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RABIES WORKING PARTY: WORKSHOP MEETING TO ASSESS THE 'ONTARIO' MODEL

by

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RABIES WORKING PARTY:
WORKSHOP MEETING TO ASSESS THE 'ONTARIO' MODEL

(Imperial College, London, July 9-11 1984)

F.G. Ball and P.J. Bacon

PREFACE

Before the main workshop session on the 'Ontario' model, 4 short papers were read by members of the RSS group both to keep other members of the group aware of recent developments and to giving the Canadian visitors a flavour of the group's past and present interests. Most of these short papers are already in press elsewhere, and are accordingly only listed below, with references, but a short synopsis is given of Ball & Hutley's presentation.

1. A. J. Crowley — Rabies today: the current world scene. Beran & Crowley, 1983.

2. F. G. Ball & S. R. Huttley — Do cycles disappear with stochasticity? (A re-appraisal of Anderson et al's model.

Anderson et al. (1981) proposed a deterministic homogeneously mixing epidemic model for the spread of fox rabies. This model, with appropriate parameter values, predicted a three yearly cycle of fox rabies prevalence, as observed in Europe. However, during the troughs of the model epizootics, the density of rabid foxes became very small and it seemed likely that such epizootics would have become extinct if stochastic effects had been incorporated into the model. The purpose of this paper is to study stochastic formulations of Anderson et al and related models, with particular emphasis on the above mentioned phenomenon of "fade out".

Monte Carlo simulations were performed of the natural Markov stochastic version of Anderson et al's model. The parameter values were the same as in Anderson et al's paper. Various values of the carrying capacity (K) were considered and rabies was introduced into populations at carrying capacity. Even with initial fox population sizes of 20,000 no endemic outbreaks occurred, indeed all of the simulated epidemics became extinct during the first or second cycle.

A modified verson of Anderson et al's model was considered in which fox births occurred at one point in time each year, rather than uniformly throughout the year. Again no stochastic endemic outbreaks occurred, though they were still predicted by the deterministic model. The deterministic model was sensitive to both the time and level of rabies introduction, the stochastic model much less so.

Finally the effect of the initial susceptible population size, SI say, on the course of the stochastic epizootics was considered when the population carrying capacity K = 20,000. For small values of SI rabies died out quickly, for values of SI of the order of K rabies "burnt itself out" during the first two cycles, however for intermediate values of SI (SI K/2) endemic outbreaks occurred. This might have interesting implications with regard to rabies control, though the limitations of the homogeneously mixing nature of the model must not be forgotten.

3. D. Mollison — Sensitivity analysis of simple epidemic models. Mollison 1984, 1985a; Mollison & Kuulasmoa, 1985.

4. B. McA.Sayers — Analysis of spatial patterns of rabies. Sayers, 1985.

1 INTRODUCTION

The RSS working party on Quantitative Aspects of the Spread of Rabies met at Imperial College, London, on July 9, 10, 11, 1984, to allow a group of Canadian workers, who have developed a computer model appropriate for the control of fox rabies in Ontario, to describe and demonstrate their model. This model is complex with numerous parameters (more than 30) and as such quite distinct from any model developed by British workers. The aspirations of the meeting were two-fold. On the one hand it was hoped that this model would be of direct use to those responsible for the control of a possible rabies epizootic in Britain and also that the demonstration of the model would increase the insight of British rabies modellers, who up to now have concentrated on simple models, into the mechanisms underlying the spatial and temporal dynamics of rabies propagation. In return the Canadians hoped that British workers' understanding and experience of simple epidemic models would help them in determining, and consequently eliminating, redundant parameters in their model.

The meeting commenced with 4 short papers given by members of the British working party (see preface for details). The remaining two and a half days of the meeting were devoted exclusively to the Canadian model. A detailed and comprehensive "Users Guide" to the Canadian model, henceforth called "The Ontario rabies model" was circulated at the meeting. An account of the model will also shortly be appearing in the book entitled "Population Dynamics of Rabies in Wildlife" which is being edited by Philip Bacon and published by Academic Press (Bacon 1985). We shall only provide a broad overview of the Ontario Rabies Model here, though at pertinent points we shall give page references to the "Users Guide".

2 THE ONTARIO RABIES MODEL

2.1 Introduction D. Voigt

The Ontario Rabies Model has been developed as a management tool to (a) aid the development and evaluation of fox rabies vaccination strategies and (b) increase our understanding of the ecology of wildlife rabies vectors and its relationship to the spread of disease. Detailed biological information has been specifically collected to allow construction of the model since this was the approach most credible to the managers. The model is still under development, the underlying philosophy being to initially include all factors that might have an effect on the course of an outbreak and then eliminate any redundant parameters, indeed the model's constructors have attempted to explicitly fill the gaps left by previous models of fox rabies. This approach contrasts sharply with that adopted by most British modellers, whose philosophy has been to first construct a simple model with few parameters and then generalize it so that, hopefully, the effect of each parameter is well understood.

2.2 Overview

The Ontario model is a "Monte Carlo" spatial simulation model. The spatial structure is provided by a rectangular array of cells, each cell corresponding to a fox home range. Currently the model caters for a maximum of 200 cells, thus the largest possible square grid is 14 x 14 cells. The time unit of the model is a season (Winter, Spring, Summer and Autumn), reflecting respectively the breeding, denning, pup rearing and dispersal of foxes, though the incubation and spread of rabies is modelled on a monthly basis within the coarser time scale. The foxes are classified into male/female, juvenile/adult and into 5 disease states, namely (i) healthy susceptible, (ii) rabid infection, (iii) rabid late incubating, (iv) rabid early incubating and (v) healthy immune, giving a total of 20 different fox types. (In the current version of the model there is only a single incubating class). The incubation period follows a geometric distribution, with time step one month, following which a rabid fox can infect neighbouring foxes according to seasonal contact rules. Juvenile foxes have the opportunity to disperse during autumn or late winter, which may further enhance the spread of disease. During dispersal a fox may leave the study area in which case it is replaced by an ingressing fox, whose sex and disease state is determined by probabilities that remain fixed throughout the time of simulation. Also during the autumn and winter local movement of foxes is permitted to aid the formation of mating pairs and locally balance fox density. Litter sizes and mortalities are regulated annually and seasonally respectively to adjust actual population densities towards 'target', carrying capacity, values.

After an initial (user determined) population settling period, rabies is introduced into a rectangular region of the study area by infecting foxes just prior to the autumn dispersal; the size and location of the injection area and the intensity of initial infection are again determined by the user.

Vaccination of foxes against rabies is allowed by the model. Like rabies infection, vaccination is over a rectangular region of the study area and for each vaccination activity the user specifies the year and season of vaccination, the location and size of the vaccination region and the vaccination rate over this region.

The model has various output possibilities which are described on pages II.16 to II.23 of the users guide. In particular one can obtain time series plots of the changes in both the fox population and rabies, taken over the study area as a whole, and seasonal maps depicting the distribution of foxes and rabies over the study area (see appended example figures of these plots).

2.3 The major subroutines

We now describe more fully those subroutines which clearly have an important influence on the spread of rabies in the model, namely those concerned with spacing and dispersal, contact between foxes and mortality and reproduction. As mentioned earlier the form of these subroutines and the data used within them are based upon the results of extensive field studies of the red fox in Ontario and, further, those data are independent of data on the spread of rabies in Ontario.

2.3.1 Spacing and dispersal (Users guide pages I.10-I.16)

The subroutine SPACE operates in autumn and winter only and permits the local movement of foxes to establish new territories and find mates. For each cell the surrounding territories are classified as either "adjacent" (A) or "neighbouring" (N) according to the following diagram.

```
N N N N N
N A A A N
N A * A N
N A A A N
N N N N N
```

SPACE takes the cells in the study area in a random permutation. For each cell the juveniles first search their A cells and then their N cells for any empty cells, and move if they find an empty cell. Then if there is more than one male fox in the range under consideration the A and N cells are searched for male-free ranges and the excess males moved accordingly. Finally if males are present without females the A and N cells are searched for unattached mates.

Dispersal is achieved by the subroutine DISPER. There are 3 dispersal times, 2 in the autumn and one in the winter, the time of dispersal for a given fox being determined by parameters P(23)-P(25)*. All male juveniles disperse but only a proportion P(13) of female juveniles disperse. Two types of dispersal are catered for, drift dispersal in which a fox gradually moves from his "parent" home range to a neighbouring A or N range and directed dispersal in which a fox travels some distance in a straight line and then looks among the neighbouring territories for somewhere to settle. The probabilities of drift (DR) and directed (DI) dispersal are governed by parameters P(10)-P(12).

In drift dispersal the fox searches its A and N territories for a more desirable territory. The fox then moves to this territory taking a time T which is exponentially distributed with mean given by parameter P(34).

In directed dispersal the fox travels a straight line in a random direction, all directions being equally likely, for a distance (D) which is exponentially distributed with mean P(15) for females and P(16) for males. The time taken is given by $T = D(0.04 + V)$, where V is exponentially distributed with mean P(32) for females and P(33) for males. The fox then performs drift dispersion from its new location to find a favourable home range.

During dispersion rabies can be transmitted by either a rabid dispersing fox traversing a home range containing susceptible foxes or a normal dispersing fox traversing a home range containing rabid foxes; the underlying probabilistic mechanisms of the spread of infection are the same for both cases. The time t_i spent by a dispersing fox in a given cell is given by

$$t_i = \frac{\text{distance traversed in given cell}}{\text{total dispersal distance}} \cdot T \cdot$$

The probability this fox contacts a given fox in that cell is $1-\exp(-P(8).t_i)$ and a proportion P(9) of contacts between a susceptible and rabid fox result in the transmission of infection. All such contacts are treated independently and for a fox undergoing directed dispersal the directed and drift components of its dispersal are treated separately.

* P(X) refers to parameters in the Ontario model, a complete parameter listing is given in Appendix 1.A: these are fully explained on pages II.27-29 of the "Users guide" and in Voigt et al. 1985.

2.3.2 Contact

The subroutine CONTAC governs the non-dispersal component of the spread of infection. This process is seasonal and obeys the following rules. In spring an adult infective infects all the foxes in its range. In summer a juvenile infective will infect a given neighbouring juvenile with probability P(1). In winter an infected male will infect a given adjacent female with probability P(4). During all seasons an infected adult will infect a given neighbouring adult with probability P(2) and for all seasons except spring an infected fox will infect a given fox within its own range with probability P(3). Again all possible infections are statistically independent.

2.3.3 Reproduction and mortality

Reproduction and mortality are controlled by the subroutines REPROD and MORTF respectively. Initially the user determines the proportion of barren females, P(5) for juveniles and P(6) for adults, and the mean and standard deviation of litter size, MU(1) and SIGMA(1) for juvenile females and MU(2) and SIGMA (2) for adult females; the litter sizes are assumed to be normally distributed. There are 16 mortalities, MORT(1) to MORT (16), referring to the mortality during each of the 4 seasons of the 4 normal fox types (see page II.28 of the Users guide). It is only the relative values of these mortalities that are important since the subroutine BALNC is used to modify the mortalities to produce a stable population (see Users guide page I.6 to I.8). BALNC also calculates seasonal target population densities for a population in equilibrium and during the course of a model run the mortalities are continually adjusted to bring the population density into line with the target values. The rate of return of the population density towards its target value is controlled by P(30), there being a lower limit on the adjusted mortality, controlled by P(36), to prevent unrealistic ageing of the fox population. The mean litter sizes are also adjusted during the course of a run, to aid the return of the population density to its carrying capacity level, the rate of this adjustment being controlled by P(37).

2.4 Sensitivity analysis

A pilot sensitivity analysis was described in which 4 parameters, three relating to contact probabilities (P(1), P(4) and P(9)) and the target carrying capacity (P(31)) were each varied at two levels. Thus there was a total of 2^4 runs of the model and for each run the following output responses were considered.

1. Total population.
2. Non rabies mortality.
3. Rabies mortality.
4. Non dispersal infections.
5. Dispersal infections.
6. Ingressor infections.

Each run was for a period of 25 years and for each of the above response variables the mean value over the final 20 years of a run was recorded. The sensitivity of each of the response variables to the four parameters was analysed separately treating the experiment as a 2^4 factorial analysis of variance. Two such analyses were described, one concerning the total population, in which the three contact parameter main effects were significant at the 1% level but the carrying capacity was not significant at the 5% level (the reason for this is explained in Section 3.1) and another concerning non-rabies mortality, in which all 4 parameter main effects were significant. It should be noted that in both of these preliminary analyses all parameter interactions were incorporated into the residual error possibly thereby inflating it unreasonably.

2.5 Model runs made during the workshop

The results of several simulation runs of the Ontario model with various parameter values typical of the Canadian situation (initial rabies introductions, vaccination policies etc.) were presented; readers requiring details are referred to Voigt et al. 1985. During the workshop the model was also run with parameter values appropriate for possible fox rabies epidemics in Bristol and Wales. The results of some of these runs are illustrated in Appendix 2. There were also some runs of the model in which the parameter values were made as homogeneous as possible: thus all sixteen mortalities were set to some common value, as were other age or sex dependent parameters (indeed the population was constrained to be all female!). The point of this exercise was to see whether the behaviour of this simplified model was any different from that with age/sex/seasonal dependent parameter values.

3 DISCUSSION

Throughout the meeting there was a considerable and far ranging discussion concerning the Ontario rabies model. We shall not provide detailed minutes of these discussions but rather give a broad summary subdivided into various topics.

3.1 Structure and complexity of the Ontario model

There was considerable debate concerning the complexity of, and the number of parameters in, the Ontario model. On the one hand there was the view that a model is only credible if it incorporates all known characteristics of the fox population and the rabies virus that might conceivably have some effect on the course of an outbreak, whilst opposing this was the view that a parameter should not be included in a model if its effect was not understood. The danger of this latter approach is that an important parameter might be completely omitted from the model although, of course, the parameters about which one has good biological information are not necessarily the ones having greatest effect on the course of an outbreak. The Ontario model was constructed with the idea of performing sensitivity analyses to determine the important parameters but to perform fully comprehensive sensitivity analyses would require an inordinate amount of computer time. It was stressed that sensitivity to changes in the model structure should be studied in addition to sensitivity to changes in parameter values.

