ECOLOGICAL STABILITY THEORY

- AN ANALYSIS OF METHOD

by

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"... most people will accept any kind of nonsense if it is stated with enough assurance. We don't like uncertainties, and we very much want to believe that experts, with their computers and other fancy tools, can come up with reliable answers. They can't, and if you look closely you will usually find all kinds of qualifications. But few of us bother to read the small print."

William Davis (1978)

"Whatever temperament we may have, we should be used to receiving our impressions, of whatever kind, exclusively from nature. We should be impregnated and saturated with nature, and think only what it makes us think."

Jean-Francois Millet

(in a letter to Alfred Sensier, quoted by William Hunt, 1882)

"The effort to understand is one of the very few things that lifts human life a little above the level of farce, and gives it some of the grace of tragedy."

Steven Weinberg (1978)

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Abstract

A set of experiments is described which examines interspecific competition in the flour mite, Acarus siro L. 1758. These experiments were based on a previously published theoretical model, being designed to provide data for that model. The experimental results are discussed within the framework of the model. Speculations are made concerning the life history of the flour mite, and also concerning more general aspects of ecology.

The theoretical basis of the model is examined and criticized, and the criticisms shown to apply equally to a number of developments in theoretical ecology. The philosophy underlying the criticized approach is contrasted with a holistic view of ecological events, using quotation as the main form of evidence. Some suggestions are made about future experiments.

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Preface

Scientific methods and systems of thought are in some respects like organisms - they arise and evolve in one environment, perhaps migrate or disperse, and adapt or fail in other environments. The criterion by which they are tested is a complex mixture of utility and validity. There has seldom been need for formal examination of the suitability of a method for a particular area of study. This may reflect the selective efficiency of scientists, or it may reflect the simplicity of the developed sciences - a simplicity which allows rapid differentiation of valid/utilitarian and invalid/inutilitarian methods. The epistemology of chemistry and physics has been accessible - the objects of study precisely and accurately definable, and interactions bound by simple rules. The epistemology of biology may not be so easily debated, especially in those areas furthest from the physico-chemical.

What follows is an analysis of a method of interpretation, drawn from the physical sciences, applied to higher levels of biological organization. There are differences between those properties required of an object for the proper and valid application of this system of interpretation, and those properties which may reasonably be assumed for biological systems. The intended result of this analysis is a statement of these differences.

CHAPTER ONE - INTRODUCTION

A significant portion of the research being carried out in ecology, both theoretical and experimental, is concerned with stability. In contrast to the everyday use of the word with its imprecise admixture of constancy, predictability and desirability, the definition most commonly used is borrowed from the study of the dynamics of mechanical systems (see Section 1.1.4), and the methods used there have been transplanted to ecology in order to erect a theoretical framework within which the behaviour of populations and communities may be studied. This work is perhaps best characterized by the research of Professor Robert May, whose major publications (see Bibliography) have done much to encourage the application of these precise methods to ecology.

With this framework established, the effects on population (community) stability of various processes (such as competition, predation and symbiosis) and system states (diversity, age structure and intrinsic time delays) have been examined (e.g. Gardner and Ashby 1970, May 1972 onwards) with a view to formulating a general theory of ecology. In 1974 May, Conway, Hassell and Southwood presented a theoretical discussion of the effects of time delays and density dependence on the stability of single species populations. Included was a mathematical model of a multiple age class species exhibiting intraspecific competition. The experimental system described in following chapters was designed to measure the degree of competition between the various age classes of a real population in order to test the suitability of the model.

As background to the discussion which occurs in later chapters, the development of the methods and ideas which comprise what might be called 'The Stability Theory of Ecological Systems' will be sketched, together with a discussion of some elements of competition theory and a description of the experimental system to be used.

1.1 The Stability Theory of Ecological Systems

The origin of this body of ecological theory lies in the observation that, generally speaking, species are well adapted for continued existence in their environment. For much of human history this was ascribed to a grand divine plan of harmony and co-existence. With the gradual acceptance of the ideas of natural selection and evolution came the realisation that the apparently ordered and static state of things was the result of a continuing power struggle, in which the combatants were striving to replace each other. That the face of nature changed so little and ran so predictably from season to season implied the presence of regulatory mechanisms which could temper the competitive and exploitative excesses of organism; thus, following the presentation of simple models describing the growth of suitably regulated populations came inquiries into the possible mechanisms of regulation. Opinion polarized with respect to this question. On the one hand were those who extended the fundamental biological property of co-ordination to the population to state, in effect, that individual organisms and groups of such organisms were co-ordinated by mechanisms operating within and between these entities. On the other hand were those who attributed the regulation of natural populations largely to the patterns, vagaries and inconsistencies of climate and weather. The resolution of this dialogue between the proponents of the random and deterministic worlds was never explicitly concluded, but in the nineteen-sixties the attention of researchers into population regulation was progressively confined to mechanisms of the density-dependent type. In the late 'sixties and early 'seventies the concepts of stability and equilibrium were gradually defined, and the investigation of regulatory mechanisms was then formalized according to the tenets of the dynamical systems theorists of the physical sciences. This situation prevails to the present day, and the opinions of this 'classical' school of theoretical ecologists have great influence where decisions about large biological systems have to be made. The importance of these decisions in terms of a pressing human need and desire to control and manipulate the natural resources of the planet, in addition to the fundamental requirement of justified and logical progression in science, makes necessary a detailed and critical examination of this body of theory.

1.1.1 Early population models - Pearl and Verhulst.

Stability analysis, the mathematical core of ecological stability theory, demands a mathematical description of the process under study in the form of differential or difference equations.

Population models vary considerably in structure and application, and also in the extent to which they may be validated with respect to real i.e. empirical, systems. At one extreme they can be simply a convenient shorthand description of dynamics, for example (in a difference equation form) :

$$X_{n+1} = kX_n \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (1)$$

for which the only hypotheses that may be stated and directly tested are of the form :

The function f(X) is an adequate description of the pattern of change of the real variable X ....(a)

although a hypothesis of this form might suggest a hypothesis concerning the real system, for example, in a system where the population is well described by the equation :

$$X_{n+1} = 2X_n \quad \text{..............................} (2)$$

the hypothesis might be presented that :

Every adult is replaced by two offspring ....(b)

At the other extreme the model may be a complex structure co-ordinating the validated results of hypotheses concerning component population processes. For example, hypothesis (b) combined with a validated statement that :

Immature organisms have a mortality of 25% ....(c)

results in a model for adult dynamics of :

$$X_{n+1} = 1.5X_n \quad \text{..............................} (3)$$

These extremes of descriptive and synthetic models, conforming to the opposites of 'top-down' and 'bottom-up' analyses, delimit a spectrum of modelling approaches in which real- and descriptive- hypothetical statements are combined in all possible manners.

It is important at this point to distinguish these two modes of analysis : the descriptive mimics the behaviour of the whole without regard to mechanism; the synthetic, in describing the behaviour of components of the whole, more often than not assumes the manner of their interaction.

In 1920 Pearl and Reed echoed the work of Verhulst eighty years earlier (1838) in presenting a descriptive population model in which the rate of population increase declined as the population itself increased. The importance of this was that a ceiling was imposed on the size of population, which implied that some form of regulation was operating. A description of this model, also known as the logistic model, is to be found in most texts of basic ecology. The exact formulation of the model varies, but it is commonly presented in the form :

$$\delta N/\delta t = rN\ (1 - K/N) \qquad \text{.........................(4)}$$

K is referred to as the carrying capacity of the environment for the population in question, and is in the same units as the population size variable N. Hence when N is equal to K the rate of population change is zero. With this differential form of the logistic equation, the model population increases smoothly to the equilibrium value (K). However, in a difference equation form (which more closely approximates the case of populations with non-overlapping generations) the behaviour of the population depends on the relative values of rate of population increase and carrying capacity. If the logistic is given in the following form (Maynard Smith 1968) :

$$X_{n+1} = (cK + 1 - cX_n)\ X_n \qquad \text{......................(5)}$$

then if $cK > 2$, small displacements from the equilibrium value result in divergent oscillations away from equilibrium; if $cK < 1$, the population approaches the equilibrium density without oscillations; and if $1 < cK < 2$, the population approaches the equilibrium with convergent oscillations.

Varley, Gradwell and Hassell (1973) consider that the model is adequate only for populations of simple animals, or those with overlapping generations and low rates of increase per generation.

1.1.2 Regulation and the question of density dependence

The essential feature of models of the Pearl-Verhulst type is that the regulation of the population is proportional to the size of the population. The importance of this type of mechanism in natural systems was the subject of a major ecological debate in the nineteen-fifties culminating in the Cold Spring Harbor Symposium of 1957 (see Bibliography under names of individual authors listed below for reference details) when representatives of the opposing factions met face to face. Although a great many publications relevant to this question had appeared before the meeting, by restricting attention to this one particular gathering of ecologists, the benefit of adapted and considered opinions is gained rather than the uncriticized and undeveloped statements of the earlier papers.

The cause of the 'regulation by density dependence' school was championed by Nicholson, who had been a major force in the development of the principle for the previous twenty years. The opposition 'regulation by environmental variation' school was represented by Andrewartha, Birch and Milne. The continued argument between these schools was the result of the refusal of either side to accept the limitations of their respective lines of logical development, because of the desire of both to lay down some general principle. That synthesis was possible, and that regulation was a variable thing, density or environmentally controlled according to circumstance, was demonstrated at this Symposium by the contributions of Reynoldson, Dobzhansky and Lewontin. However it is clear that the sympathies of these latter lay with the more biological approach of Andrewartha, Birch and company, rather than with Nicholson and his allies. They moved the emphasis from 'environmental' to 'variation' and developed arguments based on the flexibility, variability and adaptedness of living things. Conceding that density dependent mechanisms existed and were important regulatory devices, they expressed their belief in the greater importance of evolution-based and behavioural regulatory strategies.

1.1.3 Definitions of stability

When ecologists speak of the stability of ecosystems, to what property of the ecosystems are they referring ?

An obvious candidate is numbers of organisms, and this has become the criterion by which the stability of ecosystems and populations is judged. These groups of organisms are adjudged to be stable if their dynamics are such that deviations from environmentally set equilibrium levels tend to be compensated for.

An alternative to numbers of organisms as a measure of stability is types of organism, the structure of the ecosystem, qualitative as opposed to quantitative relationships. Ultimately this approach stresses the persistence of a group of organisms or of the association between species. This is the primary concept underlying the use of the word 'resilience' by Holling (1973). A definition of the word given in the Shorter Oxford Dictionary is :

Elasticity ; the power of resuming the original shape or position after compression, bending etc.

In using the word resilience in relation to ecological systems, we must carefully define that property of these systems which corresponds to 'shape or position' in the above definition. Holling stated that 'resilience determines the persistence of relationships within a system and is a measure of the ability of these systems to absorb changes of state variables, driving variables and parameters, and still persist.

It is obvious that Holling was concerned here with the ability of systems to retain topological integrity under changing conditions. The sole requirement is that the components of the system persist. Thus the measurement of resilience involves the delimiting of conditions under which a system will persist. The greater this range of conditions, the greater the resilience of the system.

Let us consider the idea of resilience within the framework of Hutchinson's (1957) hypervolume model in which all the environmental variables affecting a system are regarded as dimensions of some hyperspace.

Now for any system we can define the following terms :

a) The volume of persistence, V_p, which is the set of conditions under which the system can persist indefinitely (retain its integrity indefinitely).

b) If it is possible for V_p to be discontinuous with respect to system topology, then those constituent hypervolumes in which continuity is retained will be termed volumes of resilience, V_r.

We can distinguish within the volumes of resilience an outermost layer where there is a significant chance of the system being forced out of the volume of persistence to disintegration by chance events. This will be termed the shell of random vulnerability, S_r. Where a volume of resilience is so small as to be identical with its shell of random vulnerability it will be termed a volume of instability, V_i.

c) Within any volume of resilience there might be sets of conditions under which system composition is not significantly dependent on environmental variables. These will be termed volumes of stability, V_s, as systems moving into such volumes would undergo transition to some numerically stable state.

d) Outside the volume of persistence will lie a set of conditions which, although not allowing indefinite persistence of the system, does not force immediate disruption of the system i.e. it can recover from a chance transition into such conditions. This set is termed the shell of extinction, S_e.

Returning to numerical ideas of stability, these are concerned with the mechanisms of response of populations to their own changing numbers. The nomenclature and methods used to describe the varieties of response are drawn from the control system theory developed in engineering (see, for example, Willems, 1970). The system may be described as stable, neutrally stable or unstable depending on its response to change being negatively reactive, unreactive or positively reactive respectively. A stable resonse may be oscillatory or asymptotic according to the trajectory of its reaction.

In terms of these definitions, the niche concept is concerned with the position of the volume of persistence in hyper space, resilience is concerned with the size of this volume, and stability is concerned with the mode of transition between points within the volume (the degree of damping applied to the transitions).

The use of the word resilience by Holling, and the definition of the terms above, was done under the assumption that the systems described were at either the population or the community level of biological organization. Even restricting 'system' to these levels (and it is not necessary to be so restrictive in applying the framework of definitions given) the environment hypervolume concept is not sufficient to fully explain the idea of resilience.

In addition to the physiological resilience thus measured, there is the tactical or behavioural resilience displayed, for example, by populations migrating away from unfavourable conditions or the production of resistant life stages in the face of unfavourable conditions (man's activity in altering his immediate environment for his own benefit, as an example of Lewontin's (1957) creative homeostasis, must be thought of as one of the highest forms of this behavioural resilience).

1.1.4 Stability analysis

The usual procedure for examining the stability features of a system is to construct an equation describing the system behaviour, linearize the equation and then solve it, the solution being characterized by a parameter whose value delimits the possible modes of behaviour of the system and which is a measure of the strength of regulatory feedback within the system. For a system described by a number of equations, a set of parameters delimiting behaviour is produced.

The details of such procedures for typical biological systems are well illustrated by Maynard Smith (1968) and May (1974). Using May's description, the general case of a community of m species is described by a community matrix A, the elements of which, a_{ij}, describe the effect of species j on species i near equilibrium. The characteristic roots or eigenvalues, λ_j, of A describe the system behaviour : the system is stable if all the eigenvalues have negative real parts (they may be complex numbers). However, as May notes, that one or more eigenvalues has a positive real part only implies 'that there is not a stable equilibrium point. Perturbations will initially grow, but the neighbourhood analysis leaves their ultimate fate uncertain. Eventually terms of order x^2 and higher'(lost during linearization)'become important, and non-linearities decide whether the perturbations will grow until extinctions are produced, or whether the system may settle into some limit cycle. Likewise even if the equilibrium point is stable to small perturbations, as shown by the neighbourhood analysis, its response to severe buffetings is not necessarily known.'

This type of analysis has been applied to many biological situations, as shown by the variety of examples in May's book (1973a).

1.2 Competition

The study model is specifically concerned with the effects of competition between members of the same species. In a most general sense competition is the state of conflict existing between two organisms that require the same resource. The extension of this concept to conflict between groups of organisms is made at the risk of neglecting the competition which must, at least potentially, exist within a group. Competition can only occur where there is some common need, and the degree of competition is likely to be most severe where the requirements of the antagonists are most similar - thus intraspecific competition has a greater potential force than interspecific competition. Simple models of competition processes appeared soon after Pearl and Reed (1920) published their model of a regulated single species population. These early models have been the major source of inspiration, in detail as well as in general form, for the subsequent development of competition theory.

1.2.1 Lotka-Volterra models and Gause's principle

Lotka, in 1925, and Volterra, in 1926, published mathematical models representing the growth of two species on a single resource. The basic growth functions were adapted logistic equations, which can be stated in the following form :

$$\delta X_1/\delta t = r_1X_1((K_1 - X_1 - \alpha X_2)/K_1) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots(1)$$

$$\delta X_2/\delta t = r_2X_2((K_2 - X_2 - \beta X_1)/K_2) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots(2)$$

where X_1 and X_2 are the numbers of the two competing species; α and β the competition coefficients representing the inhibitory effect of species 2 on species 1, and vice versa, respectively; K_1 and K_2 the respective carrying capacities.

Such a form of relationship was shown to be an adequate description of interactions between real species by Gause (1934) for protozoan populations and by Crombie (1946) for competition between two species of grain beetle. It is generally agreed, however, that the Lotka-Volterra model is only suitable for simple populations. Nevertheless, because of the mathematical tractability of these equations, there has been considerable research on the properties of such models. Lotka himself recognized that there were four possible outcomes of the interaction described by equations (1) and (2), these depending on the relative values of the competition coefficients and the carrying capacities :

(a) for $K_1/\alpha > K_2$ and $K_2/\beta < K_1$: species 2 is eliminated from competition.

(b) for $K_1/\alpha < K_2$ and $K_2/\beta > K_1$: species 1 is eliminated from competition.

(c) for $K_1/\alpha < K_2$ and $K_2/\beta < K_1$: there is a possible equilibrium between the species, but this is unstable and the usual outcome is the elimination of one species, this species determined by the initial population sizes.

(d) for $K_1/\alpha > K_2$ and $K_2/\beta > K_1$: there is a stable equilibrium resulting from the fact that each species has a greater inhibitory effect on itself than on its competitor species.

Gause (1934) demonstrated these experimentally, and the principle that 'species competing for limited resources can only co-exist if they inhibit the growth of competing species less than their own growth'(Ayala, 1970) has become known as Gause's Principle. The validity and significance of this principle have been contentious issues and although they were discussed in a British Ecological Society Symposium in 1944, the matter was then eclipsed by the density dependence debate until Hardin redefined ('complete competitors cannot co-exist') and renamed it (the Competitive Exclusion Principle) in 1960.

1.2.2 The varieties of competitive situation

Various attempts were made to make more precise the definitions of competition processes and situations. These were part of a general trend towards greater formalism in ecological phraseology - a trend which, though to be welcomed in principle, was ill-served in practice and which deserves a thorough reappraisal.

Birch (1957a) discussed the meanings of the word competition in use at that time with respect to a classification of the environment of an organism presented by Andrewartha and Birch (1954), in which there were seven categories. Four of these represented groups of organisms, and the remainder weather, food and 'a place to live'. The four organism categories were : animals of the same species; non-predators utilising the same resources; non-predators not utilising the same resources; and predators.

Birch recognized four uses of the word competition, varying in the specificity of the definition.

His first meaning has the strictest definition : competition is defined as occurring when a number of animals, seeking to utilize common resources, are a source of actual or potential harm to one another by virtue of their common requirements. The second meaning of competition includes that of the first definition, but is extended to include what might be called accidental harm. The examples with which Birch illustrates this definition include habitat destruction and the ingestion of extraneous organisms with the normal food material. Although this addition appears at first to be quite distinct from meaning I, it relies on conclusive evidence that there is no resource overlap between the two species and hence no source of potential conflict. With further thought however, the empirical truth of the conflict draws attention to the resource which is required in common, though perhaps required in different ways. There is no less a conflict between two species, one requiring a plant as food and one requiring it as a place to live, than between two species both requiring a plant as food. Both interactions are of potentially incompatible species. In the same way, a man and the ant on which he treads are in conflict over 'ground upon which to walk', a subset of space or 'a place in which to live', for the habitat of each must include the routes by which the functions of life are fulfilled. The fact that these examples show a markedly one-sided competitive situation should not detract from their homology with meaning I.

The third meaning of competition is attributed to Nicholson (1937) and includes predation as a competitive process. The justification given by Nicholson is that competitive situations are characterized by a decrease of chance of survival as the density of the competitor population increases. Birch admits of no resource for which they compete. However, it might be said that they compete for the right to survive and reproduce, that the common resource is that intangible, species persistence. Nevertheless this process lacks the bilateral antagonistic component commonly associated with competition.

The fourth meaning of competition noted by Birch includes two markedly dissimilar examples - examples which I cannot reconcile as being representative of a single class of definition, except in Birch's statement that both are used in genetics and evolution. The first, in which competition is taken to include 'the struggle of organisms against harmful physical (climatic) .... factors' as well as the more conventional biological struggle, is surely one which must be rejected if competition is to have any practical use as a term in ecology. But the second, illustrated by the example of selective mating is, to my mind, as much a case of competition as any that could be stated. It seems to be a very good example of 'exploitation' competition in the sense used by Park (1954, cited by Birch in his definition of meaning I), and as such properly belongs within the compass of meaning I.

The definition of competition, indeed the definition of most ecological phenomena, has progressed very little further in terms of widely acceptable meanings. What has been done is to simplify definitions, variously by restriction or generalization, to forms which can be represented in conventional mathematical symbolism. The model which follows arose through such a process of degenerative definition.

1.2.3 The study model

The model which initiated the experimental study to be described was presented in the second part of the paper by May et al (1974). It follows a discussion of the effects of time delays on the stability of certain single age class models with density dependence. As several of the comments relating to these single age class models are pertinent to the discussion of the multiple age class model, both parts of the paper will be summarized.

The paper is generally concerned with the interaction of time delays and potential rates of population change. A term is defined, the characteristic return time (T_R), as a measure of the rate of return of a population to equilibrium. For the logistic model, this return time is the reciprocal of the instantaneous growth rate (r) :

$$T_R = 1 / r \text{ ....(3)}$$

It is shown that, for the density dependent growth model :

$$N_{t+1} = \lambda N_t^{1-b} \text{ ....(4)}$$

with unit generation time and at equilibrium, the characteristic return time is the reciprocal of the coefficient of density dependence, b, the rate of change of mortality (as a k-value) against log population density :

$$T_R = 1 / b \quad \text{.............................(5)}$$

Two types of time delay are recognized. One, τ, is associated with generation time; the other, T, represents a more general class of delay.

Stability characteristics are analysed for the specific example of the model described by equation (4), and for its differential equivalent, with a time delay element introduced :

$$dN_{(t)}/dt = -\beta \ln(N_{(t-T)}/K)\, N_{(t)} \quad \text{........................(6)}$$

(β is the characteristic return rate, $1/T_R$, and equals b/τ - hence the equivalence of b with $1/T_R$ at unit generation time)

The stability conditions for these models, the difference and differential models, are given in Tables 1.2.1 and 1.2.2 respectively.

In general terms the difference model may be given as :

$$N_{t+1} = (f\,(N_t))\, N_t \quad \text{.............................(7)}$$

(f (N_t) is the density dependent net growth rate from generation to generation)

Again the stability properties are dependent on the rate of change of density dependent mortality at equilibrium, and with b defined as :

$$b = -(d \ln f/d \ln N)^* \quad \text{........................(8)}$$

(* denotes equilibrium) the stability properties are again given by Table 1.2.1

The general differential model with time lag T is expressed as :

$$dN_{(t)}/dt = (\ g(N_{(t-T)})\ )\ N_{(t)} \quad \text{.......................(9)}$$

As for the difference case, with β defined as :

Table 1.2.1[*] Stability criteria for the difference model :

$$N_{t+1} = (\lambda N_t^{-b})\, N_t$$

Range of b	Range of T_R	Stability	Comments
$b < 0$	$T_R < 0$	Unstable	Exponential growth
$0 < b < 1$	$T_R > \tau$	Stable	Exponential damping
$1 < b < 2$	$0.5\tau < T_R < \tau$	Stable	Oscillatory damping
$b > 2$	$T_R < 0.5\tau$	Unstable	Diverging oscillations

Table 1.2.2[*] Stability criteria for the differential model :

$$\delta N(t)/\delta t = -\beta \ln\left[N(t-T)/K\right] N(t)$$

Range of ' T'	Range of T_R	Stability	Comments
$\beta T < 0$	$T_R < 0$	Unstable	Exponential growth
$0 < \beta T < e^{-1}$	$T_R > T_e$	Stable	Exponential damping
$e^{-1} < \beta T < \pi/2$	$2T/\pi < T_R < T_e$	Stable	Oscillatory damping
$\beta T > \pi/2$	$T_R < 2T/\pi$	Unstable	Diverging oscillations

---

[*] from May _et al._ (1974)

$$\beta = -(N\ dg/dN)^* \quad \ldots\ldots(10)$$

the stability properties are again given by Table 1.2.2

A number of models incorporating density dependence are examined (Table 1.2.3), and for these the equilibrium density, N^*, and the coefficient of density dependence, b, are defined in terms of each model's parameters.

For these models, with $b < 2$, the global stability properties are the same as the neighbourhood properties. For the first model, equation (4), this is also true for $b > 2$. However, for the other models with $b > 2$, stable limit cycles result.

Some mention is made of models which for $b > 2$ show neutrally stable cycles. Such models are dismissed by May et al because the functions have discontinuities in the slope, with the comment that 'Strict discontinuities of this kind are biologically unrealistic'.

The analysis of multiple age class models is analogous to that of models of interacting single age class species. The analysis is developed for the case of two age classes, larvae and adults, which occur concurrently.

With density dependence of natality and survival, the system can be described :

$$L_{t+1} = f(L_t,A_t)\ A_t \quad \ldots\ldots(11)$$

$$A_{t+1} = p(L_t,A_t)\ L_t \quad \ldots\ldots(12)$$

combining these we get :

$$A_{t+1} = p(L_t,A_t)f(L_{t-1},A_{t-1})A_{t-1} \quad \ldots\ldots(13)$$

and so possible equilibrium points are given by :

$$\left.\begin{array}{c} p(L^*,A^*)f(L^*,A^*) = 1 \\ L^* = f(L^*,A^*)A^* \end{array}\right\} \quad \ldots\ldots(14)$$

Again the stability of these equilibrium points is determined

Table 1.2.3* Some models displaying density dependence.

Density dependence function f(N)	Reference	N*	b
λN^{-b}	Haldane (1953)	$\lambda^{1/b}$	b
	Morris (1959)		
	Varley and Gradwell(1963)		
$\lambda \exp(-\alpha N)$	Cook (1965)	$(\ln\lambda)/\alpha$	$\ln\lambda$
	May *et al*(1974)		
$1+r/1+r(N/K)$	Skellam (1952)	K	$r/1+r$
	Pielou (1969)		
	Utida (1967)		
$\lambda/1+(N/J)^c$	Maynard Smith (1973)	$J(\lambda-1)^{1/c}$	$c(\lambda-1)/\lambda$
$1+r(1-N/K)$	Maynard Smith (1968) May (1973a)	K	r
$\lambda_0+\frac{(\lambda_1-\lambda_0)}{1+\exp(S(N-J))}$	Usher (1972)	$J+\frac{\ln((\lambda_1-1)/(1-\lambda_0))}{S}$	
	Pennycuick, Compton and Buckingham (1968)		$\frac{(SN^*)(1-\lambda_0)(\lambda_1-1)}{(\lambda_1-\lambda_0)}$

---

* from May *et al*. (1974)

by the rates of change of density dependence at equilibrium, these being given by the coefficients, b_{ij}, in the regressions :

$$\ln A_t - \ln L_{t+1} = (\text{constant}) + b_{LA}\ln A_t + b_{LL}\ln L_t \;\ldots\ldots\ldots\ldots(15)$$

$$\ln L_t - \ln A_{t+1} = (\text{constant}) + b_{AL}\ln L_t + b_{AA}\ln A_t \;\ldots\ldots\ldots\ldots(16)$$

The significance and interpretation of the coefficients, b_{ij}, are described in Figure 1.2.1 and Table 1.2.4 respectively. The stability condition is given by :

$$2 > 1+b_{AA}b_{LL} - (1-b_{AL})(1-b_{LA}) > |b_{AA}+b_{LL}| \;\ldots\ldots\ldots\ldots\ldots\ldots(17)$$

(cf. $2 > b > 0$ for the single age class model)

Examples of stability boundaries are given in Figure 1.2.2 . The stability condition for a five age class model, as would be required for Acarus siro, is correspondingly more complex.

1.3 The Experimental System

In a study of this sort, in which the experiments are prompted by a previously developed theoretical model, the animal on which to carry out the experiments is chosen primarily on the basis of the explicitly stated assumptions and requirements of the model, some consideration also being given to the practical problems of experimentation.

The particular reasons for the choice of Acarus siro as the experimental study animal are given below, after which are given some details of current knowledge of the animal. These details have not been chosen so as to give a balanced and substantially complete picture, rather they have been chosen so as to facilitate the development of ideas and logical arguments in later sections. Because of this they are incoherent and fragmented, but the inelegance thus introduced was felt to be a happy alternative to the lengthy, and largely irrelevant, description which a fuller expos-

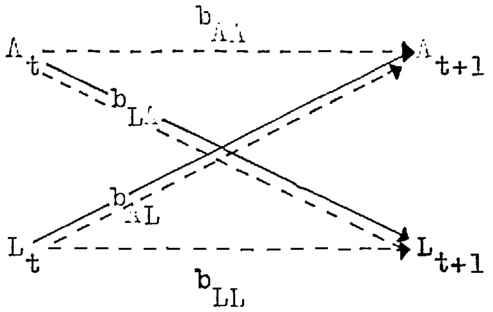


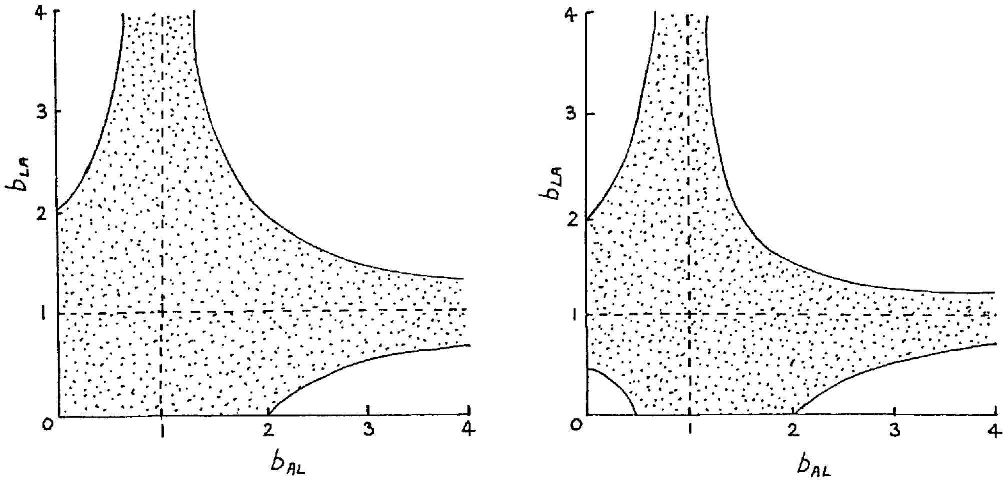
Figure 1.2.1* A two age class system

Continuous lines indicate successive developmental stages ; broken lines represent density dependent relationships as shown by the different coefficients.

Table 1.2.4* Biological interpretation of b coefficients

	Density dependence in fecundity
b_{LA}	Effect on larval recruitment at time t+1 of adult crowding at time t
b_{LL}	Effect on larval recruitment at time t+1 of larval crowding at time t
	Density dependence in larval survivorship
b_{AL}	Effect on adult recruitment at time t+1 of larval crowding at time t
b_{AA}	Effect on adult recruitment at time t+1 of adult crowding at time t

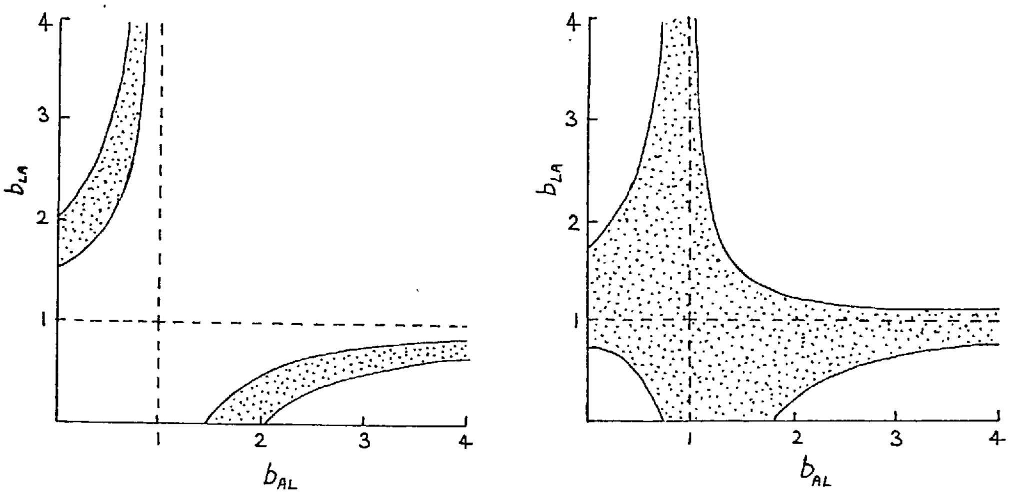
* from May et al (1974)



(a) when $b_{AA} = b_{LL} = 0$

(b) when $b_{AA} = 0.5$

$b_{LL} = 0$



(c) when $b_{AA} = 1.5$

$b_{LL} = 0$

(d) when $b_{AA} = b_{LL} = 0.5$

Figure 1.2.2* Stability boundaries for different values of the density dependent coefficients b_{LA} and b_{AL}.

* redrawn from May et al (1974)

ition of the biology of Acarus siro would have entailed. Most of this additional information is given by Hughes (1976) or Solomon (1962), or in the works cited therein.

1.3.1 The choice of experimental animal

The following criteria were set to limit the choice of animal, in line with the requirements of the theoretical model (May *et al*, 1974) and with the limitations of experimental procedure :

a) The animal must have a number of easily distinguishable age classes or life stages.

b) The animal must be amenable to handling and observation under controlled conditions.

c) The animal should have a short generation time, so as to maintain a rapid turnover of animals, and hence of experiments. (As size and generation time are somewhat correlated, there is a potential conflict between this criterion and criteria a) and b))

d) The animal should be capable of using a foodstuff of standard composition which can be weighed and delivered accurately to the experimental system (This criterion was introduced so as to allow the determination of the effect of food availability on age class interactions).

e) The animal should have been the subject of a significant amount of previous research, so that basic physiological data and tested experimental techniques are already available.

f) A preference would be given to animals from stock cultures of known history where, hopefully, some stabilization of the gene pool would have taken place.

1.3.2 Acarus siro - life history and description

The Flour Mite (Acarus siro, L., 1758) is a major pest of stored food, especially stored cereal products, in the temperate areas of the world. Its economic importance has led to its extensive study, primarily in order to develop methods of control of the animal. Outside the stored food environment, or other very similar environments, the animal is probably fungivorous.

Under normal conditions the life cycle has five stages (see Figure 1.3.1), but under extreme conditions some strains of A.siro may produce a sixth stage interposed between the normal third and fourth stages and adapted for dispersal.

The EGG is a small (120um long) ellipsoid from which, about four days after oviposition, hatches a hexapod LARVA. After a couple of days or so (depending on environmental conditions) of feeding and general activity the larva enters a resting stage in preparation for the first ecdysis. During this resting stage the larva assumes a much rounded body form with the limbs withdrawn inside the larval skin. The PROTONYMPH which emerges after ecdysis is octopod - the fourth (hindmost) pair of legs having developed. The protonymphal stage is divided into active and resting periods in the same way as the larval stage. Emerging from the second ecdysis we get either the DEUTONYMPH or the rare HYPOPUS. The latter is a heteromorphic form adapted for phoretic dispersal. The mechanisms controlling its formation and apolysis have not been elucidated. When it does apolyse it gives rise to a deutonymph indistinguishable from those produced by a normal protonymphal ecdysis. After a further period of feeding and growth the deutonymphal resting stage is formed from which emerges a sexually

Figure 1.3.1 The life cycle of <u>Acarus siro</u>

(the adult mite is redrawn from Hughes, 1976)

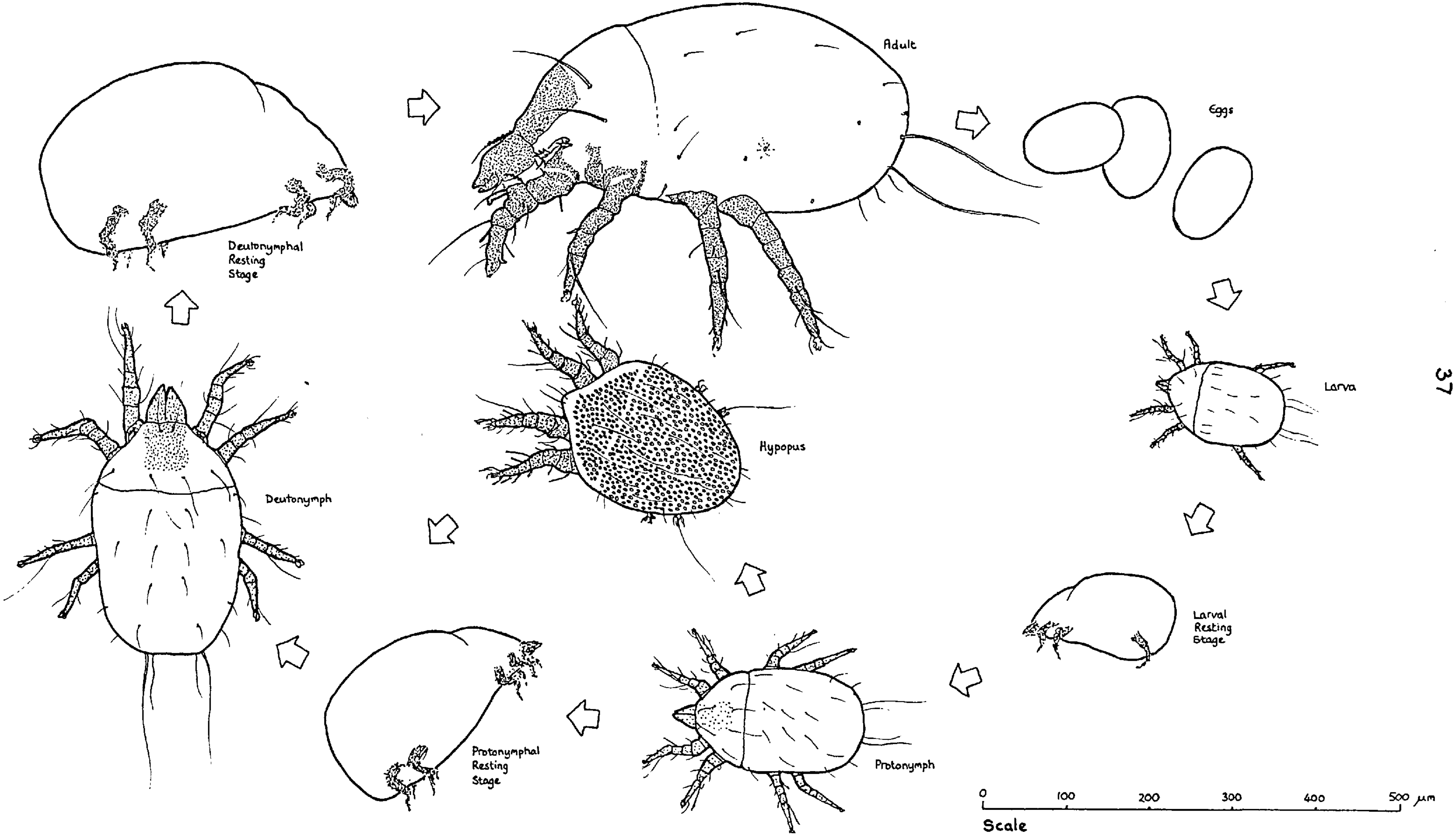

Adult
Eggs
Larva
Larval Resting Stage
Protonymph
Protonymphal Resting Stage
Deutonymph
Deutonymphal Resting Stage
Hypopus
0
100
200
300
400
500 µm
Scale

Figure 1.3.1.

mature ADULT. The female begins to lay eggs two days after mating, laying between twenty and thirty eggs per day for about twelve days. The eggs are laid singly.

The morphology and physiology of A.siro are probably best approached on a taxonomic basis. Acarus siro belongs to the family Acaridae of the order Astigmata of the subclass Acari. As a member of the Acari it is a small arachnid arthropod showing little visible external evidence of segmentation, and having six legs as a larva and eight legs as an adult. As an astigmatid mite it has a soft, lightly sclerotized, lightly pigmented cuticle which acts as the main respiratory surface and which also controls the water relationships of the animal (in the specific case of A.siro Solomon, in 1966, has presented results which indicate that an active water transport system is present). Acarid mites are free-living, associated with insects or found in the nests of small mammals. They usually have well developed claws and the males commonly possess anal and tarsal suckers to assist in copulation. Members of the genus Acarus show further sexual dimorphism in that the males have an enlarged, heavily sclerotized, first pair of legs, which bear a spur on the femur (Figure 1.3.2).

