UNIVERSITY OF STRATHCLYDE

"LONG TERM CHANGES IN A LABORATORY INSECT POPULATION"

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Thesis submitted in partial fulfilment of the
Degree of Doctor of Philosophy

1985

ABSTRACT

The work reported in this thesis falls into two distinct sections: in chapters 2-4 a simple, continuous-time, birth and death model is employed to explain the gross dynamic features of Nicholson's (1957) control blowfly population data; in chapters 5 and 6 the emphasis is upon investigating how age affects blowfly vital rates.

In chapter 2, model specific parameter estimates through time are made and the conclusion is reached that selection for competitive resilience is taking place during the blowfly experiments.

In chapters 3 and 4, the quantitative and qualitative consequence of the time-dependent parameter estimates are considered, both deterministically and with noise incorporated. It is made clear that the alteration in dynamic behaviour observed in Nicholson's control population is consistent with a shift in the vital rates occurring so as to cause stabilization (i.e. a shift from behaviour characteristic of the unstable region of parameter space to that of the stable region). Given the time-dependent parameter estimates, the model provides a satisfactory simulation of the data.

In chapters 5 and 6, recent data of Readshaw and van Gerwen's (1983) is considered. These data are of blowfly survival and fecundity for populations maintained at various, constant densities. In chapter 5, the dependence of adult death rate on age and density is unravelled and the strong dependence of mortality upon age is made clear. A necessary by-product of the investigation of density dependent mortality is an inferred, time-dependent age-structure of the control population.

In chapter 6, the time-dependent maturation times of the control population are estimated. The estimates are definitely erroneous, this being due to no account being taken of the selection for competitive resilience previously demonstrated. Despite the maturation time estimates being wrong, the results are then used, in conjunction with a fit to development-dependent fecundity data, in an attempt to determine how age and density jointly govern blowfly fecundity.

ACKNOWLEDGMENTS

I would like to take this opportunity to express gratitude to the following people: Drs Roger Nisbet and Bill Gurney for their patience, support and irreprovable supervision during my Studentship, Dr Peter Maas for occasional but much appreciated help with the computers, Steve Blythe for help, advice and friendship, Professor Edward Eisner for support when I needed it, The Science and Engineering Research Council for my grant and last, but certainly not least, Morag, for everything.

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CHAPTER ONE

1. INTRODUCTION

1.1 PROEM

Ecologists are interested in why natural populations fluctuate; this interest may be motivated by a desire to control agricultural pests, fight transmitted diseases, conserve wild life, manage natural resources such as fish stocks or 'merely' a desire to understand basic ecological principles. Studying population fluctuations under natural conditions is, however, difficult and understanding the underlying causes of fluctuations is awkward due to the many (and often unrealised) confounding factors encountered in the field. The study of natural populations is, of course, essential to comprehending how populations interact in the real world but the attempt to understand basic principles of population dynamics is often undertaken under simplified and well-controlled laboratory conditions.

Insect populations have been studied extensively for a long time, due primarily to the abundance of insect pests in agricultural and economic settings. Insects, though, are also relatively easy creatures to study in the laboratory and thus make good 'guinea-pigs' in trying to understand general principles of population regulatory mechanisms.

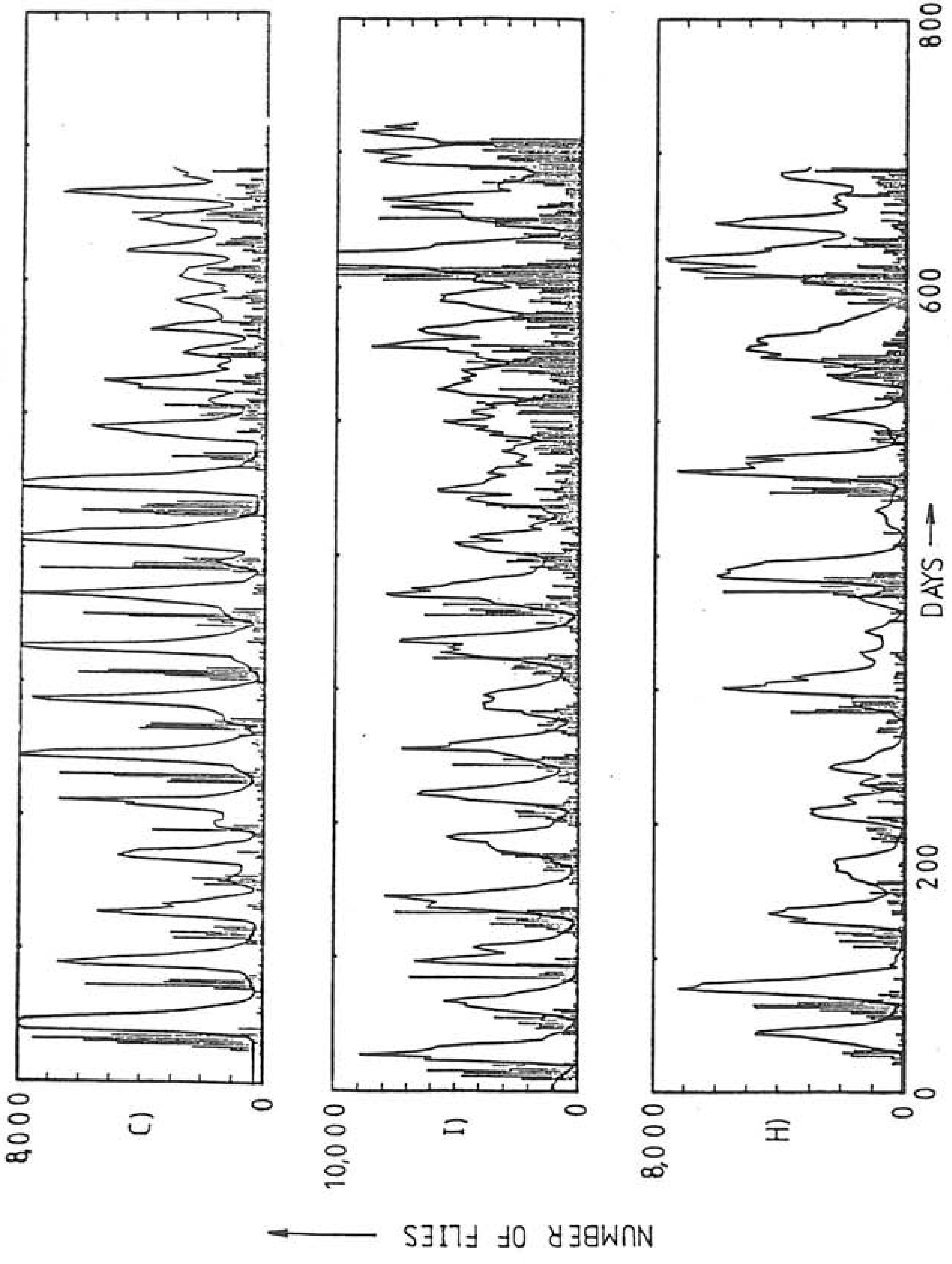
There are many well-known and oft-quoted laboratory insect population studies examining either single or mixed cultures under various experimental conditions. The duration and sampling frequency of such experiments also varies greatly (e.g. Pratt, 1943 on *Daphnia magna* for 100 days sampling every 2 days; Crombie, 1945 on the beetle *Rhizopertha* for about 300 days sampling every 2 weeks; Birch, 1953 on the weevil *Calandra oryzae* for over 90 weeks and sampling once a month; Huffaker, 1958 on a predatory mite and its prey for 7 months, sampling weekly; Huffaker, Shea and Herman, 1963 on the same system but for 60 weeks; Park, Leslie and Mertz, 1964 on *Tribolium castaneum* for 800 days and sampling every month; Lloyd, 1965, 1968 on *T.castaneum* for 35 weeks and sampling each week). Some of the best known of all such population studies, however, are those carried out by Nicholson (1950, 1954a, 1954b, 1957, 1960) using the Australian sheep blowfly *Lucilia cuprina* as an experimental animal in attempts to elucidate fundamental mechanisms of animal population regulation. These studies were not only extensive in scope but lasted for long periods (up to 722 days) and were sampled, uninterrupted, at a high frequency (every 2 days). The length and high sampling frequency of these experiments provide particularly good data with which to work and it is the longest of Nicholson's experiments (1957, Fig. 8) that are the subject of investigation in this thesis.

1.2 NICHOLSON'S EXPERIMENTS

The Australian entomologist A. J. Nicholson used the blowfly Lucilia cuprina (Wied.) as an experimental animal to investigate population oscillations caused by competition for food (1950), 'compensatory reactions' (1954a) and the self-adjustment of populations to change (1957). It is one particular dataset (see Fig. 1.1I) from this later paper (Nicholson, 1957, Fig. 8I) that forms the main target of investigation in this thesis. Hereafter, all references to 'the data' or 'the experiment' refer to this experiment.

An outline of the experiment is given in Nicholson (1957, p163) Brillinger, Guckenheimer, Guttorp and Oster (1980 p67) provide the following description:

"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 eggs hatched overnight. Adult food consisting of .4 gram ground liver, dried in a desicator, 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."


8,000
C)
0
10,000
I)
0
8,000
H)
0
0
200
600
800
DAYS →
← NUMBER OF FLIES

Unfortunately, Nicholson (1954b, 1957, 1960) never gives any more details about the experimental design than those reported by Brillinger et al (1980). The following comments, though, are useful in understanding the experiment.

Carbohydrate (supplied as sugar) and water are essential to adult blowflies and larvae - without both, they cannot long survive (Rasso and Fraenkel, 1954). Nicholson intended, by supplying carbohydrate and water on an ad lib basis, that adult mortality should not be influenced by density. Protein (supplied as ground liver) is not necessary for survival but is necessary for successful reproduction (Evans, 1936; Dorman et al, 1938; Hobson, 1938; Rasso and Fraenkel, 1954; Harlow, 1956; Orr, 1964; Roberts and Kitching, 1974; See Wu, 1978 for review.)

Protein is not only essential in reproduction for nutritional reasons but also (Nicholson 1960) because blowflies lay their eggs on it in respnse to having taken a protein meal. Although never explicitly stated in any of Nicholson's papers, the counting of eggs would thus be greatly facilitated as they would all be contained in the liver which was replaced daily. A further inference about the experimental procedure is that, in order to count the number of flies that finally emerged from eggs laid on any particular day, each daily batch of eggs must have been kept separate from other batches and only the adult flies (or possibly pupae) transferred to the main population cage. Such an inferred experimental procedure is similar to that employed by Wu (1978) when replicating Nicholson's experiments.

The experiment described above was an 'adult food limited' (afl) experiment. Nicholson (1954b) also performed experiments in which larval food was limited whilst adult food was supplied ad lib; these experiments, which will be mentioned later, will be termed 'larval food limited' (lfl).

The 1954b afl and lfl experiments were conducted to investigate the mechanism of population balance. The 1957 experiment, however, was in fact a control run. Nicholson performed eight similar runs in an attempt to study the 'frequency response' of the system to a periodic driving force; in future these runs will be referred to as the 'driven' experiments. The results of two of these runs, in which protein input varied from 50 to 500 mg d^{-1} with a 20 or 80 day period, are shown in Fig. 1.1 (C & H respectively).

Nicholson (1954b, 1957, 1960; see Clark, Geier, Morris and Hughes, 1967, for review) explained the violent oscillations seen in the blowfly experiments in terms of density-dependent fertility and the lag (egg to adult development time) inherent in the blowfly life-cycle. Apart from explaining the basic oscillatory behaviour, Nicholson also invoked the observation that the age-structure was changing over each population cycle in order to explain certain fine-details such as double or triple peaking (Nicholson, 1954b legend to Fig. 3; Readshaw, 1981) on the population fluctuations.

Nicholson (1957, 1960) explained the change in dynamic behaviour observed in Fig. 1.1 I around the four hundredth day, in terms of selection acting to produce flies capable of laying eggs in the absence of protein - i.e. a reduction in the level of 'scramble' competition (Nicholson 1954b; Varley, Gradwell and Hassell, 1973; Gurney, Blythe and Nisbet, 1980) which Nicholson considered to be the underlying cause of population oscillations (Nicholson, 1954b p19; see Maynard-Smith, 1974 pp 38-42). This explanation was supported by experimental evidence that post-experimental flies could, indeed, lay eggs in the absence, or near absence, of protein (Nicholson, 1957 p 171).

That Nicholson's (1957) 'driven' experiments (Fig. 1.1 C & H) synchronized, or phase-locked, with the 'driver' (i.e. the variable protein input rate) was taken by Nicholson as confirmation of his hypothesis (1933) that populations tend to conform to climatic change. Nicholson did not attempt to explain why the population subjected to a 20-day, variable protein-input rate (Fig. 1.1c) first of all cycled with a period precisely double that of the driver but then (from around the five hundredth day) exhibited a period equal to that of the driver.

1.3 A REVIEW OF PREVIOUS MODELLING OF NICHOLSON'S BLOWFLY POPULATION DATA

The wealth of information in Nicholson's data and the various possible mechanisms responsible for the observed population fluctuations were not the subject of mathematical enquiry until some 15-20 years after Nicholson's original publications. Beginning in 1973, however, until the present time, there has been a considerable amount of effort put into examining Nicholson's data or in using it as an example to support the notion that 'chaotic' (i.e. - c.f. Oster and Ipaktchi, 1978 - 'apparently random motion within a bounded attracting region'; see also e.g. May, 1974b; 1975; Li and Yorke, 1975; Kadanoff, 1983) behaviour might be common in Biological populations.

Much of the enquiry into Nicholson's experiments has focussed on characterising gross features of the data (e.g. how the population oscillations arise); effort has also been put into trying to understand how fine-detail arises. In this and the following section I shall consider both of these aspects.

May (1974a pp 100-102) and Maynard-Smith (1974 pp 38-42) consider Nicholson's (1954b) adult food limited experiment and both seek to explain the blowfly population dynamics using time-delayed, continous-time models. May considered the time-delayed logistic model (Hutchinson, 1948) and concluded that the population was limit-cycling - the limit-cycles being generated by the time-delayed regulatory mechanism (density-dependent fecundity) in the model. He estimated, based upon his analysis of the model, that the egg to adult development time should be 9 days. Despite the surprisingly good, qualitative fit to the data that May produced (see also Auslander, Oster and Huffaker, 1974), he recognized that the 'true' egg to adult development time was about 11 days (Nicholson, 1957 Fig. 6E). Maynard-Smith used a biologically more reasonable model with two free parameters (the time-delayed logistic has only one) but did not attempt a simulation of the data. Maynard-Smith's broad conclusions are in agreement with those of May and Nicholson - that the delay in the regulatory mechanism is the primary cause of the oscillations.

Hassell, Lawton and May (1976) sought to characterise about 30 insect populations as either stable, unstable or chaotic. This characterisation was accomplished by estimating parameters from population data (mainly life-tables) for a generalised, single-species, difference equation model due to Hassell (1975) and by plotting the estimates on the stability diagram for the model. All but two of the insect populations were characterised as stable and only one of those remaining two - Nicholson's blowflies - as chaotic. Hassell et al based their parameter estimates on Nicholson's (1954b) larval food limited experiment, not the adult food limited experiment. Varley, Gradwell and Hassell (1973) had previously characterised the same experimental population as being unstable; Gurney, Blythe and Nisbet (1980) also characterised the 1954b lfl populations as unstable. Hassell et al's characterisation of the blowfly populations proved seminal in promulgating the idea that the blowfly populations (including adult food limited ones) are chaotic. Apart from the fact that their estimates are based on the larval food limited data, the validity of Hassell et al's assertion is in doubt because their conclusions depend very much on the particular discrete-generation model that they employed. Wu (1978) attempted to model replicates of Nicholson's experiments using Leslie-Matrix models; he concluded that (Wu, 1978, p 53) '.... discrete generation models are not appropriate for modelling this population". That discrete-generation models are structurally inappropriate in modelling the blowfly populations is also discussed in Nisbet and Gurney (1982 chs 2 and 8). Essentially, in the larval food limited experiments the blowflies do seem to display approximately discrete generations but in adult food limited experiments reproduction is continuous, implying overlapping generations. Whilst, therefore, a discrete-time model may have been appropriate, as used by Hassell et al when characterising the larval food limited experiment, it must certainly be inappropriate to generalise the result of 'chaos' to adult food limited experiments - a fault which, it will be seen, has been all too frequently made.

Oster (1976) and Oster and Guckenheimer (1976) studied the behaviour of a time-delayed, birth and death model, derived from the von Foerster (1959) equation. They examined the bifurcation behaviour of the model and indicated when chaotic solutions might arise. In both papers, Nicholson's (1957) experiments were used as examples of the possibility of such chaotic behaviour but no attempt to estimate model parameters from the data was made. In the words of Oster and Guckenheimer (1976 p 343) concerning how the population oscillations might arise:
"naturally the mechanism of bifurcations suggests itself".

Oster and Ipaktchi (1978) studied the dynamics of a continuous-time birth and death model (equivalent to that studied by Gurney, Blythe and Nisbet, 1980). They concentrated on defining the conditions for stability, instability and chaos. Although the model was a biologically realistic representation of the blowfly populations, again no attempt was made to estimate parameters from the raw data - the conclusion that the blowfly populations might be chaotic being seemingly presupposed. A similar, implicit characterisation of the blowfly populations as being chaotic is made by Charlesworth (1980 pp 63-65); it is merely shown that the chaotic solutions to a discrete-time model may appear which are similar to the (1957 afl) blowfly population trajectories.

Wu (1978) attempted to determine whether or not the blowfly populations display chaotic behaviour. His approach was not to estimate parameters from Nicholson's data for a biologically sensible model but to replicate Nicholson's experiments and to model the resultant data using Leslie-matrix models. He (p52) concluded that "an animal may have intrinsic chaotic behaviour". He said nothing, however, about how such "intrinsically chaotic individuality" (sic) might influence population dynamics and, as mentioned above, he also concluded that discrete-time models were an inappropriate modelling approach.

Nicholson's blowfly populations, then, have increasingly come to be thought of as displaying chaotic behaviour. This has arisen, however, primarily due to circumstantial evidence and only one attempt (Hassell et al, 1976) to estimate parameters for a particular model; that model may, though, be fraught with difficulties as it assumes discrete generations. That so little attempt to estimate the parameters controlling the dynamic behaviour of the blowfly populations has been made is due possibly to the fact (May and Oster, 1976; Poole, 1977) that it is practically impossible to distinguish the chaotic behaviour that may be generated by non-linear deterministic models from random processes.

Because characterisations of the blowfly populations as chaotic are all - with the exception of Hassell et al (1976) - lacking in quantitative verification, Gurney et al (1980) sought to determine quantitatively the nature of Nicholson's (1954b) blowfly population fluctuations (i.e. whether they are driven quasi-cycles, self-sustaining limit cycles or chaos). Their classification depended upon both the stability analysis of a biologically plausible delay-differential equation model and parameter estimates from Nicholson's (1954b) adult and larval food limited data. Gurney et al concluded that in both adult and larval food limited cases, the fluctuations were self-sustaining limit cycles. Examination of further work, reported in Blythe, Nisbet and Gurney (1982, see Fig. 10), reveals that chaos is not a sensible possibility given the estimated parameter ranges for either adult or larval food limited populations.

1.4 OVERVIEW OF THE THESIS

None of the continuous time models alluded to in section 1.3 explicitly include age-structure but approximate it by containing time-lags to represent larval development periods. Such "gross representation" models are primarily of use in investigating and characterising dynamic properties of populations that occur over generation times or longer. Time delay models may produce a repetitive fine structure as a simple numerical response given appropriate parameter values (see e.g. Oster, 1977a; Gurney et al, 1980) or when deterministically driven. By 'fine structure' I here mean pattern or fluctuations that take place over a time much shorter than a generation.

In general, however, it has been pointed out that an understanding of how fine-structure might arise deterministically in the blowfly populations necessitates a knowledge of the age structure of the population and how vital rates depend upon age (Nicholson, 1954b; 1957; 1960; Auslander, Oster and Huffaker, 1974; Oster and Takahashi, 1974; May, 1974a; Oster, 1976, 1981; Readhsaw and Cuff, 1980; Gurney et al, 1983; Readshaw and van Gerwen, 1983). This, of course, was also realised by Wu (1978) who investigated such age dependences in blowfly vital-rates and used age structure (Leslie-matrix) models. Although Wu was unsuccessful in modelling his replicate experiments, Oster (1977a and b) used 'von Foerster-like' equations with which he was able to simulate Wu's data 'passably well' (Oster, 1981, Fig. 2).

Although, then, the desirability of age structure models has been recognised, little attempt has been made to dig into the age structure of Nicholson's blowfly populations. This is hardly surprising as Nicholson's data does not include age structure information. Brillinger et al (1980; see also Oster, 1981) did try to infer age-structure in Nicholson's data by making assumptions concerning how mortality acts dependent upon both density and age. Their attempt, though, was marred by the unavailability of experimental evidence upon which to found their assumptions. Only recently, however, Readshaw and van Gerwen (1983) have performed various experiments to investigate how fecundity and survival of blowflies depend upon both age and density. The results of these experiments provide a basis for investigating the age-structure of Nicholson's blowfly populations. This is the subject of chapters 5 and 6.

In chapter 5, age and density dependent survival is investigated based on Readshaw and van Gerwen's data. This investigation also permits the inference of age-structure in the control population. In chapter 6 the development rate of adults from emergence to maturity is considered and the results, although recognised to be erroneous, are combined with the inferred age-structure in an investigation of age-specific fecundity.

Prior to considering details of age dependencies it is desirable to clarify both how and why the gross population dynamic features arise in Nicholson's experiments. In chapters 2 to 4, therefore, a gross representation model will be employed to show that population attributes represented by model-specific parameters are changing throughout the experiment (chapter 2) and that although the population is at first best characterised in the unstable (but not chaotic) region of parameter space, selection eventually causes the population to be best characterised as stable (chapter 3). This stabilization is sufficient to explain the alteration in dynamics that occurs in both the control and the 20-day driven experiment (chapter 4).

1.5 MODELLING

1.5.1

We are not concerned here with long-term predictions or the exposition of general ecological possibilities. Our gross-representation model need not then be 'tactical' nor 'strategic' in the sense of May (1974a); we require a model that is a testable model of the blowfly population dynamics. We are interested in determining how and why the dynamic changes observed in Nicholson's (1957), adult food limited, blowfly populations occur. To achieve these ends a model that can describe the general features of the population is required. Such a model should firstly be capable of explaining behaviour such as the limit cycles observed in Nicholson's (1954b) afl data and the apparently similar, fairly regular cycles seen for the first 400 days in Nicholson's (1957) control run. The model must, however, also be capable of producing the alteration in dynamic behaviour that occurs in the control run.

1.5.2 FORMULATION OF THE MODEL

It is possible to construct a model with simple age-structure by writing down linked balance equations for all developmental stages (see Gurney, Nisbet and Lawton, 1983). Nicholson's (1957) experiments, however, all permitted ad lib feeding for larvae and the only expected density dependence in the population, and therefore also in the model, should occur in the adult stage. For this reason all pre-adult stages may be lumped together, leaving only an adult class (the N class) for which, as no emigration and immigration is possible, we can write the instantaneous rate of change as

$$\frac{dN}{dt} = R(t) - D(t) \qquad (1.1)$$

where R(t) is the recruitment to the adult population at time t and D(t) is the total number of adult deaths at time t. All that now remains is to select suitable functional forms for the per capita vital rates.

Because we have lumped all of the pre-adult stages, if we assume that in the competition-free experimental circumstances, that all individuals always develop at the same rate, then we may represent the lumped age classes by a single delay, τ. This delay must, if it is to make dynamic sense, be equal to the time taken for an individual to develop from egg to maturity. The adult class, therefore, is assumed to consist entirely of mature individuals.

In reality, not all adults are mature but spend the first few days of life as immatures. Essentially, this assumption will mean that estimates of the model parameters will be valid only in a model specific-sense - an estimate of maximum per capita fecundity, for instance, will not be a true estimate of per capita fecundity of mature flies in Nicholson's experiments but for the N-class individuals of the model. In practice, this will not affect the period of population fluctuations predicted by the model but it will effect the population levels predicted at oscillation maxima and minima.

Given the delay, τ, recruitment to the adult class at time t must equal the number of eggs laid τ days ago multiplied by some egg survival factor. The presumed lack of competition between all pre-adult stages permits the assumption of a density independent death rate for pre-adults. This, taken with the constant development time, τ, implies a constant egg to mature adult survival, s. Recruitment to the N-class at time t, therefore, is given as

$$R(t) = E(t-\tau)\, s \qquad (1.2)$$

where E(t) is the number of eggs laid at time t. We require now, to find a functional form relating egg production to the adult population size at the time of egg production. As protein is supplied at a constant rate, Φ, this is the same as seeking a direct link between the rate of protein supply per adult (f mg d^{-1}) and the per capita rate of egg production (E(f) eggs $fly^{-1} - d^{-1}$).

This link has already been investigated by Gurney et al (1983 p 487) who found, with the assumption of scramble competition, an acceptable fit to the data inferred from Nicholson's experiments, with an exponential function of the form

$$E(N(t)) = Q \exp\left[\frac{-N(t)\ f_o}{\Phi}\right] \qquad (1.3)$$

where Q is the maximum per capita fecundity and f_o is a characteristic feeding rate. Combining equations (1.2) and (1.3) gives an expression for recruitment to the N-class at time t.of

$$R(t) = Qs\ N(t-\tau)\ \exp\left[\frac{-N(t-\tau).f_o}{\Phi}\right] \qquad (1.4)$$

Possible density-dependence of the death rate is discussed in chapter 2. For now, assume that death rate is density independent and that there is a constant per capita death rate, δ. Combining this assumption with equations (1.1) and (1.4) gives the fully specified model describing the rate of change in mature adults as

$$\frac{dN}{dt} = Qs\ N(t-\tau)\exp\left[\frac{-N(t-\tau).f_o}{\Phi}\right] - \delta.N(t) \qquad (1.5)$$

As specified, the model has time independent parameters, the precise values of which govern the dynamic behaviour of the population. In this form the model may be used to simulate adequately the limit cycles observed in Nicholson's (1954b) afl experimental population or even the repetitive behaviour seen for the first four hundred days of the (1957) control experiment. The model cannot, however, be used to represent a population which undergoes an apparent change in behavioural regime (e.g. from behaviour characterised as unstable to stable). If, then, we wish to use the model to describe the (1957) control data in which an apparent behavioural shift does occur, we must not specify time invariant parameter values but instead admit time-dependency. In chapter 2, estimates of $Qs(t)$, $\delta(t)$ and $f_o(t)$ are made.

Equation (1.5), hereafter referred to as the G-B-N model, is of course only a partial specification of a model - we still need a description of the initial conditions. Nicholson (1957) started his experiments by placing 1000 pupae in a cage and beginning counts 2 days later. All solutions to models will, therefore, start with an innoculation of 1000 adults at time zero and will have an initial history of zero population. Because Nicholson's data are presented in 2-day blocks, the population size being integrated over each datum interval, all solutions to equation (1.5) will be displayed as population size averaged over the prior two days.

The solutions presented in the thesis are all obtained using a modified predictor-corrector algorithm - 'Solver' (Maas, Nisbet and Gurney, 1982) - implemented on either a Western Digital Microengine or a Sage II minicomputer.

CHAPTER TWO

PARAMETER CHANGES AND ESTIMATION

2.1 INTRODUCTION

Nicholson (1957 p. 163) noted a number of obvious alterations in the population behaviour of his control experiment. Specifically, he noted that the average population size, and the population size at oscillation minima, seemed to be rising as the experiment progressed. He proposed that this was due to selection acting during the experiment to produce flies with an improved egg laying capacity. He tested this assertion experimentally and found, quite remarkably, that post-experimental flies could, unlike wild or laboratory stock flies, produce eggs in the absence of protein; fig. 2.1.1 shows 100-day, mean populations plotted against time, and fit with an exponential regression time to emphasize the large and unequivocable rise in mean population size.

Another notable change apparent in the control population occurs at around 400 days into the experiment. Before this point there is a fairly regular, cyclic behaviour which then gives way in the later stages to a less regular and not so obviously periodic pattern. Power spectra (Figs. 2.1.2a and b) of these two experimental portions are revealing; Fig. 2.1.2a shows that in its

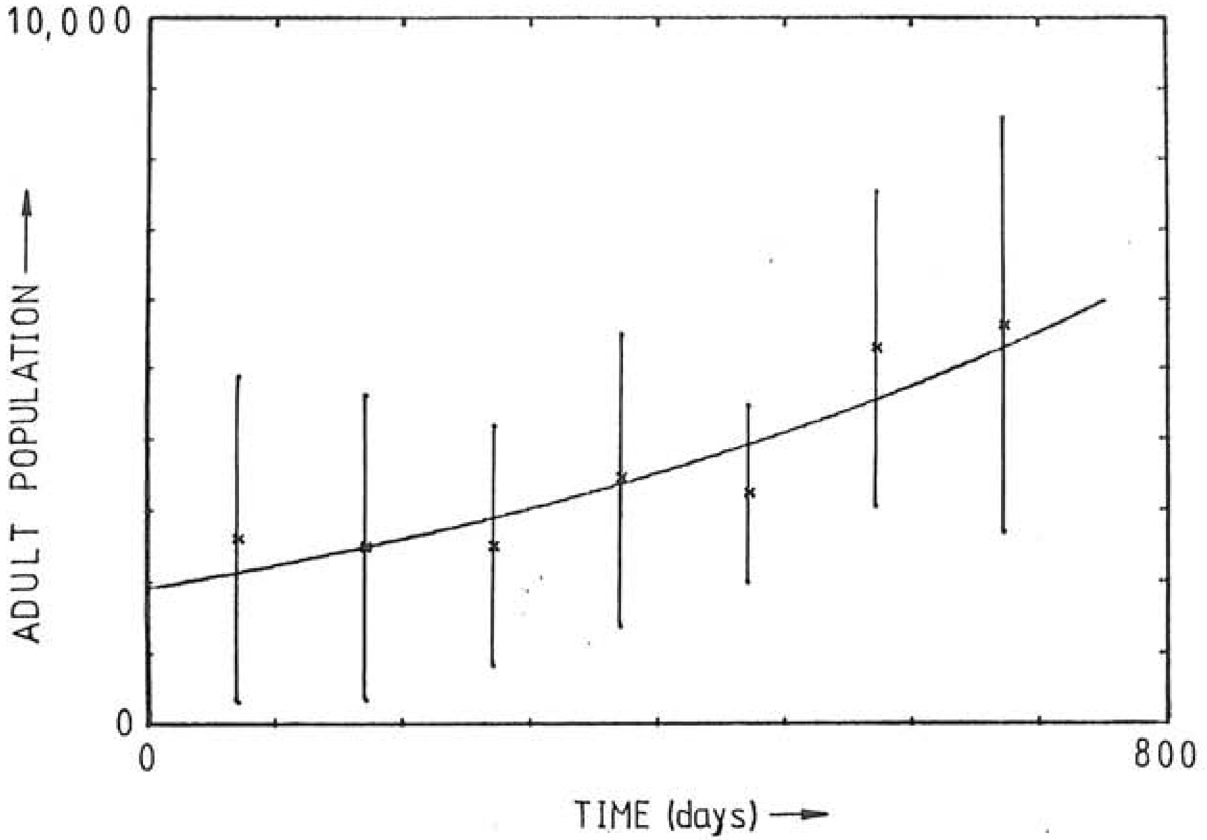


FIG. 2.1.1 100-day mean populations (± standard deviation) plotted against time for Nicholson's (1957) control experiment (see Fig. 1.1I). The continuous line is an analytic fit to the means to emphasize the gradual increase in population levels with time.

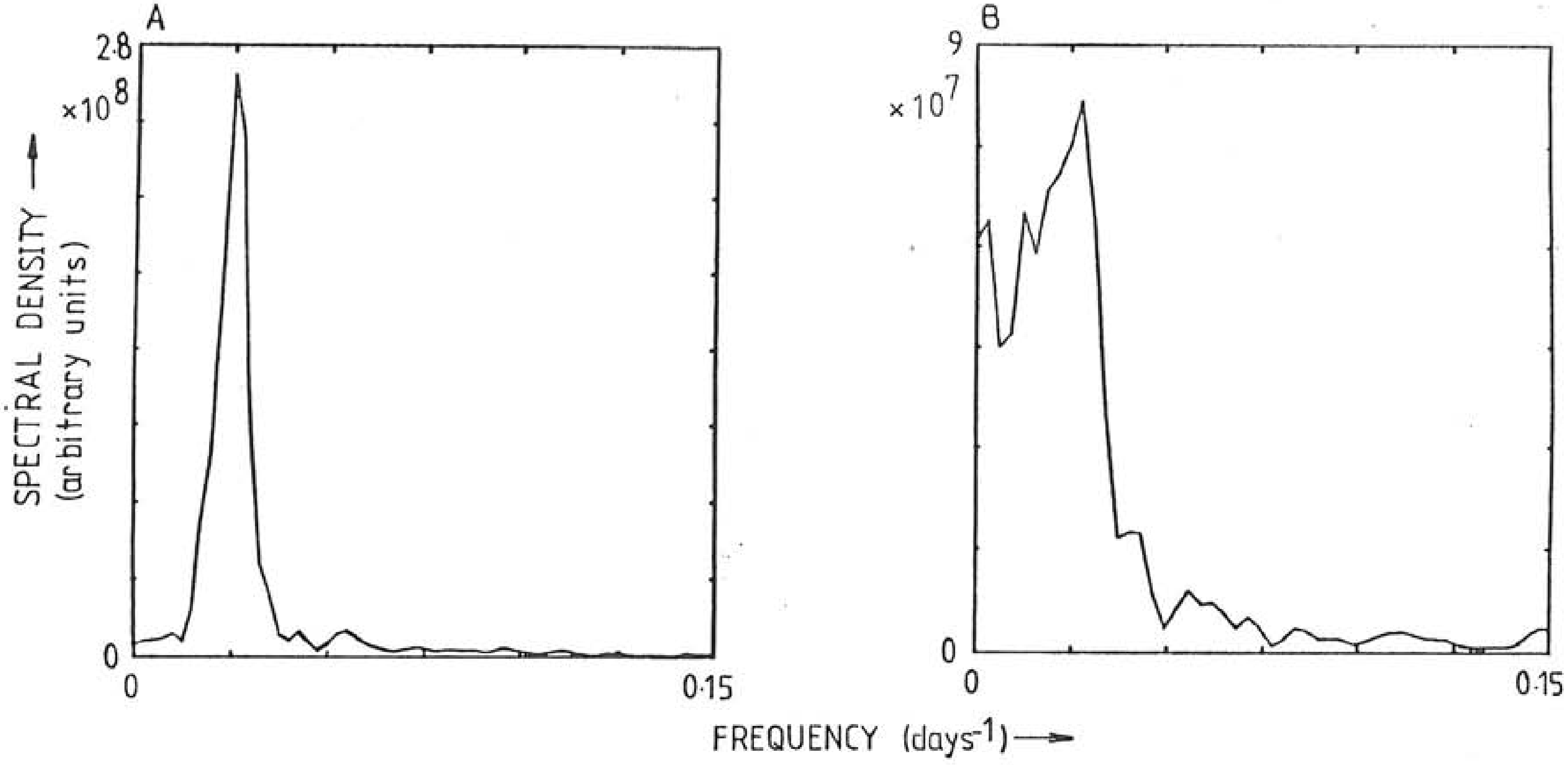


FIG. 2.1.2 Power spectra of the control data (Nicholson, 1957; see Fig. 1.1I). A) $0 < t \leq 400$ days B) $400 < t < 720$ days.

earlier stages, the population fluctuates with a period of 40 (± 2) days. Fig. 2.1.2b clearly indicates that the dynamics change - the behaviour of the population in the later stages is barely cyclic at all; the spectrum, in fact, is indicative of a great deal of broad-band noise.

This shift from strongly cyclic behaviour to essentially non-cyclic fluctuations is also apparent, but manifests itself differently, in the experiment subjected to a 20-day variable protein-input regime (see Fig. 1.1c). Again, there is a clear change in dynamic behaviour - this time about 500 days into the experiment. Over the first 500 days Fig 2.1.3a illustrates that there is a dominant period of 40 days (equivalent to twice the driving period) which then gives way, as shown in Fig. 2.1.3b, to a twenty day cycle (equal to the driving period). This behaviour begs to be explained (see Appendix 1 and Fig. A1.2) as synchronization of the natural limit cycle to the half-harmonic of the driving frequency giving way to a simple capturing of the (stable) system by the driving force ('periodically driven quasi-cycles', Nisbet and Gurney, 1982, ch. 7). This apparent shift from behaviour characterised as unstable to stable in the driven experiment now suggests that the shift in behaviour in the control is similarly caused and that the power spectra (Figs. 2.1.2a and b) are representative of a perturbed limit cycle and a stable, underdamped system subjected to noise.

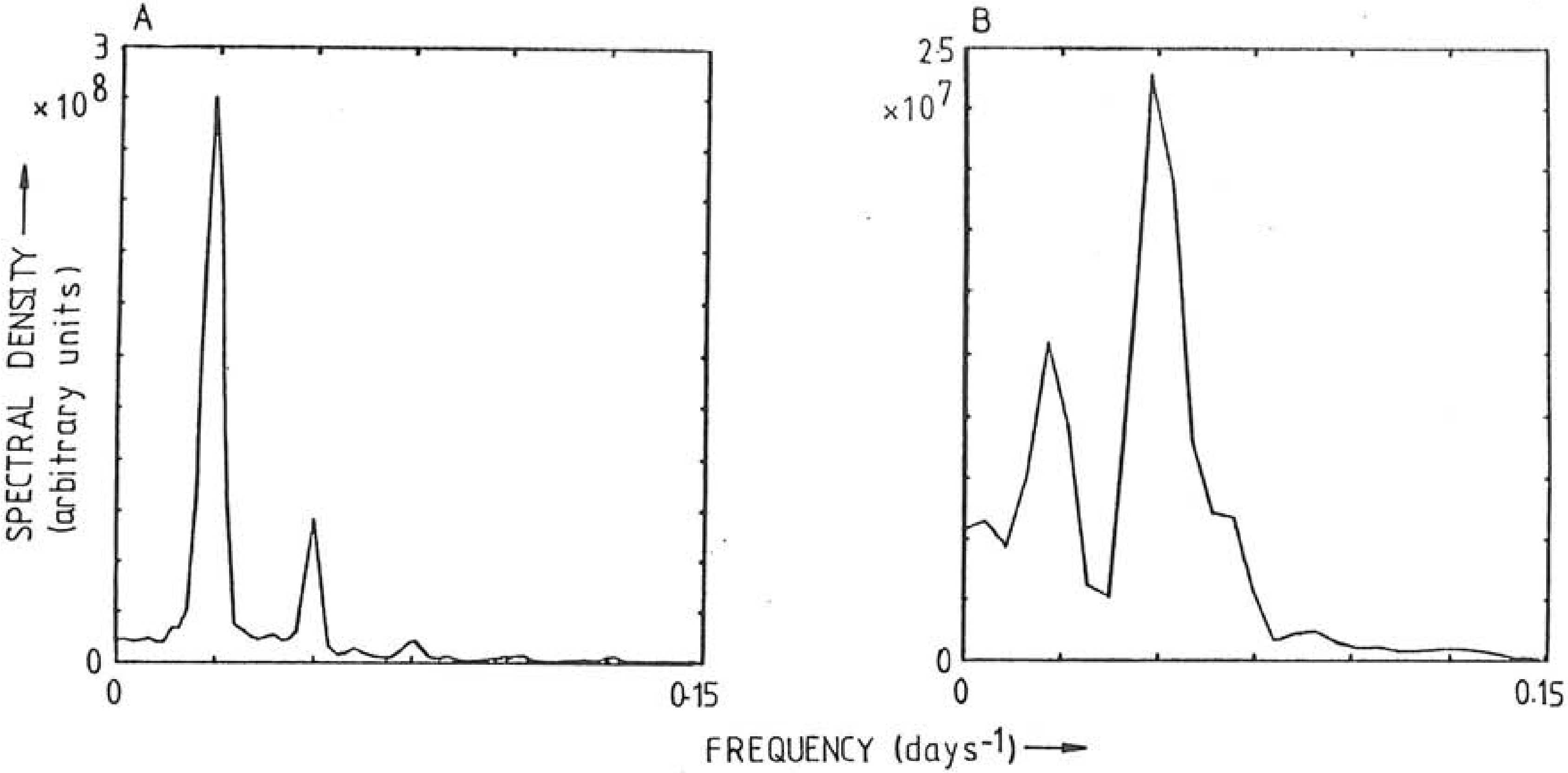


FIG. 2.1.3 Power spectra of the data from the 20-day driven experiment (Nicholson, 19G; see Fig. 1.1C.) A) $0 < t \leqslant 500$ days. B) $500 < t < 684$ days.

In summary, the average population size in the control experiment is increasing with time.

In both the control and 20-day driven experiments, the observed dynamics and power spectra are consistent with a shift from behaviour characteristic of the unstable region of parameter space to behaviour characteristic of the stable region. With this in mind, estimates through time of the parameters of a model describing the blowfly population dynamics - the G-B-N model - are derived in the following sections.

2.2 DEATH

2.2.1 DO DEATH RATES VARY?

That per capita, daily death rate varies greatly is clear (see Appendix 6, Fig. Ab.1) from the raw data presented by Brillinger et al (1980). Gurney et al (1980) estimated the death rate for a similar experimental population (Nicholson, 1954b - adult food limited case) by plotting the log of population sizes, during declines to oscillation minima, against time. During these periods, recruitment approaches zero and the slope of the resulting plotted lines is an estimator of the per capita death rate, δ. A similar exercise has been carried out for the 1957, control data, yielding the following results.

$$\delta = 0.17 \pm 0.02 \quad d^{-1},$$

The 1957 control experimental population had access to 0.4 g protein per day, the 1954b afl experimental population had access to 0.5 g protein per day. Gurney et al estimated per capita death rate for the 1954b population as

$$\delta = 0.27 \pm 0.025 \quad d^{-1},$$

The ten individual measurements upon which the 1957 estimate (0.17 ± 0.02 d^{-1}) is based are quite variable and show neither a consistent decrease nor increase with time. A dependence of death rate on some other quantity (or quantities) is indicated - the obvious first candidate being density.

2.2.2 IS DEATH RATE DENSITY-DEPENDENT?

Previous workers' perception of the relationship between death rate and density is ambiguous. Oster (1976) says that blowfly death rates are 'nearly random' whilst Brillinger et al (1980) claim a 'clear indication that the adult death rate is density-dependent'.

It can be seen that death rate does tend to increase with density (Fig. 2.2.1) but that there is a great deal of variation. The fitted regression line in Fig. 2.2.1 accounts for only a small amount of the variation in the data ($r^2 \simeq 0.21$). The large amount of variability seen in Fig. 2.2.1 may well be due to the confounding effects of age and possibly history dependence.

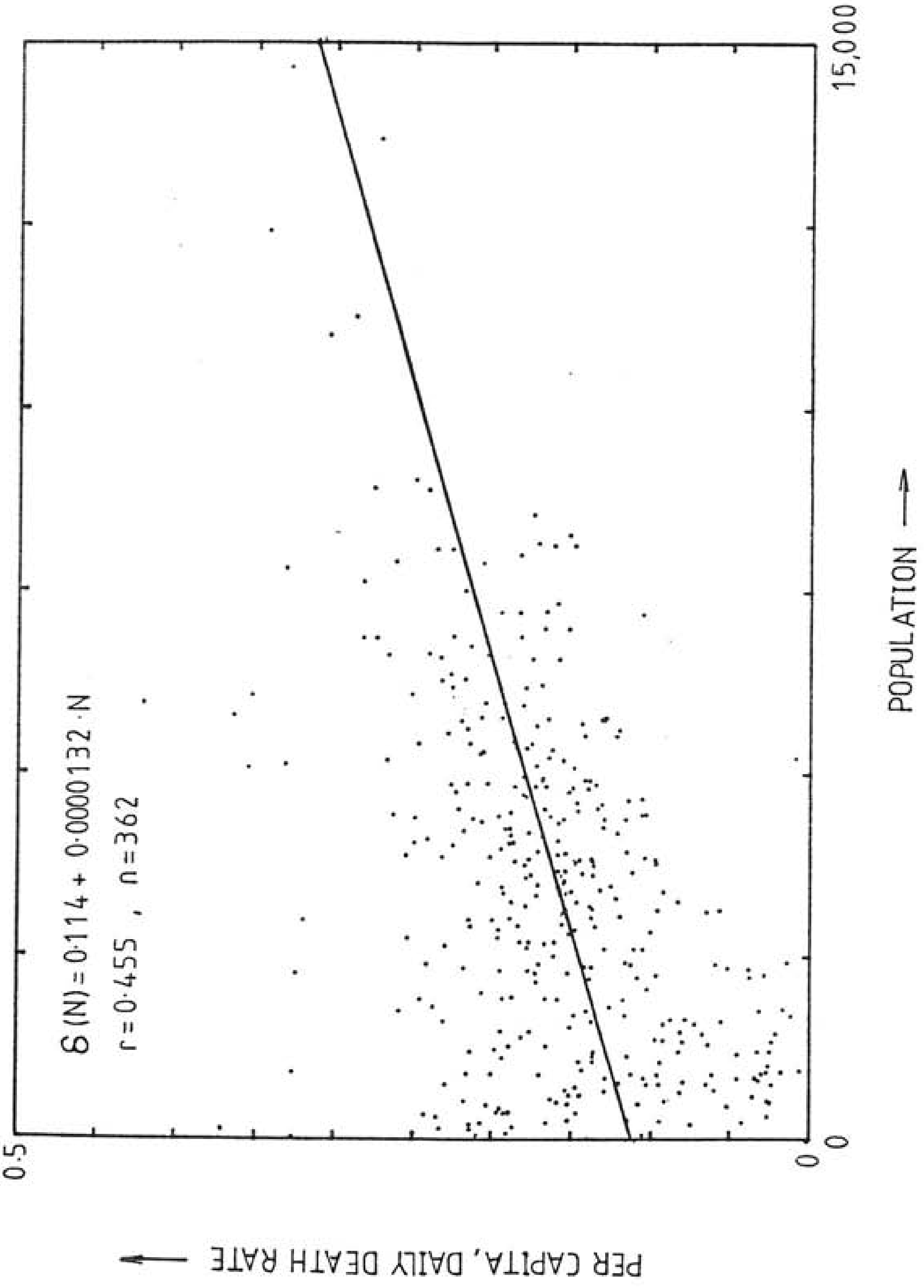

δ (N) = 0·114 + 0·0000132·N
r = 0·455 , n = 362
PER CAPITA, DAILY DEATH RATE
0.5
0
0
15,000
POPULATION

Fig. 2.2.2 is a plot of death rate versus age for the cohort of individuals comprising the initial population; it is clear that age may have a pronounced effect on mortality. That history might be important is intuitively reasonable - the probability of an individual dying depends not only on current events but also on the health of that individual, a state which is dependent upon (at least recent) past events. Precise details of the effects of age and density on mortality are investigated more fully in chapter 5, together with possible history dependence.

