

EMPIRICAL MODELLING OF POPULATION TIME SERIES DATA:
THE CASE OF AGE AND DENSITY DEPENDENT VITAL RATES

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ABSTRACT. The total numbers of births and deaths in a population are given at discrete equispaced time intervals. It is assumed that the birth and death rates depend on age, the population size and possibly time. Further it is assumed that the rates fluctuate randomly from individual to individual. The problem is to estimate average birth and death rates and the age structure of the evolving population. Results are presented for a population of sheep blow-flies maintained under stable conditions for a two year period (361 observations) by A. J. Nicholson.

1. INTRODUCTION. Statistical analyses of population data have generally concentrated on the cases where birth and death rates depend on age alone (see for example Chiang (1968), Gane (1975), Pollard (1973)) or linearly on population size alone (see for example Bartlett (1966), Keiding (1975)). In the first case the ages of the individuals concerned have been assumed known. In the second case the age structure is ignored.

In a variety of practical situations birth and death rates are non-linear functions of both age and population size. A variety of theoretical and simulated results have been derived for such populations in the deterministic (nonstochastic) case. Oster (1977) presents a review of this case. Supposing $N(t, x)$ to be the number alive in the population at time

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t aged x such studies have typically been based on the system of equations

$$\frac{\partial N(t, x)}{\partial t} - \frac{\partial N(t, x)}{\partial x} = -\mu(t, x)N(t, x),$$

$$N(t, 0) = \int \beta(t, x) N(t, x) dx$$

with $\mu(\cdot)$ the death rate (force of mortality) per individual and $\beta(\cdot)$ the corresponding birth rate. Functions $(N(t, x))$ satisfying the above equations, for plausible cases of $\mu(\cdot)$ and $\beta(\cdot)$, can evidence an extremely broad range of behavior with a rich bifurcation structure as parameters are varied. (See Guckenheimer, Oster and Ipaktchi (1977).) The results that have been obtained are instructive; however their usefulness in practical situations is not clear because, among other things, (i) measurement error is ever present, (ii) individuals differ drastically in propensity to die, (iii) in general only aggregate data (i. e. non age structured) is available, (accurate life tables for populations with nonstationary age distributions are extremely rare in the ecological literature) (iv) adequate criteria for comparing models and data are lacking and (v) the solutions are unstable, so estimation of parameters is virtually impossible.

This paper is concerned with the problem of estimating nonstationary age structures and age-and-density-dependent death rates given aggregate stochastic data. The most detailed set of experiments in the age-and-density-dependent case were undoubtedly carried out by A. J. Nicholson, (Nicholson 1950)). This data has been modelled deterministically by Auslander et al (1974) with a variety of models. These models share many of the apparent qualitative features of the data. Here we begin a more quantitative assessment of the data and immediately find that some of the earlier assumptions are questionable.

2. NICHOLSON'S EXPERIMENTS. During the 1950's the Australian entomologist A. J. Nicholson carried out an extensive series of experiments concerning the population variation of *Lucilia cuprina* (the sheep blowfly) under various conditions. Nicholson maintained populations of the flies on various diets (some constant, some fluctuating), experiencing

different forms of competition (between larvae and adults, for egg laying space, etc.), and under many other conditions. One list that we have shows 145 major experiments. In this paper we report on the analysis of one cage of Nicholson's L97 experiment, "influence of periodic environmental changes of intrinsic oscillations". This cage was actually a control maintained under constant conditions.

The blowfly's life cycle is made up of a number of stages of varying durations (see Mackerras (1933)). The principal stages and their approximate durations are listed in table 1.

Table 1.

Stage	Duration
egg	12-24 hours
larva	5-10 days
pupa	6- 8 days
immature adult	4 days
mature adult	1-35 days

The durations listed are only meant to be suggestive. Great variations are observed, for example with temperature. The observed time to emergence (from egg to immature adult) for the population studied in this paper varied between 10 and 16 days.

Since the sex ratio is close to 1:1, we shall assume equal numbers of males and females in the models. Mackerras (1933). The development of the reproductive organs in the female is dependent on diet: sufficient protein is required for egg development. Egg laying in sexually mature females occurs in bursts several days apart, with the interval increasing as the female ages. The death rates for the larval and pupal stages are low. Table 3 in the Appendix gives an indication of the dependence of the adult mortality on age.

We turn now to the specific details of Nicholson's L97 cage I experiment. On 19 May 1954 1000 pupae were set up in a perspex box with a balsa wood grid on top of them to retain pupal cases. Food consisted of lump sugar and moistened cotton wool pad. Practically all flies emerged

overnight. Adult food consisting of .4 gram ground liver, dried in a desiccator, was added to the cage on 20 May. This quantity was added daily. Measurements were first made on 21 May. The basic data recorded were total counts of emerged or dead flies at two day intervals and the dates when the emerged flies had been laid as eggs. The experiment continued until 10 May 1956. Table 3 provides the bidaily data on adult population size, adults emerging, eggs laid and adults dying. Nicholson's final count of the flies in the cage was 6701. (This differs from the figure of 6806 derived by accumulating emergences and deaths.)

* Figure 1 presents graphs of the square roots of the basic data.

The adult population is seen to oscillate dramatically with a period of approximately 35-40 days. The population was maintained on a restricted protein diet. The competition for food when the population size was large meant that the females did not receive enough protein to realize their maximum fecundity. Indeed a comparison of adult population with eggs laid, shows that at the beginning of the experiment virtually no eggs were laid when the population size exceeded a certain level. The few eggs laid meant that the population would soon drop sharply. The subsequent generation however, being smaller, faced less intense competition for food and their fecundity increased. An alternation of large and small generations resulted and hence the oscillations evident in the Figure.

From the Figure the egg, emergence and death series also oscillate with periods of 35-40 days, the egg series leading the adult series by 12-14 days; emergences lead adults by 0-2 days and deaths lag adults by 0-4 days. These intervals are in accord with the averages indicated in table 1.

3. INITIAL DATA ANALYSES. Foremost in Nicholson's design of experiment I was the notion that competition was to occur in egg laying only, death rates were to depend on age alone. Figure 2 presents graphs of the birth and death rates and of the proportion of eggs not emerging.

*The square root is graphed to provide more nearly constant variability in the series.