The adults of A.siro have colourless bodies, with gnathosoma and legs varying in colour, according to diet and age, from pale yellow to reddish brown (Figure 1.3.1). The chelicerae are distinctly toothed (Figure 1.3.3). The dorsal hysterosomal setae and the tarsi vary in length according to quality of diet in the pre-adult period. On tarsi I and II solenidion omega one (ω_1), a sensory organ, is recumbent and the angle between the dorsal surface of the tarsus and the anterior face of the solenidion rarely

Figure 1.3.2 Sexual dimorphism in adult mites of the species *Acarus siro*

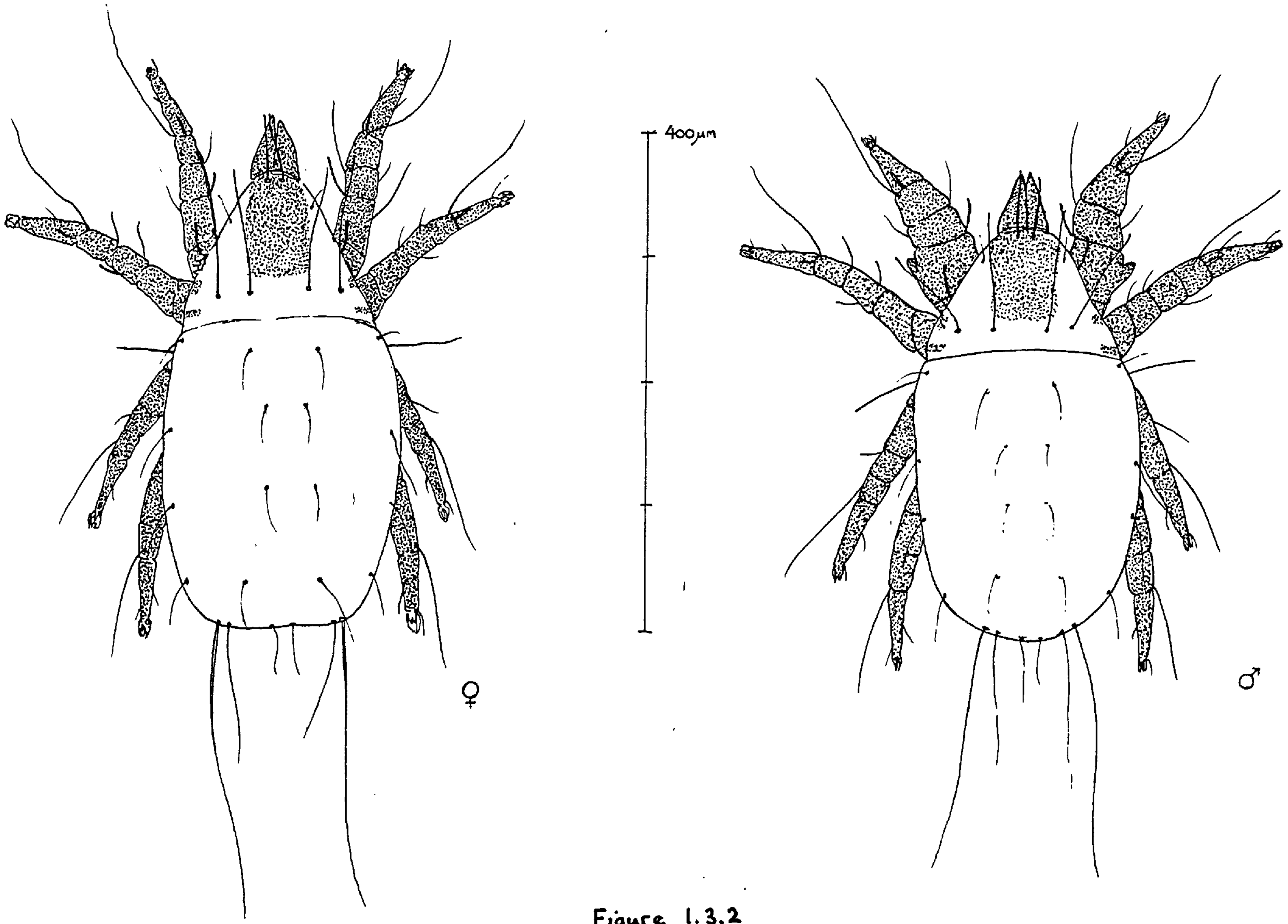


Figure 1.3.2

Figure 1.3.3 Mouthparts of Acarus siro

a) Latero-ventral view of the anterior region : Gr.or. Grandjean's organ, inf. infracapitulum, pod.c podocephalic canal, p.sh. propodosomal shield, su.s.I supracoxal seta of leg I. (from Evans, Sheals and McFarlane, 1961)

b) Internal view of chelicera : m.s. mandibular spine, c.sp. conical spur (from Hughes, 1976)

c) Dorsal view of gnathosoma with the chelicerae removed : m. mala, la. labrum, p. palp, pe.c. pedipalpal coxa (from Hughes, 1976)

d) External view of a chelicera of a mite from the experimental stock culture.

In each case the line adjacent to the figure represents 0.05mm .

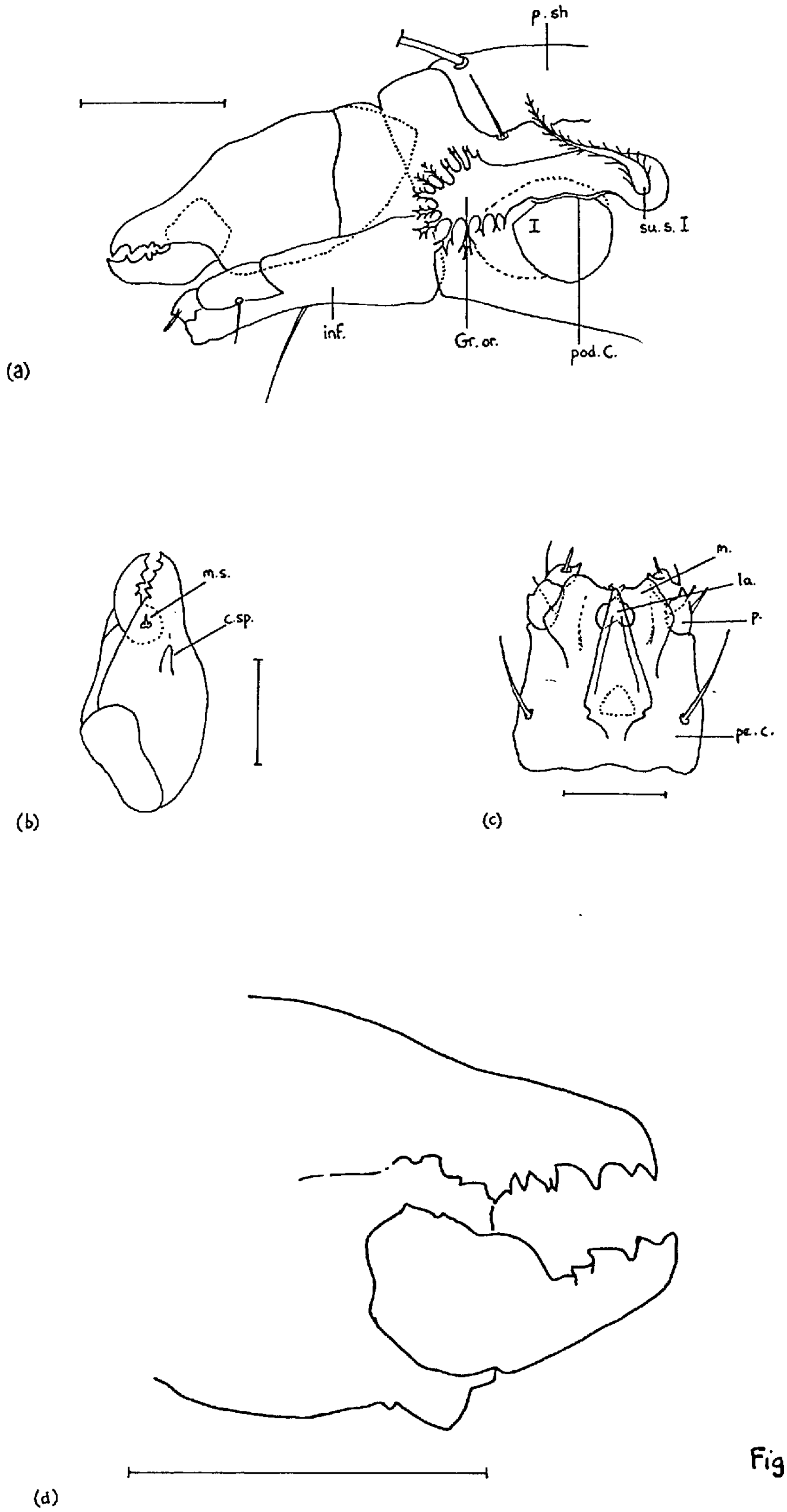


Figure 1.3.3

exceeds 45 degrees. It is broadest at the base, then narrows before swelling out into a terminal expansion. This solenidion is very important in distinguishing A.siro from the closely related A.farris and A.immobilis (Figure 1.3.4).

There is a pair of dorsal 'oil glands' from which originates a lipoid material which spreads over the cuticle and probably gives rise to the pungent, minty smell associated with infestations of A.siro (Solomon 1946).

The most important physical (climatic) variables affecting A.siro are temperature and humidity. The effect of various combinations of these two variables on the rate of increase of the mite is shown in Figure 1.3.5(d). The optimum conditions, as far as rate of increase and generation time (Figure 1.3.5(a)) are concerned, appear to be 25°C and >80%RH. However if total egg output and juvenile mortality (Figures 1.3.5 (b) and (c) respectively) are examined the optimum appears to be 15°C and >80%RH.

Limiting conditions have been examined by many authors but the most complete record is that of Cunnington (1965) and his results are shown in Figure 1.3.6 . Cunnington also made extensive comparisons of the results of earlier authors. The data are mainly concerned with the completion of the life cycle, although A.siro will survive more extreme conditions dependent in part on the stage of the life cycle involved - for example, individual mites have survived for periods of up to fifteen months at 0°C given suitable humidity conditions (Ushatinskaya 1954, cited in Cunnington 1965). There is also a case reported by von Wahl (1923, cited by Solomon 1943) of A.siro living in fermenting tobacco at a temperature of 55°C, but this observation has never been repeated.

Figure 1.3.4 Tarsus II of various Acarus species showing taxonomically important features (spine, S, and solenidion omega one, ω_1) :

a) <u>Acarus siro</u>, an individual taken from the experimental stock culture.

b)* <u>Acarus siro</u>

c)* <u>Acarus immobilis</u>

d)* <u>Acarus farris</u>

In each case the line adjacent to the figure represents 0.01mm .

* redrawn from Griffiths (1964b)

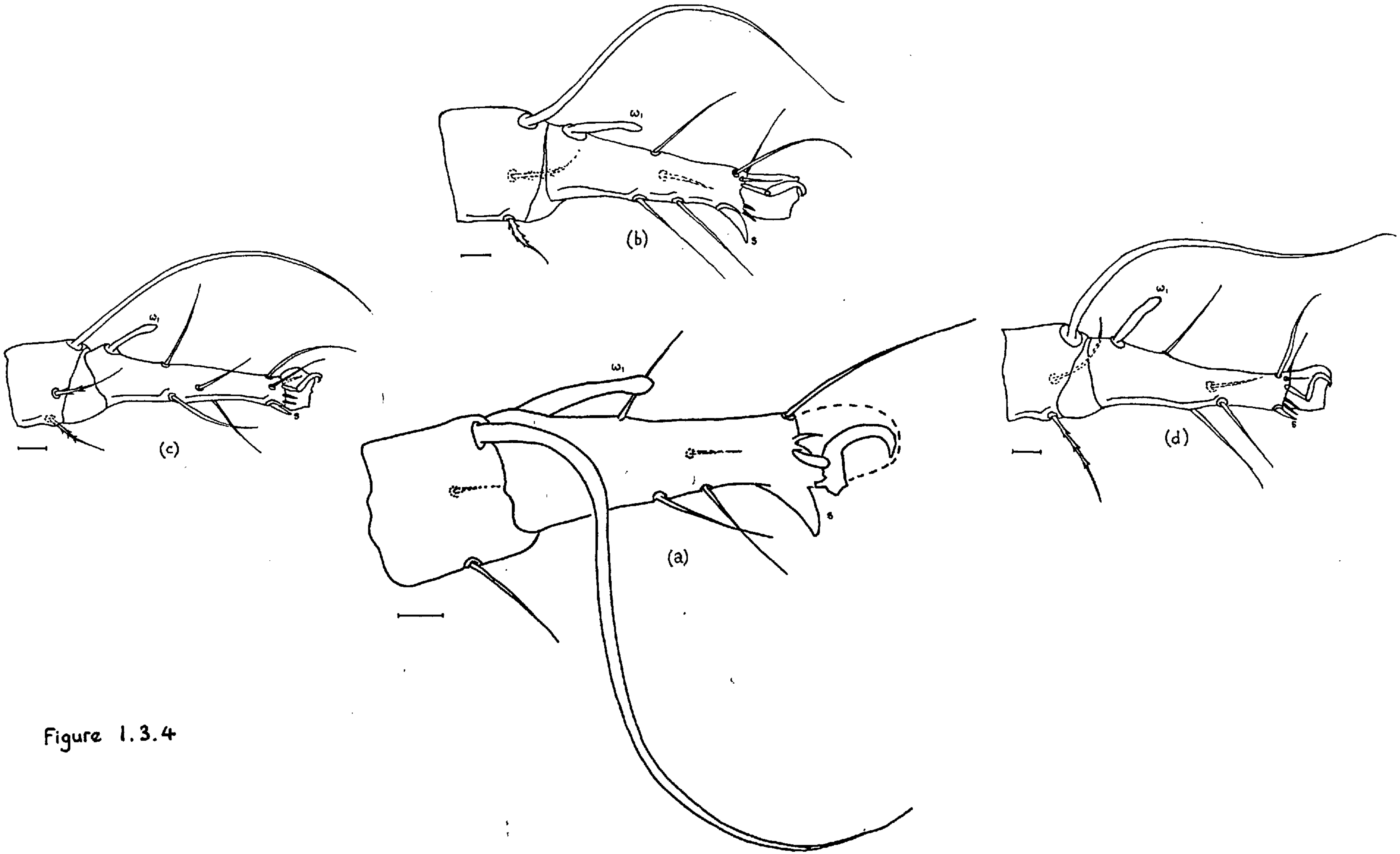


Figure 1.3.4

Figure 1.3.5 Life-history and physical limits of the Flour Mite, Acarus siro L., reared without crowding, on wheatgerm. (from Solomon 1957)

(a) Period of development, in days, from laying of egg to production of first F_1 egg.

(b) The daily egg-output of a female rises to a peak and declines again; only the totals of eggs laid are shown.

(c) Mortalities are very variable; the diagram is based on means of a series of experiments.

(d) Rates of self-multiplication per week, calculated approximately from data of categories (a), (b) and (c); also maximum survival periods beyond the limits for complete development.

Figure 1.3.6 Physical limits for complete development of the grain mite, Acarus siro L. (after Cunnington 1965)

○ conditions under which the life cycle was completed;

● conditions under which eggs failed to hatch or development was incomplete.

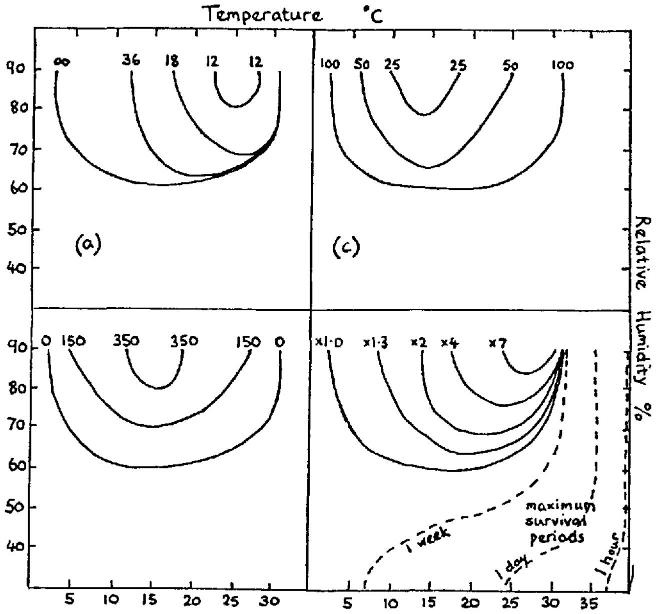


Figure 1.3.5

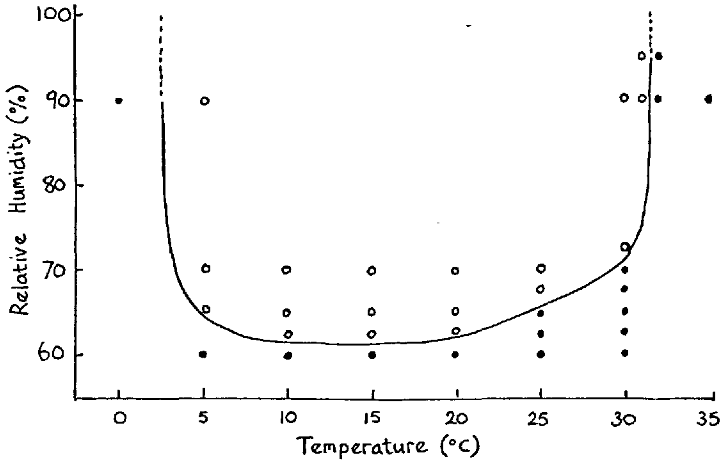


Figure 1.3.6

Cunnington also comments in detail on the effect of these factors on the world distribution of A.siro .

Hughes (1943) examined the effects of various oxygen and carbon dioxide concentrations on A.siro. In enclosed cultures, the mites became anaesthetized after reducing the oxygen concentration to between 5.0 and 6.3%, the carbon dioxide increasing to between 9.75 and 10.5%; the mites recovered after a few hours exposure to fresh air. Hughes also observed that mites were killed by exposure to pure carbon dioxide after seventy-two hours; and would survive forty-eight hours, but not seventy-two hours under an atmosphere of nitrogen. He further demonstrated that the system was cyanide sensitive and therefore probably of a cytochrome/cytochrome oxidase type, but that the mites could recover from the effect of absorbed cyanide in between twelve and twenty-four hours, thereby indicating either that the animals produced fresh cytochrome in that period, or that they succeeded in metabolizing the cyanide.

1.3.3 Acarus siro - general ecology

Of its relationships with other organisms, the most important are those with the fungi, and that with the Prostigmatid mite Cheyletus eruditus (Schr.)

Under the conditions in which A.siro thrives in stored food products various fungi are also likely to be found. Although they remove some food material and so, in some respects, compete with the mite, they are themselves a source of food, the benefits of which vary according to the species involved. A.siro has been shown to consume between 0.01 and 0.05mg of Neurospora crassa per day at 80°F(29°C) and 73%RH (Pimental et al, 1960); and Sinha (1966) has shown it to grow well on Nigrospora sphaerica, Alternaria tenuis and Trichothecium roseum; while Griffiths et al(1959) showed it to exhibit a preference for Aspergillus amstelodami, A. repens and A.ruber over A.candidus, A.ochraceous and A.flavus (this paper also included details of the process of feeding on fungi). On the other hand Solomon et al (1964) demonstrated a possible toxic effect of the fungus Sporendonema sebi on the growth of A. siro on wheat germ flakes.

Cheyletus eruditus is the most important predator of A.siro, and under certain conditions has been seen to effect extensive and successful control over populations of the Flour Mite. The variable success of the predator in this relationship is most probably explained on the basis of the difference between the climatic requirements of the two mites. Figure 1.3.7 shows the effects of these differing requirements on the interaction between the mites in terms of rates of population increase.

Other predators of A.siro, of more infrequent occurrence, include Cecid fly larvae and Gamasid mites (Solomon, 1962).

Parasites and microbial pathogens of the mite have been studied very little - a single unspecified sporozoan is mentioned by Solomon (1962).

In stored cereals A.siro competes with other mites and with insects for the food available. It has been suggested by Sinha (1968) that selective mycophagy allows sufficient separation for co-existence within the mite community. Hughes (1976) has cited the resistance of A.siro to high carbon dioxide concentrations as a factor giving the mite a competitive advantage over insects. However, the small size of Acarus and its great powers of increase are probably its greatest assets in competing with the larger

Figure 1.3.7[*] Effects of temperature and humidity on _Acarus siro_ and _Cheyletus eruditus_

(a) Lines of equal rates of net increase of A. siro as calculated approximately from results of rearing experiments; eg. 2 stands for a doubling of numbers per week (when increase is unhindered). The 1.0 line marks the tolerance limits; beyond this, conditions are lethal, but only very slowly in the shaded area.

(b) Corresponding diagram for the predator, C.eruditus. Further results show that the 1.0 line should extend down to include 50% R.H.

(c) On enlarged scale, the tolerance limit lines (A) for A.siro, and (B) for C.eruditus. The line C passes through those temperature and humidity combinations in which the calculated rates of increase for the two species are equal.

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[*] redrawn from Solomon (1962)

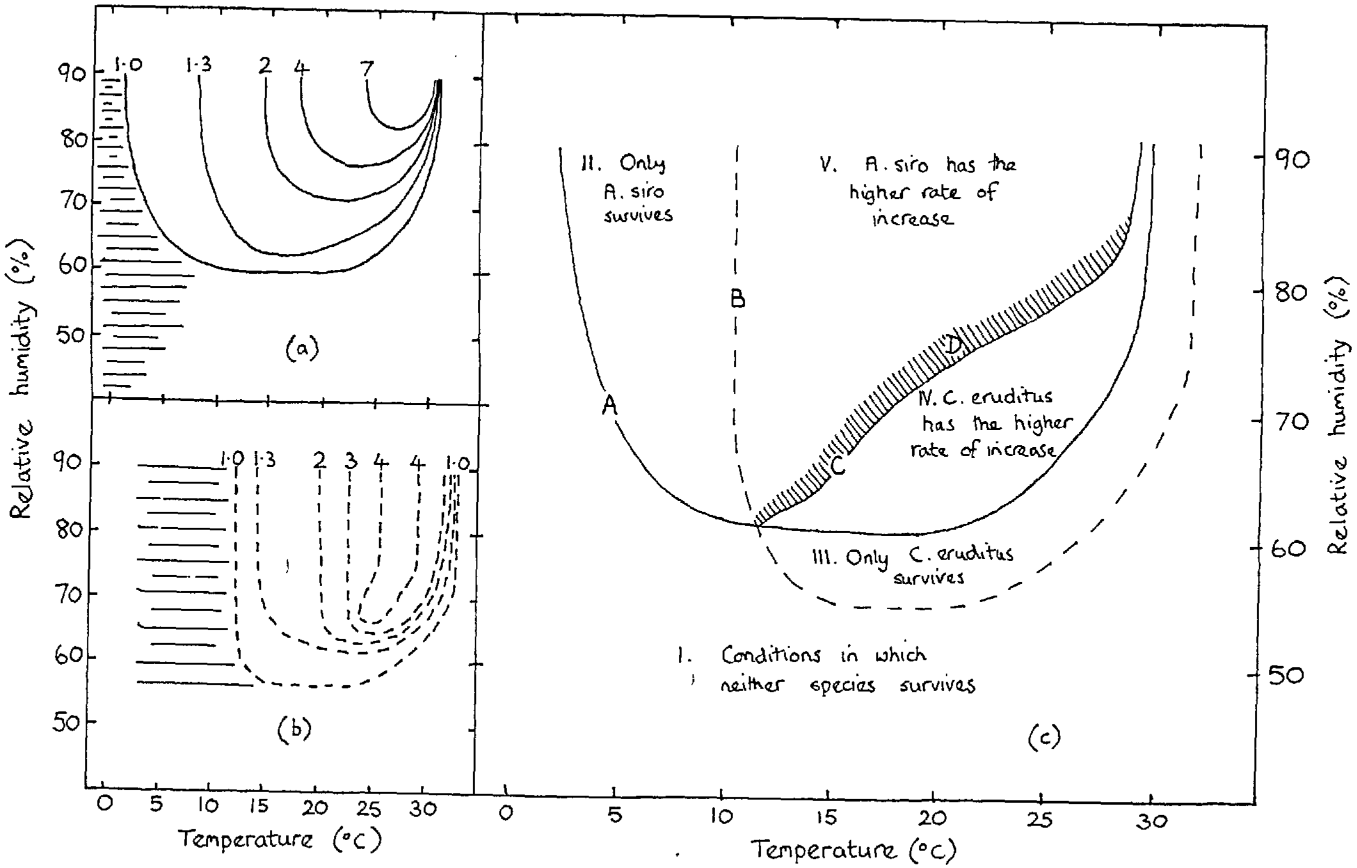

1·0
1·3
2
4
7
90
80
70
60
50
(a)
1·0
1·3
2
3
4
4
1·0
90
80
70
60
50
(b)
0
5
10
15
20
25
30
Temperature (°C)
Relative humidity (%)
II. Only A. siro survives
V. A. siro has the higher rate of increase
B
A
D
C
IV. C. eruditus has the higher rate of increase
III. Only C. eruditus survives
I. Conditions in which neither species survives
(c)
0
5
10
15
20
25
30
Temperature (°C)
90
80
70
60
50
Relative humidity (%)

Figure 1.3.7

arthropods.

The final group of organisms which interacts with A.siro is very diverse, the members of the group being linked by the fact that they provide a means of transport for the hypopus of A.siro in its dispersal from unfavourable conditions. The hypopi have been found for example on the mole flea (Hystrichopsylla talpae) and the rat flea (Ceratophyllus fusciatus), and honey bees (Apis mellifera) (Hughes, 1959) - all examples in which the phoresy relates to habitats commonly supporting populations of A.siro. It seems likely that close examination of the scavenging and ecto-parasitic fauna of other A.siro habitats would extend the list of insect carriers, and the probability of birds and mammals acting directly as carriers is similarly high.

Apart from its occurrence in stored food, especially processed cereal products, Acarus siro has been recorded as occurring in the deep litter of broiler houses and in disused bee-hives (Hughes 1976), active beehives, solitary bee (Bombus) nests and fresh dung Evans, Sheals and McFarlane, 1961), arable soils (Sorokin, 1951; Sheals, 1956), and in the nests of : rodents and moles (Hughes, 1959); the tree sparrow (Sandner and Wasylik, 1973); and sparrow, martin, pigeon, jackdaw and swallow (Woodroffe, 1953). Of the bird nest habitats, only the nests of pigeons have been seen to support large populations of Acarus siro.

CHAPTER TWO - EXPERIMENTAL METHODS

The methods used for maintaining stock cultures of Acarus siro, and for carrying out experiments on the animals, are generally those recommended by the staff of the M.A.F.F. Pest Infestation Control Laboratory at Slough. The initial stock of Acarus siro was provided by this establishment. Except where otherwise stated the methods are those described by Solomon and Cunnington (1964) or minor modifications of these.

2.1 Culture Methods

Stock cultures were held in 50ml conical flasks, closed with a tight plug of non-absorbent cotton wool. To maintain a standard humidity these flasks were enclosed in glass dessicator jars containing a saturated solution of potassium chloride, giving a relative humidity of $85\pm1\%$ (for the temperature range 20-30°C) (Solomon, 1951). These jars were kept in rooms in which the temperature was maintained at 25 ± 2°C.

2.1.1 Culture medium

The food medium used, both for routine culture and for experimental purposes, was a mixture of dried yeast powder (Yestamin 20) and ground wheat-germ flakes (Bemax), in a ratio of three parts yeast to one part wheat-germ (by weight). The wheat-germ flakes were ground to a fine powder in amounts of approximately 100cc using a small domestic grade electric coffee grinder (Moulinex) operated for fifteen seconds.

2.1.2 Sterilization

Where necessary containers and food media were sterilized by the use of propylene oxide (1,2 epoxypropane) within sealed containers - steel jars of the type commonly used in microbiological

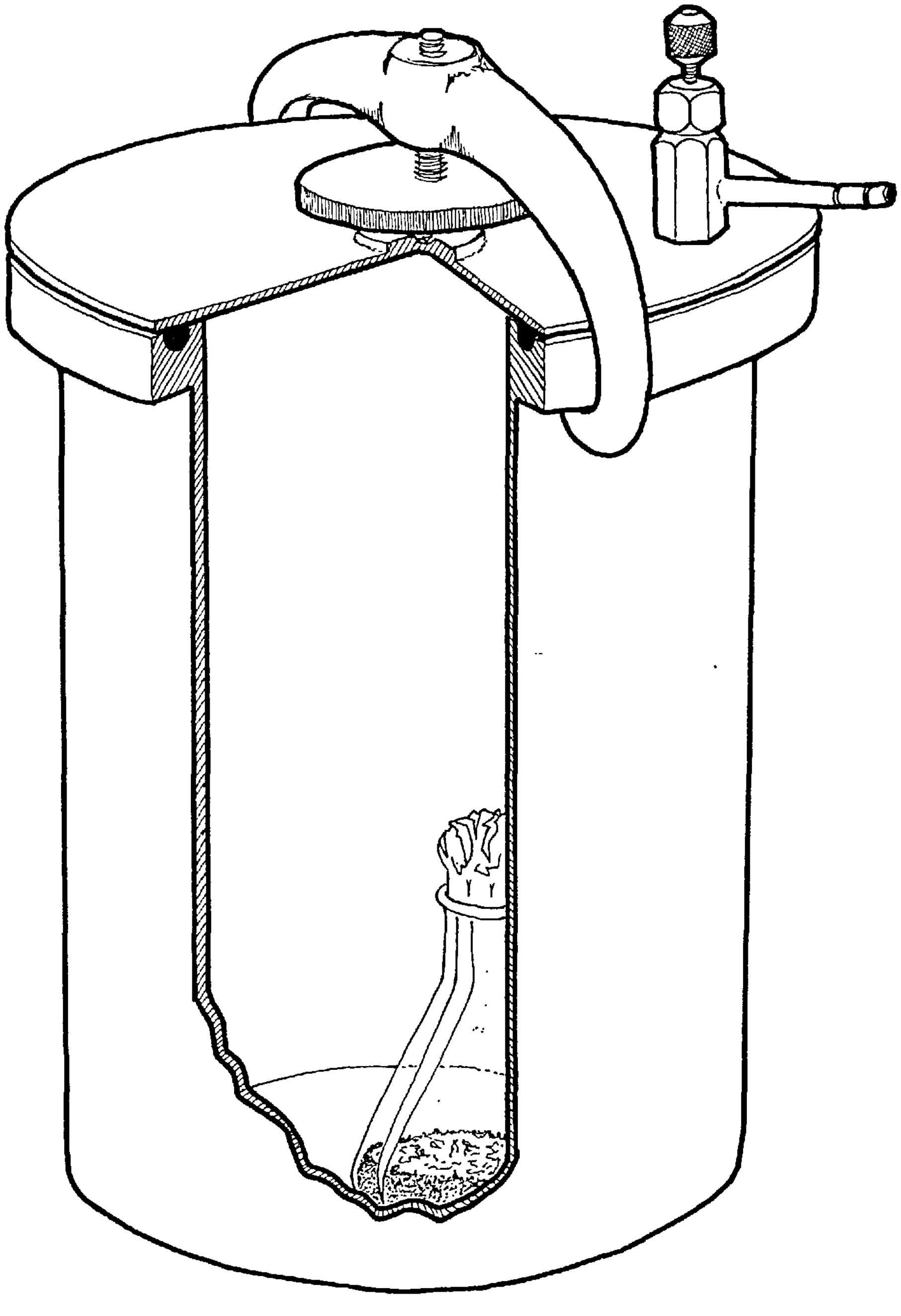


Figure 2.1.1 Steel Anaerobic Jar

research for the culture of anaerobic organisms. The propylene oxide was added at the rate of 2ml per litre volume to be sterilized, the items remaining in contact with the sterilant for twenty-four hours, after which the container was unsealed and sterilized items allowed to stand for one week to allow remaining traces of propylene oxide to diffuse away. The cotton wool bungs used for all containers were assumed to be a sufficient barrier to reinfection subsequent to the sterilization procedure.

2.1.3 Maintenance of stocks

Stocks were sub-cultured at intervals of eight to ten weeks, when the mites had increased sufficiently in number to cause discolouration and a slight deterioration of the food medium. Approximately one-half cubic centimetre ($\frac{1}{2}$cc) of an old culture was transferred to each of four flasks containing 25cc of food medium, these having been previously sterilized as above and then acclimatized to normal culture conditions (25°C and 85%RH) for at least twenty-four hours. The new cultures were then labelled on the outside of the flasks with the date of inoculation, using either a waterproof fibre-tip marker or a chinagraph pencil, and then removed to the dessicator jars in the controlled temperature room.(Old cultures were not immediately discarded but retained, sometimes with the addition of further food medium, to allow further morphological and behavioural observations) To maintain a sufficient oxygen concentration in the cultures the dessicator jars were opened twice weekly to allow free circulation of air.

2.1.4 Reserve stocks

In addition to those cultures described above , in which at least four flasks of mites were available at any one time, additional stocks were kept as a long term reserve at a lower temperature of 4°C in a refrigerator. These were held in 100ml conical flasks containing about 50cc of food medium, and sub-cultured at six-monthly intervals : two flasks being maintained at all times. Otherwise the conditions of culture were as for normal stocks.

2.1.5 Measurement of humidity

Relative humidity was estimated with cobalt thiocyanate paper (Solomon, 1957) using a disc comparator. Using this method it was possible to estimate the humidity to within ± 1.25% (the comparator disc being calibrated in 5% intervals)

2.2 Growth Curve for Acarus siro Individuals

It was necessary, before starting experiments directly concerned with intraspecific competition, to have information concerning the size range and duration of the various life stages of Acarus siro under the planned experimental conditions. For this purpose day by day studies were conducted of the development of individual mites from eggs of known age (i.e. interval since oviposition), and from the results obtained a practical means of identifying the various life stages from a large mixed age-class culture was developed.

2.2.1 Study methods (See Figure 2.2.1)

The study was carried out using modified Robertson cells (Robertson 1944, Solomon and Cunnington 1964) at a temperature of 25°C, relative humidity of 85% and using the standard yeast/wheat-germ medium. Ten adult female mites were placed in a one inch (1") diameter Robertson cell with excess food. On each day following the eggs laid were removed from the cell, and individual eggs transferred to half inch ($\frac{1}{2}$") diameter Robertson cells

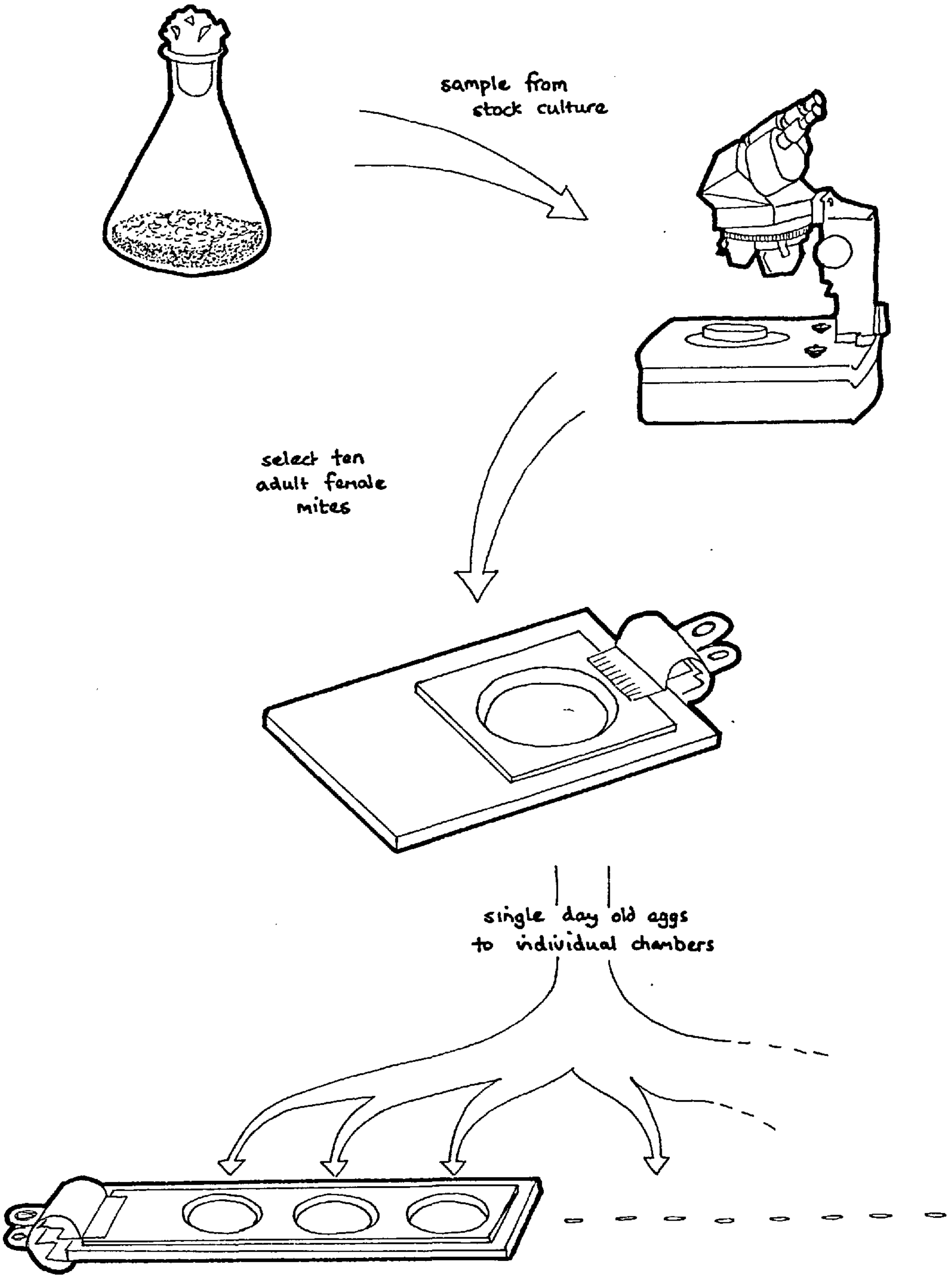


Figure 2.2.1 Procedure for growth curve study

supplied with food, these cells being labelled with the date of oviposition of the egg and a number unique to that egg. Daily observations were subsequently made on each individual, the following information being recorded :

a) The life stage of the mite.

b) The maximum body length of the mite, measured using an eye-piece micrometer.

c) Times of ecdysis.

d) Sex, where the mite developed to the adult stage.

Only a small number of mites was examined (twenty in all), but this was felt to be sufficient for the purpose of the study when the results from these mites had been examined.

2.2.2 Study results

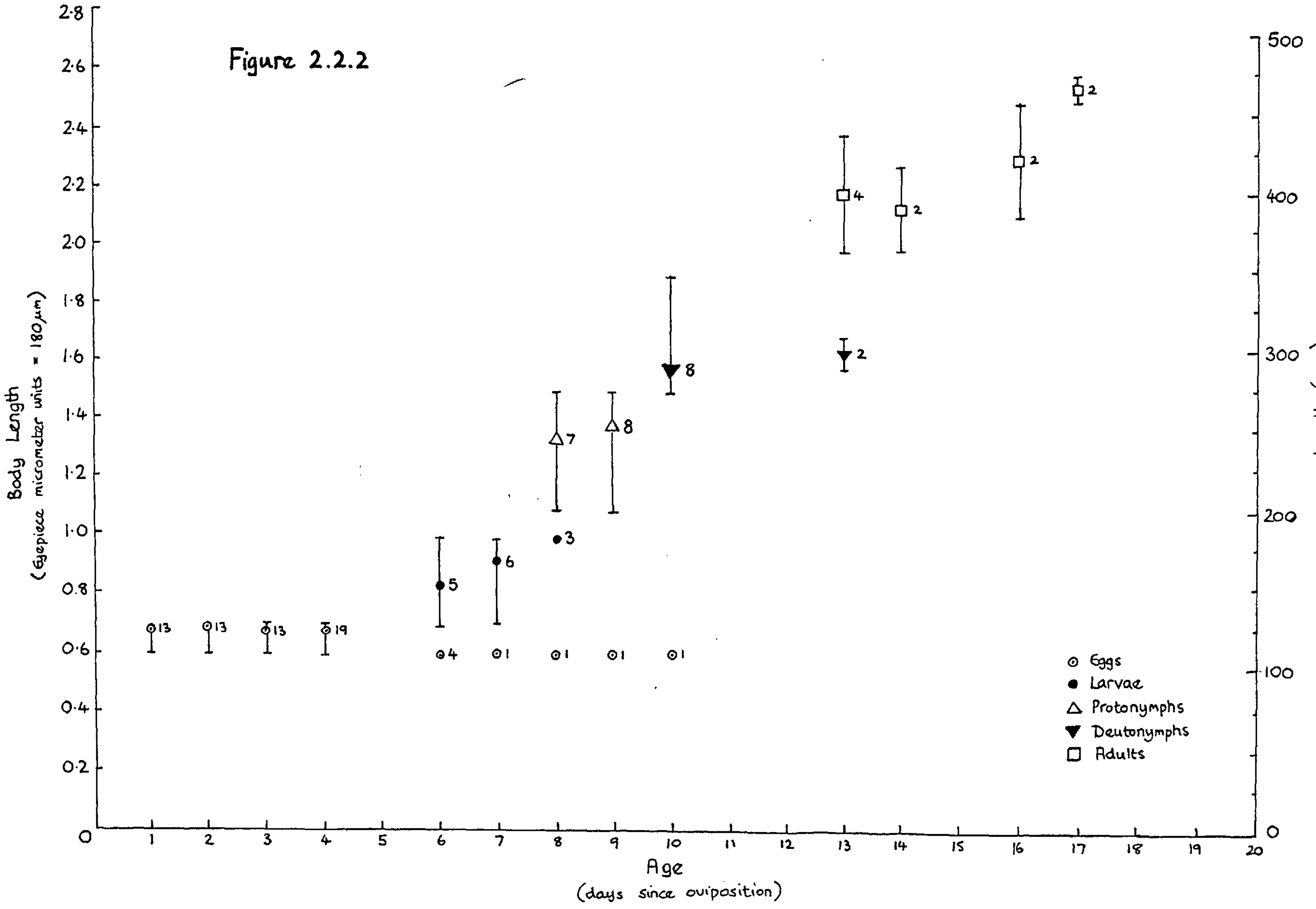
These are shown in graphical form in Figure 2.2.2 . The life stages are fairly well demarcated by size, and it was felt that this fact, together with the obvious morphological features of some of the stages would be sufficient to allow their practical separation.