The need to identify the important components of the Ontario model was often stressed. Two specific suggestions in this direction were to (a) identify the particular structural feature of the model responsible for the cyclic behaviour of rabies outbreaks and (b) elaborate the role played by the "expected net reproductive rate", E[R], of the disease (ie the mean number of "contacts" made by a rabid fox) in the spread of rabies. For (a) it seems possible that the inherent "linked difference equations with a time delay and non-linear feed-back of seasonal reproduction" might well suffice. For (b) it was suggested that the model be run in "rabies free" mode and the number of "contacts" calculated (the CONTAC routine only operates in 'Rabies' mode) and averaged out over the fox population to provide an estimate of E[R] (this would, of course, only apply to initial conditions for an outbreak). The dependence of this estimate on factors such as season and carrying capacity could then be studied to enhance our understanding of the model. It was pointed out that for the Ontario model, as indeed for most other rabies models, E[R] is approximately directly proportional to fox density, irrespective of the carrying capacity of the study region, whereas in the field E[R] is likely to be dependent on both fox density and carrying capacity. This could explain the non-significance of the carrying capacity parameter in the sensitivity analysis described earlier.

Finally it should be emphasised that the Ontario model is a Monte Carlo simulation of an underlying theoretical stochastic model. Thus two runs of the model under identical conditions will not usually yield the same results, (unless the seed of the pseudo random number generator is initialised to the same value for both runs). Therefore the more runs of the model we do with a given set of initial conditions and parameter values, the greater our confidence in the results. Generally, the more complex the model the longer each simulation run takes, and as large simulation models consume considerable amounts of computing time, for example each year of the Ontario model takes about 6 minutes to simulate on a micro (DEC personal computer Professional 350), there is a pressing need to structure the model as simply as possible, consistent with it providing an adequate reflection of reality. (A new version is currently (November 1984) being tested on a VAX computer. Eds).

3.2 Size of study region

It was pointed out that given the current size of the study region and the fairly high spatial mobility of foxes, the present version of the model is in some sense more akin to a homogeneous mixing model than to a true spatial model (eg. currently only $(14-4)^2/14^2$, $\simeq$ 51%, of cells have all their neighbouring A and N cells within the simulated study area). This is indeed borne out by the qualitative similarity of the model's output to that of a simple stochastic homogenous mixing model. A larger study area would be required to realistically investigate spatial epidemics, incorporate habitat heterogeneity and assess the long term effects of a vaccination strategy, because, currently, every egressing fox is replaced by an ingressing one, which has a fixed (user/determined) probability of being rabid. The current size of the study region is limited by computer memory constraints and imposes serious 'boundary constraints' for some analytical purposes.

(N.B. The new VAX version overcomes these constraints (but cannot be carried around for demonstration purposes!) Eds, Nov 1984).

3.3 Behaviour of rabid foxes

The movement and contact behaviour of rabid foxes in the Ontario model is precisely the same as that of normal foxes. The depth of knowledge on the behaviour of normal foxes in Ontario is excellent but we wish to stress that good data on the behaviour of rabid foxes is required most urgently by rabies modellers. It was suggested that where there is an advancing wave of fox rabies, such as on the European continent, an attempt should be made to monitor both the behaviour of rabid foxes and the progression of rabies through a susceptible population. Such a study should initially start in advance of the wavefront to obtain baseline data as has been done in Canada for the Ontario model. It was recognised that such a study would be very difficult to carry out, however, as the RSS group has recommended before, such data are most critical to a proper understanding of wildlife rabies, both in Europe and Canada.

3.4 The British situation

At the request of British officials who would be concerned with rabies control policy if the disease got into the UK (members of the RSS group present at the meeting) a brief discussion was held as to how the Ontario model might aid refinement of the British 'Rabies control contingency plans'. The main differences are that British plans envisage control by killing, not vaccination, and that spread is likely to be from a point source not on a wide front.

After this discussion the Canadians offered to make some additions to their model to allow it to simulate control killing and provide copies for use by the British officials and other interested researchers. (N.B. These changes have now been made, and the new version is currently being tested. Eds. Nov. 1984).

3.5 Output variates and their representation

In its most complete form the output from the Ontario model is a multi-variate spatial time series. For both the purposes of wildlife management and model simplification it will be necessary to condense this output so that it can be readily assimilated. There was a brief discussion on how this might be achieved. For example if one was interested in the cyclic behaviour of the density of rabies cases one might consider the mean and variance of the period of oscillation, the mean and variance of the amplitude of oscillation and the mean and variance of the density of rabid foxes; an alternative approach would be via the spectrum. However, this is rather an artificial situation; what really should determine the model outputs considered are the uses for which the model is intended and they in turn should determine the parameters and structure of the model.

3.6 An assessment of the results using data typical for an area of Wales
H.G. Lloyd

The spatial progression of rabies in foxes must depend upon complex relationships of a wide range of behavioural characteristics of foxes and of the virus. Any attempt to simulate the incidence and prevalence of the disease in foxes and its spatial and temporal progression would require an input of all the features pertinent to the epidemiology of the disease, presented quantitatively in such a way that each receives its proper weighting relative to another.

Off-the-cuff data for variable parameters of fox biology observed in Wales were used as required for input to the model, not so much to test it but to observe the kind of output the model would produce. The simulation area was 14 x 14 km in size and the model was run for a seven year period. The display of prevalence and spread over this period was impressive and even if, as in this particular instance, the result could not be taken to be representative (because of the possible inaccuracy of the input data) it would nevertheless provide a valuable method for assessing the effectiveness of differing degrees of fox control. The model engendered much interest among MAFF staff present, to the extent that requests for access to the model were made. A small MAFF study group has been formed to examine and use the model in due course.

4 CONCLUDING COMMENTS

At the close of the meeting there was a general feeling amongst all participants that the main objectives, as outlined in the introduction, had been admirably achieved. Our Canadian colleagues were specifically looking for a peer review of the Ontario model. They received several valuable comments, criticisms and suggestions concerning both the detail and structure of their model, many of which are outlined in the previous discussion. The British rabies modellers were impressed by the attention to biological detail and convenient output facilities of the Ontario model, and those who favour simple models felt that their understanding of fox rabies and its modelling had been enhanced from the detailed presentation of the Ontario model.

Everybody was extremely grateful to the Canadians for the excellent presentation of their model. The success of the meeting can be judged by the fact that several British workers, including those responsible for the control of any possible rabies epizootic in Britain, desired copies of the Ontario model to aid their research. Clearly the Ontario model is credible to both biologists and wildlife managers; the next step must be to simplify it to increase its credibility to mathematicians, in such a way that its biological credibility is maintained.

5 RECOMMENDATIONS

The group felt that the following points would improve the realism and understanding of the Ontario model. No attempt has been made to put these points "in order or priority", since priorities will differ between mathematicians interested in spatial epidemic processes and managers concerned with controlling actual localised outbreaks.

a) Identification of those features of the model responsible for cycles of rabies incidence, to permit closer comparisons with simpler models.

b) Simulations in larger 'study areas'. The present 'edge effects' could be quite severe and may make the model rather similar to 'homogenous mixing' and highly sensitive to a few rabid "imigrants". It is unlikely that turning the simulated area into a torus would help unless the size were also increased considerably.

c) There appears to be a minor error in the User Guide formula for calculating the probability that a dispersing fox contacts, and infects foxes in the cells it disperses through.

d) The model structure appears to make contacts closely dependent on fox densities and largely independent of 'carrying capacity'. More evidence that this assumption is reasonable would help assessment, as it could force the model to behave unrealistically similarly to simpler models with the same assumption.

e) Further investigations of the Ontario model should consider some changes to its structure and formulation (eg (d) above) as well as to its parameter values and the size of the simulated area.

f) The detail and complexity of the present Ontario model, plus constraints on computing time, will make a fully comprehensive analysis both difficult and time-consuming. Some thought could usefully be directed to devising a simpler version for comprehensive analysis, the findings from which could be used to direct fewer runs of the full model to investigating more complex details.

6 ACKNOWLEDGEMENTS

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APPENDICES

Appendix 1.a gives a list of the input values, and their explanations, as contained in the control file for running the Ontario model.

Appendix 1.b tabulates results from the model using the control file values from Appendix 1.a.

The results of this simulation (values in Annex 1.a and tabulated results Annex 1.b) are shown graphically in Appendix 2.1, which presents a time-series of graphs: Year 1, Spring, Summer, Autumn, Winter; Year 2, Spring, Summer, Autumn, Winter, etc. For each Year and Season two maps (representing the 14 x 14 grid cells of the simulation study area) are shown side-by-side. The left-hand square represents total foxes, the right-hand rabid foxes: on both the density of shading represents the spatial densities of (i) foxes and (ii) rabid foxes (means and standard deviations are printed between the maps). Below the maps a graph of densities (with different scales for (i) total foxes and (ii) rabid foxes) against time (time reached by simulation so far) is also shown.

For comparison, the results of a second simulation, differing only from the first in that rabies was started in a corner, not the centre, of the 'study simulation grid' (as represented by the maps in these figures). Note that this second simulated outbreak died out after 6 years, whereas the former continued for over 15 years. See Discussion 3.2 and Recommendation 5.b for likely reasons for these differing behaviours.

ANNEX 1.a

```
DEBUG    .FALSE. this is bristol model center injection
TERMIN   .false. TERMINAL  OUTPUT
LOG      .true.  LOG OUTPUT  (FOR MAPPING)
SETTLE     5     YEARS TO LET SETTLE BEFORE SAVING START CON
NTRIALS    1     NUMBER OF TRIALS (RUNS) ((0:CONTINUE EVEN W
LRUN      15     MAX NUMBER OF YEARS FOR THE RUN
P(1)       0.05  PROB. JUV. INFECTING NEIGH. JUV. SUMMER
P(2)       0.05  PROB. ADLT INFECTING NEIGH. ADLT ALL SEASON
P(3)       0.10  PROB. ANY FOX INFECTING OTHER CELL MEMBERS
P(4)       0.225 PROB. OF MALES INFECTING NEIGH. FEMALES WIN
P(5)       0.35  PROB. OF JUV. FEMALE BARREN
P(6)       0.10  PROB. OF ADLT FEMALE BARREN
P(7)       0.50  PROB.  OF MALE OFFSPRING
P(8)       0.60  CONST. IN FORMULA FOR PROB. OF CONT. IN TIM
P(9)       0.25  PROB. OF GETTING RABIES GIVEN CONTACT
P(10)      0.50  PROB OF DI FOR FEMALE
P(11)      0.80  PROB OF DI FOR MALE
P(12)      1.00  PROB OF DR
P(13)      0.10  PROB OF FEMALE DISPERSING
P(14)            PROP. INGRESS OF EGRESS ( SET TO 1.0 IN PRG
P(15)      0.80  DISTANCE FEMALE FOXES DISPERSE (KM)
P(16)      3.00  DISTANCE MALE FOXES DISPERSE (KM)
P(17)      1.00  PROB. INGRESSING FOX IS IN HEALTH STATE 0
P(18)      1.00  PROB. INGRESSING FOX IS IN HEALTH STATE 1 +
P(19)      1.00  PROB. INGRESSING FOX IS IN HEALTH STATE 2 +
P(20)      1.00  PROB. INGRESSING FOX IS IN HEALTH STATE 3 +
P(21)      1.00  PROB. INGRESSING FOX IS IN HEALTH STATE 3 +
P(22)      0.2   PROB. INGRESSING FOX IS FEMALE
P(23)      0.1   PROB. OF DISPERSING IF K=1
P(24)      0.167 PROB. OF DISPERSING IF K=2 + P(23)
P(25)      1.000 PROB. OF DISPERSING IF K=3 + P(24) = 1.0
P(26)      1.00  PROB. OF R1 TO DEATH IN INCUB
P(27)      1.00  PROB. OF R2 TO R1 IN INCUB
P(28)      0.00  PROB. OF R3 TO R2 IN INCUB
P(29)      0.42  PROB. OF R3 TO R1 IN INCUB
P(30)      0.20  MORTALITY ADJUSTER FOR STANDARD CONDITIONS
P(31)     36.00  CONTROL POINT FOR FOX DENSITY (FOXES PER CE
P(32)      1.00  PARAMETER FOR DIRECTED DISPERSAL TIMES FOR
P(33)      0.50  PARAMETER FOR DIRECTED DISPERSAL TIMES FOR
P(34)      8.00  PARAMETER FOR DRIFT DISPERSAL TIMES
P(35)      5.00  MAXIMUM NUMBER OF LITTERS PERMITTED IN ONE
P(36)      7.00  NUMBER OF YEARS WHICH 5% OF FOXES SURVIVE T
P(37)      1.00  REPRODUCTION FEEDBACK ADJUSTER
ROW       14     NUMBER OF ROWS
COL       14     NUMBER OF COLUMNS
V(1)       1   # VACC ACT/     YR,SN,RATE,LLR,LLC,URR,URC
V(2-8)                          1  3 0.00   1   1  14  14
MU(1)      3.5   MEAN LITTER SIZE FOR JUVENILES
MU(2)      5.0   MEAN LITTER SIZE FOR ADULTS
SIGMA(1)   2.00  STD. DEV OF LITTER SIZE FOR JUVENILES
SIGMA(2)   2.00  STD. DEV OF LITTER SIZE FOR ADULTS
MORT(1)    0.20  MORTALITY WINTER J F
MORT(2)    0.14                  A F
MORT(3)    0.20                  J M
MORT(4)    0.12                  A M
MORT(5)    0.10  MORTALITY SPRING J F
MORT(6)    0.05                  A F
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Annex 1.a
continued

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MORT(7)    0.10                      J M
MORT(8)    0.05                      A M
MORT(9)    0.14  MORTALITY SUMMER    J F
MORT(10)   0.05                      A F
MORT(11)   0.16                      J M
MORT(12)   0.05                      A M
MORT(13)   0.26  MORTALITY FALL      J F
MORT(14)   0.16                      A F
MORT(15)   0.34                      J M
MORT(16)   0.18                      A M
ROWSIZ     1.00  HORIZONTAL SIZE OF CELL
COLSIZ     1.00  VERTICAL SIZE OF CELL
           2   7   7   8   8VIRUS INJECT:NCASE/CELL,LLR,LLC,
    1092606542  SEED FOR THIS RUN
```
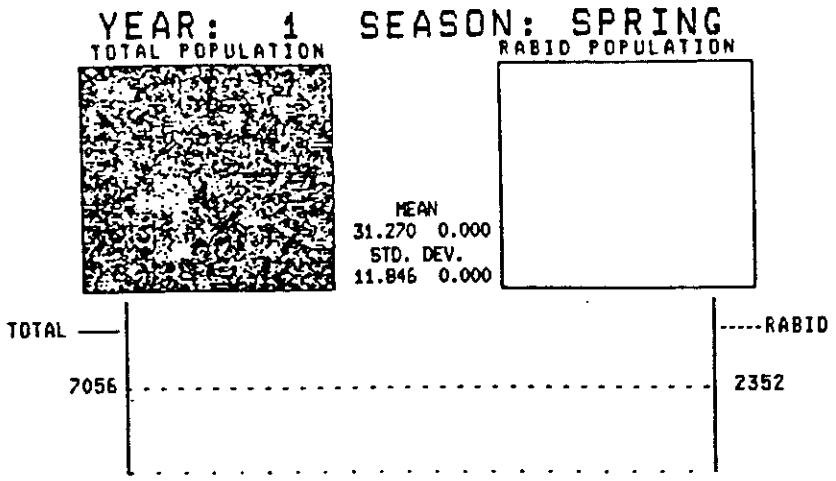
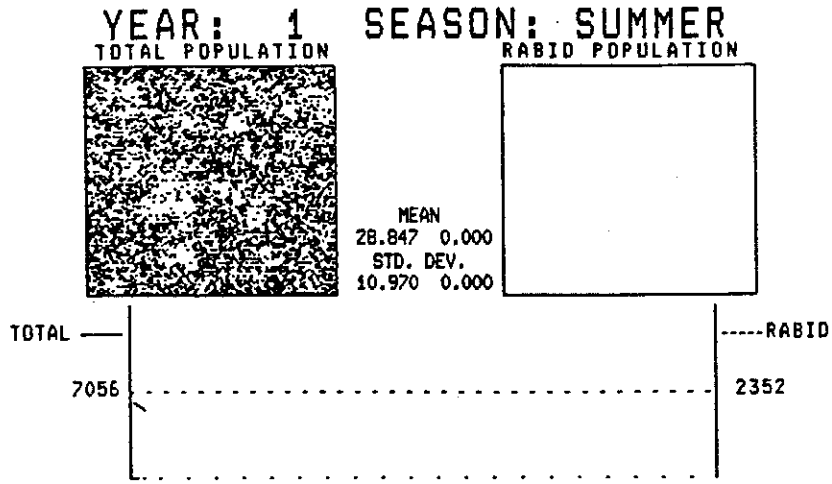