The latter series fluctuates about the level of 10 per cent throughout most of the series (the various spikes occur when the number of eggs is small). However, towards the end there is a definite rise, suggesting that Nicholson's experiment might be collapsing.*

The birth rate series varies immensely with the population series, just as Nicholson arranged. During the last 200 days there is a clear suggestion that the flies are now laying eggs at population sizes which earlier would have inhibited egg laying. Nicholson (1960) regards this as evidence that selection had occurred favoring flies able to lay eggs at higher population levels (i.e. lower protein). (Later in the paper it will be seen that the population is younger at the later stages so that this rise may be caused by younger flies being more fecund. We remark that at the end of this experiment, Nicholson carried out a further experiment and found that these flies could lay eggs with much less protein.)

The simple death rate series is also quite variable. This is expected because of the varying age composition. However, close examination of the upper two graphs of Figure 2 suggests that the death rate is generally higher when the population size is large. Figure 3 is a scatter diagram of death rate and population size. It presents a clear indication that the adult death rate is indeed density dependent —contrary to Nicholson's design. Later we will construct a model of the dependence of the death rate on age and population size.

4. A DETERMINISTIC APPROACH TO AN AGE STRUCTURED POPULATION. We consider the case of discrete time, $t = 0, 1, 2, \dots$. Let

N_t = the adult population size at time t .

\underline{N}_t = the population vector. The entry in row i gives the number of population members aged $i-1$ at time t , $i=1, \dots, I$.

E_t = the number of entrants (pupae emerging), aged 0, to the adult population in the time period $(t-1, t)$.

\underline{E}_t = the entrant vector, having E_t in row 1 and 0 in the other rows.

*Nicholson (1960) observed that the flies left at the end of the experiment laid eggs with a much higher proportion never emerging than the original strain of flies. It may be this that causes the rise.

D_t = the number dying in the time period $(t-1, t)$.

$\tilde{P}(\tilde{N}_t)$ = the survival matrix. If the population vector is \tilde{N}_t then the entry in row $i+1$, column i gives the proportion surviving from age i to age $i+1$. The remaining entries are 0.

The population variation is described by

$$\tilde{N}_{t+1} = \tilde{P}(\tilde{N}_t) \tilde{N}_t + \tilde{E}_t + 1, \tilde{N}_0 = \underline{0}. \quad (1)$$

The population size at time t is

$$N_t = \underline{1}' \tilde{N}_t \quad (2)$$

with $\underline{1}$ the unit vector.

The complete trajectory of the population may be projected from the sequence of entrants, E_t , if the survival matrix $\tilde{P}(\cdot)$ is given. The death series is given by

$$D_t = N_{t-1} - N_t + E_t. \quad (3)$$

These equations do not represent a complete system for determining future population sizes from current ones. We still need an expression for tomorrow's entrants E_{t+1} in terms of the population history:

$$E_{t+1} = f(\tilde{N}_t, \tilde{N}_{t-1}, \dots). \quad (4)$$

Nicholson's assumptions about his experiments correspond to the hypotheses that $\tilde{P}(\tilde{N}_t)$ is a constant matrix and that $f(\tilde{N}_t)$ is a nonlinear function which tends to zero with increasing population size.

Models of this kind for experiments similar to Nicholson's were studied by Wu (1976). He conducted population experiments with blowflies, which attempted to realize a model in which competition was within a single cohort during the larval stage of the insect. He measured, independently, the mortality parameters and the function (4) describing emergences for the blowflies on which his experiments were conducted. Wu carried out simulations and found them to present a similar aspect of periodicity and irregularity as the experiments. Indeed, in these experiments there is good quantitative agreement between the data and the model.

With Nicholson's experiments, estimates of the model parameters must be based upon the population data itself and independent experiments

testing the model's assumptions cannot be done with the same flies. Ipakchi et al (1980) have investigated deterministic models for Nicholson's data. They estimated the model parameters by no criteria other than producing final simulations which gave qualitatively the correct visual appearance. In this paper we attempt to investigate Nicholson's data in a more systematic fashion.

Note that models can produce simulations which appear irregular or "chaotic" despite the fact that they are deterministic (Guckenheimer, et al, 1977). Thus it is a reasonable hypothesis that the aperiodicity of Nicholson's data is primarily a consequence of deterministic causes. The underlying dynamical system described by equations (1) and (4) seems to be one which possesses "sensitivity to initial conditions"; individual trajectories diverge from one another with increasing time. Future asymptotic behavior can be predicted only in a statistical sense. Our eventual aim is to assess the validity of this hypothesis, but adequate tests to do so have yet to be developed. We begin here by examining the statistics of Nicholson's data in order to determine whether his assumptions are consistent with the experimental results. Our analysis will show that modifications to the deterministic model should be made to allow for density dependent mortality.

In the remainder of the paper we shall focus upon the relationship between the death series D_t and the population series N_t . This is an important step in reconstructing the age structure \tilde{N}_t of the population from the experimental data E_t, D_t . Without a model for the mortality of individuals of different ages, one cannot recover an estimate of the trajectory of the population through the phase space of the deterministic model. The aggregate data for N_t must be split into age classes to obtain \tilde{N}_t . As noted above, Nicholson assumed that adults were well supplied with the resources of survival so that per capita mortality should have been independent of population size. This assumption is embodied in a deterministic model with constant matrix \tilde{P} . Let us turn now to an analysis of the data via stochastic models which call into question this independence of \tilde{P} on \tilde{N}_t .

5. A STOCHASTIC APPROACH. In any real population the age structure vector $N_t + 1$ will not be uniquely determined by values of $E_t + 1$ and N_t , as equations (1) and (4) imply. Rather it is appropriate to replace equation (1) by

$$N_t + 1 = \mathcal{P}(N_t) N_t + E_t + 1 + \xi_t + 1 \tag{6}$$

with $\xi_t + 1$ an error variate. Supposing $E(\xi_t + 1 | N_t) = 0$, and arguing conditionally on the emergence series, equation (1) is replaced by

$$E(N_t + 1 | N_t) = \mathcal{P}(N_t) N_t + E_t + 1.$$

The extent to which the population will follow a trajectory determined by iterating equation (1) will depend on the stochastic variability of ξ_t .

Given only the data for total emergences and total adult population, (E_t, N_t) , $t = 1, \dots, T$ we shall now present a method for forecasting the population size and estimating both the age and density dependent survival matrix and the population age-structure vector N_t . We emphasize that the method is not restricted to stationary age distributions.