Meanwhile, for use in the ensuing modelling and simulation exercise, and to emphasize that mean death rate probably does increase a little during the experiment, a simple analytic fit of death rate against time is presented; Fig. 2.2.3 shows an exponential regression line fitted to 100-day, mean death rates plotted against time.

2.3 FECUNDITY AND COMPETITIVE RESILIENCE

2.3.1 A SIMPLE APPROACH TO ESTIMATING Qs

According to Nisbet and Gurney (1982 p. 302), if the amplitude of the blowfly population cycles is sufficient to produce a minimum population which is substantially smaller than that population able to achieve maximum

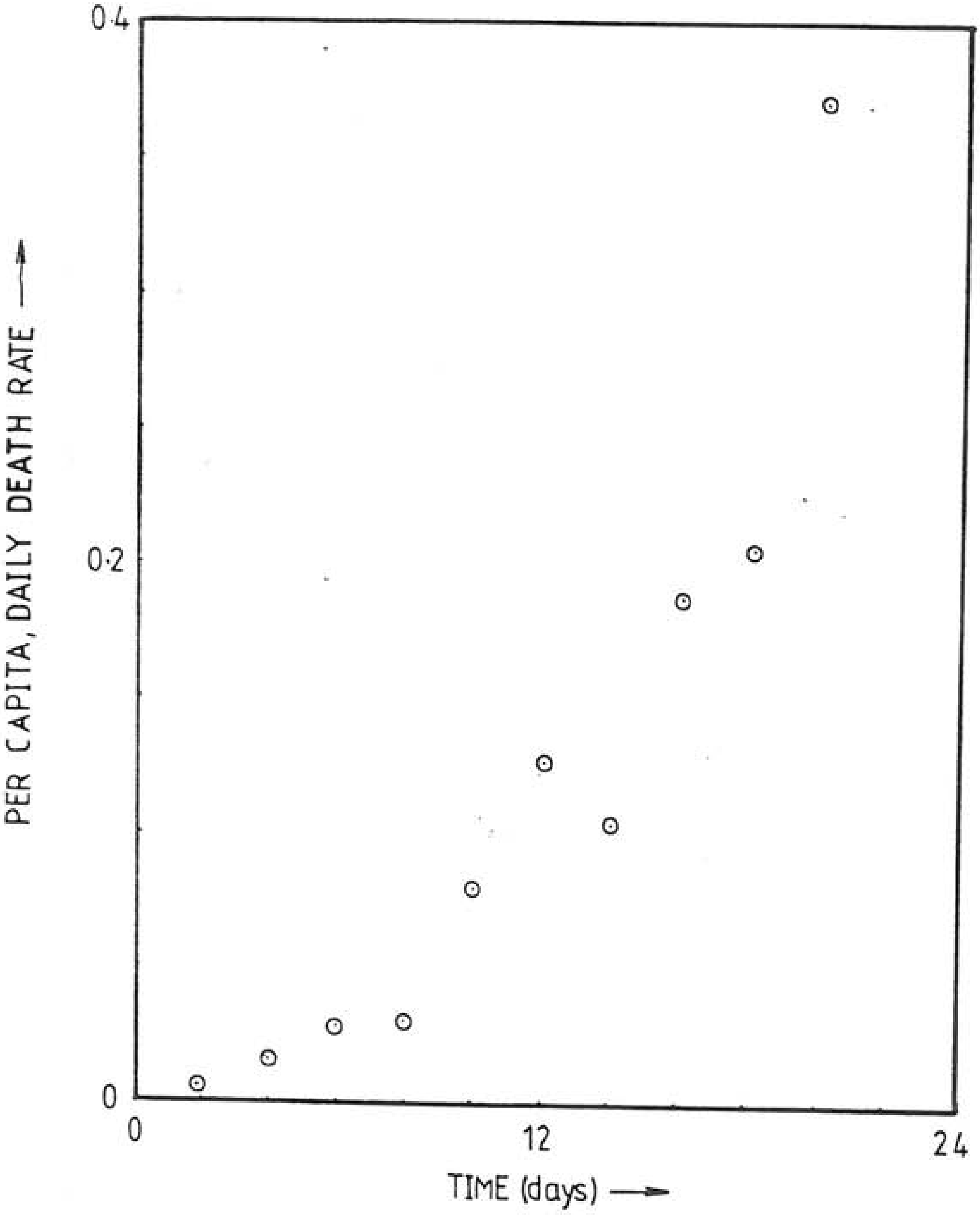
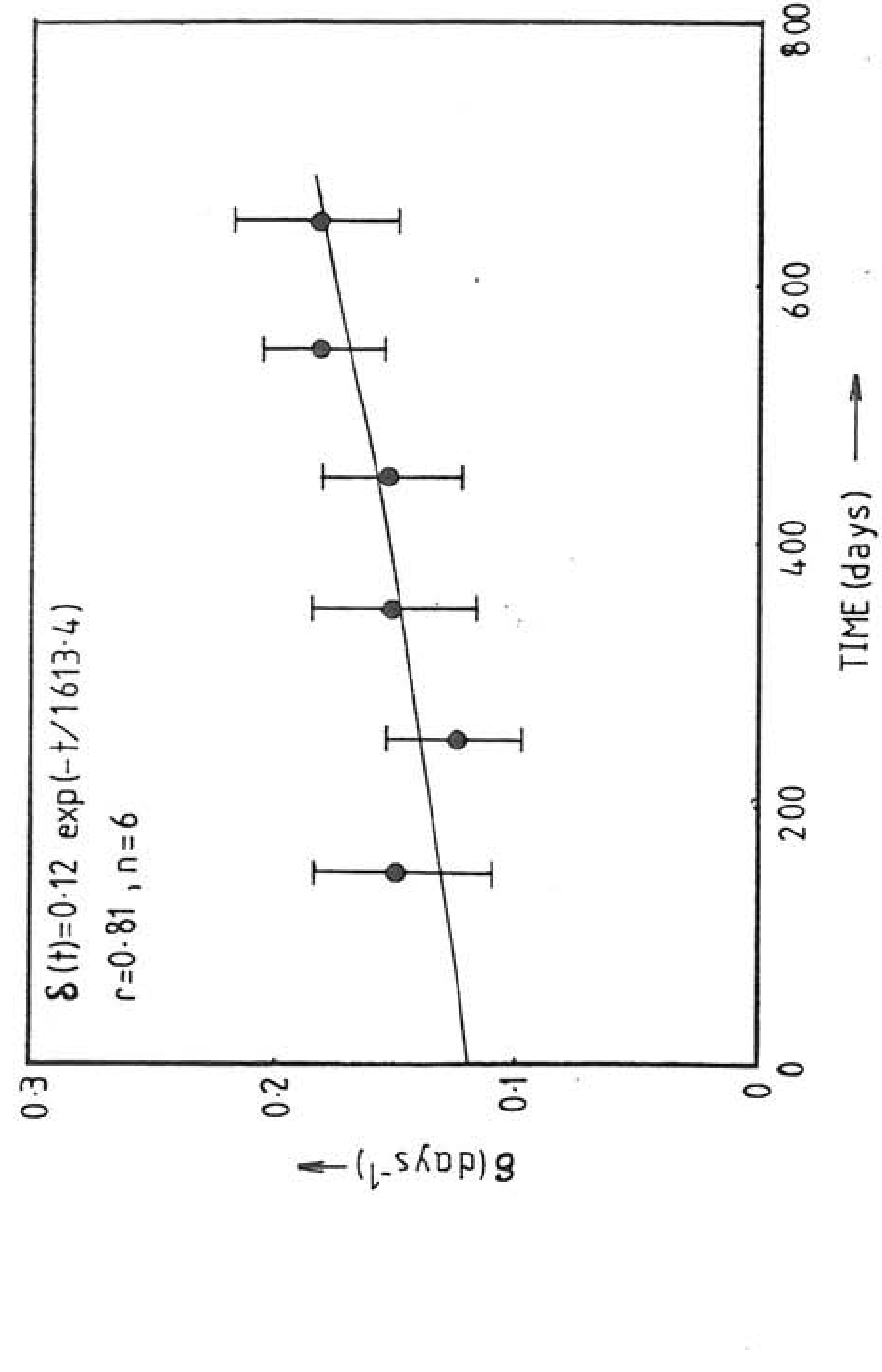


FIG. 2.2.2 Daily, per capita adult death rate plotted agains time for the initial cohort of flies in the (1957) control experiment.


δ (t)=0·12 exp(−t/1613·4)
r=0·81 , n=6
0·3
0·2
0·1
0
δ (days⁻¹) →
0
200
400
600
800
TIME (days) →

reproductive success ($\Phi(t)/f_o(t)$ - see equation 1.4), then the recruitment curve against time will have a form characterised by a double peak. Nicholson's (1954b) adult food limited population data satisfies this condition and it is thus possible to estimate fecundity, Qs, from

$$\frac{\text{MAX. EGG PRODUCTION RATE x SURVIVAL}}{\text{POPULATION AT TIME OF MAX. PRODUCTION}} = Qs\ e^{-1}$$

Gurney et al (1980) deduced values of Qs. for the (1954b) afl population of

$$1.4 < Qs < 7.4$$

and hence concluded that the blowfly population cycles could only be explained as limit-cycles - because, with the assumption that $\tau D = 14.8$ days (an egg to mature adult approximation) the possible values of $Qs\ \tau D$, for the possible range of $\delta\tau$, all lie within the unstable region of $Qs\tau - \delta\tau$ parameter space.

A like exercise has been performed for the 1957 control data (for which - see Fig. 1.1I - the double peak criterion is justified). Qs estimates for the first three cycles are large, some greater than 30; over these initial cycles, however, the population is strongly influenced by initial conditions and estimates are likely to be unreliable. For the remaining 17 cycles measured, Qs is estimated as

$$1.9 < Qs < 7.1$$

which is clearly compatible with Gurney et al's estimated range.

If τ is again taken to be 14.8 days, the Qs τ estimates lie in the unstable region of parameter space for all sensible estimates of death rate, δ.

The individual Qs estimates, though, also tend to decrease with time and come to approach the stability boundary. This simple method of estimating Qs leads, then, to the idea that the maximum per capita fecundity might be declining with time and this seems to contradict Nicholson's perception of flies developing an increased egg laying capacity; this point will be returned to in the discussion.

Just as Qs estimates show evidence of declining, so too do f_o estimates - f_o is the amount of protein available, per capita, at the time of maximum egg production and is estimated as the average over each double peaked egg production cycle. The equilibrium population for the G-B-N model is given by

$$N^* = (\Phi/f_o) \ \ln (Qs/\delta) \qquad (2.1)$$

It can be seen, therefore, that a decline in f_o may result in the observed, gradual population increase.

In order to achieve a more rigorous characterization of the variation in Qs and f_o values throughout the experiment, the following statistical approach was adopted.

2.3.2 A REGRESSION TECHNIQUE FOR ESTIMATING Qs and f_o

The obvious, simple approach to estimating Qs and f_o is to transform the egg production function (1.2) into a form suitable for linear regression analysis -

$$\ln (E(t)/N(t)) = \ln Q. - (N(t)/\Phi)f_o \qquad (2.2)$$

In order to estimate Qs rather than Q, however, we need to use not E(t) but the number of viable eggs which were produced at time t, $E_v(t)$.

A plot of $\ln (E_v(t)/N(t))$ vs. $N(t)/\Phi$ yields, then, a straight line of intercept lnQs and slope f_o. Using the linear regression technique allows for the easy calculation of standard errors on the point estimates of Qs and f_o and also yields, of course, the linear correlation coefficient, r, a measure of the goodness-of-fit.

Apart from the usual underlying assumptions of least-squares fitting (e.g. randomly distributed, random errors), the added assumption is implicitly made that the transformation of the data to a linear form should not unduly bias the estimates of Qs and f_o.

A linear fit will, though, be greatly influenced by points that lie well to the right (on the 'tail') of the recruitment hump where the population is high and egg production is low. As the important attributes of the recruitment function for Qs and f_o estimation are the position of the peak and the slope of the approach to the peak, a decision was made to weight points in proportion to egg production. Weighting in this manner mitigates against points of high or low N. The most weighted points have high egg production and middle range N. Counting/sampling errors should therefore be of less importance and unlikely to introduce bias.

The results of analysis for various regression interval lengths of less than 100 days are presented in Appendix 2. Table 2.3.1 summarizes results for a regression interval of 100 days. Standard errors are not included in Table 2.3.1 but are shown in Fig. 2.3.1. Notice that the error bars on the Qs estimates are not symmetrical - this is due to the fact that Qs is estimated as exp (intercept ± standard error).

TABLE 2.3.1 Qs and f_o estimates obtained from 100-day regression intervals. A) data abutting start of experiment. B) data abutting end of experiment.

midpoint of regression interval (days)	Qs	f_o	r	number of data points used in the analysis
A) 51	5.86	0.37	-0.61	38
151	3.93	0.53	-0.80	41
251	2.50	0.44	-0.86	46
351	2.79	0.32	-0.82	49
451	0.89	0.18	-0.69	50
551	1.00	0.13	-0.61	50
651	1.27	0.10	-0.58	49
B) 71	4.21	0.36	-0.61	38
171	3.70	0.52	-0.81	45
271	2.33	0.43	-0.86	46
371	3.27	0.34	-0.85	49
471	0.78	0.14	-0.56	50
571	1.33	0.16	-0.48	50
671	0.90	0.09	-0.67	45

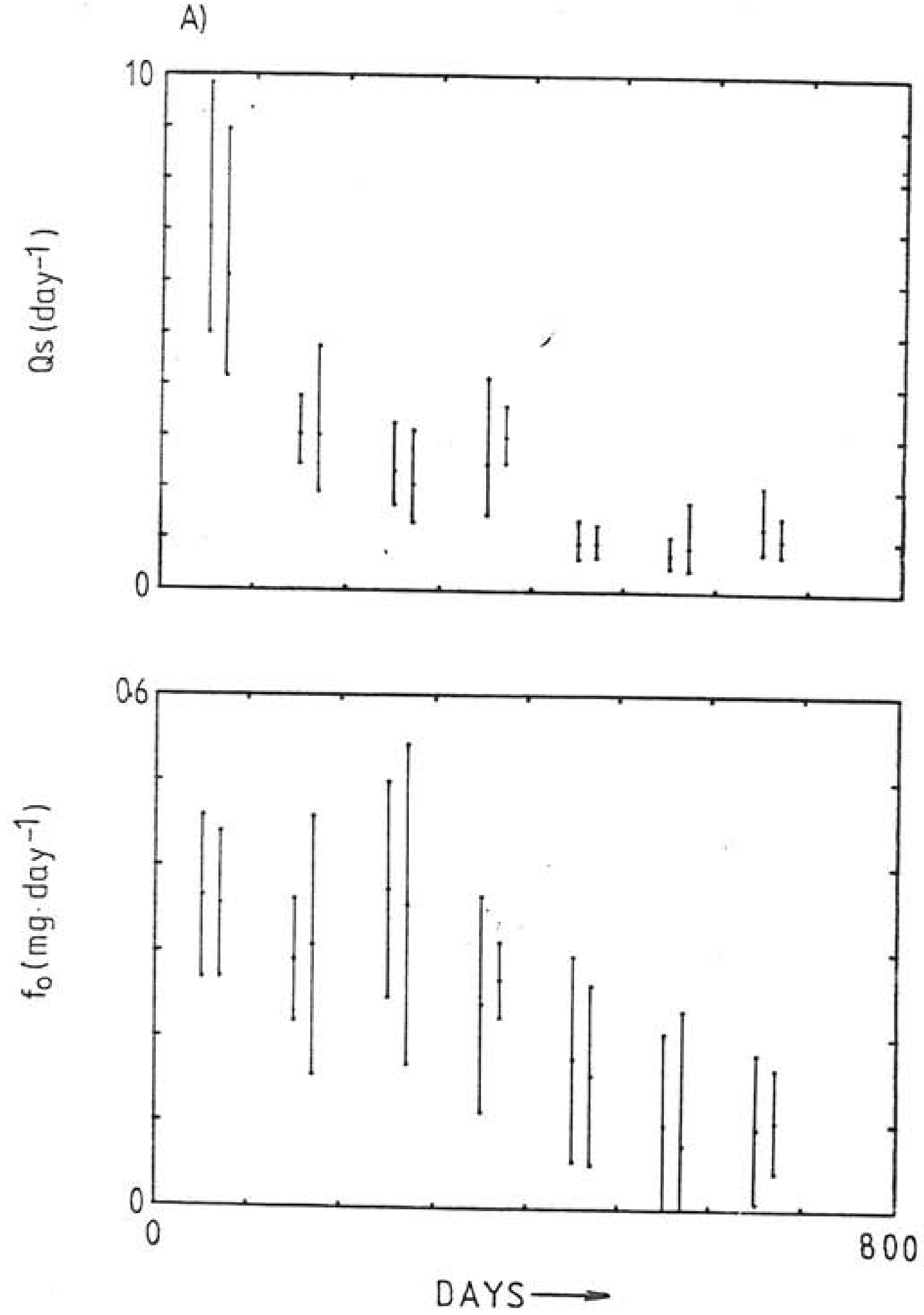


FIG. 2.3.1 Estimates (± standard errors) of A) Qs and B) f_o against time obtained from weighted linear regression analysis with intervals of 100 days. Results for regression intervals abutting both the start and end of the data are shown.

To emphasize the shift in parameter values throughout the experiment, the estimates are fitted with exponential regression lines of the form $y = a \exp\{-t/to\}$. Table 2.3.2 lists fits of this form for $y = Qs$ and $y = f_o$, together with correlation coefficients, for various lengths of regression interval. Clearly, the length of the regression interval makes little difference to the overall pattern of gradual decline. These fits were obtained by regressing $\ln y$ on t and thus the linear correlation coefficients are only a guide to the reliability of the heuristic properties of the exponential regression fits which will be utilized later in simulations (chapters 3 & 4).

2.3.3 CHECKING FOR BIAS/CONSISTENCY IN THE PARAMETER ESTIMATES

The linear regression model was adopted under the assumption that transforming the data would have little effect on the parameter estimates obtained. The weighting procedure was adopted to further reduce any effect that the transformation might have. For the results to be of use it is necessary to test these assumptions.

It is simple to derive equations for estimating Qs and f_o by a non-linear least-squares procedure (see Appendix 2). Computation, however, involves iterative procedures and it is not easy to obtain standard errors for the

TABLE 2.3.2 EXPONENTIAL REGRESSION FITS TO Qs and f_o POINT ESTIMATES OBTAINED FOR DIFFERENT LENGTHS OF REGRESSION INTERVAL. A) DATA ABUTTING START OF EXPERIMENT, B) DATA ABUTTING END OF EXPERIMENT.

LENGTH OF REGRESSION INTERVAL (DAYS)	$QS = QS(0)e^{-t/t_o}$			$f_o = f_o(0)e^{-t/t_o}$		
	$Qs(0)$	t_o	$r(Qs)$	$f_o(0)$	t_o	$r(f_o)$
40	5.84	325.8	-0.72	0.54	384.3	-0.85
60	6.73	292.7	-0.87	0.58	357.6	-0.95
80	6.66	294.2	-0.87	0.61	336.5	-0.93
900	6.28	296.7	-0.89	0.58	342.8	-0.94
100(A)	5.92	313.5	-0.88	0.49	399.6	-0.93
100(B)	5.96	325.5	-0.90	0.53	379.2	-0.90
ALL DATA	6.21	308.7	-0.82	0.55	366.3	-0.91

estimates or a measure comparable with r, the linear correlation coefficient.

Estimates using the procedure outlined in Appendix 2 have been made for the regression intervals of 100 days abutting the start of the experiment. The outcome of the analysis is presented in Fig. 2.3.2 which shows both linear, weighted estimates and non-linear, unweighted estimates for Qs and f_0.

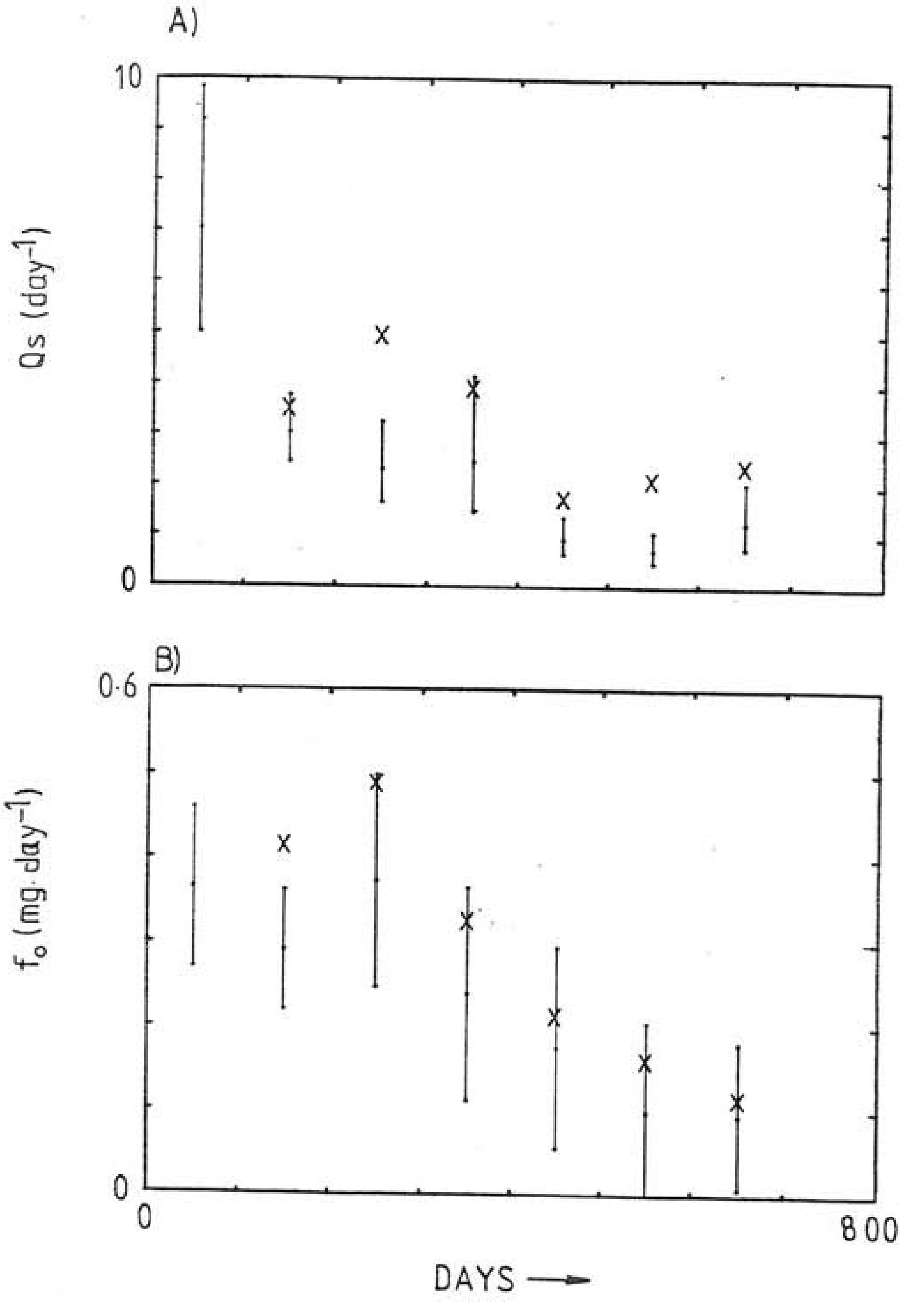


FIG. 2.3.2 Estimates (± standard errors) as in Fig. 2.3.1 from regression intervals of 100-days abutting the start of the data, plotted against time together with estimates (X) obtained for th same intervals using an unweighted, non-linear regression analysis A) Qs B) f_o.

The Qs estimates obtained using the linear analysis are all lower than their non-linear counterparts (Fig. 2.3.2a). This is due to the linear analysis rather than the weighting procedure - an unweighted linear analysis actually yields even lower estimates. This is caused, presumably, by the linearised 'tail' of the recruitment hump exerting a disproportionately strong influence and causing a reduction in the estimated value of ln Qs. The weighting procedure, whilst not fully compensating for the linear transformation does, at least to some extent, 'prevent the tail wagging the fit'. Not only are the non-linear estimates all higher than the weighted, linear ones, but they do not even all lie within one standard error. We do not, though, have estimates of standard errors for the non-linear estimates and a comparison, therefore is difficult. Nevertheless, the non-linear estimates do exhibit a decline through time which is consistent with that observed for the weighted, linear estimates.

Estimates of f_0 obtained using the non-linear analysis are consistently greater than their weighted, linear counterparts. All but one of the non-linear estimates do, though, lie within one standard error of the weighted, linear estimates. The general pattern of decline is consistent for the two analytic approaches.

In summary, the weighted, linear procedure produces estimates of Qs and f_0 which are lower than would be obtained with a non-linear fitting procedure. The overall pattern of decline is seen with both procedures and the results of the adopted, weighted linear regression appear robust.

2.4 DISCUSSION

We have established that

i) both population at oscillation minima and overall mean population are rising during the course of the experiment,

ii) per capita death rate rises throughout the experiment (see Fig. 2.2.3). There is, however, a large amount of variability in the death rate when plotted against population size (Fig. 2.2.1) - any density-dependent relationship is, therefore, well-disguised; the effects confounding any density-dependent relationship are possibly age (see Fig. 2.2.2) and history,

iii) the maximum per capita fecundity of adults decreases with time whilst f_0 (the reciprocal of which is a measure of 'competitive resilience') also declines.

Nicholson perceived an increased egg laying capacity in the blowflies; this seems to be contrary to the above statement that fecundity declines. What precisely Nicholson meant by 'egg laying capacity' is, however, unclear. He (Nicholson) may have been referring to population egg output but it is much more likely that the allusion is to the individuals in the population. If we are to consider Nicholson's remark as referring to individuals then there are two explanations which may account for the seeming inconsistency.

Firstly, Nicholson may not have been referring to per capita fecundity or 'competitive ability' (Aiken and Gibo, 1979) - but to the fecundity of <u>mature</u> individuals in the population. Our estimates of Qs refer to <u>all</u> adults and it is thus possible that a changing ratio of immature to mature flies results in the observed decline in Qs. We do not know how the fecundity of mature adults varies through time.

Secondly, let us consider why f_o declines. The reciprocal of f_o is a measure of competitive resilience. This is not to be confused with competitive ability (or fecundity). Competitive resilience does not refer to a capacity to lay eggs per se but to the ability to lay eggs in the circumstances of competition for resources. Nicholson's 'egg laying capacity' may - as is suggested by Oster (1981) with reference to Guttorp (1980) - be a reference to competitive ability or it may have been a reference to competitive resilience.

Why then does f_o decline? I would suggest that the decline in f_o is an outcome of selection acting to produce competitively resilient flies. Examples of unintended selection in the laboratory do exist. Van Den Ende (1973) reported the selection of 'sticky' bacteria in a predator-prey system; bacteria that evolved the ability to adhere to the walls of a glass culture-vessel were more able to escape predation in an otherwise homogeneous (and dangerous) environment. Bazin and Saunders (1978) reported apparently spontaneous changes in population densities of a bacterial prey and an acrasidan predator. Agur (pers. comm.) has noted that certain strains of a laboratory stock of a stored-product beetle display an increased tendency towards cannibalism.

Selection, then, may be acting to enhance competitive resilience rather than to increase fecundity, the selective pressure being competition for a limited protein supply. It is often presumed (c.f. Calow (1978, p87)) that selection acts to increase fitness, defined as gross, replicative capacity (i.e. 'competitive ability'), but this is only necessarily true if resources are unlimited. Fitness may be a measure of the extent to which a particular trait comes to monopolize the available resources (Lotka, 1922). In the blowfly population it is this latter process that occurs. Such a process is self-reinforcing - as competitive resilience increases so does competition (selective pressure) for resources - it is a genetic feedback mechanism (Pimentel, 1961).

I believe that it is this genetic feedback which causes the change in parameters which will be shown in the next chapters to underlie the observed population dynamic changes.

CHAPTER 3

THE DYNAMIC CONSEQUENCES OF CHANGING VITAL-RATE PARAMETERS IN A CONSTANT ENVIRONMENT

3.1 INTRODUCTION

In this chapter the steady state behaviour and local stability analysis for the G-B-N model are presented. An indication of how the parameter changes described in the previous chapter will influence behaviour is then made.

The G-B-N model assumes that all adults are mature and incorporates a density-independent death rate. These are definite simplifications and thus a few model variants, which alter these assumptions, are considered.

As this is the first point in the thesis where the dynamic behaviour predicted by particular models is mentioned, it is worth reiterating that these models are presented as testable models of the laboratory population under consideration. The final test of the models is the quality of the simulations that are to follow; that is, whether or not they capture the gross dynamic properties that are patent in the data.

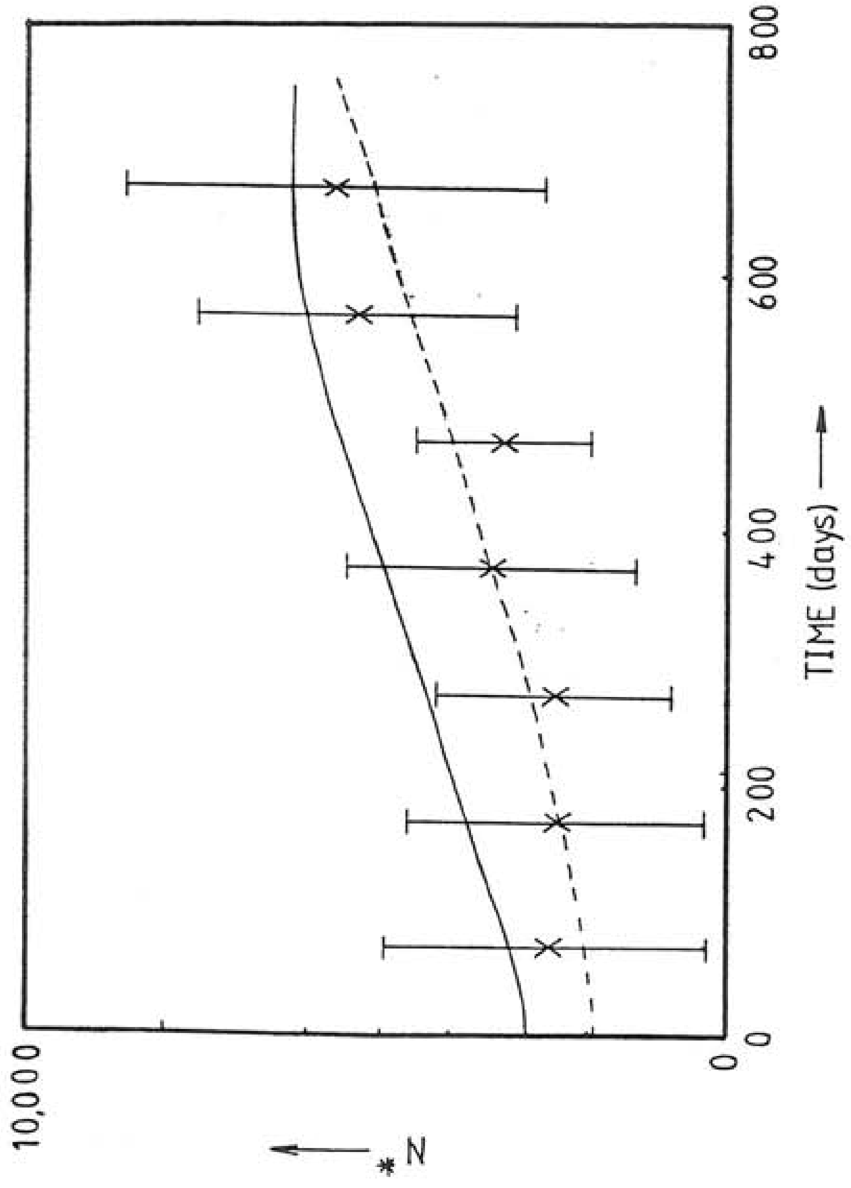
3.2.1 BEHAVIOUR OF THE G-B-N MODEL AND THE PREDICTED CONSEQUENCES OF CHANGING PARAMETERS

The equilibrium population of the G-B-N model is given by equation (2.1). Fig. 3.2.1 is a plot of the predicted equilibrium population based on the estimated parameter changes, against time. As all of the parameters (δ, Qs and f_o) are changing with time, the plot is essentially a sequence of predicted, instantaneous population equilibria.

Also shown in Fig. 3.2.1 are the 100-day mean population levels and an analytic fit to those points. Clearly, whilst the predicted equlibrium population rises in a similar manner to the mean population, it is consistently greater (typically by between 1000 and 1500).

An idea of the dynamic behaviour to be expected may now be gained by examining the behaviour of the model linearised about the steady state. Fig. 3.2.2 shows the local stability boundary in $Qs\tau$ - $\delta\tau$ parameter space together with an estimate of how $Qs\tau$ and $\delta\tau$ are changing during the course of the experiment.

The population plainly begins in the unstable region (of parameter space) and we should, therefore, expect to see the population exhibiting limit-cycles. Fluctuations which could very plausibly be perturbed limit-cycles are


10,000
0
N*
0
200
400
600
800
TIME (days)

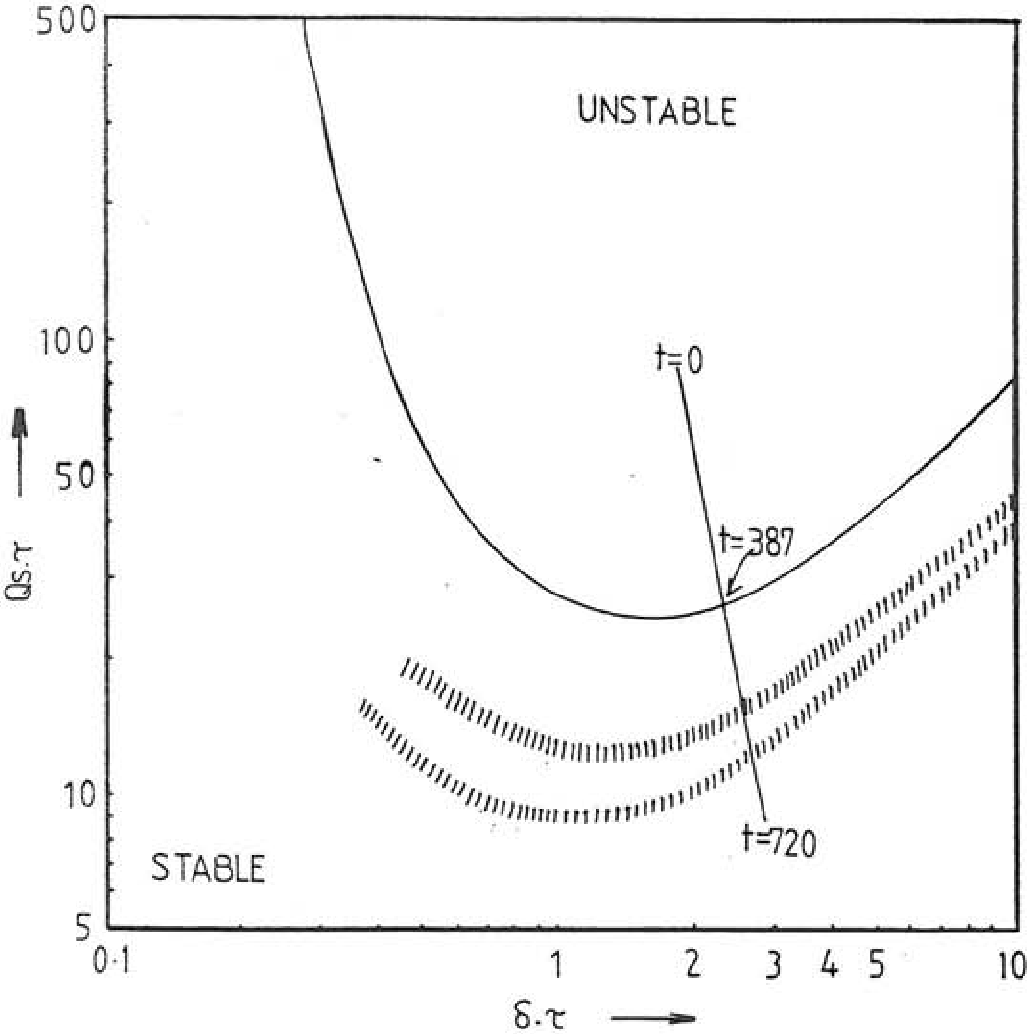


FIG. 3.2.2 The local stability boundary for the G-B-N model. The fuzzy contours are lines of constant coherence number equal to 5 and 0 (critical damping). The line indicates how $Qs.\tau$ anc $\delta.\tau$ are estimated to change during the course of the experiment.

observed in the experiment for about the first 400 days (see section 2.1.2). In the deterministic simulation these limit cycles will, of course, be more regular than those observed experimentally.

The local stability boundary is crossed at 390 ± 5 days and the stable region is entered; at first the population is in the underdamped region but gradually passes into the overdamped region passing in turn through areas that might roughly be called characteristic of strong, weak and non-cyclic behaviour. In Fig. 3.2.2 these areas are delineated by fuzzy contours representing coherence numbers (n_c) of 5 and 1. The coherence number is, in a static environment, a measure of the number of cycles over which the amplitude of those cycles reduces by a factor e (Nisbet and Gurney, 1982, ch. 4 p 98).

A deterministic simulation should then, considering the trajectory over the stability diagram, display limit cycle behaviour for about the first 390 days but then exhibit a gradual, cyclic approach to the predicted equilibrium value - equilibrium only being reached towards the end of the simulation.

3.2.2 THE MODEL WITH DENSITY-DEPENDENT DEATHS

The relationship between density and mortality is not strong (see section 2.2.2); it is confused, most probably due to the effects of age and history dependence (see chapter 5). Although in later simulations there is not any intention to use a density dependent death rate, it is pertinent to investigate the effects that such a mechanism might have on model behaviour. In this way it is possible to answer the questions - could a density dependent death rate alter the predicted equilibrium population or the timing of passage across the local stability boundary (the 'switching time') and could any change in prediction be compatible with the observed, experimental results?

If mortality depends linearly on population size as is weakly suggested by Fig. 2.2.1, then death rate is of the form

$$\delta(t) = \delta_o + \Delta N(t) \qquad (3.1)$$

where $\delta_o = 0.114 \quad d^{-1}$

and $\Delta = 1.32 \times 10^{-5} \; d^{-1} \; N^{-1}$,

The equilibrium population for the G-B-N model modified to incorporate density dependent mortality is now found iteratively from

$$N^*(t) = (\Phi/f_o(t))\ln(Qs(t))/(\delta_o + \Delta N^*(t))) \qquad (3.2)$$

A plot of $N^*(t)$ against time, based on the parameter estimates obtained in chapter 2, is shown in Fig. 3.2.3.

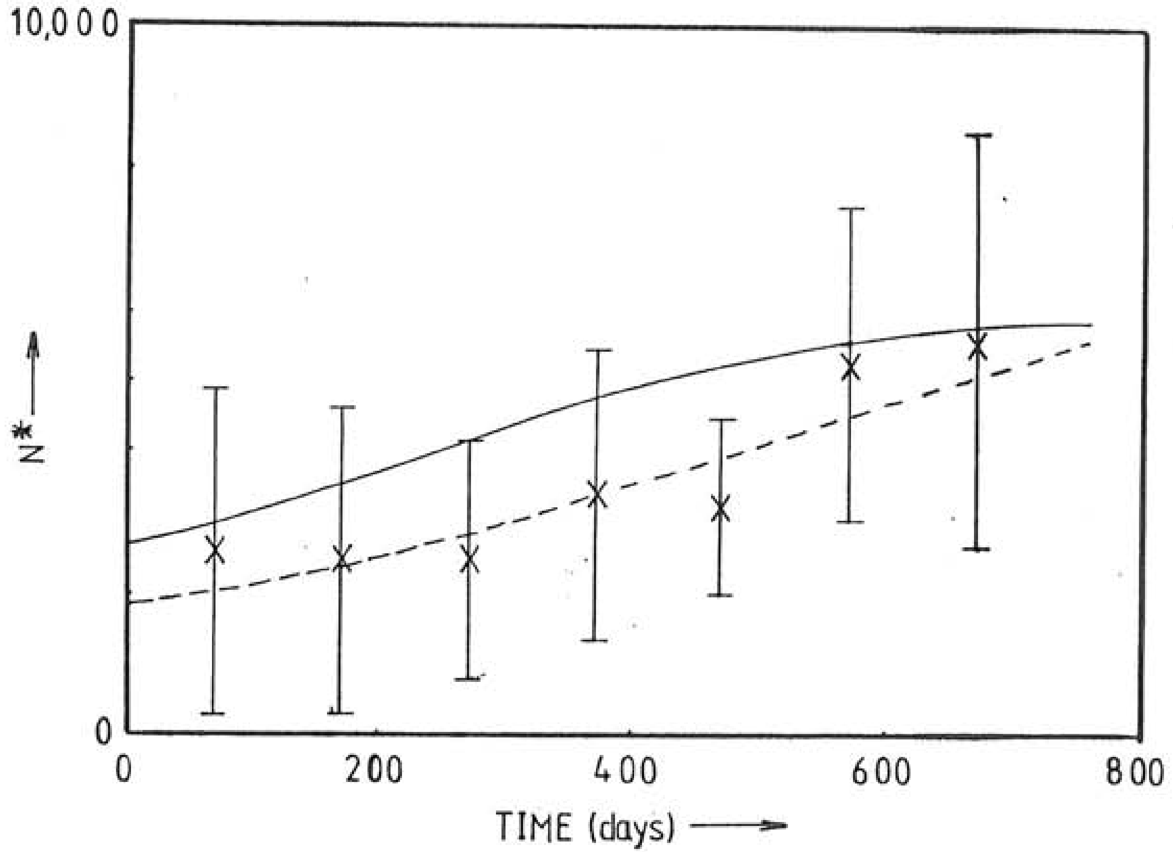


FIG. 3.2.3 As for Fig. 3.2.1 but N* is now for the model with density dependent mortality.

The predicted equilibrium population is clearly not very different from that for the density independent death rate model (Fig. 3.2.1).

A density dependent death rate will, in general, enhance the stability of a model - for instance, if population levels increase, the resultant increase in death rate will tend to counter the population increase and cause population levels to decrease, thus the death rate will itself decrease and so on... The linearly dependent death rate equation (3.1) achieves this enhanced stability for a wide range of δ_0 values (see Fig. 3.2.4) but not if δ_0 is 'too low'. There is an interesting (i.e. instability rather than stability is enhanced) effect for very low δ_0 values; such values, however, are much lower than that which we will be considering and are not of immediate interest.

For $\delta_0\tau = 1.69$ the local stability boundary rises as $K(\equiv\Delta\tau\Phi/f_0)$ increases. K, in fact, based upon the f_0 estimates obtained in chapter 2, varies from < 0.15 at $t = 0$ days to > 0.6 at $t = 400$ days. Clearly, therefore, the effect of a density dependent death rate would be to bring forward the onset of stability predicted in 3.2.1. In fact, the switching time would be brought forward from 390 days to under 290 days - a difference of 100 days!

