adult females from the previous time periods was calculated by multiplying the number of adult females by factors of survival for the time periods.

The main equation for determining reproductive females was:

```
RFEML=SPLT(8,ITIME)-SPLT(11,ITIME-1) X FACTOR(ITIME)
  -(SPLT(11,ITIME-2) X FACTOR(ITIME) X FACTOR(ITIME-1))
  -(SPLT(11,ITIME-3) X FACTOR(ITIME) X FACTOR(ITIME-1)
  X FACTOR(ITIME-2)).
```

The number of young/litter was assumed to be four, the modal number/litter calculated by Asdell (1964). The reproduction was calculated as the product of reproductive females and the number of young/litter.

```
REPRD=RFEML X XNL
```

Bendell (1959) found the mortality of young on control islands to be 96 percent; therefore, the mortality of young was assumed to be .96 of the total produced.

```
DYNG=BENDL X REPRD
```

The reproduction for the time period, calculated as a function of the mortality of the young, was:

```
SPLT(10,ITIME)-REPRD-DYNG.
```

The number of reproductive females was assigned to the population structure:

```
SPLT(11,ITIME)=RFEML,
```

and control was returned to the main program.

If the simulated time period was not within the reproductive season, the reproduction subroutine was not called, and the number of young produced and the number of reproductive females was assigned as 0.

The rest of the population structure was then calculated; i.e., the total numbers of adults, juveniles, males and females. The population structure of the time period was printed, as were the factors of survival (IJM,IJF,IAM,IAF and KSURV).

Finally, the simulation period was incremented by one. and control was returned to the beginning of the simulation portion of the program (DO 12 ITIME=2,27).

Identification of the System

As indicated in the results, the model is considered to represent the population dynamics even though the total numbers of the observed, estimated and simulated populations are different. The simulation closely represented the spring and winter periods, however, it predicted significantly higher numbers during the summer and fall. This discrepancy was expected since the trapping success during the summer and fall was less than the other two periods.

During the summer and fall periods, the study area was drier than during the other two periods. Casual observation indicated that there was a wide variety of seeds. roots and insects potentially available as food. The low trapping success during these periods was probably due to the competition of baits with natural foods. This assumption is supported by the fact that during the last trapping period of the fall, water covered most of the study area, and the trapping success doubled from the previous trapping period.

The unexpected frequency of juvenile males during late November of 1972 could be accounted for by extending the breeding season in the model a few weeks. It is a fair assumption that the breeding season in the swamp could be longer, due to the fact that the breeding season as defined in the model was assumed to be the same as that further north in Maryland.

It is suggested that in future studies of _Peromyscus leucopus_ in the swamp that a more intensive and varied trapping scheme be used. A full ten-day trapping period would probably be desirable, at least during the summer and fall. Also, studies on control areas might indicate food preferences, and selected baits might increase trapping success. Concurrent use of tracking data (see Sheppe, 1965), using smoked paper at bait stations, could help determine what other mice are on a given study area.

The International Biological Program conducted intensive studies of trapping small mammals (1971) and found that a dense-line grid (see Figure 7) was useful for determining density, and immigration. It is suggested that a similar scheme be utilized in future studies of _P. leucopus_ in the swamp in order to determine the significance of immigration and emigration.