Suppose that the survival matrix depends on N only through the population size $N = \mathbf{1}' N$. Then the model takes the form

$$N_t + 1 = \mathcal{P}(N_t) N_t + E_t + 1 + \xi_t + 1 \tag{6}$$

$$N_t = \mathbf{1}' N_t. \tag{7}$$

In control systems engineering terminology equation (6) is called the state equation and (7) the observation equation. The methodology of that field suggests an approach to the problems of forecasting and estimation.

Were the matrix $\mathcal{P}(N_t) = \mathcal{P}_t$ nonrandom and the process ξ_t Gaussian white noise with covariance matrix \mathcal{V}_t , then one could use the Kalman-Bucy filter:

$$\begin{aligned} E\{N_{t+1} | N_u, u \leq t + 1\} &= \mathcal{M}_{t+1} \\ &= \mathcal{P}_t \mathcal{M}_t + E_{t+1} + A_{t+1} (N_{t+1} - E_{t+1}) \mathcal{P}_t^{-1} \mathcal{P}_t / \mathbf{1}' A_{t+1}, \\ \mathcal{V}_{t+1} &= \mathcal{P}_t \mathcal{V}_t \mathcal{P}_t' - A_{t+1} \mathbf{1}' A_{t+1}' / \mathbf{1}' A_{t+1}, \end{aligned} \tag{8}$$

with

$$\begin{aligned} \mathcal{M}_0 &= 0, \mathcal{V}_0 = 0, \mathcal{V}_t = \text{var}\{N_u | N_u, u \leq t\}, \\ A_{t+1} &= \mathcal{V}_t + \mathcal{P}_t \mathcal{V}_t \mathcal{P}_t' = \text{var}\{N_{t+1} | N_u, u \leq t\}. \end{aligned} \tag{9}$$

(See Liptser and Shiriyayev (1978), page 66.)

The above expressions assume E_t, \mathcal{V}_t to be known. In the case that they are unknown but can be parametrized so that the model is identifiable, the parameters may be estimated by maximizing the log likelihood

$$-1/2 \sum_{t=2}^T \log \sigma_t^2 - 1/2 \sum_{t=2}^T (N_t - \mathbf{1}' \mathcal{P}_{t-1} N_{t-1} - E_t)^2 / \sigma_t^2 + C \tag{10}$$

with C a constant, $\sigma_t^2 = \mathbf{1}' \mathcal{V}_{t-1} \mathbf{1} = \text{var}\{N_t | N_u, u \leq t-1\}$ subject to the conditions (8), (9). (See for example Gupta and Mehra (1974).)

Theorem 13.4 of Liptser and Shiriyayev (1968) shows that the expressions (8), (9) continue to hold when $E_t = \mathcal{P}(N_t); \mathcal{V}_t = \mathcal{V}(N_t)$. However with respect to the problem under consideration in this paper, a substantial departure from the assumptions is caused by the undoubted variation in $\mathcal{V}(\cdot)$ with N_{t-1} not just with N_{t-1} . (The departure from a Gaussian distribution is expected to be less important.) Below, a bootstrap procedure will be developed for dealing with this difficulty.

We have assumed that the survival matrix depends only on the population size N . Now, suppose that its functional form is known up to a finite dimensional parameter, θ . Specifically write it as $\mathcal{P}(N_t; \theta)$.

The updating equation (8) is not appropriate since $\mathcal{V}(\cdot)$ depends on the full population vector N . An intuitively reasonable alternative is

$$\mathcal{M}_t + 1 - E_t + 1 = \mathcal{P}(N_t; \theta) \mathcal{M}_t (N_t + 1 - E_t + 1) / (\mathbf{1}' \mathcal{P}(N_t; \theta) \mathcal{M}_t) \tag{11}$$

wherein the projected values are updated proportionately, to yield the measured total $N_t + 1$. Equation (11) may be obtained from (8) by choosing A_{t+1} proportional to $\mathcal{P}(N_t) \mathcal{M}_t$. (Were the entries of $(N_t + 1)$ given $N_u, u \leq t$ independent Poisson variables then $A_{t+1} = \mathcal{P}(N_t) \mathcal{M}_t$.)

Empirical evidence, to be presented later, suggests that it is reasonable to take σ_t in equation (10) proportional to N_{t-1} . Hence maximizing expression (10) comes down to minimizing

$$\begin{aligned} &\sum_{t=2}^T (N_t - \mathbf{1}' \mathcal{P}(N_{t-1}; \theta) \mathcal{M}_{t-1})^2 / N^{t-1} \\ \text{or equivalently} &\sum_{t=2}^T (\mathcal{O}_t - \sum_{l=1}^I q_{l,t-1} (N_{t-1}; \theta)^m_{l-1, t-1})^2 / N^{t-1} \end{aligned} \tag{12}$$

where $q_i(N; \theta) = \text{Prob}\{\text{individual aged } i, \text{ dies aged } i \text{ given population size } N\}$.

The data fitting procedure we employ below can be described as follows:

- 1) Evaluate the \hat{m}_t via expression (11) employing a trial value of θ .
- 2) Determine an estimate of θ by minimizing expression (12) using the evaluated \hat{m}_t .
- 3) Take the estimate of θ as the new trial value in 1). Iterate until the trial value and the estimate becomes the same.

The values m_t evaluated via expression (11) at the final stage, provide estimates of the age structure of the population throughout the time period of observation. They will be used to fit an age and size dependent fertility function.

6. RESULTS. Two death rate models were fitted to the adult data:

(a) an additive model

$$q_x, N, N_{-1}(\theta) = \alpha_x + \beta N + \gamma N_{-1} \quad (13)$$

and (b) a multiplicative model

$$q_x, N, N_{-1}(\theta) = 1 - (1 - \alpha_x)(1 - \beta N)(1 - \gamma N_{-1}). \quad (14)$$

Here x is age, N is the population size at beginning of the current interval and N_{-1} the population size at the beginning of the preceding interval. The first model was selected because of its simplicity, and the second because it corresponds to independent age and size mortality forces operating on the flies.

The parameter values $\beta, \gamma = 0$ correspond to the case of no density dependence. If $\alpha_x = \alpha$ for all x , then age plays no role in mortality.