ANNEX 1.b

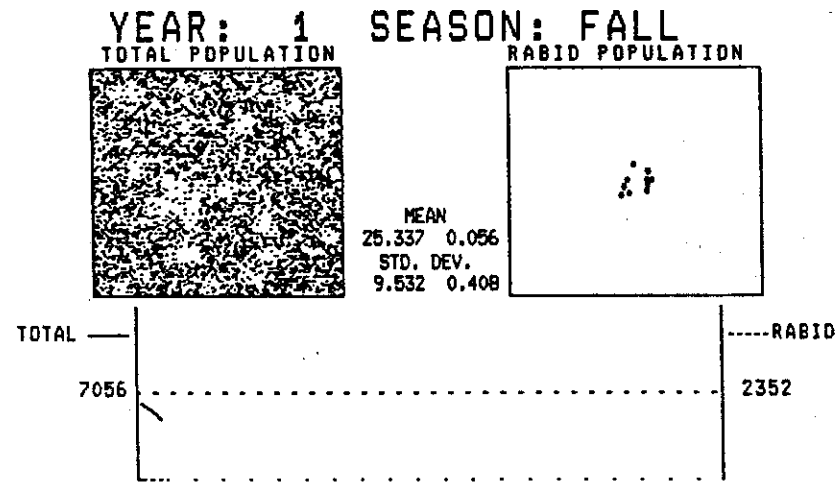
YEAR	POP	NMORT	RMORT	CONT	DINCON	DEXCON	SURV	BARRJ	BARRA	CONRT	MRT J/A	AVEL
1	6443	4024	0	0	0	0	0.656	0.449	0.102	0.000	2.52 3.58	5
2	6183	3786	0	0	0	0	0.656	0.597	0.119	0.000	2.48 3.53	5
3	6281	3834	0	0	0	0	0.656	0.644	0.134	0.000	2.57 3.76	5
4	6076	3674	0	0	0	0	0.656	0.669	0.156	0.000	2.31 3.38	4
5	6123	3716	0	0	0	0	0.656	0.697	0.171	0.000	2.42 3.68	5
1	6129	3679	48	333	6	0	0.656	0.707	0.196	3.424	2.41 3.75	5
2	6112	1341	4480	5127	15	3	0.656	0.704	0.202	1.088	3.41 3.61	5
3	1906	394	1422	1505	0	0	0.656	0.386	0.119	1.058	15.42 14.33	16
4	501	235	104	122	1	0	0.656	0.258	0.333	1.139	8.04 15.00	16
5	1114	613	28	41	0	0	0.656	0.356	0.042	1.464	12.33 14.97	16
6	2569	1103	747	989	14	0	0.656	0.544	0.070	1.231	6.99 13.28	15
7	3415	944	1943	2193	2	1	0.656	0.577	0.196	1.080	7.00 12.40	13
8	2356	838	1026	1288	3	1	0.656	0.647	0.211	1.177	5.40 12.97	15
9	2108	758	884	945	4	0	0.656	0.633	0.286	1.041	6.73 13.05	15
10	2303	1030	481	502	1	0	0.656	0.524	0.107	1.016	7.37 13.51	15
11	3164	1675	72	340	6	0	0.656	0.672	0.080	3.009	4.92 11.97	13
12	3881	971	2464	2636	9	1	0.656	0.786	0.372	1.027	3.76 8.29	10
13	2290	688	1221	1366	2	0	0.656	0.604	0.176	1.084	6.73 13.25	14
14	1615	474	904	1015	7	1	0.656	0.633	0.286	1.081	5.58 13.84	15
15	1120	474	302	299	0	0	0.656	0.507	0.037	0.977	6.65 14.27	15

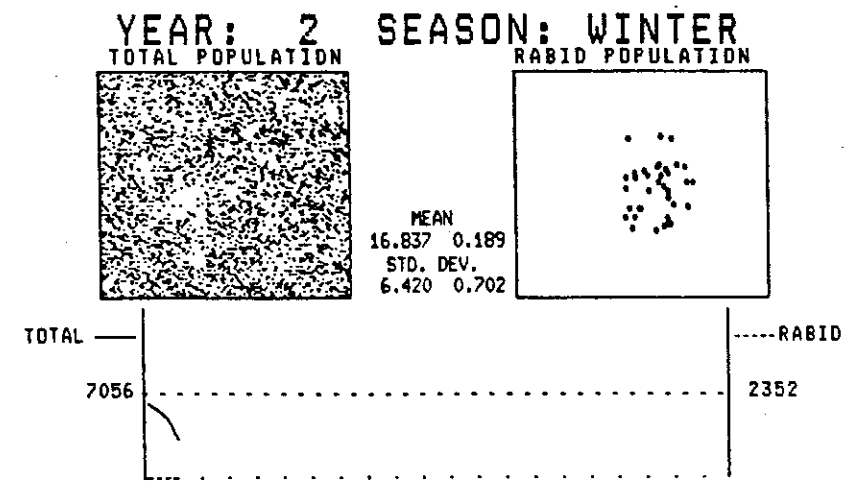
YEARS OF DIEOUTS (FIRST RABIES FREE YEAR):
0