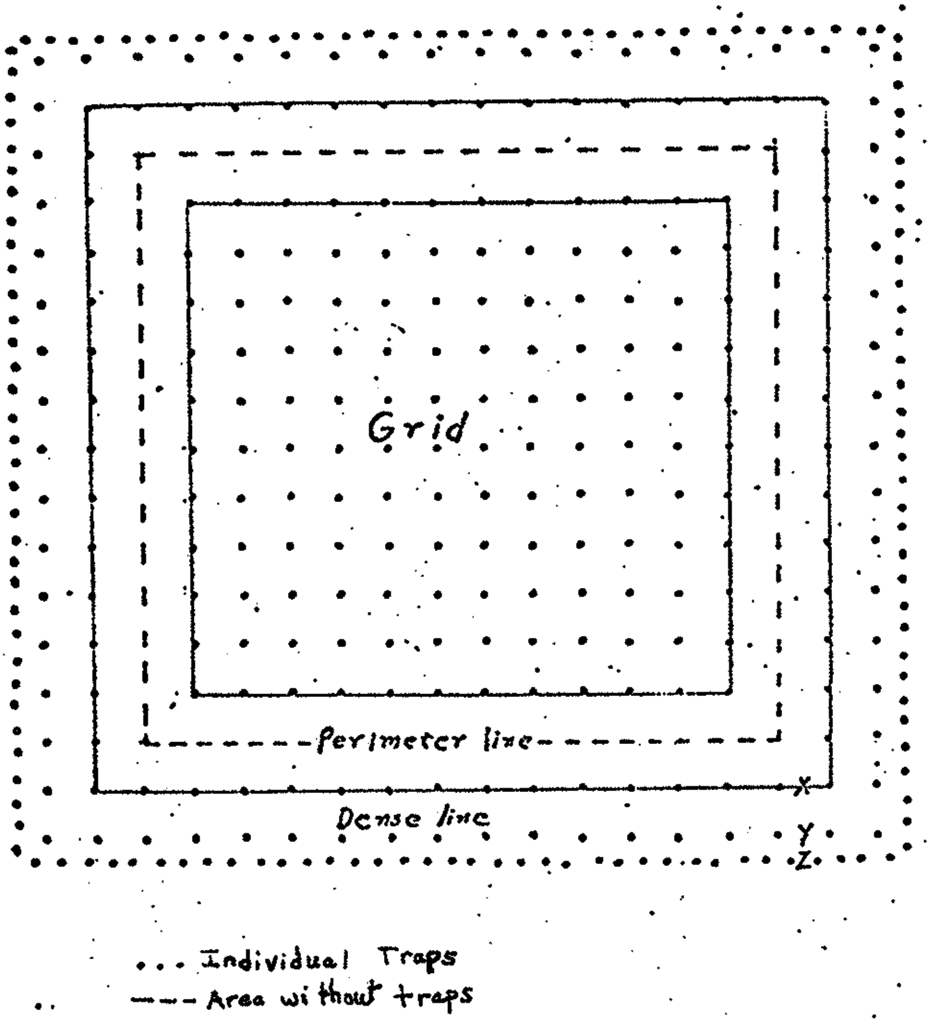
The IBP also compared several methods of estimating small mammal populations, and found that the Jolly stochastic method (1965) gave the best results. It is suggested that this approach be utilized since it, too, accounts for immigration and emigration. Other methods of population estimation should not be used unless the assumptions for their use can be met. For example, the method of Eberhardt (1969) would not be useful since the assumptions about recapture classes during a trapping period are not met.

Evaluation of Constants

Once the system was identified, the constants were changed in order to evaluate their importance to the model. Extreme upper and

FIGURE 7. A schematic diagram of the Desert Biome grid and dense-line design. The dense line is made up of three lines: X, Y, and Z from the innermost to the outermost. The perimeter line is imaginary and contains no traps.

Taken from N. R. French, C. O. Jorgensen, M. H. Smith and B. G. Maza. Comparison of Some IBP Population Estimates Methods. Special Report, July 1971, Office of the Chairman, USNC/IBP.


Grid
Perimeter line
Dense line
X
Y
Z
... Individual Traps
--- Area without traps

lower values were assigned in order to increase the probability of including the values due to natural variation within the system.