Figures 4 and 5 show $q_x, N, N_{-1}(\theta)$ for the two models in the case of a small population $N, N_{-1} = 1$, a large population $N, N_{-1} = 8000$, an increasing population $N = 5000, N_{-1} = 2000$ and a decreasing population $N = 2000, N_{-1} = 5000$.

In terms of the criterion (12), the product model (14) provides the better fit, (see Table 2), however the lower three curves of the two figures are almost identical.

The dominant feature is the apparent substantial dependence of death rate on the population size; contradicting Nicholson's desired experimental setup.

Table 2 provides a listing of various of the models that were fit to the data. The S corresponding to "persistence" is defined as

$$\sum_{t=2}^T (D_t - \hat{D}_{t-1})^2 / N_{t-1}^2.$$

If one views the problem as one of developing a predictor for the death series, this S measures the adequacy of predicting by the most recent value. The case of α_x corresponds to (Nicholson's desired) dependence of mortality on age alone. The case $\alpha + \beta N$ corresponds to random age-independent mortality.

Table 2
S for various models

q_x, N, N_{-1}	S
persistence	13.964
α	7.011
α_x	6.688
$\alpha + \beta N$	5.605
$1 - (1 - \alpha_x)(1 - \beta N)$	3.894
$\alpha_x + \beta N$	3.843
$\alpha_x + \beta N + \gamma N_{-1}$	3.609
$1 - (1 - \alpha_x)(1 - \beta N)(1 - \gamma N_{-1})$	3.531
ARMA (1, 1)	3.001

10 age intervals

7. DIAGNOSTICS. Figure 6a provides a graph of the observed death series, D_t and the fitted series \hat{D}_t (one-step predictor), based on the product model of the previous section. The two series are generally quite close together. Even split peaks are traced fairly accurately.

Figure 6b plots the values $(D_t - \hat{D}_t) / N_{t-1}$ of weighted residuals between the model and the data. This graph makes it clear that a fair amount of autocorrelation remains in the error. If the model fit the data very well,

such autocorrelation would not be present. From the stand-point of prediction there is information remaining in the data that has not been utilized.

Autoregressive moving average models were fit to this residual series and an ARMA (1, 1) scheme was found to fit fairly well. S was further reduced by this procedure as shown in Table 2.

Figures 7 and 8 provide scatter diagrams of the values $(D_t - \hat{D}_t, N_{t-1})$ and $((D_t - \hat{D}_t) / N_{t-1}, N_{t-1})$. The wedging apparent in Figure 7 suggests strong dependence of the residual variance on the population size. This dependence is still present when the residuals are normalized by $\sqrt{N_{t-1}}$. It is not apparent in Figure 8, suggesting that the standard error may be taken as proportional to the population size. This remark is the source of the N_{t-1}^2 term in S of (12). Parenthetically, were the variation in the numbers dying multibinomial, then one would have

$$\text{var} \{ D_t | N_t \} = \sum_x N_t x q_x (1 - q_x).$$

These values, when estimated, are considerably smaller than the empirical values $(D_t - \hat{D}_t)^2$. The extra variation in the population may be ascribed to, among other things, the variable sex ratio in the population and the inherent variability between individuals of the population. Taking note of the ages of individuals and the population sizes of the preceding two time periods leaves a fair amount of variation.

8. DISCUSSION. A variety of things become possible once the death probability function q has been estimated. Foremost among these is the construction of the age structure $\hat{N}_{x,t}$, = the estimated number aged x at time t . These values are important, for example, in understanding the dependence of birth intensity on age and population size. This was the principal focus of Nicholson's experimental design in this case.

Figures 9a, b show the $\hat{N}_{x,t}$: initially each of these series oscillates as successive cohorts march along in time. Eventually the numbers in the older age classes appear to stabilize somewhat. Further, it is clear that in the later stages of the experiment very few insects were surviving to a very old age. Note that the population is not becoming stable.

Figure 10 makes this last remark more apparent. It is a graph of the

average age of the population as a function of time. After an initial period of strong oscillations, this function settles down; moreover the population is apparently becoming younger.

It was remarked earlier that the flies were apparently being selected to lay eggs at low protein levels, as the experiment progressed. Figure 10 shows that it is also possible that this change in egg laying behavior might have been due to younger flies being more effective at egg laying.

9. FURTHER WORK. Quite a number of interesting problems remain to be studied. These include:

- a) the statistical properties of the estimates,
- b) estimation of the birth rate function and other parameters of the complete life cycle,
- c) the relevance, if any, of the deterministic dynamic behavior of the mean values,
- d) the statistical properties of forecasted population sizes based on the fitted model,
- e) the form of the optimal controller (timing, amount, age-dependence),
- f) the improvement, if any, resulting from the use of alternate estimates of the age structure (e.g. based on all, not just past data),
- g) developing nonparametric estimates of the dependence of the vital rates on age and population size.