ANNEX 2.1a

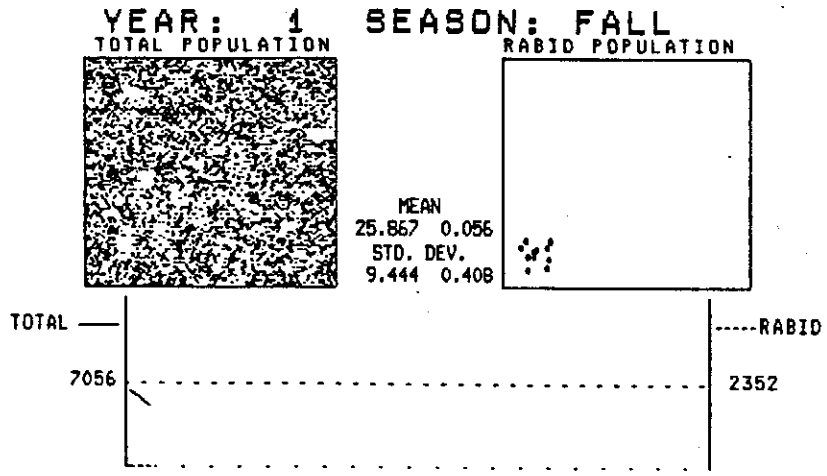

YEAR: 1 SEASON: SPRING
TOTAL POPULATION
RABID POPULATION
MEAN
31.270 0.000
STD. DEV.
11.846 0.000
TOTAL
RABID
7056
2352

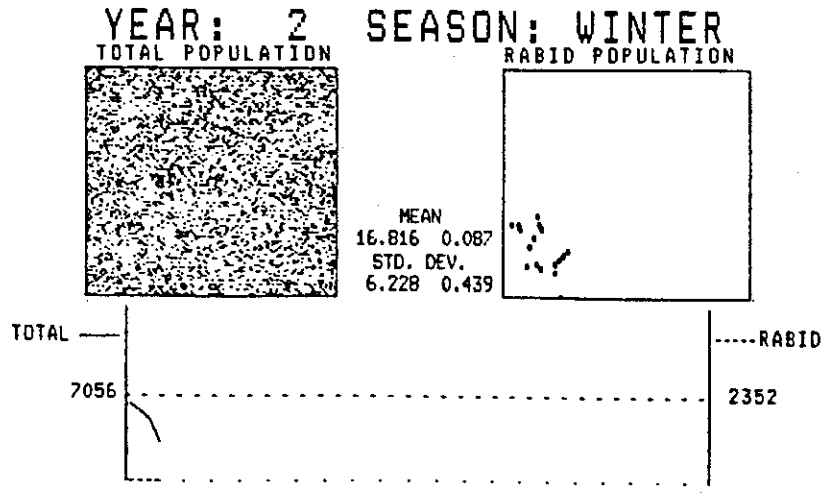

YEAR: 1 SEASON: SUMMER
TOTAL POPULATION
RABID POPULATION
MEAN
28.847 0.000
STD. DEV.
10.970 0.000
TOTAL
RABID
7056
2352


YEAR: 1 SEASON: FALL
TOTAL POPULATION
RABID POPULATION
MEAN
25.337 0.056
STD. DEV.
9.532 0.408
TOTAL
RABID
7056
2352

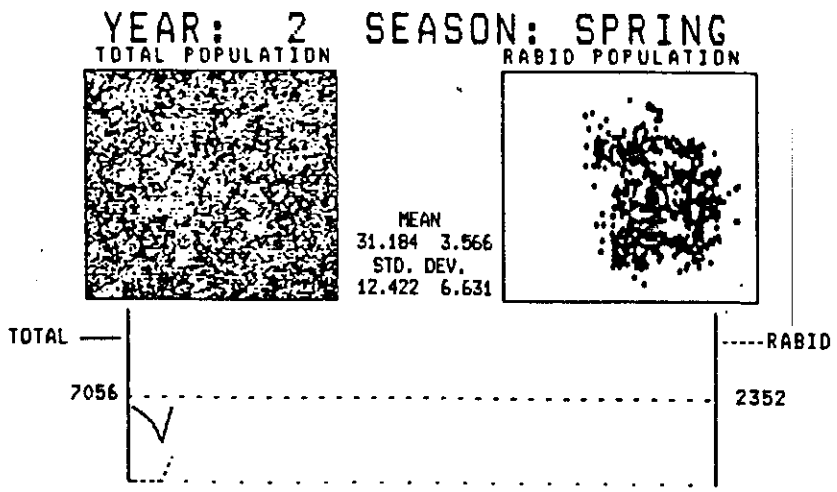

YEAR: 2 SEASON: WINTER
TOTAL POPULATION
RABID POPULATION
MEAN
16.837 0.189
STD. DEV.
6.420 0.702
TOTAL
RABID
7056
2352

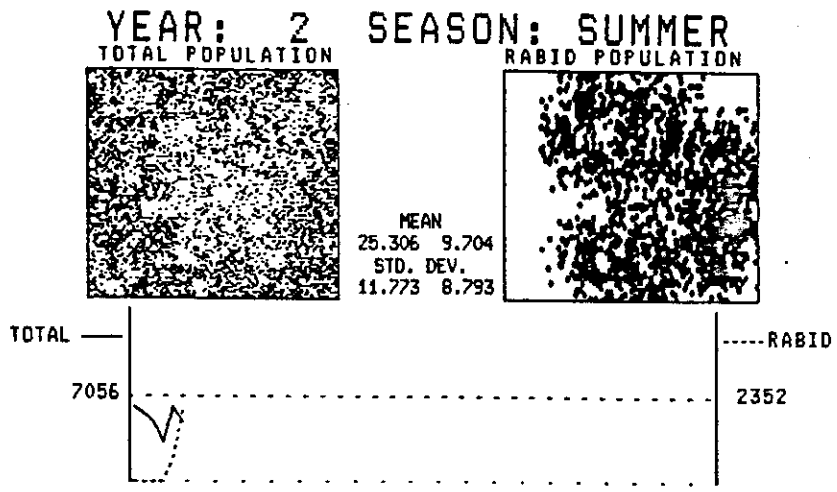
2.2a

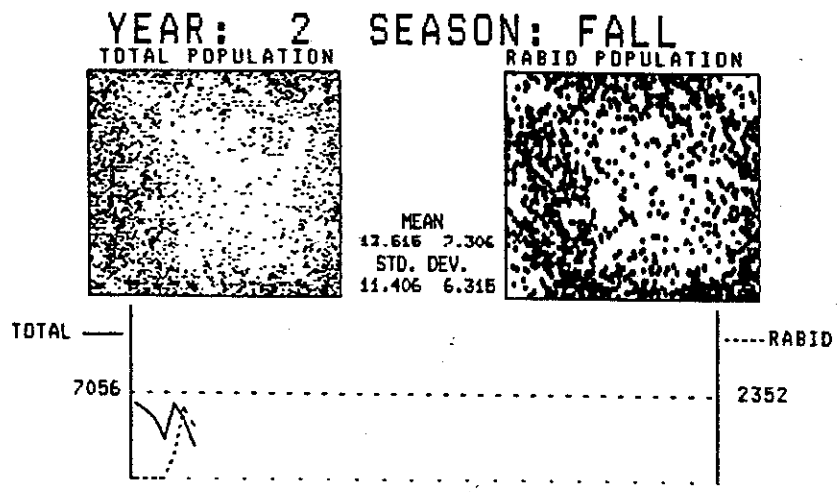

YEAR: 1 SEASON: FALL
TOTAL POPULATION
RABID POPULATION
MEAN
25.867 0.056
STD. DEV.
9.444 0.408
TOTAL
RABID
7056
2352

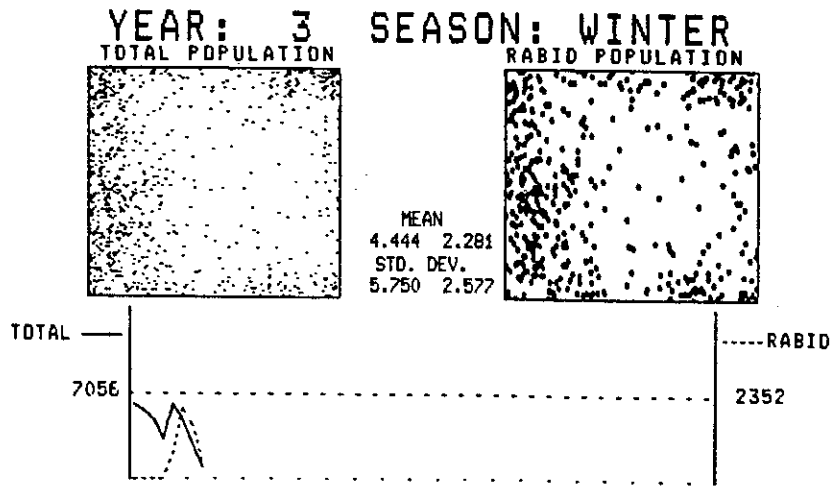

YEAR: 2 SEASON: WINTER
TOTAL POPULATION
RABID POPULATION
MEAN
16.816 0.087
STD. DEV.
6.228 0.439
TOTAL
RABID
7056
2352

2.1b

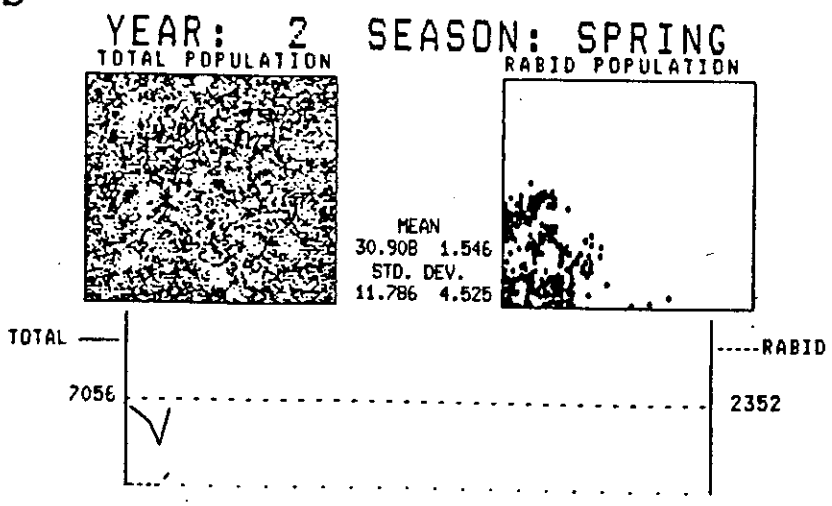

YEAR: 2 SEASON: SPRING
TOTAL POPULATION
RABID POPULATION
MEAN
31.184 3.566
STD. DEV.
12.422 6.631
TOTAL
-----RABID
7056
2352

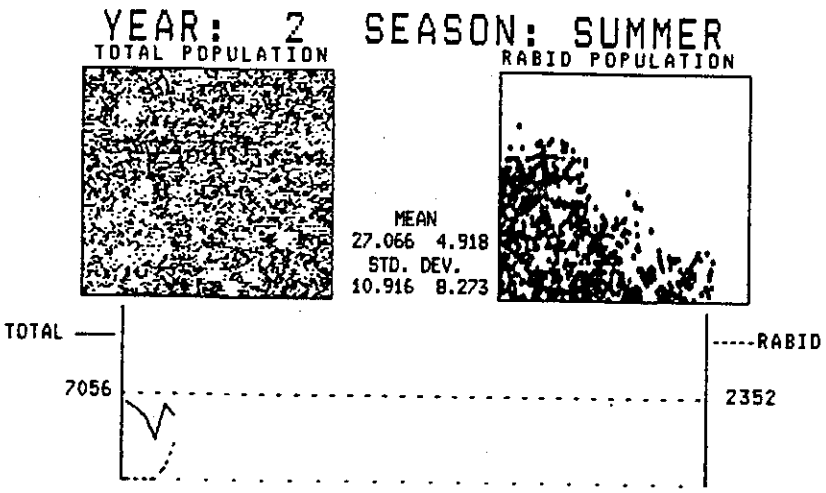

YEAR: 2 SEASON: SUMMER
TOTAL POPULATION
RABID POPULATION
MEAN
25.306 9.704
STD. DEV.
11.773 8.793
TOTAL
-----RABID
7056
2352

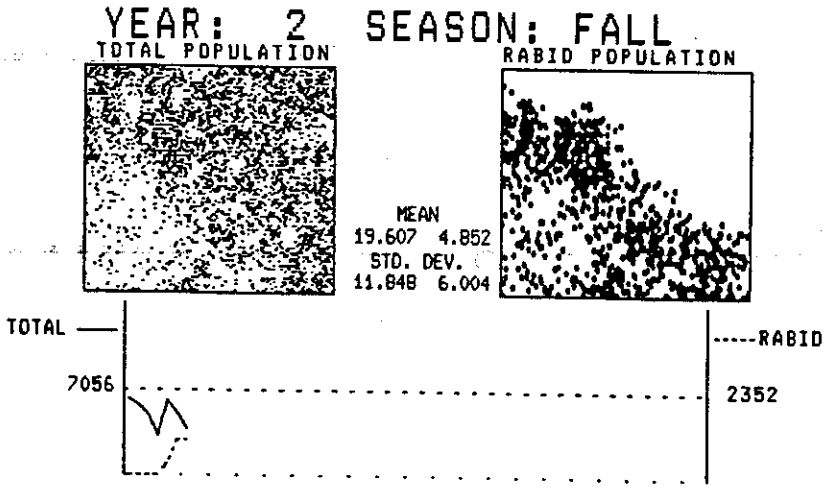

YEAR: 2 SEASON: FALL
TOTAL POPULATION
RABID POPULATION
MEAN
12.616 7.306
STD. DEV.
11.406 6.316
TOTAL
-----RABID
7056
2352

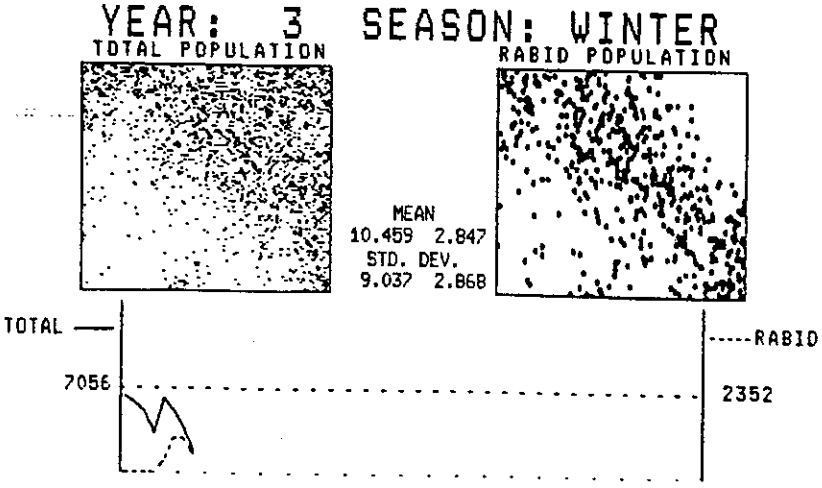

YEAR: 3 SEASON: WINTER
TOTAL POPULATION
RABID POPULATION
MEAN
4.444 2.281
STD. DEV.
5.750 2.577
TOTAL
-----RABID
7056
2352