The evaluation was done by including a looping statement (a DO-loop) that enclosed the simulation portion of the program. The statement for this process was

```
DO 1100 ND=NA,NB,NC.
```

The statement assigned the constant being incremented (ND) an initial value (NA), and the population was simulated for the year period; the constant was then incremented by NC, and the simulation was repeated. The incrementation and consequent simulation was repeated until the constant was equal to the upper value (NB). Following the last simulation for the constant, control was transferred to a DO-loop enclosing the incrementation DO-loop, the input value of the constant was reassigned, and the next constant was incremented.

The constant in the model responsible for the most change of the simulated population size was the mortality rate of the young. With a standardized mortality rate of .96, the population increased from 16 to 20 during the summer period; with a modified mortality rate of .8, the population increased from 16 to 32 during the smae period. If the mortaility rate had been 1., the population would have been exterminated in about five months (Bendell, 1969). Bendell studied populations on control islands of Lake Opinicon, Ontario, and found that the mortality of young decreased from .96 to .6 when the populations were given additional food supplies (survival from 6/140 to 64/161).

Evaluation of the variable, food/m^2, indicated that a range of one gram of food/m^2 (assuming a limiting range) would cause a one- to two-fold difference in the size of the population. Also, during the standardized simulation (no incrementation), the index of food availability was the only calculated variable that limited the population. These observations, and the role of food in affecting the mortality rate of the young, indicate that the study of food availability is a prime consideration for explaining the population dynamics of Peromyscus leucopus in the Dismal Swamp. Since there is no data available, it is particularly important to determine the amount of potential food/m^2 during different seasons. The food consumption has been documented by Sealander (1952), and is probably sufficient for future studies of population dynamics. Although food availability may be of prime importance, there is also a possibility that it may not be as important as suggested by the model. Golley (1962) found that Peromyscus leucopus stores a large amount of seeds and nuts for winter use. Also, it was observed that mice in the Dismal Town area nested in trees, and it was observed during preliminary studies of February, 1971 that white-footed mice traversed extensive areas covered with water by climbing on fallen branches. The importance of food availability may be a function of the amount of food stored, and the mice's efficiency in finding the food stored.

Evaluation of the other constants of the model indicates that unless the constants are significantly different than defined by the model, further studies of the constants would not be useful for explaining the population dynamics of P. leucopus in the Dismal Swamp. However, significantly higher densities of mice would change the relative importance of these constants. For example, the home range size of males had a more significant effect on the population than the home range size of females. This difference is due to the significantly higher number of males than females in the simulation. Also, if the number of adult females had been greater, the number of young/litter and the breeding season may have had more effect. If the the total density had been greater, the relative size of both male and female home ranges may have had more effect.

Further simulations, evaluating more than one constant at a time, may be useful for determining experimental design. For example, the number of young/litter may have a more significant effect if the mortality rate of the young is lower. It is suggested that any future study of ecological factors affecting the populations of *Peromyscus leucopus* in the Dismal Swamp concurrently include a rigid trapping scheme for determining density and age-sex structure. If there are any significant differences between the densities of future studies and this study, the constants should be re-evaluated at an early date, and the experimental design modified accordingly.

CONCLUSIONS

Probably the most significant contribution of a model such as described is that of experimental design. The logical format forces the formulation of precise relationships, and, due to the operational nature of the relationships, indicates the form and amount of data required in the experiment.

The lack of experimental design is apparent in the literature of population ecology. Data used to explain population dynamics is often fragmented, incomplete, or composed of isolated values with dubious usefulness. Simulation models can decidedly assist the data collection effort, even though by their inherent limitations, such models do not represent the entire system.

The emphasis in the construction of this model has been empirical rather than analytical. By using a large number of simple equations which are solved numerically, the model is not restricted by assumptions of linearity, and it can evaluate a wide range of input data. Theory development, including model construction, is incomplete without verification, and therefore further expansion of the model will require experimentation in the laboratory and the field.

The model is not a final explanation of the population dynamics of _Peromyscus leucopus_ in the study area. The constants were taken from studies done in upland forests; and the data collected was that needed only to identify the selected variables of interest, i.e., the population structure. However, the model does identify several of the most significant ecological factors that affect the population dynamics of the white-footed mouse, and can be a useful guide for further studies in the Great Dismal Swamp.