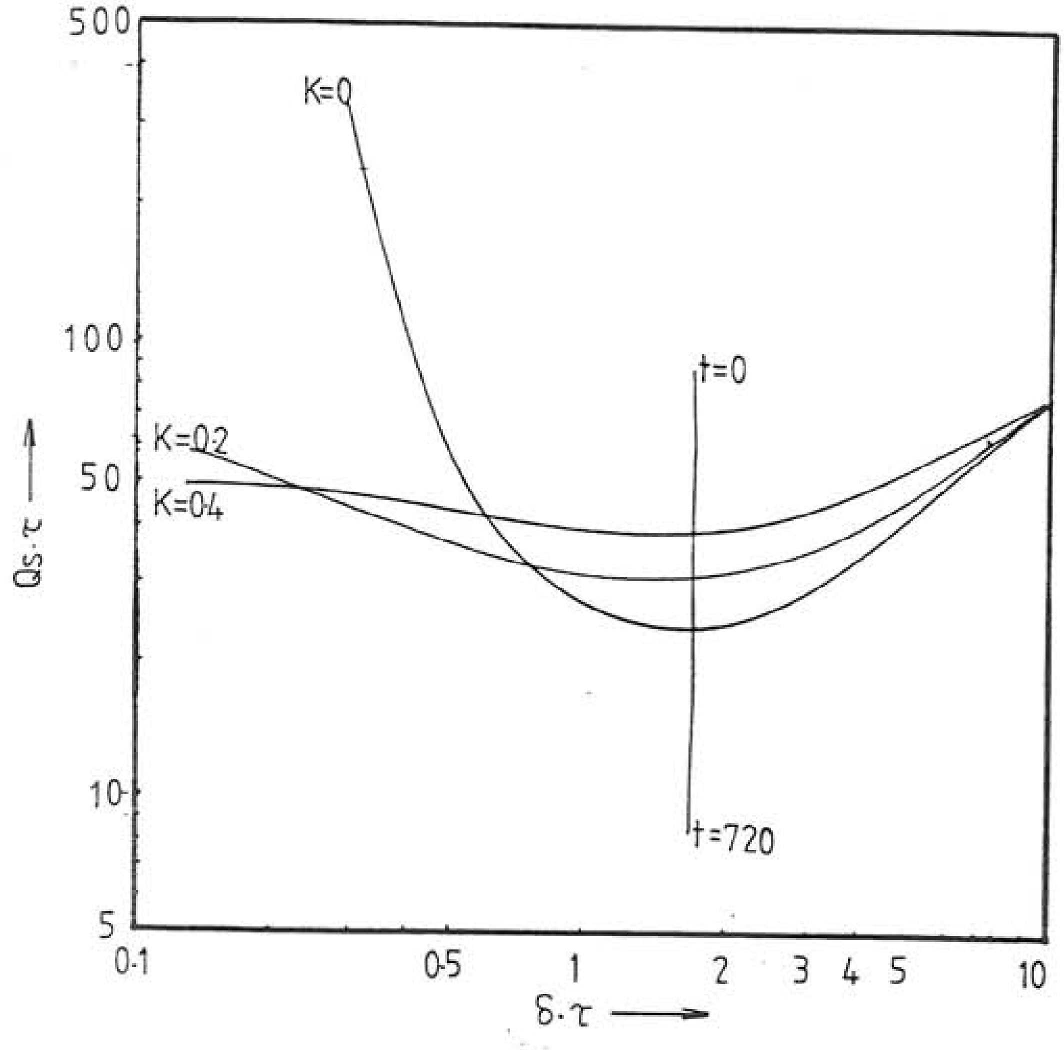


FIG. 3.2.4 Local stability boundaries for the density dependent death rate model. When K = 0 the model is equivalent to the G-B-N model. As time progresses, K, which is dependent upon f_o, increases. The line indicates how $Qs.\tau$ is estimated to change during the experiment. The local stability boundary is crossed at 285 < t < 290 days.

If the weak density dependence observed in mortality is of importance, its neglect in simulations will have little effect on overall, mean population levels but a pronounced effect on the switching time at which stability occurs. That the experimentally observed switching time is in accord with that predicted by the density independent death rate model is indicative that a purely density dependent death rate is not a sufficient explanation for the observed variations in mortality. The need to investigate age and history effects is strengthened. This is the stuff of chapter 5.

3.2.3 SPLITTING TOTAL ADULT POPULATION INTO SEPARATE IMMATURE AND MATURE CLASSES

It was suggested at the end of chapter 2 that the fecundity of mature adults as opposed to all adults may or may not be declining but that the observed decline in Qs might only be a concomitant of a model in which all adults are lumped together. An investigation of the effects of age structure is undertaken in chapters 5 and 6, but it is useful at this stage to consider whether or not a simple splitting of the total adult population into immatures and matures is possible.

It is easy (Gurney et al, 1983) to model the total adult population, N, as separated immature, I, and mature, M, classes and by the inclusion of an extra splitting of τ into τ_I and τ_L (for Immature adult and Larval delays) to

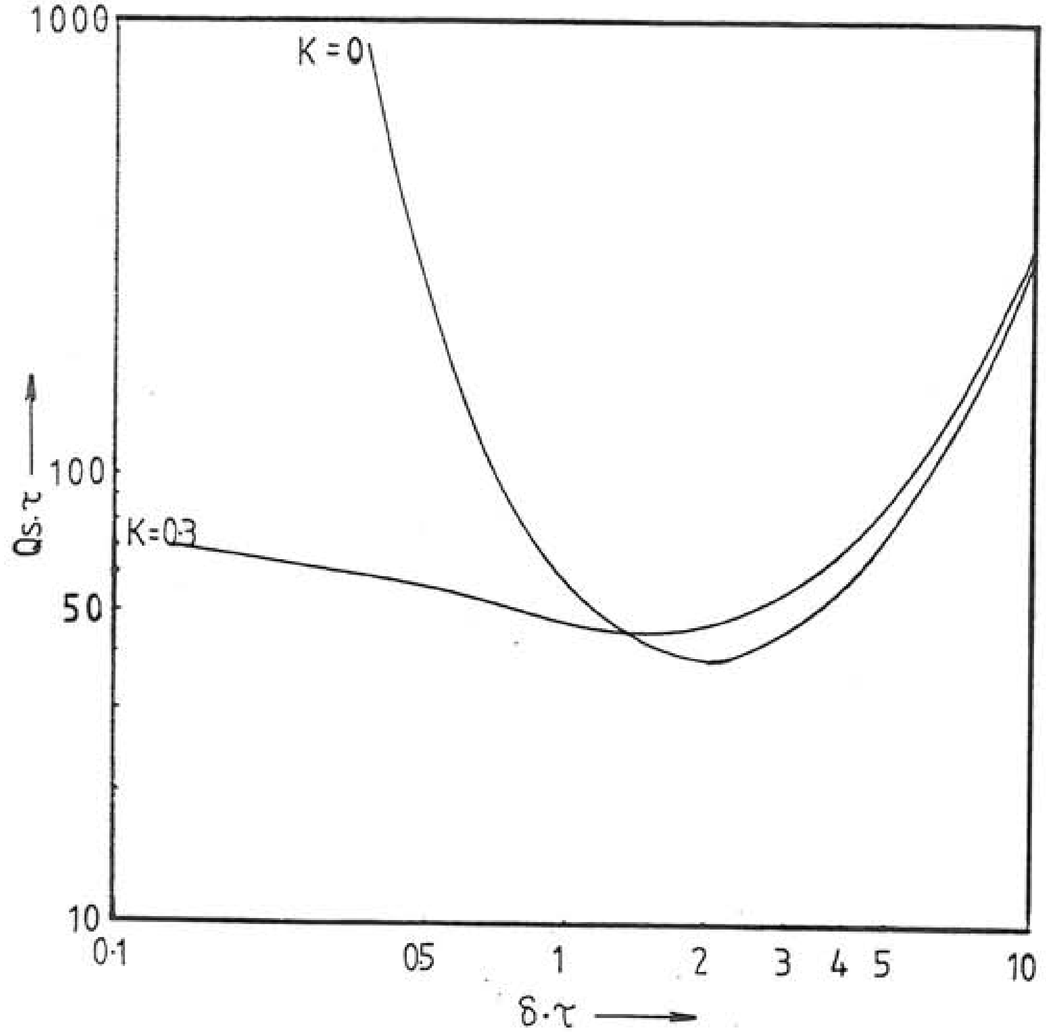


FIG. 3.2.5 Local stability boundaries for the I/M split model. For both density independent death rate (K = 0) and density dependent death rate (K = 0.3), the boundaries are calculated with τ_L = 11 days and τ_I = 4 days.

keep all 'book-keeping' consistent. Such a model yields stability boundaries like those shown in Fig. 3.2.5. This type of analysis, however, is of little utility unless estimates for Qs referring to mature individuals only, and estimates for the death rates of immature, δ_I, and mature, δ_M, individuals can be made.

These parameter estimates obviously depend upon how N is split into I and M classes which, in turn, depends upon assumptions concerning the length of τ_I and the assumed values of δ_I and δ_M. A few simple, investigative attempts have been made.

If δ_I is assumed to be zero, as is suggested by Nicholson (1957, Fig. 6) or very low (0.013 d^{-1}), as is suggested by Fig. 2.2.2, then the calculated mature population often (predominantly when population levels are very high) goes negative and, as if to compound the misery, eggs continue to be produced at such times. To prevent this biological implausibility, δ_I may be assumed equal to δ_M. Such assumptions lead to attractive I/M splits but these are specious, the assumptions are wholly unreasonable.

Although, therefore, the model analysis is straightforward, the data splitting is not and there is little information that can usefully be gained until the age-classes can be realistically separated. This endeavour is left until chapters 5 and 6.

3.3 DETERMINISTICALLY SIMULATING THE CONTROL EXPERIMENT

Fig. 3.3.1 shows the deterministic simulation of the 1957 control experiment. As predicted in 3.2.1, the overall mean population rises with time. Also, as observed by Nicholson, the population size at oscillation minima rises steadily as the experiment progresses. The power spectrum (Fig. 3.3.2a) of the simulation for the first 400 days reveals that the period of the simulated cycles is close (40 ± 2 days) to that of the experimentally observed cycles over the same period (38 ± 2 days). Whilst, however, the simulation continues to display such cyclic behaviour after 400 days, the data are essentially aperiodic. The amplitude of the predicted cycles is somewhat greater than that observed experimentally and the population minima and maxima are also greater. Eventually, as the simulation progresses, the cycles damp out, finally tracking the instantaneous equilibrium after about 600 days.

3.4 DISCUSSION

The deterministic simulation of the 1957 control experiment captures the gross features of the data, but, in the absence of age-structure and/or noise, there is little fine-detail present.

The prediction of the switching time by the G-B-N model, given the parameter estimates, is in good agreement with

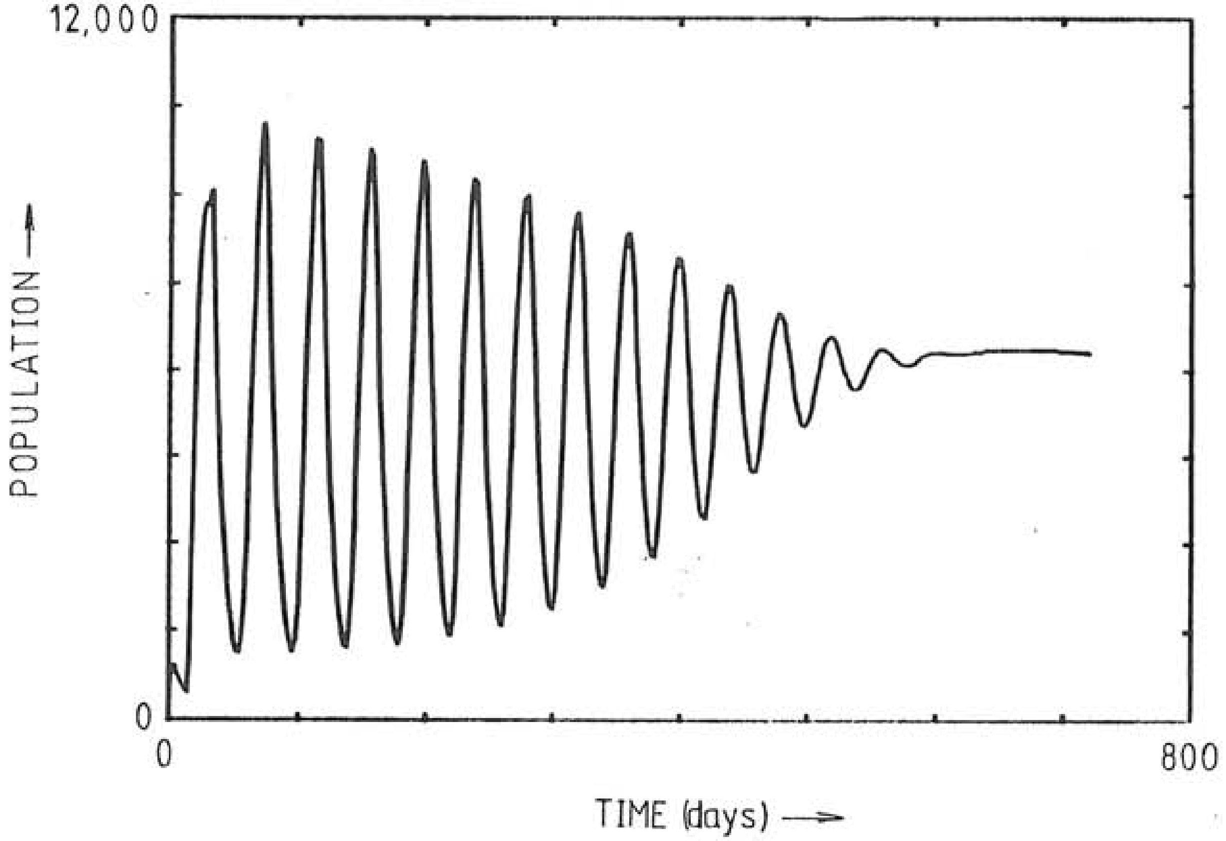


FIG. 3.3.1 Deterministic simulation of the control data based on the parameter estimates obtained in chapter 2.

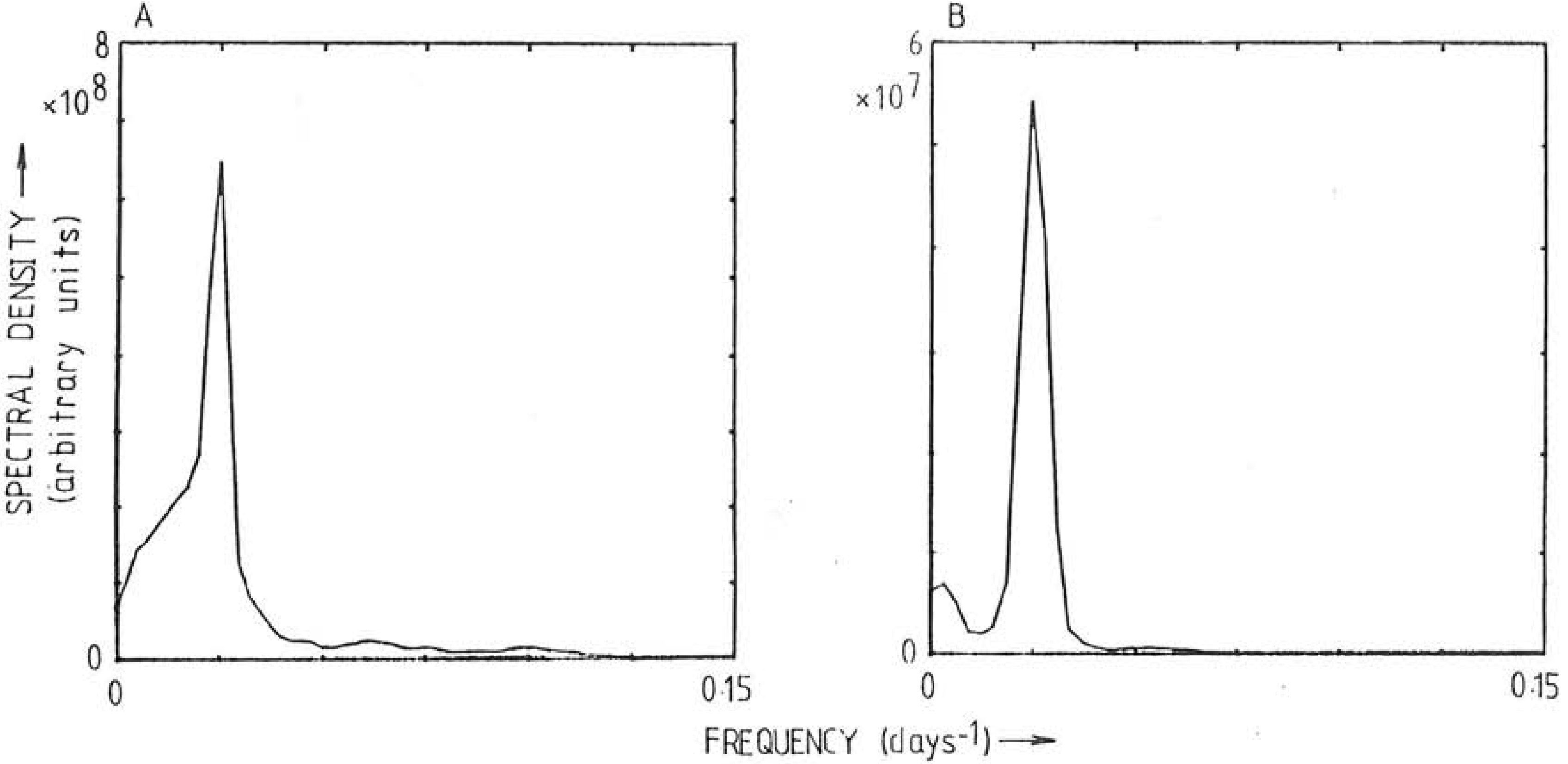


FIG. 3.3.2 Power spectra of the simulation (Fig. 3.3.1).

A) 0 < t ⩽ 400 days. B) 400 < t < 720 days.

that observed experimentally - the same cannot be said of the switching time predicted by the density dependent death rate model. Two things may be said about this. Firstly, density dependent mortality per se, taking no account of age or other effects, is not a good description of the death process in the blowfly experiments. For modelling purposes, in the absence of explicit age-structuring, density independent mortality is justifiable. Secondly, the G-B-N model was heuristically derived and was accepted (Gurney et al, 1980) as a valid model of the blowfly populations on the grounds that it provided a satisfying qualitative fit to the data and was in good quantificative agreement; the accurate prediction of switching time is a further empirical justificaton for the adoption of the model.

In section 1.2 attention was drawn to previous characterisations of Nicholson's blowfly populations as being chaotic; the results of this chapter confirm the earlier contention that this is not the case. Far from being chaotic, the 1957 control population eventually moves towards stability. That the population is initially unstable, however, is in agreement with characterisations of the 1954b data by Maynard-Smith (1974), May (1974a) and Gurney et al (1980).

With the exception of the blowflies, none of the species considered by Hassell et al (1976) were classified as chaotic; all but one, indeed, were deemed to display dynamic stability. That stability is the norm amongst laboratory populations as well as natural populations is supported empirically by Thomas, Pomerantz and Gilpin (1980) and by Mueller and Ayala (1981a,b,c); both sets of authors reporting exclusively on Drosophila spp. - Thomas et al on 27 and Mueller and Ayala on 25.

Both Thomas et al and Mueller and Ayala, having demonstrated that stability is the normal state for laboratory Drosophila populations, attempt to explain how such a condition might arise. Thomas et al invoke group selective arguments whilst Mueller and Ayala look no further than the level of the individual.

Thomas et al argue that populations with chaotic dynamics are likely to go extinct sooner than non-chaotic populations. Their idea is that selection acts at the level of the group by favouring populations which are likely to persist longer. Clearly, in the case of a single population of blowflies, such an argument is not valid. The 1957 control population is not, like the Drosophila populations of Thomas et al, stable throughout the experiment (stability having already been selected), but stabilizes during the experiment. Any genetic mechanism underlying such stabilization must be acting at the level of the individual.

It seem probable that the stabilization of the 1957 control population occurs as a result of a trade-off between competitive ability and competitive resilience. How, precisely, this occurs is beyond the scope of this discussion but Nicholson's blowfly data is now seen to be useful in investigating the evolution of stability - it is the only good population data in which stabilization has (demonstrably) taken place.

CHAPTER 4

THE DYNAMIC CONSEQUENCES OF CHANGING VITAL-RATE PARAMETERS IN A VARIABLE ENVIRONMENT

4.1 INTRODUCTION

In this chapter, the effects of changing vital-rate parameters are investigated in both deterministically and randomly varying environments. In section 4.2 a deterministic simulation of Nicholson's 20-day driven experiment (Fig. 1.1a) is presented. This simulation is included as a test of the argument forwarded in the preceding chapters, that the parameter changes (particularly of f_o) are an outcome of selection, mediated by competition for protein.

The deterministic simulation of the control experiment (Fig. 3.3.1) exhibits a gradual approach to stability; the control data, however, displays large fluctuations in the later stages of the experiment. Such fluctuations can be explained as resonant quasi-cycles which may arise due to either exogenous or endogenous perturbations. Whether or not any noise in the blowfly experiment is demographic rather than environmental is considered in section 4.3. Simulations are then performed which incorporate stochasticity.

It is not intended by incorporating stochasticity that the data might be faithfully reproduced. Performing stochastic simulations is a route to strengthening the argument that the altered dynamics observed in the experiment are truly caused by changes in fecundity, death rate and competitive resilience.

4.2 SIMULATING THE 20-DAY, DRIVEN EXPERIMENT

It was argued in chapter 2 that the altered dynamics perceived in both the control and 20-day driven experiments could best be explained by stabilization of the population with time. It is now intended to use the parameter estimates obtained for the control experiment in an attempt to simulate the driven experiment. The question to be answered is this: is the apparent stabilization of the driven experimental population caused by a similar mechanism to that operating in the control?

4.2.1 PREDICTING THE SIMULATED BEHAVIOUR

In the 20-day driven experiment, a 40-day cycle predominates for about 500 days and then gives way to a series of cycles with a period of 20 days. In chapter 2 this behaviour was explained as possibly being synchronization to the half-harmonic of the driving frequency whilst the population was unstable, followed by a simple capturing of the (now) stable population by the driver. Invoking the same mechanisms now leads to the prediction, given the $Qs\tau D$-$\delta\tau D$ trajectory of Fig. 3.2.2, that the deterministic simulation should display a dominant period of 40 days over the first (roughly) 390 days which will then give way to a period of 20 days. The average population should rise throughout the experiment as f_o declines.

4.2.2 THE SIMULATION

Fig. 4.2.1 shows a deterministic simulation of the 20-day driven experiment. This simulation used the parameter estimates (for Qs, δ and f_o) obtained from the control data and used to produce the undriven simulation (Fig. 3.3.1). The protein supply, Φ, in the driven simulation is step-wise pyramidal, following precisely that used experimentally.

As with the simulation of the control, the general features of the data are captured by the deterministic simulation. In particular, the 40-day cycle eventually gives way to a 20-day cycle (see Figs. 4.2.2a and b). The switching-time, however, is much earlier in the simulation than in the data - notice that the power spectrum (Fig. 4.2.2b) of the simulation after the 500th day, reveals only a 20-day period. In the data (see Fig. 2.1.3b) there is still a 40-day periodicity evident in the later stages.

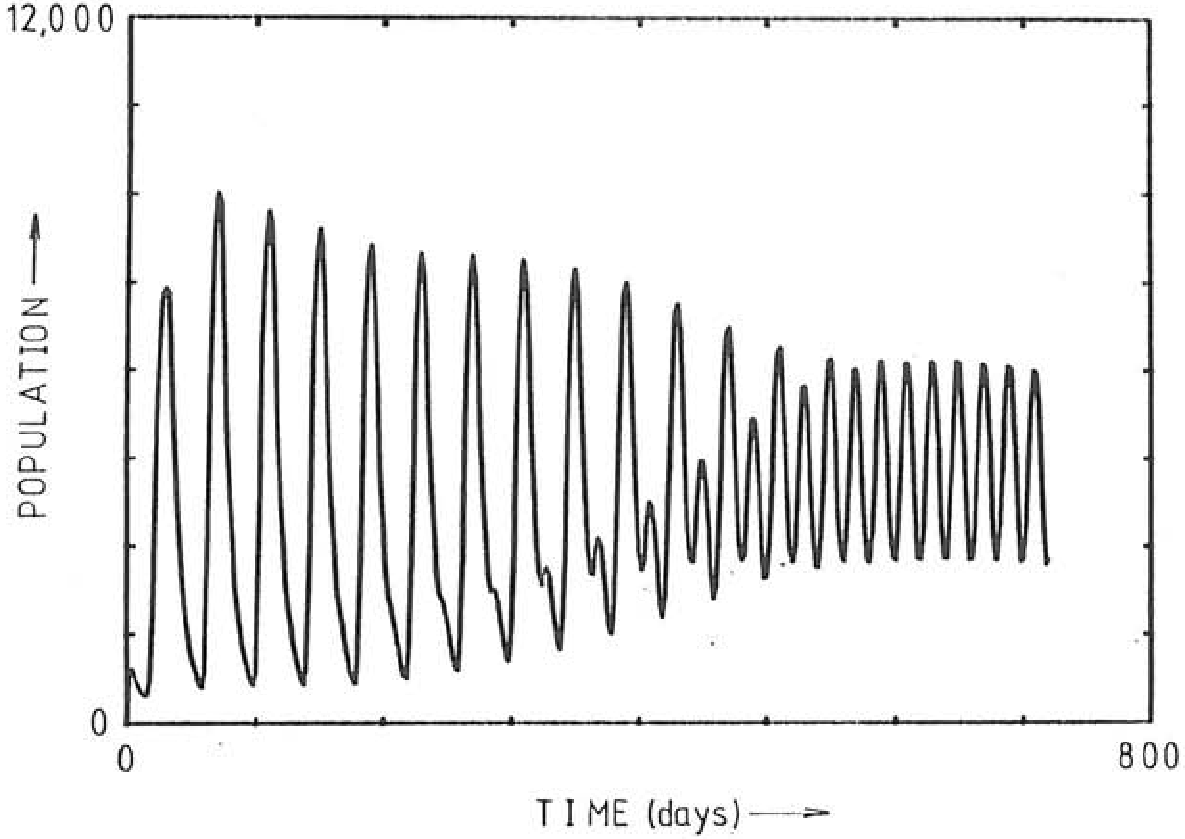


FIG. 4.2.1 Deterministic simulation of the 20-day, variable protein input experiment. The simulation is based on the parameter estimates for the control data.

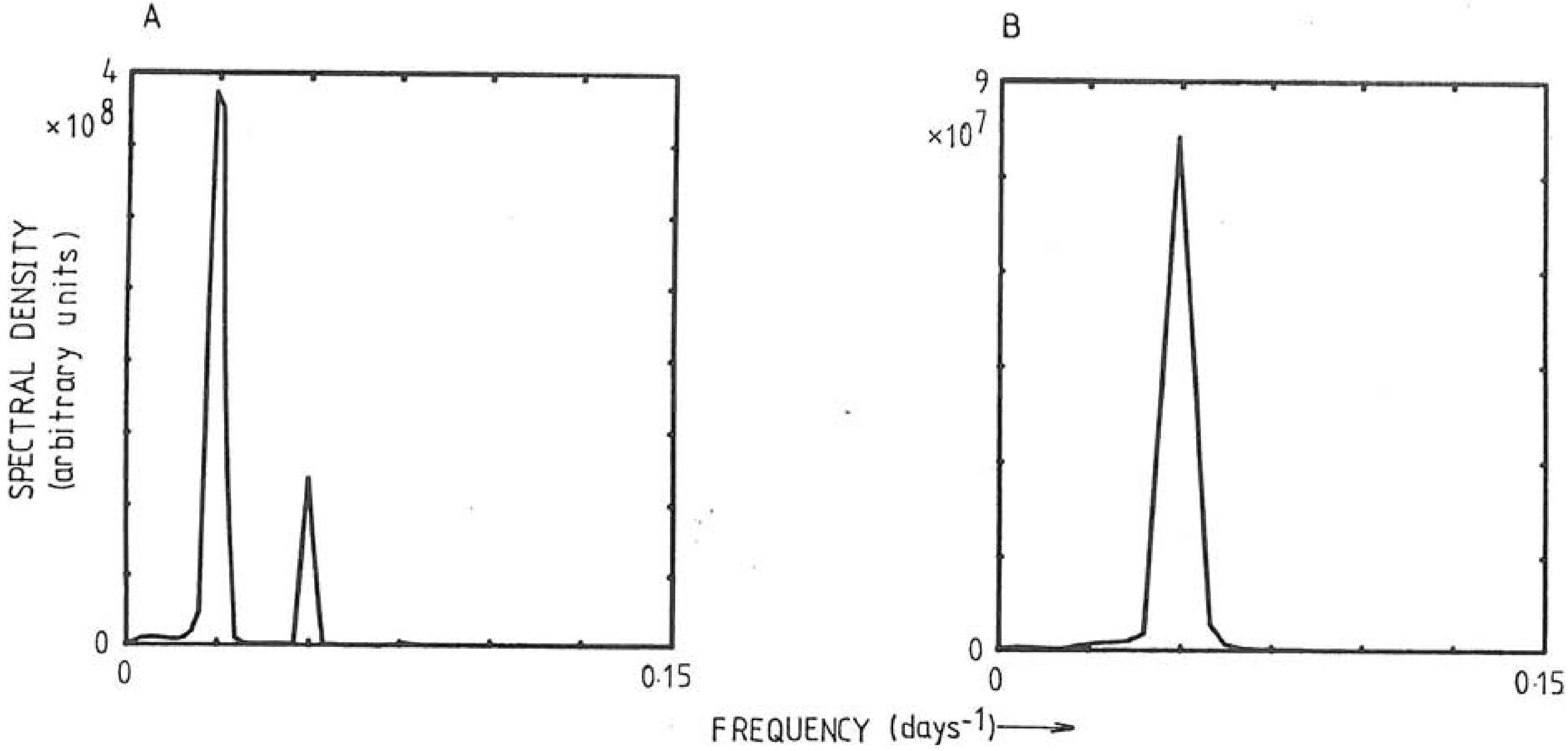


FIG. 4.2.2 Power spectra of the simulation shown in Fig. 4.2.1.

A) $0 < t \leqslant 500$ days. B) $500 < t < 720$ days.

4.2.3 DISCUSSION

That the general features of the driven simulation are similar to those observed in the experiment is indicative of a similar, stabilizing mechanism in operation. The rate at which this mechanism operates, however, is different in the control and driven experiments. This may be argued as being supportive of the argument that selection is the underlying, stabilizing force.

The rate at which competitive resilience evolves (i.e. at which f_0 declines) must depend upon the selective pressure, competition for protein. The only difference between the control and driven experiments is the protein input rate and hence the force of selection in the two experiments must differ; consequently, the rate of evolution of competitive resilience will also differ and the switching-time from instability to stability will not be the same in the two experiments.

That both the control and 20-day driven populations stabilize during the course of experimentation is indicative that individual selection is a sufficient explanation for the evolution of stability. The suggestion at the end of chapter 3, that Nicholson's control data might be beneficially utilized in studying the evolution of stability should be extended to include the 20-day driven data.

4.3 INCORPORATING STOCHASTICITY

4.3.1 IS THE NOISE DEMOGRAPHIC OR ENVIRONMENTAL?

Births and deaths are essentially random events resulting in the appearance or disappearance of a single individual. The fluctuations that may thus be produced are said to be driven by "demographic stochasticity" (or "whether or not God plays dice", Turelli, 1982). The process is only important, however, when populations are small, i.e. when the coefficient of variation ($\equiv \sqrt{N}/N$) is large. In Nicholson's control experiment the adult population almost never falls below 300 flies implying a maximum coefficient of variation of less than 6%. We may therefore conclude that simple demographic stochasticity is not important.

To convince the reader that demographic stochastic effects are, indeed, small, Fig. 4.3.1 shows a simulation of the control experiment subject to demographic stochasticity. The procedure used in constructing this simulation is outlined in Appendix 3. The simulation is virtually indistinguishable from its deterministic counterpart (Fig. 3.3.1) except that during the last 200 days, a small amount of jitter is discernible. Incorporating demographic stochasticity does not cause endogenous resonant quasi-cycles whilst the population is characterised as stable; if, therefore, the population fluctuations observed in the later part of the control experiment are quasi-cyclic and if the system has been

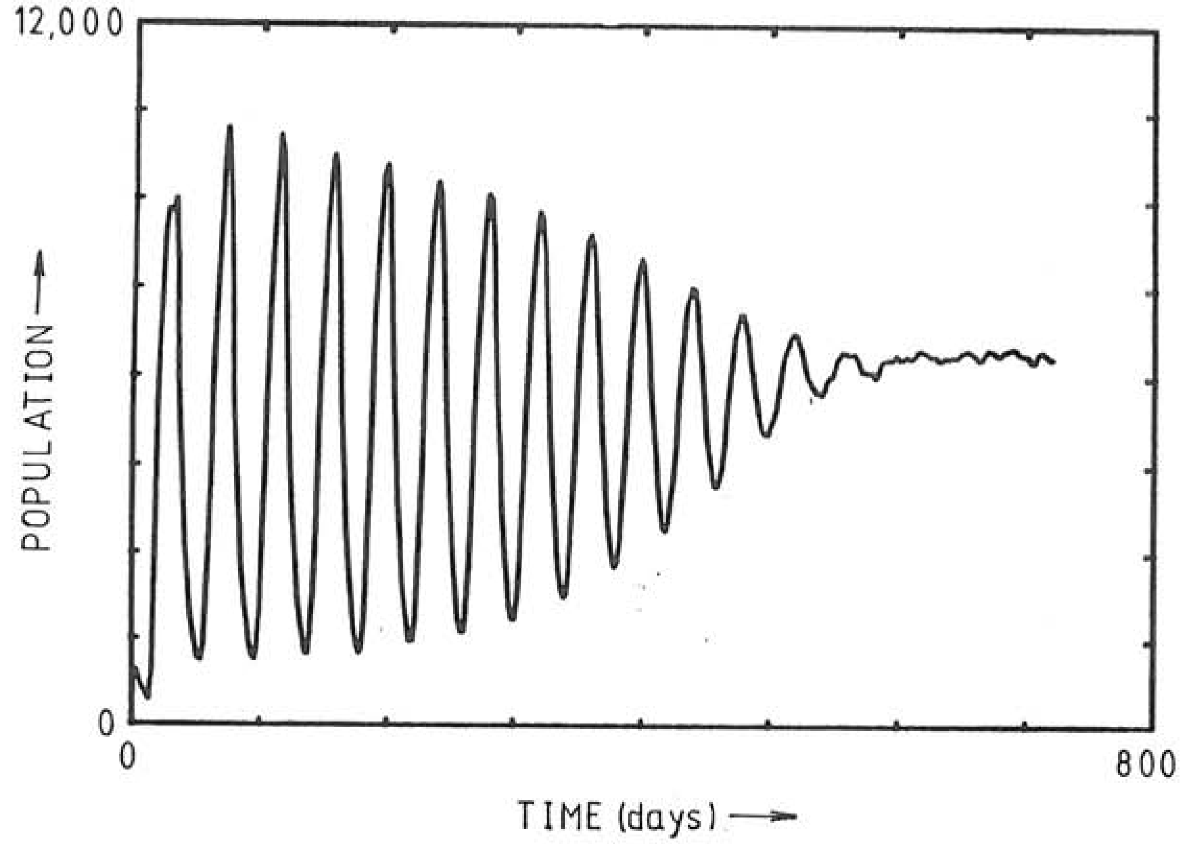


FIG. 4.3.1 Simulation of the control experiment incorporating demographic stochasticity as outlined in Appendix I.

correctly characterised, such cycles must be exogenously induced.

Environments may vary unpredictably through time (environmental stochasticity) in ways that are often assumed to affect all individuals equally. Over a 2-day interval, such variations will be averaged to some extent; also, in a well-controlled laboratory experiment, environmental variability should be small. Environmental stochasticity might also, therefore, be expected not to have a large effect; Nisbet and Gurney (1982 p298) indicate, indeed, the expectation that if quasi-cycles are a valid representation of the blowfly populations, then such cycles would be driven by demographic noise. Even a small environmental variation may, however, have a large effect on the stable, underdamped population (Nisbet and Gurney, 1976b; 1982 ch 7 p255 - "exogenous resonant quasi-cycles") - the spectral density of the population fluctuations being proportional to that of the environmental noise.

It is possible to measure the noise due to environmental effects in the data if we assume that our parameter estimates for the birth and death rates are deterministically valid and that demographic stochastic effects are small in comparison to environmental fluctuations. At any time, the data contains the actual birth and death rate information and we already have estimates of these rates through time. The difference (or 'residuals') between the actual and predicted series should, if the estimates are correct, be a measure of the wobble induced in the vital rates by stochastic environmental variations.

If, however, the estimates are deterministically inadequate (due to unconsidered demographic factors) then we might also see additional pattern in the residual series - specifically, periodicities representing age or density effects. Let us consider both birth and death rate residuals in turn.

A) BIRTH RATE RESIDUALS

Birth rate residuals plotted against time are shown in Fig. 4.3.2. The series is calculated as

$$\text{BIRTH RATE (DERIVED FROM DATA)} \\ - \langle Qs(t)\rangle \exp\{-N(t)\langle f_0(t)\rangle/\Phi\}$$

where '$\langle\rangle$' denotes the estimated parameter value at time t, derived in chapter 2.

Prediction is clearly imperfect; birth rate is often largely underestimated. A close inspection of the residual series reveals, however, that following each underestimate, there is a smaller overestimate. It is

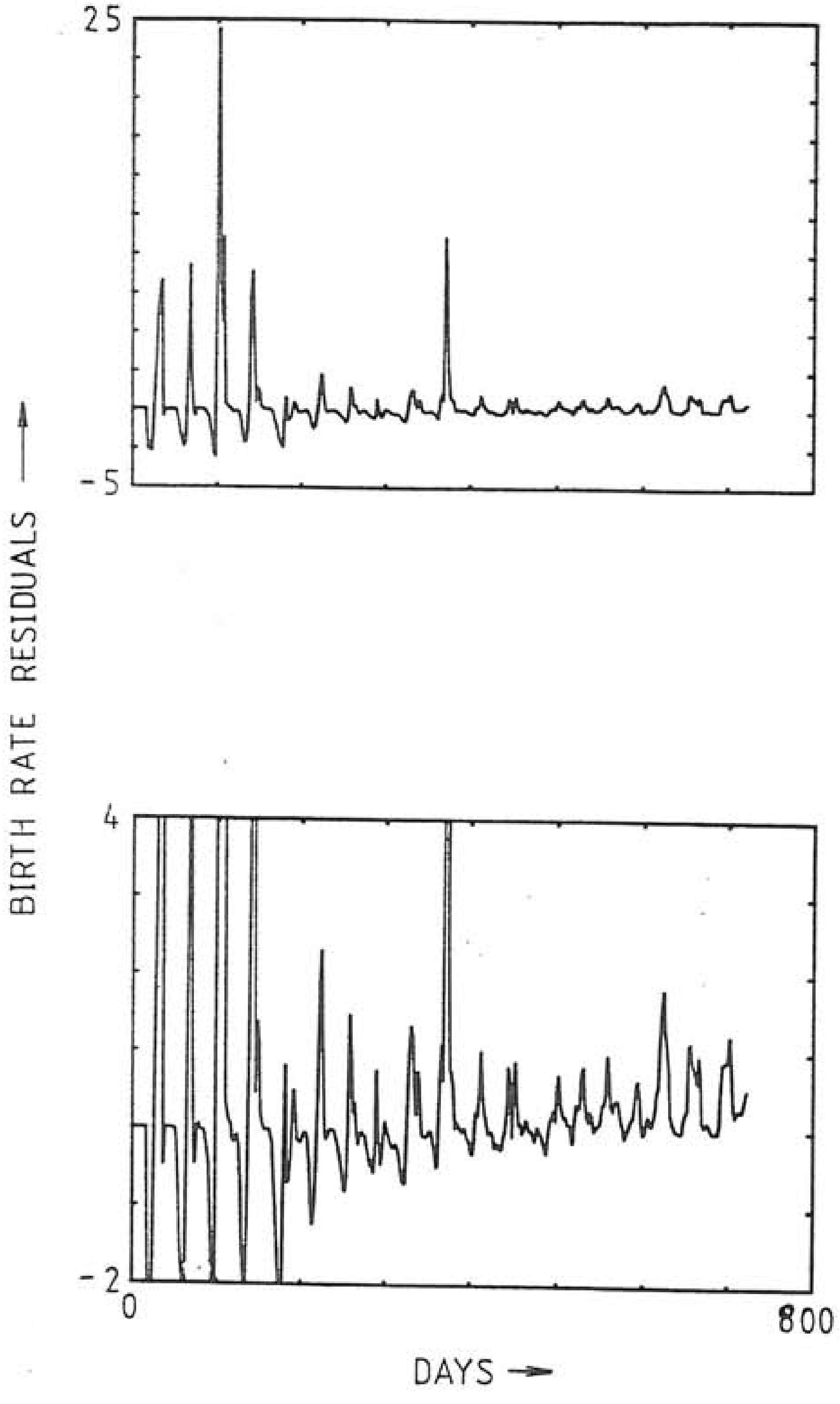


FIG. 4.3.2 Birth rate residuals (= actual-predicted birth rate) plotted against time.

apparent from the power spectra (Figs. 4.3.3a and b) of the birth rate residuals that over the first 400 days of the series the deterministic errors in prediction are due to two different mechanisms, one occurring with a period of 38 (± 2) days which is almost equal (see Fig. 2.1.2) to a population cycle - and one with a period roughly equal to a single generation length (19 ± 2 days). These two periods may represent, respectively, density and age effects. That the generation length period is not apparent in the power spectrum after the 400th day (Fig. 4.3.3b) is supportive of this notion as, if the population is indeed stabilizing, the age-structure is more stable after this time.

It was argued previously in chapter 2 that over the first few population cycles, the age-structure of the experimental poulation is greatly influenced by the initial conditions. The large discrepancies observed between prediction and reality over the first 200 days may be due to this factor; for times after day 200, prediction is much better. Notice that not only has the single generation period disappeared after the 400th-day but that the total power is also much reduced.

B) DEATH RATE RESIDUALS

Fig. 4.3.4 shows death rate residuals plotted against time. The series is calculated as

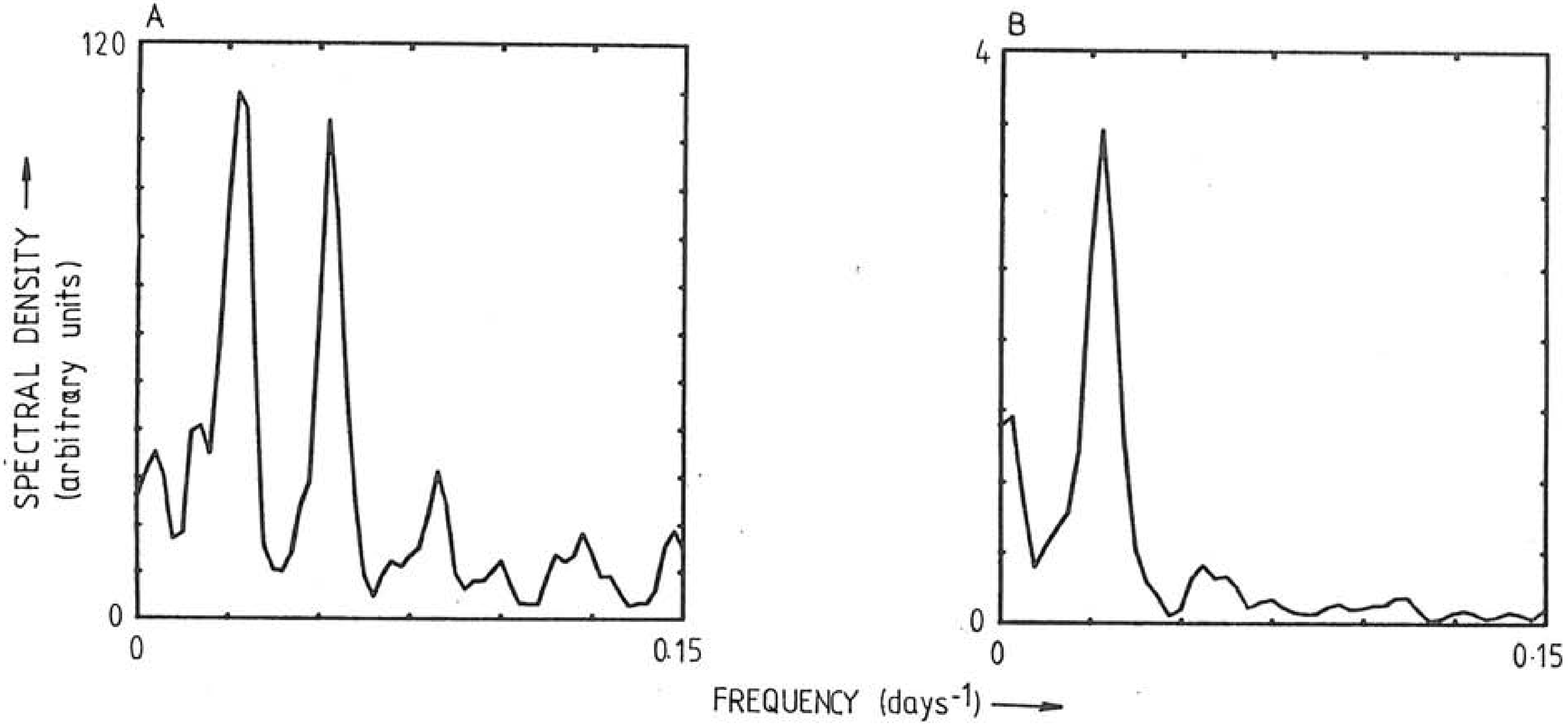


FIG. 4.3.3 Power spectra of the birth rate residuals series.

A) $0 < t \leqslant 400$ days B) $400 < t < 720$ days.