2.2.3 Visual recognition of life stages

All examinations of live mites were carried out using a stereoscopic bench microscope with 1.25x objectives and 10x eyepieces. At this level of magnification the hexapod larvae were easily distinguishable from the other stages, as were the adult males with their heavily sclerotized and spurred fore-legs. The other stages being largely separable on a size basis only, it was felt that some visual index which would obviate the use of a micrometer eyepiece was necessary in order to cut down the time spent in handling individual mites. The resting stages, larval

Figure 2.2.2 The development of individual mites of the species Acarus siro, from the time of their oviposition to maturity. The bars indicate the range of body size (length) observed for each age, the position of the symbol on the bar indicating the mean size. The number of individuals observed for each age is given alongside the relevant bar.

Figure 2.2.2


Body Length
(Eyepiece micrometer units = 180µm)
Body Length (µm)
Age
(days since oviposition)
0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
2.6
2.8
100
200
300
400
500
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
13
13
13
19
4
1
1
1
1
5
6
3
7
8
8
2
4
2
2
2
⊙ Eggs
● Larvae
△ Protonymphs
▼ Deutonymphs
□ Adults

and two nymphal, are usually present in high numbers in mixed populations (though not always, as it was noticed that sometimes cultures apparently became synchronized in growth, so that there were periods when no resting stage mites could be detected) and are sufficiently different in size as to be easily distinguishable, and therefore to act as a reference for the classification into stages of the other mites surrounding them. This proved the most convenient and reliable method of sorting the life stages in that period before the recognition of the differences became automatic, and acted as a useful checking procedure thereafter.

2.3 Experiments on Intraspecific Competition

The general plan of experiment was to measure mortality rates of mites under various conditions of population structure, population density and food availability. These particular experiments were concerned with the measurement of mortality rates in small populations whose members are of a single life stage, and were seen as providing base-line measurements against which to guage the effects of life-stage interactions on mite mortality. It was hoped thus to abstract some measure of the coefficients of competition between and within life-stages, as required by the model described earlier (see Section 1.2.3)

The experiments were planned so as to measure mortality rates over four day periods (this being approximately equal to the duration of the life stages - see Figure 2.2.2). Therefore the mites taken for experiment were those which had recently ecdysed i.e. the youngest mites of a particular life stage, in order to more closely identify the experimental periods with the life stage periods. The mites were counted into small perspex cells, in which there was a measured amount of food. After four days under standard atmospheric conditions the surviving mites were counted, using a binocular microscope at 12.5x magnification.

After a preliminary round of experiments was carried out to gain an approximate measure of the rates of mortality to be expected under the planned experimental conditions, a standard set of mite densities and food concentrations was decided upon and used for the experimental regime proper. Only the nymphal stages and adult females were used for experiment, time setting a restriction on the number of life stages which could be examined across the full range of conditions, and ease of handling favouring post-larval mites. Adult females only were used because of the marked sexual dimorphism exhibited in the adult stage (particularly in terms of size). Males and females could be visually separated in the juvenile stages but separation here was thought to be of lesser importance than in the adult stage, because of the absence of size or behavioural differences.

The preliminary experiments were restricted to mortality rates of adult females under the following conditions :

a) At 20µg food/cell : mite densities of 30,20,15,10 per cell

b) At 40µg food/cell : mite density of 15 per cell

c) With 5 mites per cell : 20,40,100,200,300,400 and 500 µg food per cell

For the main experimental program, all combinations of the following conditions were examined :

a) 20,150,300 and 450 µg of food per cell

b) 1,5,10,15,20,25,30 mites per cell

c) Adult female, deutonymph and protonymph mites a total of eighty-four combinations of conditions. Sufficient replicates were undertaken so as to guarantee the observation of at least one hundred mites under each set of conditions e.g. four replicates for those involving thirty mites per cell, eight for those involving fifteen mites per cell, twenty for those with five mites per cell etc.

2.3.1 Preparation of experimental chambers

All experiments were carried out using Robertson cells (the dimensions of which are shown in Figure 2.3.1). The cell bases were cut from black filter paper (Whatman No.29) and attached to the black perspex cell bodies with shellac. The internal junction of base and cell body was thickly coated with shellac as a seal against mite escape. The cell covers were of glass, formed by bisecting 75mm x 38mm microscope slides, and held firmly to the body of the cell by small Bulldog clips. The details of the procedure for assembling cells are given in Figure 2.3.2 . Labelling of the cells was done directly on the perspex surface using a yellow 'Chinagraph' pencil.

After use the cells were dissembled and cleaned as shown in Figure 2.3.3 . During the second stage of dissembly minor damage could occur to the basal edge of the cell cavity in the process of removing shellac from the cell wall. This damage, in the form of small nicks and cracks in the edge, was largely occluded by the subsequent shellac seal and so, although cumulative, seldom allowed the escape of mites (during the course of the experiment fewer than ten cells were discarded for this reason)

2.3.2 Preparation of mites for experiment

Under normal conditions of culture mites are present through

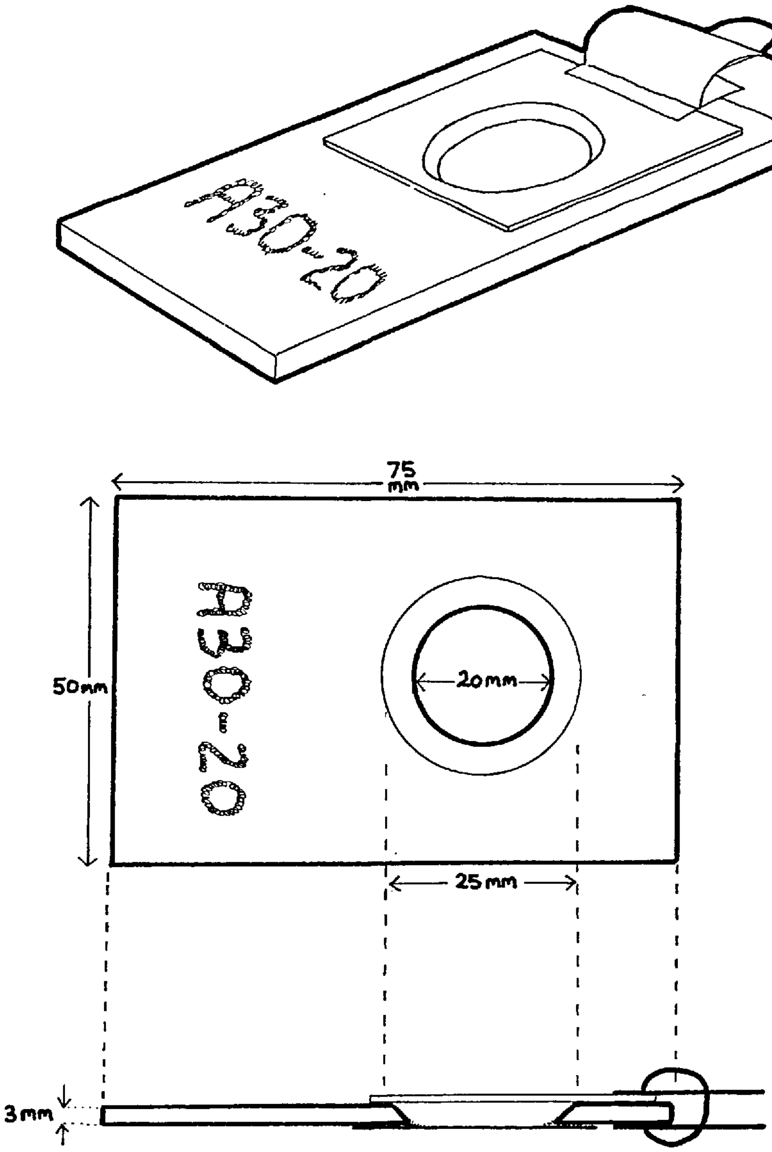


Figure 2.3.1 Robertson cell

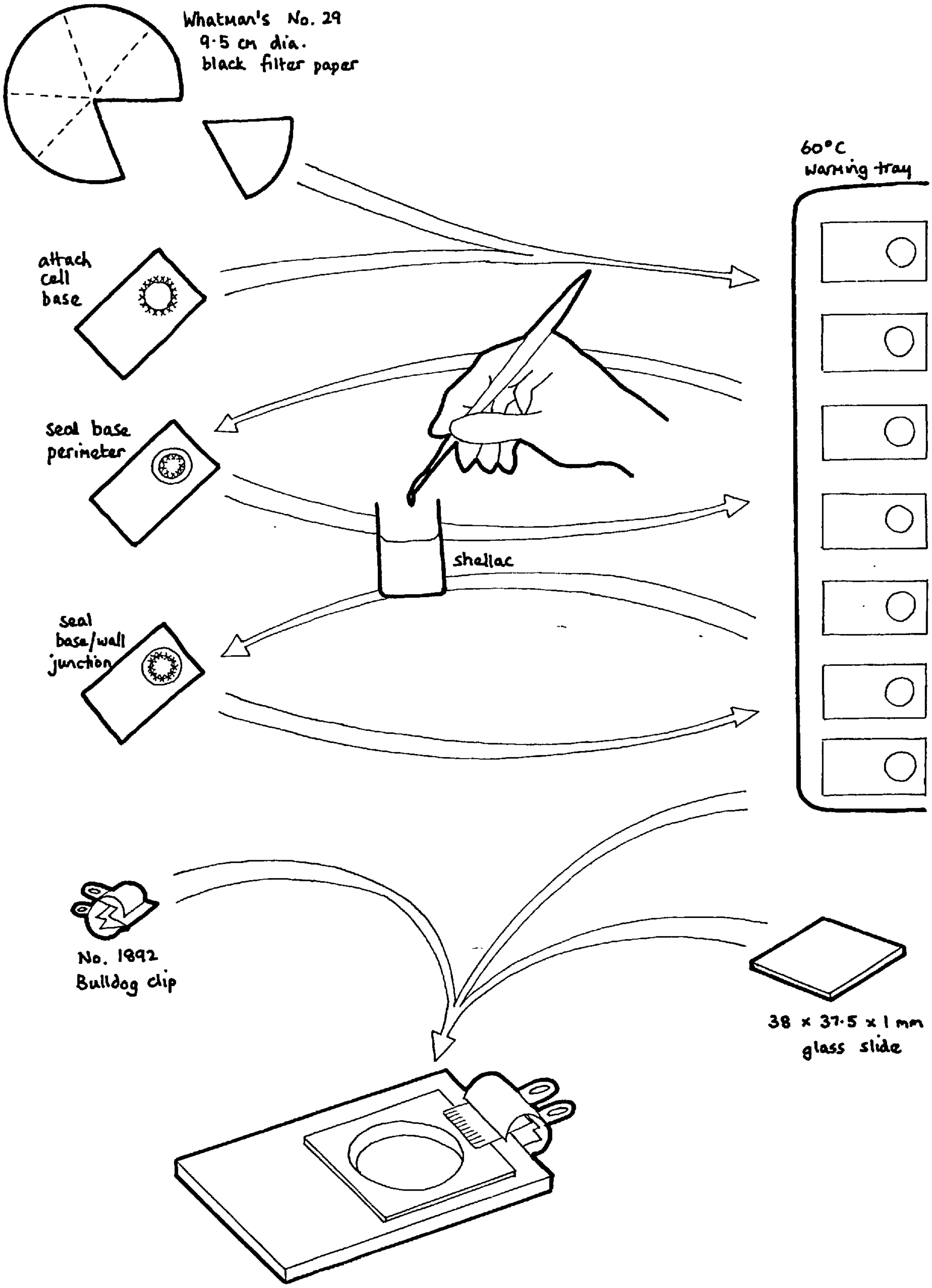


Figure 2.3.2 Procedure for assembly of experimental cells

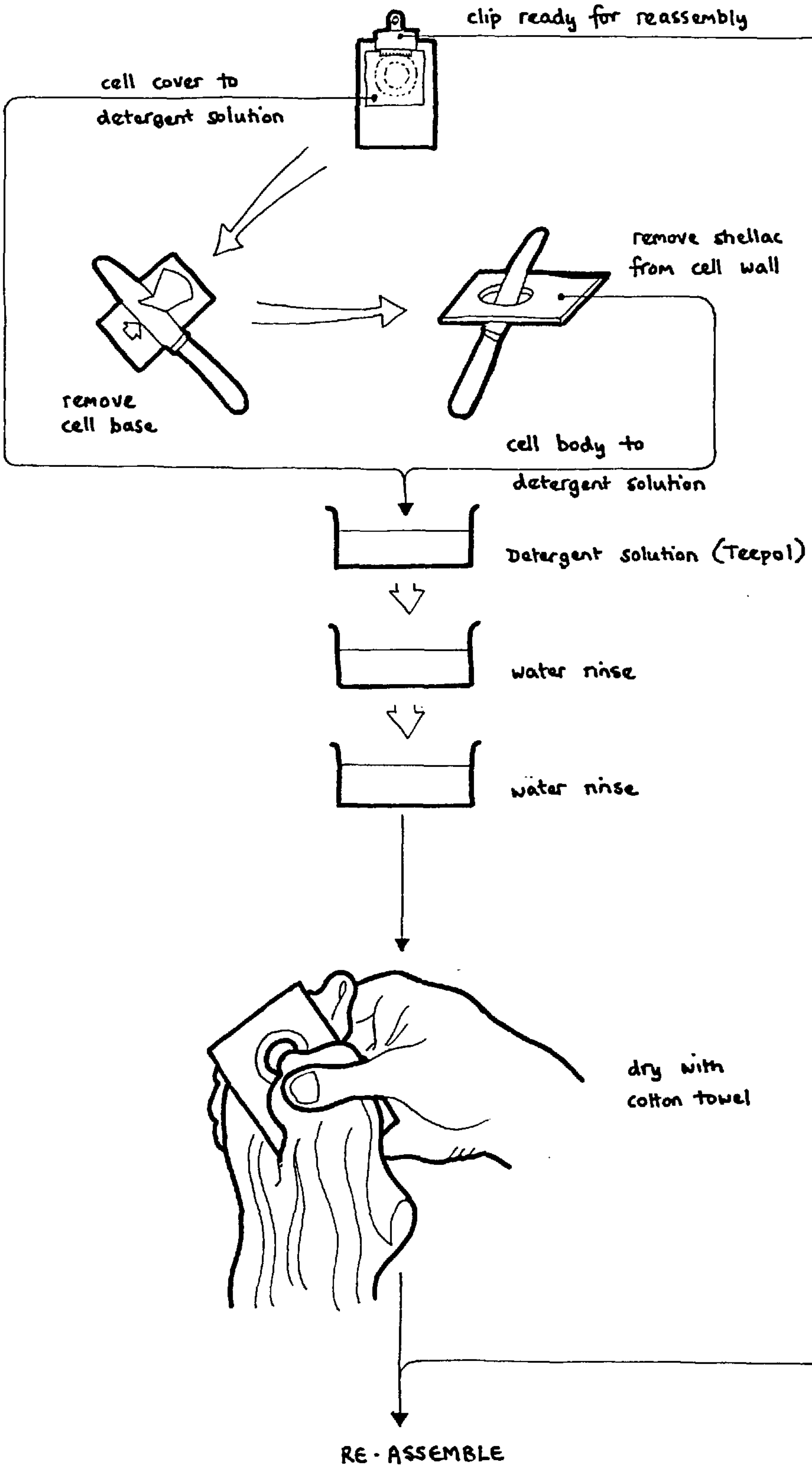


Figure 2.3.3 Procedure for dissembly of experimental cells

the bulk of the medium. Even when small quantities of culture are removed and spread on a flat surface, for example in a petri dish, it is difficult to minimize the three-dimensional quality of the mixture without damaging the organisms. This, together with the propensity of the mites to stick to each other and to collect food particles and other debris on their body surfaces, makes difficult the problem of removing individuals, unaccompanied by extraneous matter, for experiment. To overcome this, a washing procedure was devised which greatly facilitates the subsequent manipulation of individual mites. The procedure is illustrated in Figure 2.3.4 .

When the suspension is filtered it forms a sludge on the surface of the cotton filter. Vacuum filtration and the subsequent absorption stage remove moisture from the sludge, but the consistency is still sufficiently soft to allow mites to burrow out and move freely on the surface. Large numbers of mites are usually free within fifteen minutes of filtration, and an estimate can then be made of the availability of the various life stages for experiment. The mites, now held in the sealed petri dish, are then stored in a refrigerator until required, so as to slow the growth of any fungi which might have infected the culture during the washing and filtration routines.

Within the petri dish the mites tend to aggregate towards the centre of each filter disc, but are to be found on all of the surfaces of the interior. A humidity gradient, humidity decreasing radially outwards from the centre of the sludge mass, probably accounts for this distribution of mites.

2.3.3 Delivery of food to experimental chambers

In view of the small amounts of food expected to be consum-

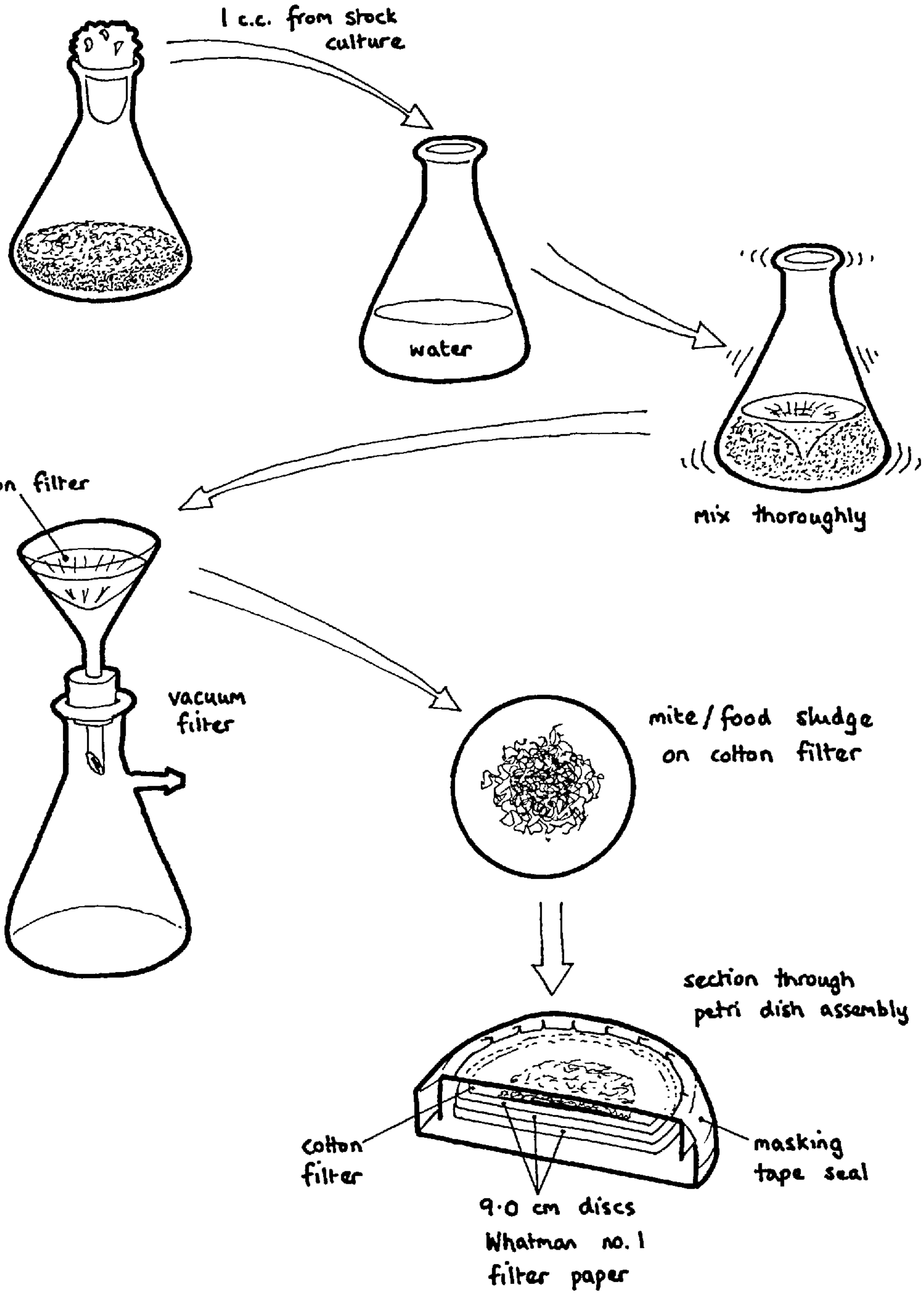


Figure 2.3.4 Procedure for preparation of mites for experiment

ed per day by individual mites, and the necessity to deliver the yeast/wheat-germ mixture in measured amounts, apportioning of the food to the cells in the form of a suspension in water was thought to be most suitable.

It was necessary to limit the total amount of suspension applied to any one cell because of the problem of cockling of the filter-paper cell base. It was found that amounts less than 0.05ml would not cause this problem.

During preliminary tests of the food mixture suspension it was noticed that a significant proportion of the solids came out of suspension rapidly, thereby causing a difference between the nominal concentration of the suspension and that delivered to the cells. A measure of this difference (at a standard time of ten seconds after thorough mixing of the suspension) was gained experimentally (see Table 2.3.1 et seq) and used subsequently to calculate the adjustments of dry weights of ingredients required to give a particular delivered concentration of suspension.

Three standard suspensions of the yeast/wheat-germ mixture were used during the course of experiment, these giving 2, 10 and 15 milligrams food per millilitre of suspension (the last replacing the second as a standard after the preliminary run of experiments). The amount of food delivered to individual cells in experiment ranged from 20µg to 500µg. The minimum food aliquot was adjudged, prior to experiment, to be insufficient for a single mite for the duration of observation and to be, therefore, functionally equivalent to no food, whilst avoiding the problem, in later mathematical manipulation of data, of zero numerical values.

Table 2.3.1 Calculation of solids in suspension.

Cup no.	Initial wt(g)	Suspension	Final wt(g)	Wt of solids(g)
1	0.0737	1.0 WG	0.0802	0.0065
2	0.0680	1.0 WG	0.0752	0.0072
3	0.0674	1.0 WG	0.0740	0.0066
4	0.0702	5.0 WG	0.1027	0.0325
5	0.0697	5.0 WG	0.1006	0.0309
6	0.0582	5.0 WG	LEAKAGE - NO RESULT	
7	0.0601	0.5 Y	0.0640	0.0039
8	0.0665	0.5 Y	0.0696	0.0031
9	0.0679	0.5 Y	0.0724	0.0045
10	0.0633	5.0 Y	0.1004	0.0371
11	0.0660	5.0 Y	LEAKAGE - NO RESULT	
12	0.0667	5.0 Y	0.1049	0.0382
13	0.0630	CONTROL	0.0630	0.0000
14	0.0714	CONTROL	0.0716	0.0002

Four fifty-millilitre water suspensions were made : two of ground wheatgerm, containing 1.000g (1.0 WG) and 5.000g (5.0 WG) solids, and two of yeast powder, containihg 0.500g (0.5 Y) and 5.000g (5.0 Y) solids. Three half-millilitre aliquots were taken from each suspension and deposited in foil cups, which had previously been numbered, dried to constant weight at 150°C and weighed accurately. After further drying to constant weight at 150°C, the cups were again weighed (two cups were discarded because of leakage). The concentrations of the two suspensions were then calculated from the weight of solids figures, and compared with the nominal concentrations.

For wheatgerm the actual concentration was found to be 66% of the nominal concentration, and for yeast powder the actual concentration was found to be 76% of the nominal concentration. For the purpose of adjusting subsequent suspensions, these transference figures were rounded to 65% and 75% respectively.

After dosing with food, the cells were stored upright (on end with chamber upmost) in glass dessicator jars at 4°C and a relative humidity of 85% to await inoculation.

2.3.4 Inoculation of cells

The dessicator jars containing the cells to be inoculated were removed from storage at 4°C and held at room temperature for an hour as a stage in equilibration to experimental conditions, and to avoid problems of condensation within the cells during inoculation. The petri dish containing the mites was unsealed and positioned on the stage of a low power binocular microscope. The top of the dish was removed and the contents illuminated from above.

Cells were removed from the dessicators in batches of twelve (to help reduce the time each was exposed to the drier conditions of the laboratory). Each cell was opened in turn and the requisite number of mites transferred from the petri dish to the cell by means of a micro-dissection needle (15x.0056mm) affixed to a matchstick held in a clutch pencil holder. When a batch of cells had been inoculated, it was taken for incubation at 25°C, a note being taken of the time half-way through the inoculation of that batch.

Mites were used from all localities within the petri dish as accessible, layers of paper and cloth being removed as necessary. Care was taken to isolate any material removed to the bench top by surrounding it with a barrier of paraffin (liquid and/or wax). As a further measure to avoid contamination of the general laboratory area with mites, the microscope stage and surroundings were frequently swabbed with cotton wool soaked in 70% alcohol. When all the cells for a given run of experimental replicates had been completed the petri dish assemblage was resealed and the outside surface wiped clean with alcohol. The bench surface, microscope and all utensils used, including trays used to transport cells between laboratory and controlled temperature rooms, were then thoroughly cleaned.

2.3.5 Experimental logistics

The experiments were run on a seven day cycle : three days preparation of materials and four days of incubation. Two cycles could be maintained simultaneously by overlapping the incubation time of one with the preparation time of the other (see Figure 2.3.5)

DAY ONE : Cells inoculated on day four of the previous cycle were removed from the C.T. room, each batch being removed 96 hours after it had been put in for incubation. The numbers of mites surviving in each cell were recorded. Dead mites were distinguished by their dehydrated appearance or, in doubtful cases, by the absence of response to bright light and heat (by increasing the power of the illuminating lamp). The dead mites were also counted as a check against the escape of mites from the cells during incubation. After the counting operation the cells were put into a dessicator containing anhydrous calcium chloride in order to kill the remaining mites by dehydration. The cells were then taken apart and cleaned (Section 2.3.1).

DAY TWO : The cells were re-assembled and stored in dessicator jars at 85%RH and laboratory temperature. A sample of mites was then filtered from the stock culture (Section 2.3.3). When the majority of mites had freed themselves from the

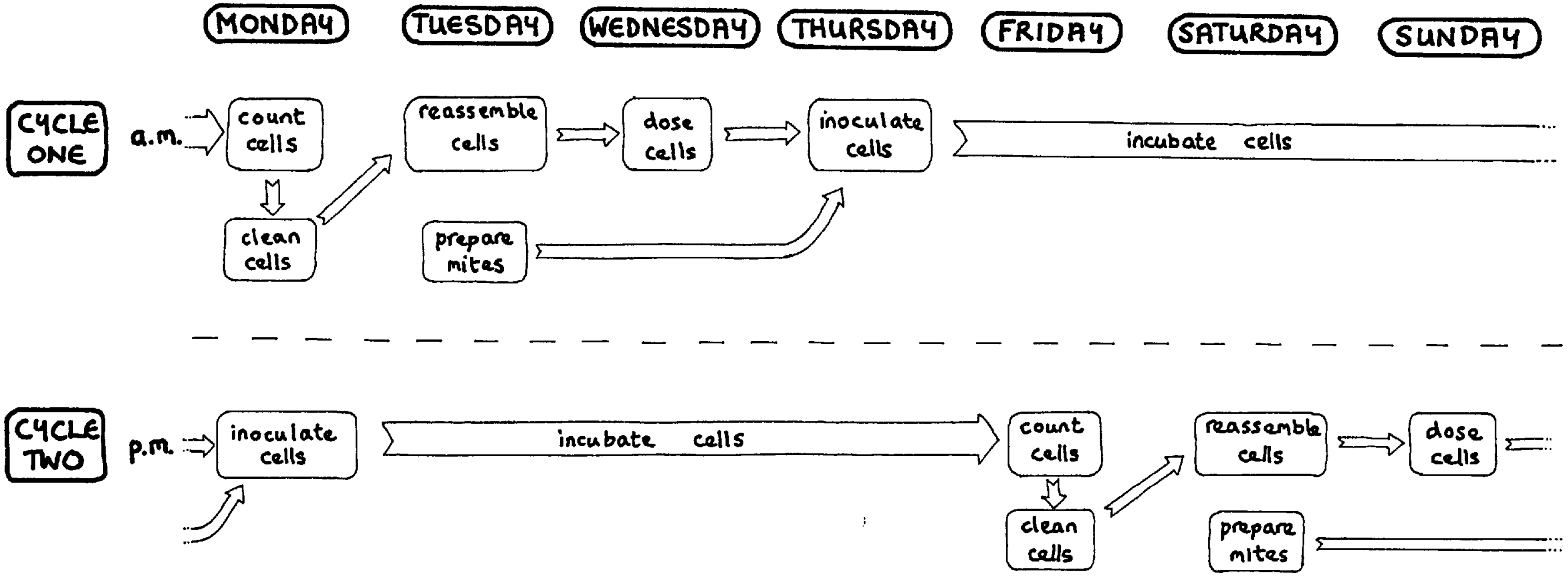

MONDAY
TUESDAY
WEDNESDAY
THURSDAY
FRIDAY
SATURDAY
SUNDAY
CYCLE ONE
a.m.
count cells
clean cells
reassemble cells
dose cells
inoculate cells
incubate cells
prepare mites
CYCLE TWO
p.m.
inoculate cells
incubate cells
count cells
clean cells
reassemble cells
dose cells
prepare mites

Figure 2.3.5

food sludge a visual estimate was made of the population structure so as to determine which experimental conditions might be fulfilled in the current week's batch of cells - often one or two life stages would predominate, therefore allowing experiments utilizing those stages. When a decision had been made in this matter, the cells were labelled with details of the treatment - mite life stage, mite numbers and amount of food e.g.:

A30 - 20 : thirty adult mites with 20µg food,
P5 - 450 : five protonymphs with 450µg food.

The labelling was marked directly onto the surface of the cell using a yellow wax ('Chinagraph') pencil - see Figure 2.3.1

DAY THREE : The experimental cells were dosed with the required amounts of food (Section 2.3.3).

DAY FOUR : The cells were inoculated with the required types and numbers of mites, and then stored at 25°C and 85%RH (see Section 2.3.4)

DAYS FIVE - SEVEN : Incubation period.

CHAPTER THREE - EXPERIMENTAL RESULTS

The overall patterns of mortality under varying conditions of mite density and food availability are shown in Figures 3.0.1 (for the preliminary data set) and 3.0.2 a-c (for the primary data set). The values shown are percentage means.

The preliminary set of experiments, over a limited range of conditions and using only the adult mites, will be described first. The results from this set were used to finalize the details of the primary set, and also to develop a model relating mortality to food availability and mite density. The results of experiments for both the preliminary (Section 3.1) and primary (Section 3.2) sets are given in two forms : the basic data are summarized by tables of standard moments for each condition set; and the effects of density and food availability on mortality are displayed in graphs of mean k-value mortality against these variables. K-value plots have been used rather than percentage mortalities so as to display explicitly, where appropriate, the coefficient of density dependence, b; and simple mean values used because the mortality distributions cannot be distinguished from a binomial pattern, where the variance is linked to the mean (see Section 3.3).

Additionally, for the primary data set, the relationship between mortality and the amount of food available per mite is graphed for various attributes of the individual - volume, surface area, volume/surface area ratio : these calculated assuming the mites to be ellipsoids of age independent proportions, the ratios of the major semi-axes being 14:6:3, with the size ratios of the life stages estimated as :

Figure 3.0.1 Preliminary experimental set - patterns of mortality for adult mites of the species *Acarus siro* under various conditions of mite density and food availability.

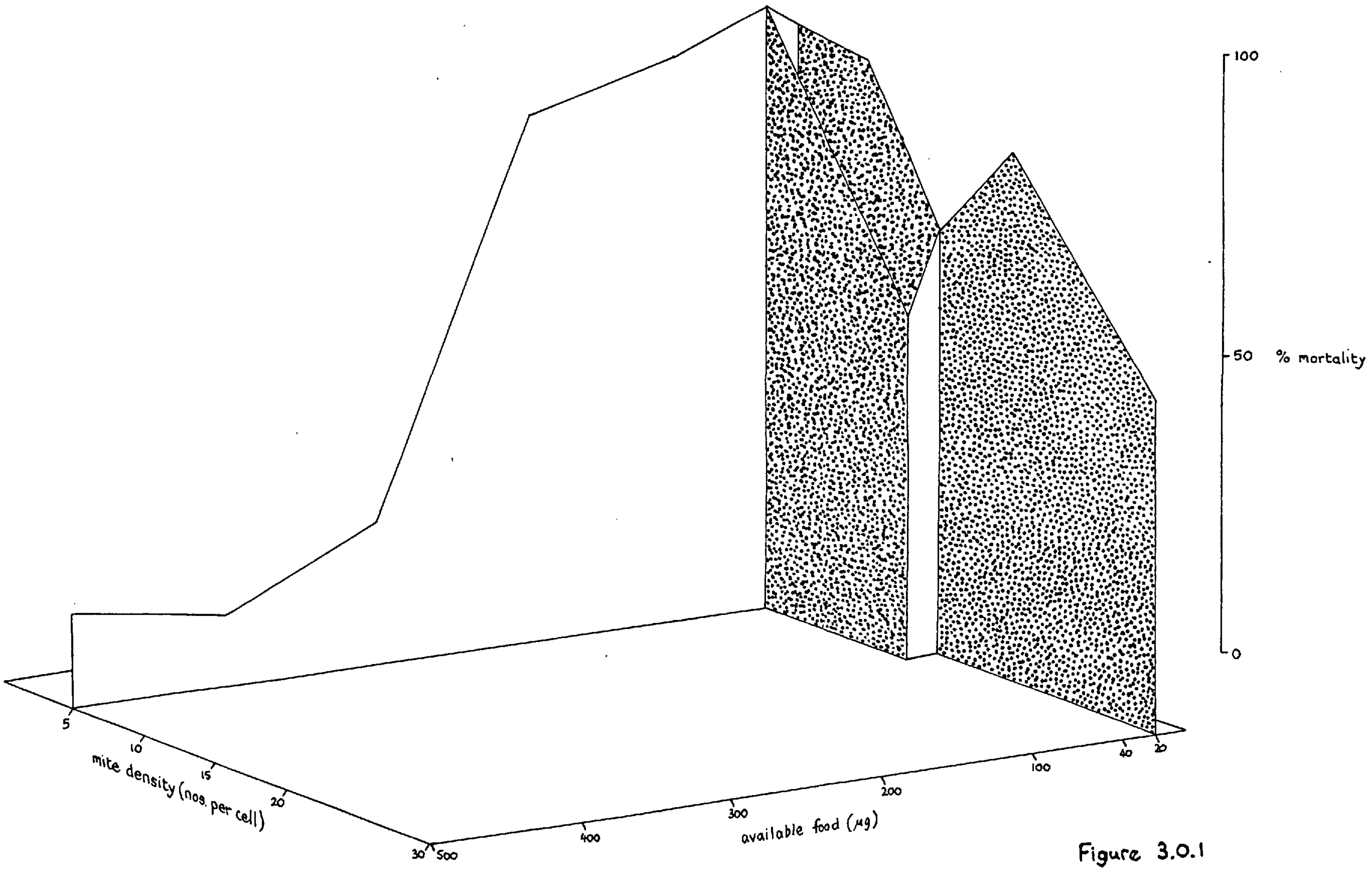

100
50
0
% mortality
5
10
15
20
30
mite density (nos. per cell)
500
400
300
200
100
40
20
available food (µg)

Figure 3.0.1

Figure 3.0.2 primary experimental set - patterns of mortality for mites of the species <u>Acarus siro</u> under various conditions of mite density and food availability :

a) adult mites

b) deutonymph mites

c) protonymph mites

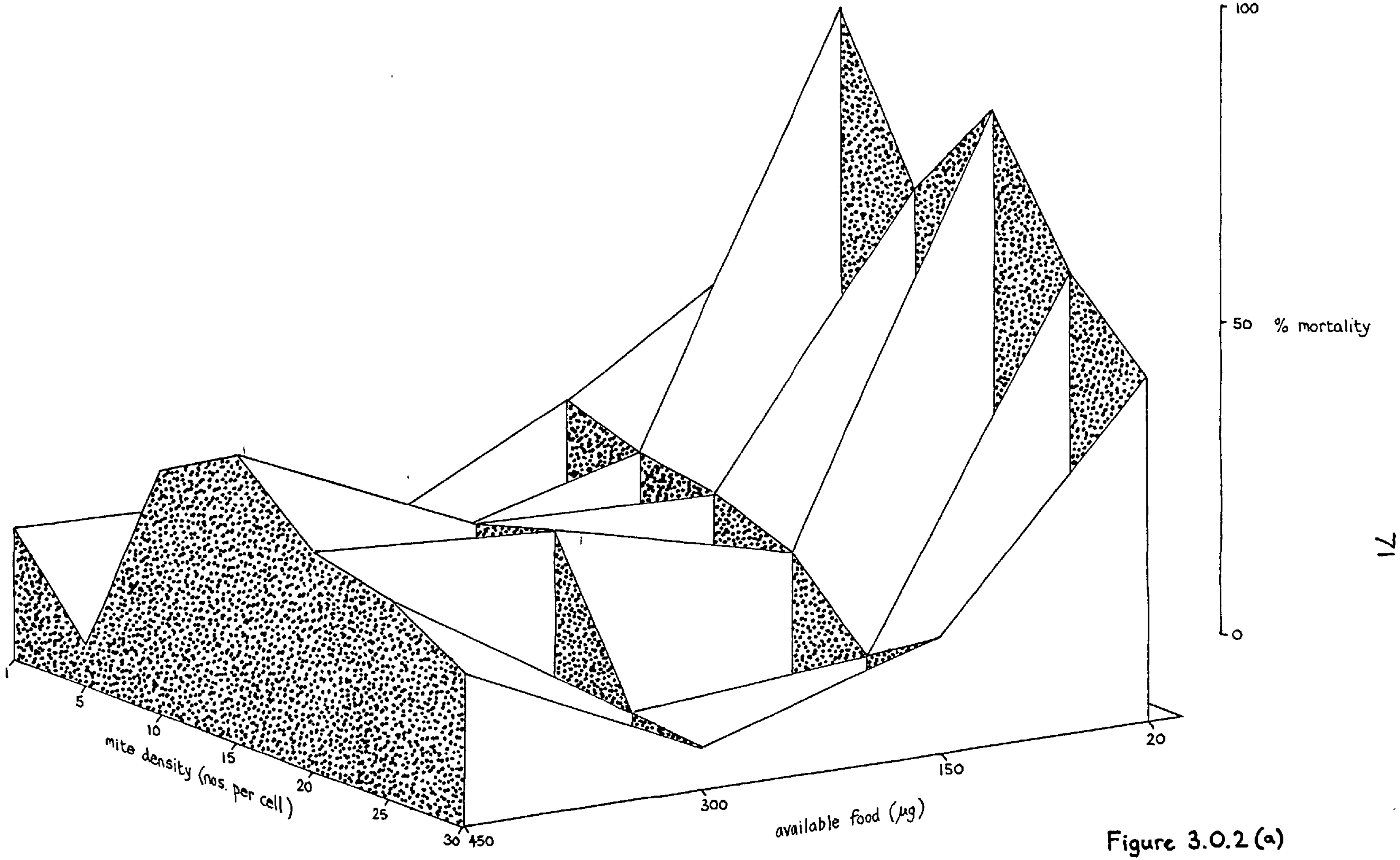

100
50
0
% mortality
1
5
10
15
20
25
30
mite density (nos. per cell)
450
300
150
20
available food (μg)