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APPENDIX

Table 3

EGGS	NONEMERGING EGGS	EMERGING	DEATHS	TOTAL	EGGS	NONEMERGING EGGS	EMERGING	DEATHS	TOTAL	EGGS	NONEMERGING EGGS	EMERGING	DEATHS	TOTAL
0	0	949	0	949	26	5	1270	2186	3952					
0	0	4	10	14	30	0	30	40	70					
0	0	0	53	53	321	0	0	10	331					
2149	121	0	172	1328	392	18	410	521	912					
4827	458	0	107	5463	333	10	343	443	774					
2024	120	0	149	2393	1369	15	1384	165	3008					
3373	176	0	102	3649	1292	19	1311	163	2455					
446	0	1763	108	2241	977	92	1069	17	1996					
133	2	447	150	600	1336	48	1384	51	1435					
17	1	752	2005	2777	450	152	602	227	877					
58	0	1953	464	2417	3057	41	3098	438	3536					
0	10	2419	3056	5475	166	1	167	540	707					
6	1	1966	2266	4233	1071	4	1075	1092	2173					
133	2	132	120	265	27	0	27	127	154					
0	0	36	120	156	70	0	70	127	197					
25	0	85	121	206	100	10	110	171	271					
0	0	17	34	51	364	18	382	171	553					
58	30	0	37	95	115	0	115	150	265					
461	111	5	163	640	364	10	374	150	524					
1638	47	0	102	1787	106	2	108	168	274					
1524	266	41	107	1938	80	0	80	182	262					
2339	10	0	60	2449	303	0	303	472	775					
1423	0	424	34	1867	472	16	488	523	911					
1389	220	1511	49	3220	502	172	674	542	1216					
1617	7	1317	160	2841	5050	422	5472	179	6264					
936	7	2016	61	2897	3020	101	3121	162	3483					
19	4	148	102	273	1461	0	1461	173	1634					
0	8	1884	184	2072	1526	174	1700	173	1873					
0	0	2856	1859	4715	802	96	898	1016	1914					
0	0	469	1291	1760	568	338	906	311	1217					
0	0	955	1211	2166	1244	0	1244	75	1319					
1	2	157	197	356	1662	145	1807	187	2094					
8	1	45	37	50	5050	432	5482	179	6061					
71	0	0	22	93	3020	101	3121	162	3483					
578	0	0	116	694	1461	0	1461	173	1634					
6537	51	77	146	7205	1526	174	1700	173	1873					
1296	4	45	77	1422	526	48	574	542	1076					
451	11	0	47	519	136	10	146	1016	1914					
1664	44	185	35	2008	156	19	175	75	233					
358	302	0	68	660	247	0	247	187	434					
81	1	1771	1075	3549	623	0	623	1308	1931					
62	5	1607	1075	3794	779	0	779	162	941					
39	2	1674	1075	3851	478	0	478	472	950					
0	0	190	1146	1336	1075	0	1075	542	2057					
0	0	70	1146	1216	1075	0	1075	916	2091					
10	1	1501	1598	3100	1075	0	1075	1061	2136					
172	15	1771	216	3989	416	44	460	1071	1531					
626	108	1607	216	3557	1319	112	1431	276	1715					
1216	108	1674	1075	3851	1319	135	1454	295	1749					
2109	25	190	1146	3220	1926	90	2016	172	2186					
2360	102	31	146	2639	975	76	1051	602	1653					
2328	102	31	146	2639	1075	0	1075	1061	2136					
744	130	33	24	931	616	28	644	108	754					
745	900	1072	160	2817	699	252	951	57	1008					
2019	167	174	160	2350	1908	147	2055	126	2181					
672	0	0	108	780	352	62	414	140	554					
0	0	0	108	108	472	60	532	107	639					
0	0	0	108	108	131	0	131	102	233					
33	5	1052	412	1489	150	3	153	108	261					

EGGS	NONEMERGING EGGS	EMERGING	DEATHS	TOTAL	EGGS	NONEMERGING EGGS	EMERGING	DEATHS	TOTAL	EGGS	NONEMERGING EGGS	EMERGING	DEATHS	TOTAL
1766	155	147	105	701	1178	90	1126	512	3203					
2091	302	143	182	1762	1601	110	1491	861	2706					
2577	302	528	108	1188	1717	196	909	695	2711					
2333	293	694	158	1778	1031	90	323	737	2178					
1388	158	178	285	760	2573	280	196	737	2352					
5915	144	144	730	2519	2625	1507	1507	717	3567					
124	13	2440	1312	4851	1745	143	1599	670	3155					
110	2	1628	2423	4851	1321	182	2139	812	3155					
110	2	2180	1657	5374	1942	130	2149	963	3771					
65	15	1235	1696	4713	433	435	2425	1873	3771					
126	11	4323	1669	7367	2009	194	2016	1377	4553					
71	4	806	2721	3235	254	19	2016	254	3801					
71	4	46	1706	2639	2518	19	641	1959	3501					
339	31	1	1264	2417	2404	228	1579	1959	3501					
941	152	1	1159	2404	1652	138	1271	1866	4365					
1709	174	61	493	1768	2657	1571	134	1244	3394					
766	51	115	142	479	4169	484	1526	1889	3869					
6267	570	62	166	402	2525	165	165	11	782					
2709	550	397	47	254	1492	188	188	11	2677					
15220	6355	1057	61	604	1197	346	1603	250	4600					
1166	94	1762	175	1342	2236	338	109	980	5119					
756	66	1161	1057	3228	819	60	1599	1599	5399					
1254	94	1075	584	3228	1238	59	1287	1281	4592					
206	16	2873	4267	7433	2082	84	2131	1226	4831					
233	47	1412	3333	7519	322	252	2216	1339	4630					
1024	76	5092	4954	6956	164	174	1474	195	4819					
1185	11	1218	2480	5334	460	642	501	175	3664					
112	11	834	134	134	416	416	1060	1102	3016					
521	43	605	421	1099	271	271	1779	131	3016					
287	36	943	1356	2442	199	402	1510	131	3016					
1904	67	46	1567	1901	354	354	268	1390	4168					
11377	145	431	499	1190	282	36	268	2682	5446					
976	165	161	395	1422	437	374	5115	2882	5477					
2660	234	165	525	1488	118	108	1907	879	2579					
205	44	492	224	1269	1466	115	2606	2606	7233					
274	1790	477	298	1569	270	122	1108	2903	6484					
1209	1	1888	266	380	1120	120	2394	1575	5713					
663	45	428	65	280	142	15	2062	1325	5713					
397	16	2652	153	404	212	102	2062	2666	6604					
725	48	1828	188	494	217	102	420	1420	6604					
14	3	1076	556	313	217	291	538	1420	6604					
14	12	1566	156	402	282	255	230	1420	6604					
14	12	47	153	404	217	291	538	1420	6604					
14	12	1828	188	494	217	102	420	1420	6604					
14	12	1076	556	313	217	291	538	1420	6604					
14	12	1566	156	402	217	102	420	1420	6604					
14	12	47	153	404	217	291	538	1420	6604					
14	12	1828	188	494	217	102	420	1420	6604					
14	12	1076	556	313	217	291	538	1420	6604					
14	12	1566	156	402	217	102	420	1420	6604					
14	12	47	153	404	217	291	538	1420	6604					
14	12	1828	188	494	217	102	420	1420	6604					
14	12	1076	556	313	217	291	538	1420	6604					
14	12	1566	156	402	217	102	420	1420	6604					
14	12	47	153	404	217	291	538	1420	6604					
14	12	1828	188	494	217	102	420	1420	6604					
14	12	1076	556	313	217	291	538	1420	6604					
14	12	1566	156	402	217	102	420	1420	6604					
14	12	47	153	404	217	291	538	1420	6604					
14	12	1828	188	494	217	102	420	1420	6604					
14	12	1076	556	313	217	291	538	1420	6604					
14	12	1566	156	402	217	102	420	1420	6604					
14	12	47	153	404	217	291	538	1420	6604					
14	12	1828	188	494	217	102	420	1420	6604					
14	12	1076	556	313	217	291	538	1420	6604					
14	12	1566	156	402	217	102	420	1420	6604					
14	12	47	153	404	217	291	538	1420	6604					
14	12	1828	188	494	217	102	420	1420	6604					
14	12	1076	556	313	217	291	538	1420	6604					
14	12	1566	156	402	217	102	420	1420	6604					
14	12	47	153	404	217	291	538	1420	6604					
14	12	1828	188	494	217	102	420	1420	6604					
14	12	1076	556	313	217	291	538	1420	6604					
14	12	1566	156	402	217	102	420	1420	6604					
14	12	47	153	404	217	291	538	1420	6604					
14	12	1828	188	494	217	102	420	1420	6604					
14	12	1076	556	313	217	291	538	1420	6604					
14	12	1566	156	402	217	102	420	1420	6604					
14	12	47	153	404	217	291	538	1420	6604					
14	12	1828	188	494	217	102	420	1420	6604					
14	12	1076	556	313	217	291	538	1420	6604					
14	12	1566	156	402	217	102	420	1420	6604					
14	12	47	153	404	217	291	538	1420	6604					
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14	12	47	153	404	217	291	538	1420	6604					
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14	12	1076	556	313	217	291	538	1420	6604					
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14	12	1076	556	313	217	291	538	1420	6604					
14	12	1566	156	402	217	102	420	1420	6604					
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14	12	1076	556	313	217	291	538	1420	6604					
14	12	1566	156	402	217	102	420	1420	6604					
14	12	47	153	404	217	291	538	1420	6604					
14	12	1828	188	4										