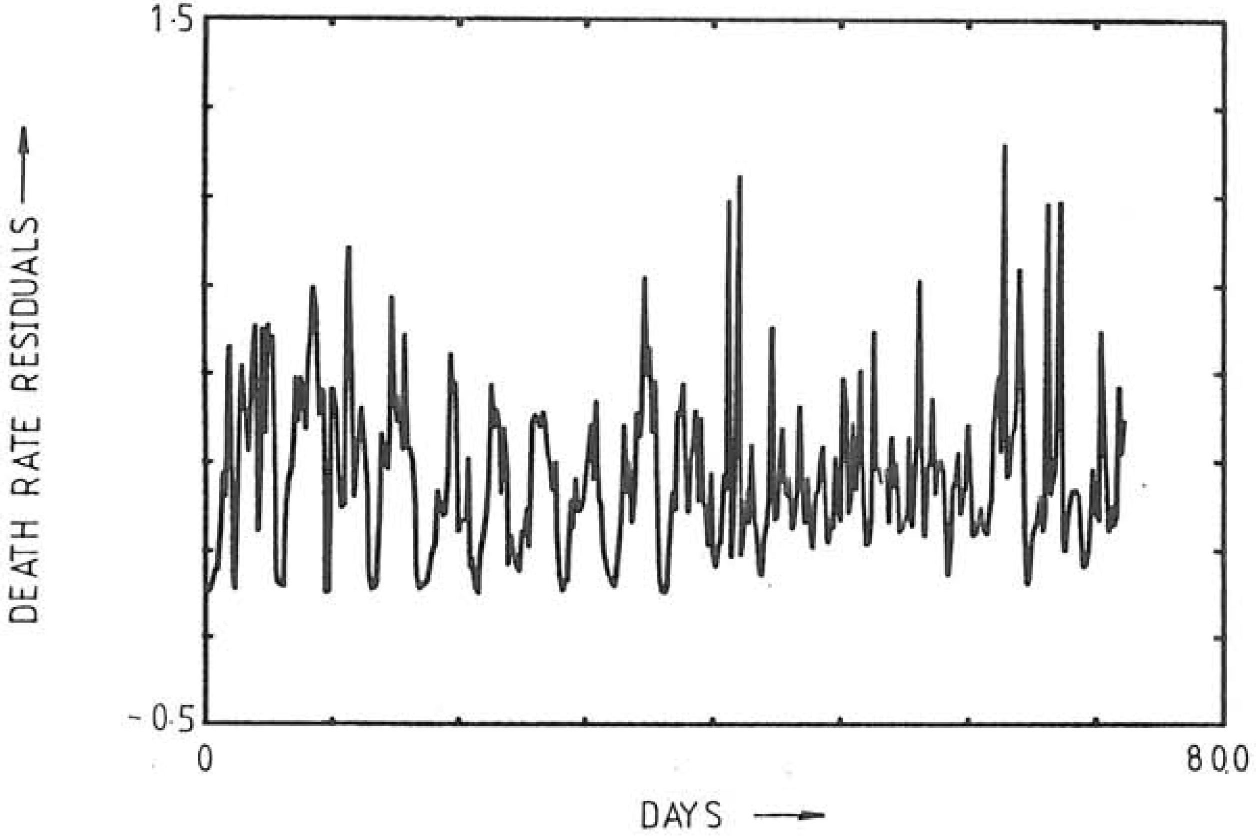


FIG. 4.3.4 Death rate residuals (= actual-predicted death rate) plotted against time.

DEATH RATE (derived from data) - $\langle \delta(t) \rangle$

As with birth rate, prediction is imperfect - again being largely underestimated. The power spectra (Figs. 4.3.5a and b) of the death rate residual series indicate, though, a different underlying cause of imprecise prediction. Fig. 4.3.5a reveals that errors in death rate prediction of the unstable population (i.e. t < 400 days) are cyclic with a period of one population cycle. There is no evidence, however, of a single generation effect. It was argued in chapters 2 and 3 that death rate is only weakly density dependent (being also dependent upon age). The lack of a single generation period in the death rate residuals series is, therefore, slightly surprising because we would expect to see evidence of age, as well as of density dependence.

After the 400th day, when the population has stabilized, the death rate residuals do not display a strong periodicity (see Fig. 4.3.5b) equal to that of a population cycle. The power spectrum reveals that discrepancies between the actual and predicted death rates are much more certainly due to noise alone.

In summary, both birth and death rate predictions are imperfect due to neglect of both density and age effects. There is evidence, though, that the vital rates also vary unpredictably - due, presumably to random, environmental variations.

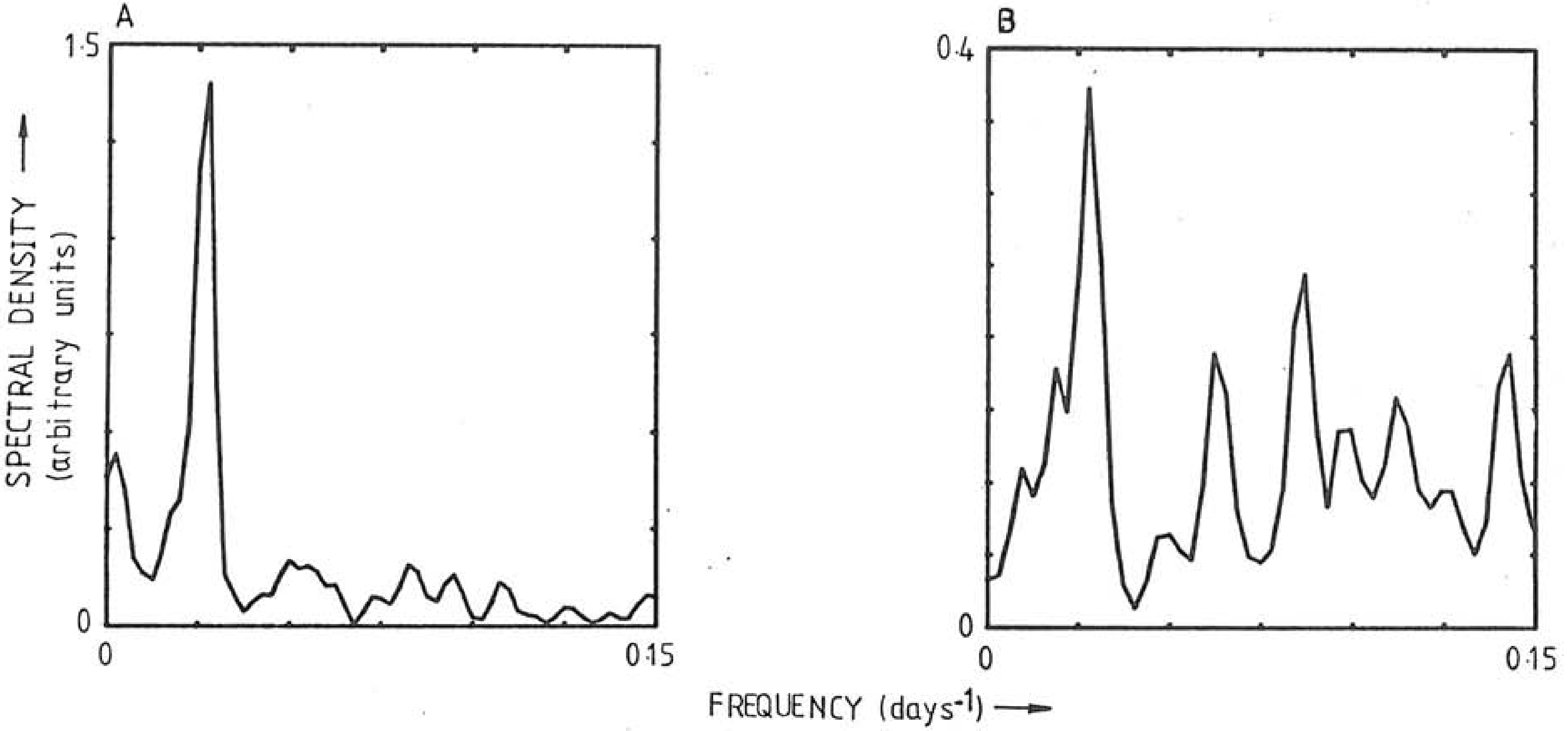


FIG. 4.3.5 Power spectra of the death rate residuals series.

A) 0 < t ⩽ 400 days B) 400 < t < 720 days.

4.3.2 MEASURING THE NOISE AND SIMULATING THE EXPERIMENT

For times less than 400 days the population is characterised as unstable and the observed fluctuations as limit cycles. Environmental noise might perturb such limit cycles and may cause variations in amplitude and even non-repetitive fine structure. We are primarily interested, however, in determining whether or not our characterisation of the population after the 400th day, as stable but influenced by external noise is a reasonable one. To test the characterisation we may measure the noise from the power spectra of the residual series after t = 400 days and simulate the experiment incorporating this noise. The method of incorporation is described in appendix 3.

Essentially, birth and death rates will be calculated as

$$V(t) = V_{DET}(t) + S_v^{1/2}\,\gamma(t) \qquad (4.1)$$

where

$V(t)$ = Vital rate at time t

$V_{DET}(t)$ = the deterministic estimate of the vital rate at time t

S_v = the spectral density of the noise associated with the residual series

$\gamma(t)$ = Gaussian white noise of zero mean and unit spectral density.

S_V is estimated for birth and death rates (S_B and S_δ respectively) from the power spectra shown in Figs. 4.3.3b and 4.3.5b as

$$S_\delta^{1/2} = 0.25$$

$$S_{\beta 1}^{1/2} = 0.20 \qquad \text{for } f > 0.05 \text{ d}^{-1}$$

$$S_{\beta 2}^{1/2} = 0.60 \qquad \text{for } 0 < f \leqslant 0.05 \text{ d}^{-1}$$

S_δ is simply the mean spectral density of the death rate residual series after the 400th day (Fig. 4.3.5b). $S_{\beta 1}$ is the mean spectral density of the birth rate residual series (Fig. 4.3.3b) for frequencies greater than 0.05 d^{-1} and thus ignoring the dominant period; $S_{\beta 2}$ is the mean spectral density of the same power residual series for all frequencies shown. To test for the importance of the periodicity present in the birth rate residual series after the 400th day, a simulation with a sinusoidally variable element of Qs is included. Such a deterministically variable portion of Qs is equivalent to representing the dominant period in Fig. 4.3.3b as a delta-function. The amplitude of the continuous (sine) function is taken as $Z^{1/2}$ where Z is the total power present in the peak of the power spectrum. For the simulation with the dominant period present at a frequency of $f = 0.025$ d^{-1}, Qs is represented as

$$Qs(t) = Qs_{DET}(t) + 0.2 \sin(0.157\ t) + S_{\beta 1}{}^{1/2}\ \gamma(t) \qquad (4.2)$$

Fig. 4.3.6 shows a simulation with δ varying deterministically and Qs varying stochastically ($S_{\beta 1}^2 = 0.2$). The effect of such stochastic variation about the deterministic trend in Qs is plainly small - the simulation is barely distinguishable from the deterministic (Fig. 3.3.1) or demographically stochastic (Fig. 4.3.1) analogues for the first 500 days and even after this time, only fluctuates weakly. Increasing the stochastic variability in Qs ($S_{\beta 2}^2 = 0.6$; see Fig. 4.3.7), however, causes larger fluctuations in the stable region but leaves the limit cycles essentially unperturbed. Adding a periodic element (using equation 4.2) has no apparent effect on the limit cycles but produces a capturing of the stable system which then oscillates at the driving frequency (Fig. 4.3.8).

Adding stochastic variation ($S_{\delta}^{1/2} = 0.25$) about the deterministic trend in death rate (Fig. 4.3.9) has a much more dramatic effect. Such variation not only causes considerable perturbation to the limit cycles - even repeatedly causing double-peaks - but induces large quasi-cyclic fluctuations over the last 300 days of the simulation. Fig. 4.3.10a shows a simulation with death rate varying as in Figs 4.3.9 but with additional birth rate variation ($S_{\beta 2}^2 = 0.6$). This is shown for comparison with the data (Fig. 4.3.10b); power spectra (Fig. 4.3.11a-d) of the simulation and data are also

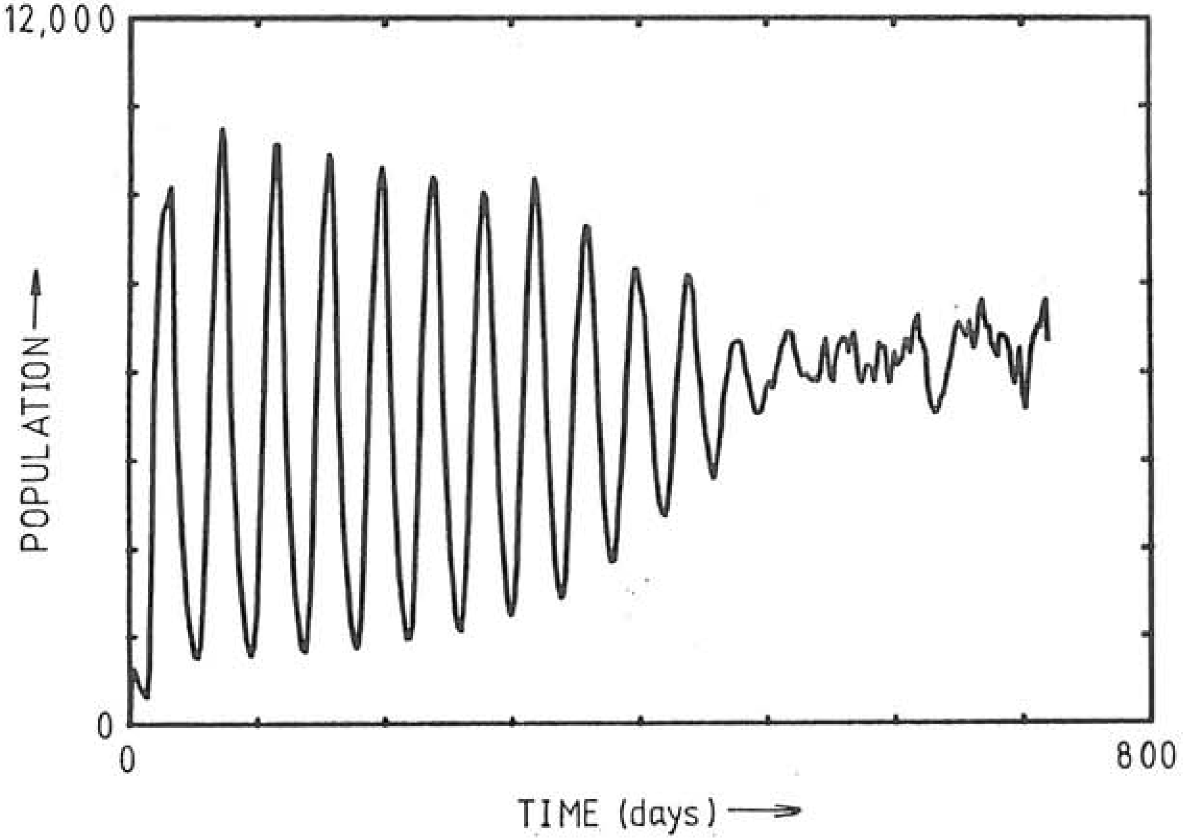


FIG. 4.3.6 Simulation of the control experiment with Qs. varying stochastically ($Qs(t) = QS._{DET}(t) + 0.2\ \gamma(t)$).

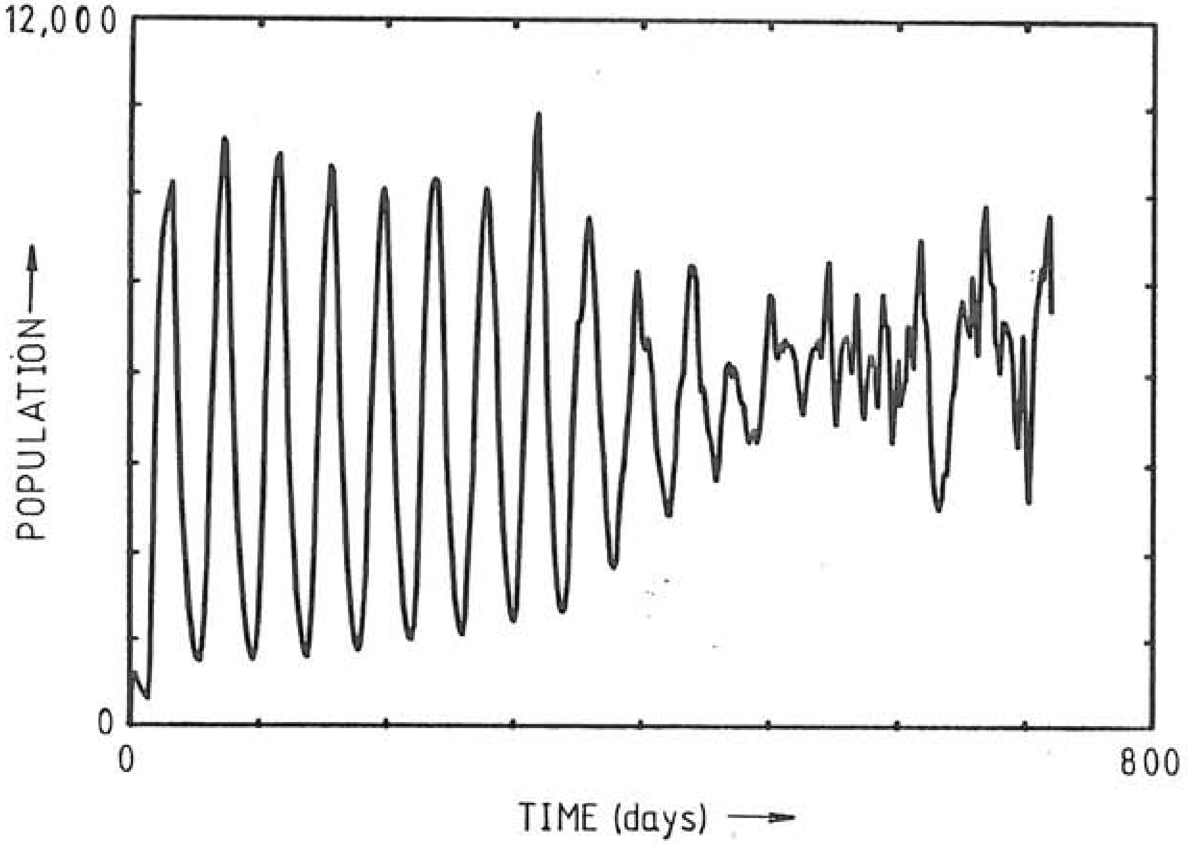


FIG. 4.3.7 Simulation of the control experiment with Qs. varying stochastically ($Qs(t) = Qs_{DET}(t) + 0.6\ \gamma(t)$).

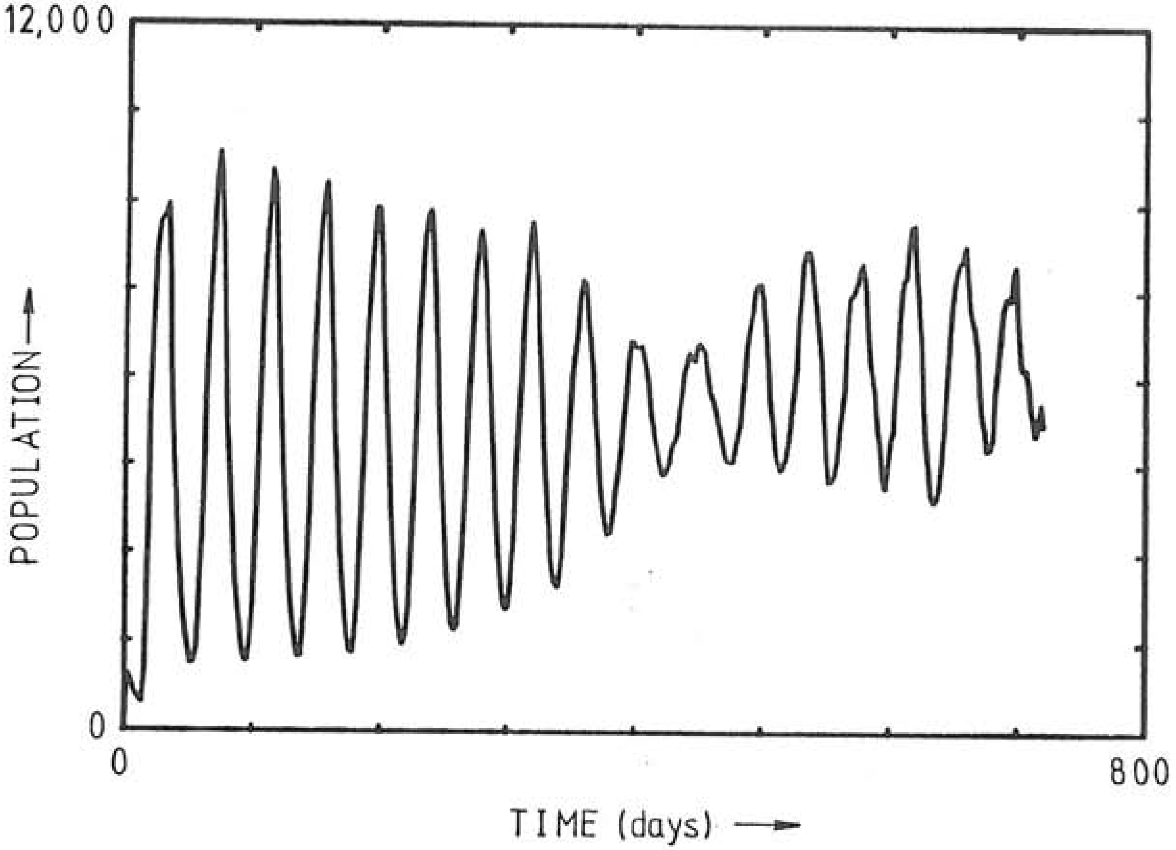


FIG. 4.3.8 Simulation of the control experiment with Qs. varying stochastically ($Qs(t) = Qs_{DET}(t) + 0.2\gamma(t) + 0.2 \sin(0.157\ t)$).

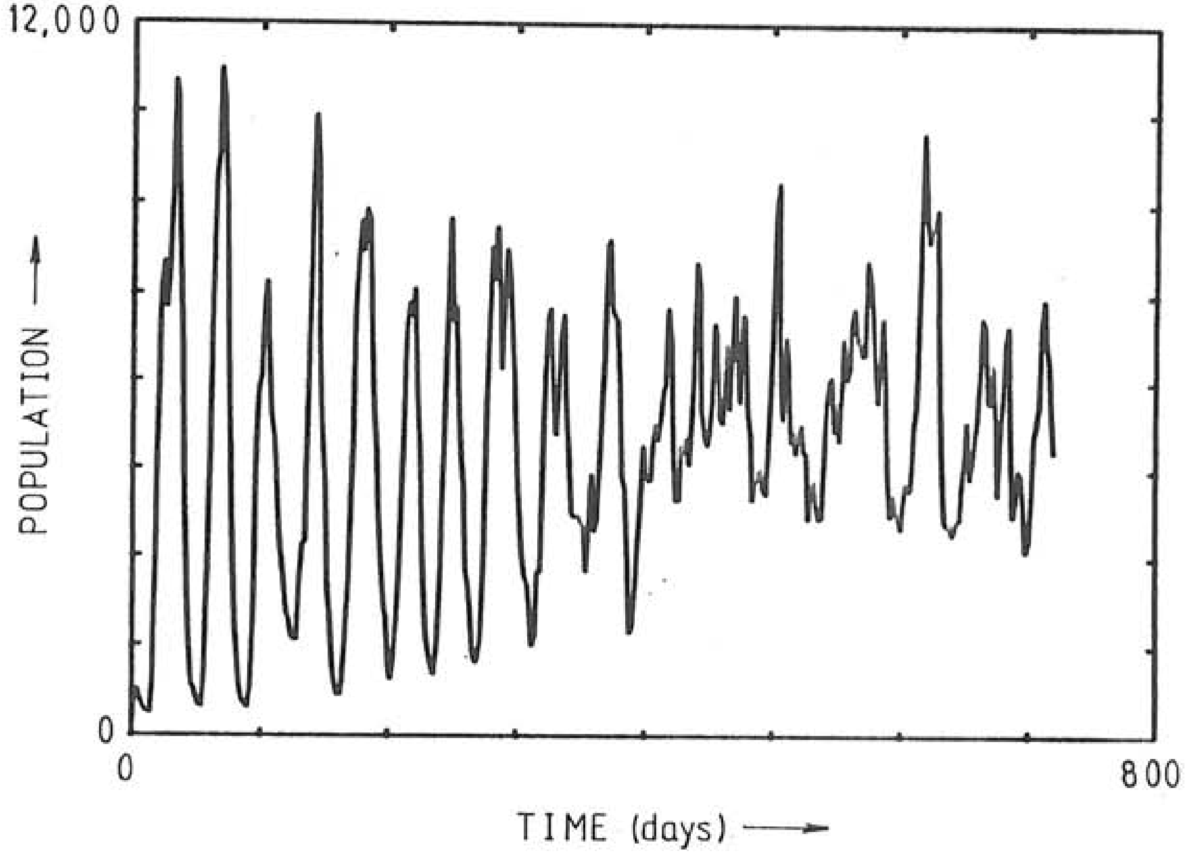


FIG. 4.3.9 Simulation of the control experiment with δ varying stochastically ($\delta(t) = \delta_{DET}(t) + 0.25\,\gamma(t)$).

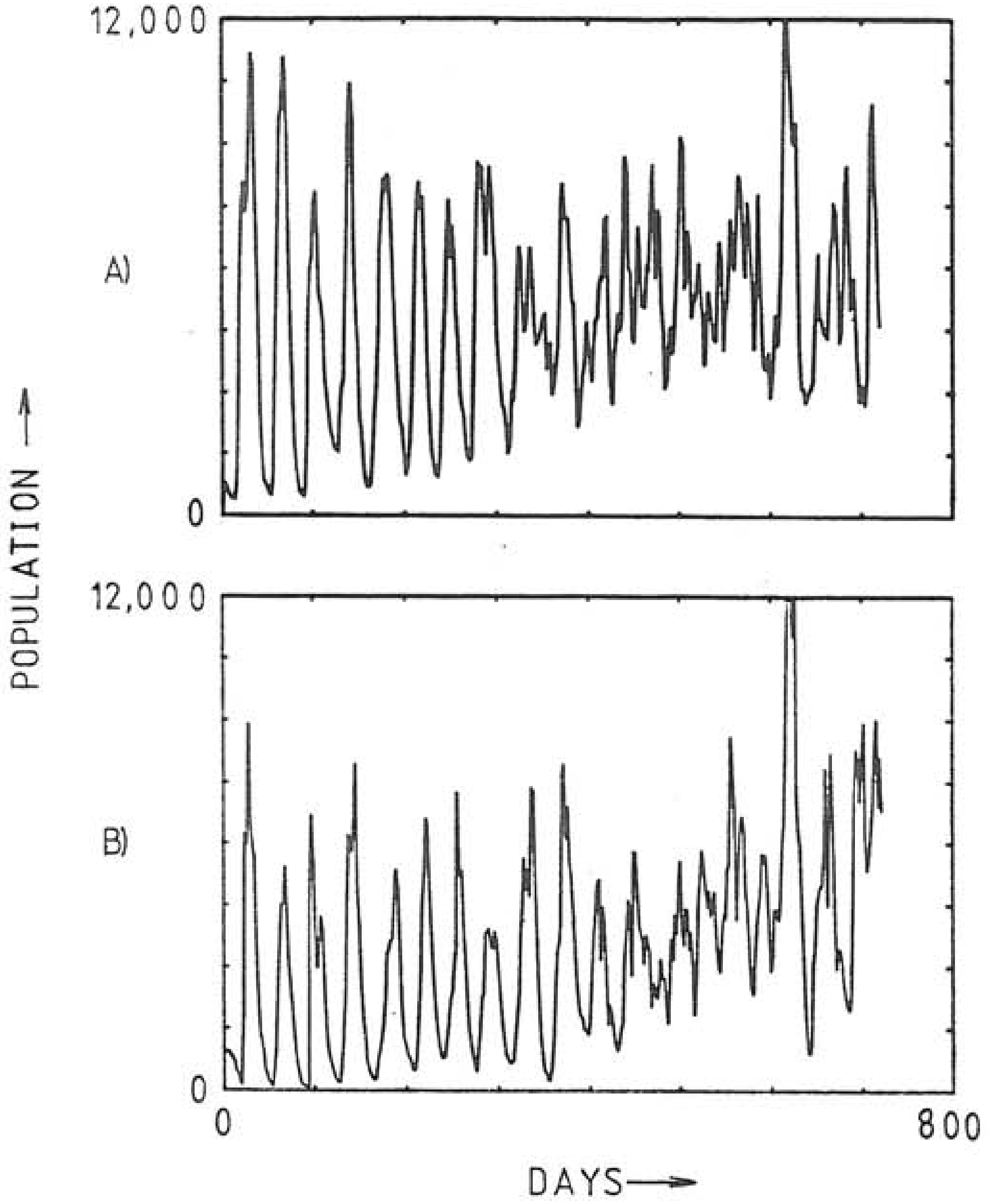


FIG. 4.3.10 A) Simulation of the control data with stochastic Qs and δ (δ as in Fig. 4.3.9, Qs as in Fig. 4.3.7). B) the control data.

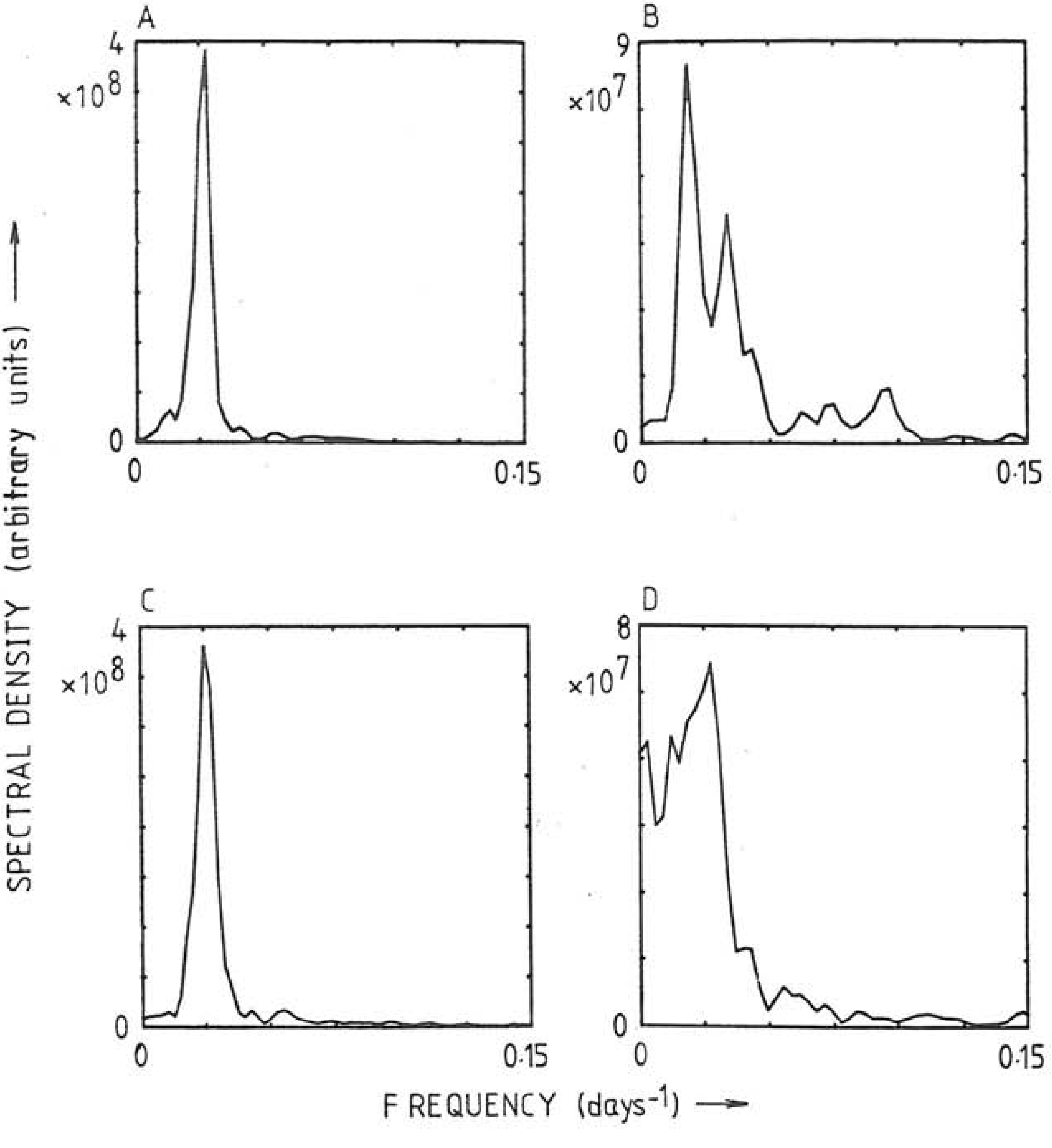


FIG. 4.3.11 Power spectra of the simulation 4.3.10A and the control data (4.3.10B).

- of the simulation	A)	$0 < t \leq 400$ days
	B)	$400 < t < 720$ days
- of the control data	C)	$0 < t \leq 400$ days
	D)	$400 < t < 720$ days.

shown. The qualitative similarity between the simulation and the data is clearly caused by the stochastic variation in the death rate rather than the birth rate.

Although the power spectra in Fig. 4.3.11 illustrates the similarities between data and simulation (i.e. like periods - 40 ± 2 vs. 38 ± 2 days - for the limit cycles giving way to 'broader band' noise in the later stages), there is one feature of the simulation that deserves special mention. The extra 'peak' in the power spectrum of the simulation after t = 400 days (see Fig. 4.3.11b) represents a period of 10-11 days and is not present in the power spectrum of the data (Fig. 4.3.11d). This extra peak appears in all simulations in which the death rate is assumed to vary stochastically. This is due to the way in which such variation is added; the modulus of the transfer function of the G-B-N model with stochastic death rate has an unusual form (see Appendix 4) in which there is more than one peak, the height and precise positioning of which depend upon the precise values of Qs and δ.

That a similar extra peak does not occur in the power spectrum of the data is a reminder that, although the simulation is appealingly similar to the data, the way in which this has been achieved may ignore certain important details of deterministic effects in the death rate.

4.4 DISCUSSION

The deterministically driven simulation of Nicholson's 20-day driven experiment, using parameter estimates obtained from the control data, displays qualitatively similar behaviour to the driven data; this strengthens the idea that the estimates and the model are good representations of the blowfly experiments. Further, that the rates of the caducity producing dynamic changes differ in the control and driven experiments, suggests that the mechanism underlying the vital rate changes is natural selection. This selection must be acting at the level of the individual and both the control and driven experiments are perhaps excellent candidates for the study of the evolution of stability in animal populations.

The dynamic behaviour of the driven experiment is, then, well explained by the hypothesis of stabilization. That the simulations with stochastic variation in the vital rates are qualitatively good facsimilies of the control data suggests that the same mechanism (i.e. stabilization) also affords a satisfactory (and indeed satisying) explanation for the quasi-cyclic behaviour seen in the control data after the 400th day.

Demographic stochastic effects on the control data are shown to be small; measuring environmental stochastic effects is observed by the deterministically imprecise prediction of the vital rates. This imprecision is due to neglect of age-structure in particular, and at least in the case of mortality, density dependence. Including environmental stochasticity in simulations produces fluctuations similar to those observed experimentally - such variability has the most marked effect when introduced in the death rate. This reflects, possibly, the relatively good, deterministic description of birth rate dependent upon density (but not age) and the lack, thus far, of any good deterministic explanation of the variability in death rate.

So far we have employed a model which is a parsimonious descrition of the blowfly population. Despite the lack of complexity, this model has yielded qualitatively good and quantitatively acceptable simulations of the data and has proved, perhaps unexpectedly, to be remarkably heuristic. Heuristic, that is, in the sense that the model has not only led to insight into what underlies the gross population dynamic changes but also through its shortcomings, has focussed attention on the details that need further investigation. Although simple, the model has proved particularly useful in laying to rest the notion that the control dataset is chaotic. Indeeed, the model and parameter estimation exercise has shown that the population behaviour is best characterised by a gradual movement from unstable to stable parameter space caused by selection to increase competitive resilience.

The major weakness of the model lies in its lack of ability to explain the detailed deterministic pattern of the population fluctuations. We must now progress to an inquisition into how age and density (and perhaps history or 'health') influence birth, death and maturation rates. This is the stuff of chapters 5 and 6.

CHAPTER 5

THE DEPENDENCE OF MORTALITY UPON AGE AND DENSITY AND THE INFERENCE OF AGE-STRUCTURE IN THE CONTROL POPULATION

5.1 INTRODUCTION

In chapters 2-4, a simple non-structured model was employed to describe and to explain gross features of the blowfly population dynamics; in this and the ensuing chapter, our attention will be upon how age and density jointly influence vital rates. Clearly, in order to investigate the detailed dependencies of fecundity and death upon age and density, we need access to results of experiments that investigate the problem. Although Nicholson, as pointed out in chapter 1, noticed and commented upon the importance of a changing population age-structure, he neither recorded the ages of flies in the population at any time nor did he examine experimentally how age affects vital rates. There are obvious reasons for this, not least that collecting such data is both very difficult and very expensive.

Experiments to investigate directly how age affects vital rates have, however, been recently performed (Readshaw and van Gerwen, 1983). In these experiments, cultures of _L. cuprina_ were kept at various constant densities as they aged. This was achieved by adding similarly aged flies to cultures to replace individuals as they died. Protein was supplied at the same constant rate in each constant density experiment. The data recorded (see Appendix 7) were the number of eggs laid each day and how many of these survived, also how many of the original population survived. These few recordings, each day, provide a basis for investigating how age and density affect survival (and hence death rate). In the process of investigating age and density dependent death rate it is also possible to infer age-structure in the control population. This age-structure may then, after examining how long adults take to mature throughout the experiment, be used to investigate age-dependent fecundity (see chapter 6).

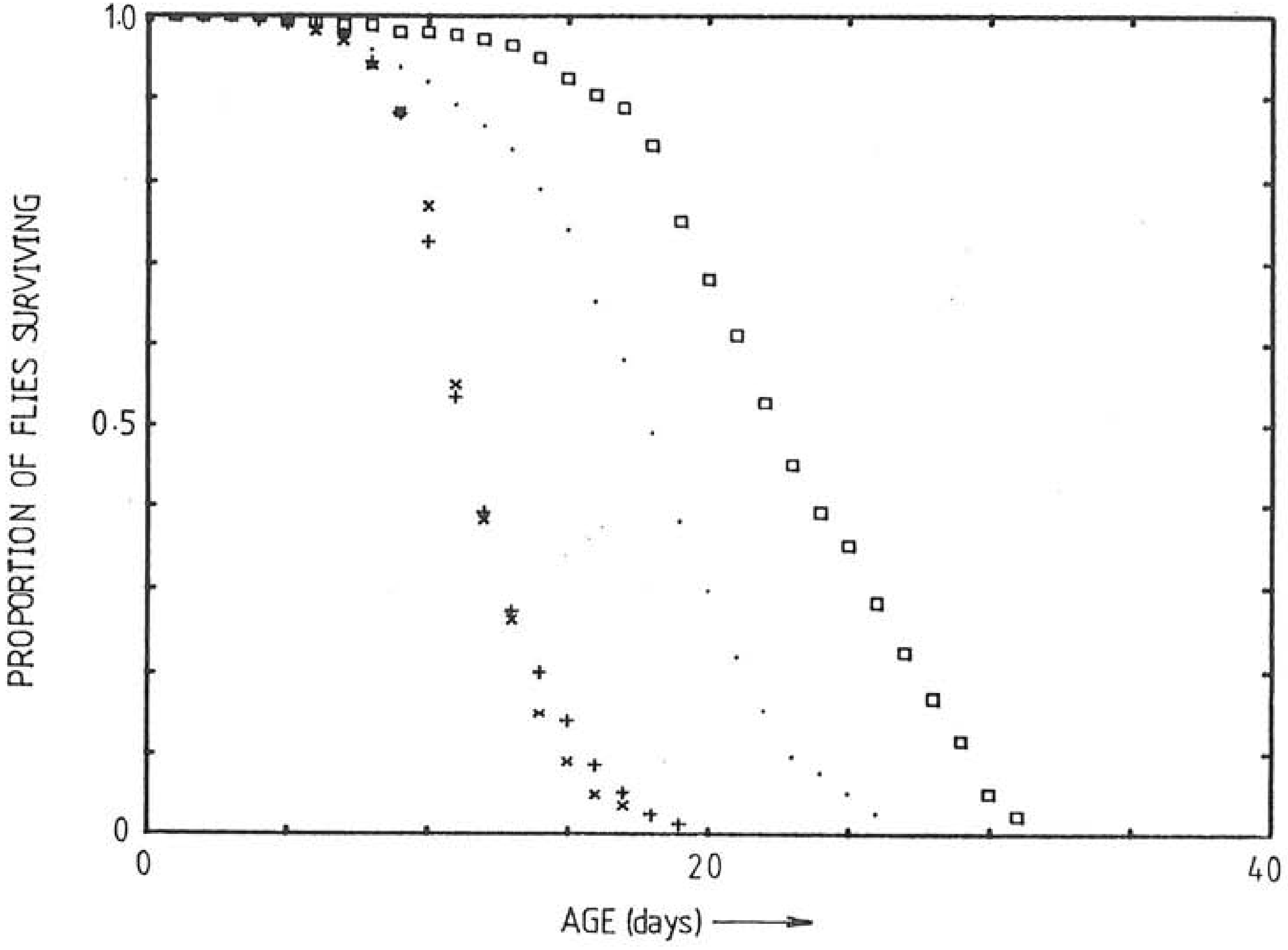
Readshaw and van Gerwen did not attempt any age-structuring of Nicholson's data based upon the results of their constant density experiments; they confined their discussion to the comments that density affects survival and that fecundity is age-specific and hence, might cause fine-structure in the blowfly populations.

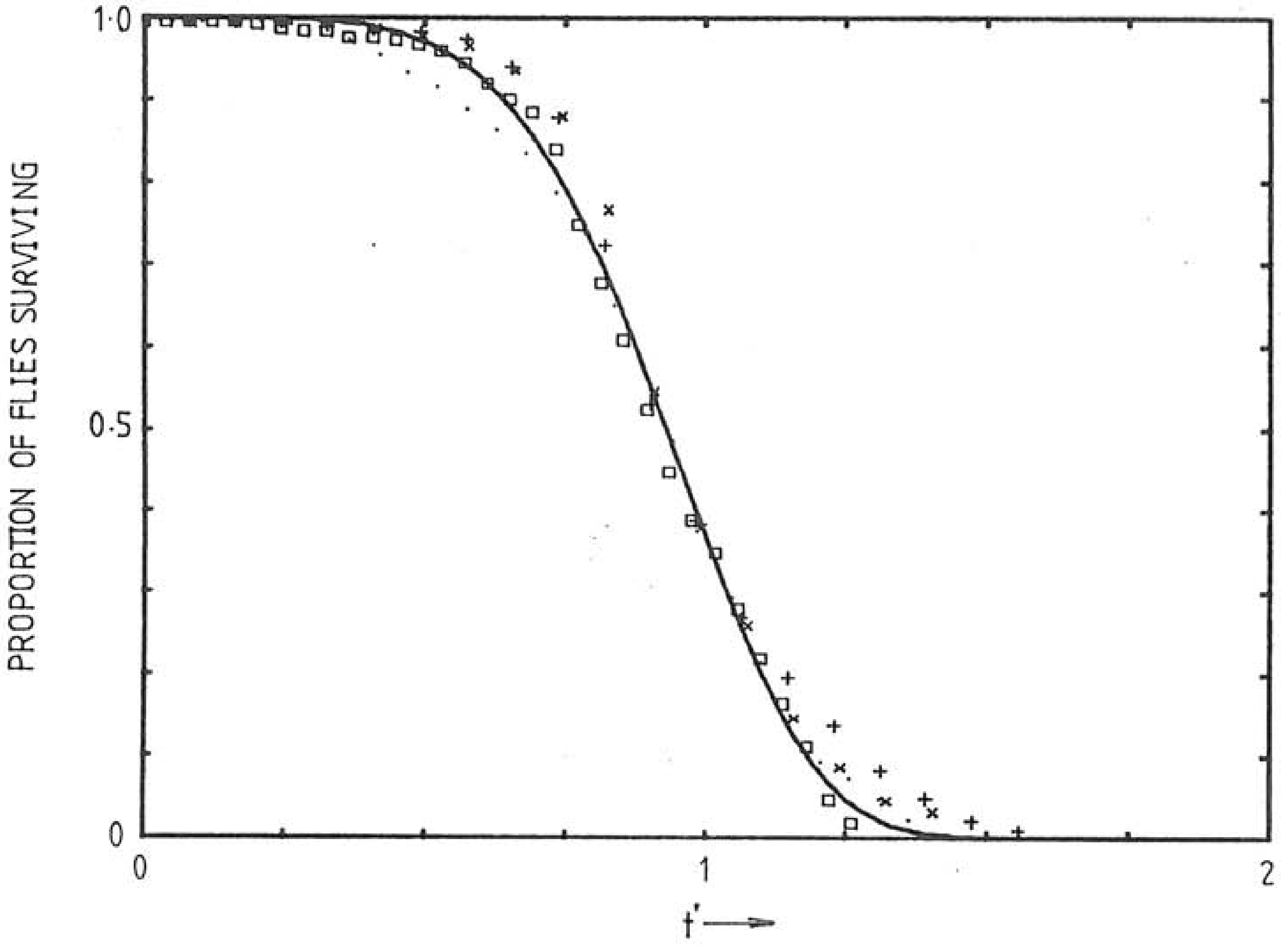
An attempt to age-structure Nicholson's (1957) control data has, however, already been made by Brillinger, Guckenheimer, Guttorp and Oster (1980). These authors assumed that the birth and death rates of individuals in the control population depended either multiplicatively or additively upon age and density. Also, they assumed that the rates fluctuated randomly from individual to individual. Brillinger et al's attempt to age-structure the control population is, unfortunately, marred by the unavailability at the time of empirical evidence concerning age-dependencies. Indeed, in the light of Readshaw and van Gerwen's experimental results, it can be seen that Brillinger et al's final age-structuring is based upon an apparently unsound assumption; specifically, Brillinger et al assumed that death rate depended linearly upon age whereas it will be seen in section 5.2 that the dependence is in fact upon age to the fourth power!