LITERATURE CITED

Asdell, S. A. 1964. Patterns of mammalian reproduction. Comstack Publ. Assoc., Ithaca, N.Y. 670 pp. 2nd Ed.

Barton, R. F. 1970. A primer on simulation and gaming. Prentice-Hall, Inc., Englewood Cliffs, N.J. 239 p.

Bendell, J. F. 1959. Food as a control of population of the white-footed mice, Peromyscus leucopus noveboracensis (Fisher). Can. Journ. of Zool. 37: 173-209.

Bridges, K. W. Discussion paper for analysis of ecosystems, Desert Biome. Unpublished.

Buell, M. F., A. N. Langford, D. W. Davidson and L. F. Ohmann. 1966. The upland forest continuum in northern New Jersey. Ecol. 47: 416-432.

Clark, F. H. 1938. The age at sexual maturity of mice of the genus Peromyscus. J. of Mamm. 19: 230-234.

Dean, G. W. 1969. Forests and forestry in the Dismal Swamp. Va. J. Sci. 20: 166-173.

Eberhardt, L. L. 1969. Population estimates from recapture frequencies. J. Wildlife Mgmt. 33: 28-39.

Forrester, J. W. 1968. Principles of systems. Wright Allen Press, Cambridge, Mass. 2nd Ed.

French, N. R., C. O. Jorgensen, M. H. Smith and B. G. Maza. 1971. Comparison of some IBP population estimates methods for small mammals. Special Report, July, 1971. Office of the Chairman, USNC/IBP.

Golley, F. B. 1962. Mammals of Georgia. A study of their distribution and functional role in the ecosystem. University of Georgia Press, Athens.

Henry, E. F., J. Chudoba and H. C. Porter. 1959. Soil Survey of Norfolk County, Virginia. U. S. Dept. Agr., Soil Cons. Serv., Soil Surv. Rep., Series 1953, No. 5. 53 p.

------------. 1970. Soils of the Dismal Swamp of Virginia. Va. J. Sci. 21: 41-46.

Jackson, W. B. 1952. Populations of the woodmouse (Peromsycus leucopus) subjected to applications of DDT and Parathion. Ecol. Monogr. 22: 259-281.

Jameson, J. R. 1955. Some factors affecting the fluctuations of Microtis and Peromyscus. J. of Mamm. 35: 206-20[illegible]

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration -- stochastic model. Biometrika 52: 225-247.

Kearny, T. H. 1901. Report on a botanical survey of the Dismal Swamp region. Contrib. U. S. Nat. Herb. 5: 321-550.

Kowal, N. E. 1971. A rationale for modeling dynamic ecologic systems. p. 123 to p. 194. In B. C. Patten (ed), Systems analysis and simulation in ecology. Academic Press, New York and London.

McCarley, H. 1964. Ethological isolation in the cenospecies Peromyscus leucopus. Evol. 18: 331-332.

Meanly, B. 1968. Notes on Dismal Swamp plants. Atlantic Natur. 23(2). 5 p.

Metzgar, L. H. 1971 Behavioral propulation regulation in the woodmouse Peromyscus leucopus. Am. Midl. Nat. 86(2): 434-448.

Nicholson, A. J. 1941. The homes and social habits of the woodmouse (Peromyscus leucopus noveboracensis) in southern Michigan. Am. Midl. Nat. 25: 196-223.

Patten, B. C. 1971. Systems analysis and simulation in ecology. Academic Press, New York and London. 607 p.

Platt, J. R. 1964. Strong inference. Sci. 146: 347-353.

Rageot, R. H. de. 1965. An introduction to the Great Dismal Swamp. Wildlife in N.C. 29: 7-9, 23.