EGGS	NONEMERGING EGGS	EMERGING	DEATHS	TOTAL
2293.	262.	72.	917.	936.
1822.	76.	571.	609.	698.
1926.	114.	565.	303.	383.
3428.	413.	2259.	346.	3386.
3465.	383.	2182.	1031.	4547.
3826.	1011.	1475.	1199.	4823.
1711.	175.	1479.	1332.	4970.
1019.	96.	1624.	1684.	4940.
1952.	65.	2266.	1392.	4940.
1767.	238.	1703.	5172.	7626.
1351.	178.	4769.	2325.	4487.
917.	18.	4361.	3071.	6901.
227.	40.	1240.	2765.	6766.
456.	47.	1277.	2876.	5165.
638.	92.	1162.	777.	2919.
609.	79.	1273.	3417.	5417.
1520.	152.	636.	699.	3162.
4004.	505.	24.	881.	2523.
3131.	276.	572.	807.	2230.
2877.	200.	357.	692.	1955.
2533.	200.	625.	644.	1936.
4535.	432.	1053.	605.	2366.
4127.	844.	2930.	629.	7290.
1759.	300.	3609.	1500.	8306.
2899.	506.	2282.	2511.	8027.
3393.	628.	1884.	2901.	7010.
3257.	510.	3451.	2392.	8943.
3485.	600.	3192.	4514.	6185.
5895.	516.	2070.	3040.	5766.
5907.	2704.	2253.	149.	6214.
3671.	1522.	7613.	149.	7007.
0.	0.	3094.	2201.	6154.
0.	0.	3250.	2615.	9043.
0.	0.	3510.	4485.	6683.
0.	0.	2319.	3747.	6103.
0.	0.	4967.	3783.	6603.
0.	0.	2483.		