5.2 INVESTIGATING AGE AND DENSITY DEPENDENCE IN THE DEATH RATE USING READSHAW AND VAN GERWEN'S DATA

Fig. 5.2.1 shows survival (as proportion of original population) plotted against time for blowfly populations kept at four different, constant densities. Survival, and by implication, death rate are clearly dependent upon both density (flies die more quickly at higher densities) and time since emergence (if death rate was independent of age, the survival curves would be simple, negative exponentials).

To investigate how density and age affect death rate we now need a suitable collapse of the four survival curves shown in Fig. 5.2.1. If, quite arbitrarily, we scale each curve by the time taken, t_o, to reach some level of survival - which we will take to be e^{-1} ($\simeq 37\%$) - then the four curves all collapse onto one (Fig. 5.2.2). The collapsed data is


1.0
0.5
0
PROPORTION OF FLIES SURVIVING
0
20
40
AGE (days)


PROPORTION OF FLIES SURVIVING
1·0
0·5
0
0
1
2
t′ ⟶

well fit by the function

$$S(t') = \exp\{-t'^{5}\} \qquad (5.1)$$

where t' is time scaled by t_0 and $S(t')$ is survival to time t'.

This particular form of survival function is a so-called Weibull-distribution, (Metz, 1974; Kalbfleisch and Prentice, 1980) and necessarily implies that (and is implied by) the death rate must be of the simple, multipicative form

$$\delta(a) = \alpha\ a^{n} \qquad (5.2)$$

where a is adult age since emergence and $n = 4$.

The parameter α is age-independent but density dependent and by calculating α though time in Nicholson's experiment we can examine how the death rate is influenced by density. We do, of course, already know the values of α for the four constant population densities examined by Readshaw and van Gerwen; we are seeking, though, to estimate α against time during an experiment in which density is fluctuating. Throughout the experiment, therefore, we will be implicitly assuming that the history of flies does not affect their current, instantaneous propensity to survive. Although this seems implausible, it will be justified post hoc in section 5.3.

We must also make some assumptions about how α varies during any datum interval. Clearly, deaths, emergences, population density and α are all continuous through time - but the data are in two-day blocks and we must assume something about α during each interval. The simplest thing is to let α be constant over each datum-interval with an effective value $\hat{\alpha}_t$, written subscript t to emphasize the assumed lack of continuity.

In order to estimate $\hat{\alpha}_t$ we must now define the arbitrary age-classes into which the control data will be split. In the course of estimating $\hat{\alpha}_t$ it will prove necessary to keep track of how many individuals there are, during each datum interval, in each age-class. The inferred age-structure is, therefore, a necessary (but valuable) by-product of investigating density dependence.

Consider age-class i spanning $a_{iL} \rightarrow a_{iH}$ where $a_{iH} - a_{iL} = \Delta a$, then

$$a_i = 2i - \frac{\Delta a}{2} \; ; \; a_{iL} = a_i - \frac{\Delta a}{2} \; ; \; a_{iH} = a_i + \frac{\Delta a}{2} \qquad (5.3)$$

So that we have age-classes 1,3,5 . . . spanning 0-2, 2-4, 4-6 days etc...

Now, given (5.2), we can define survival through any age-class i to mature out at time t + Δa as

$$S_i(t) = \exp\{-\hat{\alpha}_t \int_{a_{iL}}^{a_{iH}} x^4\, dx\} \qquad (5.4)$$

$$= \exp\{-\hat{\alpha}_t \Psi_i\} \qquad (5.5)$$

where

$$\Psi_i = a_i^4\, \Delta a + \frac{1}{2}\, a_i^2\, \Delta a^3 + \frac{1}{80}\, \Delta a^5 \qquad (5.6)$$

which is thus a constant for each age-class during any time interval.

We now have to combine equation (5.5) with the raw, experimental data if we are to evaluate $\hat{\alpha}_t$ and investigate the relationship between α and density. We can proceed by inferring that the number of deaths in each age-class is given by

$$d_i(t) = X_i(t)\ \{1 - S_i(t)\} \qquad (5.7)$$

where $X_i(t)$ is the sub-population in age-class i at time t. The total deaths in the population, which we know, must then equal

$$D(t) = \sum_{i=0}^{\infty} X_i(t)\{1-S_i(t)\} \qquad (5.8)$$

Combining equations (5.5) and (5.8) then yields the transcendental equation

$$D(t) \;=\; \sum_{i=0}^{N} X_i(t)\{1-\exp(-\hat{\alpha}_t\Psi_i)\}. \qquad (5.9)$$

where N is larger than the number of age classes in which we are interested. We know $X_1(0)$ and can solve equation (5.9) using a Newton-Raphson procedure to determine $\hat{\alpha}_0$. The survival of the $X_1(0)$ individuals into $X_3(2)$ may then be calculated from equation (5.5) and $X_1(2)$ is known; $\hat{\alpha}_2$ may then be calculated from the updated age-structure, and so on for the entire data series to produce both values of α_t and an inferred age-structure.

Starting, then, with empirical relationships between survival and density, we have obtained by a simple scaling procedure, a survival function, equation (5.1), which implies a death rate, equation (5.2), multiplicatively dependent upon age to the power four and a quantity $\hat{\alpha}_t$ which will contain the density dependent portion of the death rate. The relationship between $\hat{\alpha}_t$ and N_t may now be investigated. Also, by calculating $\hat{\alpha}_t$ we have had to infer an age-structure which will be useful in examining age-dependence in fecundity.

5.3 RESULTS

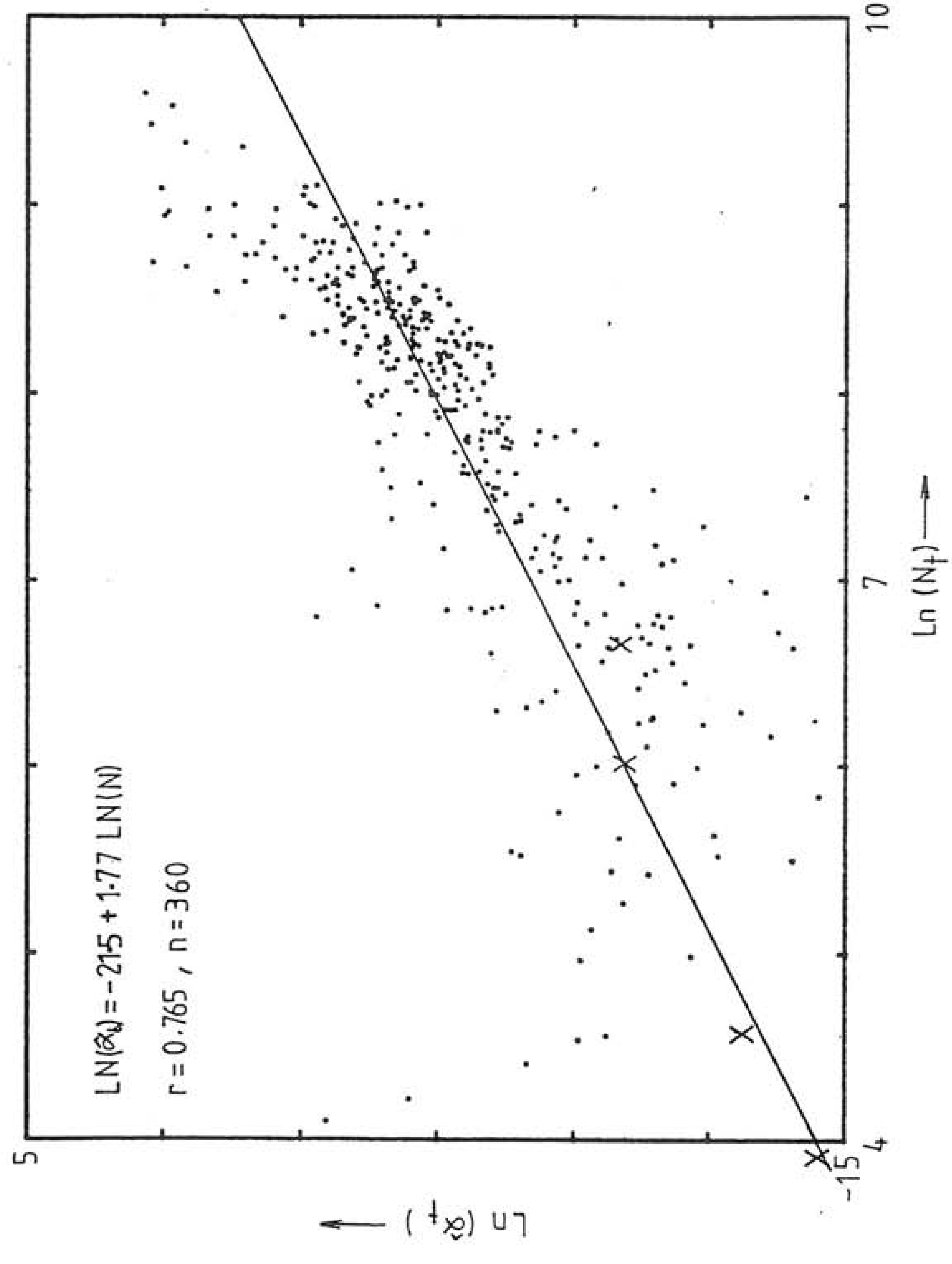
The scatter diagram (Fig. 2.2.1) of death rate against density indicated a weak relationship - r was 0.45, we were accounting for only 21% of the variance. The relationship between $\hat{\alpha}_t$ and N_t is, however, much stronger. Fig. 5.3.1 is a plot of $\ln(\hat{\alpha}_t)$ vs. $\ln(N_t)$; a fitted regression line now accounts for almost 60% of the variance ($r = 0.77$). In section 5.2.3 we made the assumption that history did not affect current survival chances - tnis may now be justified. If $\ln(\hat{\alpha}_t)$ is regressed, not against $\ln(N_t)$ but against a weighted history of population sizes, then the resulting r values may be increased; the effect, however, is small - we cannot increase r by more than a very small amount (0.01). Whilst, therefore, history does have an effect, it is trivial compared to current conditions. N_t, of course, already covers a two-day period and we are necessarily accounting for some recent history, perhaps this is why the relationship between $\hat{\alpha}_t$ and N_t is so good.

Based upon the relationship between $\ln(\hat{\alpha}_t)$ and $\ln(N_t)$ we can now write a death rate function explicitly dependent upon powers of both age and density as

$$\delta(a,N) = K\, N_t^{1.8}\, a^4 \qquad (5.10)$$

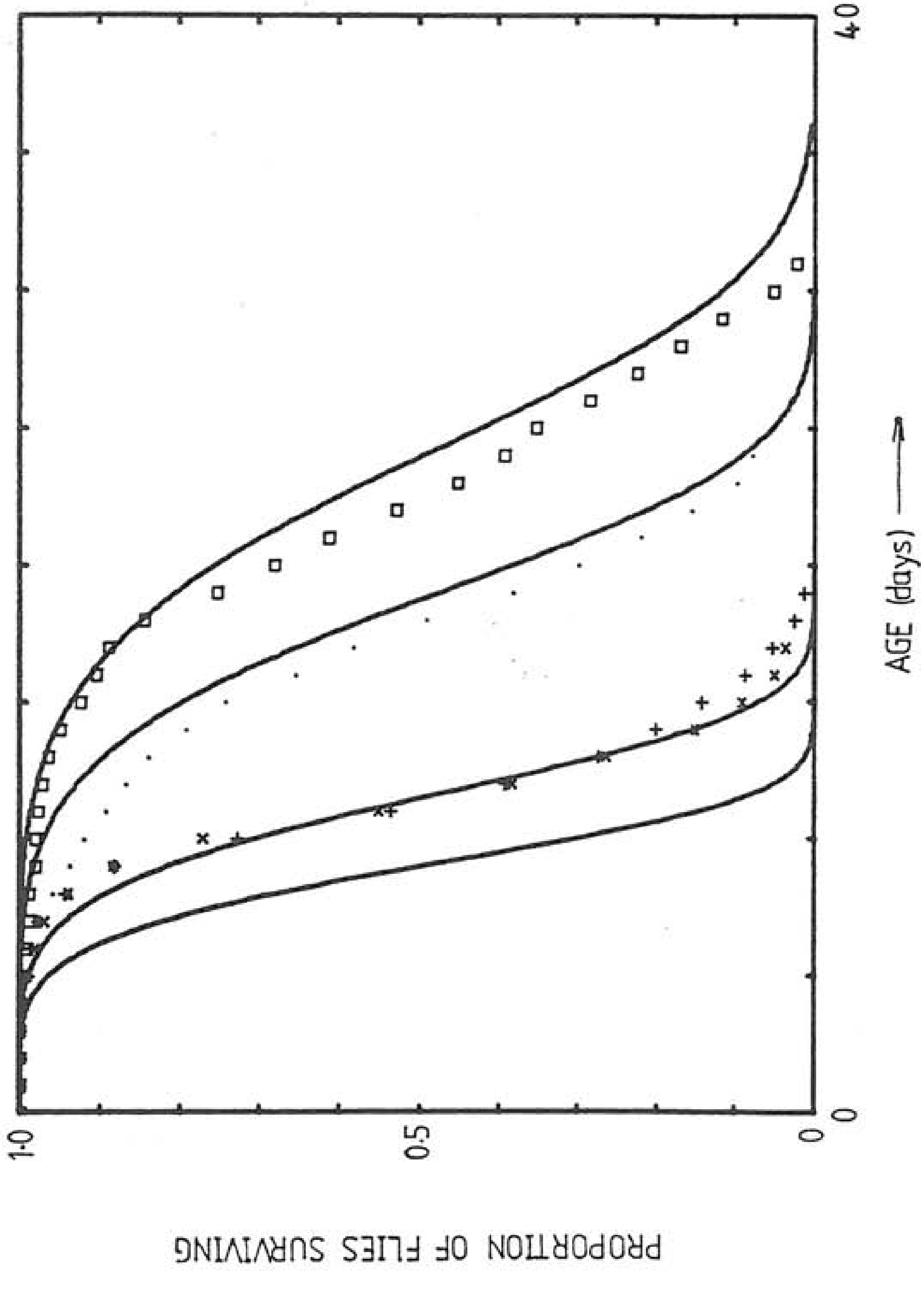
where $$K = 4.35 \times 10^{-10}\, N^{-1.8} d^{-5},$$

We are now in a position to test the self-consistency of our analysis. If we plot values of $\ln(\alpha)$ derived from the scaling factors used in the original data collapse (see


LN(αt) = -21·5 + 1·77 LN(N)
r = 0.765 , n = 360
Ln (αt) ⟶
Ln (Nt) ⟶
5
-15
4
7
10

(section 5.2.2) against the natural logs of the constant densities at which the data were obtained (the 'x' points in Fig. 5.3.1) then these points lie close to the fitted regression line. The regression line is a fit to the data obtained at predominantly high and varying densities yet the data upon which the analysis is based are for relatively low and constant density experiments. That the analysis results in a fit for $\ln(\hat{\alpha}_t)$ vs. $\ln(N_t)$ which is consistent with the original data is reassuring - the correlation between $\ln(\hat{\alpha}_t$ fitted) and $\ln(\alpha$ data) at the experimental constant densities is, in fact, 0.97.

As a further test we may derive (based upon equation (5.10)) the expected survival curves for the constant densities used by Readshaw and van Gerwen. Such curves compare well with the data (Fig. 5.3.2) for three experiments but are discrepant for the highest density. If the contrary result was for the lowest density then we might conclude that the relationship (5.10) is robust at all but very low densities. The discrepant result, though, is at the highest experimental density and may possibly best be explained as an 'odd' result. It would have been useful if Readshaw and van Gerwen had performed at least one higher density experiment. Nevertheless, we may confidently expect our expression for the death rate equation (5.10) to be valid for all densities observed in Nicholson's experiments. One possible caveat is that the data in Fig. 5.3.1 appear to display a tendency to deviate upwards from


PROPORTION OF FLIES SURVIVING
1·0
0.5
0
0
40
AGE (days) ⟶

the fitted regression line at high densities. This may well be due to an 'interference' effect. That is, although flies are fed ad libetum with water and carbohydrate and are therefore not expected to compete for these resources, at high densities it may become physically difficult or impossible for all flies to gain access to these essential supplies. In other words, at very high densities, scramble competition may not be a valid assumption.

Let us now, however, turn our attention to the inferred population age-structure. The calculated mean age of blowflies against time is shown in Fig. 5.3.3. Clearly, whilst the population is cycling so too is the mean age. Later, as the population may be characterised as entering stable parameter space (see chapter 3), so then does the mean age appear 'stable'. The surprising thing about the variations in mean age is that as the population stabilises, the mean age declines to a value of about 3 days. L. cuprina typically take 5-7 days (with an observed minimum of 4 - Mackerass, 1933) to mature.

If we now consider the age-structure in 2-day age-classes against time (Fig. 5.4.3) we see individuals being recruited to the population and forming cohorts which march along through time, gradually diminishing in size until they disappear altogether. As time progresses we see that there are fewer and fewer older individuals in the population - that young flies come to predominate.

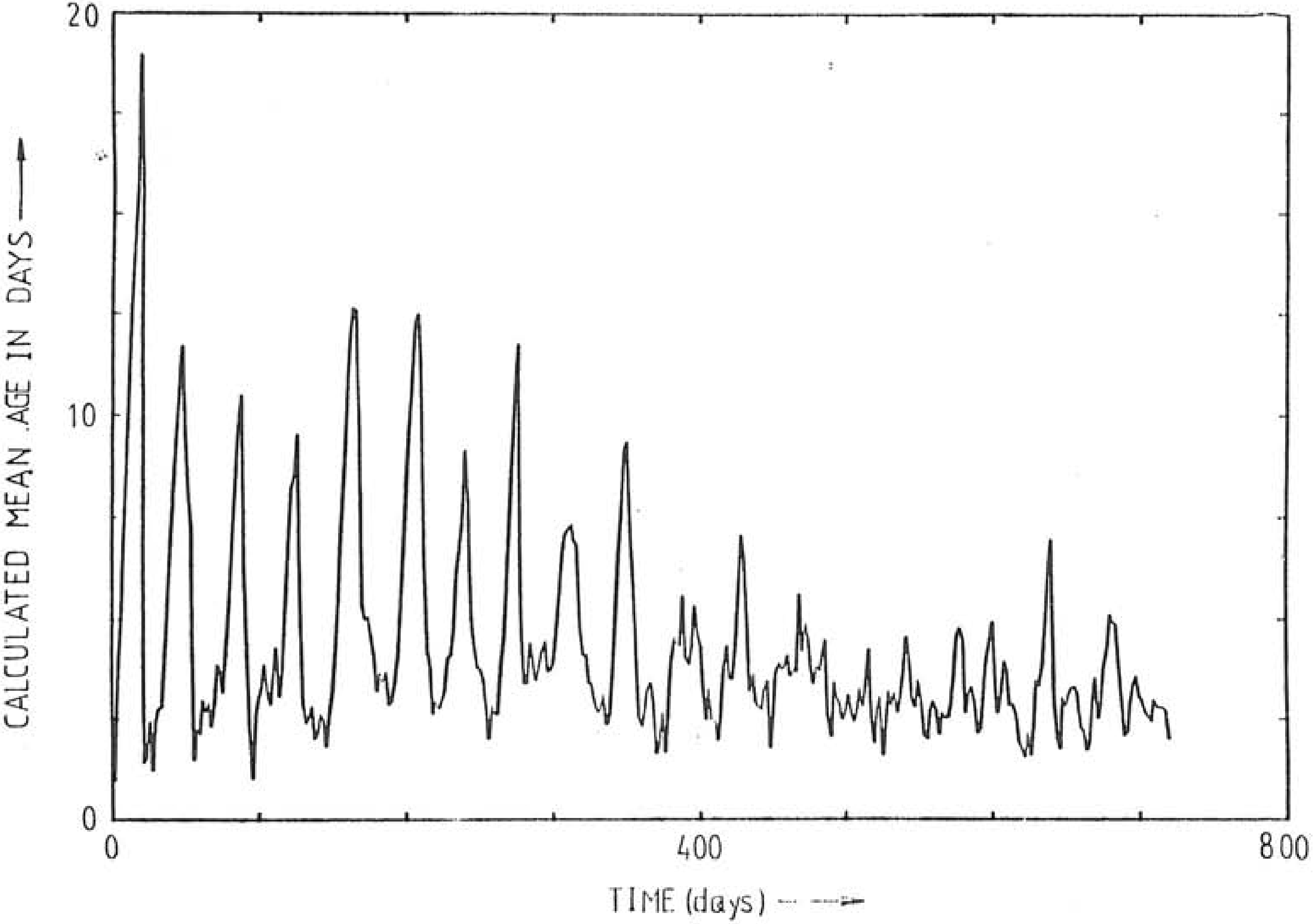
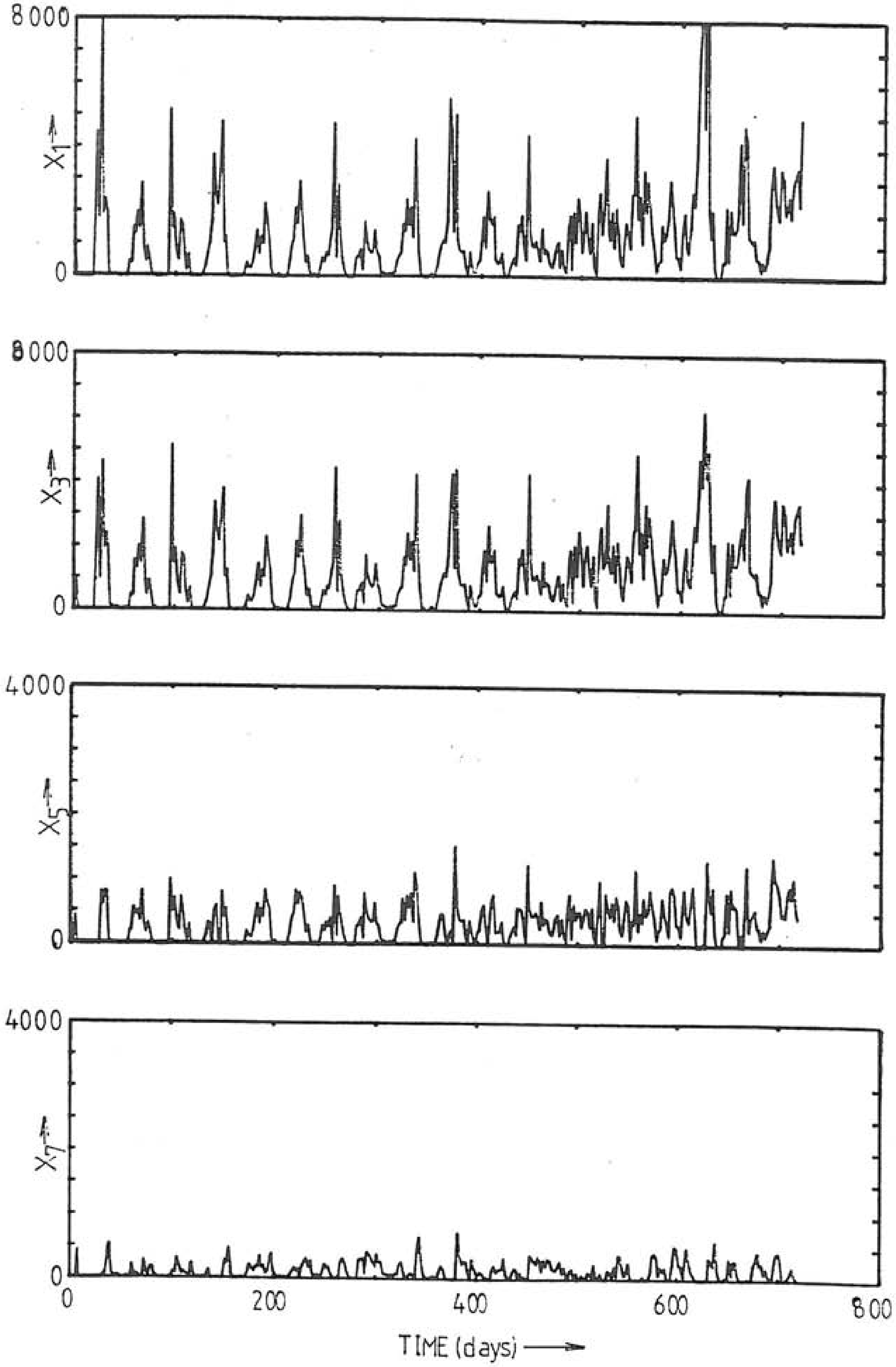
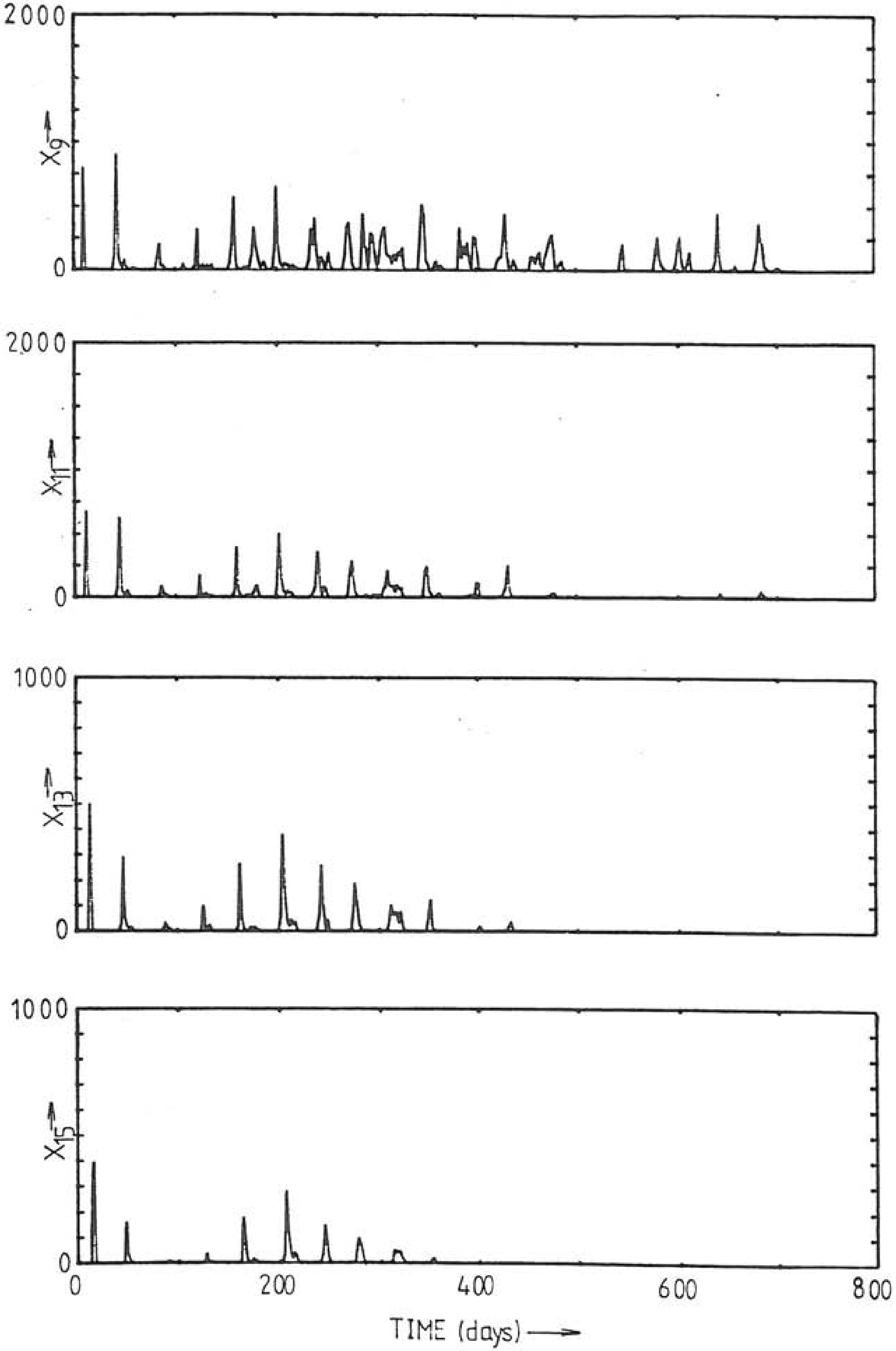
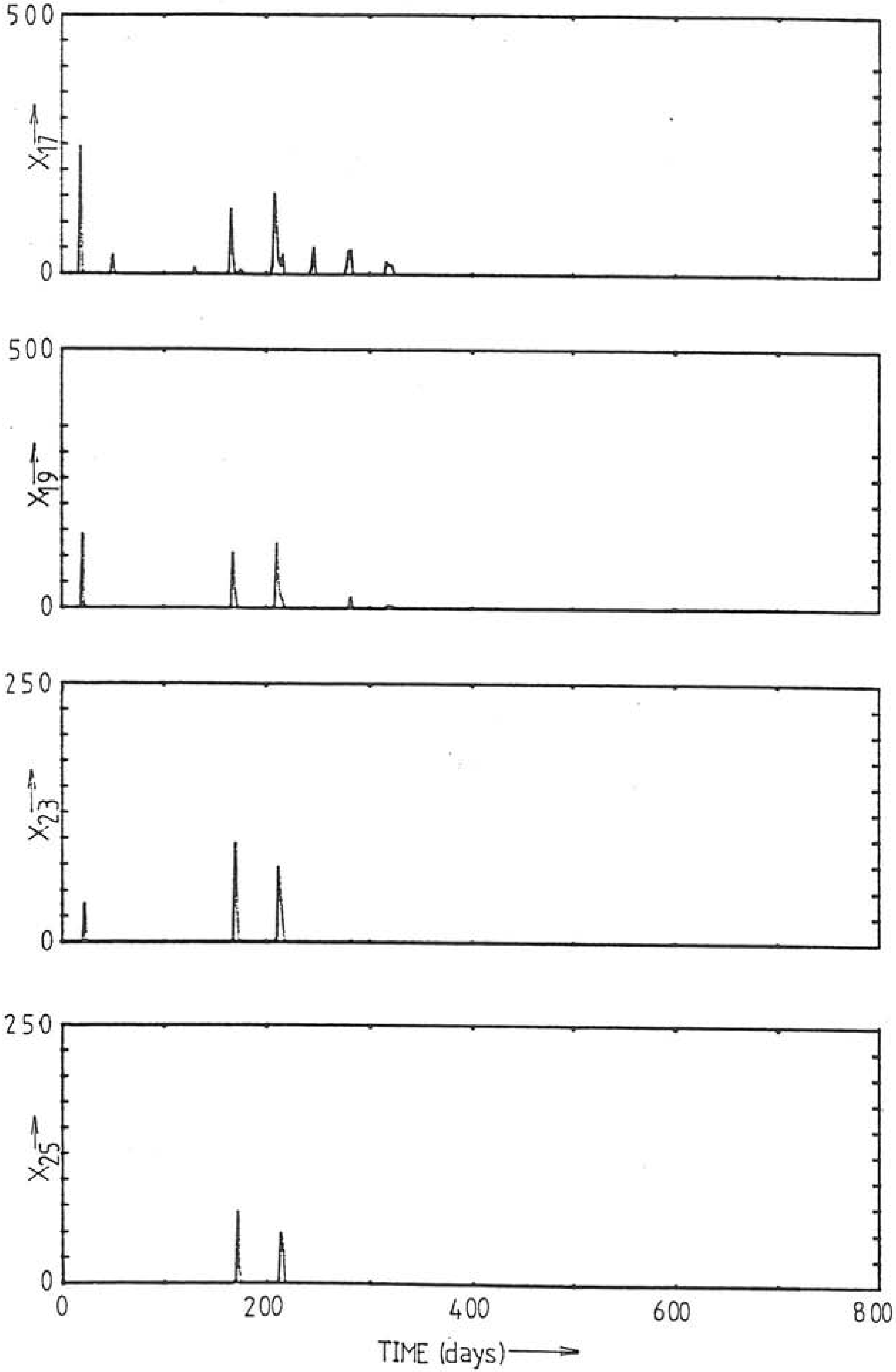


FIG. 5.3.3 Calculated mean age of adult blowflies against time.


8000
0
X1
8000
0
X3
4000
0
X5
4000
0
X7
0
200
400
600
800
TIME (days)


2000
0
X_9
2000
0
X_{11}
1000
0
X_{13}
1000
0
X_{15}
0
200
400
600
800
TIME (days)


500
0
X_{17}
500
0
X_{19}
250
0
X_{23}
250
0
X_{25}
0
200
400
600
800
TIME (days)

5.4 DISCUSSION

It was seen in chapter 2 that the relationship between death rate and density, without taking account of age, is not good. When age is taken into account (see Fig. 5.3.1) the relationship is very strong. This improvement, moreover, is not restricted to the constant density environment but has been demonstrated in Nicholson's control experiment when population density fluctuates wildly. Already, then, the investigation of age-specific mortality shows how important age can be. That strong age dependencies coupled with a fluctuating mean age and age distribution might produce fine-structure on population oscillations is clear. It now remains, after estimating maturation-time variations, to use the inferred age-structure to investigate age-dependent fecundity.

The age-structure of Nicholson's control population has been inferred using a procedure which produces results consistent with the data from Readshaw and van Gerwen's constant density experiments. The inferred age-structure is also in line with Nicholson's observations and the findings of chapters 2-4 of this thesis. Consider the following.

Selection acts to produce flies capable of producing eggs in the near (or even total) absence of protein. Such flies must, if we reasonably assume that protein remains necessary for vitellogenesis, utilise protein acquired as larvae in order to produce eggs. If flies are unable to call upon protein acquired during the larval stage, then they do not need to spend time competing for and ingesting protein as adults - ovarian development may proceed immediately after emergence and maturation times might reduce to the time taken for ovarian development which is typically about 2 days.

The results of the analysis, then, may be justified because younger individuals come to predominate and because maturation rates ought (if the analysis in chapters 2-4 is correct) to decline. This, of course, is 'just-so' justification; the correctness of the inferred age-structure cannot be formally tested, but, as has already been shown, the analysis is self-consistent and the results may be used with some confidence in an attempt to relate fecundity to age and density (see chapter 6).

To conclude, it is worth pointing out that performing constant density experiments of the type conducted by Readshaw and van Gerwen is a relatively cheap, short and easy exercise compared to the long, Nicholson-style, population experiment in which no age-specific data is recorded. I would suggest to experimentalists that conducting constant density experiments as a prelude to a long population study would be a very worthwhile and potentially illuminating exercise. Provided the survival data recorded at constant densities collapses to a Weibull distribution, a Nicholson-type experiment in which only recruitment and deaths are recorded, might then be performed with the knowledge that a time-dependent, age-structure could be inferred. The utility of such an inferred age-structure would depend, of course, on the results of the constant density experiments extending to the variable density situation; this, though, may be tested easily after the first one or two population cycles.

CHAPTER 6

MATURATION TIME ESTIMATION AND AGE AND DENSITY DEPENDENCE IN FECUNDITY

6.1 INTRODUCTION

In the previous chapter, the time-dependent age-structure for Nicholson's (1957) control population was inferred based upon the results of Readshaw and van Gerwen's constant density experiments. In this chapter, data from the same experiments will be used to estimate how maturation times vary throughout Nicholson's experiment; maturation time is here defined as the time from emergence until flies first lay eggs. This has been carried out with the intention of combining the maturation time estimates and the inferred age-structure with Readshaw and van Gerwen's egg production data in order to estimate how per capita fecundity, dependent upon both density and age since emergence, varies through time. As will become clear, however, the results of the maturation time estimation, as evidenced by the estimated number of mature individuals at any time, are not consistent with Nicholson's egg laying results. This problem will be discussed in terms of the increasing competitive resilience demonstrated in chapters 2-4.

Because of the difficulty in estimating maturation times, the estimation of maximum age and density-independent, per capita fecundities is awkward. Although it has not as yet been possible to estimate fecundities satisfactorily, an approach to the problem is presented; this approach will work only when the problem of estimating maturation times has been solved.

6.2.1 ESTIMATING MATURATION TIMES

In order to estimate how maturation times vary throughout Nicholson's control experiment we must seek a relationship between the rate of development of adults from emergence to maturity (defined as the age at which eggs are first laid) and feeding rate. The only, and very limited, data available for this are those of age at which flies first lay eggs at each of the constant densities investigated by Readshaw and van Gerwen. There are only four experimental densities and we therefore only have four data points to work with. As in previous chapters, we will assume that competition is of the scramble type and hence that feeding rate, $f(t)$, is given as food available, Φ, divided by the population size, $N(t)$. If we plot the age at which eggs are first laid, τ_I, against f then we cannot sensibly fit the data with any 'standard' development rate function such as the Michaelis-Menten. If, though, we plot τ_I against ln f then the data are well fitted by a straight line (Fig.

6.1); one function which provides such a fit and which has the properties of maximum growth and feeding rates is

$$g(f) = \frac{g_{max}}{1 + \ln\left[\frac{f_{max}}{f}\right]} \quad \text{if } f \leqslant f_{max}; \quad g = g_{max} \text{ otherwise} \tag{6.1}$$

where g_{max} and f_{max} are the maximum development and feeding rates respectively.

If we now assume that there is a critical state of development, S_c, at which maturity is triggered then, under constant food conditions

$$S_c = g(f)\ \tau_I \tag{6.2}$$

and we therefore expect τ_I to be given by

$$\tau_I = \frac{S_c}{g_{max}} [1 + \ln f_{max}] - \frac{S_c}{g_{max}} \ln f \tag{6.3}$$

The line fitted to the data (Fig. 6.1), therefore, has a slope of (S_c/g_{max}) and intercept $(S_c/g_{max})[1 + \ln f_{max}]$. The data are well fitted by the function (6.1) and we obtain values of f_{max} and g_{max} of

$$f_{max} = 68 \text{ mg d}^{-1},$$

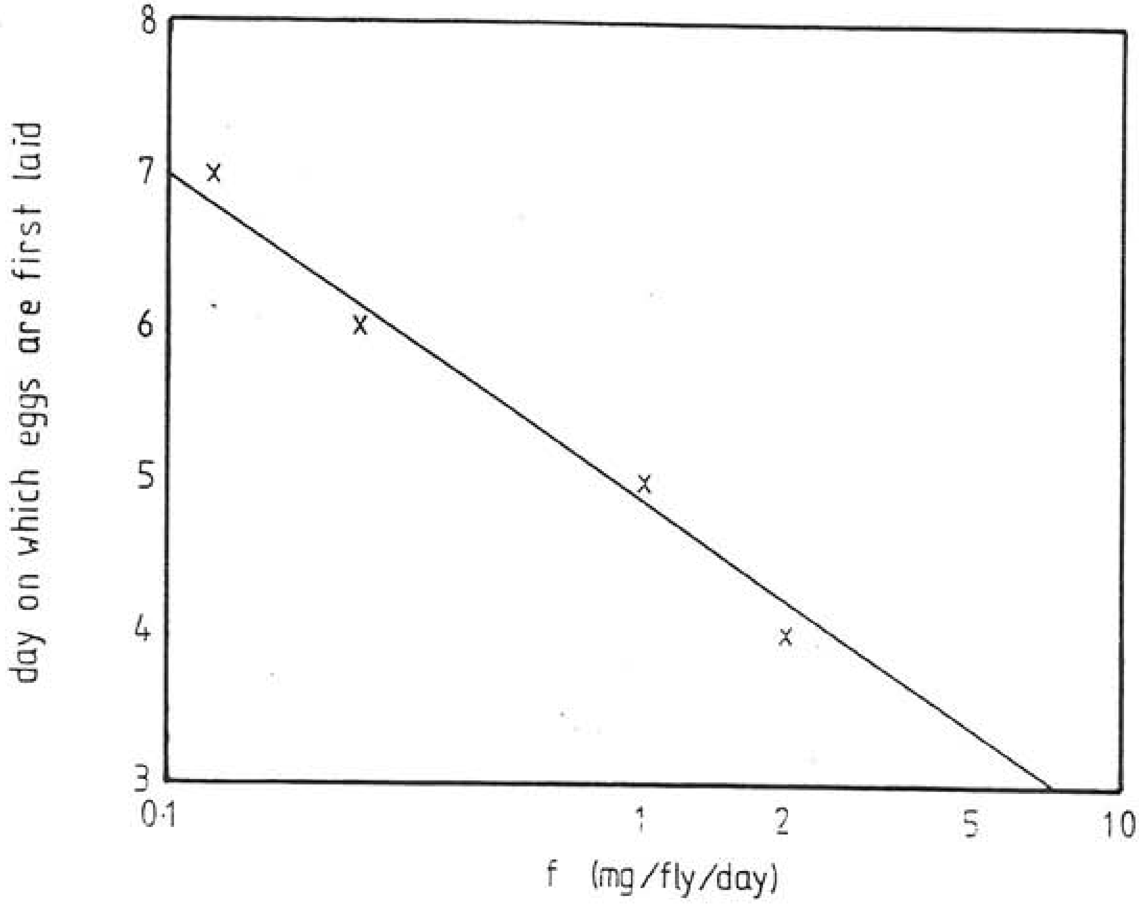


FIG. 6.2.1 Time to first egg laying plotted against ln (f) for each of Readshaw and van Gerwen's (1983) constant density experiments.

$$g_{max} = 1.07\ S_C.$$

If we now assume that the development function (6.1) is valid not just at constant densities but when densities vary, and hence that feeding rate is time dependent and given as protein input rate, Φ, divided by population size, $N(t)$, we may represent development rate during Nicholson's control experiment as

$$g(t) = \frac{1.07\ S_c}{1 + \ln\left[\frac{68\ N(t)}{\Phi}\right]} \qquad (6.4)$$

and hence expect the maturation time to be given by

$$1 = \int_{t-\tau_I(t)}^{t} \frac{1.07\ dx}{1 + \ln\left[\frac{68}{\Phi}\right] + \ln N(x)} \qquad (6.5)$$

which may be recast as a differential equation

$$\frac{d\tau_I}{dt} = 1 - \frac{g(t)}{g(t-\tau_I(t))} \qquad (6.6)$$

and can be solved, subject to appropriate initial conditions (see Appendix 5), to calculate $\tau_I(t)$ throughout the experiment.

6.2.2 RESULTS

Fig. 6.2.2 shows the calculated age to maturity plotted against time. Not surprisingly, as the population density fluctuates, so too does the estimated maturation time. Also, as the population rises through time then so too does the estimated maturation time; this being because the development rate equation (6.4) is assumed to be purely density dependent.

By combining estimates of $\tau_I(t)$ with the inferred age-structure, it is possible to estimate the number of mature individuals at any time (see Fig. 6.2.3). The estimated $\tau_I(t)$ values are, though, unquestionably wrong; it often happens that a zero population of mature adults is estimated when eggs are, in fact, being laid (see Appendix 8). The problem occurs increasingly as time progresses.

Notwithstanding the difficulties in assessing $\tau I(t)$, a method for estimating age-dependent fecundities is provided and the results of applying the method using the erroneous maturation time estimates are shown.