Ramsey, E. W., K. R. Hinkle and L. E. Benander. 1970. Waters of the Dismal Swamp. Va. J. Sci. 21: 81-83.

Rood, J. P. 1966. Observation of Peromyscus in captivity. Am. Midl. Nat. 76: 496-503.

Sealander, J. A., Jr. 1952. Survival of Peromyscus in relation to environmental temperature and acclimation at high and low temperatures. Am. Midl. Nat. 46(2): 257-311.

Sheppe, W. 1965. Characterisitics and uses of Peromyscus tracking data. Ecol. 46: 630-634.

Snyder, D. R. 1956. Survival rates, longevity, and population fluctuations in the white-footed mouse, Peromyscus leucopus, in southern Michigan. Misc. Publ. of the Mus. of Zool., Univ. of Mich. No. 95. 33 p.

Stickel, L. F. and O. Warbach. 1960. Small mammal populations of a Maryland woodlot. Ecol. 41: 269-286.

Wingo, A. L. 1949. Virginia's soils and land use. The Baughman Co., Richmond, Va. Vol. XXXI, No. 8, 323 p.

Walker, S. W. 1972. Plant Succession in the Great Dismal Swamp of Virginia. M. S. Thesis. Old Dominion University, Norfolk, Va. 52 p.

Wecker, S. C. 1964. Habitat selection. Sci. Amer. 211(4): 109-116.