Figure 3.0.2 (a)

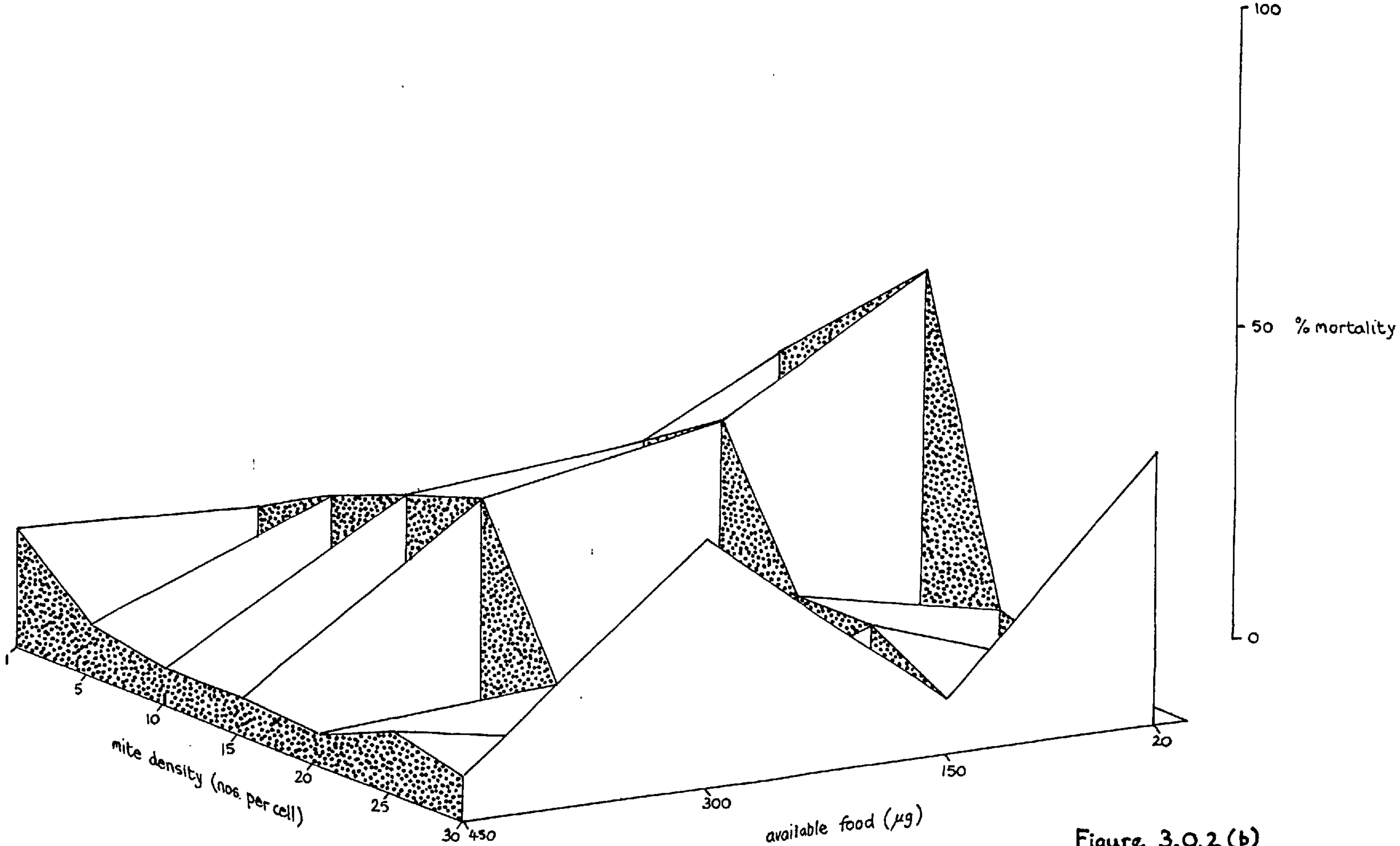

100
50
% mortality
0
1
5
10
15
20
25
30
mite density (nos. per cell)
450
300
150
20
available food (µg)

Figure 3.0.2 (b)

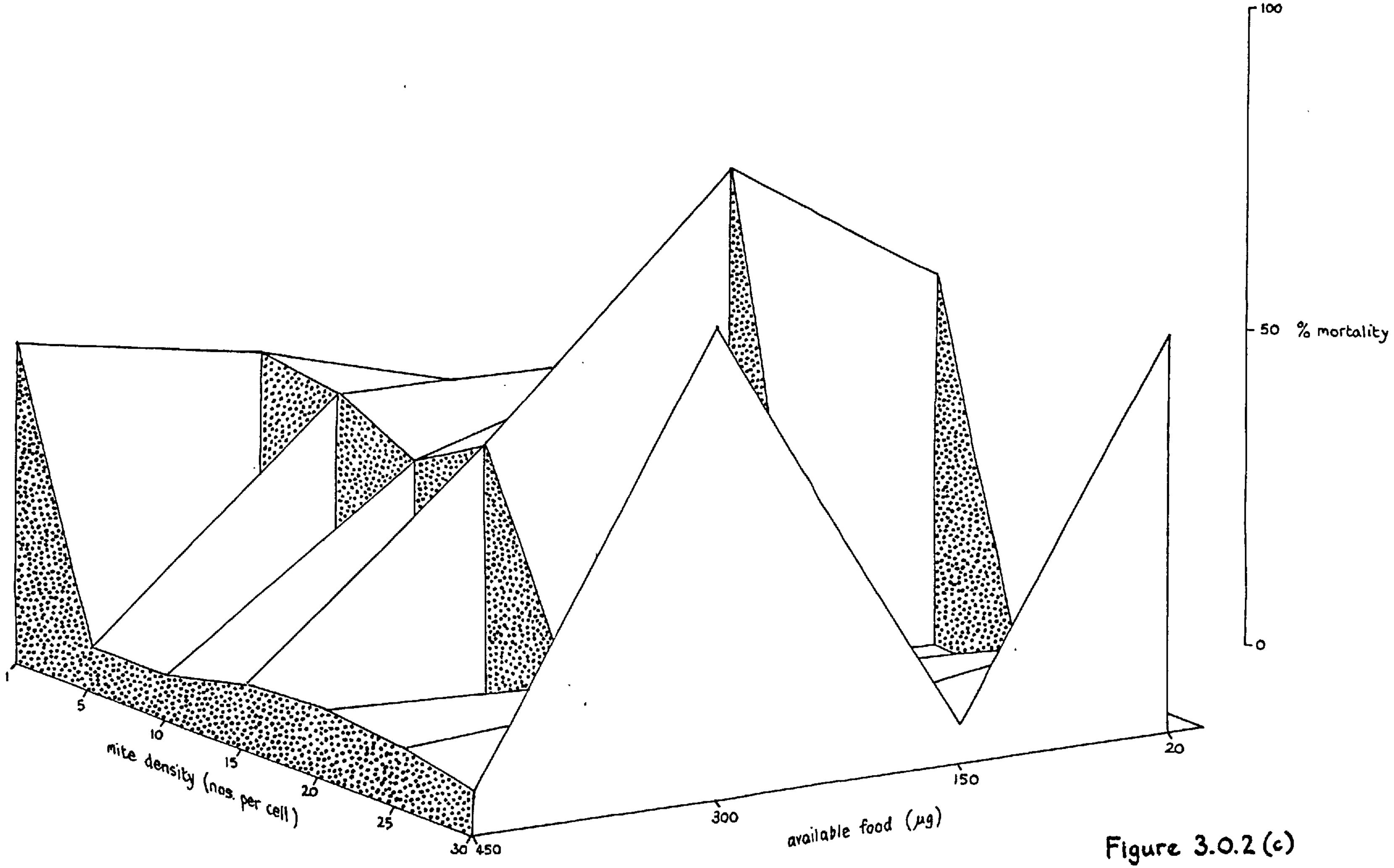

100
50 % mortality
0
1
5
10
15
20
25
30
mite density (nos. per cell)
450
300
150
20
available food (μg)

Figure 3.0.2 (c)

	Adult	Deutonymph	Protonymph
Volume	1	0.377	0.125
Surface area	1	0.522	0.25
Vol./surface	1	0.722	0.5

3.1 Preliminary Results

A priori consideration of the life history of Acarus siro leads to the conclusion that numerical stability, as a result of damping density dependence, would be most beneficial, in the evolutionary sense, if it were displayed in that phase of population history between successive infestations. Regardless of the nature of the habitat of the animal in this phase it is likely to be relatively poor in food compared with the infestation habitat and as a consequence the population will probably be in decline. Assuming that transmission of individuals from infestation to infestation has some probabalistic component, then it seems reasonable to expect that some mechanism might be present to prolong the life of such a residuum of the population - in effect producing a decelerating asymptotic decline to a constant population level. With this in mind these preliminary experiments have been set at food levels spanning the presumed daily requirement of the individual (see Section 1.3.3), at density levels much below those encountered in the infestation phase (estimated at 280,000 per gram of grain by Solomon, 1945), and with a qualitatively different physical distribution : the inside surfaces of the experimental cells rather than the bulk aggregation of mites characteristic of infestations (the experimental condition is probably close to the presumed transition phase location in the floor of silos and other food storage areas).

The results from this set of experiments are summarized in Table 3.1.1 and presented in detail in Appendix A. Transformed to k-value mortalities the results are displayed plotted against log-transformed values of density (Figure 3.1.1) and available food (Figure 3.1.2), and against log food per mite (Figure 3.1.3). K-value mortality decreases both with increasing food availability and with increasing mite density, in both cases the relationship being convex curvilinear over the range of conditions studied, though in the case of the food relationship there is a suggestion of a small constant residual mortality unaffected by any increase in food.

The apparent mid-point maximum of the mortality v. food/mite relationship (Figure 3.1.3) is an experimental artefact : low values of food/mite being obtained by using high mite densities - the effect of these high densities in reducing mortality masking any effect of reduced food. Mite mortality is probably best described by a relationship of the form :

$$\%\ \text{mortality} = (100 - x)(1 - 1/f(F))(1 - 1/g(M)) + x$$

where the functions f(F), of food availability, and g(M), of mite density, are monotonic curves (asymptotic to constant mortality) scaled such that f(F)max and g(M)max equal 1; and x is the unexplained residual mortality.

3.2 Primary Experimental Set

The conditions of experiment here were determined by the results of the preliminary set, a complete square design being adopted to cover the major change of mortality levels exposed in that preliminary analysis.

The results from this set of experiments are summarized in

Xa-b	$\bar{m}$	$\bar{m}/a$	σ^2	σ^2/a	n
A5-20	4.80	0.960	0.16	0.032	10
A10-20	9.50	0.950	0.25	0.025	10
A15-20	10.70	0.713	5.01	0.334	10
A20-20	17.60	0.880	6.04	0.302	10
A30-20	16.50	0.550	4.45	0.148	10
A5-40	5.00	1.000	0.00	0.000	10
A15-40	8.50	0.567	2.00	0.133	8
A5-100	4.70	0.940	0.21	0.042	10
A5-200	4.40	0.880	0.44	0.088	10
A5-300	1.20	0.240	0.96	0.192	10
A5-400	0.60	0.120	0.24	0.048	10
A5-500	0.80	0.160	1.16	0.232	10

Table 3.1.1 Summary of results for the preliminary experimental set :

X : Life stage (A adult, D deutonymph, P protonymph)

a : number of mites per experimental replicate

b : amount of food per experimental cell

$\bar{m}$: mean mortality

$\bar{m}/a$: percentage mean mortality

σ^2 : variance

σ^2/a : percentage variance

n : number of experimental replicates

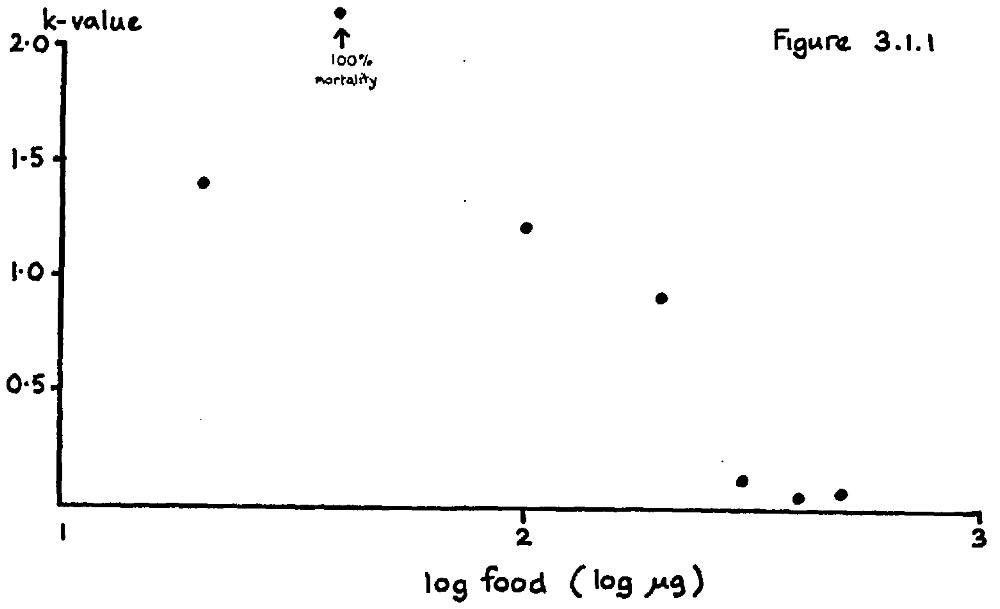


Figure 3.1.1

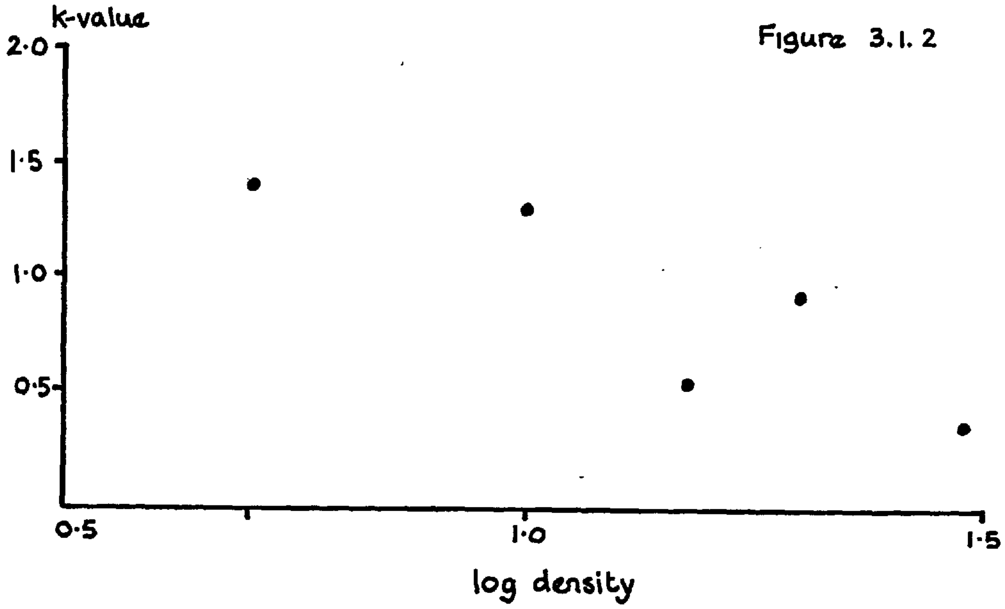


Figure 3.1.2

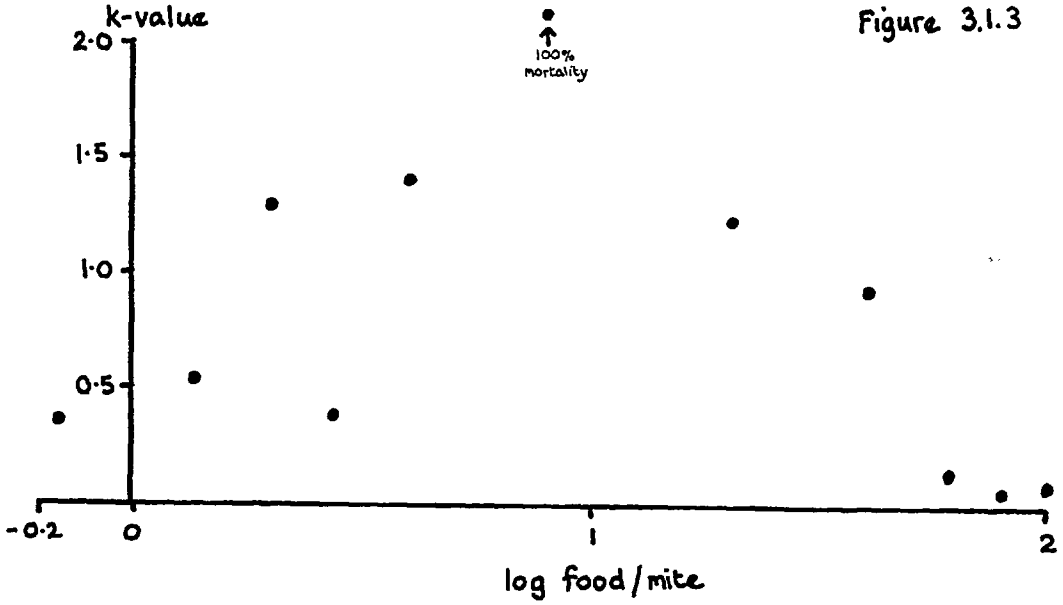


Figure 3.1.3

Tables 3.2.1 - 3.2.3, grouped according to mite life stage, and presented in detail in Appendix B. As in Section 3.1 k-value mortalities are displayed, plotted against log density (Figure 3.2.1 a-l), log food (Figure 3.2.2 a-u), log food/mite (Figure 3.2.3), log food/(mite vol/surface) (Figure 3.2.4), log food/mite-surface area (Figure 3.2.5) and log food/mite volume (Figure 3.2.6).

A least squares linear regression analysis (Harnett, 1970) was carried out on the log density and log food relationships and the results are summarized in Tables 3.2.4 and 3.2.5. As can be seen from the last columns (values of r^2 - the coefficients of determination), the fitted lines generally explain little of the variation displayed, but food levels do explain more than mite density levels in terms of linear relations.

3.3 Patterns of Distribution of Data

Given the experimental design used, the simplest hypothesis that can be realistically examined with respect to the results is that the probability of death is a function of experimental conditions, that this probability is constant and equal for each mite under a particular experimental condition, and that the death of one mite has no effect on the probability of death of any other mite with which it shares a cell. This is equivalent to stating that the distribution of mortality values can be described as a binomial distribution in which the probability of death is a function of mite density, mite age class and food availability. Accordingly, for each possible mortality category at each experimental condition, a theoretical frequency of observation can be calculated, according to the formula :

Xa-b	$\bar{m}$	$\bar{m}/a$	σ^2	σ^2/a	n
A5-20	2.70	0.540	4.71	0.942	20
A5-150	1.70	0.340	2.01	0.402	20
A5-300	0.75	0.150	0.79	0.158	20
A5-450	0.35	0.070	0.23	0.046	20
A10-20	9.50	0.950	0.25	0.025	10
A10-150	3.00	0.300	3.20	0.320	10
A10-300	2.00	0.200	2.20	0.220	10
A10-450	3.90	0.390	0.89	0.089	10
A15-20	10.70	0.713	5.01	0.334	10
A15-150	4.25	0.283	3.44	0.229	8
A15-300	4.38	0.293	13.98	0.932	8
A15-450	6.88	0.458	2.61	0.174	8
A20-20	17.60	0.880	6.04	0.302	10
A20-150	4.60	0.230	2.24	0.112	5
A20-300	6.57	0.329	4.24	0.212	7
A20-450	7.00	0.350	3.43	0.172	7
A25-20	16.75	0.670	1.19	0.048	4
A25-150	2.75	0.110	3.69	0.148	4
A25-300	2.00	0.080	0.00	0.000	4
A25-450	8.00	0.320	2.00	0.065	4
A30-20	16.50	0.549	4.45	0.148	10
A30-150	5.60	0.188	4.24	0.141	5
A30-300	2.00	0.065	1.00	0.033	4
A30-450	7.00	0.235	5.50	0.183	4

Table 3.2.1 Summary of results of the primary experimental set for adult mites (expressed as in Table 3.1.1)

Xa-b	$\bar{m}$	$\bar{m}/a$	σ^2	σ^2/a	n
D5-20	1.80	0.360	2.26	0.452	20
D5-150	1.05	0.210	1.75	0.350	20
D5-300	1.15	0.230	1.73	0.346	20
D5-450	0.40	0.080	0.34	0.068	20
D10-20	1.13	0.113	1.11	0.111	8
D10-150	3.10	0.310	1.49	0.149	10
D10-300	2.80	0.280	3.56	0.356	10
D10-450	0.56	0.056	0.91	0.091	9
D15-20	8.67	0.579	2.00	0.133	9
D15-150	5.88	0.391	10.36	0.691	8
D15-300	4.75	0.318	8.94	0.596	8
D15-450	0.88	0.059	0.61	0.041	8
D20-20	1.80	0.090	1.36	0.068	5
D20-150	3.20	0.160	2.16	0.108	5
D20-300	1.40	0.070	1.04	0.052	5
D20-450	1.00	0.050	0.40	0.020	5
D25-20	1.25	0.050	1.19	0.048	4
D25-150	4.00	0.160	1.50	0.060	4
D25-300	1.00	0.040	0.50	0.020	4
D25-450	2.50	0.100	0.75	0.030	4
D30-20	13.00	0.432	2.80	0.093	5
D30-150	2.75	0.093	3.19	0.106	4
D30-300	11.75	0.390	34.19	1.140	4
D30-450	2.25	0.075	0.69	0.023	4

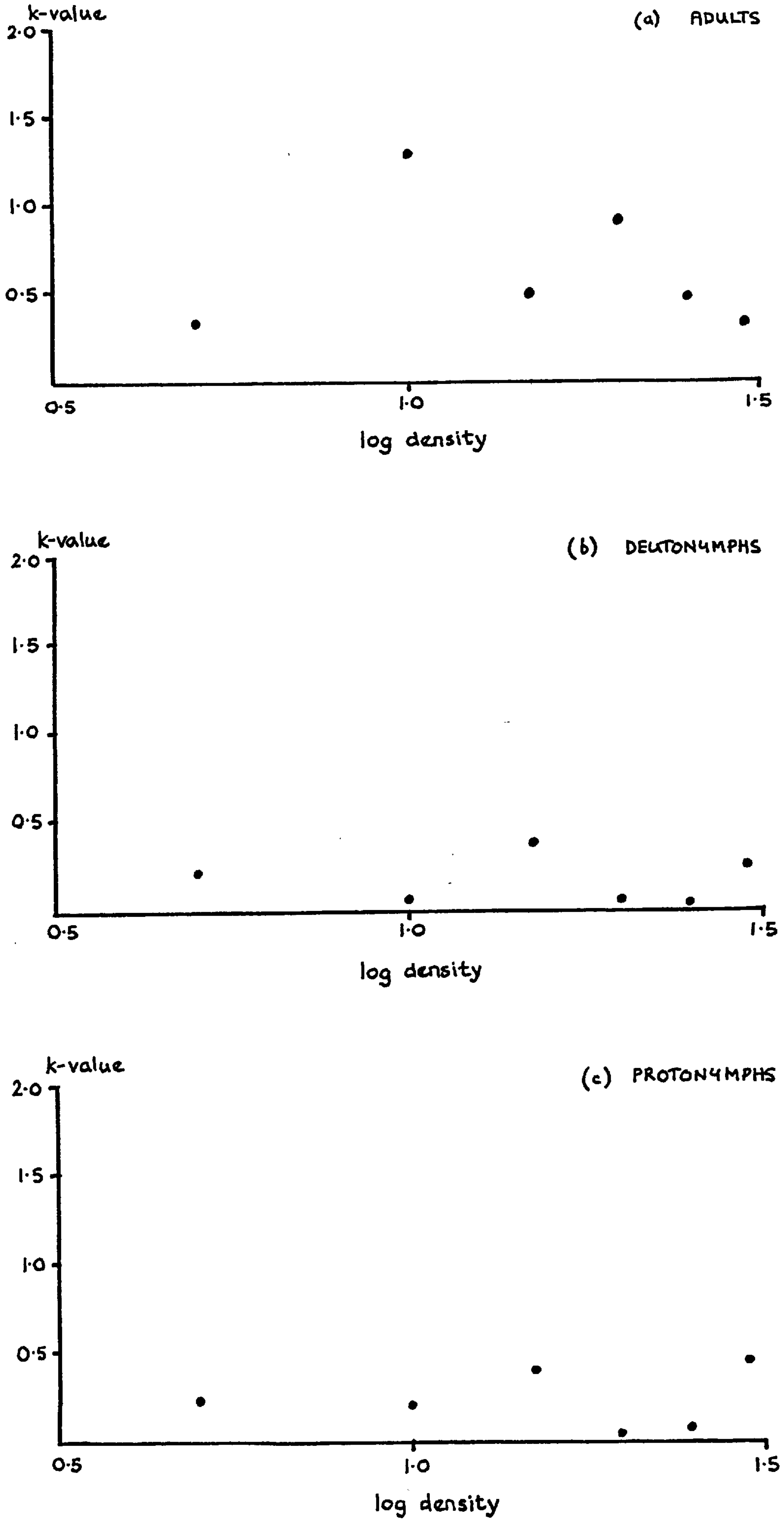
Table 3.2.2 Summary of results of primary experimental set for deutonymph mites (expressed as in Table 3.1.1)

Xa-b	$\bar{m}$	$\bar{m}/a$	σ^2	σ^2/a	n
P5-20	1.85	0.385	2.43	0.486	20
P5-150	2.00	0.400	3.10	0.620	20
P5-300	2.05	0.410	2.55	0.510	20
P5-450	0.35	0.070	0.63	0.126	20
P10-20	3.40	0.340	2.04	0.204	10
P10-150	4.70	0.470	2.41	0.241	10
P10-300	3.50	0.350	7.45	0.745	10
P10-450	0.70	0.070	0.61	0.061	10
P15-20	8.70	0.579	8.21	0.547	10
P15-150	11.90	0.794	2.89	0.193	10
P15-300	6.25	0.418	14.94	0.996	8
P15-450	1.50	0.103	1.50	0.100	8
P20-20	0.80	0.040	0.56	0.028	5
P20-150	1.20	0.060	0.56	0.028	5
P20-300	1.80	0.090	2.16	0.108	5
P20-450	2.20	0.110	0.16	0.008	5
P25-20	2.75	0.110	2.19	0.088	4
P25-150	1.50	0.060	4.25	0.170	4
P25-300	3.00	0.120	6.50	0.260	4
P25-450	2.50	0.100	0.25	0.010	4
P30-20	18.50	0.617	25.05	0.835	10
P30-150	1.80	0.060	2.16	0.072	5
P30-300	22.25	0.743	4.69	0.156	4
P30-450	2.00	0.068	0.50	0.017	4

Table 3.2.3 Summary of results of the primary experimental set for protonymph mites (expressed as in Table 3.1.1)

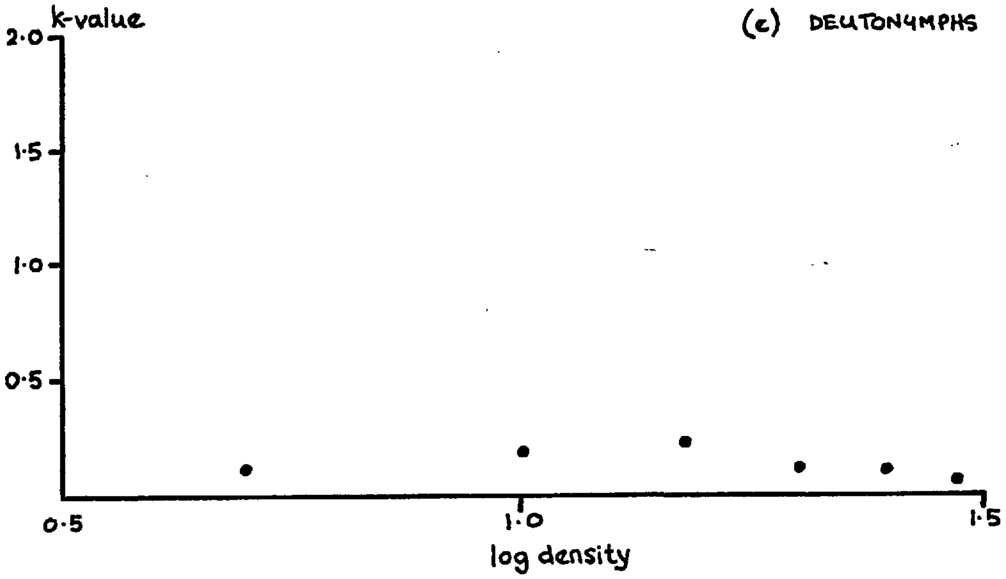
20µg food per cell

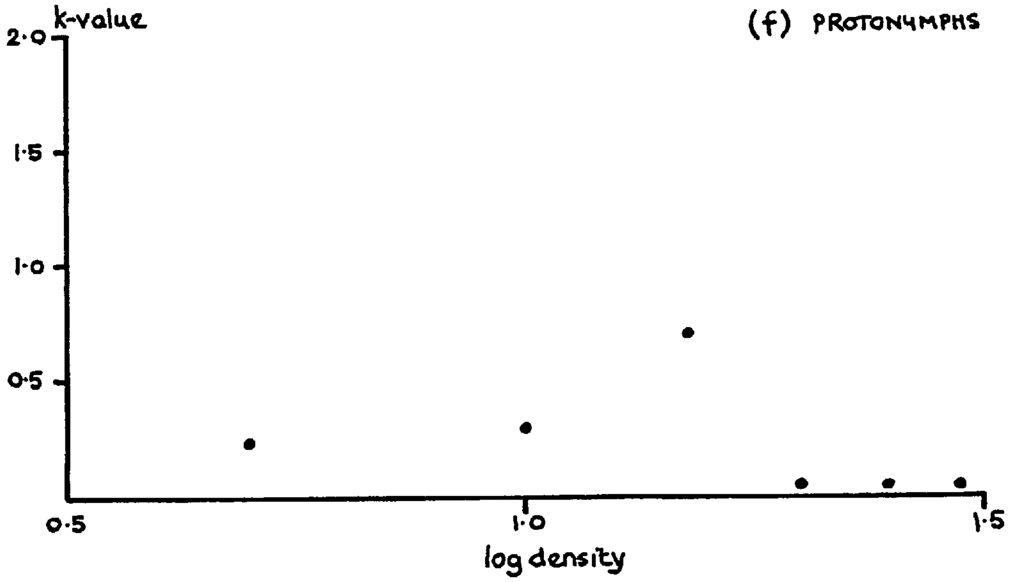
Figure 3.2.1



150µg food per cell

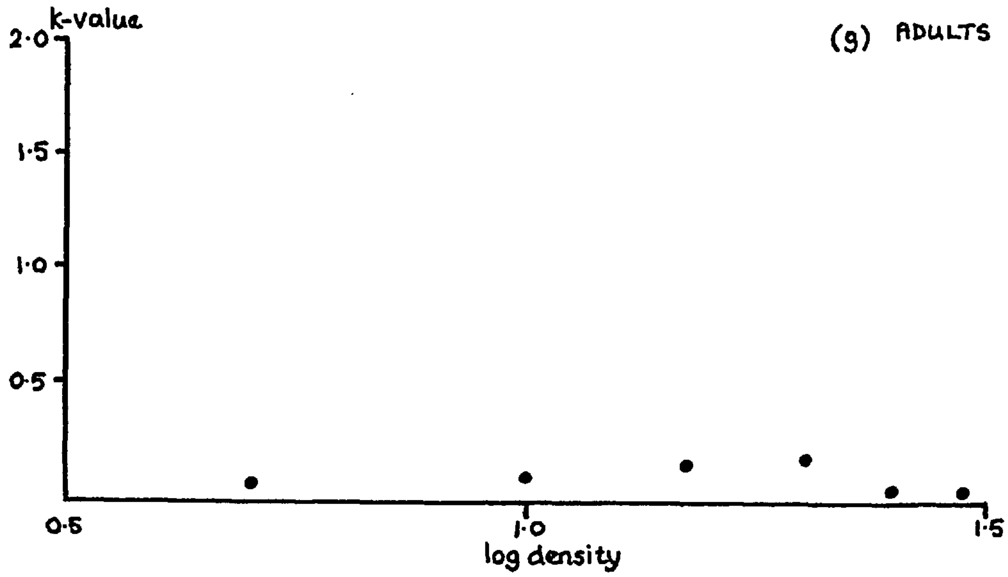
Figure 3.2.1 (contd.)

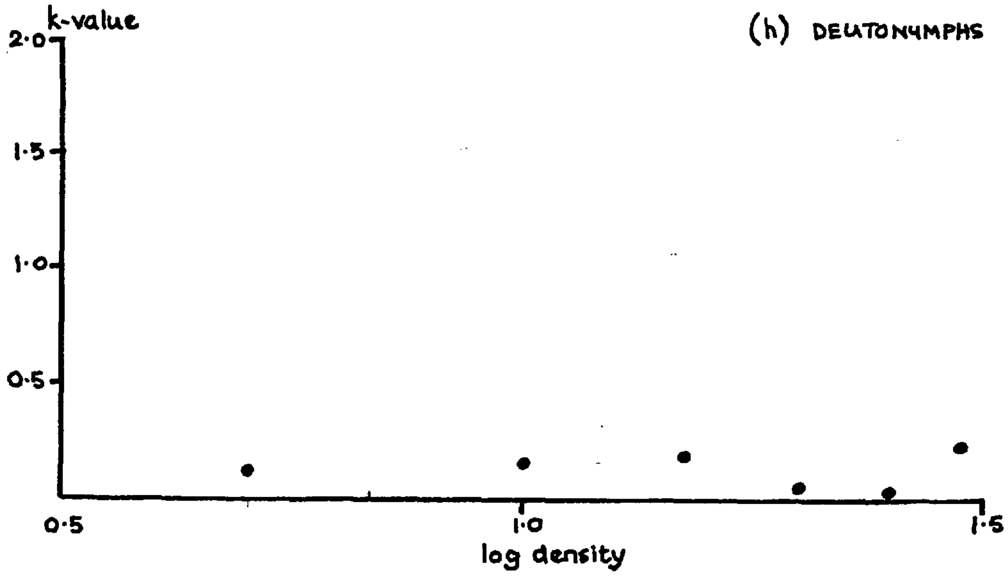


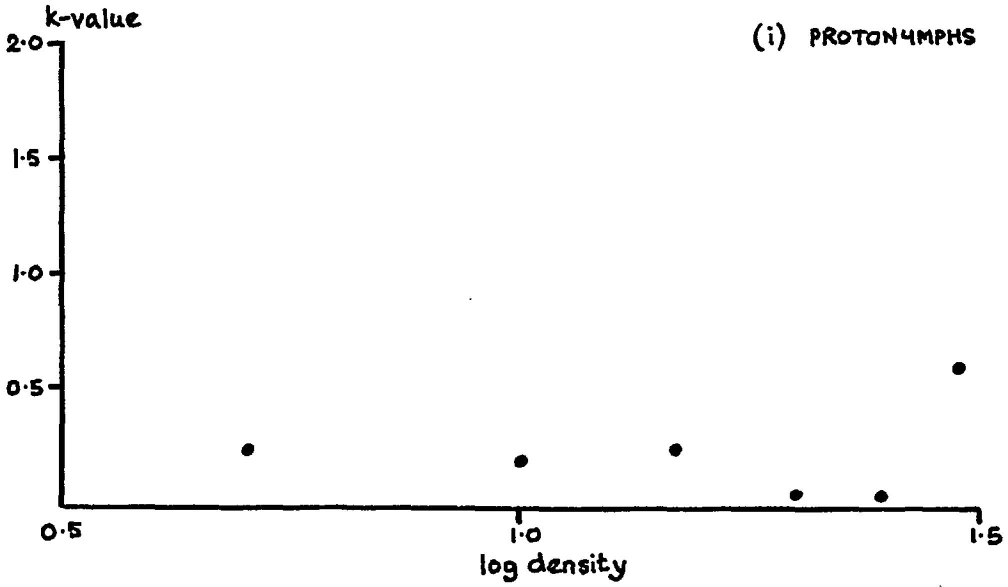


300μg food per cell

Figure 3.2.1 (contd.)

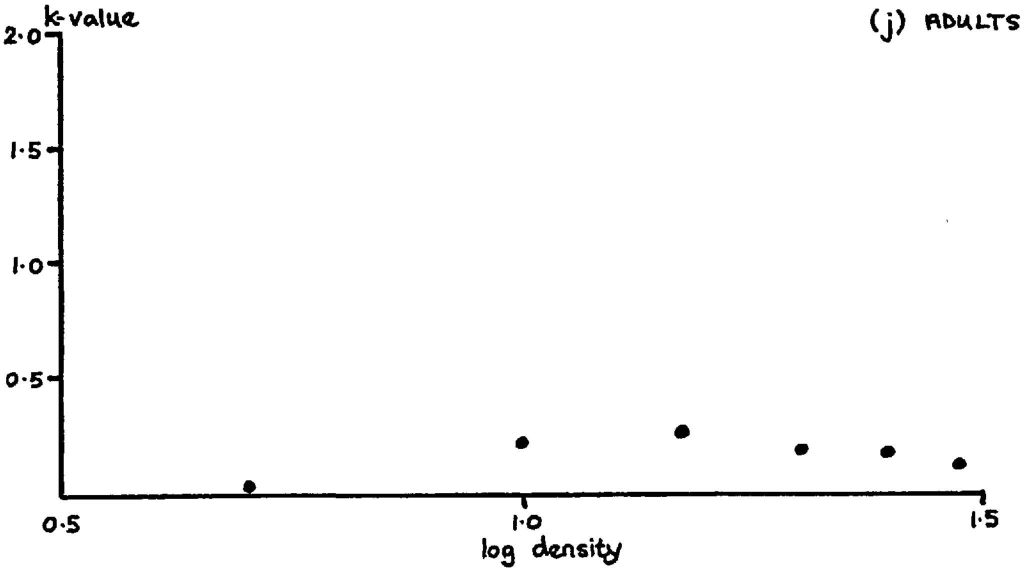


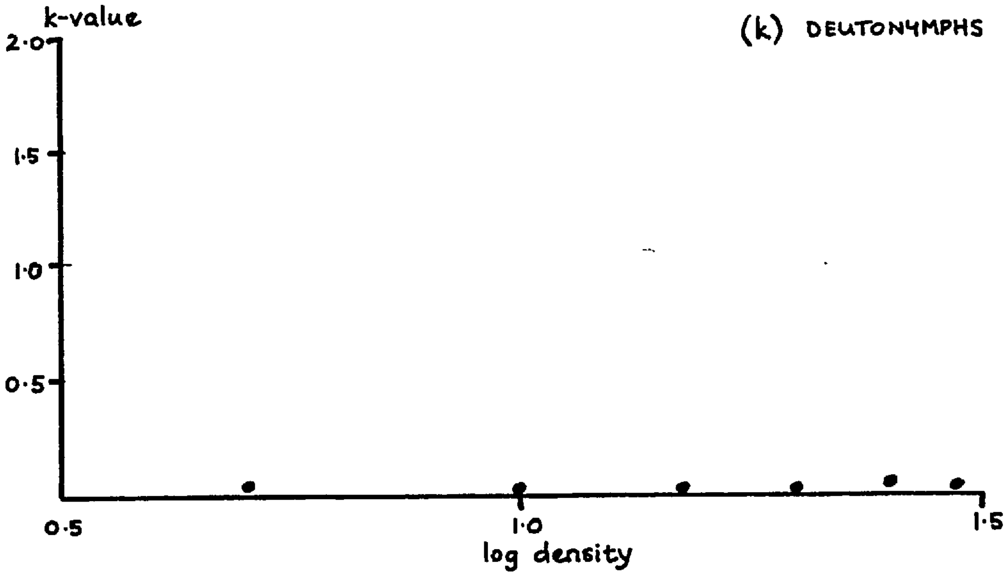


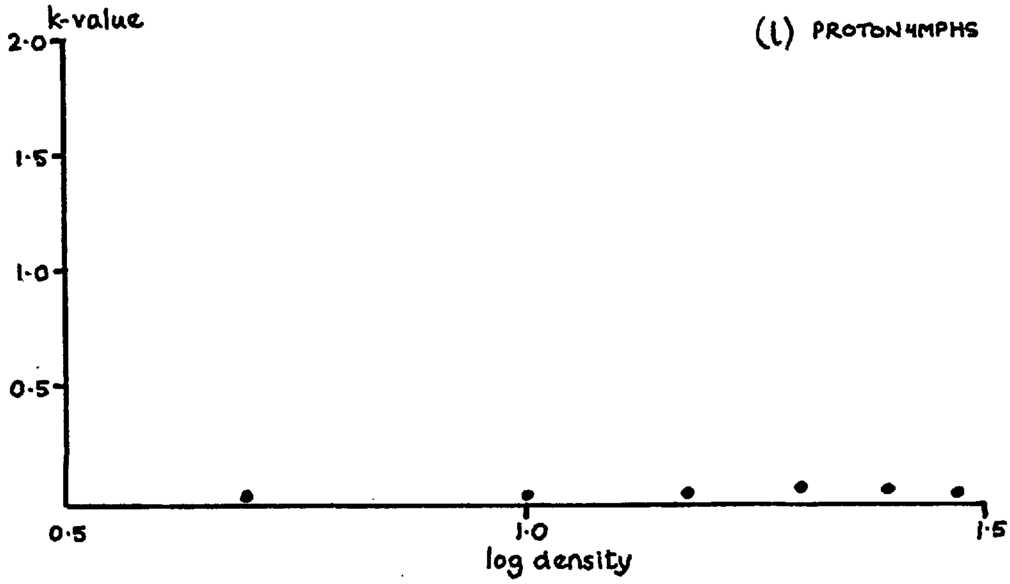


450µg food per cell

Figure 3.2.1 (contd.)