6.3.1 ESTIMATING DENSITY AND DEVELOPMENT-DEPENDENT FECUNDITY

Readshaw and van Gerwen recorded, for each constant density experiment, the number of eggs layed each day and

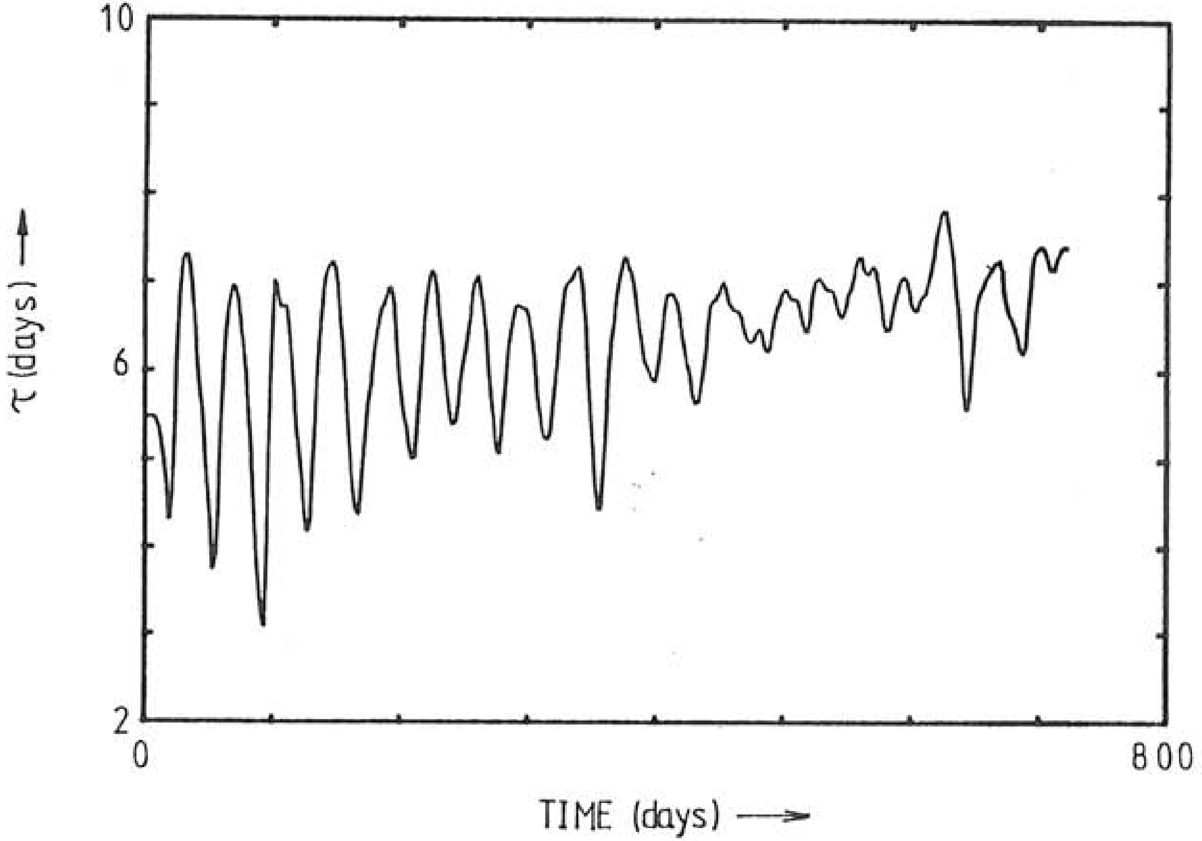
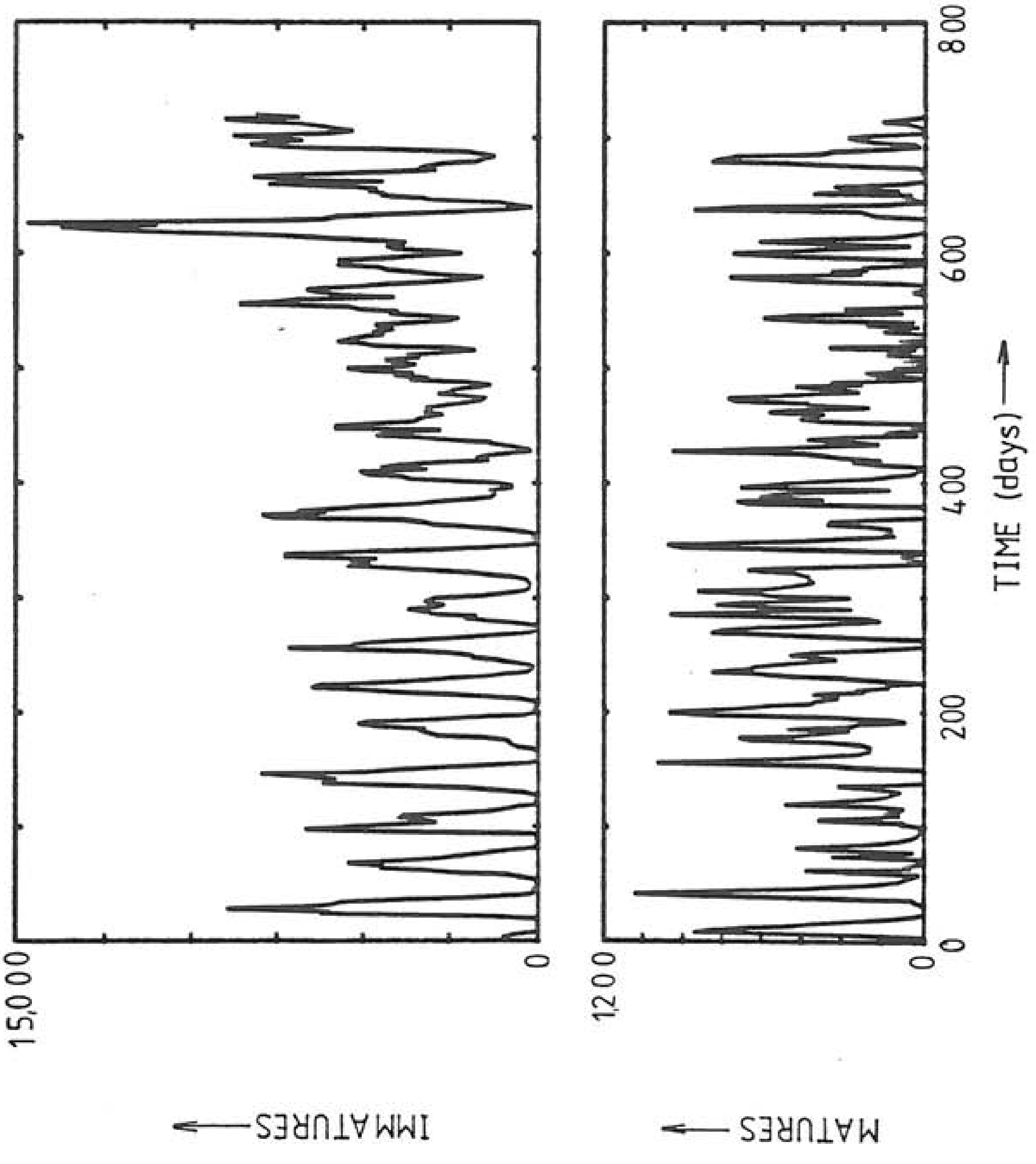


FIG. 6.2.2 Estimated maturation times through time for Nicholson's (1957) control experiment.


15000
0
IMMATURES
1200
0
MATURES
0
200
400
600
800
TIME (days)

how many of these survived. To examine the relationship between fecundity and age and density we have plotted (Fig. 6.3.1) the three-day averaged fecundity against age since maturity (based on the results in section 6.2) for each constant density experiment. The fecundities are normalised by the maximum observed fecundity for each constant density experiment. It is clear that at lower densities, flies continue to lay eggs for longer and also that the peak in fecundity is later (though not necessarily in terms of real age rather than age since maturity). Also, but not clear from Fig. 6.3.1 due to the normalisation, at lower densities, many more eggs are produced per fly per day.

As with the survival data, we now seek to collapse the four, normalised fecundity curves onto a single curve by scaling the 'age since maturity' axis of Fig. 6.3.1. The scaling factors, t_o, used in the survival data collapse (section 5.2) also prove satisfactory in collapsing the four fecundity curves (Fig. 6.3.2) and the scaled data are fitted acceptably by the function.

$$\frac{\overline{\beta}}{\overline{\beta}_{\max}} = \exp\{m^{-1}\}(q/q_o)\exp\{-m^{-1}(q/q_o)^m\} \qquad (6.7)$$

where

$$q = (a-\tau_I)/t_o$$

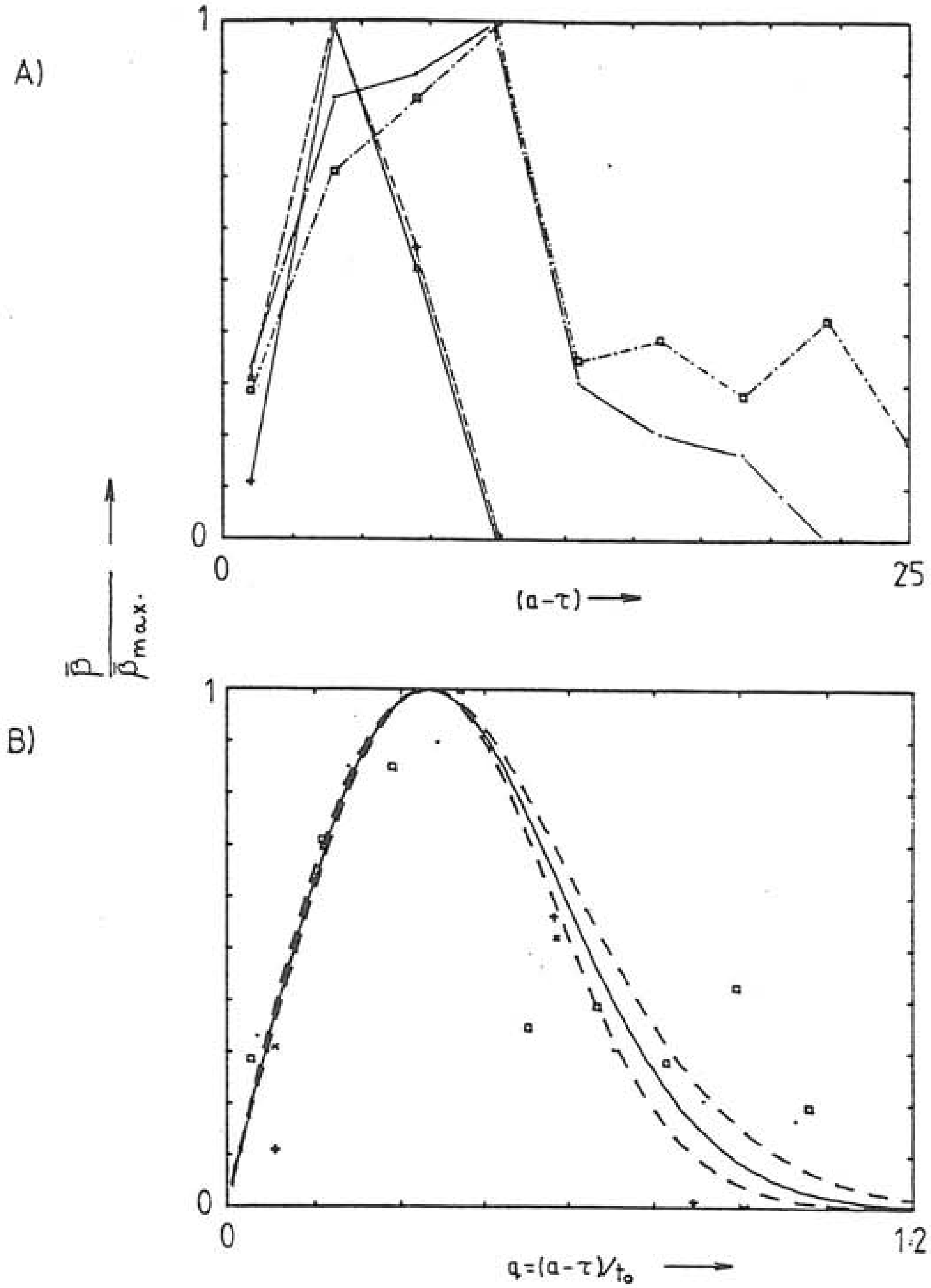
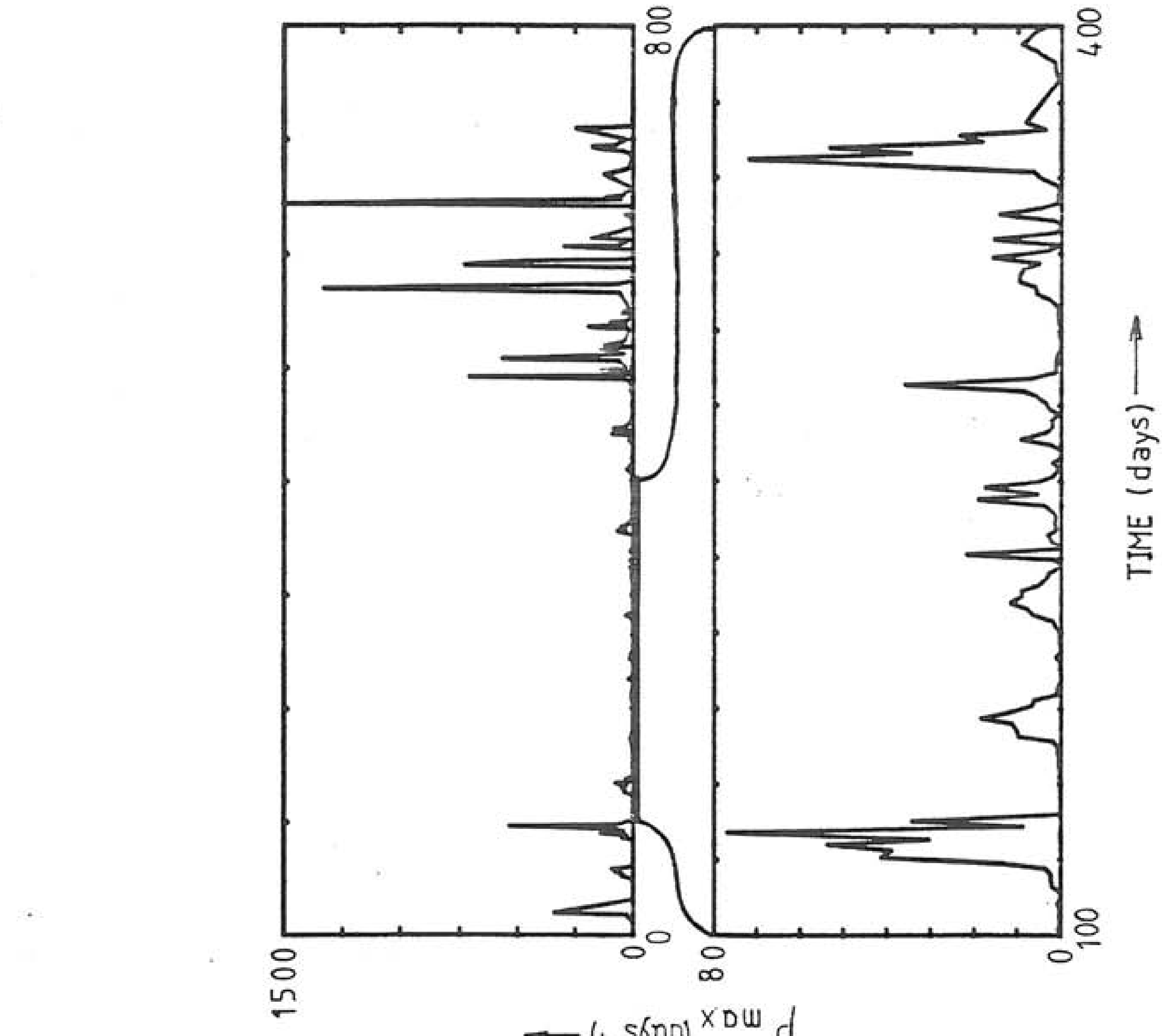


FIG. 6.3.1 Three-day average fecundity, normalised by the maximum three-day averaged fecundity plotted against A) age since maturity ($a-\tau$) and B) age since maturity scaled by the t_o values used in the survival data collapse of chapter 5. Based on Readshaw and van Gerwen's (1983) data.

□: 50 flies per cage, •: 100 flies per cage,

+: 400 flies per cage, X: 800 flies per cage.


β max (days⁻¹) →
1500
0
80
0
0
800
100
400
TIME (days) →

$\overline{\beta}$ = the three day averaged fecundity.

and

$m = 2.3 \pm 0.3$

$q_o = 0.35$.

This function (6.7) is presented, not as a definitive best-fit to the data, but as an adequate and satisfactory description of the unambiguously humped relationship between normalised fecundity and the density-independent state of development, q.

It is now possible to proceed from equation (6.7) to calculate $\beta_{max}(t)$, the maximum per capita fecundity, throughout Nicholson's control experiment. If the subpopulations in the structured population at time t are given as X(q,t) then it is evident from equation (6.7) that

$$E(t) = \beta_{max} \exp\{m^{-1}\} \int_{q=0}^{\infty} X(q,t)(q/q_o)\exp\{-m^{-1}(q/q_o)^m\}dq \tag{6.8}$$

We do not know the values of X(q,t) but we do have estimates of X(a,t). If we map the X(a,t) populations into X(q,t) using the relationships

$$q_{iH} = (a_{iH} - \tau_I(t))/t_o(t) \qquad (6.9)$$

$$q_{iL} = (a_{iL} - \tau_I(t))/t_o(t)$$

where $\tau I(t)$ are known from section 6.2 and $t_o(t)$ are known from chapter 5, then we will obtain a series of unequally spaced q-intervals for which we know each subpopulation. Assuming that within each interval, at any time, there is a flat q-distribution, we may subdivide the q-intervals into any small number of units of known population size. We may then find $\beta_{max}(t)$ by evaluating equation (6.8) using Simpson's approximation.

6.3.2 RESULTS

The β_{max} estimates obtained using the approach outlined in section 6.3.1 are shown in Fig. 6.3.2. Clearly, β_{max} fluctuates between very high and low values, especially towards the start and over the last 300 days of the experiment. Over the last few hundred days, though, the high $\beta_{max}(t)$ estimates are caused by the extremely low - often zero - mature population estimates. Only in the middle of the experiment, during the period 100-400 days might we be at all confident that the $\beta_{max}(t)$ estimates are in any way 'sensible' or representative of reality. Before this time the population is heavily influenced by initial conditions and after this period our maturation rate estimates are distinctly questionable.

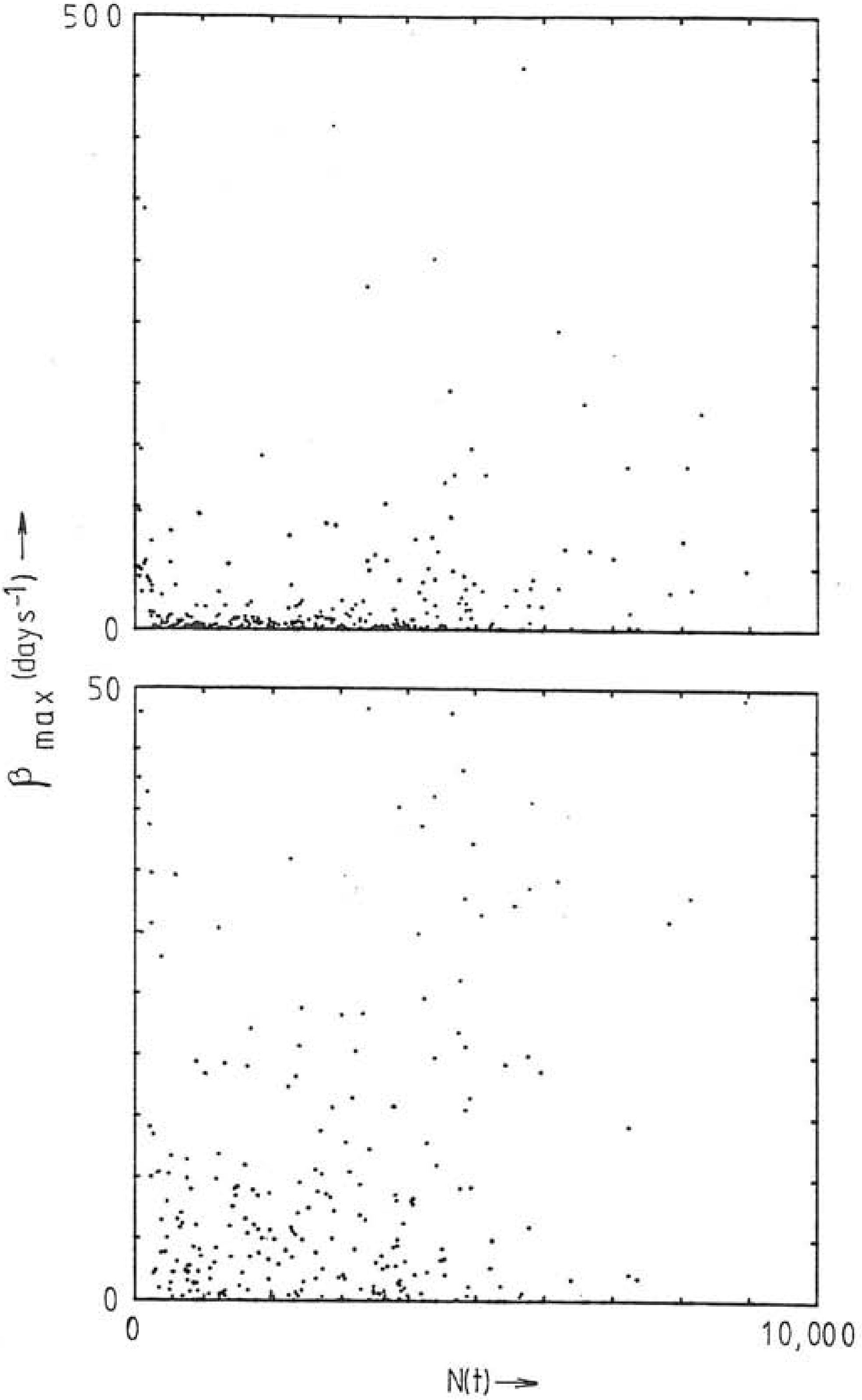


FIG. 6.3.3 Calculated β_{max} against total population size, N(t) for Nicholson's (1957) control experiment.

If our $\beta_{max}(t)$ estimates are good then we should expect to see some clear relationship between $\beta_{max}(t)$ plotted against $N(t)$; clearly (see Fig. 6.3.3), there is no relationship. The same lack of correlation occurs for just the data from the middle of the experiment. It must be concluded that the $\beta_{max}(t)$ estimates are not useful.

6.4 DISCUSSION

In the previous chapter we saw that the mean age of flies decreased as the experiment progressed and justified this result in terms of an hypothesised, gradual decline in maturation times. The justification was founded upon the results of chapters 2-4, in particular the demonstration that f_o declines during the experiment.

The maturation time estimates shown in Fig. 6.2.2 are based on experiments carried out with flies that had not been exposed to conditions conducive to evolving an increased competitive resilience. The neglect, in estimating $\tau_I(t)$, of the evolution that occurs during the experiment is a serious flaw - if we are to understand successfully how τ_I varies throughout the experiment then we must, in some way, incorporate realistically the decline in f_o into our development rate function.

Unfortunately, interpreting the decline in f_o and linking this with the development dynamics is not easy. If we are to keep our differential equation describing the rate of change of τ_I with time, equation (6.6), then we might allow f_{max} to decline in some way as time passes. We do not know, however, and therefore could not confidently interpret any possible results of an analysis based on such an assumption, how the decline in f_o manifests itself in ways other than the ability to lay eggs in the absence of protein. If flies, as suggested in section 5.3, utilize protein resources acquired whilst in the larval stage, then maybe not only f_{max} declines but S_c also - S_c, remember, does not refer to a physical size but to a developmental state. Similarly, the development rate function (6.4), actually comprises more than just one, simple process. As competitive resilience increases, the complex of processes underlying development, and therefore the development rate itself, must change.

Essentially, then, we cannot confidently incorporate a realistic change in the development rate. We cannot calculate $\tau I(t)$ in a meaningful way unless we have access to further information as to precisely how the decline in f_o is brought about and precisely what concomitant effects this produces.

Despite the difficulties in assessing $\tau_I(t)$, a method has been presented for calculating development dependent fecundities. Good estimates of such fecundities have not been obtained because of the difficulties in estimating maturation times. The difficulties arise due to the lack of a reasonable method of incorporating the evolution of competitive resilience into the development rate function, equation (6.4). Until a realistic estimate of maturation times has been achieved, it is best to keep the β_{max} estimation procedure in abeyance.

Although no final estimation of age/development-dependent fecundities has been achieved, the method used in the previous section to infer age-structure and characterise age and density dependent mortality, together with the approaches to evaluating maturation times and β_{max}, illustrate the importance of age as a factor influencing vital rates and provides a possible route, given some modification, to accomplishing successfully a disentanglement of how age and density jointly influence population dynamics.

CHAPTER 7

SUMMARY

The objective of the work reported in this thesis is the understanding of the dynamics of Nicholson's (1957) control blowfly population data (Fig. 1.1I). To this end, a continuous time, birth and death model has been successfully employed to explain gross dynamic features of the data; particularly, an apparent change in behaviour after about 400 days. This has been followed by an attempt to decouple the effects of age and density on the blowfly vital rates.

The starting point for the work is the observation (Chapter 2) that the blowfly population subjected to a 20-day variables protein-input rate (Fig. 1.1c) may best be explained as displaying behaviour characteristic of an unstable system for about 500 days but that this then gives way to behaviour characteristic of a stable system. To be more precise, for the first 500 days, a clear 40 day population cycle is evident and later a 20 day cycle predominates; this behaviour is explained as synchronization of the natural limit cycle to the half harmonic of the driving frequency giving way to a simple capturing of the (now stable) system by the driving force. The observation of a change in behavioural

regime in the 'driven' experiment suggests a similar explanation for the change in dynamic behaviour perceived in the control run and implies that the factors controlling stability must somehow change during the course of the experiment.

The stability properties of the model are governed by daily, per capita, adult, maximum fecundity (Qs) and death rate (δ) and the egg to maturity development time (τ). The equilibrium population size is also controlled by the parameter f_o, which is a characteristic, per capita protein intake rate (the reciprocal of which is a measure of how well flies are able to compete - i.e. competitive resilience). How these vital rate parameters vary through time was estimated in Chapter 2. Death rate was measured directly from Nicholson's raw data but Qs and f_o were estimated using a weighted linear regression technique. It was shown that all three parameters varied systematically as the experiment progressed; in particular, Qs and f_o declined. It was suggested that the mechanism underlying these changes was selection for competitive resilience, the selective pressure being competition for the limited protein available.

The estimates obtained in Chapter 2 were, of course, for model specific parameters. In Chapter 3, however, it was shown how the equilibrium population through time, calculated from the parameter estimates, is consistent with the experimentally observed mean population. Also, when the $Qs\tau$-$\delta\tau$ estimates through time were plotted as a trajectory over the stability diagram for the model, it was shown that the estimates are consistent with a shift from unstable to stable behaviour and, furthermore, that the time at which the stability boundary is crossed is in agreement with the shift in behaviour perceived in the data.

The parameter estimates are shown to be representative of the experimental population (chapter 3). A deterministic simulation of the data based on the estimates displays, however, a gradual approach to stability whilst the control data displays large fluctuations in the later stages. These fluctuations may be explained as resonant quasi-cycles which arise due to stochastic perturbations. To test, therefore, if the deterministic characterisation of how the parameters vary and influence dynamic behaviour is valid, the effects of demographic and environmental noise were considered in Chapter 4. It was shown that both deterministic birth and death rate prediction are far from perfect. When, however, noise, as measured from the vital rate residual series (i.e. actual-predicted values), is introduced into the vital rates, simulations of the experiments display not only perturbed limit cycles for the first 400 days but also noisy quasi-cyclic behaviour for the latter part of the runs. This simulated behaviour is appealingly similar to that observed experimentally and the model and the parameter estimates are adjudged to be a good representation of the blowfly experiments.

Whilst the work reported in Chapters 2-4 was in progress, data concerning the blowfly vital rates became available (Readshaw and van Gerwen, 1983). This data is of adult survival and fecundity for populations of L. cuprina kept at four different constant densities.

In Chapter 5 the survival data from the constant density experiments is considered; these data collapsed neatly and provided a satisfactory separation of the effect of age and density on mortality. The importance of age was made very apparent; death rate, in fact, depends on age to the power four! Knowing the influence of age on survival it then proved possible to investigate the age-independent, density-dependence of death rate; a strong relationship was found. The method used to investigate density-dependence also led necessarily to the inference of a time-dependent age-structure in Nicholson's control population.

In Chapter 6 an attempt was made to estimate how maturation times (i.e. the adult age at which flies first lay eggs) vary throughout the control experiment. This attempt was based on a maturation time - feeding rate relationship derived from Readshaw and van Gerwen's data.

The results are definitely wrong but, nevertheless, were used in conjunction with the inferred age-structure and a development-dependent fecundity relationship (again based on the constant density experimental data) to estimate maximum per capita, age-independent fecundities through time. No relationship with density was found for these estimates.

The results of Chapter 3 were discussed in terms of the evolution of stability. It was suggested that both Nicholson's control and 20-day driven data are of potential use in studying why animal populations tend to be stable and how such stable dynamics evolve. Both experiments represent, as far as I am aware, the only population data in which stabilization has demonstrably taken place.

Because selection for competitively resilient flies must be genetically mediated and selection for competitive resilience is the process by which population stability is brought about, the use of genetic models of the blowfly populations is a possibility for future work. It has been gratifying, though, that the non-genetic model used in Chapters 2-4 has, by the simple expedient of admitting time-dependent parameters, explained adequately why the observed alteration in dynamics occurs. Although the construction of a genetic model is appealing, the utility of the simpler approach is worthy of emphasis.

Before considering the usefulness of the age-dependency investigations, it is worthwhile pointing out that the assumption has been made implicitly throughout this thesis that males and females may be lumped together with impunity. The sex ratio in L. cuprina populations certainly does tend to 1:1 (Mackerass, 1933) but males and females must differ in some respects. Mackerass has observed that over a three day interval when flies were emerging from pupae, males predominated early on. I do not know, however, how differently adult males and females survive or compete for limited resources. A few experimental investigations into blowfly sex differences might be valuable.

The first thing of interest in the age-dependence investigations was the discovery of an extremely strong dependence of death rate upon age. Whether or not this is a blowfly or experiment specific result I do not know; it would be interesting to know how age affects mortality in other insects but such data is not available.

The procedure used to investigate age-independent, density-dependent death rate led to an inferred population age-structure throughout the experiment. Conducting short and relatively cheap, constant density experiments as a prelude to performing long and expensive studies can be seen, therefore, to be potentially very rewarding. Given certain testable assumptions the time-dependent age-structure may be calculated simply from the easy to collect births and deaths data of a longer experiment. If age-structured data is to be collected then such an approach is extremely valuable and cannot be overstressed.

In Chapters 5 and 6 all investigations were based on Readshaw and van Gerwen's data. These data were collected at low and constant densities but the derived relationships were used to investigate a population in which densities were both predominantly high and very variable. This may well be why the attempt to estimate maturation times in Chapter 6 was not successful. More likely, though, the difficulties of Chapter 6 arose because no account was taken of the evolution of competitive resilience. During Nicholson's experiments the flies became able to lay eggs in the absence of protein and the maturation time to feeding rate relationship must have changed as the experiment progressed. Only when adequate account is taken of changes in competitive resilience will it be possible to investigate age-independent, density-dependent fecundities using the methods of Chapter 6.

The gross dynamic features of Nicholson's control population have, I believe, been well explained. It still remains, however, to further investigate and to understand short-term poplation variations. Such comprehension will depend upon a detailed examination of how age, density and perhaps sex and history affect the vital rates. The analysis of Chapter 5 has provided a good insight into how death rates are so affected, the endeavour to comprehend fecundity dependencies is underway.

Nicholson's data was much investigated during the 1970s but in recent years has received little attention. The data are still, however, amongst the most complete available and if the age effects can be understood, might yet be an excellent basis against which to test new age-structure modelling techniques and may provide insight in to why population age-structure changes occur and how important such changes might be.

APPENDIX 1 - FORCED SYSTEMS

The experiment that is the main focus of interest in this thesis was conducted as a control for a series of experiments in which the protein-input rate was varied. It was originally intended that the subject of this thesis should be the effect of environmental variations on population dynamics. Although this has not come to pass, a numerical analysis of the G-B-N model subjected to a variable protein input rate has been carried out and will be reported here as the results lead to the hypothesis forwarded at the start of chapter 2. Essentially, the results of the numerical analysis permit an interpretation of Nicholson's (1957) control and 20-day driven experiments in which the values of Qs, f_0 and δ are changing through time. It was this interpretation that motivated the work that is reported in the thesis.

All natural populations are subject to both deterministic and stochastic fluctuations in at least certain aspects of their environments. That environmental variability plays a significant role in causing population fluctuations has long been appreciated. The literature on the effects of deterministic fluctuations (Uvarov, 1931; Andrewartha and Birch, 1954; Skellam, 1967; Oster and Takahashi, 1974; Coleman, 1979; Coleman, Hsieh and Knowles, 1979; May, 1981; Sanchez, 1983; also Clark, Geier, Morris and Hughes, 1967; see Levins, 1968; Fretwell, 1972 and Krebs, 1972 for reviews) and stochastic fluctuations (e.g. May, 1973a; 1974a; Roughgarden, 1975; Turelli, 1978; Boyce and Daly, 1980) abounds.

In this thesis, the influence of stochastic variability is discussed in chapter 4; in chapters 2 and 3, the experiments are treated as deterministic. Deterministic variability may have profound effects on a non-linear system - specifically it may cause synchronization or subharmonic resonance (see, e.g. Rayleigh, 1883; Ludeke, 1942; Minorsky, 1963, ch. 19; Jones and Sleeman, 1983; Jordan and Smith, 1977, ch. 7; Nisbet and Gurney, 1982, ch. 2). A knowledge of these effects and how they might arise in the G-B-N model is essential to understanding the interpretation of the control and driven experiments which appear in chapter 2.

The importance of synchronization and subharmonic resonance has been recognised in other areas of biological science (e.g. Winfree, 1967; 1980; Hao, 1982; Takahashi and Menaker, 1984) but the phenomena have been paid little attention by population biologists (notable exceptions being Oster and Takahashi, 1974; Oster, 1977a; Nisbet and Gurney, 1976; 1982, ch. 2). This lack of attention being possibly due, as discussed by Nisbet and Gurney (1982) to their probable lack of importance for population modelling.

WHAT ARE SUBHARMONIC RESONANCE AND SYNCHRONIZATION?

Synchronization, or "phase-locking", only occurs in nonlinear systems when, in the absence of an applied force, the system would be characterised as a limit cycle (i.e. having an unstable local equilibrium point). Entrainment to the driving frequency, or a subharmonic of the driving frequency, may occur when the system is driven at, or near, its natural (limit cycle) frequency or a harmonic thereof. The nearness to the natural frequency at which synchronization may occur is dependent upon the strength of the driving force.

Subharmonic resonance only occurs in systems characterised as stable and underdamped. If the driving oscillation is small, then normally the system exhibits a similar, small oscillation (the amplitude and phase of which may be calculated using the transfer function of the system); as the stimulus strength increases, however, the nonlinearities in the system may cause resonances. In the case of the G-B-N model, the nonlinearities cause recovery after population upswings and downswings to be respectively fast and slow. When, therefore, the population starts a cycle well below equilibrium, it may not be able to rise fast enough before being dragged down again by the driving force. Recovery, though, is fast and enables the population to quickly pass equilibrium on the second upswing (if half-harmonic resonance) and the second peak is effectively amplified. The slow recovery after the subsequent downswing results in the low population level at the beginning of the next, subharmonic cycle.

DRIVING THE G-B-N MODEL

In order to investigate the effects of a variable protein-input rate on the blowfly population, Nicholson varied the supply of ground liver from 50 $mg.d^{-1}$ to 500 $mg.d^{-1}$. The rate was increased or decreased in 50 mg. steps with the period of variation, varying in 10-day intervals, from 10 to 80 days.

Variation is incorporated into $\Phi(t)$, for numerical analysis of the driven G-B-N model, not in the step-wise pyramidal form used experimentally but, for ease of computation, continuously as

$$\Phi(t) = \Phi_o(1 + \beta \cos \omega t) \tag{A1.1}$$

Combining (1.5) and (A1.1) gives

$$\frac{dN}{dt} = Qs \quad N(t-\tau) \exp\left[\frac{-N(t-\tau) \; f_o(t-\tau)}{\Phi_o(1 + \beta \cos \omega t)}\right] - \delta N(t) \tag{A1.2}$$

where f_o will, in general, be constant. Qualitatively, the continuous approximation (A1.1) to the protein-input rate yields similar numerical results to those obtained using a step-wise pyramidal form. Quantitatively the two differ with the continuous function leading to a higher, time-averaged population. It is straightforward to perform a stability analysis on (A1.2) and to derive the transfer function from the linearised dynamic. It is thus possible to characterise the amplitude and phase differences of the population cycles when driving with low β-modulation in the stable region of parameter space. In order to investigate the behaviour of the model when driven in the unstable region (in which we might expect synchronization) or in the stable, underdamped region with high β-modulation (in which we might expect subharmonic resonance), it is necessary to resort to numerical analysis.

A pair of $Qs\tau$-$\delta\tau$ parameter values (50, 0.5) was chosen for investigation of the stable, underdamped region. The point describes a system which has a natural frequency, as determined from the transfer function, of $\omega'(\equiv 2\pi f\tau) = 1.81$ - this corresponds to a natural period of 51.4 days. When β is 'large enough', subharmonic resonance may occur if the driving frequency is at or close to the natural frequency or 3/2 or 2 times the natural frequency. Subharmonic effects, however, are not apparent in the data and, as the adult larval food limited populations have previously been characterized as unstable, the phenomenon of resonance has not been exhaustively studied.

Numerous solutions to (A1.2) were obtained with $Qs\,\tau$ = 150 and $\delta\tau = 3.5$ with $\beta = 0.08$. These values were chosen based upon Gurney et al's (1980) estimates for the 1954b afl experiment. The driving frequency, ω', was varied from 0 to 6.0. Fig. A1.1a shows the undriven limit cycle - note the double-peaked structure that arises with the particular parameter values used (see, section 1.3). Fig. A1.1b shows how the population, when driven close to its natural frequency, synchronizes to the driving frequency; Fig. A1.1c illustrates synchronization of the natural limit-cycle to the half-harmonic of the driving force. The results of the synchronization analysis are summarised in Fig. A1.2.

The dashed line in Fig. A1.2 indicates how the population would behave in the absence of an external driving force. Synchronization to the driving frequency is seen in the region S_1 and to the half-harmonic of the driving frequency in the region $S_{1/2}$. There are a number of points (a, b and c) in the region S_1 which do not lie on the abcissa. Two of these points, a and b, lie in an area in which long transients (of about 20 years or more) are common. Nicholson's 80-day driven experiment (Fig. 1.1H) lies in this region and may best be explained as a transient with a 'beating' of the natural limit-cycle frequency and the driving frequency. The point c,

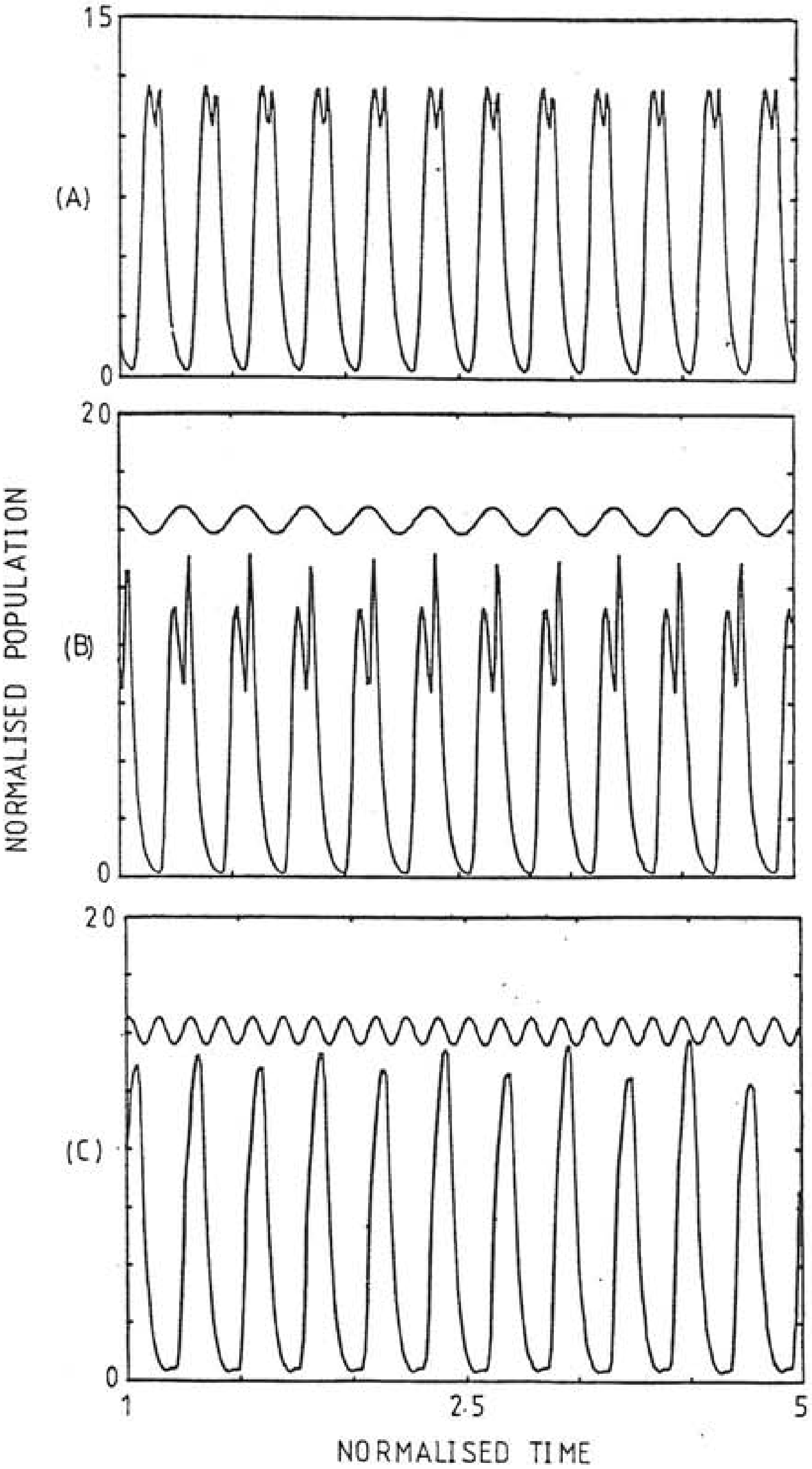
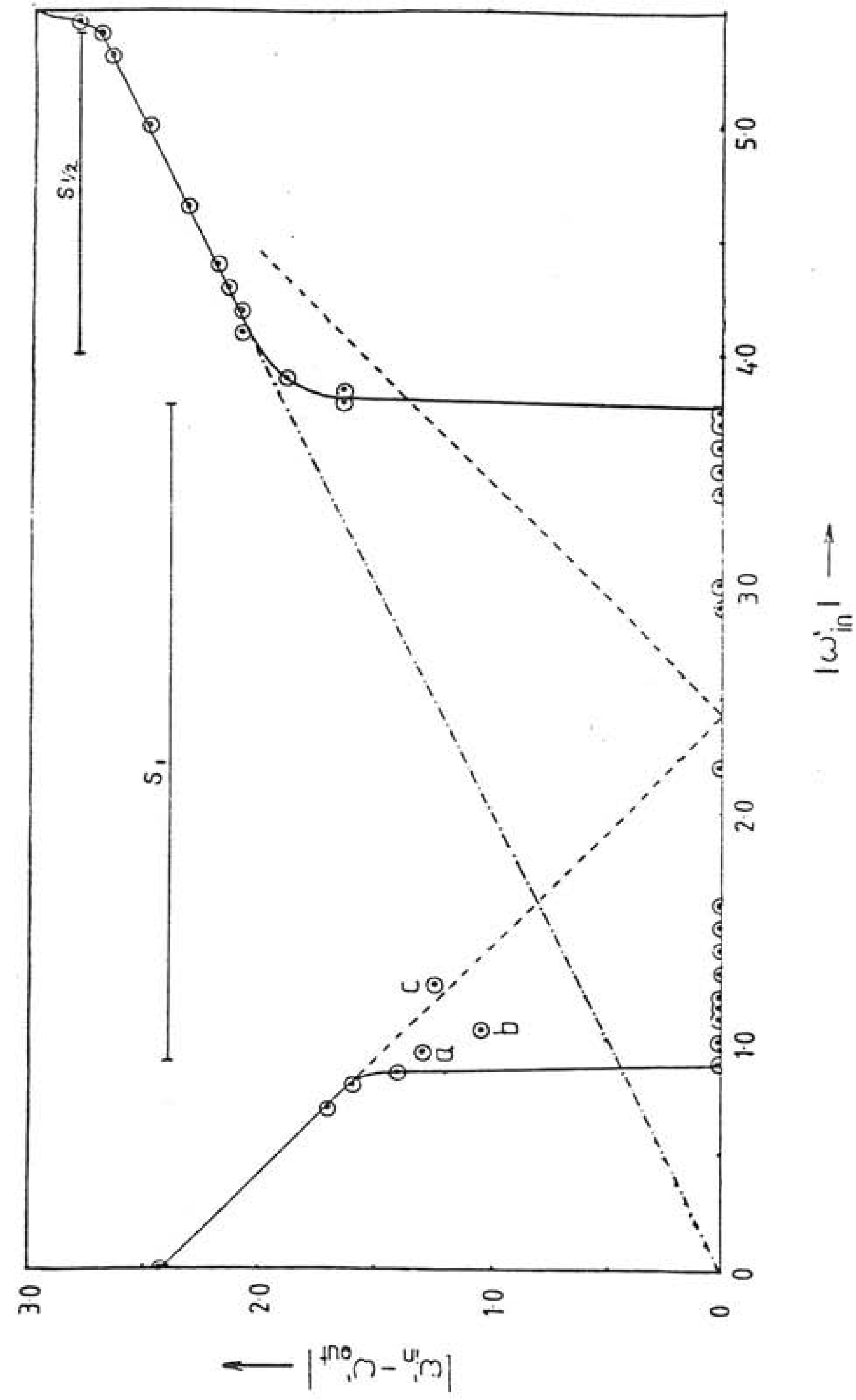


FIG. A1.1 Solutions to the driven G-B-N model displayed as normalised population against normalised time

A) $\omega' = 0$ B) $\omega' = 2.3$ C) $\omega' = 4.6$.



$|\omega'_{in} - \omega'_{out}|$ →
0
1·0
2·0
3·0
$|\omega'_{in}|$ →
0
1·0
2·0
3·0
4·0
5·0
S_1
$S_{1/2}$
a
b
c

however, does not fall into this long-transient category but lies on the driving frequency axis at very close to the natural frequency of the undriven system. Very long solutions have been obtained, but, even when the transient has decayed, the model still exhibits the natural limit-cycle frequency when driven at this frequency. I am uncertain how to interpret point C; the point represents, however, a driving frequency which has no immediate relevancy to our study.

In section 2.1.2 the results of Nicholson's twenty-day driven experiment are interpreted in the light of the results summarized in Fig. A1.2.

APPENDIX 2 - STATISTICS

THE NON-LINEAR LEAST SQUARES FIT.

Let $\chi^2 = \sum_i w_i \, (y_i - a \, x_i \, e^{-v_i b})^2 \; ; \; i = 1..N$

we seek now to minimise χ^2 w.r.t. a and b

$$\frac{\partial \chi^2}{\partial a} = 0 = -2 \sum_i w_i \, x_i \, e^{-v_i b} (y_i - a x_i \, e^{-v_i b})$$

$$\frac{\partial \chi^2}{\partial b} = 0 = 2a \sum_i w_i x_i v_i \, e^{-v_i b} \, (y_i - a x_i \, e^{-v_i b})$$

rearranging leads to two expressions for a

$$a_1 = (\sum_i w_i \, y_i \, x_i \, e^{-v_i b})/(\sum_i w_i \, x_i^2 \, e^{-2v_i b})$$

$$a_2 = (\sum_i w_i \, y_i \, x_i \, v_i \, e^{-v_i b})/(\sum_i w_i \, x_i^2 \, v_i \, e^{-2v_i b})$$

but a_1 MUST equal a2; therefore, if a value of b is obtained for which $a_1 = a_2$, the best fit values of a and b are found.