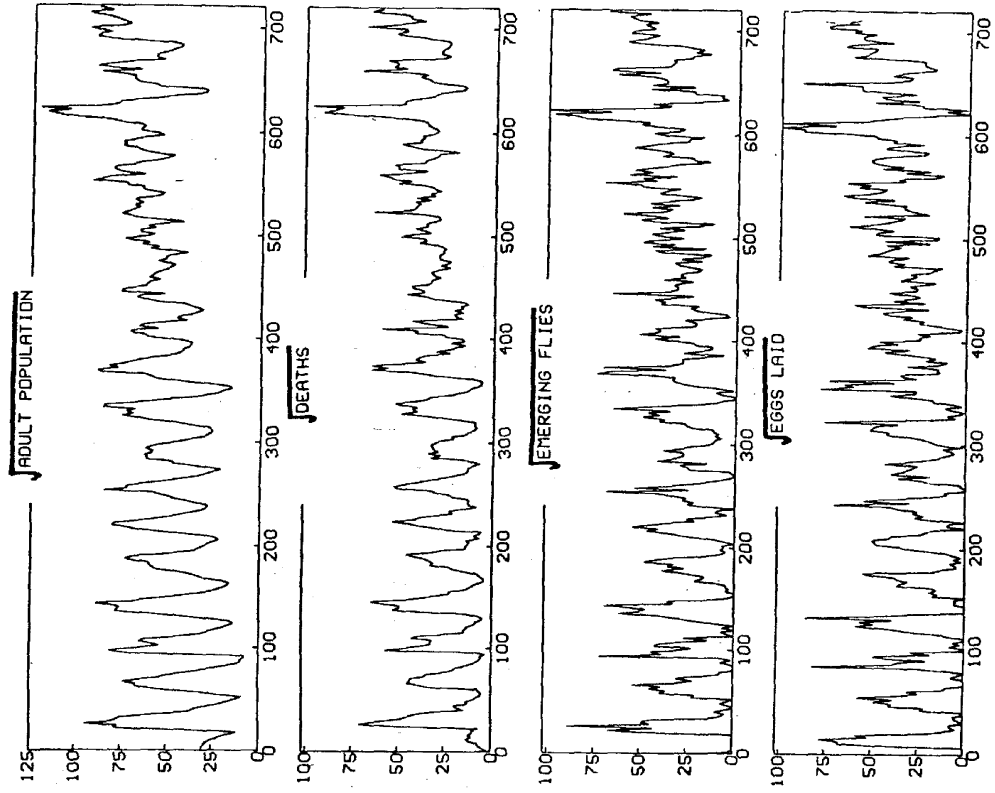


FIGURE 1

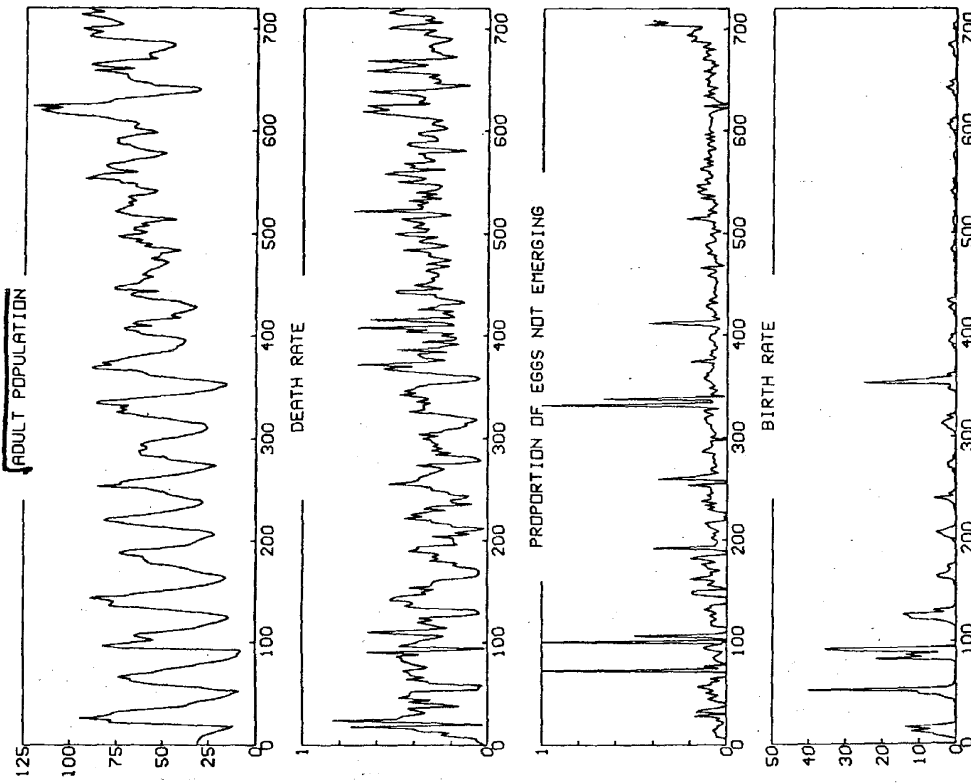


FIGURE 2

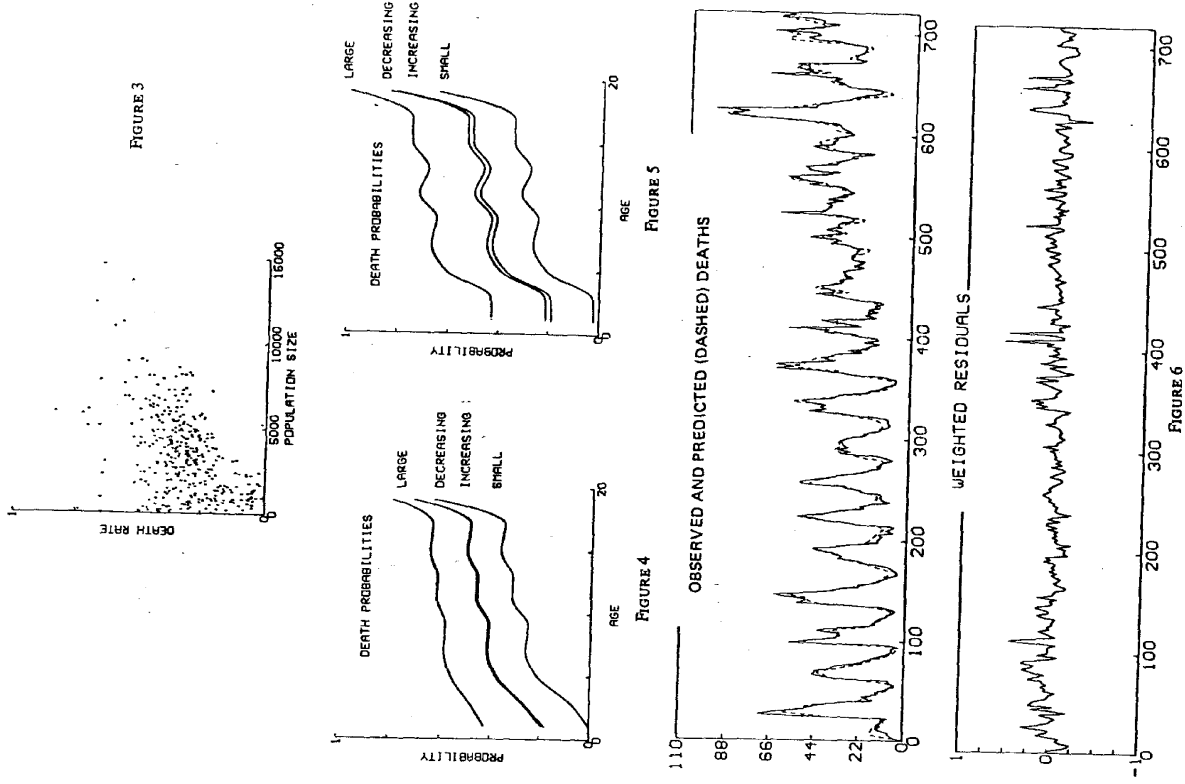


FIGURE 3

FIGURE 4

FIGURE 5

FIGURE 6

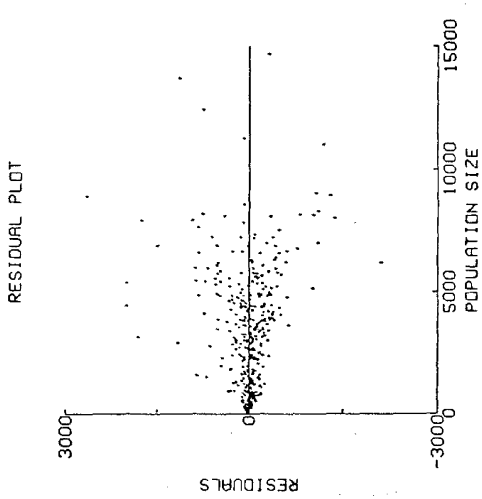


FIGURE 7