2.2b

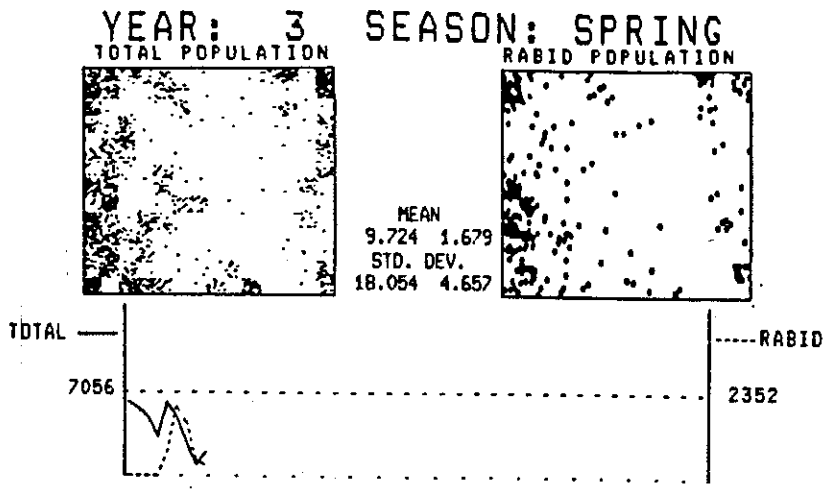

YEAR: 2 SEASON: SPRING
TOTAL POPULATION
RABID POPULATION
MEAN
30.908 1.546
STD. DEV.
11.786 4.525
TOTAL
RABID
7056
2352

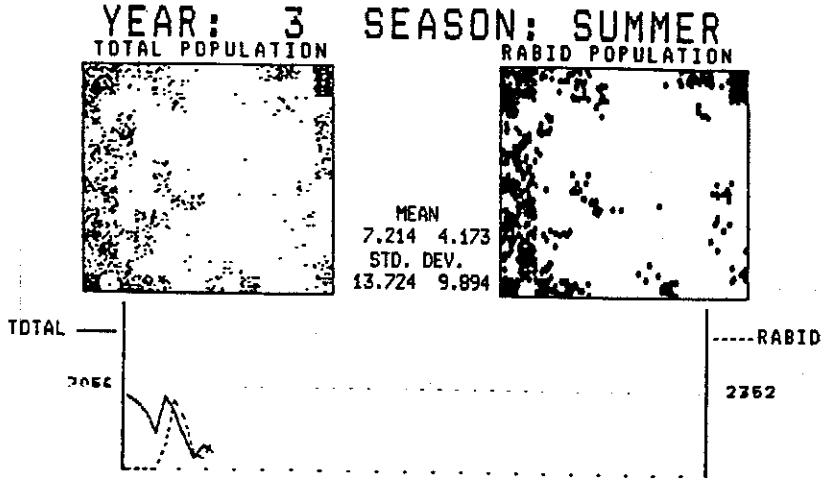

YEAR: 2 SEASON: SUMMER
TOTAL POPULATION
RABID POPULATION
MEAN
27.066 4.918
STD. DEV.
10.916 8.273
TOTAL
RABID
7056
2352

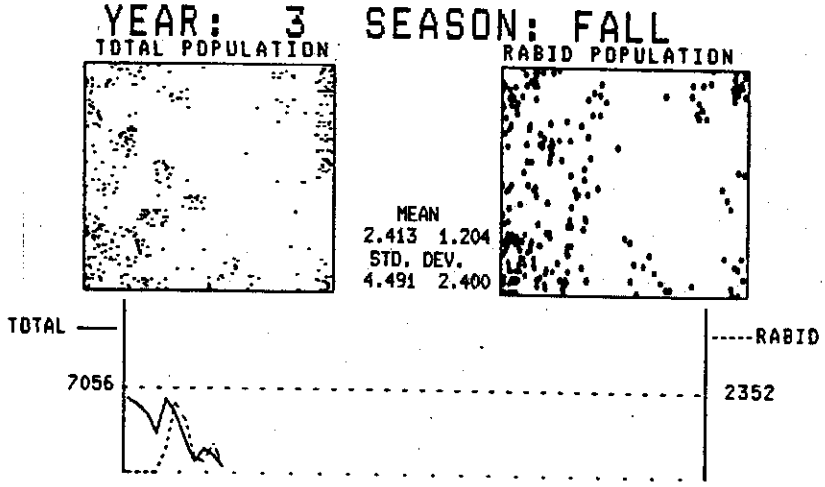

YEAR: 2 SEASON: FALL
TOTAL POPULATION
RABID POPULATION
MEAN
19.607 4.852
STD. DEV.
11.848 6.004
TOTAL
RABID
7056
2352

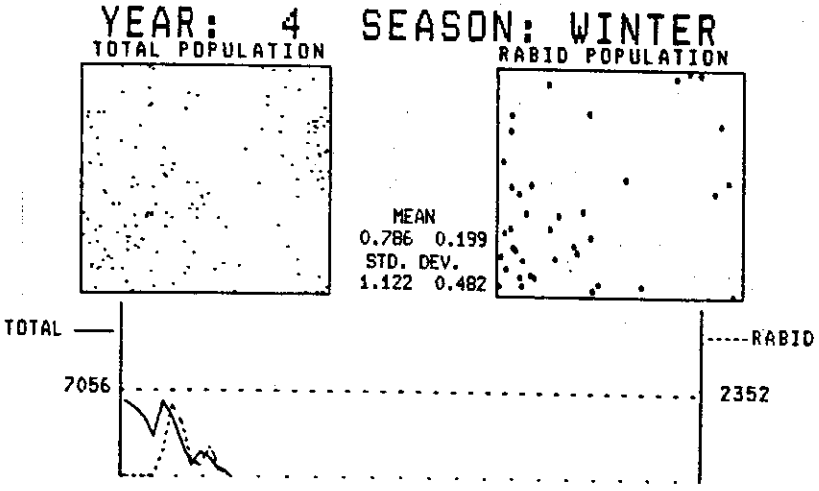

YEAR: 3 SEASON: WINTER
TOTAL POPULATION
RABID POPULATION
MEAN
10.459 2.847
STD. DEV.
9.037 2.868
TOTAL
RABID
7056
2352

2.1c

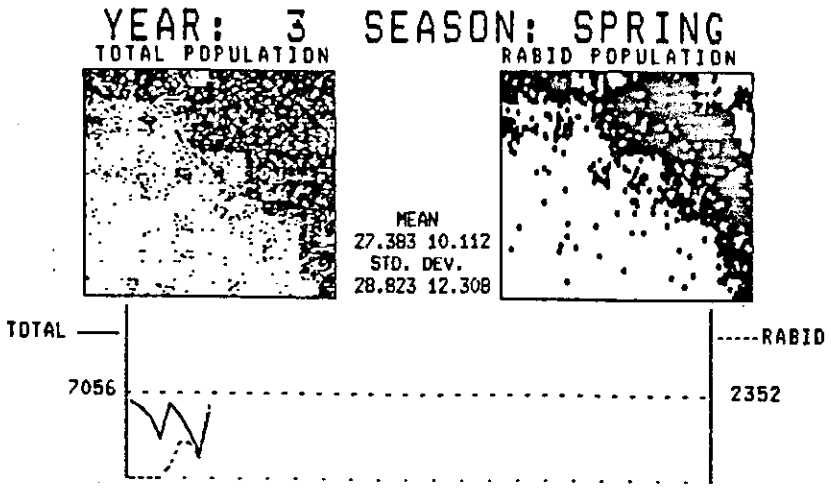

YEAR: 3
SEASON: SPRING
TOTAL POPULATION
RABID POPULATION
MEAN
9.724 1.679
STD. DEV.
18.054 4.657
TOTAL
RABID
7056
2352

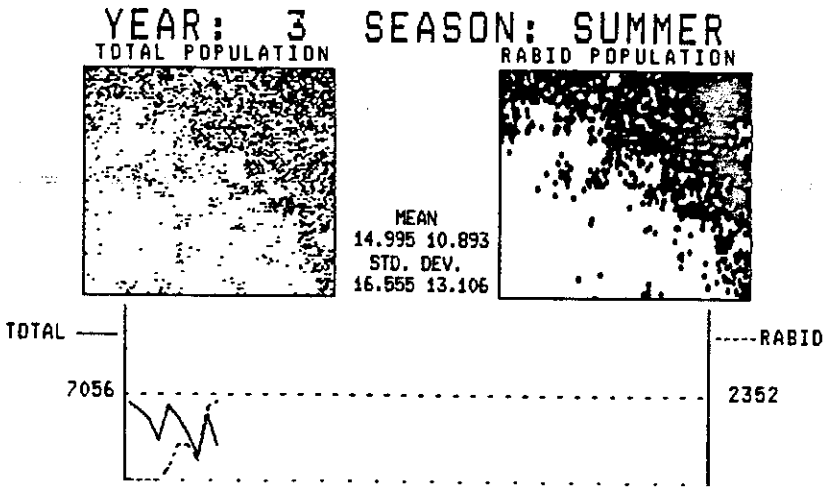

YEAR: 3
SEASON: SUMMER
TOTAL POPULATION
RABID POPULATION
MEAN
7.214 4.173
STD. DEV.
13.724 9.894
TOTAL
RABID
2352

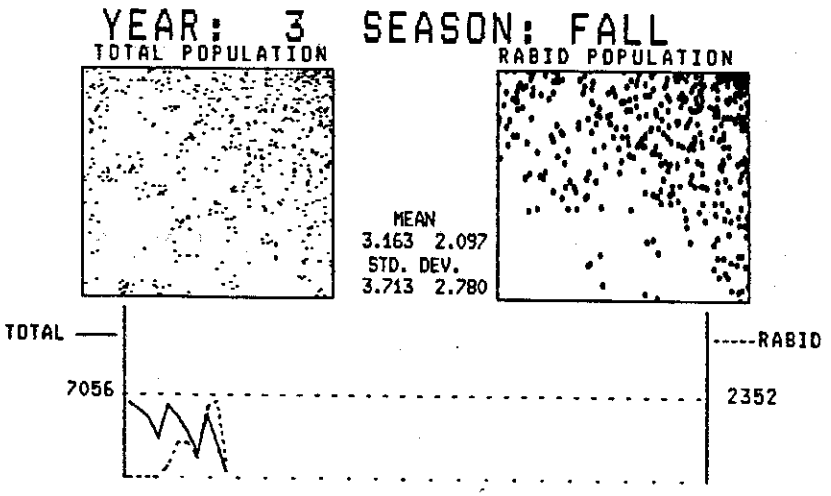

YEAR: 3
SEASON: FALL
TOTAL POPULATION
RABID POPULATION
MEAN
2.413 1.204
STD. DEV.
4.491 2.400
TOTAL
RABID
7056
2352

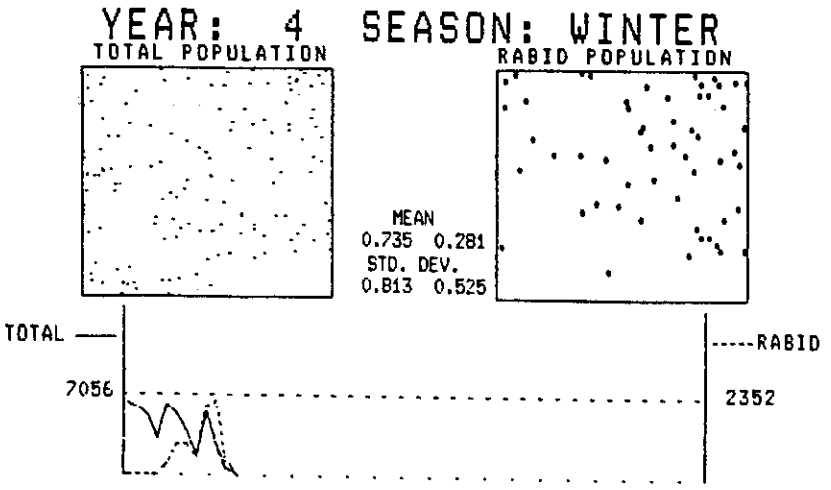

YEAR: 4
SEASON: WINTER
TOTAL POPULATION
RABID POPULATION
MEAN
0.786 0.199
STD. DEV.
1.122 0.482
TOTAL
RABID
7056
2352

2.2c

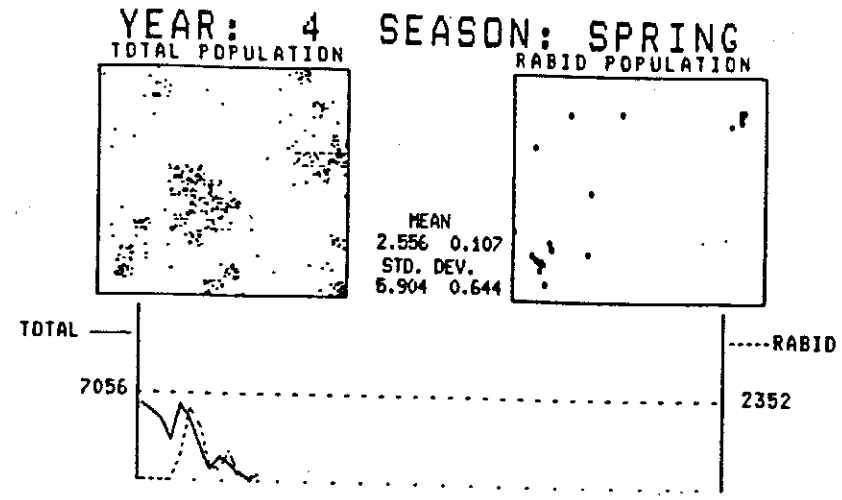

YEAR: 3 SEASON: SPRING
TOTAL POPULATION
RABID POPULATION
MEAN
27.383 10.112
STD. DEV.
28.823 12.308
TOTAL
RABID
7056
2352

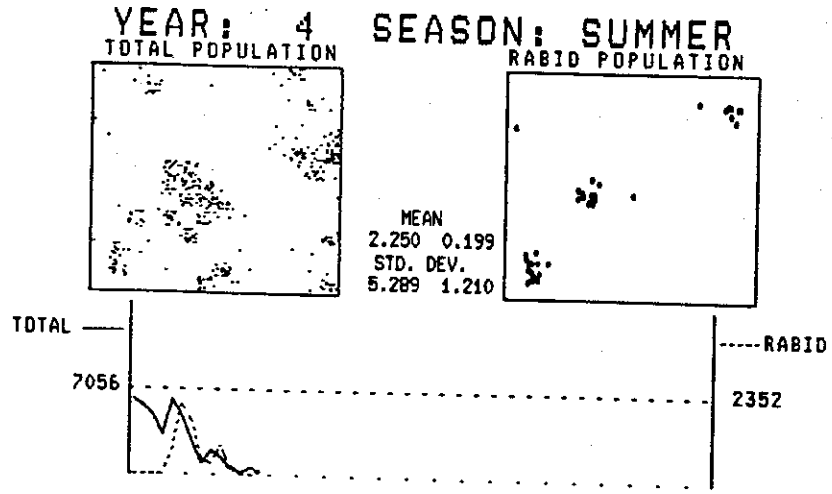

YEAR: 3 SEASON: SUMMER
TOTAL POPULATION
RABID POPULATION
MEAN
14.995 10.893
STD. DEV.
16.555 13.106
TOTAL
RABID
7056
2352