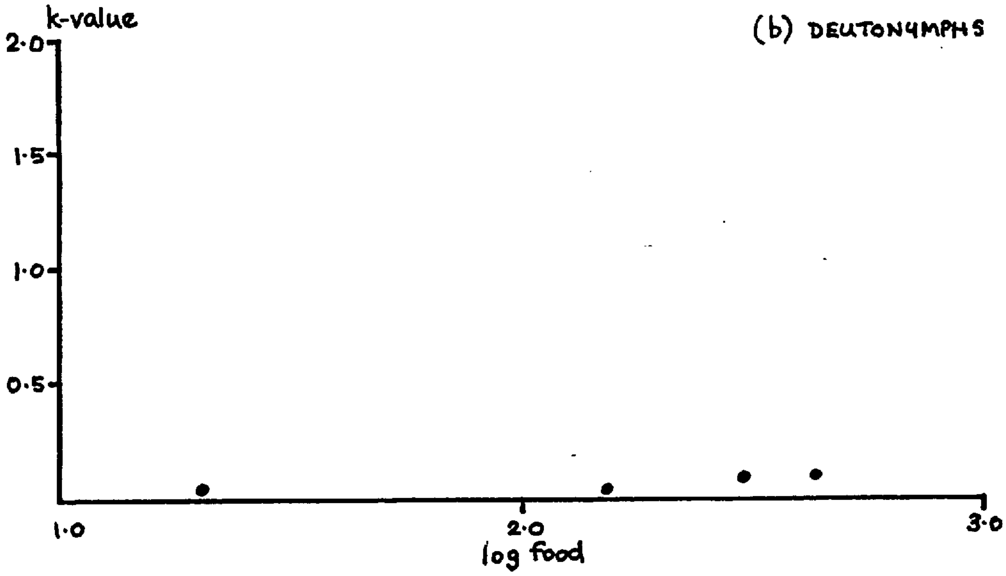


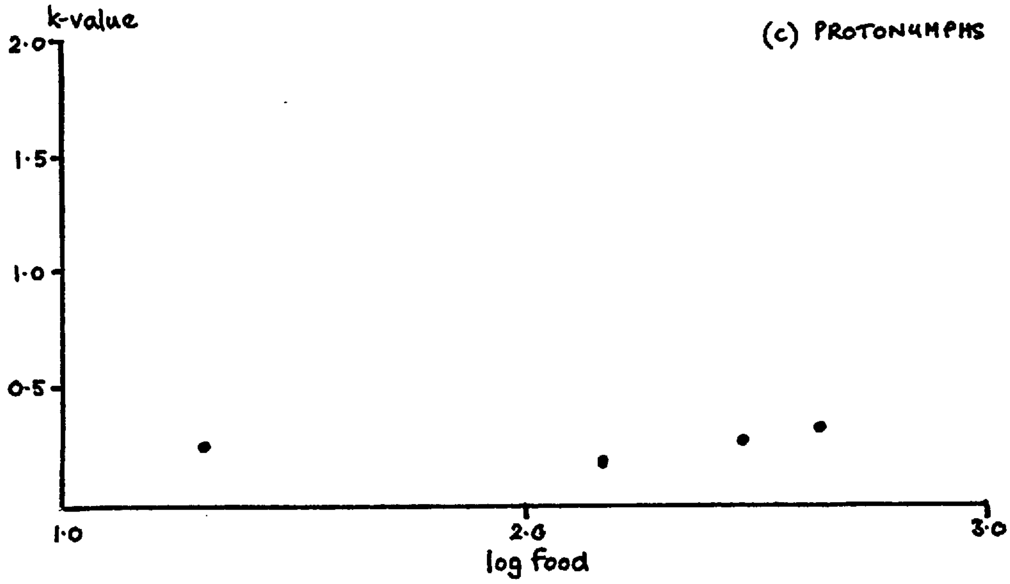




1 mite per cell

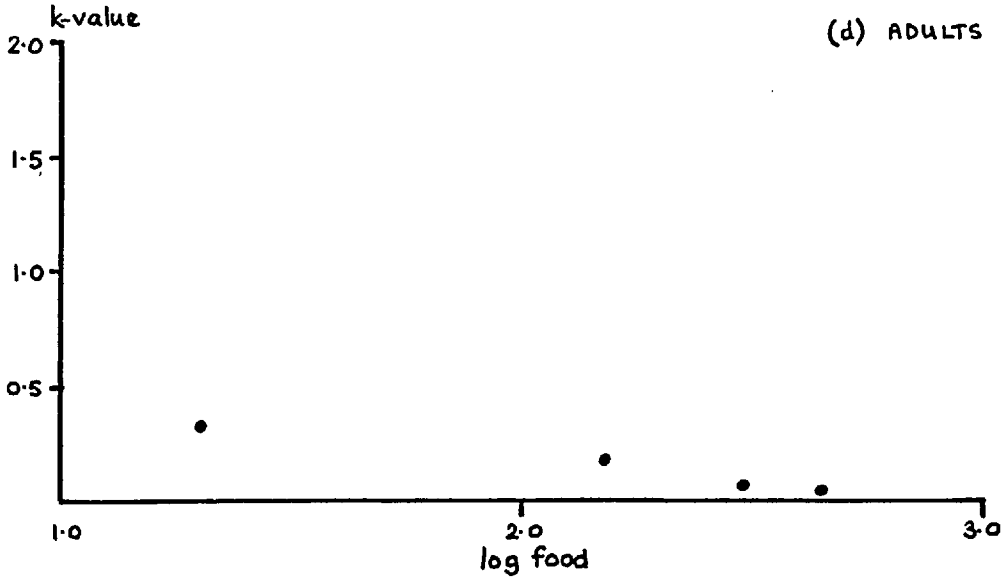
Figure 3.2.2

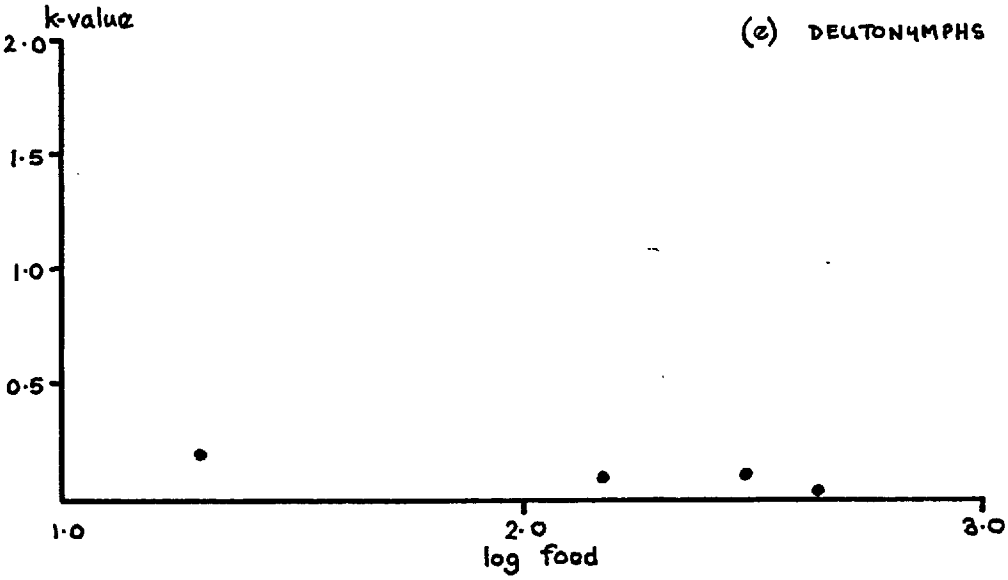


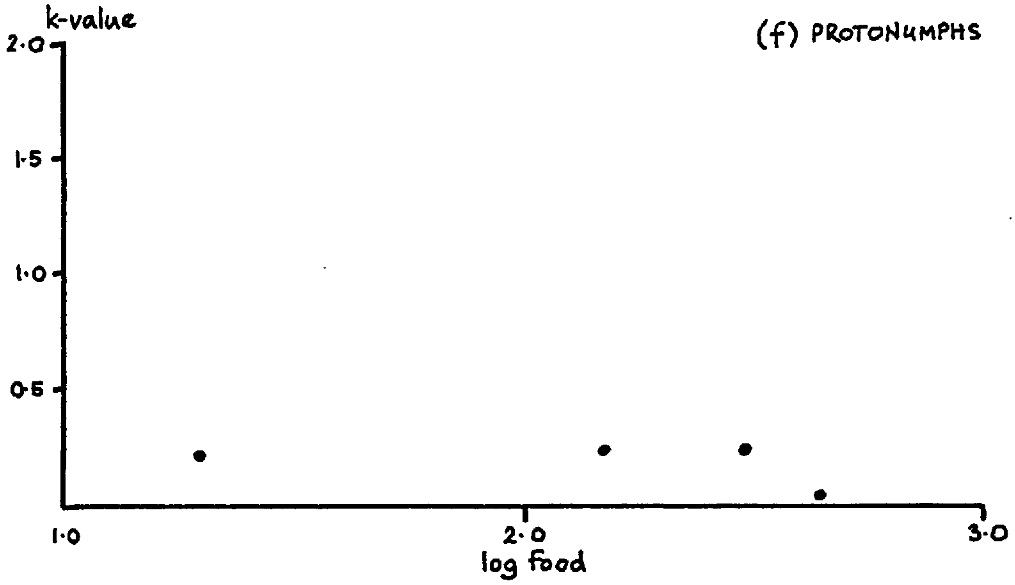


5 mites per cell

Figure 3.2.2 (contd.)

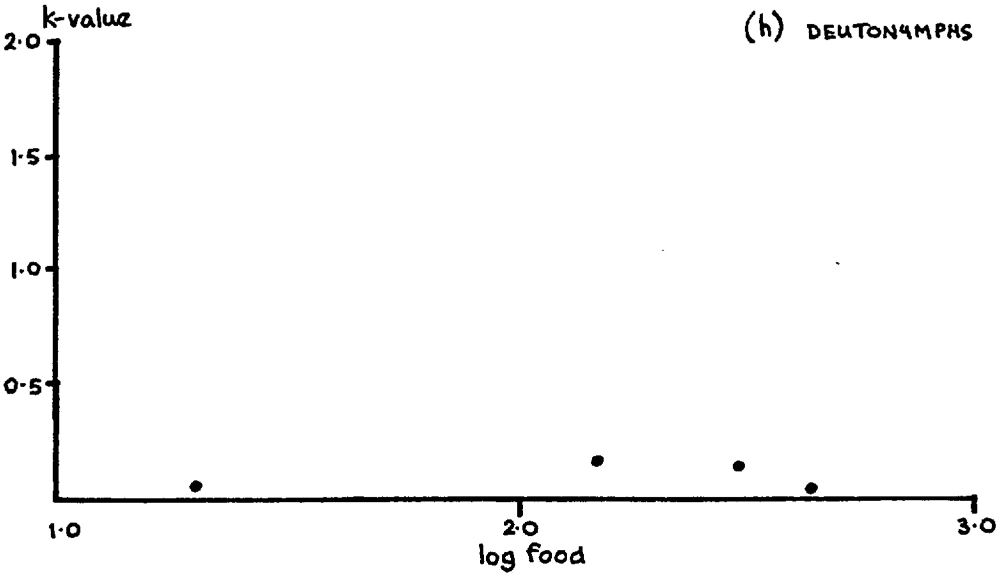


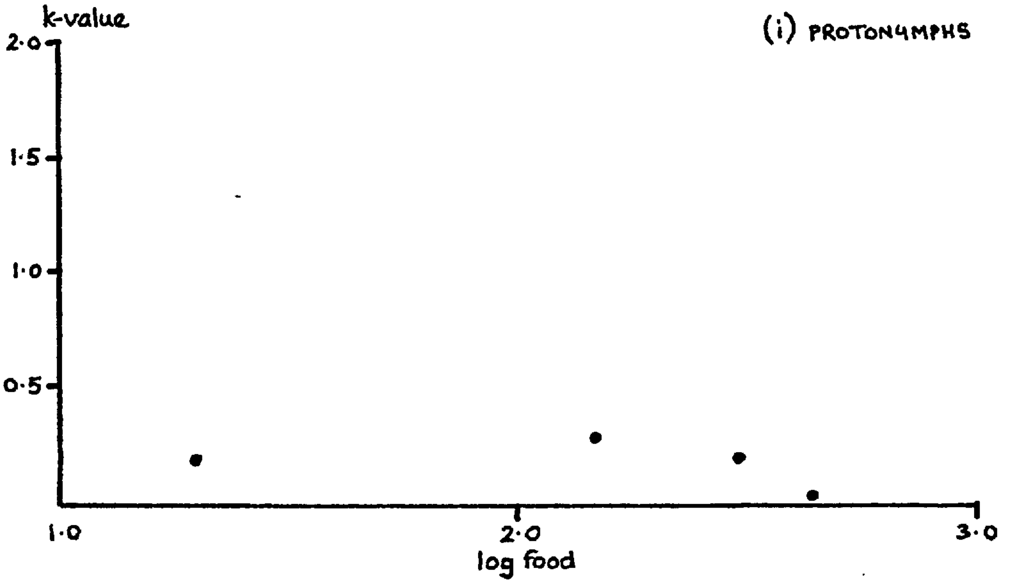




10 mites per cell

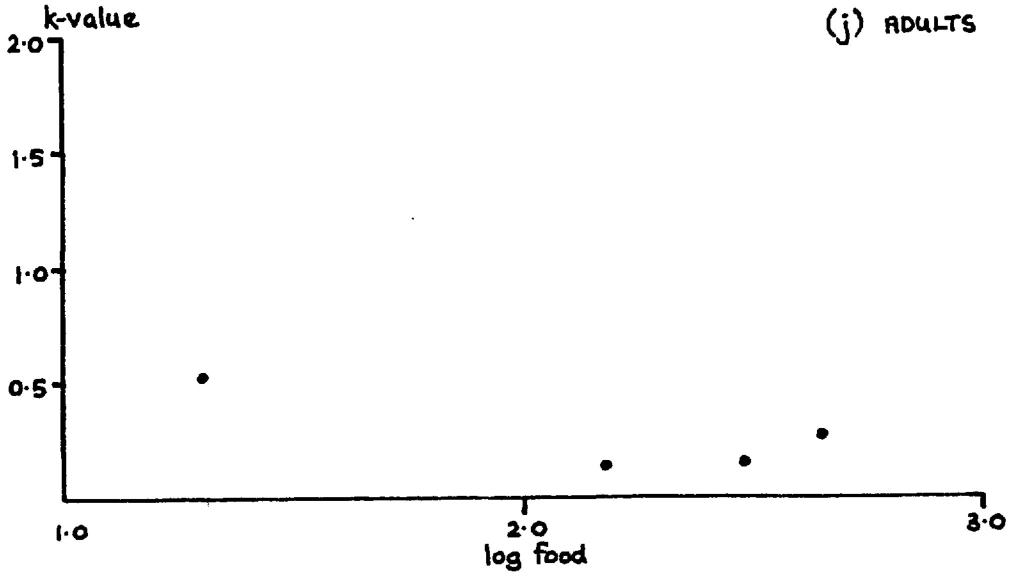
Figure 3.2.2 (contd.)

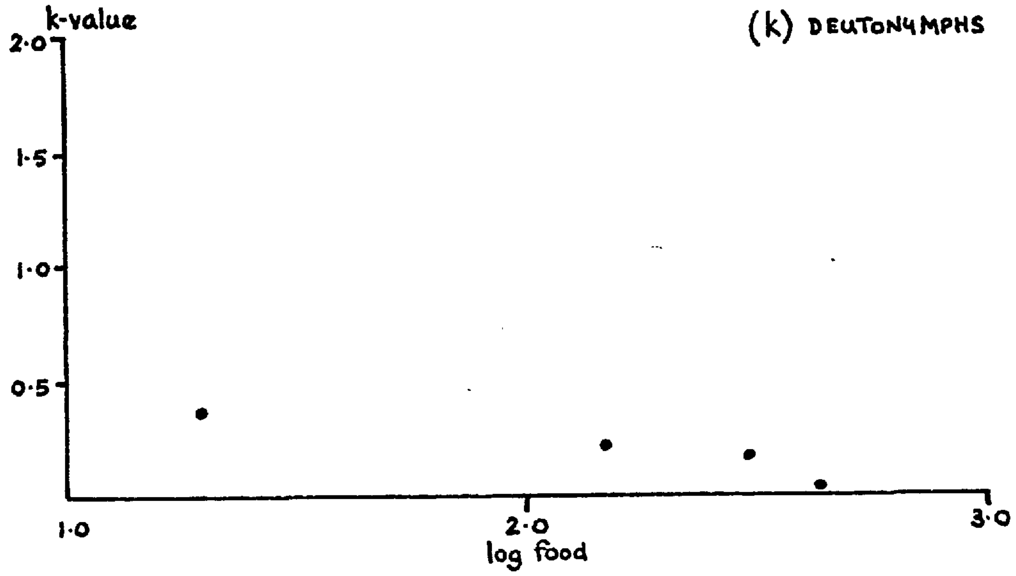


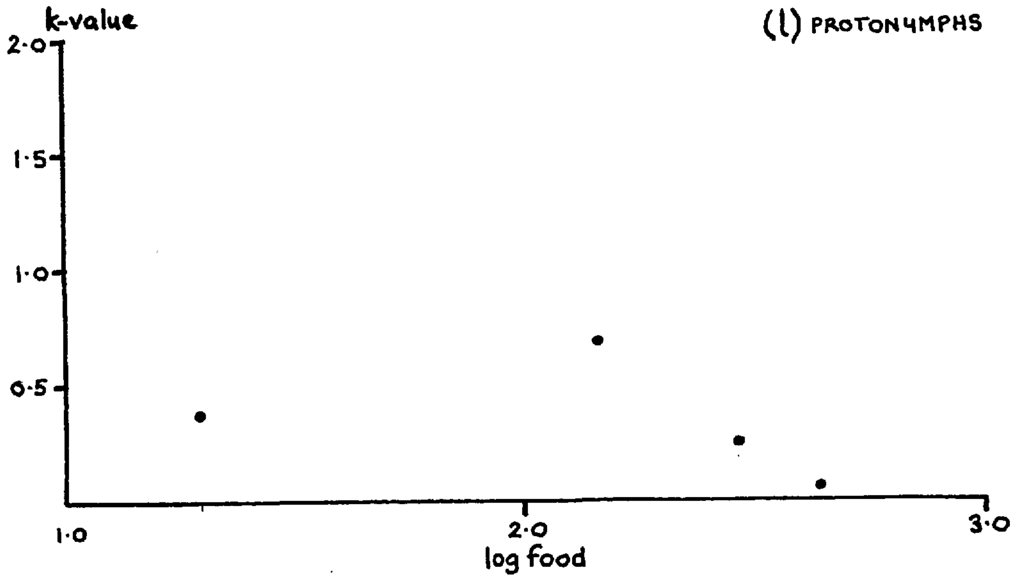


15 mites per cell

Figure 3.2.2 (contd.)

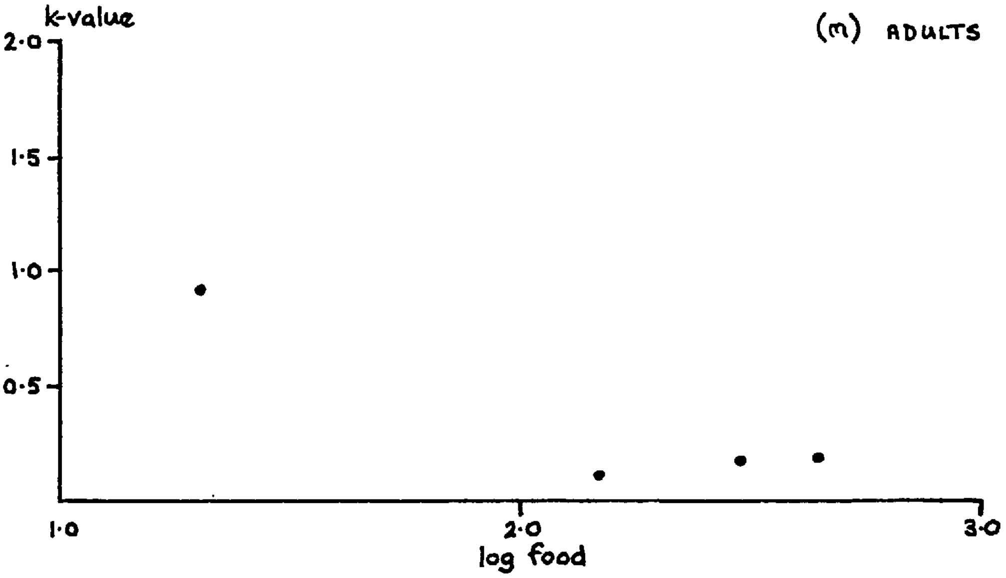


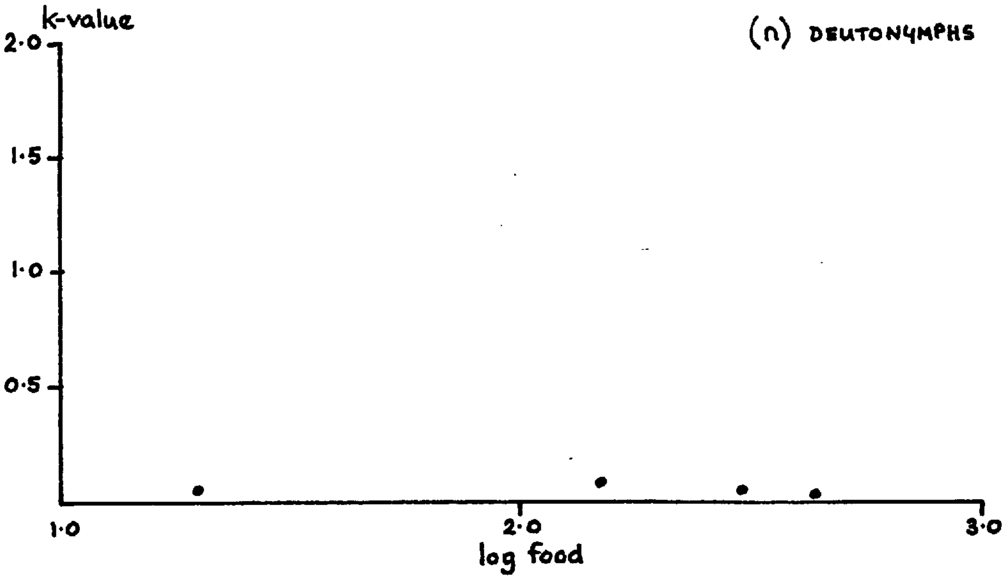




20 mites per cell

Figure 3.2.2 (contd.)

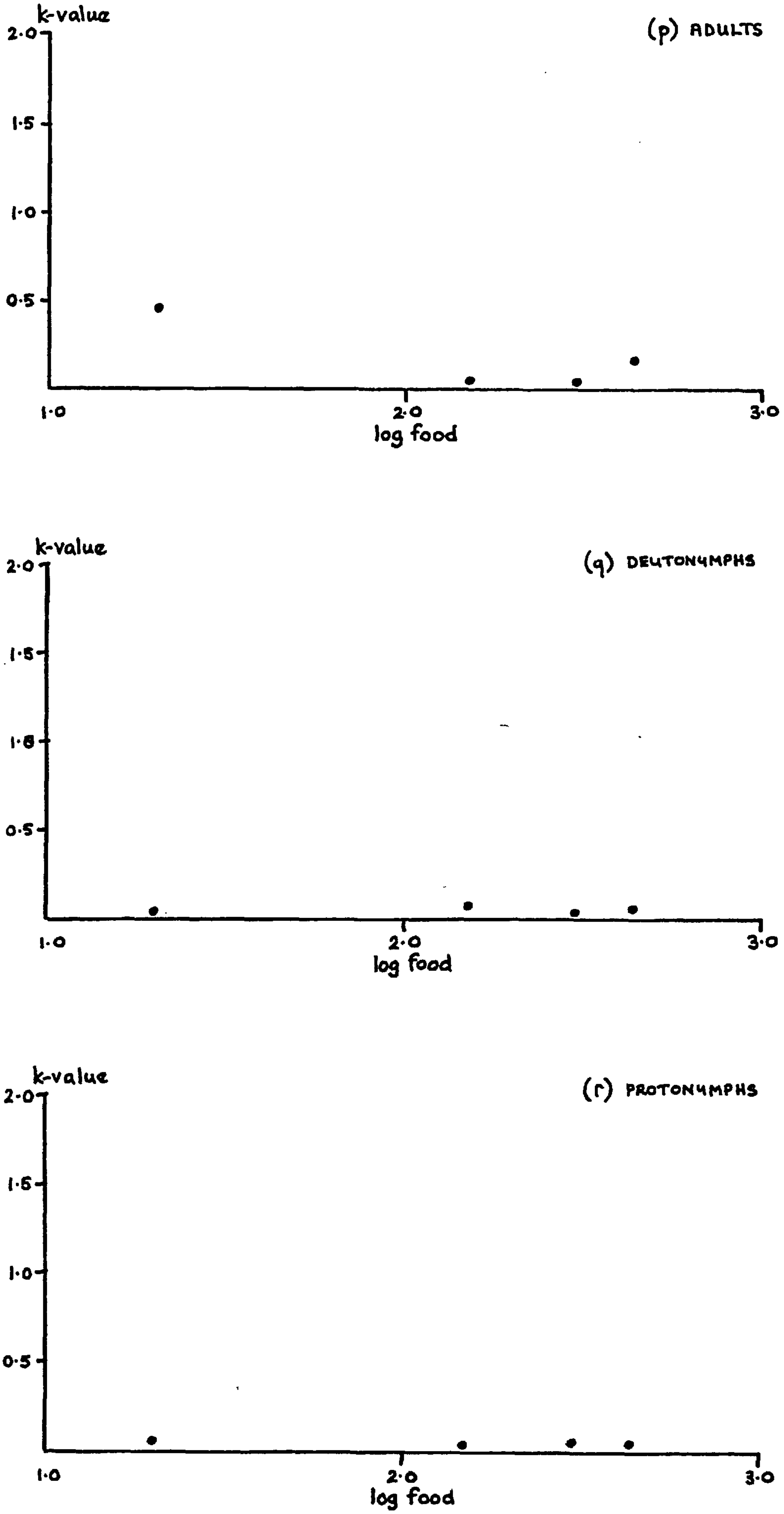

(m) ADULTS


(n) DEUTONYMPHS


(o) PROTONYMPHS

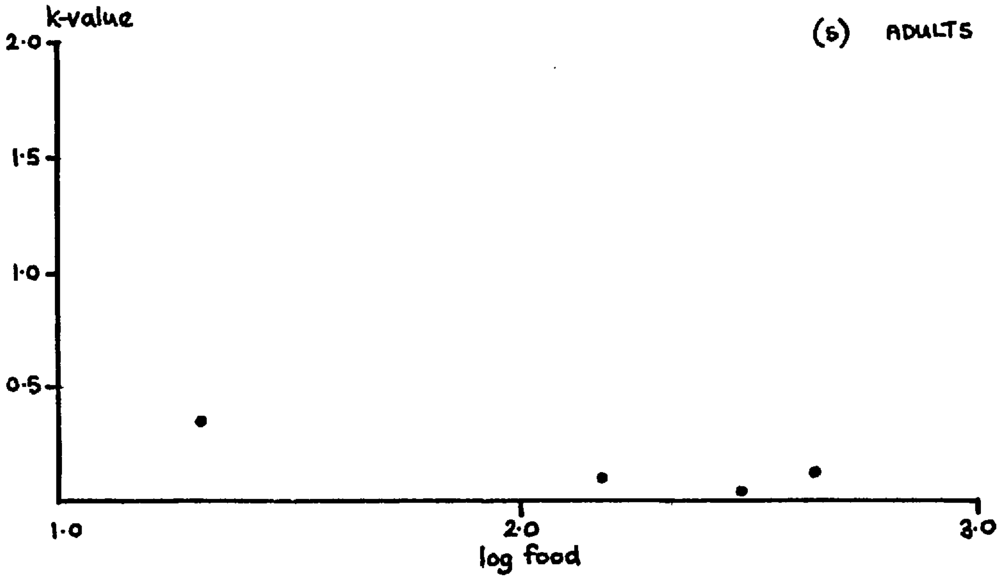
25 mites per cell

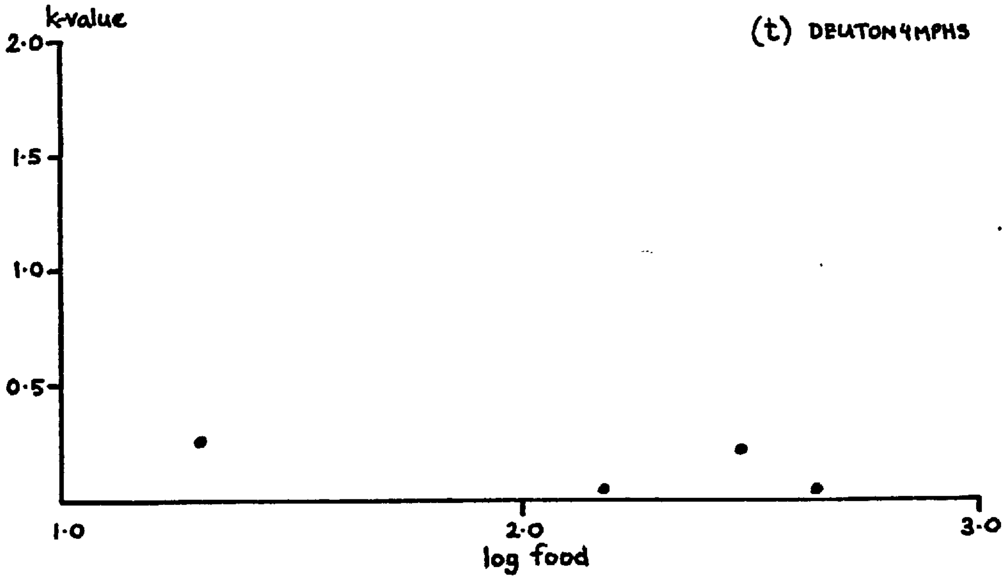
Figure 3.2.2 (contd.)

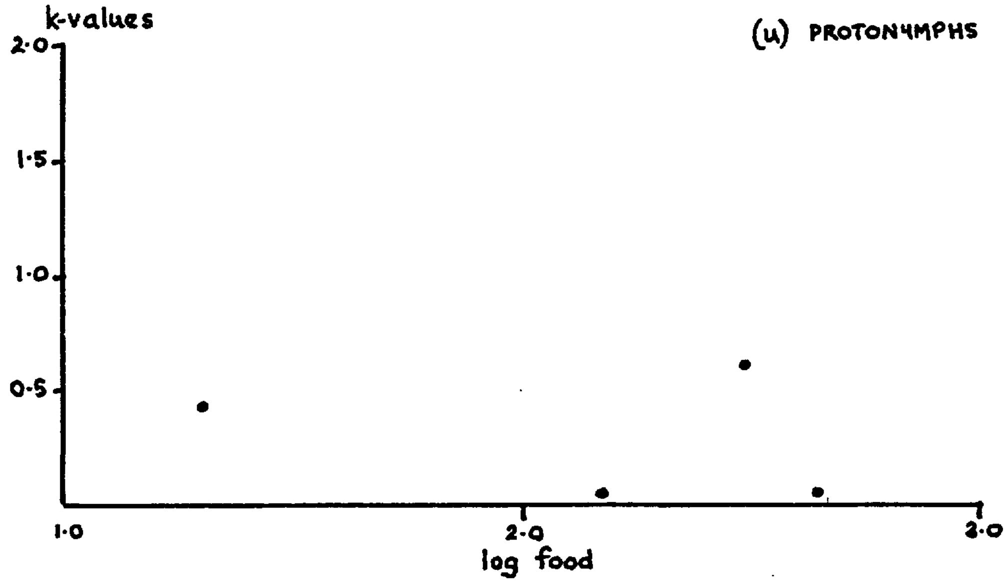


30 mites per cell

Figure 3.2.2 (contd.)