The linear least squares fit was performed using standard equations (Bevington, 1969). The standard errors were calculated according to the equations given by Ezekiel and Fox (1957 - ch. 17 and Appendix) and the sums of squared residual terms used in the calculation of r, were derived based on the method outlined in Hogg and Craig (1978, p 44).

Both of the above methods for estimating Qs and f_o have been implemented using Pascal programs. They have been checked by hand calculation and a recent U.C.S.D. Pascal version (author, Blythe) of the SIMPLEX method (Caceci and Cacheris, 1984). The results obtained using the simplex method provided a very satisfactory and rigorous check of the least-squares fitting routines.

Results obtained using the weighted, linear regression are presented in chapter 2 and below in Table A2.1.

TABLE S1

cycle mid-point	r	n	Qs	Qs+S·E·	Qs−S·E·	f_o	f_o+S·E·
2.1000E1	-6.9032E-1	1.4000E1	9.1681	1.6737E1	5.0219	5.2135E-1	1.0428E-1
6.1000E1	-8.5360E-1	1.4000E1	4.5293	6.7847	3.0237	6.9265E-1	4.7386E-1
1.0100E2	-5.8076E-1	1.6000E1	6.0200	1.7141E1	2.1142	3.0735E-1	4.3984E-2
1.4100E2	-8.5323E-1	1.5000E1	5.1871	7.2636	3.6941	5.1380E-1	3.5111E-1
1.8100E2	-8.0187E-1	2.0000E1	2.0934	2.9958	1.4628	4.7758E-1	2.7291E-1
2.2100E2	-8.7725E-1	1.8000E1	2.3812	3.0308	1.8708	4.3439E-1	3.3686E-1
2.6100E2	-7.7770E-1	1.8000E1	2.7407	3.5791	2.0987	4.5872E-1	2.9651E-1
3.0100E2	-9.0741E-1	2.0000E1	2.5011	3.0580	2.0455	4.7166E-1	3.7869E-1
3.4100E2	-8.4756E-1	1.9000E1	5.1355	7.7383	3.4081	4.0994E-1	2.7532E-1
3.8100E2	-8.1346E-1	2.0000E1	1.4158	2.0315	9.8677E-1	2.2718E-1	1.3233E-1
4.2100E2	-8.4246E-1	2.0000E1	1.7649	2.3007	1.3540	3.3085E-1	2.2029E-1
4.6100E2	-3.1826E-1	2.0000E1	2.3984E-1	3.4797E-1	1.6531E-1	5.8320E-2	-7.8013E-2
5.0100E2	-3.6629E-1	2.0000E1	6.4873E-1	1.0778	3.9049E-1	9.4266E-2	-1.2101E-1
5.4100E2	-7.2816E-1	2.0000E1	1.3192	1.6835	1.0325	1.4780E-1	6.6250E-2
5.8100E2	-5.9210E-1	2.0000E1	9.2042E-1	1.4611	5.7980E-1	1.3419E-1	-1.1531E-2
6.2100E2	-6.9354E-1	1.9000E1	2.8222	4.1972	1.8976	1.3946E-1	4.8225E-2
6.6100E2	-5.5411E-1	2.0000E1	1.0148	1.8102	5.6891E-1	1.1768E-1	-2.2517E-2
7.0100E2	-7.8754E-1	1.6000E1	8.0132E-1	1.0161	6.3153E-1	7.5783E-2	3.8510E-2
3.1000E1	-5.9453E-1	2.3000E1	6.7602	9.8132	4.6570	5.2869E-1	2.3901E-1
9.1000E1	-6.3258E-1	2.1000E1	5.6882	1.8258E1	1.7722	3.5325E-1	6.5734E-3
1.5100E2	-7.9077E-1	2.5000E1	3.8665	4.2145	3.5473	4.9303E-1	4.4717E-1
2.1100E2	-8.7659E-1	2.8000E1	2.4362	3.2871	1.8056	4.6473E-1	3.4849E-1
2.7100E2	-8.2986E-1	2.8000E1	2.6826	3.5654	2.0184	4.5771E-1	3.2165E-1
3.3100E2	-7.9629E-1	2.9000E1	3.7548	5.1398	2.7166	4.0165E-1	2.7678E-1
3.9100E2	-8.0741E-1	3.0000E1	1.3682	1.8937	9.8844E-1	2.4068E-1	1.5273E-1
4.5100E2	-7.3043E-1	3.0000E1	8.6773E-1	1.2361	6.0913E-1	1.8256E-1	7.9168E-2
5.1100E2	-5.0889E-1	3.0000E1	7.7256E-1	1.2201	4.8917E-1	1.1887E-1	-5.2091E-2
5.7100E2	-6.8339E-1	3.0000E1	1.1280	1.5139	8.4044E-1	1.3707E-1	5.1243E-2
6.3100E2	-5.3613E-1	2.9000E1	1.4895	1.8649	1.1896	1.0111E-1	5.0894E-2
6.9100E2	-6.6813E-1	2.6000E1	7.7595E-1	1.1036	5.4555E-1	8.0598E-2	2.2431E-2
4.1000E1	-7.1771E-1	2.8000E1	7.2097	9.0094	5.7695	5.9199E-1	4.5309E-1
1.2100E2	-6.6150E-1	3.1000E1	4.8190	9.5935	2.4207	3.7187E-1	1.4376E-1
2.0100E2	-8.4608E-1	3.8000E1	2.2073	3.0195	1.6136	4.4325E-1	3.0122E-1
2.8100E2	-8.5014E-1	2.8000E1	2.6540	3.3400	2.1029	4.6838E-1	3.4794E-1
3.6100E2	-8.4254E-1	3.9000E1	3.3638	4.8905	2.3136	3.3104E-1	2.3241E-1
4.4100E2	-7.3784E-1	4.0000E1	8.8776E-1	1.2967	6.0777E-1	1.9597E-1	6.3554E-2
5.2100E2	-5.7996E-1	4.0000E1	8.2151E-1	1.1631	5.8025E-1	1.1275E-1	3.3445E-3
6.0100E2	-5.4849E-1	3.9000E1	1.7619	2.1743	1.4277	1.2761E-1	7.5500E-2
6.8100E2	-6.2451E-1	3.6000E1	7.9021E-1	1.2260	5.0931E-1	8.1058E-2	5.0173E-3
4.6000E1	-6.9987E-1	3.3000E1	9.4041	1.7238E1	5.1304	6.5029E-1	2.3746E-1
1.3600E2	-6.6201E-1	3.6000E1	2.4165	4.5945	1.2710	3.1404E-1	9.5662E-2
2.2600E2	-8.7058E-1	4.1000E1	2.9167	3.8764	2.1946	4.7926E-1	3.5269E-1
3.1600E2	-7.9325E-1	4.4000E1	3.3501	4.2379	2.6482	4.1737E-1	3.2800E-1
4.0600E2	-7.7898E-1	4.5000E1	1.1638	1.7095	7.9230E-1	2.1308E-1	1.0866E-1
4.9600E2	-4.2068E-1	4.5000E1	5.9017E-1	8.4522E-1	4.1209E-1	1.0381E-1	-3.2529E-2
5.8600E2	-5.5379E-1	4.4000E1	1.6004	2.4425	1.0487	1.2544E-1	1.6655E-2
6.7600E2	-6.3739E-1	4.1000E1	8.3926E-1	1.3016	5.4114E-1	8.5685E-2	8.6725E-3
5.1000E1	-6.1097E-1	3.8000E1	5.8583	1.4846E1	2.3118	3.6958E-1	1.1080E-2
1.5100E2	-8.0408E-1	4.1000E1	3.9262	5.0300	3.0646	5.3254E-1	4.0788E-1
2.5100E2	-8.5511E-1	4.6000E1	2.5038	3.3773	1.8562	4.4393E-1	3.1420E-1
3.5100E2	-8.2005E-1	4.9000E1	2.7855	4.0591	1.9115	3.1761E-1	2.1116E-1
4.5100E2	-6.9441E-1	5.0000E1	8.8578E-1	1.2926	6.0698E-1	1.8131E-1	6.2517E-2
5.5100E2	-6.0951E-1	5.0000E1	1.0017	1.4993	6.6922E-1	1.3115E-1	-1.2853E-4
6.5100E2	-5.8016E-1	4.9000E1	1.2749	1.9191	8.4692E-1	1.0191E-1	1.9988E-2
7.1000E1	-6.1480E-1	3.8000E1	4.2088	1.2292E1	1.4423	3.6442E-1	4.7067E-2
1.7100E2	-8.1483E-1	4.5000E1	3.6959	4.0429	3.3786	5.2022E-1	4.7411E-1
2.7100E2	-8.5899E-1	4.6000E1	2.3300	3.0055	1.8063	4.3433E-1	3.1509E-1
3.7100E2	-8.4862E-1	4.9000E1	3.2682	4.3981	2.4286	3.4032E-1	2.6253E-1
4.7100E2	-5.5788E-1	5.0000E1	7.7492E-1	1.1420	5.2582E-1	1.3804E-1	9.1182E-3
5.7100E2	-4.7645E-1	5.0000E1	1.3261	2.6395	6.6626E-1	1.1601E-1	-8.4353E-2
6.7100E2	-6.6581E-1	4.5000E1	8.9695E-1	1.3697	5.8737E-1	9.3168E-2	2.1025E-2
3.6100E2	-6.6206E-1	3.2900E2	1.7287	3.0222	9.8882E-1	1.5983E-1	5.8981E-2

APPENDIX 3 - INCORPORATING STOCHASTICITY

A) SIMULATIONS INCORPORATING DEMOGRAPHIC STOCHASTICITY

If a particular realization contains N individuals at time t, and if the time interval dt is very short, and hence the probability of multiple births or deaths during dt is negligible, then the population change dN which occurs during dt is a random variable with possible values 0, ± 1, and has the statistical expectation value

$$\begin{aligned} E\{dN\} = &(+1) \times \{\text{probability of a birth during dt}\} \\ &+(-1) \times \{\text{probability of a death during dt}\} \\ &+(0) \times \{\text{probability of no change during dt}\} \end{aligned} \tag{A3.1}$$

A3.1 clearly implies

$$E\{dN\} = \{B(N) - D(N)\}dt \tag{A3.2}$$

and $$E\{(dN)^2\} = \{B(N) + D(N)\}dt \tag{A3.3}$$

A3.2 states that the expected population during dt is the same as would be predicted by a deterministic model. A3.3, however, is not so easily interpreted and has the property that $E\{(dN)^2\}$ is proportional to dt and not to dt^2.

If we assume that dt is small enough to allow the neglect of terms of order dt^2 and higher, the actual change in population of any one replicate may be written

$$dN = \{B(N) - D(N)\}dt + \eta(t)\ \{B(N) + D(N)\}^{1/2}dt \quad (A3.4)$$

where η is a random variable with zero mean and unit variance. Because, though, N is restricted to take only integer values, the probability distribution of $\eta(t)$ is strange.

Except for very small populations, any population change which might significantly affect the birth and death probabilities must be the result of a large number of statistically independent births and deaths. A3.4, therefore, may be employed to describe the population change, dN, which occurs over a relatively long time interval, dt, but with $\eta(t)$ now (by the Law of Large Numbers) having a probability distribution close to normal.

If, then, the time scales inherent in our model allow us to both regard η as normally distributed (i.e. dt large) and regard N as continuous (i.e. dt small) then A3.4 may be recast as

$$dN = \{B(N)-D(N)\}dt + \{B(N) + D(N)\}^{1/2}\, dw(t) \qquad (A3.5)$$

where dN and dt are infinitesimally small and dw(t) - a Weiner increment - has the statistical properties

$$E\{dw(t)\} = 0 \qquad \text{for all } t$$
$$E\{(dw(t))^2\} = dt \qquad \text{for all } t$$
$$E\{dw(t)dw(t')\} = 0 \qquad \text{unless } t = t'$$

The stochastic differential equation, A3.5, may now be rewritten in the form used to create the demographic stochastic simulation in chapter 4.

$$\frac{dN}{dt} = B(N) - D(N) + \{B(N) + D(N)\}^{1/2}\, \gamma(t) \qquad (A3.6)$$

where

$$\gamma(t) = dw(t)/dt \qquad (A3.7)$$

The righthand side of I6 may be interpreted as the sum of 'deterministic' and 'stochastic' contributions to dN(dt).

$\gamma(t)$ is Gaussian white noise which is calculated in all simulations presented in chapter 4 using the noise-generator built into the differential equation solving program 'Solver' (Maas et al, 1982).

B. SIMULATIONS INCORPORATING ENVIRONMENTAL STOCHASTICTY

If we make the discrete-to-continuous approximation A3.5 with the additional assumption of a well-behaved driving function, $\Phi(t)$, then the population is described by the non-linear, stochastic differential equation

$$dN(t) = \{B(N,\Phi(t)) - D(N,\Phi(t))\}dt + \{B(N,\Phi(t)) + D(N,\Phi(t))\}^{1/2}\, dw(t) \qquad (A3.8)$$

Now assume that the 'wobble', $f(t)$, in the environmental variable $\Phi(t)$ affects the birth and death probabilities additively so that they take the forms

$$B(N,\Phi(t)) = B(N,\Phi^*) + b(N)f(t)$$
$$D(N,\Phi(t)) = D(N,\Phi^*) + d(N)f(t)$$

and A 3·8 becomes

$$dN(t) = \{B(N,\Phi^*) - D(N,\Phi^*)\}dt + \{b(N)-d(N)\}f(t)dt + \{B(N,\Phi(t)) + D(N,\Phi(t))\}^{1/2}\, dw(t) \qquad (A3.9)$$

If the population fluctuations due to demographic stochasticity are small compared to the driven fluctuations, the last term in A3.9 may be neglected to leave

$$dN(t) = \{B(N,\Phi^*) - D(N,\Phi^*)\}dt + \{b(N) - d(N)\}f(t)dt \tag{A3.10}$$

If the assumption of a well-behaved driving function is now violated and f(t) allowed to be Gaussian white noise of spectral density S_Φ,

$$\text{i.e} \quad f(t) = S_\Phi^{1/2} \; \frac{dw_\Phi(t)}{dt} \tag{A3.11}$$

then

$$\frac{dN}{dt} = B(N,\Phi^*) - D(N,\Phi^*) + \{b(N)-d(N)\}S_\Phi^{1/2} \; \gamma(t) \tag{A3.12}$$

Equation A3.12 is of the form used in the environmental stochastic simulations of chapter 4. Because Gaussian white noise, however, has infinite variance, the birth and death probabilities may become negative - in simulations this is prohibited for obvious reasons of biological sensibility.

APPENDIX 4 - TRANSFER FUNCTION FOR THE MODEL WITH A STOCHASTICALLY VARYING DEATH RATE.

The scaled G-B-N model with a time-dependent variation in death rate is

$$N'(t') = Qs\tau N'(t'-1)\exp\{-N'(t'-1)\}-\{\delta + \epsilon(t')\}\tau N'(t') \qquad (A4.1)$$

where

$$N' = Nf_o/\Phi \; ; \; t' = t/\tau$$

The linearized dynamic is then

$$n'(t') = -\alpha\, n'(t') - \beta f(t') + \gamma\, n'(t'-1) \qquad (A4.2)$$

where

$\alpha = \delta\tau$

$\beta = \ln(Qs/\delta)\tau$

$\gamma = \ln(Qs/\delta)$

defining $\tilde{n}(\omega)$ as the Fourier transform of n(t) and $\tilde{f}(\omega)$ as the transform of f(t), where $\omega = 2\pi\tau/T$ yields

$$\tilde{n}(\omega)[i\omega + \alpha-\gamma\, e^{-i\omega}] = -\beta\, \tilde{f}(\omega) \qquad (A4.3)$$

The transfer function, $T(\omega)$, is then calculated as

$$T(\omega) = \tilde{n}(\omega)/\tilde{f}(\omega) = \frac{-\beta}{[i\omega+\alpha-\gamma e^{-i\omega}]} \qquad (A4.4)$$

and the modulus of the transfer function, $|T(\omega)|$, is found as

$$|T(\omega)| = (Re^2 + Im^2)^{1/2} \qquad (A4.5)$$

where

$$Re = -\beta(\alpha - \gamma \cos \omega)/B.L. \qquad (A4.6)$$

$$Im = \beta\ (w + \gamma \sin \omega)/B.L. \qquad (A4.7)$$

$$B.L. = (\alpha - \gamma \cos \omega)^2 + (\omega + \gamma \sin \omega)^2$$

Figs A4.1 a-d show $|T(\omega)|$ vs. ω at times 400-700 days. The double peaked structure described in 4.3.2 is clearly seen; at greater ω values smaller peaks are also evident.

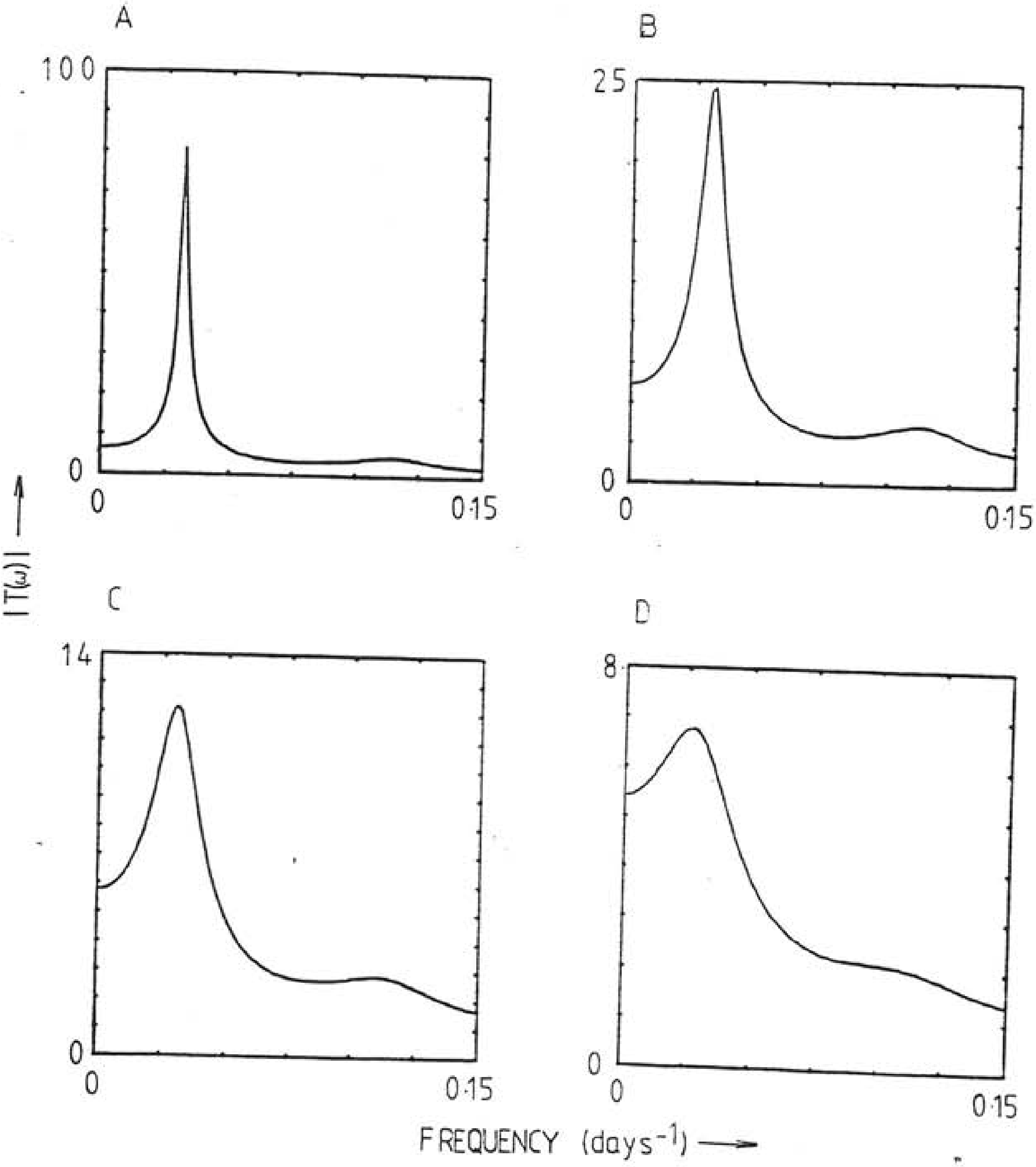


FIG. A4.1 Transfer functions for the G-B-N model with a stochastic death rate. The figures are based on the parameter estimates obtained in chapter 2 at A) t = 400 days B) t = 500 days C) t = 600 days D) t = 700 days.

APPENDIX 5 - MATURATION RATE ESTIMATION

We expect τ_I to be given by

$$1 = \int_{t-\tau_I(t)}^{t} \frac{1.07\,dx}{1+\ln\left[\frac{68}{\Phi}\right]+\ln N(x)} \qquad \text{(A5.1)}$$

This may now be recast as a differential equation:

$$0 = \frac{d}{dt}\left[\int_{t-\tau I(t)}^{t} g(x)\,dx\right] \qquad \text{(A5.2)}$$

$$= g(t) - g(t-\tau I(t))\left[1 - \frac{d\tau_I}{dt}\right] \qquad \text{(A5.3)}$$

$$\frac{d\tau_I}{dt} = 1 - \frac{g(t)}{g(t-\tau_I(t))} \qquad \text{(A5.4)}$$

We now want to calculate the initial conditions for solving (A5.4). If we choose a starting point of t = 8 days then we know the population history up until this time:

t/days	0	2	4	6	8
N(t)	0	948	942	911	858

and at t = 8 days, τ_I will be given as the solution of

$$1 = 1.07 \int_{t-\tau_I(8)}^{t} \frac{dx}{1+\ln\left[\frac{68}{\Phi}\right] + \ln N(x)} \qquad \text{(A5.5)}$$

If we assume a flat age-distribution within each datum interval then (A5.5) is equivalent to solving

$$1 = 1.07 \int_0^2 \frac{dx}{-0.772 + \ln(858 + 26.5\,x)}$$

$$+ 1.07 \int_0^2 \frac{dx}{-0.772 + \ln(911 + 15.5\,x)}$$

$$+ 1.07 \int_0^L \frac{dx}{-0.72 + \ln\,(942+3\,x)} \qquad (A5.6)$$

for L

The integral $\int_a^b \frac{dx}{Z + \ln(N+Mx)}$ is not, however, suitable for quantification and we require a suitable change of variable; therefore let $Z = \ln A$

then the bottom line (B.L.) becomes

$$\begin{aligned} B.L. &= \ln A + \ln(N + Mx) \\ &= \ln(A(N + Mx)) \\ &\equiv \ln y \end{aligned}$$

now $\frac{dy}{dx} = AM \Rightarrow dx = \frac{1}{AM}\,dy$

so

$$\int_a^b \frac{dx}{Z + \ln(N + Mx)} = \frac{1}{AM} \int_{y_1}^{y_2} \frac{dy}{\ln y}$$

where
$$y_1 = A(N + Ma)$$
$$y_2 = A(N + Mb)$$

From Gradshteyn and Ryzhik (1980 p. 204).

$$\int \frac{x^n\,dx}{\ln x} = \mathrm{Li}\,(x^{n+1})$$

and from Gradshteyn & Ryzhik (1980, p. 929)

$$\mathrm{Li}\,(x) = \mathrm{Ei}\,(\ln x).$$

Abramowitz and Stegun (1965, tables 5.1) may now be consulted and the problem is soluble - equation (A5.5) becomes

$$1 = 0.0874 \int_{396.5}^{421} \frac{dy}{\ln y} \qquad (A5.7)$$
$$+ \; 0.1494 \int_{421}^{453.3} \frac{dy}{\ln y}$$
$$+ \; 0.7342 \int_{435.3}^{y^L} \frac{dy}{\ln y}$$

Evaluating (A5.7) is straightforward and we finally obtain L = 1.496 days. $\tau_I(8)$ is then calculated as 2+2+1.496 = 5.496 days.

APPENDIX 6 - RAW DATA

This Appendix contains the raw data for Nicholson's (1957, Fig. 8 I,C & H) experiments. The control data (run I) is the same as that presented in Brillinger et al (1980); it is included here for easy reference. The data for the 20 and 80 day driven experiments (runs C & H respectively) was created by hand measurements of the graphically presented data (Clark, Geier, Morris & Hughes, 1968 p114). The picture was copied, enlarged on to tracing paper and then hand measured.

CONTROL DATA

time	numbers	eggs	non-emerging eggs	emergences	deaths
2.0000	9.4800E2	0.0000	0.0000	9.4800E2	0.0000
4.0000	9.4200E2	0.0000	0.0000	4.0000	1.0000E1
6.0000	9.1100E2	0.0000	0.0000	0.0000	3.1000E1
8.0000	8.5800E2	0.0000	0.0000	0.0000	5.3000E1
1.0000E1	8.0100E2	2.1490E3	1.2100E2	0.0000	5.7000E1
1.2000E1	6.7600E2	4.6270E3	2.6000E2	0.0000	1.2500E2
1.4000E1	5.0400E2	4.5230E3	2.8100E2	0.0000	1.7200E2
1.6000E1	3.9700E2	6.0300E3	4.5800E2	0.0000	1.0700E2
1.8000E1	2.4800E2	2.6840E3	1.2000E2	0.0000	1.4900E2
2.0000E1	1.4600E2	3.3730E3	1.7600E2	0.0000	1.0200E2
2.2000E1	1.8010E3	4.4400E2	9.0000	1.7630E3	1.0800E2
2.4000E1	6.2350E3	1.3300E2	2.0000	4.4870E3	5.3000E1
2.6000E1	5.9740E3	1.7000E1	1.0000	1.8300E3	2.0910E3
2.8000E1	8.9210E3	5.6000E1	2.0000	7.9520E3	5.0050E3
3.0000E1	6.6100E3	5.8000E1	1.0000E1	1.9530E3	4.2640E3
3.2000E1	5.9730E3	0.0000	0.0000	2.4190E3	3.0560E3
3.4000E1	5.6730E3	6.0000	1.0000	1.9660E3	2.2560E3
3.6000E1	3.8750E3	2.5000E1	3.0000	1.3200E2	1.9300E3
3.8000E1	2.3610E3	3.0000E1	1.0000	3.6000E1	1.5500E3
4.0000E1	1.3520E3	0.0000	0.0000	1.6000E1	1.0250E3
4.2000E1	1.2260E3	0.0000	0.0000	8.5000E1	2.1100E2
4.4000E1	9.1200E2	5.4800E2	3.0000E1	1.7000E1	3.3100E2
4.6000E1	5.2100E2	4.6100E2	4.7000E1	0.0000	3.9100E2
4.8000E1	3.6300E2	1.6380E3	1.1100E2	5.0000	1.6300E2
5.0000E1	2.2900E2	1.5240E3	6.6000E1	4.1000E1	1.7500E2
5.2000E1	1.4200E2	2.3380E3	2.7000E2	1.0000E1	9.7000E1
5.4000E1	8.2000E1	1.4730E3	1.0500E2	0.0000	6.0000E1
5.6000E1	5.4200E2	3.2870E3	3.4600E2	4.9400E2	3.4000E1
5.8000E1	9.3900E2	1.3670E3	2.2000E2	4.2400E2	2.7000E1
6.0000E1	2.4310E3	6.1700E2	5.2000E1	1.5410E3	4.9000E1
6.2000E1	3.6890E3	9.3600E2	7.6000E1	1.3170E3	6.1000E1
6.4000E1	4.5430E3	1.1200E2	4.0000	2.0160E3	1.1600E3
6.6000E1	4.5350E3	9.1000E1	8.0000	1.4960E3	1.5040E3
6.8000E1	5.4410E3	0.0000	0.0000	2.8930E3	1.9920E3
7.0000E1	4.4120E3	0.0000	0.0000	8.5500E2	1.8840E3
7.2000E1	3.0220E3	0.0000	0.0000	4.6900E2	1.8590E3
7.4000E1	2.6560E3	1.0000	1.0000	9.2500E2	1.2910E3
7.6000E1	1.9670E3	4.7000E1	2.0000	5.2200E2	1.2110E3
7.8000E1	1.2950E3	8.0000	1.0000	5.5000E1	7.2700E2
8.0000E1	9.1500E2	0.0000	0.0000	4.5000E1	4.2500E2
8.2000E1	5.5100E2	7.7000E1	3.0000	0.0000	3.6400E2
8.4000E1	3.1300E2	5.9800E2	3.7000E1	0.0000	2.3500E2
8.6000E1	1.6700E2	6.8140E3	5.1300E2	0.0000	1.4600E2
8.8000E1	9.5000E1	1.5370E3	9.1000E1	5.0000	7.7000E1
9.0000E1	9.3000E1	1.2960E3	4.8000E1	4.5000E1	4.7000E1
9.2000E1	6.0000E1	4.5100E2	1.1000E1	2.0000	3.5000E1
9.4000E1	6.8000E1	1.8630E3	1.8500E2	4.7000E1	3.9000E1
9.6000E1	5.2590E3	2.4080E3	3.0300E2	5.2050E3	1.4000E1
9.8000E1	6.6730E3	3.5800E2	2.9000E1	1.4960E3	8.2000E1
1.0000E2	5.4410E3	8.4700E2	1.9000E1	1.9570E3	3.1890E3
1.0200E2	3.9870E3	1.4000E1	1.4000E1	8.5500E2	2.3090E3
1.0400E2	2.9520E3	0.0000	0.0000	5.0100E2	1.5360E3
1.0600E2	3.6480E3	6.2000E1	5.0000	1.7710E3	1.0750E3
1.0800E2	4.2220E3	4.0000	2.0000	1.6070E3	1.0330E3
1.1000E2	3.8890E3	3.9000E1	2.0000	6.7400E2	1.0070E3
1.1200E2	2.2950E3	0.0000	0.0000	1.9700E2	1.7910E3
1.1400E2	1.5090E3	0.0000	0.0000	7.0000E2	1.4860E3
1.1600E2	9.2800E2	1.0700E2	0.0000	0.0000	5.8100E2
1.1800E2	7.3900E2	1.7200E2	1.5000E1	1.6000E1	2.0500E2
1.2000E2	5.6600E2	8.2800E2	6.9000E1	4.3000E1	2.1600E2
1.2200E2	3.8300E2	1.2160E3	1.0800E2	0.0000	1.8300E2
1.2400E2	2.7400E2	2.1090E3	1.2300E2	3.7000E1	1.4600E2
1.2600E2	1.9200E2	3.4600E3	2.5100E2	0.0000	8.2000E1
1.2800E2	2.2600E2	2.4380E3	2.2900E2	1.0500E2	7.1000E1
1.3000E2	5.1900E2	3.2340E3	1.7500E2	3.2600E2	3.3000E1
1.3200E2	1.2240E3	1.5740E3	1.3000E2	7.2900E2	2.4000E1
1.3400E2	2.2360E3	7.4450E3	9.0000E2	1.0720E3	6.0000E1
1.3600E2	3.8180E3	2.0190E3	1.6700E2	1.7470E3	1.6500E2
1.3800E2	6.2080E3	6.7200E2	6.2000E1	3.7940E3	1.4040E3
1.4000E2	5.9960E3	0.0000	0.0000	2.5760E3	2.7880E3
1.4200E2	5.7890E3	0.0000	0.0000	2.2200E3	2.4270E3
1.4400E2	6.6520E3	0.0000	0.0000	3.2480E3	2.3850E3
1.4600E2	7.9390E3	0.0000	0.0000	4.8080E3	3.5210E3
1.4800E2	4.8680E3	3.3000E1	5.0000	1.0520E3	4.1230E3
1.5000E2	3.9520E3	2.6000E1	5.0000	1.2700E3	2.1860E3
1.5200E2	2.7120E3	3.2000E1	6.0000	9.5000E1	1.3350E3
1.5400E2	1.7340E3	0.0000	0.0000	3.0000	9.8100E2
1.5600E2	1.2240E3	3.2100E2	1.0000E1	0.0000	5.1000E2
1.5800E2	7.0300E2	2.3000E2	2.5000E1	0.0000	5.2100E2
1.6000E2	5.0800E2	3.9200E2	3.0000E1	1.8000E1	2.1300E2
1.6200E2	3.6600E2	2.5300E2	1.6000E1	1.0000E1	1.5200E2
1.6400E2	2.7900E2	3.2400E2	6.3000E1	1.9000E1	1.0600E2
1.6600E2	2.4300E2	1.3690E3	1.5500E2	2.7000E1	6.3000E1
1.6600E2	3.4300E2	1.2520E3	9.4000E1	1.2000E2	2.0000E1
1.7000E2	7.6100E2	9.7700E2	9.2000E1	4.2500E2	1.7000E1
1.7200E2	1.0250E3	1.3360E3	4.8000E1	2.9800E2	3.4000E1
1.7400E2	1.2210E3	1.4500E3	1.5500E2	2.4700E2	5.1000E1
1.7600E2	1.6000E3	2.5200E3	2.8700E2	4.5600E2	7.7000E1
1.7800E2	2.2670E3	3.0570E3	4.1900E2	8.4700E2	2.3000E2
1.8000E2	3.2900E3	3.0200E2	1.9000E1	1.4590E3	4.3600E2
1.8200E2	3.4710E3	1.6600E2	1.9000E1	7.2100E2	5.4000E2
1.8400E2	3.6370E3	2.0000E1	4.0000	1.2580E3	1.0920E3
1.8600E2	3.7030E3	2.7000E1	3.0000	1.0450E3	9.7900E2
1.8800E2	4.8760E3	7.0000E1	0.0000	2.3000E3	1.1270E3
1.9000E2	5.3540E3	4.0000	0.0000	1.7820E3	1.2940E3
1.9200E2	4.8900E3	3.8000E1	2.0000	1.2520E3	1.7260E3
1.9400E2	3.0290E3	5.0000	2.0000	2.3200E2	2.0930E3
1.9600E2	1.9500E3	4.8000E1	3.0000	5.3000E1	1.1320E3
1.9800E2	1.2250E3	1.1500E2	6.0000	2.3000E1	7.4800E2
2.0000E2	1.0760E3	3.6400E2	1.7000E1	5.0000E1	1.9900E2
2.0200E2	9.0500E2	1.0340E3	6.5000E1	3.0000E1	2.0100E2
2.0400E2	7.7200E2	1.2950E3	1.1000E2	3.9000E1	1.7200E2
2.0600E2	6.2800E2	2.3830E3	1.4400E2	0.0000	1.4400E2
2.0800E2	4.7300E2	2.4350E3	1.8800E2	3.3000E1	1.8800E2
2.1000E2	5.3900E2	2.5350E3	1.0400E2	1.1300E2	4.7000E1
2.1200E2	8.2500E2	1.7010E3	1.1500E2	3.8300E2	9.7000E1
2.1400E2	1.7020E3	1.6010E3	1.5200E2	9.2800E2	5.1000E1
2.1600E2	2.8680E3	5.8000E2	6.2000E1	1.2010E3	3.5000E1
2.1800E2	4.4730E3	4.6000E2	5.5000E1	2.1750E3	5.7000E2
2.2000E2	5.2210E3	3.6300E2	1.8000E1	1.6680E3	9.2000E2
2.2200E2	6.5920E3	0.0000	0.0000	2.4800E3	1.6090E3
2.2400E2	6.4000E3	1.0600E2	2.0000	1.8720E3	2.0640E3
2.2600E2	4.7520E3	3.0000E1	0.0000	1.2280E3	2.8760E3
2.2800E2	3.5210E3	0.0000	0.0000	4.6100E2	1.6920E3
2.3000E2	2.7190E3	3.0300E2	1.6000E1	6.6000E2	1.4620E3
2.3200E2	1.9310E3	7.5500E2	7.7000E1	1.6500E2	9.5300E2
2.3400E2	1.5000E3	5.3600E2	3.4000E1	1.6000E1	4.4700E2
2.3600E2	1.0820E3	6.0200E2	9.6000E1	1.0600E2	5.2400E2
2.3800E2	8.4900E2	6.8800E2	3.8000E1	7.8000E1	3.1100E2
2.4000E2	7.7400E2	1.2440E3	1.7200E2	0.0000	7.5000E1

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7.2000E2 , 5.1030E3 , 0.0000 , 0.0000 , 4.9670E3 , 3.7470E3
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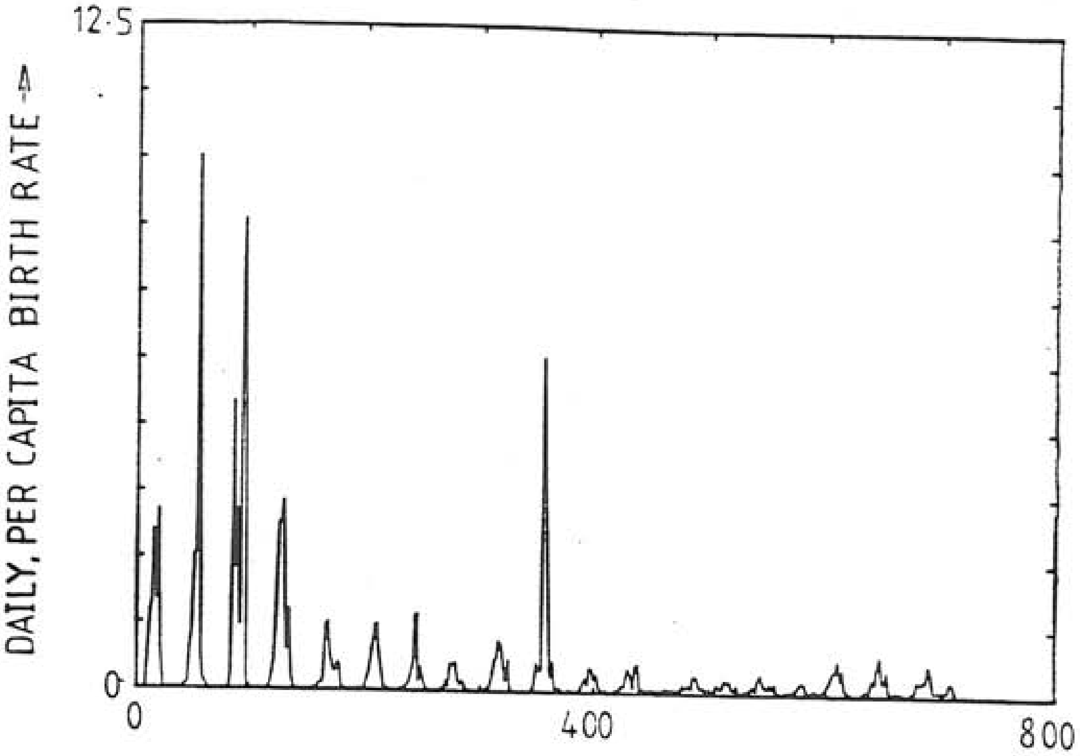
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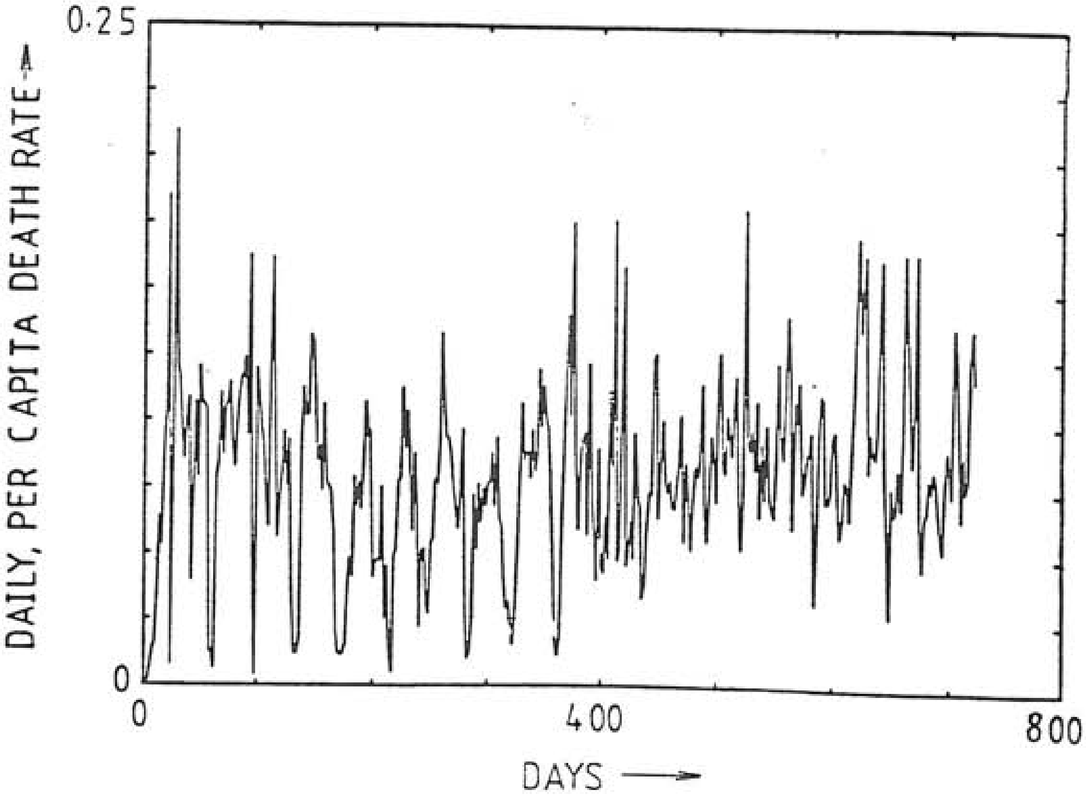
DAILY, PER CAPITA BIRTH RATE →
0
0
400
800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DAILY, PER CAPITA DEATH RATE →
0
0
400
800
DAYS →

DATA FROM THE 20-DAY DRIVEN EXPERIMENT

time	numbers	eggs
0.0000	3.0000E2	0.0000
2.0000	3.0000E2	0.0000
4.0000	3.0000E2	0.0000
6.0000	3.0000E2	0.0000
8.0000	3.0000E2	0.0000
1.0000E1	3.0000E2	0.0000
1.2000E1	3.0000E2	0.0000
1.4000E1	3.0000E2	0.0000
1.6000E1	3.0000E2	0.0000
1.8000E1	3.0000E2	0.0000
2.0000E1	3.0000E2	0.0000
2.2000E1	3.0000E2	0.0000
2.4000E1	3.0000E2	1.2308E2
2.6000E1	3.0000E2	1.0462E3
2.8000E1	3.0000E2	2.2974E3
3.0000E1	3.0000E2	4.7385E3
3.2000E1	3.0000E2	5.8462E3
3.4000E1	4.0000E2	7.5282E3
3.6000E1	6.0000E2	4.9436E3
3.8000E1	2.9000E3	6.9744E2
4.0000E1	7.8000E3	1.2308E2
4.2000E1	8.0000E3	7.7949E2
4.4000E1	8.0000E3	2.0513E1
4.6000E1	8.0000E3	2.0513E1
4.8000E1	7.8000E3	4.1026E1
5.0000E1	6.0000E3	4.1026E1
5.2000E1	4.1000E3	6.1538E1
5.4000E1	2.6000E3	2.0513E2
5.6000E1	2.2000E3	8.2051E1
5.8000E1	1.7000E3	1.4359E2
6.0000E1	1.1000E3	0.0000
6.2000E1	6.5000E2	0.0000
6.4000E1	4.0000E2	0.0000
6.6000E1	3.5000E2	2.4615E2
6.8000E1	2.5000E2	2.0513E2
7.0000E1	3.0000E2	3.0769E2
7.2000E1	3.5000E2	1.6000E3
7.4000E1	4.0000E2	5.8051E3
7.6000E1	4.0000E2	3.2410E3
7.8000E1	4.5000E2	3.0769E3
8.0000E1	5.0000E2	6.1538E2
8.2000E1	6.0000E2	4.7179E2
8.4000E1	8.0000E2	1.8462E2
8.6000E1	2.0000E3	2.0513E1
8.8000E1	6.0000E3	4.1026E1
9.0000E1	6.7000E3	1.4359E2
9.2000E1	5.7000E3	4.1026E1
9.4000E1	4.7000E3	8.2051E1
9.6000E1	3.2000E3	2.0513E1
9.8000E1	2.5000E3	0.0000
1.0000E2	1.6000E3	0.0000
1.0200E2	1.1000E3	0.0000
1.0400E2	8.0000E2	0.0000
1.0600E2	5.5000E2	5.7436E2
1.0800E2	4.5000E2	5.7436E2
1.1000E2	4.0000E2	2.9333E3
1.1200E2	3.5000E2	1.6667E3
1.1400E2	3.0000E2	3.0359E3
1.1600E2	2.5000E2	1.2923E3
1.1800E2	2.5000E2	1.6000E3
1.2000E2	3.0000E2	6.1538E1
1.2200E2	6.0000E2	2.0513E1
1.2400E2	1.8000E3	4.1026E1
1.2600E2	4.0000E3	4.1026E1
1.2800E2	5.4000E3	8.2051E1
1.3000E2	4.0000E3	6.1538E1
1.3200E2	2.9000E3	3.2821E2
1.3400E2	3.3000E3	5.1282E2
1.3600E2	2.3000E3	1.8462E2
1.3800E2	1.8000E3	1.2308E2
1.4000E2	1.2000E3	2.0513E1
1.4200E2	6.5000E2	0.0000
1.4400E2	3.5000E2	0.0000
1.4600E2	3.0000E2	2.4615E2
1.4800E2	6.0000E2	6.1538E1
1.5000E2	9.5000E2	1.9282E3
1.5200E2	1.1500E3	1.4974E3
1.5400E2	1.1000E3	2.3179E3
1.5600E2	9.5000E2	1.2513E3
1.5800E2	7.5000E2	1.6410E2
1.6000E2	7.0000E2	6.1538E1
1.6200E2	7.0000E2	6.1538E1
1.6400E2	8.0000E2	2.0513E1
1.6600E2	2.1000E3	4.1026E1
1.6800E2	4.2000E3	4.1026E1
1.7000E2	4.7500E3	2.6667E2
1.7200E2	4.5000E3	2.0513E2
1.7400E2	4.1000E3	8.6154E2
1.7600E2	2.3000E3	8.2051E1
1.7800E2	1.7000E3	4.1026E1
1.8000E2	1.2000E3	6.1538E1
1.6200E2	6.0000E2	1.8462E2
1.8400E2	4.0000E2	4.1026E1
1.8600E2	3.0000E2	3.2821E2
1.8800E2	3.0000E2	4.5128E2
1.9000E2	9.0000E2	3.6513E3
1.9200E2	1.5000E3	1.1077E3
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1.9600E2	1.6000E3	4.1026E1
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2.0200E2	1.3500E3	0.0000
2.0400E2	1.6000E3	4.1026E1
2.0600E2	2.8000E3	0.0000
2.0800E2	4.5000E3	1.2308E2
2.1000E2	4.2000E3	4.1026E1
2.1200E2	6.7000E3	2.0513E1
2.1400E2	2.2000E3	2.2564E2
2.1600E2	1.5000E3	4.1026E1
2.1800E2	1.1000E3	1.0256E2
2.2000E2	7.0000E2	2.2564E2
2.2200E2	6.0000E2	1.2308E2
2.2400E2	4.0000E2	3.0769E2
2.2600E2	3.5000E2	3.2000E3
2.2800E2	4.0000E2	3.0769E3
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2.3200E2	6.0000E2	6.7077E3
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2.4600E2	8.0000E3	1.2308E2
2.4800E2	7.0000E3	1.0256E2
2.5000E2	3.6000E3	2.2564E2
2.5200E2	2.5000E3	1.8462E2
2.5400E2	1.7000E3	2.6667E2
2.5600E2	1.3500E3	4.3077E2
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2.6000E2	7.0000E2	2.6667E2
2.6200E2	3.0000E2	8.6154E2
2.6400E2	5.0000E2	4.5128E2
2.6600E2	6.0000E2	4.1026E3
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2.8000E2	1.8500E3	6.1538E1
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2.8400E2	4.5000E3	2.0513E1
2.8600E2	7.1000E3	4.1026E1
2.8800E2	7.6000E3	2.6667E2
2.9000E2	5.0000E3	2.0513E1
2.9200E2	3.4000E3	1.6410E2
2.9400E2	2.3000E3	6.1538E1
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2.9800E2	1.0000E3	1.8462E2
3.0000E2	5.0000E2	2.6667E2
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3.0600E2	2.5000E2	3.3231E3
3.0800E2	3.0000E2	6.0923E3
3.1000E2	5.0000E2	5.1282E3
3.1200E2	5.0000E2	1.9487E3
3.1400E2	6.5000E2	4.1026E1
3.1600E2	9.0000E2	6.1538E1
3.1800E2	1.0500E3	4.1026E1
3.2000E2	1.1500E3	1.8462E2
3.2200E2	3.6000E3	6.1538E1
3.2400E2	7.2500E3	2.0513E2
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3.3000E2	4.0000E3	1.6410E2
3.3200E2	2.9000E3	5.7436E2
3.3400E2	2.0000E3	3.6923E2
3.3600E2	1.5000E3	1.0256E2
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6.7400E2  , 1.8000E3  , 2.0513E2
6.7600E2  , 2.3000E3  , 5.5385E2
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6.8400E2  , 3.1000E3  , 1.0051E3
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DATA FROM THE 80 - DAY DRIVEN EXPERIMENT