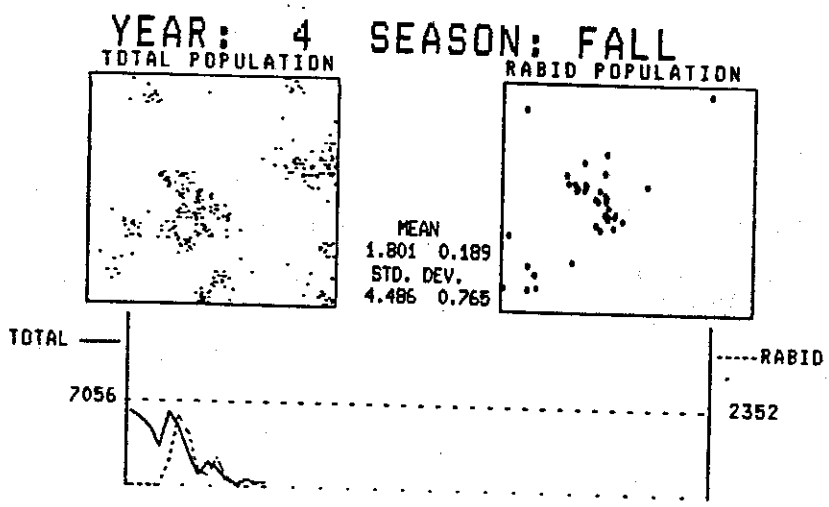

YEAR: 3 SEASON: FALL
TOTAL POPULATION
RABID POPULATION
MEAN
3.163 2.097
STD. DEV.
3.713 2.780
TOTAL
RABID
7056
2352


YEAR: 4 SEASON: WINTER
TOTAL POPULATION
RABID POPULATION
MEAN
0.735 0.281
STD. DEV.
0.813 0.525
TOTAL
RABID
7056
2352

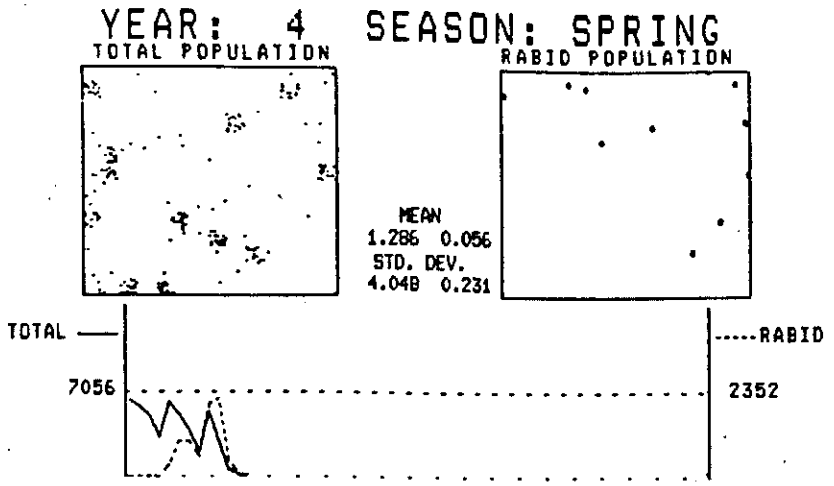
2.1d

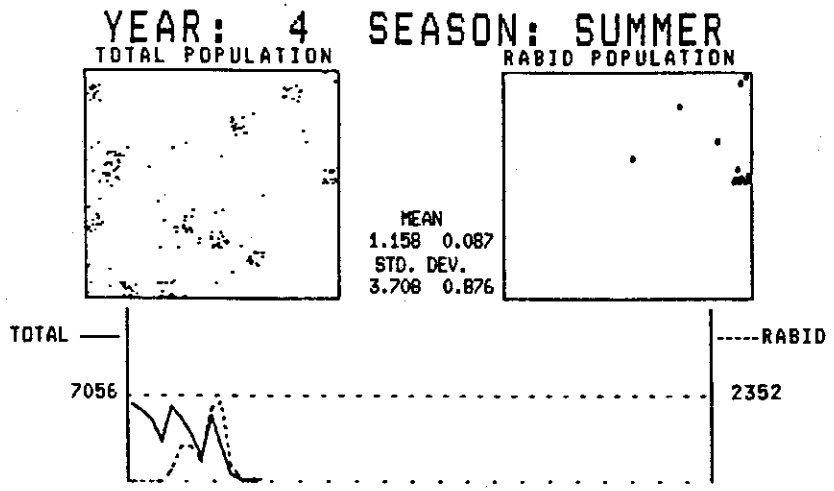

YEAR: 4
SEASON: SPRING
TOTAL POPULATION
RABID POPULATION
MEAN
2.556 0.107
STD. DEV.
5.904 0.644
TOTAL
RABID
7056
2352

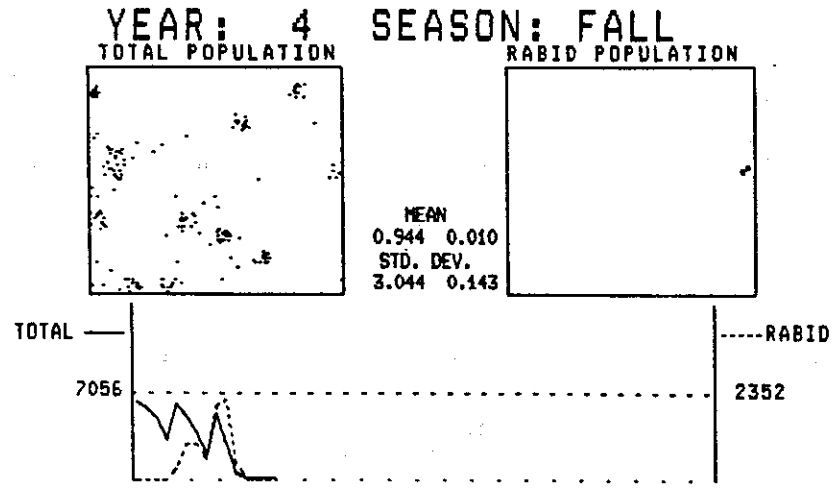

YEAR: 4
SEASON: SUMMER
TOTAL POPULATION
RABID POPULATION
MEAN
2.250 0.199
STD. DEV.
5.289 1.210
TOTAL
RABID
7056
2352


YEAR: 4
SEASON: FALL
TOTAL POPULATION
RABID POPULATION
MEAN
1.801 0.189
STD. DEV.
4.486 0.765
TOTAL
RABID
7056
2352

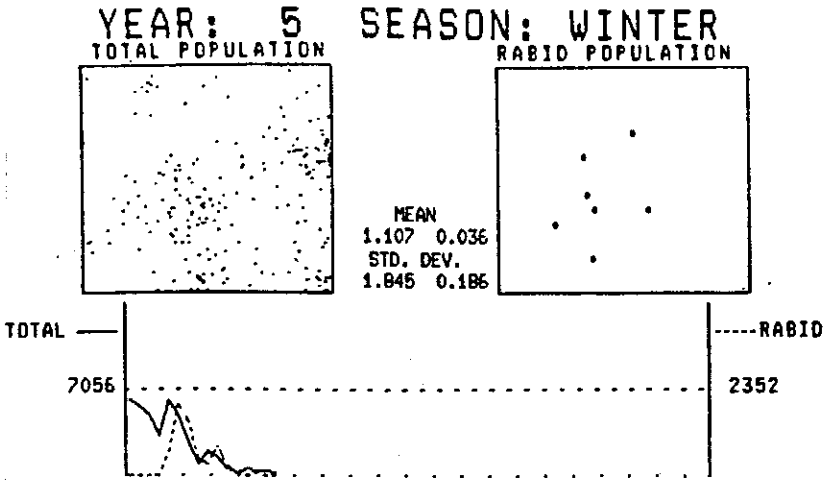
2.2d

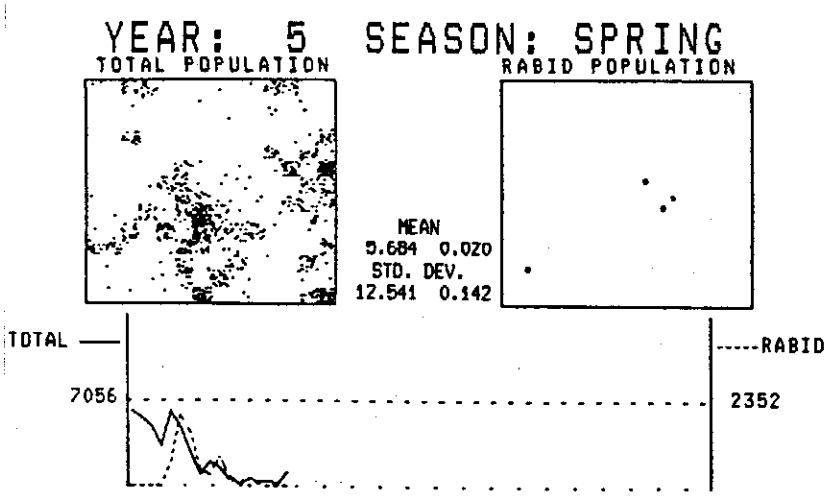

YEAR: 4 SEASON: SPRING
TOTAL POPULATION
RABID POPULATION
MEAN
1.286 0.056
STD. DEV.
4.048 0.231
TOTAL
-----RABID
7056
2352

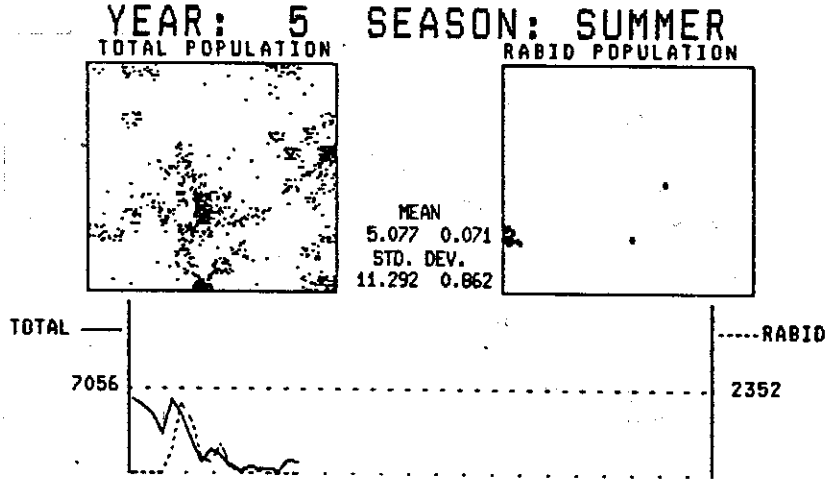

YEAR: 4 SEASON: SUMMER
TOTAL POPULATION
RABID POPULATION
MEAN
1.158 0.087
STD. DEV.
3.708 0.876
TOTAL
-----RABID
7056
2352