APPENDICES

APPENDIX I

The computer program developed to simulate the population changes of *Peromyscus leucopus*.

```
      DIMENSION SPLT(11,56),STH20(26),FACTOR(56)
      DIMENSION BIOSM(26),AMNT1(26),STH201(26)
      COMMON SPLT,XNL,TPLT,FACTOR,ITIME,I,IND,MN,BENDL
      DATA AMNT1/5*95.,8*45.,6*35.,4*45.,3*95./
      DATE BIOSM/6*.3,4*1.,5*2.,6*1.5,2*.8,3*.4/
      DATA STH201/7*.6,5*.3,4*.2,4*.01,2*.3,4*.6/
      DO 1112 I=1,26
      STH20(I)=STH201(I)
 1112 CONTINUE
      DO 113 ITIME=1.56
      FACTOR(ITIME)=0.
113   CONTINUE
  301 READ(5,300)(SPLT(IND,1),IND=1,11),NK
  300 FORMAT(11F3.0,T70,I2)
      XNL=4.
      BENDL=.96
      HRFEM=850.
      HRMALE=1100.
      PNUTT=6400.
      HSELN=4800.
      IB=3
      IE=20
      DO 114 IND=1,11
      SPLT(IND,ITIME)=0.
114   CONTINUE
      I=7
      FACTOR(1)=1,
C SIMULATE POPULATION USING 2-WEEK INTERVALS FOR 1 YEAR).
      DO 12 ITIME=2,27
      IF(ITIME-4)22,23,23
   22 A5=0.
      A6=0.
      GO TO 24
   23 SP53=SPLT(5,ITIME-3)
      IF(SP53.LE.1.)SP53=1.
      F53=SPLT(5,ITIME-2)/SP53
      IF(F53.GE.1.)F53=1.
      SP52-SPLT(5,ITIME-2)
      IF(SP52.LE.1.)SP52=1.
      F52=SPLT(5,ITIME-1)/SP52
      IF(F52.GE.1.)F52=1.
      SP63=SPLT(6,ITIME-3)
      IF(SP63.LE.1.)SP63=1.
      F63=SPLT(6,ITIME-2)/SP63
      IF(F63.GE.1.)F63=1.
      SP62=SPLT(6,ITIME-2)
      IF(SP62.LE.1.)SP62=1.
```

```
      F62=SPLT(6,ITIME-1)/SP62
      IF(F62.GE.1.)F62=1.
      A5=SPLT(5,ITIME-3)*F53*F52
      A6=SPLT(6,ITIME-3)*F63*F62
   24 S5=SPLT(5,ITIME-1)+.569*SPLT(10,ITIME-1)-A5
      S6=SPLT(6,ITIME-1)+.431*SPLT(10,ITIME-1)-A6
      S7=SPLT(6,ITIME-1)+A5
      S8=SPLT(8,ITIME-1)+A6
      ISSN=1
      TOTAR=40000.
      AMNS=(TOTAR-HSELN-PNUTT-(SPLT(5,ITIME-1)*HRMALE))/HRMALE
      IF(AMNS-S7)1122,1,1
 1122 SPLT(7,ITIME)=AMNS
      IAM=1
      GO TO 3
    1 SPLT(7,ITIME)=S7
      IAM=0
    3 XJMNS=(TOTAR-HSELN-PNUTT-(SPLT(7,ITIME)*HRMALE))/HRMALE
      IF(XJMNS-S5)5,4,4
    4 SPLT(5,ITIME)=S5
      IJM=0
      GO TO 6
    5 SPLT(5,ITIME)=XJMNS
      IJM=1
    6 AFNS=(TOTAR-HSELN-PNUTT-(SPLT(6,ITIME-1)*HRFEM))/HRFEM
      IF(AFNS-S8)8,7,7
    7 SPLT(8,ITIME)=S8
      IAF=0
      GO TO 9
    8 SPLT(8,ITIME)=AFNS
      IAF=1
    9 XJFNS=((TOTAR-HSELN-PNUTT)-(SPLT(8,ITIME)*HRFEM))/HRFEM
      IF(XJFNS-S6)11,10,10
   10 SPLT(6,ITIME)=S6
      IJF=0
      GO TO 112
   11 SPLT(6,ITIME)=XJFNS
      IJF=1
  112 TPLT=SPLT(5,ITIME)+SPLT(6,ITIME)+SPLT(7,ITIME)+SPLT(8,ITIME)
      S88=SPLT(8,ITIME)
      CONSN=AMNT1(1)*TPLT
      AVAIL=TOTAR-(STH20(I)*TOTAR)-HSELN-PNUTT
      TBIOA=BIOSM(I)*AVAIL
      IF(CONSN-TBIOA)13,13,14
   13 KSURV=0
      FACTOR(ITIME)=1.
      GO TO 15
   14 TTPLT=TBIOA/AMNT1(I)
      FSURVA-TTPLT/TPLT
      SPLT(5,ITIME)=SPLT(5,ITIME)*FSURVA
      SPLT(6,ITIME)=SPLT(6,ITIME)*FSURVA
      SPLT(7,ITIME)=SPLT(7,ITIME)*FSURVA
      SPLT(8,ITIME)=SPLT(8,ITIME)*FSURVA
      FACTOR(ITIME)=SPLT(8,ITIME)/S88
```

```
      IF(FACTOR(ITIME).GE.1.)FACTOR(ITIME)=1.
      TPLT=TTPLT
      KSURV=1
   15 IF(ISSN.GE.IB.AND.ISSN.LE.IE)GO TO 161
      SPLT(10,ITIME)=0.
      SPLT(11,ITIME)=0.
      GO TO 115
161   CALL REPROD
115   SPLT(1,ITIME)=SPLT(5,ITIME)+SPLT(6,ITIME)
      SPLT(2,ITIME)=SPLT(7,ITIME)+SPLT(8,ITIME)
      SPLT(3,ITIME)=SPLT(5,ITIME)+SPLT(7,ITIME)
      SPLT(4,ITIME)=SPLT(6,ITIME)+SPLT(8,ITIME)
      SPLT(9,ITIME)=TPLT
      WRITE(6,2)I,(SPLT(IND,ITIME),IND=1,11),IJM,IJF,IAM,IAF,KSURV
2     FORMAT(T5,I2,5X,11F6.1,2X,5I3//)
      I=I+1
      IF(I.GT.26)I=1
12    CONTINUE
      STOP
      END



      SUBROUTINE REPROD
      DIMENSION SPLT(11,56),STH20(26),FACTOR(56)
      COMMON SPLT,XNL,TPLT,FACTOR,ITIME,I,IND,MN,BENDL
      IF(TPLT.EQ.0..OR.SPLT(9,ITIME-1).EQ.0.) GO TO 44
      IF(ITIME-4)20,19,19
   20 GO TO (16,17,18),ITIME
   16 RFEML=SPLT(8,ITIME)
      GO TO 21
   17 RFEML=SPLT(8,ITIME)-SPLT(11,ITIME-1)*FACTOR(ITIME)
      GO TO 21
   18 RFEML=SPLT(8,ITIME)-SPLT(11,ITIME-1)*FACTOR(ITIME)-SPLT(11,ITIME
     *2)*FACTOR(ITIME)*FACTOR(ITIME-1))
      GO TO 21
   19 RFEML=SPLT(8,ITIME)-SPLT(11,ITIME-1)*FACTOR(ITIME)-(SPLT(11,ITIM
     *2)*FACTOR(ITIME)*FACTOR(ITIME-1))-(SPLT(11,ITIME-3)*FACTOR(ITIME
     **FACTOR(ITIME-2)*FACTOR(ITIME-1))
   21 IF(RFEML.LE.0.)RFEML=0.
      REPRD=RFEML*XNL
      DYNG=BENDL*REPRD
      SPLT(10,ITIME)=REPRD-DYNG
      SPLT(11,ITIME)=RFEML
44    RETURN
      END
```