(s) ADULTS


(t) DEUTONYMPHS


(u) PROTONYMPHS

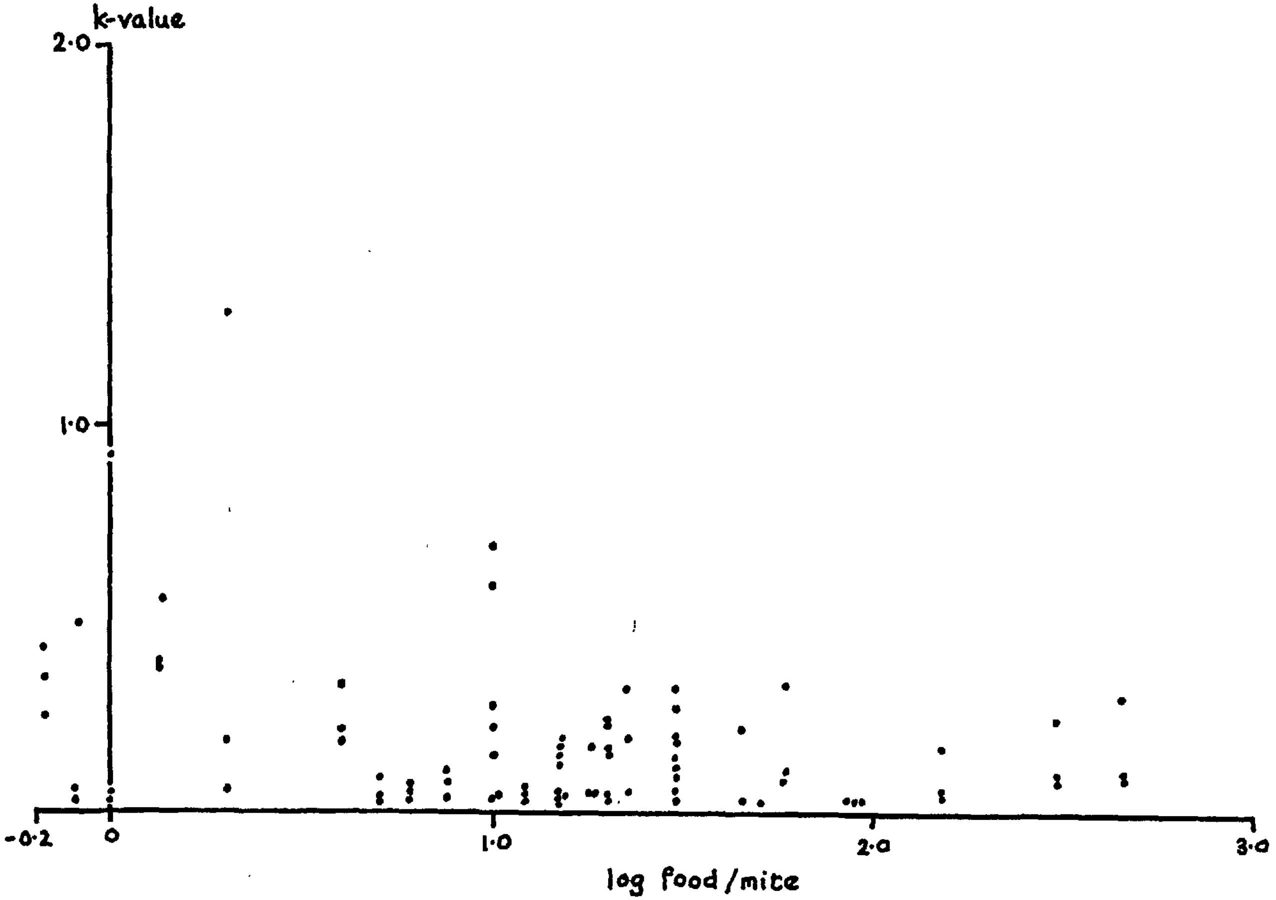


Figure 3.2.3

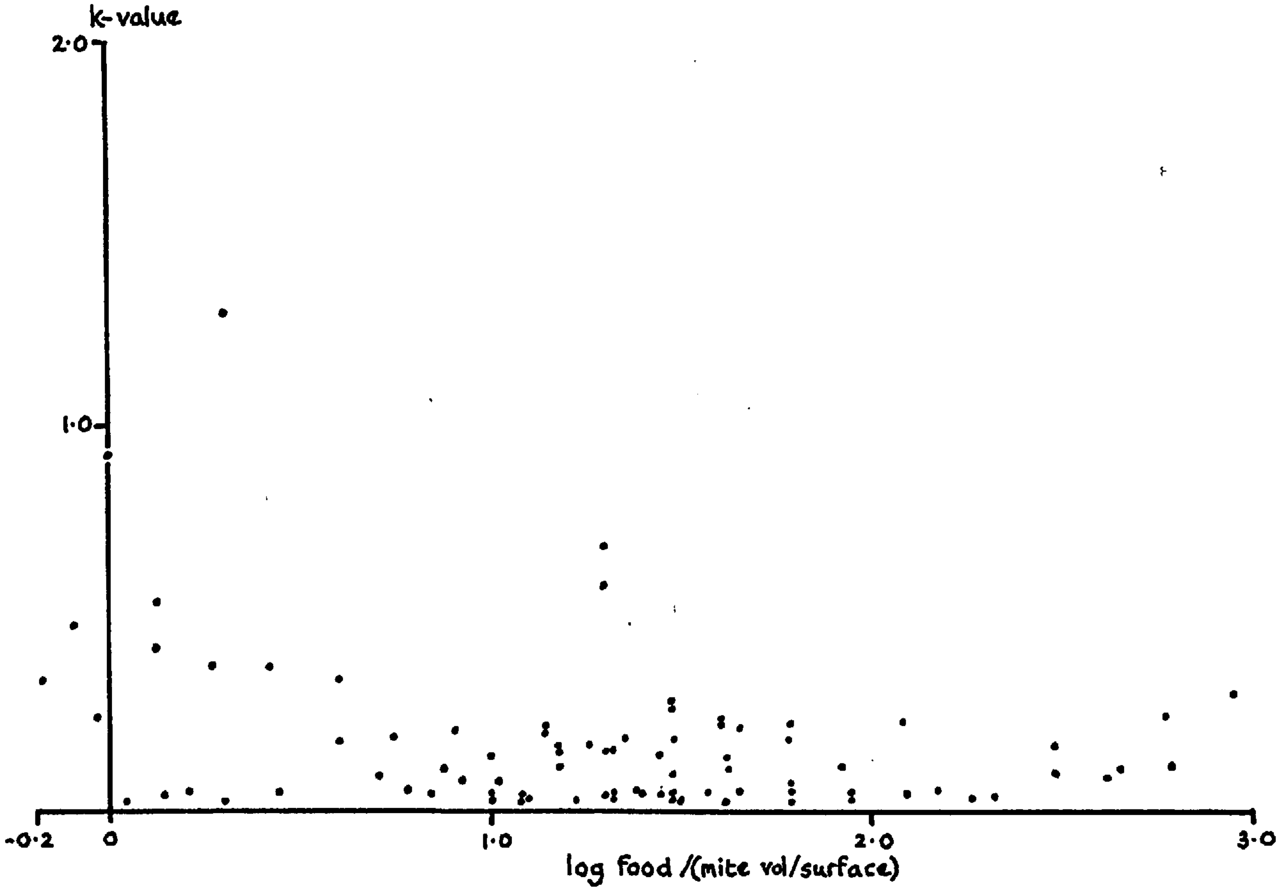


Figure 3.2.4

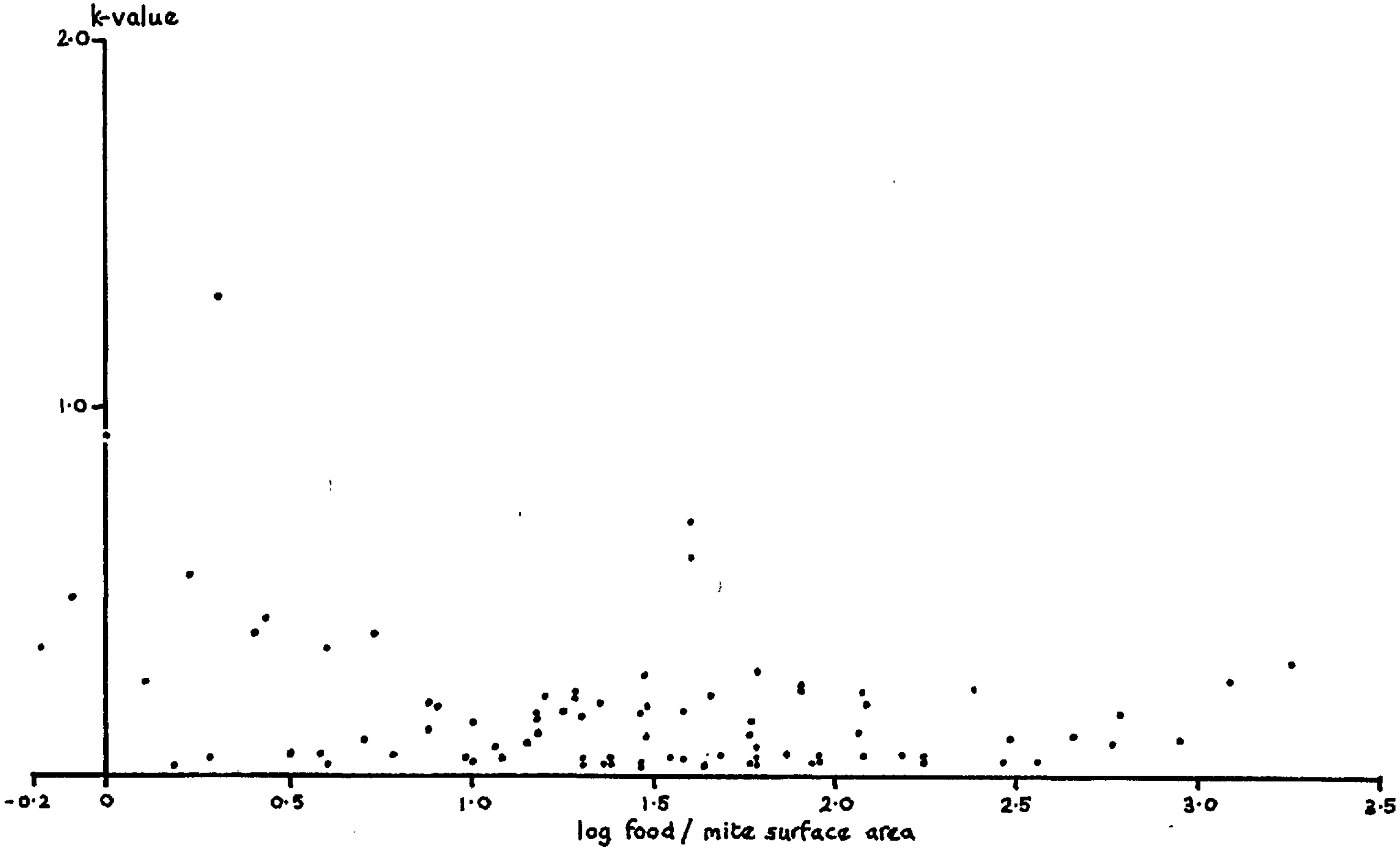


Figure 3.2.5

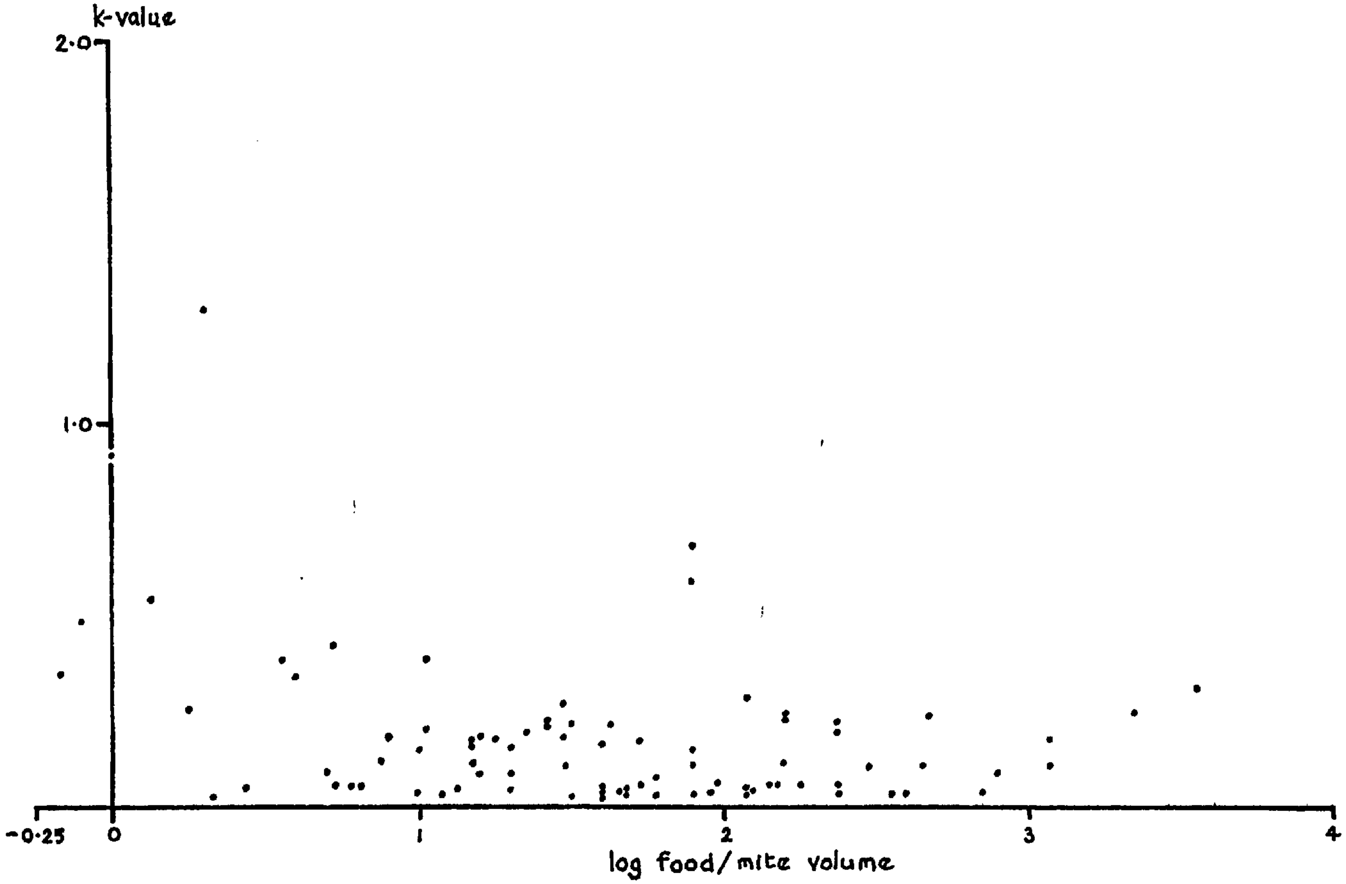


Figure 3.2.6

	$y_{0.699}$	$y_{1.477}$	intercept	slope	r^2
A20µg	1.520	0.693	2.262	-1.063	0.081
D20µg	0.330	0.130	0.510	-0.257	0.030
P20µg	0.247	0.316	0.185	0.089	0.012
A150µg	0.324	0.046	0.574	-0.358	0.060
D150µg	0.147	0.142	0.152	-0.007	0.001
P150µg	0.499	0.295	0.683	-0.262	0.014
A300µg	0.097	0.125	0.071	0.037	0.007
D300µg	0.159	0.123	0.192	-0.047	0.006
P300µg	0.375	0.206	0.527	-0.217	0.018
A450µg	0.145	0.144	0.145	-0.001	0.015
D450µg	0.037	0.029	0.045	-0.011	0.005
P450µg	0.041	0.041	0.041	-0.001	0.001

Table 3.2.4 Least squares regression analysis of the relationship between mortality and available food (logarithmically transformed)

	$y_{1.301}$	$y_{2.653}$	intercept	slope	r^2
A1	0.035	0.097	-0.024	0.045	0.820
D1	0.037	0.080	-0.004	0.032	0.496
P1	0.232	0.244	0.220	0.009	0.034
A5	1.268	-0.050	2.537	-0.975	0.299
D5	0.355	0.066	0.632	-0.214	0.088
P5	0.358	0.281	0.431	-0.057	0.003
A10	1.483	0.055	2.857	-1.056	0.481
D10	0.090	0.118	0.063	0.021	0.009
P10	0.237	0.156	0.314	-0.060	0.040
A15	0.579	0.157	0.984	-0.312	0.367
D15	0.406	0.099	0.701	-0.227	0.426
P15	0.580	0.352	0.799	-0.169	0.030
A20	1.300	0.020	2.533	-0.947	0.500
D20	0.053	0.038	0.068	-0.011	0.028
P20	0.015	0.046	-0.014	0.023	0.214
A25	0.434	0.039	0.813	-0.292	0.675
D25	0.032	0.046	0.019	0.010	0.032
P25	0.047	0.046	0.049	-0.001	0.001
A30	0.340	0.037	0.631	-0.224	0.779
D30	0.235	0.086	0.378	-0.110	0.228
P30	0.448	0.179	0.706	-0.199	0.151

Table 3.2.5 Least squares regression analysis of the relationship between mortality and mite density (logarithmically transformed)

$$E_{n:ax-y} = \frac{n!}{x!(n-x)!} P^x_{ax-y} (1 - P_{ax-y})^{n-x} r_{ax-y}$$

where : $E_{n:ax-y}$ is the number of replicates, of x mites of age class a with y µg food, expected to show n deaths per replicate; P_{ax-y} is the empirically derived mean probability of mortality for x mites of age class a with y ug food; and r_{ax-y} is the number of replicates experimentally observed for the same conditions (the assumption is made that the empirically derived mean mortality, rather than the empirically derived variance or any other derived moment, is the parameter estimate which will give the best fit binomial distribution).

The goodness of fit of the results to this binomial model cannot be estimated directly because the data is inadequate for the relevant statistical tests. The expected frequency values are too low for application of a chi-squared test and there is no estimate of mean mortalities independent of the results themselves for application of the Kolmogorov-Smirnov test.

Accordingly the relationship of variance to mean mortality (both scaled as percentages of replicate size) is graphed explicitly (Figure 3.2.7) for comment.

Figure 3.2.7 The relationship between variance and mean mortality in the data from the primary experimental set (given in Tables 3.2.1 - 3.2.3) :

a) composite of adult, deutonymph and protonymph results.

b) adult results

c) deutonymph results

d) protonymph results

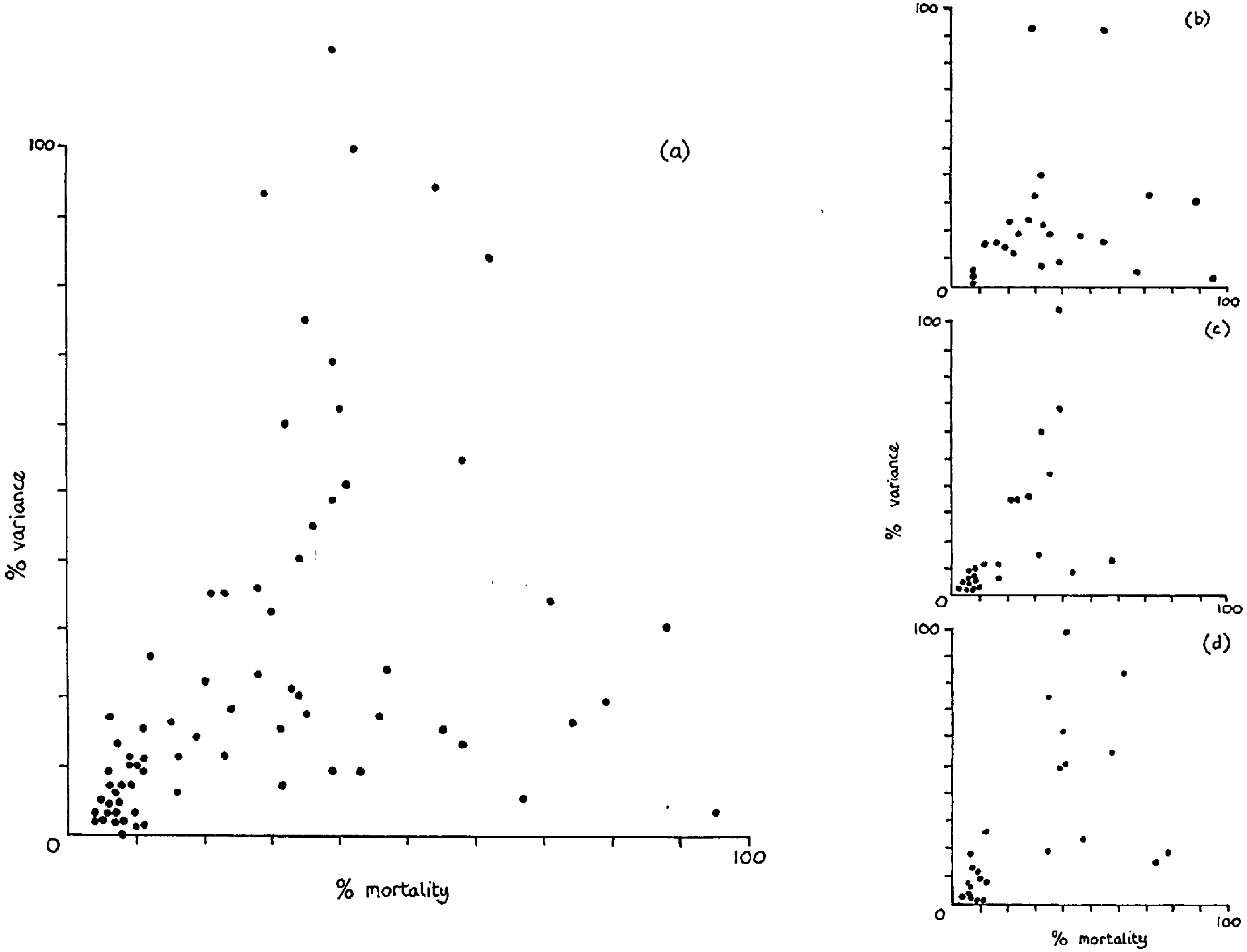

(a)
100
0
100
% variance
% mortality
(b)
100
0
100
(c)
100
0
100
% variance
(d)
100
0
100
% mortality

Figure 3.2.7

CHAPTER FOUR - ANALYSIS AND DISCUSSION

In this and subsequent chapters it will, for the most part, be convenient to present the discussion in dialectical form to maintain, concurrently, mutually antagonistic lines of argument. The participants in discussion are : ALPHA, a theoretician with reductionist sympathies; BETA, a champion of the emergent property (but above all else a sceptic); and GAMMA, the unassuming experimenter who will answer their questions.

GAMMA : Let me first apologize for the incomplete nature of the results you have seen, both in their relation to the original experimental design and in the extent of the statistical analysis.[1]

BETA : No need for apology. There's more than enough here to provoke debate of the major issues, as well as several minor, if more detailed, issues.

ALPHA : Major issues ? What major issues ? Are we not to discuss the validation of a specific model by experimental evidence ? Wasn't that the original purpose of the experiments ?

GAMMA : Well yes, it was originally, but ....

BETA : Validation, what's this talk of validation! The very idea that a scientist could consider such a thing is preposterous - it's the worst kind of inductive logic.

GAMMA (calmly continuing) : .... in considering the extent to which the results did validate the model, the question arose of whether validation had any meaning at all in this context. To which I'm sure our friend Beta will answer no.

But let us not reach for so high a level of discussion so soon. Regardless of the reason for the experiments, results were produced. We ought to discuss these first - their nature and their reliability.

4.1 Experimental Results : measures of reliability

ALPHA : What we must be concerned with is dividing the variability shown in the results according to the factors causing them, so that we might determine how much is due to errors in experimental technique. The rest must then be a property of the animals themselves.

Let us start with the explicitly defined experimental conditions. The nominal temperature was 25°C, but there was a fluctuation of plus or minus two degrees. That represents a range equal to sixteen per cent of the desired temperature, a quite considerable variation.

GAMMA : But not one that would have affected the mites. You forget that they were doubly removed from the conditions of the room itself, where the observed variation was most probably due to the opening and closing of doors. The mites were in cells contained in sealed jars, a double damping of the fluctuations experienced in the room. Although no measurements were made, I doubt that the fluctuations within the cells were more than half a degree in range.

BETA : It may be that the fluctuations were thus well controlled, but what of the actual temperature? Recognizing that the experimental arena was doubly insulated from the controlling influence of the room, could not the metabolic heat of the animals have produced temperature differences according to density ?

GAMMA : Certainly there would be production of heat proportional to density, but this would not significantly increase the temperature for the range of densities used. Solomon in 1946, citing papers by Howe and Oxley, and Oxley and Howe, both in 1944, states that Acarus siro in bulk grain at a density of eight thousand mites per hundred cc's of grain at twenty-five degrees Centigrade, would not produce a significant temperature increase 'unless a very large bulk, such as a six-metre cube, were infested throughout at this density.'. In comparison, the maximum density in experiment was thirty mites in an otherwise free volume of 1.156 cc (equivalent to 2600 mites per hudred cc's). This being the case, I think we can safely conclude that there would be no significant increase in temperature in the experimental cells as a result of metabolic activity.

BETA : Is carbon dioxide production similarly insignificant ?

GAMMA : Carbon dioxide production was also measured by Howe and Oxley in their 1944 study for the same conditions as the temperature measurement, and found to be a one per cent increase in twenty-four hours. So under the conditions of experiment, even neglecting diffusion through the base of the cells, there would be an increase in carbon dioxide of less than two per cent, which, considering the remarkable tolerance shown by Acarus siro to carbon dioxide (see Section 1.3.2), would be unlikely to have any effect.

ALPHA : I agree, and I think that the humidity controls were also sufficient to rule out significant errors of that factor. Which leaves the amount of food present as the only variable liable to cause errors. There are two sources of error here : variation in the concentration of suspensions; and variation in the quantities delivered to the cells. The preparation of relatively large amounts of suspension would have minimized the errors in weighing of solids, and the mixing and dosing procedure (see Section 2.3.3) should have overcome the effects of differential settling of suspended particles. But how much variation was there in the volumes applied to the cells ?

GAMMA : The amounts delivered were too small to allow a direct estimation of the variation, but as different numbers of drops were applied at different food levels, any significant effect of variation in applied suspension volume should be detectable as a change in variance with food level. The 20µg and 150µg food levels should have displayed the greatest variance because they were single drop applications, while the 450µg level should show the least variance being the result of three-drop applications. Looking at Tables 3.2.1 - 3.2.3 there seems to be little evidence of this.

BETA : But any droplet error would be confused by other factors affecting the variance. Figure 3.2.7 shows the relationship of variance with mortality, and mortality is affected by factors other than food level.

ALPHA : I think that for the moment we must assume no significant error in the delivery of food to the cells. The question is not one which will be resolved by analysing the data, because, as Beta says, we are dealing with a multi-variable system with many interactive effects. In any case, suspension volume error, in delivery by pipette, must surely be less significant than errors caused by differences in the quality of the suspension.

BETA : That seems reasonable, and I would think that environmental conditions other than those we've mentioned should have no effect. Lighting coditions were constant through the course of the experimental regime, and the only other factor which seems likely to affect the mites is atmospheric pressure, seasonally changing.

GAMMA : Seasonal changes were investigated, but no trend was detected. So we are left with errors resulting from undesired differences in the animals used.

ALPHA : As I remember, the mites were selected, on the basis of a visual index, to be those which had just entered the life stage desired for experiment. The variation is presumably due to error in the estimation of the size of a selected individual and should be normally distributed.

BETA : Wrong! On several counts. Of course there will be variation due to experimental error, but there may also be variation intrinsic to the population, and with a distribution which cannot be defined prior to experiment. The experimental design used seeks only gross changes in mortality due to age class. Patterns of variability within age classes are not considered. As I wish to discuss the matter later, I will not pursue it here.

As to normally-distributed errors, these are unlikely. The mites were chosen as the smallest of a particular age class. The reference objects, the resting stages, provided a lower limit to selection, but the upper limit must necessarily have been a subjective matter. This would lead to a skewed distribution of errors, a condition which would have been exacerbated when large numbers of one life stage were taken from a single extraction when, assuming an equal age distribution in the extraction, the selected mites might well show a plateau distribution, square and identical with the lower bound of the age class and exponentially declining at its upper bound (see Figure 4.1.1).

Figure 4.1.1 A possible effect of increasing sample size on the size distribution of mites taken for experiment from any life stage.

The curves are numbered in order of increasing sample size.

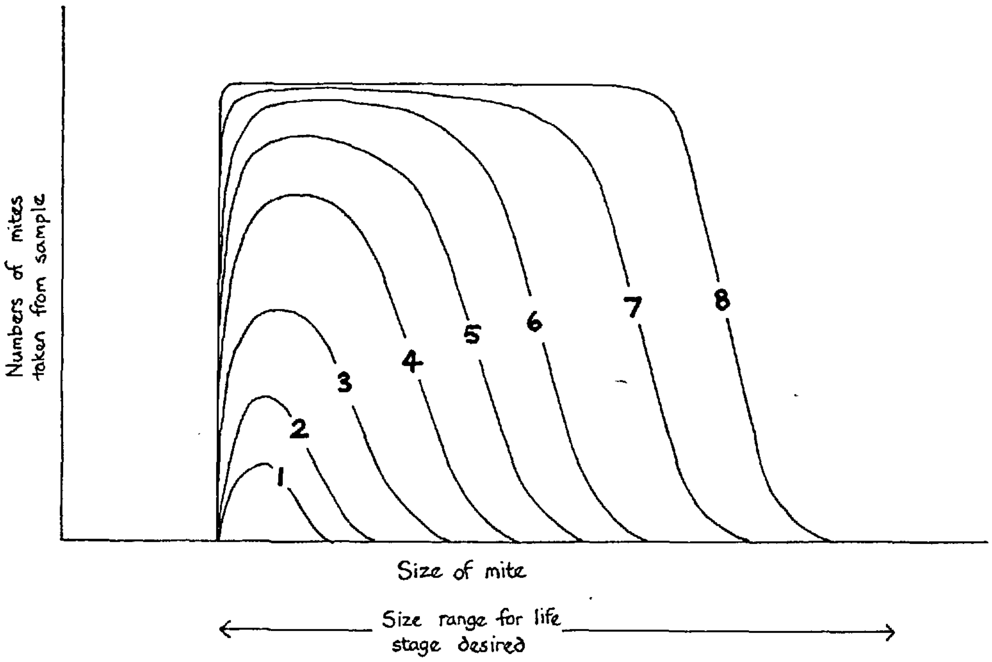

Numbers of mites taken from sample
Size of mite
Size range for life stage desired
1
2
3
4
5
6
7
8

Figure 4.1.1

GAMMA : In thinking of the way in which I selected mites, I realize that the mites put in any one particular cell usually came from the same location within the extraction dish. If that location was not the result of random movement but rather was a measure of a 'tendency to explore' of an individual mite, then this might also contribute to the heterogeneity of the mortality results.

ALPHA : That being the case you should have selected mites from only one location within the extraction dish to remove the variability due to this exploratory factor.

BETA : Not at all! The experiment sought population characteristics. All of the mites were from the same population, that is we have no reason to assume that there were reproductively isolated sub-populations. The variability is therefore a characteristic of the population and must be taken into consideration in estimating the effect of mortality responses.

4.2 Patterns of Mortality : the preliminary data

GAMMA : I think we should discuss the preliminary results and the primary results separately before discussing the consistency of one with the other. Would you agree that the general form of the model suggested for the preliminary data is correct ?

ALPHA : No. I'm not sure that I would accept an exponentially decreasing function to describe the mortality relationship to density. I think I would prefer to use a linear function.

BETA : Why ? What advantage does one have over the other in such a tentative model ? Perhaps if mortality increased with increasing density it would be preferable to assume a linear function as representing a relationship with per capita food availability, but in this case I see no reason not to assume the curvilinear relationship suggested by the data.

GAMMA : What of the relationship between mortality and available food. Is that reasonable ?

ALPHA : Certainly. One has only to assume a threshold value of food required for each individual mite and a normal distribution of threshold values in the population, to generate a curve similar to that suggested. And as far as the 'residual mortality' factor is concerned, it seems wise to allow for mortality unrelated to the experimentally-manipulated factors.

BETA : I agree. Now let us return to the density relationship. Mortality decreasing with increasing density. What does that suggest to you ? My first thought was some form of cannibalism. Although necessitating some mortality, as long as the death of one mite was sufficient to maintain the lives of a number of others, there would still be a decreasing rate of mortality if the <u>number</u> of mites dying was a function of density.

GAMMA : I'm not sure I follow that.

ALPHA : And I'm not sure that it's correct.

BETA : You must assume scramble-type competition for food - the food being eaten steadily over four days. At the lowest food density there is insufficient food for any number of mites, but the mites do not die until near the end of the experimental period, continuing to move about in the meantime. As density increases the rate of contact between mites increases, and there is some mortality proportional to this rate of contact which operates before the starvation mortality. A mite dying as a result of such contact then provides food for the remaining mites, thus alleviating the mortality expected because of the limited nominal food concentration.

ALPHA : Yes, you're right. I wasn't considering the fact of mortalities operating at different times. But what kind of mechanism did you envisage for this contact rate proportional mortality ? Did you observe anything that might suggest a possible mechanism durin the course of the experiments, Gamma ?

GAMMA : Active mites did pay a lot of attention to the bodies of dead and dying mites.

ALPHA : How could you characterize a mite as dying ?

GAMMA : Mainly by the appearance of dehydration - an obvious loss of volume and a wrinkled cuticle. Although this inevitably meant that the mites were immobile, usually dorsum downwards with legs in the air, otherwise healthy adults would often temporarily adopt this supine pose, so the distinguishing features of approaching death were the signs of dehydration.

BETA : Do you think this dehydration was a cause or an effect of dying ?

GAMMA : I tend to think that it was the ultimate cause of death, but that it resulted in most cases from some form of cuticular damage. How this damage was caused I do not know but, whether it was accidental or due to deliberate acts by other mites, it is easy to see that the rate of such occurrences could increase with mite density. The chelicerae of A.siro are quite capable of piercing cuticle, even that of larger animals : starved individuals have been seen to attack and kill the mite Cheyletus eruditus, which is a common predator of A.siro.(J.Berreen, pers.comm.)

ALPHA : Are there any clues in the results as to the mechanism responsible for death of mites ?

GAMMA : Nothing that would distinguish between accidental and deliberate damage, I think. But let us consider what the effects would be if the damage were purely accidental, resulting from contact injury. How would the mortality rate vary with density ?

BETA : We are assuming then that a certain proportion of contacts between mites result in injury, and that a certain proportion of these injuries result in a fatality and that these proportions remain constant.

ALPHA : Yes, I think that we must assume these for simplicity, though we will probably need to discuss the plausibility of these assumptions when we come to examine the case of deliberate injury. Will we further assume that the mites move randomly ?

GAMMA : I think we can simplify the argument here. Mites in cells were observed to move predominantly across the side wall area usually near the interface of cell wall and glass cover. In passing let me say that I think this behaviour may be the result of maximizing tactile contact with surrounding surfaces. But let me return to the main argument. During the course of experiment any one mite will traverse the outer perimeter of the cell many times. If we now assume that the movements of mites are independent, then the number of mites encountered, that is the number of contacts, will be proportional to the number of mites in the cell.

BETA : A point here. Are these contacts sufficiently intimate to make damage possible ? If not then we must abandon the accidental damage idea and discuss deliberate damage.

GAMMA : The mites readily clamber over each other as they move about the cell, and I feel that their tarsal claws are capable of inflicting damage even though I have no positive evidence in this matter.

ALPHA : Is there no more that we can suggest then, than that the number of fatalities is proportional to the number of mites in the cell ?

BETA : I don't think we are ready to say that without further qualifications. We have assumed a constancy of type of injury inflicted, but we have not said anything about the effect of these injuries. It seems to me obvious that the ability of an animal to recover from injury will depend on that animal's nutritional status. Therefore while the number of potentially fatal injuries will be proportional to the number of mites in a cell, the number of actual deaths will be affected by the amount of food available. Now this may be explained in that the fatalities occurred to mites which had become stuck in a supine position and therefore unable to feed, and that the negative relation of mortality to density displayed in the preliminary data could be because the regaining of an upright position depended on contact with another mite and that, as we have said, the number of contacts increases with density.

ALPHA : That wouldn't, however, explain the decline in mortality with increasing food availability at low density levels. If a mite is stuck in a supine position it wouldn't matter how much food was available, the mortality rate would be independent of food availability.

GAMMA : You are neglecting the fact that some time elapses before a mite becomes stuck in a supine pose. With no information as to the maximum rate at which a mite can eat, as to the amount of food that can be stored, or as to the amount required for simple body maintenance (remembering that the supine mite need expend no energy on locomotion), I don't think that we can reject the relationship we have already postulated which assumes threshold food requirements normally distributed through the population.

BETA : So we are suggesting now that the critical factors are the amount of time in which the mite is capable of feeding, and the amount of food available to be eaten during that time. So we have that the rate of food ingested is food limited and not ingestion-process limited, that the time available for feeding is proportional to the density of mites, and that each mite requires a certain amount of food simply to survive the duration of the experiment.

Consider the possible events at low food densities. At low mite densities the time spent supine is maximized, and hence mortality also maximized. As mite density increases, the mortality decreases until the amount of food available per mite (which is decreasing with increasing mite density) approaches the subsistence amount, when mortality increases again.

At higher levels of food availability, the target amount of food can be collected in a shorter time and hence the effect of low mite density is alleviated. A plateau of residual mortality would result if some mites had a sufficiently low maximum ingestion rate.

ALPHA : But you have just stated that there is no limitation resulting from the ingestion process.

BETA : I was speaking then of the mean response of the population.

GAMMA : There is another conflict, one of explanation with experimental conditions. The food was delivered to the cells in suspension and was concentrated at the centre of the cell base. The suggestion that the total amount of food ingested was time limited but not ingestion-process limited implies that the food must be dispersed, and that the time element accounts for movement over the field of dispersed food.

BETA : I think you are crediting your mites with a greater feeding efficiency than they have, for certainly the explanation would be rendered doubtful if the mites gathered and remained in the vicinity of the food. But you have recently told us that the mites were generally to be found on the walls of the cell, which implies that for only a small proportion of the time were they near food.

ALPHA : Or that most did not encounter the food at all.

BETA : Yes, except that, variable though it is, there is a relationship between food availability and mortality,

I think that the mites wandered the cell preferring, but not exclusively, the cell wall and feeding as they traversed the centre of the base, but having no inclination to stay there. The cell can thus be thought of, abstractly, as an extended matrix of food patches separated by distances far greater than the physical dimensions of the cell would suggest, across which the mites move at random.

ALPHA : So we have general alternatives of explanation : one based on starvation-induced death, the other on damage-induced death. Let us return to damage-induced death and discuss the possibility of deliberate damage by one mite of another. Our previous argument requires that dead mites be used as food by the survivors. In what way may we distinguish accidental from deliberate damage, and damage deaths from starvation deaths ?

BETA : Cannibalism, for that is what we are now discussing, would be difficult to demonstrate visually.

GAMMA : But could be demonstrated as the ingestion of radio-labelled tissue.

ALPHA : But that would not demonstrate the type of relationship we are seeking to establish ; it would only show the possibility of cannibalism. We need first to determine whether the mites that die do so as the result of damage or starvation, and that presumably rests on the possibility of identifying injuries on the dead mites, coupled with observation of live mites to plot the course of events leading to death.

BETA : Yes, plotting the times of death during the experiments might suggest the mechanism. If the deaths were evenly spread through time one would favour the accidental-death hypothesis, or some sort of steady rate cannibalism ; while if the deaths tended to occur near the end of the experimental period then starvation deaths or starvation-induced cannibalism would be more likely. The observed extent and manner of contacts between individuals should suggest the correct choice of hypothesis at either of these patterns of death occurrence. Again, of course, this would be only circumstantial evidence.

GAMMA : I think we may already be able to make a tentative selection of hypothesis if we review the data at our disposal. Mortality decreases both with increasing food availability and with increasing mite density. The former suggests that there is food limitation, the latter that the presence of other mites somehow allays the effect of food shortage. Our starvation death hypothesis implies that there is sufficient food, even at the lowest food levels, for up to thirty mites for four days - the continued decline in mortality with increased density suggests this. The damage-death hypotheses, whether accidental or deliberate, demand that the lowest food level be insufficient for as few as five mites for four days, in order to explain the decline in mortality with density. If we could achieve a measure of the food requirements of a single over four days we should be able to distinguish between these categories of hypothesis.

BETA : But as a final note let us remember that we have not allowed the possibility of mixed causes of death, even within the limits of our present hypotheses, nor have we mentioned infection deaths whether fungal, bacterial or protozoan. Any of these may also play a part.

4.3 Expected Patterns

BETA : It seems to me a marked feature of our discussions that we credit our population of A.siro with a remarkably high level of homogeneity. Whether our arguments are concerned with the ability of an organism to survive on a given amount of food, or survive a particular level of injury, or display intraspecific aggression at a particular starvation level, our cases are stated generally in terms of mean values of these characteristics. We are assuming a continuous and unimodal distribution of these characteristics so that we may legitimately represent them by single values. What are our reasons for making such assumptions ? In what circumstances would we expect these assumptions not to hold ? How may our conclusions be altered by relaxation of these assumptions ?

ALPHA : Our main reason must surely be the principle of parsimony - the application of Occam's Razor to prevent the adoption of complications which might divert us from the discovery of scientific truth. Scientific history attests to the need to identify critical features of objects or processes, and of the difficulty of determining mechanism where a plethora of possible causes remains unsifted. Further to this argument of simplicity is the weight of practicability in that complex interactions are at best difficult to analyse, at worst intractable.

BETA : But isn't this approach to science, this state of possible analysis, the product of the study of relatively simple systems which conform to this investigative ideal ? Let us discuss the properties of populations on the basis of current knowledge, unbiased by the need to investigate them.

When would we expect a population to be variable ? Are there life styles correlated with high variability, and can we suggest why this should be so ?

GAMMA : As a general rule I would say that the variability of a population was correlated with its position on the r-k spectrum[2], high variability being associated with r-selected organisms, low variability with k-selected organisms.

BETA : There is a rich ground for discussion in that observation, but let us first discuss the ways in which we are using the term variable. There is genetic variability which allows both continuous and discontinuous forms[3]- we need only remember the standard examples of height and eye colour, respectively, in man. There is behavioural variability - for example, in territorial birds and insects, adult males can be divided into those holding territory and those not, each group displaying different behaviour, albeit only in expression as individuals may change status, and hence behaviour, according to circumstance.[4]

ALPHA : But aren't these exceptional cases ? Wouldn't it be true to say that conformity was the general rule, and that there are good evolutionary reasons to expect this to be so ? If two genotypes compete then the genotype with lesser fitness will eventually succumb.[5] There will always be this tendency to maximize efficiency. Of course there will be changes in the selective conditions, and random events and unavoidable physical dispersion will slow down the process of selection. But I can see that these factors might well act together - there being major trends in the former which would be followed more faithfully by a population whose selective mechanisms were affected by such damping mechanisms as those latter mentioned. There would be a smoothing of response analogous to that exhibited in forecasting methods based on weighted averages.

BETA : Your argument is persuasive, and enjoys a considerable weight of academic support. But I think that there are assumptions hidden in its development which lack substance and which, because of their subtlety, have gone largely unnoticed by those who have attempted criticism previously. Before discussing these theoretical considerations however, I wish to return to the empirical and deny your claim that heterogeneous populations are exceptional. Not that I wish to suggest the opposite, that heterogeneity is the norm, merely that I do not believe there has been sufficient observation or discussion of natural populations to allow any definite statement to be made.[6] Most of the concepts used at this level, by field biologists, laboratory experimenters and theoreticians, such as species and population, are so variable in their definition as to make me doubt the value of work based on them. Each person has his own idea of their definition, but the greater part of these definitions is not explicitly examined. The explicit features of the definitions tend to be the most obvious, the common experience, characteristics of the classes of entities called species, population, etc. We are left with a superficial appearance of agreement and, with the individual man's susceptibility to the belief that the world thinks as he does, there appears the ground for confusion and false argument. Worse, when the confusion is recognized, there is a retreat to definitions based solely on common agreement. The definition of a class of sets is reduced to the caricature which is the common sub-set. Our basic intellectual drive to draw order from chaos, to attribute pattern to the complexity of events around us, over-reaches itself in the face of the richness of organic life and abandons information before its worth has been evaluated.

GAMMA : But we have to abstract information. If we merely chronicle events, assuming nothing but the correspondence of our sensory data with external objects, we would be historians not scientists.

ALPHA : And there would have been no scientific progress.

BETA : You misunderstand me. I am not proposing simple observation as the method of science. I am not denying the value and necessity of theoretical abstraction in the formulation of natural laws. I wish to remind you that there are assumptions in our accounts of ecological phenomena and that these assumptions may be critical to developed theory; and I would hope to point out alternatives and the means of examining these. We must discuss the definitions of species and population in detail later. For the moment let us discuss possible distributions of characteristics within a completely mixed group of inter-breeding individuals. What conditions would allow various types of distribution ? Square distributions, implying equal fitness of a range of genotypes, are usually looked upon with disfavour. Yet one only has to visualize total fitness as a composite quantity to realize that any one characteristic may display a number of expressed levels if these are counterbalanced by other contributions to fitness. If the number of contributory factors is high and their effects of equal order, independent sorting and alignment of the characteristcs would ensure comparable fitness over a wide range of phenotypes.[7] Discontinuities are usually thought of in terms of major allele interactions - typical Mendelian inheritance - and as such are easy to explain. But how could we explain discontinuity in an essentially continuous, multi-allele, characteristic. Easily if we postulate that these sister alleles are independent, but are each linked to other characteristics which may interact destructively, for example to produce an embryo which will not develop.[8] A contrived argument, you may say, but it is one quite compatible with current genetic knowledge. I would say that we cannot exclude any patterns of distribution of a characteristic on general a priori grounds. There can be no expected patterns, and one should certainly not expect patterns which are characterized by one or two simple parameters. Too often our approach suggests that we are disciples of Procrustes.[9]

ALPHA : What then are we to do ? Do we abandon descriptive statistics lest they bias our subsequent interpretation of events ?

BETA : No. I want more statistics, not less. I object to the bias towards unimodality. There is a stigma attached to variability, associated with an implied synonymity with error. The foundations of normal distribution theory are grounded in errors of observation, and our scientific past confines us to such thinking of dispersed results as the products of our own inept and bungling observational technique. We must be careful not to base our theoretical ideas on concepts which are, at best, borne of convenience, at worst, historical prejudice.[10] There are few studies of the composition of natural populations, or of their behaviour. Theories which presume to general explanation of such matters seem naive and premature. We need to return to observation until we can decide how we will describe what we observe.

4.4 Primary Results - compatability with preliminary hypotheses

GAMMA : An initial point as to the differentiation of damage and starvation hypotheses. The adult results (Figure 3.0.2a) show, at the lowest food levels, a decline in mortality from the five-mite to single-mite densities. This would not be expected if the damage hypothesis held, but would be possible in the starvation case if the food available was sufficient for one mite but not five.

BETA : No. The same case applies for both hypotheses if there is sufficient food for the observed proportion of single mites, but not for greater numbers. The removal of the possibility of contact injury is only important if there is insufficient alternative food, and we have as yet no means of separating these effects.