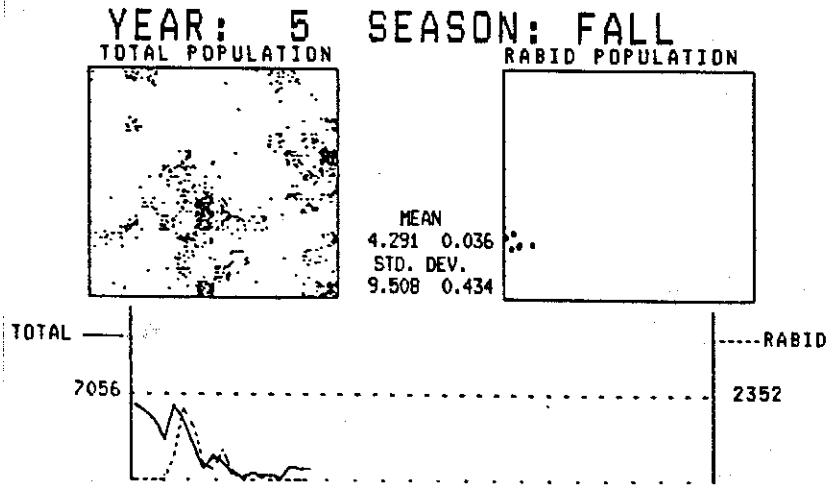

YEAR: 4 SEASON: FALL
TOTAL POPULATION
RABID POPULATION
MEAN
0.944 0.010
STD. DEV.
3.044 0.143
TOTAL
-----RABID
7056
2352

2.1e

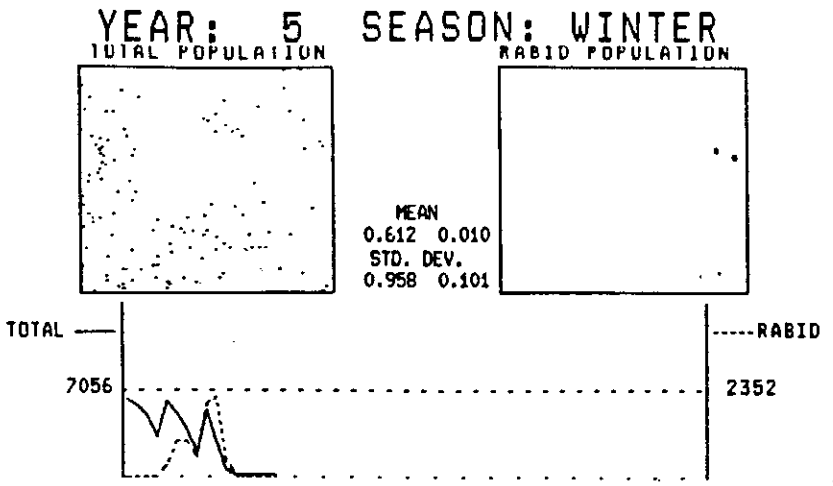

YEAR: 5 SEASON: WINTER
TOTAL POPULATION
RABID POPULATION
MEAN
1.107 0.036
STD. DEV.
1.845 0.186
TOTAL
RABID
7056
2352

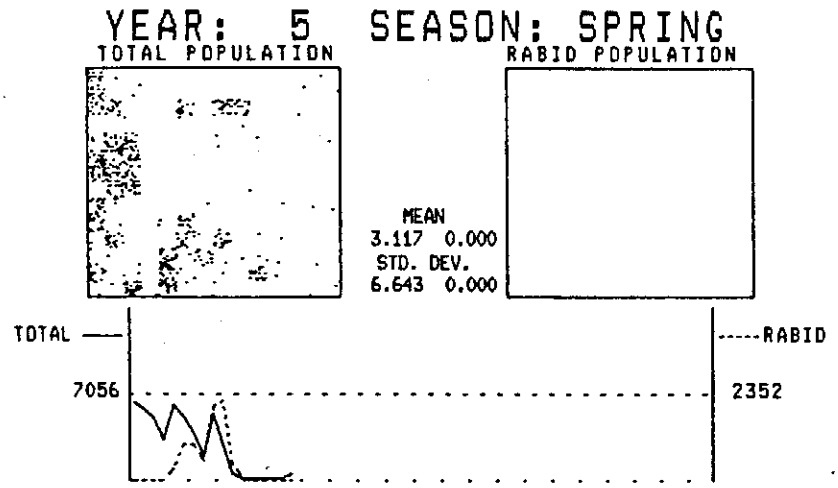

YEAR: 5 SEASON: SPRING
TOTAL POPULATION
RABID POPULATION
MEAN
5.684 0.020
STD. DEV.
12.541 0.142
TOTAL
RABID
7056
2352

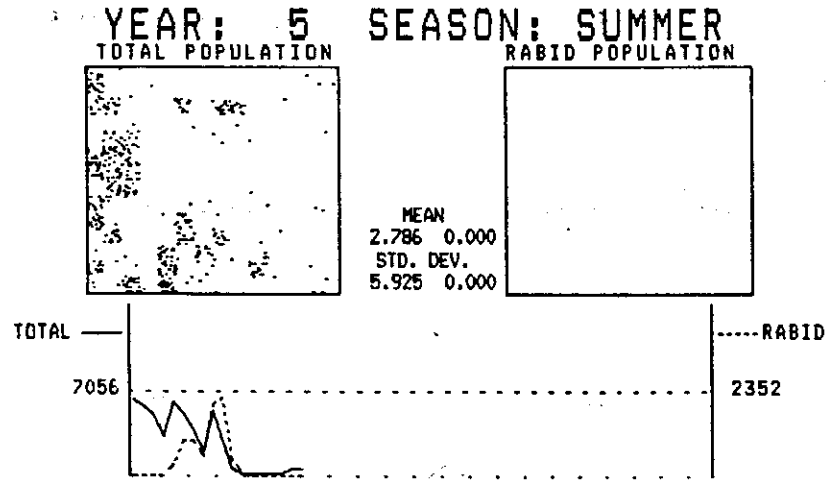

YEAR: 5 SEASON: SUMMER
TOTAL POPULATION
RABID POPULATION
MEAN
5.077 0.071
STD. DEV.
11.292 0.862
TOTAL
RABID
7056
2352

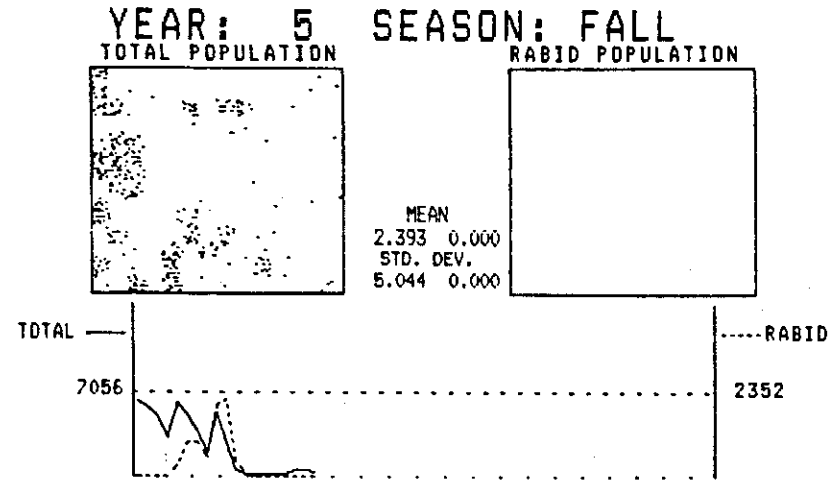

YEAR: 5 SEASON: FALL
TOTAL POPULATION
RABID POPULATION
MEAN
4.291 0.036
STD. DEV.
9.508 0.434
TOTAL
RABID
7056
2352

2.2e

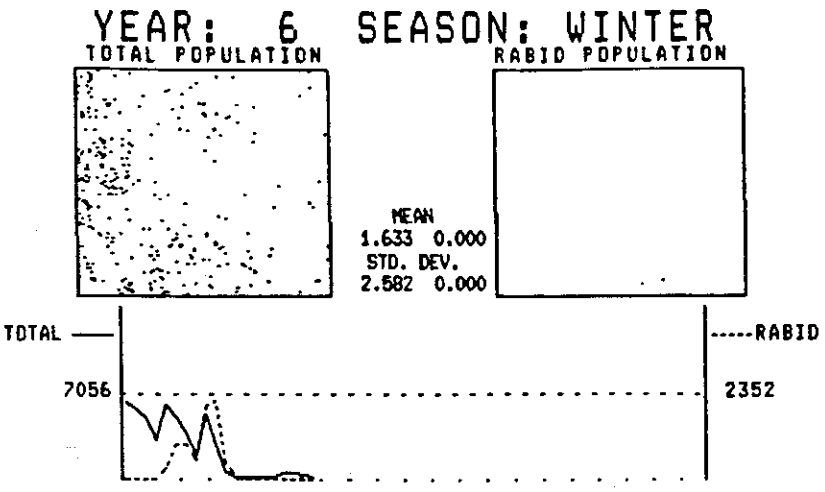

YEAR: 5 SEASON: WINTER
TOTAL POPULATION
RABID POPULATION
MEAN
0.612 0.010
STD. DEV.
0.958 0.101
TOTAL
RABID
7056
2352


YEAR: 5 SEASON: SPRING
TOTAL POPULATION
RABID POPULATION
MEAN
3.117 0.000
STD. DEV.
6.643 0.000
TOTAL
RABID
7056
2352

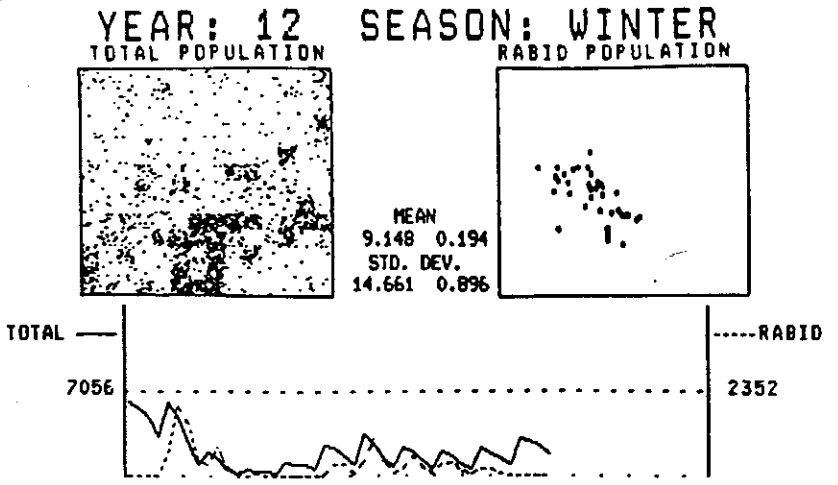

YEAR: 5 SEASON: SUMMER
TOTAL POPULATION
RABID POPULATION
MEAN
2.786 0.000
STD. DEV.
5.925 0.000
TOTAL
RABID
7056
2352

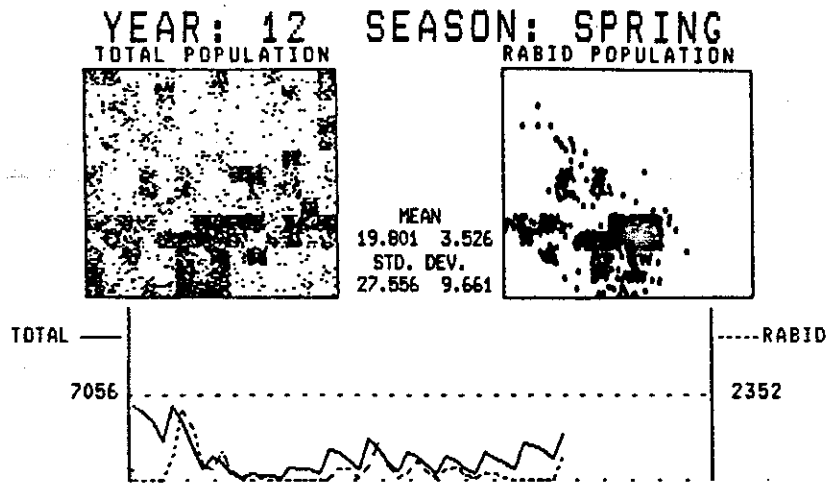

YEAR: 5 SEASON: FALL
TOTAL POPULATION
RABID POPULATION
MEAN
2.393 0.000
STD. DEV.
5.044 0.000
TOTAL
RABID
7056
2352

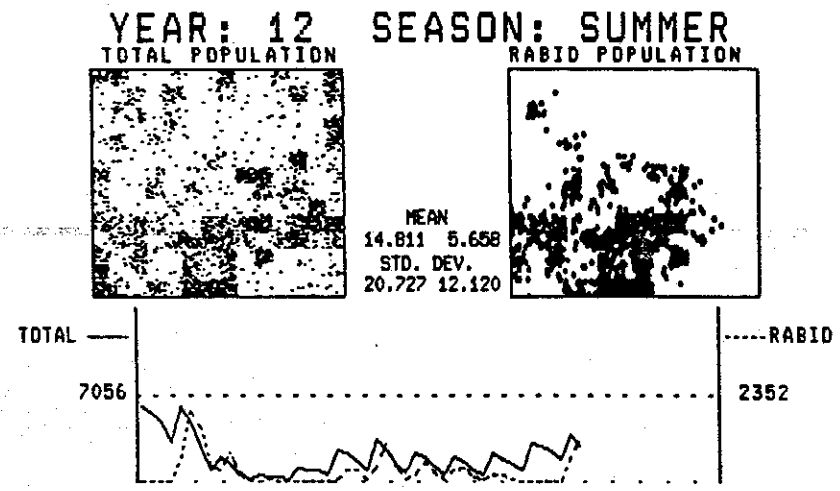
2.2f

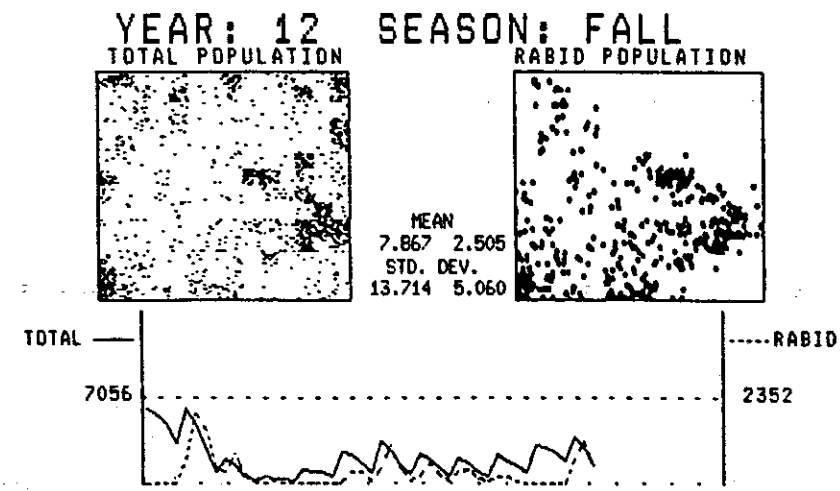

YEAR: 6 SEASON: WINTER
TOTAL POPULATION
RABID POPULATION
MEAN
1.633 0.000
STD. DEV.
2.582 0.000
TOTAL
RABID
7056
2352

2.1g

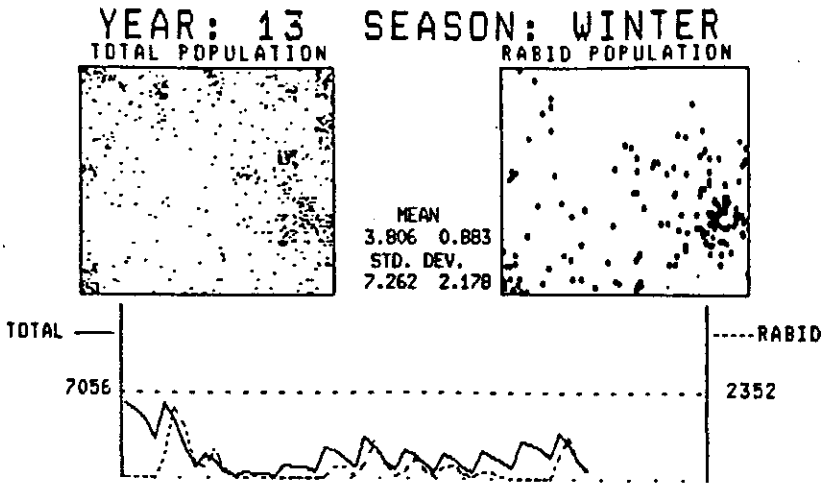

YEAR: 12 SEASON: WINTER
TOTAL POPULATION
RABID POPULATION
MEAN
9.148 0.194
STD. DEV.
14.661 0.896
TOTAL
RABID
7056
2352

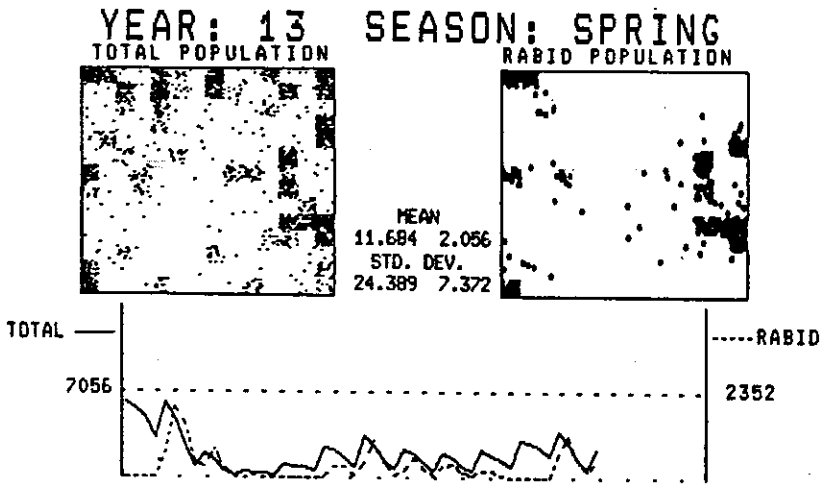

YEAR: 12 SEASON: SPRING
TOTAL POPULATION
RABID POPULATION
MEAN
19.801 3.526
STD. DEV.
27.556 9.661
TOTAL
RABID
7056
2352

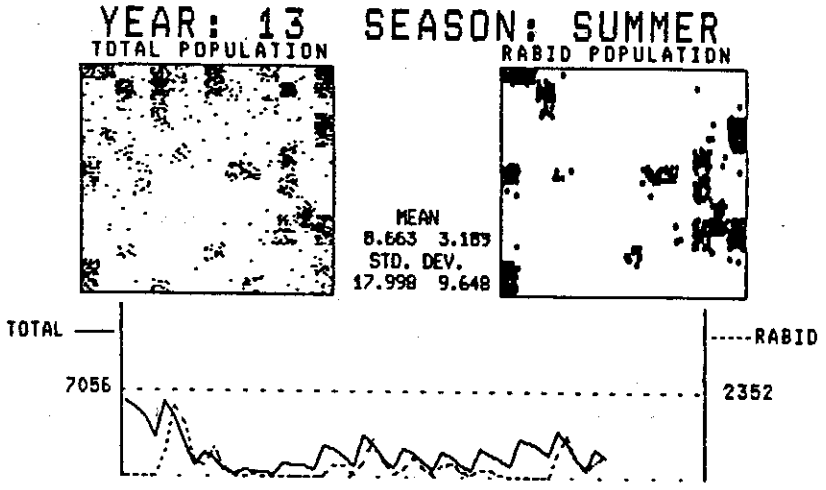

YEAR: 12 SEASON: SUMMER
TOTAL POPULATION
RABID POPULATION
MEAN
14.811 5.658
STD. DEV.
20.727 12.120
TOTAL
RABID
7056
2352