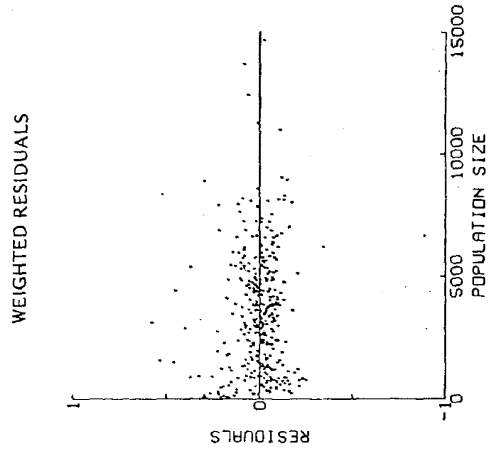


FIGURE 8

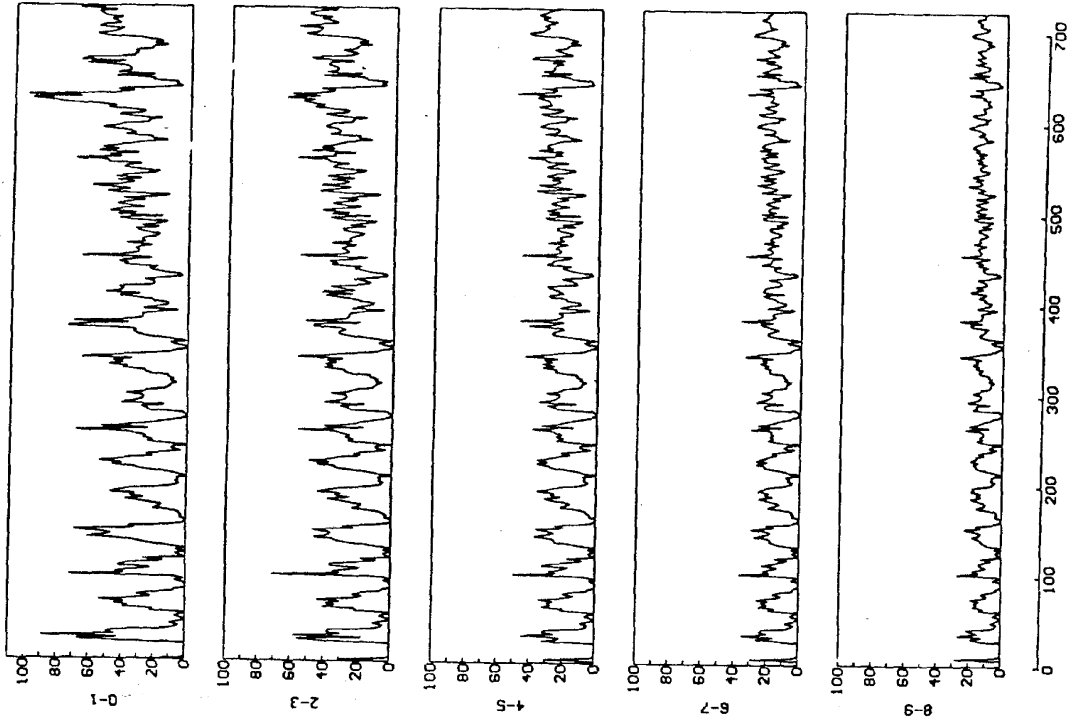


FIGURE 9a

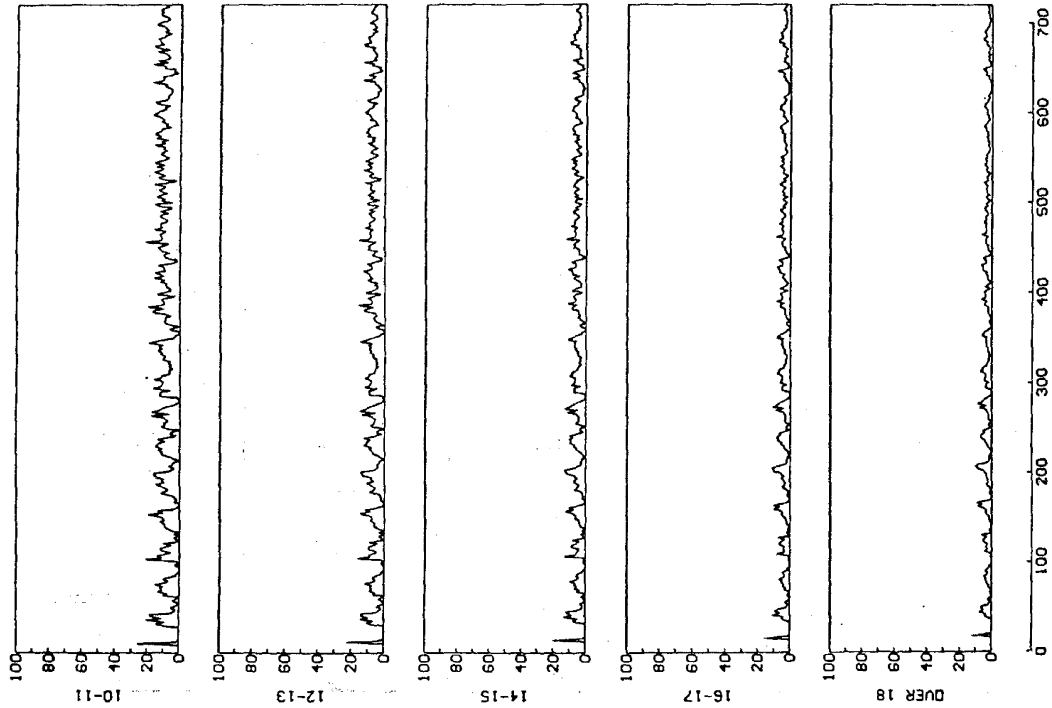


Figure 9b

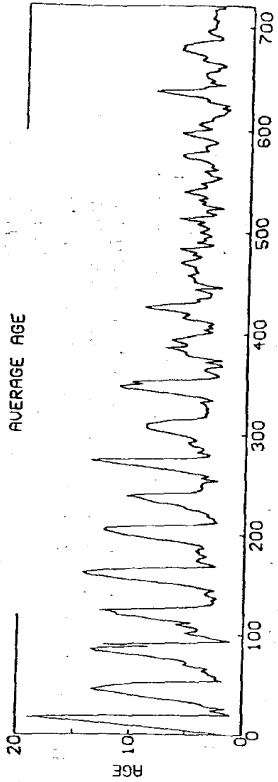


FIGURE 10

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