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4.0000	, 1.0000E2	, 0.0000
6.0000	, 1.0000E2	, 0.0000
8.0000	, 1.0000E2	, 0.0000
1.0000E1	, 1.0000E2	, 0.0000
1.2000E1	, 1.0000E2	, 0.0000
1.4000E1	, 1.0000E2	, 0.0000
1.6000E1	, 1.0000E2	, 0.0000
1.8000E1	, 1.0000E2	, 0.0000
2.0000E1	, 1.0000E2	, 0.0000
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2.4000E1	, 1.0000E2	, 3.4872E2
2.6000E1	, 1.0000E2	, 4.3077E2
2.8000E1	, 1.0000E2	, 1.6615E3
3.0000E1	, 2.0000E2	, 1.9282E3
3.2000E1	, 7.0000E2	, 1.5590E3
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3.6000E1	, 1.6000E3	, 2.0513E2
3.8000E1	, 2.2000E3	, 6.1538E1
4.0000E1	, 2.7000E3	, 1.2308E2
4.2000E1	, 3.3000E3	, 1.0256E2
4.4000E1	, 4.7000E3	, 2.4615E2
4.6000E1	, 4.6000E3	, 8.2051E1
4.8000E1	, 3.5000E3	, 8.2051E1
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5.4000E1	, 7.0000E2	, 8.2051E1
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6.0000E1	, 3.5000E2	, 1.6615E3
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6.4000E1	, 2.5000E2	, 4.6974E3
6.6000E1	, 2.0000E2	, 4.7795E3
6.8000E1	, 8.0000E2	, 3.3846E3
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7.2000E1	, 2.6000E3	, 4.5128E2
7.4000E1	, 4.0000E3	, 8.2051E2
7.6000E1	, 6.0000E3	, 5.1282E2
7.8000E1	, 7.2000E3	, 8.2051E1
8.0000E1	, 6.6000E3	, 8.2051E1
8.2000E1	, 6.4000E3	, 8.2051E1
8.4000E1	, 4.7000E3	, 8.2051E1
8.6000E1	, 3.2000E3	, 3.4872E2
8.8000E1	, 2.4000E3	, 4.1026E1
9.0000E1	, 1.7000E3	, 4.1026E1
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9.4000E1	, 2.5000E2	, 4.1026E1
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9.8000E1	, 3.4000E2	, 6.1538E1
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4.8200E2 , 7.0000E2 , 1.0256E2
4.8400E2 , 4.0000E2 , 3.6923E2
4.8600E2 , 4.0000E2 , 9.4359E2
4.8800E2 , 4.5000E2 , 1.1282E3
4.9000E2 , 6.0000E2 , 3.2821E2
4.9200E2 , 6.0000E2 , 9.6410E2
4.9400E2 , 6.0000E2 , 1.0462E3
4.9600E2 , 6.5000E2 , 1.8462E2
4.9800E2 , 8.5000E2 , 4.1026E1
5.0000E2 , 1.4000E3 , 1.2308E2
5.0200E2 , 2.2000E3 , 4.1026E1
5.0400E2 , 3.0000E3 , 4.1026E1
5.0600E2 , 2.4000E3 , 4.1026E1
5.0800E2 , 2.0000E3 , 4.1026E1
5.1000E2 , 1.3000E3 , 4.1026E1
5.1200E2 , 7.0000E2 , 1.0256E2
5.1400E2 , 5.0000E2 , 6.1538E1
5.1600E2 , 3.0000E2 , 5.1282E2
5.1800E2 , 2.5000E2 , 1.0051E3
5.2000E2 , 1.5000E2 , 7.1795E2
5.2200E2 , 1.0000E2 , 6.3590E2
5.2400E2 , 5.0000E1 , 3.2821E2
5.2600E2 , 2.0000E2 , 2.0513E2
5.2800E2 , 9.0000E2 , 6.5641E2
5.3000E2 , 1.5000E3 , 4.9231E2
5.3200E2 , 2.1000E3 , 7.3846E2
5.3400E2 , 2.3500E3 , 2.2154E3
5.3600E2 , 2.0000E3 , 2.5026E3
5.3800E2 , 1.6000E3 , 1.0256E3
5.4000E2 , 1.2500E3 , 1.7026E3
5.4200E2 , 1.6000E3 , 2.6462E3
5.4400E2 , 2.3000E3 , 1.6615E3
5.4600E2 , 3.2000E3 , 1.0051E3
5.4800E2 , 4.6000E3 , 2.6872E3
5.5000E2 , 4.0000E3 , 2.1538E3
5.5200E2 , 4.5000E3 , 6.5641E2
5.5400E2 , 5.1000E3 , 6.1538E2
5.5600E2 , 5.0000E3 , 2.8718E2
5.5800E2 , 4.4000E3 , 7.5897E2
5.6000E2 , 4.7500E3 , 7.3846E2
5.6200E2 , 4.7000E3 , 4.9231E2
5.6400E2 , 4.4000E3 , 2.0513E1
5.6600E2 , 3.5000E3 , 3.4872E2
5.6800E2 , 2.7500E3 , 2.8718E2
5.7000E2 , 2.8000E3 , 4.1026E.
5.7200E2 , 2.5000E3 , 1.2308E2
5.7400E2 , 2.0500E3 , 6.1538E1
5.7600E2 , 1.9000E3 , 4.1026E1
5.7800E2 , 1.7000E3 , 2.0513E1
5.8000E2 , 1.4000E3 , 0.0000
5.8200E2 , 1.1500E3 , 0.0000
5.8400E2 , 9.0000E2 , 6.1538E1
5.8600E2 , 7.0000E2 , 3.2821E2
5.8800E2 , 5.0000E2 , 4.7179E2
5.9000E2 , 3.0000E2 , 1.8462E3
5.9200E2 , 2.0000E2 , 1.2308E3
5.9400E2 , 2.0000E2 , 6.5641E2
5.9600E2 , 2.0000E2 , 2.2564E3
5.9800E2 , 2.0000E2 , 2.2564E3
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6.0000E2 , 4.0000E2 , 2.1128E3
6.0200E2 , 2.2000E3 , 1.8667E3
6.0400E2 , 3.1000E3 , 3.3026E3
6.0600E2 , 3.3500E3 , 3.3641E3
6.0800E2 , 3.1000E3 , 6.4410E3
6.1000E2 , 4.8000E3 , 3.3026E3
6.1200E2 , 6.4000E3 , 2.6051E3
6.1400E2 , 7.2000E3 , 7.5897E2
6.1600E2 , 4.8000E3 , 1.5385E3
6.1800E2 , 6.2000E3 , 1.5795E3
6.2000E2 , 7.6000E3 , 5.1282E2
6.2200E2 , 7.7000E3 , 3.4872E2
6.2400E2 , 6.8500E3 , 3.4872E2
6.2600E2 , 4.9000E3 , 4.5128E2
6.2800E2 , 4.3000E3 , 7.5897E2
6.3000E2 , 4.5000E3 , 7.1795E2
6.3200E2 , 3.7000E3 , 2.6667E3
6.3400E2 , 3.0000E3 , 1.3744E3
6.3600E2 , 2.6000E3 , 1.5385E3
6.3800E2 , 2.1000E3 , 1.7026E3
6.4000E2 , 1.9500E3 , 2.8718E2
6.4200E2 , 2.2000E3 , 2.0513E2
6.4400E2 , 3.3000E3 , 2.6667E2
6.4600E2 , 5.2000E3 , 4.1026E2
6.4800E2 , 6.1000E3 , 5.1282E2
6.5000E2 , 5.3000E3 , 3.0769E2
6.5200E2 , 5.1000E3 , 8.2051E2
6.5400E2 , 3.3000E3 , 6.1538E1
6.5600E2 , 2.5000E3 , 2.6667E2
6.5800E2 , 2.0000E3 , 8.4103E2
6.6000E2 , 1.9000E3 , 6.1538E1
6.6200E2 , 2.1500E3 , 0.0000
6.6400E2 , 2.3500E3 , 7.3846E2
6.6600E2 , 2.1000E3 , 2.2564E2
6.6800E2 , 2.3000E3 , 4.3077E2
6.7000E2 , 2.2000E3 , 1.9487E3
6.7200E2 , 1.7500E3 , 9.2308E2
6.7400E2 , 1.7000E3 , 6.5641E2
6.7600E2 , 1.7500E3 , 7.7949E2
6.7800E2 , 2.3000E3 , 9.0256E2
6.8000E2 , 2.9000E3 , 9.8462E2
6.8200E2 , 3.8000E3 , 9.2308E2
6.8400E2 , 4.0000E3 , 1.1282E3
6.8600E2 , 4.0000E3 , 6.1538E2
6.8800E2 , 3.2000E3 , 2.9128E3
6.9000E2 , 3.1000E3 , 2.4000E3
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APPENDIX 7 READSHAW and van GERWEN's DATA

This Appendix contains Readshaw and van Gerwen's (1983) raw data. Shown are age since emergence, number of flies, eggs laid and egg survival for four different constant density experiments.

READSHAW AND VAN GERWEN'S DATA

	50 flies per cage(fpc)			100 fpc		
age	flies surviving	eggs	% egg survival			
0.0000	2.5000E2	0.0000	0.0000	5.0000E2	0.0000	0.0000
1.0000	2.5000E2	0.0000	0.0000	5.0000E2	0.0000	0.0000
2.0000	2.5000E2	0.0000	0.0000	5.0000E2	0.0000	0.0000
3.0000	2.5000E2	0.0000	0.0000	5.0000E2	0.0000	0.0000
4.0000	2.5000E2	3.8000E2	9.4000E-1	4.9900E2	0.0000	0.0000
5.0000	2.4900E2	1.8530E3	8.7000E-1	4.9800E2	9.0400E2	9.6000E-1
6.0000	2.4800E2	2.7070E3	8.7000E-1	4.9600E2	1.5100E3	8.0000E-1
7.0000	2.4700E2	3.2180E3	9.3000E-1	4.8800E2	2.3060E3	8.4000E-1
8.0000	2.4700E2	2.7330E3	9.6000E-1	4.7900E2	2.1860E3	9.3000E-1
9.0000	2.4500E2	6.1620E3	8.3000E-1	4.6800E2	5.6660E3	8.2000E-1
1.0000E1	2.4500E2	3.2350E3	9.3000E-1	4.5900E2	4.3350E3	7.3000E-1
1.1000E1	2.4400E2	5.0220E3	5.2000E-1	4.4600E2	5.1000E3	4.9000E-1
1.2000E1	2.4300E2	5.5780E3	9.2000E-1	4.3300E2	6.0480E3	6.6000E-1
1.3000E1	2.4100E2	3.0440E3	8.9000E-1	4.1900E2	4.4300E3	7.0000E-1
1.4000E1	2.3700E2	3.9170E3	9.2000E-1	3.9500E2	8.5100E3	7.5000E-1
1.5000E1	2.3100E2	9.1050E3	8.9000E-1	3.7000E2	2.8360E3	6.9000E-1
1.6000E1	2.2600E2	1.8720E3	9.0000E-1	3.2700E2	1.7640E3	6.1000E-1
1.7000E1	2.2200E2	2.4050E3	8.8000E-1	2.3000E2	1.5040E3	5.9000E-1
1.8000E1	2.1100E2	1.0870E3	8.4000E-1	2.4500E2	1.4420E3	4.9000E-1
1.9000E1	1.8800E2	6.6200E2	5.3000E-1	1.9000E2	5.7000E2	5.2000E-1
2.0000E1	1.7000E2	3.1650E3	8.0000E-1	1.4800E2	5.9700E2	2.5000E-1
2.1000E1	1.5300E2	1.3130E3	8.3000E-1	1.0900E2	9.0500E2	4.9000E-1
2.2000E1	1.3200E2	7.3600E2	9.4000E-1	7.7000E1	2.7000E1	0.0000
2.3000E1	1.1300E2	8.4600E2	6.1000E-1	4.8000E1	2.9200E2	4.8000E-1
2.4000E1	9.8000E1	1.3440E3	5.4000E-1	3.8000E1	6.3000E1	4.6000E-1
2.5000E1	8.6000E1	2.9560E3	6.5000E-1	2.6000E1	5.3000E1	2.1000E-1
2.6000E1	7.1000E1	4.9700E2	5.9000E-1	1.3000E1	0.0000	0.0000
2.7000E1	5.6000E1	9.7000E1	1.3000E-1			
2.8000E1	4.2000E1	2.3100E2	9.0000E-1			
2.9000E1	2.9000E1	4.2700E2	4.7000E-1			
3.0000E1	1.3000E1	0.0000	0.0000			
3.1000E1	6.0000	0.0000	0.0000			

	400 fpc			800 fpc		
0.0000	2.0000E3	0.0000	0.0000	4.0000E3	0.0000	0.0000
1.0000	2.0000E3	0.0000	0.0000	4.0000E3	0.0000	0.0000
2.0000	1.9970E3	0.0000	0.0000	4.0000E3	0.0000	0.0000
3.0000	1.9950E3	0.0000	0.0000	4.0000E3	0.0000	0.0000
4.0000	1.9900E3	0.0000	0.0000	3.9840E3	0.0000	0.0000
5.0000	1.9800E3	0.0000	0.0000	3.9670E3	0.0000	0.0000
6.0000	1.9740E3	1.7000E2	4.7000E-1	3.9260E3	0.0000	0.0000
7.0000	1.9590E3	1.7500E2	9.4000E-1	3.8800E3	3.1000E2	7.2000E-1
8.0000	1.8870E3	0.0000	0.0000	3.7570E3	1.2600E2	5.9000E-1
9.0000	1.7530E3	3.5200E2	7.2000E-1	3.5340E3	6.5600E2	5.6000E-1
1.0000E1	1.4530E3	3.0000E2	7.7000E-1	3.0820E3	5.4100E2	5.5000E-1
1.1000E1	1.0690E3	1.3420E3	6.6000E-1	2.1990E3	8.1200E2	7.4000E-1
1.2000E1	7.8300E2	4.0100E2	6.6000E-1	1.5330E3	5.1000E2	6.5000E-1
1.3000E1	5.4700E2	3.1800E2	4.4000E-1	1.0550E3	4.2800E2	6.1000E-1
1.4000E1	4.0000E2	1.2000E2	1.4000E-1	6.0300E2	1.1200E2	7.3000E-1
1.5000E1	2.8200E2	0.0000	0.0000	3.6300E2	1.1200E2	7.3000E-1
1.6000E1	1.7200E2	4.0000E1	5.0000E-2	2.0400E2	0.0000	0.0000
1.7000E1	1.0700E2	0.0000	0.0000	1.4800E2	0.0000	0.0000
1.8000E1	5.0000E1	0.0000	0.0000			
1.9000E1	2.8000E1	0.0000	0.0000			

APPENDIX 8 - A PROBLEM WITH THE MATURATION RATE ESTIMATES

The data shown in this Appendix are the calculated immature and mature population sizes through time and the eggs per mature fly estimates. Whenever a 'NOENTRY' appears in the eggs per mature fly column, this signifies that eggs have been laid but also that there has been an estimate of no mature flies in the population at that time. Such an event is clearly impossible and implies an incorrect analysis.

t	I	M	E/M	I+M
2.0000	9.4800E2	0.0000	0.0000	9.4800E2
4.0000	9.4200E2	0.0000	0.0000	9.4200E2
6.0000	6.8200E2	2.2900E2	0.0000	9.1100E2
8.0000	3.0000	8.3500E2	0.0000	8.3800E2
1.0000E1	0.0000	8.0100E2	2.6829	8.0100E2
1.2000E1	0.0000	6.7600E2	6.8447	6.7600E2
1.4000E1	0.0000	5.0400E2	8.9742	5.0400E2
1.6000E1	0.0000	3.9700E2	1.3189E1	3.9700E2
1.8000E1	0.0000	2.4800E2	1.0623E1	2.4800E2
2.0000E1	0.0000	1.4600E2	2.3107E1	1.4600E2
2.2000E1	1.7630E3	3.8000E1	1.1737E1	1.8010E3
2.4000E1	6.2350E3	0.0000	NOENTRY	6.2350E3
2.6000E1	5.9740E3	0.0000	NOENTRY	5.9740E3
2.8000E1	8.9210E3	0.0000	NOENTRY	8.9210E3
3.0000E1	6.6100E3	0.0000	NOENTRY	6.6100E3
3.2000E1	5.9730E3	0.0000	0.0000	5.9730E3
3.4000E1	5.6420E3	3.1000E1	1.9355E-1	5.6730E3
3.6000E1	3.8280E3	4.7000E1	5.3191E-1	3.8750E3
3.8000E1	2.0740E3	2.8700E2	1.0453E-1	2.3610E3
4.0000E1	4.9600E2	8.5600E2	0.0000	1.3520E3
4.2000E1	1.4700E2	1.0790E3	0.0000	1.2260E3
4.4000E1	1.1700E2	7.9500E2	6.8931E-1	9.1200E2
4.6000E1	8.2000E1	4.3900E2	1.0501	5.2100E2
4.8000E1	1.5000E1	3.4800E2	4.7069	3.6300E2
5.0000E1	4.6000E1	1.8300E2	8.3279	2.2900E2
5.2000E1	5.2000E1	9.0000E1	2.5978E1	1.4200E2
5.4000E1	9.0000	7.3000E1	2.0178E1	8.2000E1
5.6000E1	4.9400E2	4.8000E1	6.8479E1	5.4200E2
5.8000E1	9.1700E2	2.2000E1	6.2136E1	9.3900E2
6.0000E1	2.2780E3	1.5300E2	4.0327	2.4310E3
6.2000E1	3.2570E3	4.3000E2	2.1767	3.6870E3
6.4000E1	4.4940E3	4.9000E1	2.2857	4.5430E3
6.6000E1	4.4620E3	7.3000E1	1.2466	4.5350E3
6.8000E1	5.4340E3	7.0000	0.0000	5.4410E3
7.0000E1	4.4080E3	4.0000	0.0000	4.4120E3
7.2000E1	3.0110E3	1.1000E1	0.0000	3.0220E3
7.4000E1	2.3240E3	3.3200E2	3.0120E-3	2.6560E3
7.6000E1	1.8560E3	1.1100E2	4.2342E-1	1.9670E3
7.8000E1	1.2550E3	4.0000E1	2.0000E-1	1.2950E3
8.0000E1	5.6400E2	3.5100E2	0.0000	9.1500E2
8.2000E1	8.7000E1	4.6400E2	1.6595E-1	5.5100E2
8.4000E1	2.5000E1	2.8800E2	2.0764	3.1300E2
8.6000E1	0.0000	1.6700E2	4.0802E1	1.6700E2
8.8000E1	5.0000	9.0000E1	1.7078E1	9.5000E1
9.0000E1	4.9000E1	4.4000E1	2.9455E1	9.3000E1
9.2000E1	3.1000E1	2.9000E1	1.5532E1	6.0000E1
9.4000E1	4.8000E1	2.0000E1	9.3130E1	6.8000E1
9.6000E1	5.2520E3	7.0000	3.4400E2	5.2590E3
9.8000E1	6.6600E3	1.3000E1	2.7538E1	6.6730E3
1.0000E2	5.4410E3	0.0000	NOENTRY	5.4410E3
1.0200E2	3.9020E3	8.5000E1	1.6471E-1	3.9870E3
1.0400E2	2.8770E3	7.5000E1	0.0000	2.9520E3
1.0600E2	3.2690E3	3.7900E2	1.6359E-1	3.6480E3
1.0800E2	3.9510E3	2.7100E2	1.4760E-2	4.2220E3
1.1000E2	3.8000E3	8.9000E1	4.3820E-1	3.8890E3
1.1200E2	2.1550E3	1.4000E2	0.0000	2.2950E3
1.1400E2	1.4120E3	9.7000E1	0.0000	1.5090E3
1.1600E2	8.5100E2	7.7000E1	1.3896	9.2800E2
1.1800E2	5.5900E2	1.8000E2	9.5556E-1	7.3900E2
1.2000E2	5.9000E1	5.0700E2	9.6331	5.6600E2
1.2200E2	5.2000E1	3.3100E2	3.6737	3.8300E2
1.2400E2	5.3000E1	2.2100E2	5.5430	2.7400E2
1.2600E2	3.7000E1	1.5500E2	2.2323E1	1.9200E2
1.2800E2	1.0900E2	1.1700E2	2.0838E1	2.2600E2
1.3000E2	4.3100E2	8.8000E1	3.6730E1	5.1900E2
1.3200E2	1.0980E3	1.2600E2	1.2492E1	1.2240E3
1.3400E2	2.0300E3	2.0600E2	3.6141E1	2.2360E3
1.3600E2	3.5110E3	3.0700E2	6.5765	3.8180E3
1.3800E2	6.1860E3	2.2000E1	3.0545E1	6.2080E3
1.4000E2	5.9960E3	0.0000	0.0000	5.9960E3
1.4200E2	5.7890E3	0.0000	0.0000	5.7890E3
1.4400E2	6.6480E3	4.0000	0.0000	6.6520E3
1.4600E2	7.9390E3	0.0000	0.0000	7.9390E3
1.4800E2	4.8680E3	0.0000	NOENTRY	4.8680E3
1.5000E2	3.9520E3	0.0000	NOENTRY	3.9520E3
1.5200E2	2.4600E3	2.5200E2	1.2698E-1	2.7120E3
1.5400E2	1.3880E3	3.4600E2	0.0000	1.7340E3
1.5600E2	2.2800E2	9.9600E2	3.2229E-1	1.2240E3
1.5800E2	3.0000	7.0000E2	3.2857E-1	7.0300E2
1.6000E2	1.8000E1	4.9000E2	8.0000E-1	5.0800E2
1.6200E2	2.8000E1	3.3800E2	7.4852E-1	3.6600E2
1.6400E2	3.5000E1	2.4400E2	1.3279	2.7900E2
1.6600E2	4.8000E1	1.9500E2	7.0205	2.4300E2
1.6800E2	1.5100E2	1.9200E2	6.5208	3.4300E2
1.7000E2	5.6400E2	1.9700E2	4.9594	7.6100E2
1.7200E2	7.9600E2	2.2900E2	5.8341	1.0250E3
1.7400E2	8.5600E2	3.6500E2	3.9726	1.2210E3
1.7600E2	9.5300E2	6.4700E2	3.8949	1.6000E3
1.7800E2	1.5850E3	6.8200E2	4.4824	2.2670E3
1.8000E2	2.8190E3	4.7100E2	6.4119E-1	3.2900E3
1.8200E2	3.1070E3	3.6400E2	4.5604E-1	3.4710E3
1.8400E2	3.3660E3	2.7100E2	7.3801E-2	3.6370E3
1.8600E2	3.2090E3	5.0000E2	5.4000E-2	3.7090E3
1.8800E2	4.6080E3	2.6800E2	2.6119E-1	4.8760E3
1.9000E2	5.1330E3	2.3100E2	1.7316E-2	5.3640E3
1.9200E2	4.8190E3	7.1000E1	5.3521E-1	4.8900E3
1.9400E2	2.9050E3	1.2400E2	4.0323E-2	3.0290E3
1.9600E2	1.5940E3	3.5600E2	1.3483E-1	1.9500E3
1.9800E2	4.5100E2	7.7400E2	1.4858E-1	1.2250E3
2.0000E2	1.2600E2	9.5000E2	3.8316E-1	1.0760E3
2.0200E2	1.0000E2	8.0500E2	1.2845	9.0500E2
2.0400E2	1.0700E2	6.6500E2	1.9474	7.7200E2
2.0600E2	6.0000E1	5.6800E2	4.1954	6.2800E2
2.0800E2	5.6000E1	4.1700E2	3.8393	4.7300E2
2.1000E2	1.4600E2	3.9300E2	6.4504	5.3900E2
2.1200E2	5.1300E2	3.1200E2	5.4519	8.2500E2
2.1400E2	1.3860E3	3.1600E2	5.0665	1.7020E3
2.1600E2	2.4650E3	4.0300E2	1.4292	2.8680E3
2.1800E2	4.2540E3	2.1900E2	2.1005	4.4730E3
2.2000E2	4.9770E3	2.4400E2	1.4877	5.2210E3
2.2200E2	6.4650E3	1.2700E2	0.0000	6.5920E3
2.2400E2	6.2650E3	1.3500E2	7.8519E-1	6.4000E3
2.2600E2	4.7410E3	1.1000E1	7.2727	4.7520E3
2.2800E2	3.3540E3	1.6700E2	0.0000	3.5210E3
2.3000E2	2.4120E3	3.0700E2	9.8697E-1	2.7190E3
2.3200E2	1.4360E3	4.9500E2	1.5253	1.9310E3
2.3400E2	8.8100E2	5.1900E2	8.6591E-1	1.5000E3
2.3600E2	2.9600E2	7.8600E2	1.0204	1.0820E3
2.3800E2	1.9800E2	6.5100E2	1.0568	8.4900E2
2.4000E2	1.5900E2	6.1500E2	2.0228	7.7400E2
2.4200E2	3.0200E2	5.6200E2	2.9573	8.6400E2
2.4400E2	8.7000E2	4.3800E2	1.1530E1	1.3080E3
2.4600E2	1.3050E3	3.1900E2	2.9028	1.6240E3
2.4800E2	1.8430E3	3.8100E2	7.9029	2.2240E3
2.5000E2	1.9340E3	4.8900E2	2.9877	2.4230E3
2.5200E2	2.5410E3	4.1800E2	1.2584	2.9590E3
2.5400E2	3.2620E3	2.8500E2	3.7544E-1	3.5470E3
2.5600E2	7.1550E3	8.2000E1	1.6585	7.2370E3
2.5800E2	5.2180E3	0.0000	0.0000	5.2180E3
2.6000E2	5.3110E3	0.0000	0.0000	5.3110E3
2.6200E2	4.2650E3	8.0000	1.0000	4.2730E3
2.6400E2	3.2670E3	3.0000	3.3333	3.2700E3
2.6600E2	1.9680E3	3.1300E2	1.3355	2.2810E3
2.6800E2	9.7400E2	5.7500E2	1.0713	1.5490E3
2.7000E2	3.0200E2	7.8900E2	1.6717	1.0910E3
2.7200E2	4.5000E1	7.5100E2	5.2730E-1	7.9600E2
2.7400E2	5.0000	6.0500E2	2.7041	6.1000E2
2.7600E2	1.3000E1	4.3200E2	2.8912	4.4500E2
2.7800E2	6.3300E2	2.6100E2	3.7356	8.9400E2
2.8000E2	1.2950E3	1.5900E2	5.1132	1.4540E3
2.8200E2	2.0560E3	2.0600E2	3.3932	2.2620E3
2.8400E2	1.7650E3	5.9800E2	3.1906	2.3630E3
2.8600E2	2.8990E3	9.4800E2	1.0042	3.8470E3
2.8800E2	3.2360E3	6.4000E2	7.4531E-1	3.8760E3
2.9000E2	3.6720E3	2.6300E2	7.8327E-1	3.9350E3
2.9200E2	2.9500E3	5.2900E2	2.2873E-1	3.4790E3
2.9400E2	2.6440E3	7.7100E2	5.0584E-2	3.4150E3
2.9600E2	3.1960E3	6.6500E2	1.0526E-1	3.8610E3
2.9800E2	3.1370E3	4.3400E2	3.7327E-1	3.5710E3
3.0000E2	2.8420E3	2.7100E2	1.1070E-2	3.1130E3
3.0200E2	1.7480E3	5.7100E2	2.9772E-1	2.3190E3
3.0400E2	1.0140E3	6.1600E2	4.8701E-1	1.6300E3
3.0600E2	4.5400E2	8.4300E2	4.9466E-1	1.2970E3
3.0800E2	2.7700E2	5.8400E2	1.0668	8.6100E2
3.1000E2	2.5500E2	5.0600E2	2.0968	7.6100E2
3.1200E2	2.3100E2	4.2800E2	4.3271	6.5900E2
3.1400E2	3.0000E2	4.0100E2	4.4040	7.0100E2
3.1600E2	3.3900E2	4.2300E2	6.3381	7.6200E2
3.1800E2	7.6700E2	4.2100E2	6.1211	1.1880E3
3.2000E2	1.3310E3	4.4700E2	5.2192	1.7780E3
3.2200E2	1.9460E3	4.8200E2	2.8693	2.4280E3
3.2400E2	3.1590E3	6.4700E2	5.1422	3.8060E3
3.2600E2	3.9590E3	5.6000E2	2.2161	4.5190E3
3.2800E2	5.4440E3	2.0200E2	1.8812E-1	5.6460E3
3.3000E2	4.8370E3	1.4000E1	7.7143	4.8510E3
3.3200E2	5.3540E3	2.0000E1	5.0000E-1	5.3740E3
3.3400E2	4.6350E3	7.8000E1	2.5641E-2	4.7130E3
3.3600E2	7.2840E3	8.3000E1	7.8313E-1	7.3670E3
3.3800E2	7.2140E3	2.2000E1	5.8182	7.2360E3
3.4000E2	5.2410E3	4.0000	1.5000	5.2450E3
3.4200E2	3.2780E3	3.5800E2	1.9832E-1	3.6360E3
3.4400E2	1.5130E3	9.0400E2	3.7168E-1	2.4170E3
3.4600E2	3.0200E2	9.5600E2	3.5879E-1	1.2580E3
3.4800E2	4.7000E1	7.1900E2	1.3783	7.6600E2
3.5000E2	6.2000E1	4.1700E2	4.0983	4.7900E2
3.5200E2	1.7700E2	2.2500E2	3.4044	4.0200E2
3.5400E2	1.3900E2	1.0900E2	6.8716	2.4800E2
3.5600E2	1.1400E2	1.4000E2	4.4764E1	2.5400E2
3.5800E2	4.8400E2	1.2000E2	3.1250E1	6.0400E2
3.6000E2	1.2200E3	1.2600E2	3.4865E1	1.3460E3

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3.6200E2 , 2.1350E3 , 2.0700E2 , 7.3768    , 2.3420E3 | 4.8200E2 , 2.3770E3 , 3.2500E2 , 5.2831    , 2.7020E3 | 6.0200E2 , 2.7050E3 , 5.4900E2 , 4.7668    , 3.2540E3
3.6400E2 , 2.9770E3 , 3.5100E2 , 1.5726E1  , 3.3280E3 | 4.8400E2 , 1.6910E3 , 4.6900E2 , 2.1983    , 2.1600E3 | 6.0400E2 , 4.0480E3 , 3.4000E2 , 1.1862E1  , 4.3880E3
3.6600E2 , 3.2620E3 , 3.3700E2 , 2.2433    , 3.5990E3 | 4.8600E2 , 1.3830E3 , 2.2900E2 , 1.2983E1  , 1.6120E3 | 6.0600E2 , 4.3270E3 , 5.5000E1 , 1.4733E2  , 4.3820E3
3.6800E2 , 3.8840E3 , 1.9700E2 , 5.9188    , 4.0810E3 | 4.8800E2 , 2.0330E3 , 3.3900E2 , 6.5634    , 2.3720E3 | 6.0800E2 , 3.8210E3 , 2.7500E2 , 2.9058E1  , 4.0960E3
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3.7200E2 , 7.9190E3 , 0.0000   ,  NOENTRY  , 7.9190E3 | 4.9200E2 , 3.1360E3 , 4.0000   , 4.3625E2  , 3.1400E3 | 6.1200E2 , 5.3300E3 , 4.3300E2 , 1.2079E1  , 5.7630E3
3.7400E2 , 6.0980E3 , 0.0000   ,  NOENTRY  , 6.0980E3 | 4.9400E2 , 4.0680E3 , 1.8800E2 , 7.0266    , 4.2560E3 | 6.1400E2 , 6.4550E3 , 1.2600E2 , 8.6167E1  , 6.5810E3
3.7600E2 , 6.8960E3 , 0.0000   ,  NOENTRY  , 6.8960E3 | 4.9600E2 , 3.5410E3 , 2.1400E2 , 5.0748    , 3.7550E3 | 6.1600E2 , 8.0240E3 , 5.1000E1 , 6.2098E1  , 8.0750E3
3.7800E2 , 5.6340E3 , 0.0000   ,  NOENTRY  , 5.6340E3 | 4.9800E2 , 4.9330E3 , 6.0000   , 7.2167E1  , 4.9390E3 | 6.1800E2 , 1.1266E4 , 0.0000   ,  NOENTRY  , 1.1266E4
3.8000E2 , 5.1330E3 , 1.0000   , 1.8500E2  , 5.1340E3 | 5.0000E2 , 5.4560E3 , 1.1200E2 , 1.7937E1  , 5.5680E3 | 6.2000E2 , 1.2430E4 , 0.0000   ,  NOENTRY  , 1.2430E4
3.8200E2 , 3.5380E3 , 6.5000E2 , 1.7231E-1 , 4.1880E3 | 5.0200E2 , 3.8740E3 , 1.0000   , 2.5400E2  , 3.8750E3 | 6.2200E2 , 1.3696E4 , 0.0000   ,  NOENTRY  , 1.3696E4
3.8400E2 , 2.7770E3 , 6.9200E2 , 7.5289E-1 , 3.4690E3 | 5.0400E2 , 3.4760E3 , 9.0000   , 2.7556E1  , 3.4850E3 | 6.2400E2 , 1.1001E4 , 0.0000   , 0.0000    , 1.1001E4
3.8600E2 , 2.0710E3 , 3.7100E2 , 7.7358E-1 , 2.4420E3 | 5.0600E2 , 4.3470E3 , 7.3000E1 , 3.4397E1  , 4.4200E3 | 6.2600E2 , 1.4667E4 , 0.0000   ,  NOENTRY  , 1.4667E4
3.8800E2 , 1.3260E3 , 6.0500E2 , 1.0744    , 1.9310E3 | 5.0800E2 , 4.3450E3 , 8.0000   , 3.0050E2  , 4.3530E3 | 6.2800E2 , 7.2420E3 , 0.0000   ,  NOENTRY  , 7.2420E3
3.9000E2 , 1.2300E3 , 5.6500E2 , 2.2195    , 1.7950E3 | 5.1000E2 , 3.3660E3 , 1.2000E1 , 1.3767E2  , 3.3780E3 | 6.3000E2 , 6.1790E3 , 0.0000   ,  NOENTRY  , 6.1790E3
3.9200E2 , 1.2980E3 , 4.2900E2 , 4.6084    , 1.7270E3 | 5.1200E2 , 3.7200E3 , 1.3300E2 , 1.9977E1  , 3.8530E3 | 6.3200E2 , 5.7690E3 , 1.7700E2 , 3.6836    , 5.9460E3
3.9400E2 , 1.3650E3 , 1.2800E2 , 7.6250    , 1.4930E3 | 5.1400E2 , 2.8160E3 , 9.0000E1 , 4.6322E1  , 2.9060E3 | 6.3400E2 , 3.9770E3 , 2.2000E2 , 1.1918E1  , 4.1970E3
3.9600E2 , 7.4200E2 , 6.7900E2 , 4.2415    , 1.4210E3 | 5.1600E2 , 1.7920E3 , 3.5000E1 , 7.2143E1  , 1.8270E3 | 6.3600E2 , 2.5190E3 , 2.4000E2 , 3.1792    , 2.7590E3
3.9800E2 , 7.7600E2 , 5.9800E2 , 4.1890    , 1.3740E3 | 5.1800E2 , 2.4760E3 , 3.4500E2 , 5.5275    , 2.8210E3 | 6.3800E2 , 9.0600E2 , 8.5900E2 , 2.4552    , 1.7650E3
4.0000E2 , 1.1630E3 , 5.0800E2 , 2.7441    , 1.6710E3 | 5.2000E2 , 4.6570E3 , 1.7000E1 , 8.8118E1  , 4.6740E3 | 6.4000E2 , 2.3200E2 , 6.8800E2 , 3.3328    , 9.2000E2
4.0200E2 , 2.2500E3 , 3.8200E2 , 5.8455    , 2.6320E3 | 5.2200E2 , 5.1010E3 , 2.0000   , 5.9850E2  , 5.1030E3 | 6.4200E2 , 7.2200E2 , 1.6000E2 , 5.3250    , 8.8200E2
4.0400E2 , 3.6450E3 , 2.0000E2 , 3.1450    , 3.8450E3 | 5.2400E2 , 5.7290E3 , 9.4000E1 , 3.4447E1  , 5.8230E3 | 6.4400E2 , 1.1390E3 , 5.0000   , 3.8520E2  , 1.1440E3
4.0600E2 , 3.9200E3 , 1.2900E2 , 5.2946    , 4.0490E3 | 5.2600E2 , 5.3730E3 , 0.0000   ,  NOENTRY  , 5.3730E3 | 6.4600E2 , 3.1010E3 , 4.1000E1 , 8.3610E1  , 3.1420E3
4.0800E2 , 4.8920E3 , 4.2000E1 , 9.4524    , 4.9340E3 | 5.2800E2 , 4.9770E3 , 0.0000   ,  NOENTRY  , 4.9770E3 | 6.4800E2 , 3.2860E3 , 8.4000E1 , 4.1250E1  , 3.3700E3
4.1000E2 , 5.0870E3 , 2.9000E1 , 2.5000E1  , 5.1160E3 | 5.3000E2 , 4.4300E3 , 0.0000   ,  NOENTRY  , 4.4300E3 | 6.5000E2 , 4.4790E3 , 5.2000E1 , 6.6423E1  , 4.5310E3
4.1200E2 , 3.1570E3 , 0.0000   ,  NOENTRY  , 3.1570E3 | 5.3200E2 , 4.6900E3 , 1.4500E2 , 8.5379    , 4.8350E3 | 6.5200E2 , 4.4020E3 , 4.0500E2 , 2.0390E1  , 4.8070E3
4.1400E2 , 4.4670E3 , 0.0000   ,  NOENTRY  , 4.4670E3 | 5.3400E2 , 4.1270E3 , 1.0000E2 , 1.1670E1  , 4.2270E3 | 6.5400E2 , 4.8580E3 , 9.6000E1 , 1.7823E1  , 4.9540E3
4.1600E2 , 3.9280E3 , 1.5900E2 , 9.1824E-1 , 4.0870E3 | 5.3600E2 , 4.5780E3 , 2.6000E1 , 8.6077E1  , 4.6040E3 | 6.5600E2 , 4.6210E3 , 3.0300E2 , 3.3650    , 4.9240E3
4.1800E2 , 2.7690E3 , 2.6200E2 , 1.0878    , 3.0310E3 | 5.3800E2 , 4.6240E3 , 2.0900E2 , 1.5158E1  , 4.8330E3 | 6.5800E2 , 5.4490E3 , 3.2800E2 , 2.9024    , 5.7770E3
4.2000E2 , 1.4360E3 , 1.5800E2 , 4.3924    , 1.5940E3 | 5.4000E2 , 3.6060E3 , 4.2000E1 , 3.9167E1  , 3.6480E3 | 6.6000E2 , 7.7450E3 , 7.5000E1 , 2.3360E1  , 7.8200E3
4.2200E2 , 1.7590E3 , 3.2100E2 , 1.7383    , 2.0800E3 | 5.4200E2 , 2.5650E3 , 4.3500E2 , 8.9471    , 3.0000E3 | 6.6200E2 , 4.4410E3 , 0.0000   ,  NOENTRY  , 4.4410E3
4.2400E2 , 1.4510E3 , 3.8300E2 , 3.1880    , 1.8340E3 | 5.4400E2 , 2.2740E3 , 5.9100E2 , 7.7885    , 2.8650E3 | 6.6400E2 , 6.8850E3 , 0.0000   ,  NOENTRY  , 6.8850E3
4.2600E2 , 9.4800E2 , 4.4500E2 , 2.0247    , 1.3930E3 | 5.4600E2 , 3.3310E3 , 4.7400E2 , 5.7321    , 3.8050E3 | 6.6600E2 , 8.1750E3 , 0.0000   ,  NOENTRY  , 8.1750E3
4.2800E2 , 2.1500E2 , 9.3900E2 , 1.8679    , 1.1540E3 | 5.4800E2 , 4.2040E3 , 8.0000E1 , 2.7025E1  , 4.2840E3 | 6.6800E2 , 6.7500E3 , 0.0000   ,  NOENTRY  , 6.7500E3
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4.3800E2 , 2.6540E3 , 4.2600E2 , 8.7958    , 3.0800E3 | 5.5800E2 , 7.5170E3 , 0.0000   ,  NOENTRY  , 7.5170E3 | 6.7800E2 , 2.6460E3 , 5.0000E2 , 8.0080    , 3.1460E3
4.4000E2 , 3.5330E3 , 2.8700E2 , 1.6850    , 3.8200E3 | 5.6000E2 , 6.8660E3 , 2.0000   , 7.3000E2  , 6.8680E3 | 6.8000E2 , 1.7410E3 , 7.8800E2 , 3.9734    , 2.5290E3
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4.7000E2 , 2.2050E3 , 4.2500E2 , 9.9294E-1 , 2.6300E3 | 5.9000E2 , 5.7330E3 , 4.0000   , 5.1175E2  , 5.7370E3 | 7.1000E2 , 6.1760E3 , 4.2000E1 , 8.7405E1  , 6.2180E3
4.7200E2 , 1.7090E3 , 7.0800E2 , 4.6610E-1 , 2.4170E3 | 5.9200E2 , 5.5390E3 , 0.0000   ,  NOENTRY  , 5.5390E3 | 7.1200E2 , 6.9310E3 , 8.0000E1 , 8.7500E-2 , 7.0110E3
4.7400E2 , 1.5000E3 , 7.2600E2 , 2.5895E-1 , 2.2260E3 | 5.9400E2 , 5.6920E3 , 4.0000   , 1.3773E2  , 5.6960E3 | 7.1400E2 , 8.0070E3 , 1.5100E2 , 0.0000    , 8.1580E3
4.7600E2 , 2.0380E3 , 5.8600E2 , 2.8038    , 2.6240E3 | 5.9600E2 , 4.5530E3 , 2.1700E2 , 7.9124    , 4.7700E3 | 7.1600E2 , 8.9980E3 , 5.5000E1 , 0.0000    , 9.0530E3
4.7800E2 , 2.7920E3 , 4.1600E2 , 2.8317    , 3.2080E3 | 5.9800E2 , 3.5120E3 , 5.5800E2 , 2.8996    , 4.0500E3 | 7.1800E2 , 6.8860E3 , 1.0000   , 0.0000    , 6.8870E3
4.8000E2 , 2.4520E3 , 2.3900E2 , 7.7866    , 2.6910E3 | 6.0000E2 , 2.1670E3 , 7.0800E2 , 3.5480    , 2.8750E3 | 7.2000E2 , 8.1070E3 , 0.0000   , 0.0000    , 8.1070E3
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