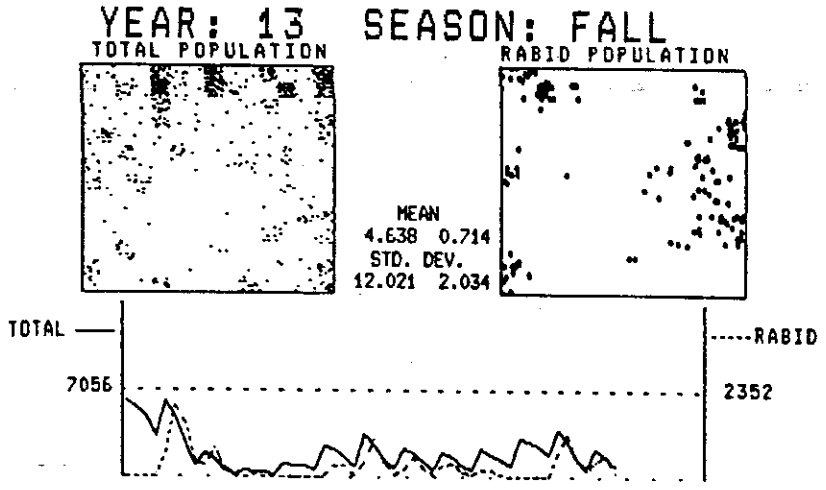

YEAR: 12 SEASON: FALL
TOTAL POPULATION
RABID POPULATION
MEAN
7.867 2.505
STD. DEV.
13.714 5.060
TOTAL
RABID
7056
2352

2.1h

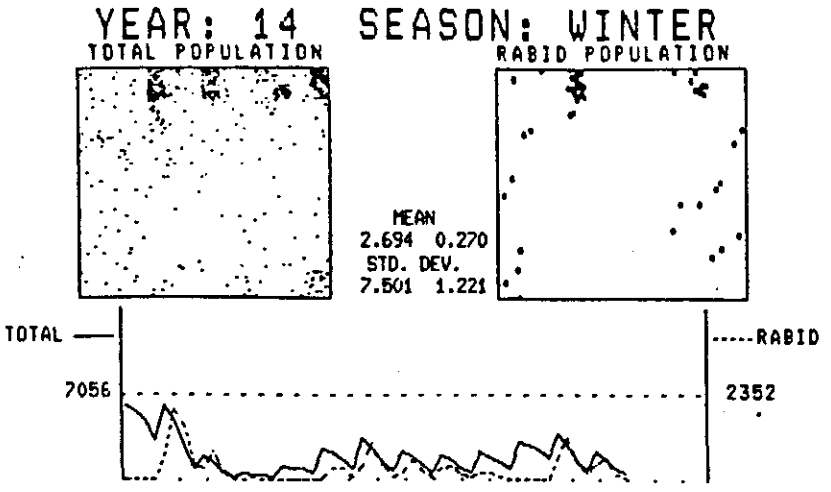

YEAR: 13 SEASON: WINTER
TOTAL POPULATION
RABID POPULATION
MEAN
3.806 0.883
STD. DEV.
7.262 2.178
TOTAL
RABID
7056
2352

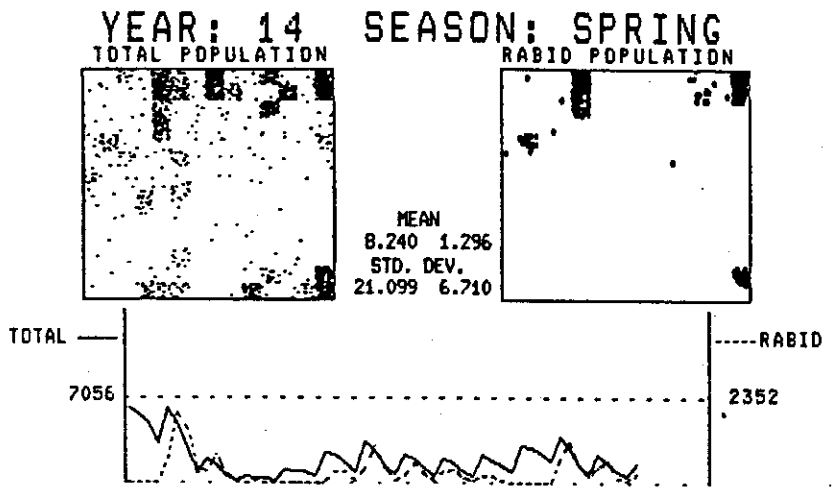

YEAR: 13 SEASON: SPRING
TOTAL POPULATION
RABID POPULATION
MEAN
11.684 2.056
STD. DEV.
24.389 7.372
TOTAL
RABID
7056
2352

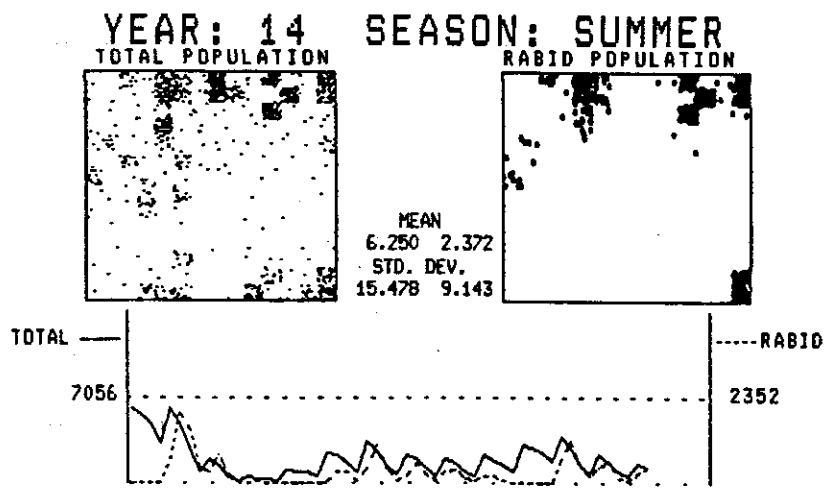

YEAR: 13 SEASON: SUMMER
TOTAL POPULATION
RABID POPULATION
MEAN
8.663 3.189
STD. DEV.
17.998 9.648
TOTAL
RABID
7056
2352

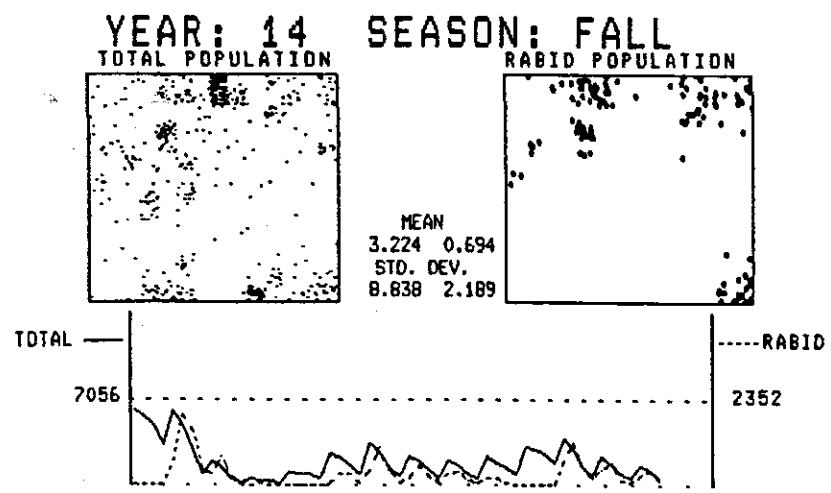

YEAR: 13 SEASON: FALL
TOTAL POPULATION
RABID POPULATION
MEAN
4.638 0.714
STD. DEV.
12.021 2.034
TOTAL
RABID
7056
2352

2.1i

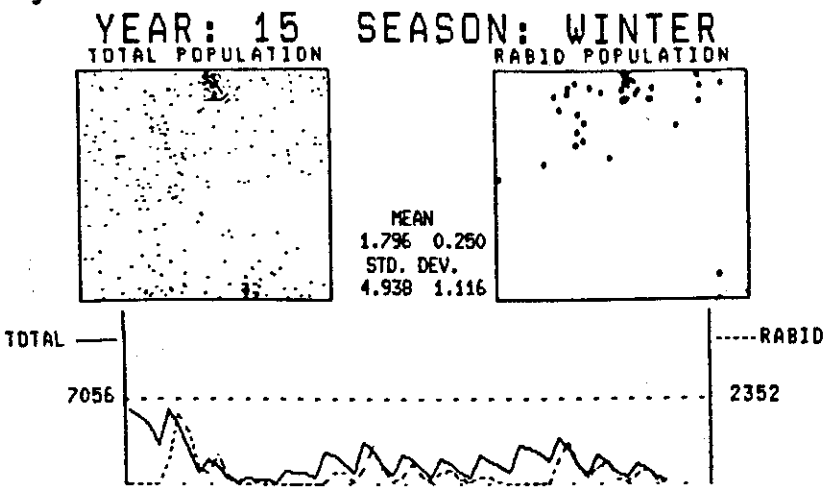

YEAR: 14 SEASON: WINTER
TOTAL POPULATION
RABID POPULATION
MEAN
2.694 0.270
STD. DEV.
7.501 1.221
TOTAL
-----RABID
7056
2352

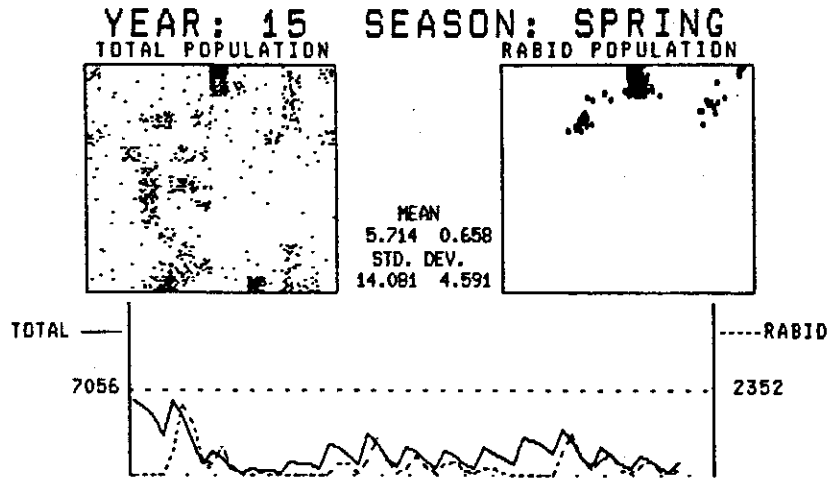

YEAR: 14 SEASON: SPRING
TOTAL POPULATION
RABID POPULATION
MEAN
8.240 1.296
STD. DEV.
21.099 6.710
TOTAL
-----RABID
7056
2352

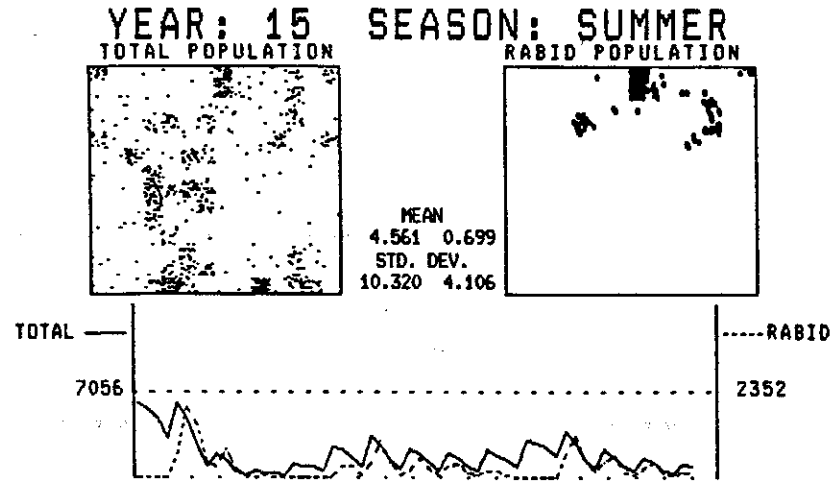

YEAR: 14 SEASON: SUMMER
TOTAL POPULATION
RABID POPULATION
MEAN
6.250 2.372
STD. DEV.
15.478 9.143
TOTAL
-----RABID
7056
2352

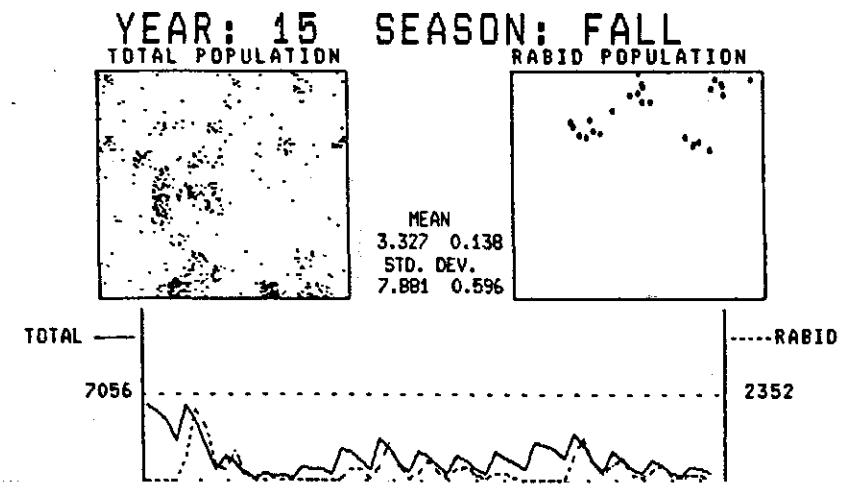

YEAR: 14 SEASON: FALL
TOTAL POPULATION
RABID POPULATION
MEAN
3.224 0.694
STD. DEV.
8.838 2.189
TOTAL
-----RABID
7056
2352

2.1 j


YEAR: 15 SEASON: WINTER
TOTAL POPULATION
RABID POPULATION
MEAN
1.796 0.250
STD. DEV.
4.938 1.116
TOTAL
RABID
7056
2352


YEAR: 15 SEASON: SPRING
TOTAL POPULATION
RABID POPULATION
MEAN
5.714 0.658
STD. DEV.
14.081 4.591
TOTAL
RABID
7056
2352


YEAR: 15 SEASON: SUMMER
TOTAL POPULATION
RABID POPULATION
MEAN
4.561 0.699
STD. DEV.
10.320 4.106
TOTAL
RABID
7056
2352


YEAR: 15 SEASON: FALL
TOTAL POPULATION
RABID POPULATION
MEAN
3.327 0.138
STD. DEV.
7.881 0.596
TOTAL
RABID
7056
2352

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