APPENDIX II

Trapping record of *Peromyscus leucopus* and *Peromyscus nuttali* from April, 1972 through March, 1973.

Date	Species	Trap No.	Animal No.	Age	Sex
April 13, 1972					
	P. nuttali	1	1401	Adult	Male
	P. leucopus	49	1403	Adult	Male
	P. nuttali	51	1405	Adult	Female
	P. leucopus	65	1407	Juvenile	Male
	P. nuttali	66	1409	Adult	Male
	P. leucopus	69	1411	Adult	Male
	P. leucopus	70	1413	Adult	Female
	P. leucopus	74	1415	Adult	Male
	P. leucopus	74	1417	Adult	Male
	P. leucopus	79	1419	Adult	Male
	P. leucopus	92	1421	Adult	Male
	P. leucopus	99	1423	Adult	Female
April 15, 1972					
	P. leucopus	91	1421	Adult	Male
	P. leucopus	90	1415	Adult	Male
	P. leucopus	88	1419	Adult	Male
	P. leucopus	78	1435	Juvenile	Male
	P. leucopus	73	1417	Adult	Male
	P. leucopus	68	1403	Adult	Male
	P. leucopus	65	1407	Juvenile	Male
	P. leucopus	63	1433	Juvenile	Male
	P. leucopus	60	1411	Adult	Male
	P. nuttali	36	1405	Adult	Female
	P. leucopus	35	1429	Adult	Male
	P. leucopus	10	1427	Adult	Female
	P. nuttali	2	1424	Adult	Female
	P. nuttali	1	1401	Adult	Male
April 16, 1972					
	P. leucopus	96	1439	Juvenile	Male
	P. leucopus	97	1421	Adult	Male
	P. leucopus	68	1433	Juvenile	Male
	P. leucopus	73	1417	Adult	Male
	P. leucopus	69	1411	Adult	Male
	P. leucopus	69	1437	Juvenile	Male
	P. leucopus	73	1407	Juvenile	Male
	P. leucopus	63	1403	Adult	Male
	P. leucopus	49	1435	Juvenile	Male
April 17, 1972					
	P. leucopus	85	1419	Adult	Male
	P. nuttali	5	1426	Adult	Female
	P. leucopus	44	1435	Juvenile	Male