GAMMA : Let us look at the general shape of the results.First note the similarity between the deutonymph and protonymph results (Figures 3.0.2 b and c). Both show a ravine of low mortality at mite densities of 20 and 25 per cell; in both, mortality, increasing with additional food at the lowest mite density, changes gradually to a decrease with additional food at the 15 mites per cell density; the pattern of mortality at the 30-mite density is similar. Overall, however, protonymph mortalities are higher than deutonymph mortalities under the same conditions. The adult mortality pattern is generally convex, tending to decrease with increased mite density over most of the range, and saddle-shaped with lower mortalities at intermediate food levels, the highest mortalities occurring where there is least total food.

I would hesitate to suggest an explanation at the moment, but the results do have form.

BETA : Yes, they are respectable; they have an element of order about them - certain symmetries and points of similarity. There is a greater complexity than was suggested by the preliminary results, and some disagreement at low food and mite levels where the adult primary results show much lower mortalities than the preliminary results.

GAMMA : Though there is greater consistency within the primary data because of that disagreement.

BETA : In that all now show moderately low mortality levels at this point. But how do our preliminary hypotheses stand ?

ALPHA : In need of adaptation. We no longer have the simple response surface implied by the preliminary results , in which mortality declines as conditions move away from those of low mite density and low food availability. In all cases, at low food levels mortality at first rises and then falls as mite density increases. Generally the effect of increasing food is to decrease mortality but though, for single mites in a cell, this is true for the adults the juveniles show an increase in mortality under these conditions; the increase being exaggerated according to the youth of the life stage involved. The independence of mortality from food availability at mite densities of 20 and 25 per cell for juveniles perhaps suggests some change in behaviour.

GAMMA : Possibly an increase in aggressive behaviour with hunger, a behavioural response overridden when a critical density was reached ....

BETA : But how is an individual to know the density of the population. Assuming that the animal has a fairly limited sensory field it would need to take a census, counting the frequency of contacts on a sample walk around the experimental arena for example, before deciding how it was going to behave.

GAMMA : I think that here you have assumed too much, and maybe underestimated dear Acarus. The mite does have a number of chemoreceptor organs and there remains the undiscovered function of the aromatic oil secreted over the body surface. The oil could easily provide a threshold switch in the mite's behavioural repertoire.

BETA : Agreed. That would provide a possible mechanism. But, even if we could show such a switch mechanism, the problem remains of identifying the causes of mortality on either side of this switching ravine, as does that of reconciling or separating the patterns of adult and juvenile mortality.

ALPHA : Of course. All we can do is suggest possibilities, and devise critical experiments and observations which will distinguish these hypotheses.[11] But let us not forget that we carried out these experiments in order to determine the stability characteristics of populations of Acarus. If we look at the k-value density plots (Figure 3.2.1), remembering that the rate of change of mortality here, the slope, is the value of b in Table 1.2.1 and determines the stability properties, we see that a stabilizing influence is present only at low to intermediate levels of mite density and then only at the lowest food levels. This might be indicative of a limited-scope mechanism whereby at very low population densities, population increase is retarded unless adequate food is present.

BETA : Can we deduce anything from the other graphs (Figures 3.2.3 - 3.2.6) ?

ALPHA : I think not. They suggest nothing to me immediately, and I think that the complexities of mortality response revealed in Figure 3.0.2 make them unhelpful in investigating the possible causes of mortality. The regression analyses are similarly superfluous.

4.5 Statistical Testing

ALPHA : What are we to make of Figure 3.2.7 ?

BETA : Nothing, I think. The relationship is variable, but we have no reason to expect it to be otherwise, and no need to specify the relationship. We need to rid ourselves of this pathological desire to put simple form on every facet of experience. I would have thought that, by now, the debate of the relative merits of distribution-free, or non-parametric, statistics and classical continuous unimodal statistics would have attracted sufficient attention to make scientists aware of the shortcomings of the latter.[12]

ALPHA : So we are denied the means of testing the significance of the mortality patterns we have seen. The overall patterns are non-linear and interactive and so not amenable to any simple analysis of trend, and the internal consistency of the data cannot be questioned because we have no a priori conception of its proper form.

BETA : Correct. We must be satisfied with the superficial appearance of the mortality results, and pause only to comment that the distributions of results merit further investigation. I commented on the overall appearance of order in the results and suggested that this in itself lent a degree of reliability to them. What statistical test would recognize such a quality. The tests are predominantly for simple forms of relationship and for differences between simple quantities. If we investigate systems with the potential for complex inter-relationships we must not bias our analyses with simplifying assumptions. Our intrinsic ability to recognize order obviously transcends our ability to present such processes in algorithmic form. If we fail to recognize this we will never develop more sophisticated methods of analysis.[13]

CHAPTER FIVE - CONJECTURAL HYPOTHESES

BETA : We have discussed the results within the framework of the model and questioned their reliability. Where do we go from here ? Do we need to go further or have we already completed a competent study ? What say you, Gamma ?

GAMMA : I can see nothing to do except to extrapolate the results to applied research, for example to the problem of controlling infestations of these mites.

ALPHA : I agree, and I think that we ought to sketch the control strategies which are suggested by the stability analysis. We should be able to deduce critical conditions of population size and growth at which control would be most effective.

GAMMA : That certainly seems a reasonable addition to the study. I am suspicious of Beta's questioning, however. He must intend to set up a line of argument to his own tastes, for I am certain that he does not regard the study as complete in its present form. And his mention of competence suggests to me that he intends to prepare the ground for a discussion of epistemological problems.[14]

BETA : I commend your perceptivity, Gamma. Problems of epistemology are certainly my final objective. But for the moment I wish to remain with Acarus siro. To delve into its past and so discover its present is my immediate concern. Now is a time for flights of fancy - to let our imaginations run free. I believe that this most essential phase of scientific enquiry ought to be made explicit. From the core of information we already have, we must extend in all directions, stretching the fabric of our logic to the point of absurdity.

ALPHA : And you intend to call this science ?

BETA : I do indeed, and I believe that nothing so characterizes science as the reign of imagination. The rest is mere bookkeeping.

GAMMA : So you dismiss data collection - in the field and in the laboratory - as unnecessary tedium. And you can baldly state that imagination - a quality common to all human pursuits - is the key characteristic of science. You have overstated your case in support of creative science, Beta. Of course science requires imagination, but the essential feature is its concern with empirical facts - direct or indirect sense data. Science is the process of compression of sense data, the abbreviation of objects and events to patterns. Imagination enters science in the generation and selection of patterns - in the provision of explanatory and self-consistent formal systems with which to compare the data.

But I would agree that imagination is necessary at this stage of investigation when, having fixed some points in the pattern of existence of Acarus siro, we need to relate these various items of information.

ALPHA : However there must be reasonable inference and extrapolation. This is always the second stage of scientific enquiry, after entities and processes have been differentiated and named. The next stage is the critical examination of the hypotheses so created, when reference is made back to the objects of experience in order to test and distinguish the relative merits of these hypotheses.

BETA : But there is a danger, in erecting hypotheses and prospective theories of complex systems, that definitions of entities and processes become confused and sometimes fused. The conceptual frameworks so formed become all-embracing, allowing no exceptions to their rules. They are thus raised to the status of metaphysical systems, rather than allowed to gravitate by process of experiment to the status of accepted science.

ALPHA : And do you believe that this description applies to ecology, Beta ?

BETA : I believe that sufficient ambiguity is contained in our definitions of the supra-organismic levels of biological organization to make this a possibility. We should, therefore, very carefully examine our attempts to manufacture theories in this area of study. It is here that diligent observation, and the imaginative extrapolation of empirical crrelates, can pin-point the flaws in our defining and reasoning processes.

GAMMA : So we consciously extend the world of 'what-might-be' in order to resolve the why and how of our world of 'what-is' ?

BETA : Yes, and we must now ask 'what-might-be' for Acarus siro, as a first step towards asking the same questions of the more general objects of our interest.

5.1 Hypotheses concerning Acarus siro

ALPHA : Where do we start ? If we have to comprehensively review the biology of Acarus, weighing all the various accounts of its behaviour and biology, any conclusions we may be able to make will be delayed greatly. Can we not be selective, and so reduce the scope of our discussion ?

BETA : Of course. But in selecting characteristics for discussion we must remain aware of the basic evolutionary framework within which Acarus siro must be assumed to exist. Every organism represents a point in a continuum of genetic material, and the attributes and characteristics of an organism are,for the most part, an expression of the selective pressures which have operated on that continuum. The differences between organisms are expressions of the differences in selective pressures, past and present, which have operated on them and their ancestors. The closer the relation between organisms i.e. the shorter the time since genetic divergence, the more precisely can structural differences be correlated with behavioural differences, behavioural differences with distributional differences, and circularly from the distributional differences, inferences made about the differences in selective pressures operating.

That the selective pressures may be viewed as goal-orienting - towards survival - and are, one assumes, generally efficient, makes productive a teleological analysis of the organism in its environment, providing that the constraints on form and function imposed by the basic genetic material are always kept in mind.

This type of approach is most likely to prove beneficial in those areas least amenable to direct observation, for example where morphological form and life history have been studied, physiological and control mechanisms can be postulated from conditional necessity, and attention thus drawn to the more critical, and hence more fruitful, areas of enquiry.

In that the environment of an organism is likely to be a subset of the purely additive range sum of the various environmental factors i.e. there will be correlations between environmental factors, and that there is interaction between the characteristics of an organism at all levels of organization which is likely to compromise the efficiency of individual mechanisms and behaviours, the observation of the animal in its natural environment must precede and delimit attempts to abstract and isolate the effects of single external factors on single behavioural sequences.

The total response of a species to its environment is a function of the physiological limitations of the organisms and of the strategic and tactical control mechanisms that have evolved, these latter being differentiated by the element of potential choice in the second.

Given information about life history and distribution, with basic generic or family biology if available, it ought to be possible to deduce statements, albeit hypothetical, about likely physiological control mechanisms, about the genetic structure of populations, species and species groups.

Reasoned verbal arguments, based on sound biological knowledge are probably better suited to the elucidation of such ideas than are the severely limited powers of currently tractable mathematical arguments.[15]

I think we should now try to pursue this type of analysis in relation to Acarus siro.

5.1.1 The question of origin

ALPHA : So this is where we 'delve into the past to discover the present'. Why do you think this so important ?

BETA : Because the evolutionary options open to any group of organisms at a particular time are the product of its ancestral history.

ALPHA : And how do you intend to carry out this historical analysis ?

BETA : Of the immediate past by examining the present habitat and considering the history of that. The habitat is larger than the organism, and the larger the object the more likely we are to be able to locate information about its past.

The more remote history of the organism I would hope to be able to deduce from a study of the close relatives of Acarus siro, where the common features should suggest the form of the ancestral type.

ALPHA : Then let us start by examining the present habitat. Where is it found, Gamma ?

GAMMA : By far the most common habitat recorded for Acarus siro is the stored cereal environment. In terms of numbers observed, recorded observations elsewhere are insignificant.[16]

BETA : Avoiding a discussion of what is or is not significant in this situation, where else has the animal been seen ?

GAMMA : As was stated earlier (Section 1.3.3), the mite has been seen in a number of more natural habitats, but these generally have obvious links with the stored cereal environment.

ALPHA : What are these obvious links ?

GAMMA : Well for example mites are found on the rat flea. Rats, like Acarus, are well known pests of cereal stores and their co-location at these sites makes the occurence of the mite on the rat flea easily explicable.

BETA : Yes, of course their common exploitation of man's food stores makes the relationship possible, but what other factors impinge on the realization of this potential state. Are the conditions we think necessary for a hypopus of A.siro to attach itself to the rat flea common enough for us to expect to have observed the attachment ? And if not, what features of the relationship have we overlooked ? In determining the critical phases of the mite's life history we must pursue our reasoning carefully around all aspects of observed behaviour. If, in fact, the hypopus randomly attaches itself to passing larger objects and that, therefore, all its recorded occurrences in 'natural' environments are the result of accidental passive dispersal, the inferences we may draw about its possible breeding behaviour, hypopus formation and so on, will be very different to those drawn from an argument based on a life history including the existence of natural and autonomous populations of Acarus siro.[17]

ALPHA : But what has this to do with the experiments which have been carried out. The results of competition, as observed, remain whatever the details of the natural life cycle may be, and presumably, with modification, apply to natural and artificial habitats.

BETA : However, conclusions regarding the gross impact of A.siro on its environment can only be drawn correctly if experiments of detail are viewed within the natural life strategy. If patterns of behaviour are displayed by the mite which ensure certain forms of hypopal dispersal, then one must reasonably assume that these elements of behaviour have evolved because hypopal dispersal is a critical phase of the life cycle. If this was the the case, the details of any competitive interactions at other phases of the life cycle, except insofar as they affected hypopal dispersal, would be relatively unimportant. To determine the gross impact of the mite we must first examine the gross features of its life history.

GAMMA : As I see it the hypopus allows two general categories of existence. It may link only successive infestations of stored food, or it may link both infestation and natural populations. But if we consider the numbers of mites involved then the natural populations must surely be insignificant. As population reservoirs they are too small to have any effect.

As well as the low number of mites involved, there must also be taken into consideration the frequency of visitation by animals likely to provide phoretic transport. The richness of the human food store must certainly attract a larger throughput of animal scavengers than any natural habitat. Thus on two counts I believe that the more natural of the observed habitats of A.siro must be discounted as important in continued species existence.

BETA : I think you are being distracted by the relative numbers in the various habitats from a true assessment of their importance. The food store habitat is rich and supports large numbers, but can we reasonably assume that direct transmission from store to store can account for the observed potential of Acarus siro to cause infestations wherever store management procedures are relaxed. I prefer to think that the mite is present with a much less patchy distribution but at very low numbers, say comparable with those of soil mites, in natural habitats such as the nests of birds and mammals. From this background reservoir the mite is free to invade and establish large populations wherever its hosts care to take it.

ALPHA : But why does this hypothesis suggest itself to you. It would mean that the mite was adapted for some habitat other than the food store, and yet several of its characteristics seem eminently suitable for that environment. Its tolerance to high carbon dioxide concentrations, for example, must surely be the result of continued selection in infestations of grain.

BETA : Yes, but the grain store need not be human. Rodents build up caches of food for future use, and in underground storage with limited ventilation, with dampness promoting germination of the grain, I would imagine high carbon dioxide concentrations to be a likely state of affairs.

As for the reasons for my belief that the animals are incursory vandals of man's food supply, let me start by reminding you of their feeding apparatus. The toothed chelicerae seem to me an adaptation more likely useful for mycophagy than for its presumed granivorous disposition.

GAMMA : But that observation does not discriminate between the proposed principal modes of life. Under the conditions in which Acarus is a pest of grain, fungal growth is also well favoured as was stated earlier (Section 1.3.3) and it has been suggested that selective mycophagy is the mechanism responsible for the co-existence of a number of granivorous mite species which would seem otherwise to have identical niche requirements.[18]

I believe that any attempt here to develop further ideas as to the details of possible histories of individual populations would be fruitless. We do not know enough of its whereabouts outside the storage areas of man's immediate concern, and if the populations in more natural habitats are of as small a size, and as dispersed, as Beta has suggested, then the problems of estimating their potential present great difficulties in sampling technique and statistical inference. We must remember that we are dealing with objects which can move through space and move purposefully, which have repertoires of behaviour which are purposefully used, and which interact purposefully with similar objects. These properties are of the highest significance and must be treated as such when we consider such questions as the importance of infrequent observations of animals in particular habitats. The more so when we remember the potential for reproduction and increase characteristic of living organisms.

ALPHA : How are you using the word 'purposefully' ?

GAMMA : Simply to imply decisions, choices between alternatives, made as the result of information received by the animal from its environment.

We have an animal which I think we must regard as essentially mycophagous, although capable of existence and increase on other foodstuffs. It is facultatively phoretic ...

ALPHA : What of the strains which cannot produce hypopi ?

BETA : If I may interrupt, I think that those strains are, most likely, artefacts of human research programmes. I would not attach too much significance to their existence, inasmuch as the fragility of the other A.siro life stages makes any major change of location very inefficient by any means other than phoresy.

GAMMA : Yes, I think we must regard those strains with the potential for the production of hypopi as typical, and bound our discussions with this assumption.

As I was saying, the mite is facultatively phoretic, with insects as vectors, and is found in human food stores and in animal nests.

ALPHA : This possible duality of habitat might explain the suggestion of an escape-and-release mechanism in the competition interactions (Section 4.4). The natural habitats are much less rich than the man-made ones, with no scope for spectacular population increase. It would therefore be advantageous to follow a density-dependent mortality regime there. The mechanism would need to exist only for relatively low densities as, barring a sudden mass immigration, the population could never outrun the imposed competitive mortality unless there was an influx of food. The population would therefore be stabilized for subsistive existence in a poor habitat.

BETA : So it seems we have a low level reservoir of small populations of Acarus siro, sending out their hypopi, at some unknown cue, on their insect fellow nest-dwellers. When these travellers chance upon some rich habitat they abandon their conservative ways and exploit the new found wealth with utmost speed. The fate of the infesting population, doomed to a short-lived if spectacular success, is relatively unimportant to the continued existence of the species because of the steady-state low-level production of the natural habitats.

GAMMA : But don't problems of continuity affect these natural populations as they do infestation populations ? Birds commonly build fresh nests yearly, and the more permanent burrows of mammals are periodically cleaned.

BETA : But probably the less frequently so as a result of the cleaning activities of the scavenging mites who, locked into a low density existence, would not be a sanitary problem themselves. In any case, if they were not selective in their choice of nests, the density of sites suitable for their existence would be generally high, and transportation between sites relatively easy. We must not think of the population as confined to a single nest, but rather as being confined to some geographical area containing a number of nests linked, as far as the mites are concerned, by the movement of their insect vectors.

This argument does require that hypopi be continually produced, and so suggests a possible preliminary test of its likelihood. The production of hypopi should be induced by conditions similar to those of nests harbouring Acarus siro. Therefore low food, low density, presence of fungi may provide the cues for hypopal production, and possibly explain the absence of hypopi in populations in decline from high density, this being the usual focus of experiments into hypopal production.[19]

GAMMA : Similarly the seasonal aspects of nest-building, clearance and so on, may imply parallel seasonal cues for hypopi. It is interesting to remember here that there may be a minimum necessary humidity for eclosion (Griffiths 1964b). Of what significance is this ? Is it connected with the summer period when nests fall into disuse, and general climatic conditions in temperate regions are least favourable to mite existence ?

However we are now only increasing the scope for further conjecture. In the absence of factual observation, let us foreclose this particular discussion and move on to discuss the close relatives of Acarus siro.

5.1.2 The Acarus siro species complex

ALPHA : Am I correct in thinking that the class of mites which may now be assigned to the species Acarus siro shows much less variability in form and distribution than previously, as a result of the creation of new species within the Acarus genus ?

GAMMA : Yes, The species was once regarded as being highly variable, but it has been demonstrated that there are a number of morphologically very similar Acarus species which, although capable of a very limited amount of gene transfer, maintain autonomous existences.

BETA : What sorts of observable difference are there between these sibling species ?

GAMMA : Differences in the structure of the hypopus for example, or of various appendages of the tarsi. For instance, of the three species initially recognized within the complex - Acarus siro, A.farris and A.immobilis - the adult of A.siro can be distinguished from adults of the other two species by the shape of a spine on the tarsus (adults of A.farris and A.immobilis are indistinguishable in this feature) , while the hypopus of A.immobilis is a non-motile form in contrast to the motile, and virtually indistinguishable, hypopi of A.farris and A.siro. A number of other sibling species have been described since the former three were distinguished, including A.calcarabellus, A.chaetoxysilos, A.macrocoryne and A.nidicolous, and here the differences involve overall body size, relative sizes and degree of pectination of setae, and again of hypopi and tarsal appendages.

ALPHA : And this sub-division of the original A.siro species to a number of sibling species largely accounts for the variability of habitat previously ascribed to A.siro ?

GAMMA : Yes it does. A.siro is now regarded as the typical stored products form, A.farris and A.immobilis being outdoor species associated with grain. A.nidicolous is, as its name suggests, a form found in nests, as are A.macrocoryne and A.calcarabellus. Other species have been found with stored foods other than cereal products.

ALPHA : This burst of speciation obviously makes much simpler the task of describing life histories, especially in terms of pest management models for the control of A.siro.

GAMMA : The recognition of these new species is not enough in itself to prove that all records of A.siro from other than stored-product environments were erroneous. Only further more thorough observation of mites in the various habitats will make that clear. The speciation does however suggest a simplification of life histories.

BETA : Only if we can truly regard these as strictly separate species. I don't believe that we can, though. The recognition that discrete populations exist, of different form and incapable of major gene transfer, is important, but rather than simplifying matters, with respect to conventional mathematical models of species, I believe that this fact once again draws into question the traditional definition of species.

Here we have a group of species which, examined across a set of characteristics, are distinguishable but which, if examined with respect to single characteristics, form sub-groups of indistinguishable forms : as with the characteristics of hypopus and tarsal spine already mentioned.[20]

So we have a multidimensional characteristics field upon which these species are points, perhaps sharing any one co-ordinate with other species. Some of the characteristics are polygenic, and intermediate forms can result from hybridization.[21] Intuitively, those species with the greatest differences should have the lowest likelihood of success in hybridization. Yet, while only a few characteristics are used to distinguish species, there is no absolute measure of genetic difference and, indeed, members of other mite species, designated as such in respect of similarly few characteristics, may be sufficiently different for successful mating to be impossible.[22] The species so far recognized, and maintained as such, are obviously stable points on this genetic landscape and it seems likely that some points on the landscape will be denied specific expression because of basic gene incompatability.[23] But there may be routes of gene flow between the recognized species through only slightly less stable hybrid intermediates. The continued proliferation of species within the A.siro species complex as a result of more thorough investigation would support this idea. There may be a number of separate gene flow routes linked only by their momentary collusion to re-create another stable species. Within this framework it is easy to see that a species could be maintained, and even reborn, by the activities of groups of individuals which, conventionally, would be regarded as different species. One need only remember the existence of ring species, where forms may exist at one location as distinct, separately breeding, species and yet be genetically linked through intermediates along a linear geographical continuum.[24]

ALPHA : Are you suggesting that we return to a single species, Acarus siro, with a plethora of habitats, morphologies and behaviours : an animal then with such catholic and cosmopolitan tastes as to be beyond the bounds of control. If so, you may certainly deny the possibility of a useful mathematical model of the pest, in line with your general antagonism to analytical modelling, but all you gain for your efforts is a return to the costly trial and error empiricism of the past.

BETA : Which is not at all what I desire, although I would question that such empiricism was any more costly than your predictive modelling.[25] And I would not suggest that the new species designations in the Acarus siro group be abandoned. They likely represent important differences, most certainly are specific ranks by current definition, and therefore need only be reviewed if the definition of species itself is reviewed.[26]

What I wish to do is to force the evolution of population modelling to take account of possible areas of uncertainty in attempting to describe any particular situation. If it is the case that explicit recognition of these areas of uncertainty renders a model unusable, or perhaps increases the variability of outcome of the model such that it becomes for practical purposes useless, then we at least have a reminder of the limitations of our knowledge, and we may tread more carefully.

While simple models and their behaviour may be interesting in themselves, the rationalization and centralization of management policies allow pest control directives to be put into practice on a very large scale. In such circumstances the degree of uncertainty of model predictions is as important as the values of the predictions.[27]

Merely by examining A.siro and its siblings in a framework only one step removed from a conventional species definition, we have posed several problems to the prospective pest controller. If we now continue to examine other, again quite plausible, complications to the conventional view, I am sure the stipulations to be attached to pest models will continue to multiply.[28]

5.1.3 Genetic switching

BETA : What I want to discuss here is the potential for individual animals to exist in different states according to their circumstances.

GAMMA : As for instance, A.siro being capable of producing hypopi under suitable circumstances ?

BETA : Certainly, but also including all changes in morphological, physiological or behavioural states where there are mutually exclusive options.

ALPHA : But would you then lump together, for example, the transitory change from feeding to moving, with the more major changes required in preparation for the formation of the hypopus ?

BETA : Yes - because it is this aspect of change that I am concerned with : the relative ease of change, with the possible types of control mechanism, and the limitations and duration of control. I think that there are interesting possibilities here which may revive the discussion of the definition of species, and which should prepare the ground for a later more thorough analysis of modelling methods.

I would like first to attempt a classification of types of change. Remember that we mean here changes which result from the selection, by some means, of a particular expressed state from a number of potential states of an individual.

GAMMA : So we are not concerned with differences between individuals in a population which are the result of absolute genetic differences between those individuals, but only with differences of expression of the same genotype ?[29]

BETA : Exactly. This type of flexibility is a major characteristic of living organisms, yet receives minimal recognition in mathematical models of populations.

ALPHA : Because it would introduce needless complication, when a statistical treatment in any case reveals the major trends and most likely outcomes.

BETA : But only for totally unstructured populations, which I would say are in a very small minority. Further, I would suggest that structured populations and variability were, by necessity, correlated and that therefore, where observed, their effect on population behaviour would be highly significant. Without variability of individuals, structuring of the population would be impossible.[30]

GAMMA : But the individual variability need not be brought about by individual flexibility. It could also result from the maintenance of genetically different strains within a population, along the lines of a balanced polymorphism.[31]

BETA : Yes - the variability need not be the result of individual flexibility. But I would argue that a population structured on the basis of individual flexibility would be more adaptable than one structured on an absolute genetic basis, if only because there would be no indispensable sub-groups of the population.[32]

But back to the classification of changes. As a first division may I suggest reversible and irreversible changes.

ALPHA : What examples of irreversible changes had you in mind? And wouldn't such change remove the increased adaptability you claim for structured populations with individual flexibility ?

BETA : I had thought of the rearing of queen bees, where the functional switch is the result of differences in diet. And no, the increased adaptability is not removed. The balance of individual forms can at all times be altered independently of the genetic derivation.

ALPHA : But your example here is of a population, all members of which are the progeny of an individual. I think that this must be regarded as a special case, a peculiarity of the social insects, and not one on which to erect universal categories.

BETA : No, I think that the feature of irreversible change is adequately illustrated here, and that the special colonial habit of the social insects lends itself more to a discussion of the definition of population than to the categorization of individual change.[33]

ALPHA : I would feel more at ease if you could give another example of irreversible change.

GAMMA : But we already have one - the acarine hypopus. As a stage in the life cycle it is one whose course must be completed. There can be no reversion to the protonymphal form.

BETA : True, it is irreversible, but it does not, I think, fulfil Alpha's requirement of changes which can result in structured populations. On reflection I began to think that Alpha was right and that this is a characteristic of colonial animals. I posed the question to myself as "Of which animals, during development, can you say 'some become ....., others become ....'?" The form is so immediately reminiscent of the differentiation of body cells that I restricted my focus to concurrent differentiation of individuals, and I admit that all of the examples which sprang to mind were of colonial animals - coelenterates, social arthropods. And of course this is reasonable - if individuals are differentiated for different tasks then, if they are to remain a cohesive population, a social structure must exist. But I have an example which I think is intermediate between the acarine hypopus and the social insect. The desert locust produces a migratory form which is morphologically and behaviourally different from the normal solitary form. The differences are maintained over generations, each capable of breeding true and yet also capable of generating the alternative form. For any individual there is the possibility of two life forms, two life styles. There is no reversible transformation of form in any individual however.[34] As another example I now recall the Western tent caterpillar, in which sluggish and active forms vary in their proportions within a population according to the age of the population.

ALPHA : But in the latter example, is there not a genetic component to the variation in form. I seem to remember that some females produced colonies of the active forms and other females colonies of the sluggish forms. That would suggest some sort of variably balanced polymorphism, rather than individual change.

BETA : Your memory is basically correct, but there was no absolute segregation of the active and sluggish forms within the offspring of single females. Only tendencies to produce more of one type.[35] Which, in an attempt to show that this need not be the result of absolute genetic difference, brings us to consider possible mechanisms of control of individual change. At what point is the form of the individual decided ? - the egg ? - the gamete ? Is the cue for switching a single one ? Double, involving the state of the parent individuals ? What possibilities exist within the currently accepted genetic framework to explain trans-generational maintenance or change of form ?[36]

GAMMA : I begin to feel lost. The purpose of our present discussion eludes me. I fail to see where we can reasonably attach this argument to Acarus siro.

BETA : We are conjuring up riders to be appended to population models, so that these may be correctly used. Acarus siro serves only as an example on which to display these imaginings. We are now discussing change, of form and behaviour, and the mechanisms which control change.

In the last section we explained the existence of Acarus siro and its very similar close relatives as stable points in a fluxing genetic manifold. Let me now propose an explanation based on genetic switching. This explanation, as the other, is neither suggested nor denied by current knowledge. The space of our ignorance here is large enough for very many explanations. I have no desire here to present the most likely explanations, but only to suggest types of explanation in such a way that fundamental properties of all organisms are revealed.

ALPHA : And what fundamental properties are these, that so much undermine our present mathematical theorizing ?

BETA : Be patient. For the moment let them remain implicit in our discussion. I am at present only preparing the ground for a major critical attack on a school of ecological modelling; what revelations there are will be best left until that time. Let us return to Acarus siro.

The differences between the various siblings of the A.siro species group are small. The different forms are generally allopatric. Let me suggest that these species are merely differences of expressed form of the same genotype, expression being controlled by environmental cues.

ALPHA : But the forms breed true under wide ranges of conditions!

GAMMA : And do not successfully interbreed to a significant degree!

BETA : Very weighty objections. It would seem my case is a poor one. But yet .... Imagine that it is the case. Then would it not be reasonable to make switching difficult so as to avoid the inefficiency of continual change with fluctuating conditions; positive hysteresis switching between a small number of states rather than the resource-diverting wastage of continuous control. And further, to avoid the necessity for the young to adapt to their environment, each generation afresh, let them come pre-adapted, the switches set across generations. And then as to the lack of success of interbreeding, it is quite reasonable that such semi-permanent switching or blocking of gene sequences would make the fusion of gametes and subsequent nuclear division difficult.[37]

GAMMA : Wouldn't the change of form have been noticed at some time ? One would expect that such a remarkable occurrence would have been recognized immediately as being important.

BETA : But of course not. Our inherited view of things is of constancy of form. Transmutation is anathema to all the sciences. An unexpected form in a supposedly pure culture would be put down to contamination; in samples from natural habitats, such semi-permanent morphs would be regarded as separate species. The change is not one that could be observed by chance. It would demand detailed and conscientious observation of the production and development of individuals from generation to generation. And this presuming the conditions for switching are known. One can guess at the cues required bearing in mind the different habitats of the supposed morphological variants and the need for threshold, or similar large inertia, switches. But there must be many possibilities. It may be that the cue involves the hypopal stage, the environment of the phoretic host or gradual rather than abrupt climatic changes. These are types of change rarely manipulated in experimental studies, but they are major features of natural environments.

ALPHA : If your surmise were correct it would be virtually impossible to demonstrate systematically. And its disproof as a hypothesis totally impossible.

GAMMA : Not so. It would be possible to analyze the genetic material directly to determine the basic synonymity. Absolute differences could be displayed to disprove postulated isogenic relationships.[38]

BETA : So the idea remains falsifiable and within the realms of science. All to the good. But what of states of affairs intermediate between our imaginative suggestions. Perhaps a genetic manifold whose stable states are themselves potentially multimorphic ?[39]

ALPHA : But this is going too far. There must be assumptions of form, rules of specific constancy, if our study is to have any practical use. Absolute scepticism may be a stimulating and amusing pastime, but it always remains an easy escape from the responsibility of setting rules.

BETA : Except when it is meant as an antidote to dogmatic reasoning; shock therapy for the convention-bound.

Certainly our ideas must remain applicable to the real world.

Science by hypothesis and experiment is intended to ensure this. It is this applied interest that must be safe-guarded from the confines of conventions borne solely of convenience. Observation sets the rules of constancy; empiricism is the conforming principle.

By accepting any one definition of species we prevent ourselves from resolving those problems most crucial to our understanding of evolution and population dynamics. The shifting composition of populations subjected to fluctuating environmental conditions, in terms of both numbers and attributes of individuals, poses great problems for those who would characterize populations by estimates of average behaviour.

5.2 General Hypotheses

GAMMA : We have already come a considerable distance from the specific subject of our study - Acarus siro - so let us now turn explicitly to questions of a more general nature. We will continue with your informal logical analysis, Beta, but we must now shift our attention from individuals of single species to groups of animals - populations and communities - and the interactions between various levels of organization of such groups.

ALPHA : What approach do you intend to take with this problem? Do you think we can productively discuss such matters remembering the difficulties that arose in discussing the responses of single species ?

BETA : I would take the line that the properties of any one level of biological organization are partially divorced from the properties of the subordinate level because of the control mechanisms of the latter. Therefore the properties of each level may be treated in a gross fashion as independent phenomena. The characteristics of the superior level can be abstracted from the lower level noise in which they are embedded.

ALPHA : I think you have defined your class of hierarchies too loosely. Such independence of levels may be a valid working hypothesis in the case of a distinctly co-ordinated system, for example the individual organism, its organs, cells etc., but without evidence of a co-ordinating system akin to the nervous system, there seems no reason to assume this independence.

BETA : But to do otherwise is to accept a view in which the properties of populations are synthesized from those of individuals, and those of the community represented as a matrix of apparently independent quantities. Difficulties arise then because the richer the total pattern becomes, the easier it is to abstract component patterns of limited application, which although in some senses allow empirical substantiation may nonetheless be spurious.

Mistakes of this sort lead to classes of definition which can be applied to any system in retrospect, but which cannot be used to predict events because they are dependent on many external variables. The unavoidable incompleteness of these definitions is explicitly recognized by their proponents in order to provide an escape clause with which to explain away events which appear not to conform.

ALPHA : But these are definitions, not hypotheses in the strict scientific sense. To attack them on the grounds of a possibly spurious correlation is quite impermissible.

BETA : I would agree with you if these definitons were left as mildly interesting, tentative and <u>independent</u> observations. However it seems to me that the ecological scientific community may attempt to meld these quasi-independent definition classes into an ecologist's periodic table, in which population structures are defined within orthogonal sequences of relationship. It is in this venture that the untested, indeed untestable, nature of these definitions becomes important. The chemists' periodic table reflects underlying similarities of structure; in contrast, these ecological definitions form a composite whose similarity with reality has been forced in a verbal equivalent of polynomial curve fitting. To stretch an analogy, while a holographic image of a telephone is a faithful superficial representation, one would not expect it to work and thus one would be unable to determine its mechanism or predict its behaviour.

GAMMA : But what sort of definition are you talking about ? Can you give examples ?

BETA : The most obvious are those which attempt to categorize populations and species on a functional level. The best known of these schemes is the r-K spectrum approach, with its admixture of related gross characteristics such as specialist/generalist, ephemeral/perpetual, and apparent/non-apparent. [40]

5.2.1 The characterization of populations

GAMMA : Would you say then that objective and universal characterizations of populations were impossible, Beta ?

BETA : I would hope not, for the term 'population' has been long used, and despite the difficulties and variations in its present use, I would like to retain it as a general term for groups of organisms with genetic intermingling slightly less than that implied by the use of a term such as deme.[41]

GAMMA : In what terms then would you ask that populations be described ?

BETA : We must examine population characteristics which transcend the properties of the individual organism.I would suggest that the first characteristics to examine are those of internal structure and of distribution. The structure indepehdent of location, that is the sub-grouping of the different types of organism - morphological or behavioural variants, could then be used in conjunction with some measure of the distribution of the sub-groups over the environmental surface they inhabit.

GAMMA : Are you considering the relative dispersion or aggregation of the individuals or of the sub-groups.

BETA : Both, separately. From the extremes of a population of clumped sub-groups of clumped individuals, to that of a population of dispersed and isolated individuals.

ALPHA : By what criterioh would you judge aggregation or dispersion. If we are talking about a classification useful for dynamic enquiries, then the index of dispersion cannot have an absolute spatial basis. An index based on relative space, scaled to individual size, is similarly inadequate in failing to distinguish fast and slow moving organisms. A functional classification must describe the rate of interaction of individuals, and therefore has to include size and mobility as scaling factors.

GAMMA : But what scale does this frequency rate have ? Again obviously not absolute - it cannot be measured in contacts per hour for instance. So it must be related to the life cycle of the organism.

ALPHA : The point is easily dealt with by measuring contacts as a percentage of time. The absolute duration of the measurement interval then controls the precision of the frequency rate estimate.

BETA : A simple measurement of contact frequency would still be inadequate, failing to distinguish the degree of clumping, the numbers of individuals contacted. A two-dimensional graphic representation showing rates of contact for individuals contacted (see Figure 5.2.1) would display both overall dispersion and gross substructuring.

Further, if a third axis were introduced - time, representing the life history cycle, changes in the patterns of contact through the life cycle could be displayed.

ALPHA : But what would be the advantage of such a display ? I think that such a representation of the interactions within a population would have the same faults as many of the descriptive indices you have been at pains to criticize - namely that, in order to construct such a representation, one must average individual patterns, thereby losing information.

BETA : Of course. But the answer to the problem is not to abandon descriptions in a search for some one definitive charactersitic. Descriptions must multiply,but only those descriptions which can be objectively justified and demonstrated. The extent of differences within populations must be explicitly discussed and estimated, and populations thus described in terms of numerous simple characteristics.

As well as contact frequencies, there are the temporal structures of co-ordinated or independent generations, measuring the relationship between genetic lines within a population, and of delayed or immediate generations, measuring the delays between parent and progeny active states.

Figure 5.2.1 A possible scheme for graphically illustrating the interactions of individuals of a species, so as to display the internal structure of populations in respect of aggregation and absolute degrees of interaction.

Case (a) might represent a species in which individuals form small stable groups which are isolated from other such groups e.g. wolf packs.

Case (b) might represent species in which individuals are dispersed, having infrequent and random contact with others e.g. spiders.

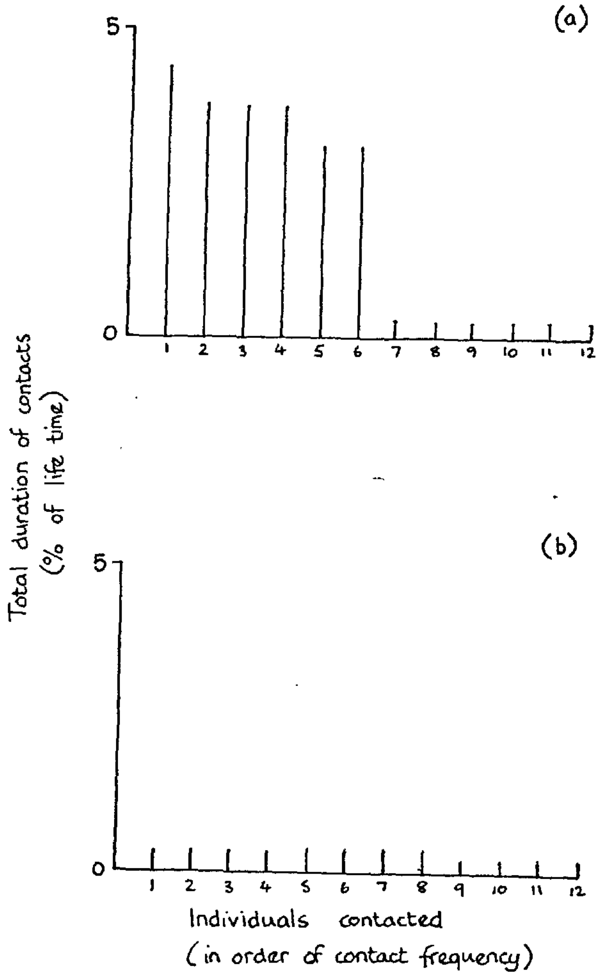

(a)
5
0
1
2
3
4
5
6
7
8
9
10
11
12
Total duration of contacts
(% of life time)
(b)
5
0
1
2
3
4
5
6
7
8
9
10
11
12
Individuals contacted
(in order of contact frequency)

Figure 5.2.1

Moving then to physiological characteristics, one must consider the mode of energy utilization : carnivore, herbivore, omnivore etcetera, and also the level of energy utilization, whether the food is of high or low quality - whether the metabolism is geared for a low ratio of useful energy to throughput energy or for near parity.

These are all simple characteristics which can be directly gained from observation. Such empirical characteristics must form the basis for our population descriptions and classifications.

ALPHA : But don't these individual characteristics then amount to the same framework as proposed by such schemata as the r-K spectrum.