Date	Species	Trap No.	Animal No.	Age	Sex
April 17, 1972 (Continued)					
	P. nuttali	47	1405	Juvenile	Female
	P. leucopus	58	1433	Juvenile	Male
	P. leucopus	60	1437	Juvenile	Male
	P. leucopus	69	1411	Adult	Male
	P. leucopus	72	1439	Juvenile	Male
April 25, 1972					
	P. leucopus	10	1427	Adult	Female
	P. nuttali	11	1401	Adult	Male
	P. leucopus	15	1441	Adult	Male
	P. leucopus	30	1443	Adult	Female
	P. nuttali	36	1445	Juvenile	Male
	P. leucopus	45	1447	Juvenile	Female
	P. leucopus	50	1429	Adult	Male
	P. nuttali	51	1405	Adult	Female
	P. leucopus	66	1433	Juvenile	Male
	P. leucopus	69	1439	Juvenile	Male
	P. leucopus	87	1421	Adult	Male
	P. leucopus	95	1449	Adult	Male
	P. leucopus	99	1415	Adult	Male
August 24, 1972					
	P. leucopus	93	1453	Adult	Female
	P. leucopus	87	1455	Adult	Male
	P. leucopus	59	1457	Adult	Male
August 25, 1972					
	P. nuttali	25	1459	Adult	Male
	P. leucopus	26	1461	Adult	Male
	P. leucopus	100	1415	Adult	Male
August 31, 1972					
	P. leucopus	31	1461	Adult	Male
	P. nuttali	38	1405	Adult	Female
September 1, 1972					
	P. nuttali	3	1424	Adult	Female
	P. leucopus	70	1467	Adult	Female
	P. leucopus	42	1469	Adult	Male
	P. leucopus	95	1465	Adult	Male
November 6, 1972					
	P. leucopus	47	1472	Adult	Female
	P. leucopus	62	1461	Adult	Male
	P. leucopus	97	1455	Adult	Male
November 7, 1972					
	P. leucopus	62	1462	Adult	Male
	P. leucopus	92	1455	Adult	Male
	P. leucopus	97	1475	Juvenile	Male

Date	Species	Trap No.	Animal No.	Age	Sex
November 28, 1972	*P. leucopus*	53	1461	Adult	Male
	P. leucopus	54	Dead	Juvenile	Male
	P. leucopus	58	1473	Adult	Female
	P. leucopus	76	1477	Juvenile	Male
	P. leucopus	77	1479	Juvenile	Male
	P. leucopus	90	1471	Adult	Male
	P. leucopus	97	1481	Juvenile	Female
	P. leucopus	97	1475	Adult	Male
March 3, 1973	*P. leucopus*	98	Dead	Adult	Male
	P. leucopus	43	1477	Adult	Male
	P. leucopus	62	1473	Adult	Female
	P. leucopus	100	1483	Adult	Male
March 4, 1973	*P. nuttali*	32	1485	Juvenile	Male
	P. leucopus	35	1487	Adult	Male
	P. leucopus	40	1489	Juvenile	Male
	P. leucopus	43	1477	Adult	Male
	P. leucopus	62	1473	Adult	Female
	P. leucopus	80	1491	Adult	Female
	P. leucopus	98	1495	Adult	Male
March 9, 1973	*P. leucopus*	80	1483	Adult	Male
	P. leucopus	30	1489	Juvenile	Male
	P. nuttali	46	1485	Juvenile	Male
	P. leucopus	72	1477	Adult	Male
	P. leucopus	73	1473	Adult	Female
	P. leucopus	93	1497	Adult	Male
	P. leucopus	77	Taken to lab	Adult	Male
March 10, 1973	*P. leucopus*	85	1491	Adult	Female
	P. nuttali	51	Unmarked	Adult	Female
	P. leucopus	25	1487	Adult	Female
	P. leucopus	32	1499	Adult	Male
	P. leucopus	35	1717	Adult	Male
	P. leucopus	57	1473	Adult	Female