BETA : No. Because the characteristics remain independent in this case. Composite frameworks make correlative assumptions. These assumptions have not been shown to have sufficient empirical support to allow any subsequent theoretical excursions from their premises. Only by returning to classifications based on simple characteristics can we hope to understand the patterns of correlation of these characteristics which we subsequently observe. We cannot expect simple schemes of classification of populations. To use skimpily researched composite characteristics as fundamental categories is an approach best left to astrologers.[41]

5.2.2 Levels of effect

GAMMA : The ordering of species in ecological systems may be regarded as a hierarchical structure.[42] In describing the many-to-few aspects of the relationships between populations and communities, there may be advantages in assuming the hierarchy to be a strict and necessary organizational arrangement.[43]

BETA : Only if it meant that fewer components of comparable complexity were needed for our models of the world. In a gross sense the components of any one level are necessarily simpler than the composite they form. But whether sufficient descriptions of one may be simpler than the other depends entirely on the partitioning and sub-structure of the higher level - on its organization.

GAMMA : So the behaviour of the higher level may be simpler than that of its individual components, or vice versa ?

BETA : Apparently so. Imagine a group A composed of individuals a. Now ignoring the possibility of some incorporeal influence affecting the entity A independently of the a's, the behaviour of A must be some function of the characteristics of the a's and of the interactions between these characteristics. Are there a priori considerations which will allow us to specify the conditions under which simplifying or complexifying interactions will take place ?[44]

ALPHA : Yes. We have already talked about the damping effects of control systems at the levels of the individual and of the population.[45] Such control systems are essential features of biological organization and must be widespread enough for us to assume that for any system level there are critical sizes of event below which no effect is observed at higher levels, because even without such damping control systems there must level events so small as to have negligible effects on higher levels of organization.[46]

BETA : You have misinterpreted the effect of structure on this transmission of effects from level to level of biological hierarchies. The true effect is not to increase the diminution of perturbations, but to increase the potential for changing the magnitude of the transmitted effect. The change may be a decrease or an increase. The nature of the change is determined by details of the structure relating the levels.

GAMMA : So one could predict the nature of transmission knowing the hierarchical structure.

BETA : Theoretically speaking the answer must be yes. But the relationships between hierarchical configurations and types of transmission have not yet been elucidated.

ALPHA : Even so, there must still be events so small as not to be transmitted.

BETA : Again, theoretically speaking, yes. But in trying to define such event categories, there remains the intrinsic difficulty that complexifying interactions are by definition those that magnify low-level component events. It must be recognized therefore that, at any level of measurement of finite precision, low-level evnts may occur, immeasurable in themselves, but causing measurable events at a higher level of organization. This may be called the holistic theorem. The component in isolation is not the same as the component in organization, and should not be regarded as such. Levels of significance of behaviour of a component can only be determined in relation to the pattern of organization in which it is embedded. Organizational structure is always the major determinant of system behaviour. This fact may only be ignored in relation to randomly organized structures, if we may call these structures, where simplifying and complexifying interactions may be regarded as nullifying each other's effect, and a normalized account of system behaviour, based on major component characteristics, assumed. For systems with the least vestige of organization, which must include all ecological systems, one cannot generally predict whether an event of any given size will have an effect on a higher level. The transmitted effect will as much depend on when and where the event occurs as on the size of the event.

ALPHA : Your argument is all very reasonable, but can you demonstrate it ?

BETA : One need only go to the literature of the design of computer logic networks for demonstration. There is a study of large numbers of similar small elements, structurally grouped for a particular purpose. Even with such well-planned organization, high level imprecisions occur because of events smaller than the functional time-base unit of the individual network elements. These are magnified in effect, accidently, because of the differential transmission times of the various logic routes of the networks. As a result of this, designs for logic networks can only be tested in prototype, or by using detailed element-by-element simulation models which operate with a precision far greater than the nominal precision of the real network. Analytic testing of the network designs is impossible.[47]

ALPHA : But this isn't a biological system.

BETA : No. It is a system of known structure and known purpose, with fewer levels of organization, fewer basic components, more uniform environmental conditions, and, by several orders of magnitude, less complex components than characterize high order biological systems.

Bearing this in mind, the use of analytical methods of enquiry for the study of biological systems seems optimistic, not to say incautious when given practical credence. The truth of the holistic theorem is itself a caution against the reductionist philosophy which has fostered such scientific methods.

5.2.3 The structure of communities

ALPHA : Would you suggest then, given that the various levels of organization may be almost impossible to relate by oonventional scientific observation, that we also view communities as entities in themselves, to be studied independently of the populations of which they are composed ?

BETA : Not quite indepently of their component populations, as I hope that a reasonable classification of populations would allow communities to be structurally defined. But I would argue that the overall behaviour of the community be examined as if it were an autonomous object under evolutionary laws. Community organization is a useful conceptual device. It has allowed ecologists to loosely identify and correlate species occupying defined geographical regions.

ALPHA : But the sort of cohesion you require demands obligate associations between populations of different species...

BETA : Or at least between types of population.....

GAMMA : And which most certainly exist - one could not have a predator population without a prey population, but often the relationship is not specifically defined.

ALPHA : Is that sort of interaction appropriate to other associations ? Are there non-specific structural blocks which are universally linked in a higher level of energy use, at a level sufficient to justify thinking of communities as cohesive assemblages ? The considerable research effort which has already been put into community ecology has failed to reveal any general and practicable rules.

BETA : That is because the research has been restricted to piece-meal plans of analysis, in which cross-sections of the community structure are examined, slices along single axes of description. Zoology-minded ecologists have usually concentrated on the analysis of food/energy pathways, either at an abstracted high level, for example the producer-herbivore-carnivore-decomposer energy schemes of Odum, or at a detailed local level where specific or generic groups are located in a food web. The corresponding analyses of the spatial and temporal aspects of community structure remain similarly isolated, either enmeshed in detail or diffused in abstraction.[48]

ALPHA : If the path to understanding communities does not lie with such ventures, then where does it lie ?

BETA : Many of the problems associated with developing elegant theories describing communities can be traced to the property of multi-scaling. In time and space the community is divided into a continuum of differently scaled systems. These systems appear to be interlocked independently of scale magnitude. Although such problems are often examined in the context of a specified interaction, there seems to be neither general theory nor even general theoretical discussion. In fact the scale problem, especially in the case of interactions of organisms of vastly different size, is very often ignored. For example, May (1973a) dismisses symbiosis as important regions, ignoring the almost universal harboring of gut-flora by animals. This relationship is truly mutualistic and virtually obligate - certainly the chances of survival of either partner are very small should the other partner cease to exist.

ALPHA : That situation is hardly one to be considered as symbiotic. The relationship is one between an organism and a fixed community which might almost be regarded as an organ of that organism.

BETA : The community is not fixed. It is determined by the material ingested by the organism, and in turn influences the physiological state of the organism. But the bounds of composition of the community, within which it continues to fulfil its obligations to the association, are flexible. The host and its gut-flora are co-adapted for mutual maintenance, but are not immune to extraneous influences and invasions by non-adapted microbes.[49]

In artificial hierarchical systems where differential scaling is present, considerable effort must be applied in order to align differently scaled levels. One need only think of the devices and processes needed in computers to integrate the temporal universes of core memory, drum memory, processor and consoles, remembering that here we have a designed and strictly ordered hierarchy, to imagine the complexity of effect possible in the relatively disordered world of biological communities.[50]

ALPHA : But that lends great support to objections to the community concept. The complexity of interaction of the organisms in any area makes highly unlikely the level of regulation required to make a cohesive whole of the species assemblage. You cannot still seriously support the community as an autonomous unit.

BETA : On the contrary, the empirical fact that, in some senses, communities can be viewed as cohesive assemblages, and have been viewed as such, suggests the degree to which individual organisms have solved the problems of co-adapted evolution.[51] Static ordering[52] – barriers and partitioning – obviously plays some part in the regulation, but dynamic controls are also necessary for those situations where barriers cannot be maintained, for example where co-scalar interactions of different sorts occur together or where an interactant is too large or too mobile for feasible barriers.[53]

This question of community evolution and the extent of its internal co-operative activity depends on the stabilization of communication between organisms, or at least on the stabilization of patterns of communication.[54] The overall stability of a community must then be viewed as the culmination of an historical sequence by which the community components become acclimatized to a particular habitat.

ALPHA :But how do you account for the development of such supra-specific structures ?

BETA : I think the explanation rests on the concept of foundation species in communities. Natural selection/evolution is a sufficient is a sufficient explanation for adaptive community structure given either climatic predictability within the generation time of the major foundation species, or a flexible foundation species.

The foundation species provides a stable habitat for colonization, and a regenerative, recursive proliferation of microhabitats necessarily occurs given immigration of suitable species.

GAMMA : Why 'necessarily occurs' ?

BETA : Imagine an isolated patch of a producer species - a plant. The plant has structure, its tissues differentiated. A herbivore species enters. It may be one that will consume entire plants or perhaps only minor portions of the plant. But there is some correlation between the consuming capacity of the herbivore and the structural complexity of that herbivore. So if we regarded each tissue of the original producer as typifying a separate microhabitat, then the addition of herbivores at least results in a conservation of unutilized habitats. If we then remember that the herbivore regularly provides further microhabitats for detritus feeders, for decomposers, and again that micro-organisms may exist in any microhabitat subsisting on throughput energy without destructive activity, then the beginnings of the microhabitat explosion can be seen.[55]

GAMMA : And if there were variations in soil structure, available sunlight or water across the producer patch, then a further source of microhabitat diversity would be available.

BETA : That is certainly true. But such fundamental diversity in the abiotic habitat is not necessary to generate further diversity at the base biotic level. Even with a uniform abiotic field, extra levels of diversity can be generated by considering scale effects of both time and space. The basic producer patch has a space component. If species enter which are small in relation to to the plants and whose mobility is small in relation to the producer patch, then point immigration allows the same basic microhabitat to be utilized by different species at different locations. This applies to phyto-parasitic and disease organisms which may then provoke a response in their host, differently according to the various species, inducing heterogeneity in the basic producer patch. Which again induces further scope for heterogeneity in successive trophic levels.

ALPHA : This is all very well, and satisfactorily explains the potential for diversity of organismic forms, but your suggestion that communities be studied in their own right must assume cohesion of the component populations within some necessary pattern of structure. Are you seriously asserting such a teleological description of populations and communities ?

BETA : The teleology is illusory, based on a neglect of fundamental characteristics of natural selection, namely that selection produces life-forms favouring persistence and that the material for selection is limited in function by its own evolutionary history. The latter constrains the solutions of the former dynamic process. As a result there must be necessary patterns of structure. All communities are solar-energy based, and use chemical-bond energy transmission. Matter must be re-cycled if a community is to persist, both because it is locally limited and because end-product accumulation would interfere with the energy fixation and transmission. Efficient energy interception requires that the producers have structural and energy-fixing components; maintenance of these involves other components. Herbivores must separate the energy-rich components from others. For each organism type the strategies for persistence range from individual production to individual persistence - the extremes suggested by the r-K selection nomenclature. The larger, longer-lived members stabilize the physical structure of the community against some environmental fluctuations by absorbing and damping these fluctuations. Ephemerals e.g.fungi, stabilize against other fluctuations, springing up to absorb transient accumulations of energy-rich and easily assimilable material which might otherwise upset the steady state of the more conservative community members.[56]

ALPHA : Again you make it sound like a planned venture to maximize energy turnover, the community geared to efficiency of transmission of energy and re-cycling of matter. A self-sufficient corporation of species dedicated to efficiency.

BETA : And again you have conjured up a teleology where none exists, by visualizing present-day community structure as the beginning rather than as the culmination of a temporal sequence.

Natural selection results in the appearance of more persistent corporeal bodies. If self-sufficiency favours persistence then a self-sufficient community will perpetuate itself. If the self-sufficiency involves re-cycling of materials in interspecific relationships then the organisms become efficient by natural selection, and must fill all habitats within the community to prevent the incursion of possibly disruptive new species.

The essence of the problem seems to revolve around the structure of the community - on patterns of type of major life style, rather than on the dubiously relevant abstractions of individual population dynamics. 'Stability' then becomes almost synonymous with 'evolved', with 'climactic'. The major features of the community are then co-adaptive action and tolerance.

The problems of stability, instability, pest outbreaks, population fluctuations etcetera, are mainly problems of semantics.

Ecology could do worse than import linguistic analysts to examine ecological systems and nomenclature. In many cases, attempts by biologists or mathematicians to clarify ideas of dynamic phenomena have, in gaining precision, perverted definitions. The caricature of reality which has thus arisen threatens our existence by its pretensions to practicality.

CHAPTER SIX - GENERAL DISCUSSION

The inadequacies of current ecological theorizing are becoming more apparent.[57] The influence of the physical sciences has had mixed results - beneficially there has come a greater awareness of mathematics, a desire for increased precision and definition; however too often this has led to an overzealous adherence to standard recipes, without regard to the nature of the raw materials. Hypothetical constructs have been erected and used as the foundations of extensively developed platforms from which to deliver universal statements, with a distinct lack of rigour in the testing of their initial assumptions.

If blame is to be apportioned for these scientific misdemeanours then a great deal must be laid at the feet of those planners who, carried away in the euphoria of the computer revolution of the 'sixties, saw digital decision making, with the power to handle huge quantities of data and the inherent precision of its algorithmic logic, as the cure for their ailing predictive powers. Their problem was to convince the doyens of the various academic disciplines to join them, so as to share the costs of these expensive machines. This was all too easy in the social climate of western civilization in those years - years of economic resurgence, quick answers, easy money, optimism and, above all, an uncompromising lack of uncertainty : he who hesitated was lost, and for the winners nothing short of mastery of the universe seemed the prize - the ages old dream of complete knowledge. Hard facts, unquestionable decisions were required- and these were produced, ream upon ream, by these new and infallible oracles. In ecology, the results of the ecological debates of the 'fifties, which had seemed poised to come to fruition in the decade following, were forgotten as naively simplistic mathematical models were resurrected by the power of computer simulation, which promised to supply the complexity of interaction so obviously missing from the models themselves, and further to give results accurate to the sixteenth decimal place.

In science generally, as elsewhere, the measure of prognoses was the cost of their production. To the ecologist came the greater monetary resources necessary for such computing pursuits, an injection of finance not unhelped by the pressure of the environmental protection lobby (which also gave ecology the prestige associated with major problem-solving disciplines). The resultant expansion of the subject, though greatly to be desired, was bought at the expense of a narrower approach to the study of the more complex levels of organism interaction - to justify the maintenance of increased resources it was necessary to continue to provide hard results. Ecologists with the desired aptitudes came into prominence, but by the end of the 'sixties they had fully utilized their somewhat limited mathematical backgrounds, and their taste for ecological games-playing was becoming jaded. Then, providentially, ecology received an influx of a particular breed of physical scientist whose own areas of research and philosophical predelictions had been overshadowed by the pseudo-mysticism of the new physics[58] (some physicists were the first scientists to realize that the spiral which promised to lead them to the solution of the universe was an infinitely receding helix - the reductionist dream was becoming a recursive nightmare), and who were ready to exploit unsullied pastures with their sophisticated analytical tools. This deus ex machina intervention revived mathematical ecology, which became complacent in the security of its powerful methods, assured of its direction despite the disquiet, disillusionment and bewilderment of other sectors of society.

An oversimplified, and perhaps in places exaggerated, picture of events. Ecological theorists are not blind to the faults that were produced by these pressures and have adapted their ideas to take account of the more obvious faults. But there has been a general unwillingness to subject the past to rigorous scrutiny - perhaps akin to the grown man's shame in remembering the follies of his adolescence. To continue to ignore the historical details is to erect an artefactual obstacle to the understanding of natural ecological processes. The more subtle assumptions fostered by the rejuvenated theories represent the greatest long term threat. It seems important to at least identify these assumptions, and where possible to discuss them in the light of relevant and current knowledge.

6.1 Ecological Stability Theory - A Critical Appraisal

GAMMA : How would you describe this area of study, Alpha ?

ALPHA : A precise definition of 'stability' was established and within the scope of this definition, the characteristics of various models of ecological systems are examined.

The definition used (see Section 1.1.4) has obvious merits - it is easily demonstrable using simple, physical (mechanical) models and further, the method used to examine the stability characteristics is easily visualized using the same sort of model - when the model is in equilibrium nudge it slightly and see what happens - if it returns to its former position or remains in its displaced position, it is stable; if it continues to move away from its originalposition it is unstable.

GAMMA : Why was a precise definition of stability necessary ?

ALPHA : Mainly because of the existence of ecological generalizations of the type 'Complex systems tend to be stable'. Obviously if such statements were to be examined critically then a universal definition of the terms used was necessary.

BETA : But it must be remembered that for there to be any advance in our knowledge of ecological systems, some point within the framework of definitions must have an empirical basis and justification. The posited relationships between the defined objects must be tested experimentally.

If the notion of stability used is generally accepted as a description of the behaviour of ecological systems, then it can be used to distinguish various proposed models of the system. And, conversely, if accepted models of a system are available they can be used to define the regulatory characteristics of that system. However ecological stability theory seems to have neither of these empirical anchors. Both the models and the stability definition are open to criticism as adequate descriptors of the real world.

ALPHA : But of course they can be criticized; they are simplifications of real world phenomena, with all the faults of abstaction.

BETA : Are the simplifications justified ? Perhaps this question will be resolved as we discuss a number of developed ecological model systems which are based on stability theory. For each we must locate the points at which the system development is empirically fixed and expand these in real world terms. These points are generally characterized by a log-linear response of a process of change to change itself.[59]

We must identify the general cases where linearity is not acceptable in such relationships.

ALPHA : But non-linear processes can always be approximated by linearity over a suitably small interval!

BETA : I entirely agree with you. That is not the type of linear approximation to which I object. I will translate my objections back to the parametric forms of the models so as to expound the real world implications.[60]

Perhaps then we will be able to delimit the areas of valid application of stability theory to ecology, and to establish guidelines for its use.

ALPHA : So you will admit that there are valid uses for stability theory in ecology ?

BETA : I think that that will be easier to discuss when we have worked through the examples, when we might also discuss the philosophy behind the method, which seems typified by Comins's (1977) statement that 'it is as good to provide an exact answer to an approximate problem as to provide an approximate answer to an exact question.' I hope to make it clear that the logical framework supporting the general application of stability analysis to ecology is tenuous and certainly demands thorough discussion, and that very often the circumstantial evidence supporting its use under specific conditions is fragile.

ALPHA : Isn't this simply an antagonism to mathematics, a yearning for the amateur naturalist's approach to ecology, a preference for simple observation over rigorous science ?

BETA : The target of my criticism isn't theory or modelling in any general sense but that specific approach which equates theory with a particular mathematical form. My motivation is a desire to refute the idea that methods can always be successfully transferred from one science to another - an idea which is regarded almost as a truism when the transfer is from that purest of sciences, physics, to chaotic, inelegant biology.

This latest excess of reductionist philosophy seems entirely at odds with the spirit of biology. Such marked intuitive disquiet as it has engendered should have provoked a rigorous discussion of the concepts involved, even if the discussion could not attain the precision and elegance of formal arguments.

ALPHA : Without formal argument your case lacks weight. If all you can do is oppose the precise formalism of modern ecological theory with ill-defined opinion, you cannot expect to be taken seriously.

BETA : Several of the most highly regarded thinkers of the century came to recognize the limitations of conventional logical analysis.[61] Perhaps we would do well not to regard this position as resulting simply from a failure to describe the world in such formal fashion, that is as a reaction to disillusionment, but rather to ascribe it to the recognition of a different classification of externals[62]; and to start along the path to understanding complex relationships by examining the properties of complex systems, unfettered by the traditional desire to differentiate and isolate.

Any reasonable discussion of the merits of these two basic philosophies can only be hindered by the circumstantial validation and exaggerated notion of applicability typical of ecological stability theory.

What can, and what cannot, be regarded as reasonable paths to knowledge of the real, that is common experience (?), world must be distinguished so as to clear the ground for productive enquiry.[63]

6.1.1 Time delays, density dependence and single species oscillations

GAMMA : How appropriate that our first example should be the paper that was the raison d'etre of the experimental work described earlier. The paper (May, Conway, Hassell and Southwood, 1974) was summarized in Section 1.2.4, but perhaps you would like to state the rationale of the arguments presented, Alpha ?

ALPHA : The stated aim of the paper was 'to identify the conditions giving rise to stability and oscillations in a single species population interacting with a maintained resource, and to state how they are fundamentally related to one another'.

Two population characteristics ($T_R=1/b, \tau$) were examined, one to do with the period of change of population number, the other to do with the rate of change of number with density.

BETA : It is important to remember that we are dealing with gross changes in number of the populations, and not merely with some mortality component of population change.

ALPHA : The one characteristic, b, is equivalent to the slope of the density-dependent mortality in K-value/log-density plots. Ranges of values of b, T_R and τ are are identified as requirements for various patterns of population change.

BETA : Relationships which are entirely fatuous! If a single b-value characterizes a K-value/log-density plot then the underlying dynamics are, by necessity, well described by the density-dependence model :

$$N_{t+1} = (\lambda N_t^{-b}) N_t$$

However one cannot argue either from oscillatory population patterns to b, T_R and τ, or vice versa, in any sense other than that of displaying synonyms within a formal, that is tautological, system; and one certainly cannot argue that certain values of b, T_R and τ give rise to stability and oscillations so as to imply that these are empirically estimable parameters of independent existence, as for instance in paragraph four of the summary : 'a general requirement for stability is that the characteristic return time, T_R be larger than the time delays (τ or T)'.

Perhaps the point will be clarified by an analogy : circles are found in nature - cross sections of plant stems and animal bones, fairy rings and numerous other examples. For each of these examples one can identify and measure various abstract properties of circles - the radius, side length of the circumscribed hexagon, $x^2 + y^2 = 1$, and so on. These properties, although describing the circle and hence the reality, are not necessarily to be identified with the reasons for the existence of the real circle - they are only descriptions.

In this light the demonstration of the fundamental relationship between the model parameters T_R and τ, although true, must be regarded as trivial.

ALPHA : Would you deny that the paper has any value then ?

BETA : The ecologically important point, and the only point at which this paper truly enters the realm of science, under a Popperian definition at least[64], is in the nature of the relationship between k-values and log-density. The analysis demands that this be linear or at least be approximated as linear in the region of the postulated equilibrium. It is here that the development is empirically fixed, and at which experimental testing may be carried out.

GAMMA : But what about the examples given ? The experimental results used to illustrate the paper appear to fit the theory well, and the paper as a whole shows great cohesion.

BETA : A cohesion which on close examination is no more than a superficial gloss. There are several points at which statements contributing to the overall tone and plausibility of the developed argument are made either with insufficient justification or are justified erroneously by implication-in-context[65], though I admit that the latter is very difficult to avoid. The illustrative examples used, of types of population response, are the most important of these false justifications.

ALPHA : What fault is there in the first example ? Population curves of three strains of the stored-product beetle Callosobruchus chinensis are given (see Figure 6.1.1). The changes shown are consistent with $\beta\tau$ values of 0.8,1.5 and 2.0

BETA : Indeed, the changes shown are consistent with those of the model at the three parameter levels you specified. But those values are estimates from the data under the assumptions of the model, and no more. Yet the implication seems to be that the differences in response are the results of analogous quantitative changes in a control mechanism common to the three strains, otherwise the example might as well contain the curves for three different species. No evidence is presented to support the common mechanism hypothesis, and although a common mechanism is likely - the three after all being strains of a single species - this is no way to conduct a scientific argument.

If one considers the variety of influences which must affect

Figure 6.1.1 Population changes in three strains of the beetle, *Callosobruchus chinensis*, under identical culture (from May *et al*, 1974, after Fujii, 1968)

Figure 6.1.2 Population changes of the water flea, *Daphnia magna*, cultured at (a) 18°C and (b) 25°C. (from May *et al*, 1974, after Krebs, 1972, and Pratt, 1943)

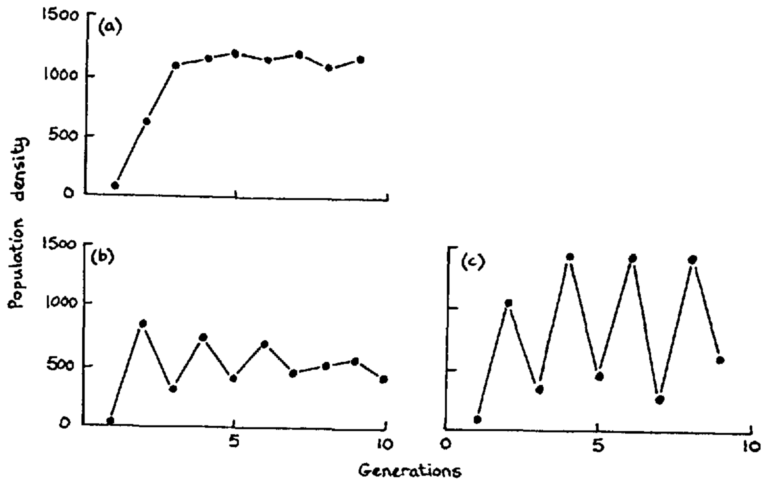


Figure 6.1.1

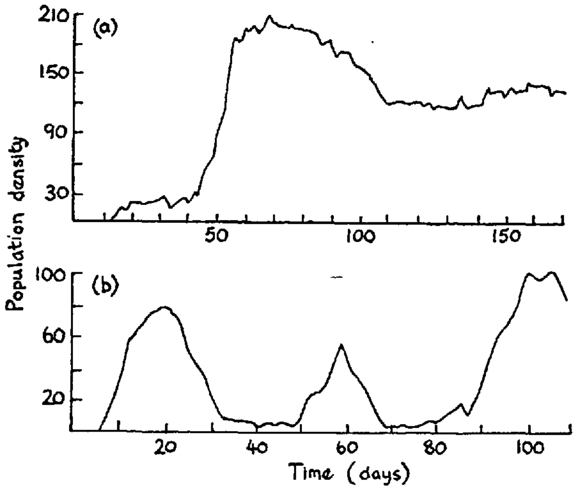


Figure 6.1.2

population number responses it seems improbable that these would interact and balance so as to produce a simply described total response. The examples suggest that under certain circumstances regulatory systems do collapse to such simple forms. The extrapolation of stability analysis conclusions to general ecological problems demands the assumption that this reduced simplified regulation is typical of all populations under all circumstances.

ALPHA : Does the second example, concerning Daphnia magna (see Figure 6.1.2), fall to the same criticism ?

BETA : Yes, again there is only a descriptive correspondence; the functional correspondence is assumed : 'Presumably, increased temperature has led to increased competition'.[66]

ALPHA : But that is a realistic and reasonable assumption, and one should always accept the simplest assumption.

BETA : Such an appeal to parsimony, though not unexpected, is quite inappropriate to this discussion. The merits, demerits and meaning of the philosophy exemplified by Occam's Razor, as applied to ecology, have not to my knowledge been discussed, let alone resolved. Suffice it to say at present that the same philosophy leads to the development of stability analysis, and it is a tautological error to support one with the maxim of the other.[67]

GAMMA : Continue with the examples before we discuss general ecological philosophy. What comments have you about the next example ?

BETA : That is even more sparsely described than the previous two. A simulation model is invoked (see Figure 6.1.3) in which increased temperature causes 'a change from monotonic damping to oscillations. This, too, is mediated through increased competition at

Figure 6.1.3 Results of a simulation model for the bug <u>Leptoterna dolobrata</u> in grassland showing the effects of temperature and the interval between egg hatch and flowering on the stability of the insect population. Heavy stippling denotes increasing oscillations; light stippling, damped oscillations; blank squares, monotonic damping . (from May <u>et al</u>, 1974)

Figure 6.1.4 Density-dependent relationships due to competition for a fixed quantity of food in laboratory experiments (a) Larvae of the sheep blow fly (<u>Lucilia cuprina</u>) (b) larvae of <u>Drosophila melanogaster</u>. (from May <u>et al</u>, 1974, after Varley <u>et al</u>, 1973)

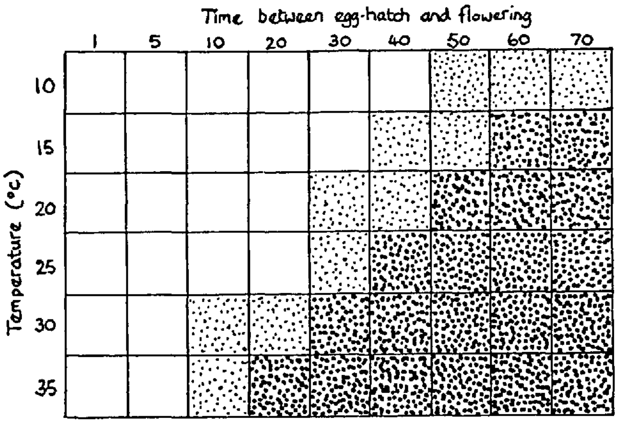


Figure 6.1.3

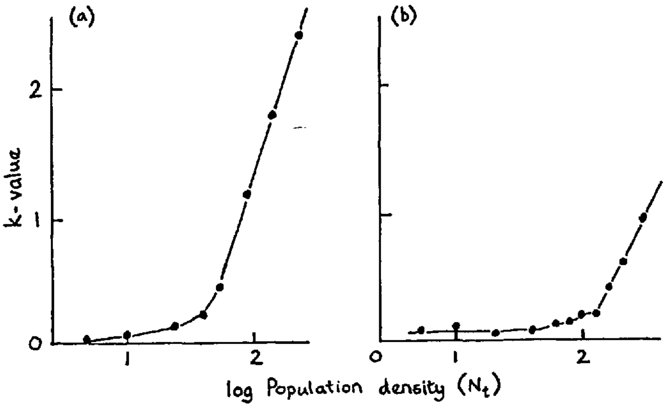


Figure 6.1.4

higher temperatures'. This last sentence suggests that the observed temperature-stability relationship might be a product of the modelling strategy rather than of the data abstracted from reality. However no details of the simulation are provided, either in this paper or in the referenced work from which the example was taken. I think, therefore, that the value of this example must also be doubted.[68]

GAMMA : So we are left with one final example to illustrate the stability model.

BETA : This last example, from Nicholson's (1954) blowfly experiments, fully illustrates the possibility of simplified responses in real populations but, as in the first two examples, this is all it evidences.[69]

ALPHA : Then you don't regard any of these examples as reasonable support for the theoretical model ?

BETA : Certainly not. But I believe their inappropriateness has been masked by the generally polished and confident presentation of the paper. There are some minor, but nonetheless irritating, points which make the presentation appear more sound than it really is.

The distinction between populations and population models is not maintained and, in an area of discussion where vocabulary is imprecise, misapprehensions rife and reading time limited, the authors have a duty to avoid such carelessness. While they may have recognized the distinction, others may not be so perceptive. As some of the general conclusions of this paper have appeared in subsequent publications as facts of ecology, a rigorous analysis of the original ideas is certainly necessary.[70]

Of more concern is the manner of the authors' dismissal of certain models which produce neutrally stable cycles. These are cast aside in such an offhand manner : 'Strict discontinuities of this kind are biologically unrealistic', that one is not surprised that the reviewers were taken in by the authority of the statement . The statement is left without direct support, and no support is forthcoming from the literature cited - the primary (mathematical) source merely states that the functions involved may not be biologically feasible. No opinion is given in either direction, and the tone of this rider is of an honest admission of ignorance of the limitations imposed by biological form.[71]

In fact, discontinuities in such functions could easily describe behavioural switches, and the strictness of a discontinuity brought about by the synchronization of a population. Both of these phenomena are well represented in the biological literature.[72]

ALPHA : The stictness of the discontinuity would be hindered by spatial separation of the individuals and could therefore be objected to on the basis of these two essential aspects of reality.

BETA : But those arguments equally apply to most population models, including those accepted by the authors of the paper we are discussing. I don't see how such criticism can properly be used in this context.

GAMMA : How would you summarize your criticisms of this paper ?

BETA : The entire development of the paper hinges on the linearity of the k-value/log-density relationship. Discussion of the realism of such a relationship is likely to be difficult and complex. The authors bypass the issue by a simple mathematical extrapolation of the assumption, classify the results of their extrapolation with tautological synonyms, and then justify their classification with examples which ambiguously conform to the desired patterns. The burden of proof for this universal classification of populations must lie with the proponents of the system, yet all they offer is the circumstantial evidence of superficial homologues, while ignoring the root of their argument.[73]

6.1.2 Stability and complexity in model ecosystems

ALPHA : You maintain that the application of stability analysis to the question of biological time delays and their effect on population behaviour is only trivial description. To what extent do you regard other applications of stability analysis as similarly flawed ?

BETA : I think that your question will best be answered by reference to a major work dealing with the analysis of stability in biological systems - the book 'Stability and Complexity in Model Ecosystems' by Robert M.May. Although Professor May is at pains to point out that the book is about model ecosystems, everywhere is the implication that these, despite their necessary abstraction and simplification, provide general insights to real biological systems.[74]

ALPHA : But the simplifications and ommissions are explicitly stated so as to allow subsequent refinement of the conclusions in the light of these additional factors.

BETA : The implicit assumption <u>remaining</u> that such an additive alteration of the models is valid. I would maintain that the orthogonality of these various characteristics of organism and environment is the critical area of discussion, and that the resolution of some major definitions of characteristics is a necessary prerequisite of the analysis of detailed interactions.[75]

However, for the moment, we should examine the details of the book discussing each point, in turn, as it arises in the text.

GAMMA : The first points made in the introduction are summaries of subsequent chapters, and so should be left to arise in detail. The ommissions from the model structures are stated - lack of evolution, lack of genetic realism, lack of environmental heterogeneity.

BETA : Disclaimers admirably phrased so as to divert rather than answer any criticism that might arise.[76]

GAMMA : There then follows a discussion of the function of general models. May describes general ecological models as 'strategic', sacrificing precision in order to grasp at general principles, and compares them with the perfect crystal model of physics. They are placed at one end of a continuum of model types, whose other end is represented by detailed and realistic 'tactical' models. The general models 'are at best caricatures of reality, and thus have both the truth and the falsity of caricatures'(p.12 : page numbers following quotations refer to May, 1973a).

BETA : Admirable defences of the tradition of modelling. But remember the points made here and, while we discuss the rest of the book, ask yourself whether, in fact, it is accuracy and not precision which is sacrificed in the models presented. The essence of caricature is the altering in proportion of characteristics of the subject, not the creation of new characteristics or new interrelations of characteristics. Here I must criticize some definitions presented in the book.

GAMMA : Which is where the second chapter starts, by presenting various meanings of stability. The first is that of neighbourhood stability 'that is, stability in the vicinity of an equilibrium point in a deterministic system'(p.13). May states that 'one is interested in the community equilibria where all the species' populations have time-independent values, that is where all net growth rates are zero'(p.13).

BETA : One is, is one ? I personally find such a state of affairs a very unlikely object of interest. So who does find it interesting ? And why ?

ALPHA : The interest is obvious. We need to know how ecological systems will respond to disturbances from their normal stable states.

GAMMA : Mankind needs to utilize the resources of the earth more fully, more efficiently. We must be able to offer predictions as to the effects of our intended manipulations of the natural world, and to offer guidelines for the construction of artificial ecosystems.[77]

BETA : Very commendable! And of course the way to do this is to examine systems in numerical stasis, and to see what happens when something upsets this precious balance.

ALPHA : With a good description of a system at equilibrium, one can then judge how well a system will cope with disturbance. The neighbourhood stability analysis judges the effects of small disturbances, the global analysis the effects of more major change. The effects can be used to classify the system as either stable, if the disturbance is diminished by the system response, or unstable if the disturbance is magnified.

BETA : But are such situations relevant to biological systems? Are populations and communities geared to numerical constancy ?

ALPHA : Not necessarily simple constancy; constant periodicity is also included in the definition of stable.

BETA : Yes, but even so, are biological systems characterized by equilibria in that sense. I would say no. Some individual populations may so be structured, but populations generally not so, and communities most definitely not so. Stable communities show neither a constant structure nor constant numbers but a constant potential response to conditions. The more stable the system, the more controlled and ordered its transitions from one structural or numerical state to another.[78]

ALPHA : You are only hiding numerical constancy by your talk of potential states. Are you not there talking of, for example, spores and other resistant stages which allow apparent sudden changes of community structure ? But these are as much individuals as are fully developed specimens.

BETA : Would you allow the same latitude of definition to less well-protected examples - to the seeds of grasses, to the eggs of fish ? If so, then the idea of numerical constancy must surely be abandoned.

But I did not mean to include only such well-defined examples of potential growth. I had in mind also the less immediately perceptible potentials of modes and levels of behaviour and metabolic process. Structural flexibility is thus partially divorced from the replacement and turnover of individual organisms.[79]

The multidimensional landscape assumed for stability analyses is set by the assumed equilibrium and the assumed, constant, functional relationships between system variables.

The true biological state is more closely represented by a response surface which is always flat over a defined area at a defined time; this stable area moves over the surface as the response equations alter parametrically and structurally, driven by external environmental variables.

ALPHA : You have replaced enquiry by tautology. You have defined systems as stable. You have dissolved away the point of discussion.

BETA : Not so, not at all! Imagine the response surface as a flexible sheet, made of thin rubber, the state of the system represented by the position of a heavy ball bearing. The sheet is suspended by its edges - the area perhaps being equivalent to the resilience concept - and the response changes represented by manipulations of the surface.

ALPHA : You still have definitional stability. However the surface is manipulated the ball bearing will find a stable equilibrium.

BETA : If the manipulations are discrete and infrequent events then that will be so, especially if the manipulations are slow. But if the manipulations combine in a continuous, rate-varying flexion of the surface, the resulting motion is very different.

ALPHA : Too responsive though. There is response to the slightest flexion of the surface; there is none of the control typical of biological systems.

BETA : Which must, therefore, be incorporated by a sculpting of the surface and the fabric of the response. A thickening of the sheet to represent the structurally stabilizing effects of large, long-lived components, for example trees, and the extension of some point system states to define plates within the surface. In short, an inertial component is added.

ALPHA : Haven't we now returned to an analogy indistinguishable from that specifying the stability analysis approach.

BETA : No, because the trajectory of the system, of the population or whatever, is determined by flexion of a surface which explicitly includes changes in the behaviour of that system, and whose fate is largely governed by boundary effects between these various areas of different behaviour.

The primary importance, however, is the change of conceptual framework involved, away from a view of ecological systems as structurally and responsively homogeneous, where changes are externally driven over a constant surface, towards a more dynamic view in which the system responds so as to nullify external change. The success of the system is determined locally by the relative rates of change, external variation versus internal behavioural/structural change, and globally by boundary considerations. These systems have evolved to maximize biotic potential (potential future biological energy utilization) not some integrative number function. It seems to me that the most important characteristic of ecological systems is their ability to absorb change; the fact that they are generally prepared for change being, of course, because they have evolved in adaptation to environmental changes which are reasonably periodic. This view is in marked contrast to the image presented by stability analysis in which system number change is assumed as a means of attaining some stable relationship with the external world and in which, therefore, the only important system mechanisms are those which alter numbers absolutely, that is, birth and death.

The absorptive model framework emphasizes the conservation of system number by structural re-arrangement. Then, with the added relativistic effects of evolutionary history and of rates of change of conditions, the situation is made ever-changing though not, I think, less easy to visualize.[80]

ALPHA : Aren't we introducing too much complexity too early. Professor May says that 'many biologically interesting models, although non-linear, correspond to relatively simple such landscapes'(p.15). This being the case, the analytic approach is undoubtedly useful for some situations.

BETA : But what are these situations and where are they ? Where do these simple biological systems abound to allow such unequivical interpretation ?[81] The statement is false, a red herring - inaccurate, circumstantial empirical padding like so much else in the book. Here, where it is important to provide examples, where examples would give a clear indication of the value of the approach examples are omitted. Elsewhere where there is sufficient interpretative ambiguity to cast doubt on the empirical evidence, examples are given.[82]

In this case a doubtful statement leads to the introduction of that absurdity par excellence, the Lyapunov Function, whose existence vindicates global assertions about stability, but which suffers from the unfortunate defect that there is 'no general way of telling whether a Lyapunov function exists in a given situation, nor of constructing it if it does exist'.[83] It is, nevertheless, in common usage and those who create and use it, at a stroke remove the problems of the local/global stability relationship and of correct dynamic characterization. Assumption is all; empiricism dead.

ALPHA : Your judgement is too harsh. Reasonable functions can be generated provided certain simplifying assumptions can be made.

BETA : Ah yes! The simplifying assumption. The prime weapon of the analytical theorist. Precursor to the realisticalizing adjustment. Of which there can be no better example than the recognition of fluctuating environmental parameters which occurs next.[84]

ALPHA : But isn't this exactly the sort of variation you wish exhibited in ecological models ?

BETA : Most certainly not. I would like to see the kind of variation actually observed in nature, with responses of the same sort as are observed in nature. But what do we have here ? Added to the previous ecological indignity of the equilibrium population we now gain the concepts of randomly fluctuating environments and finite average populations with steady average variances. To suggest that random fluctuations should be considered essential to ecological models is ridiculous. Biological systems respond to pattern in environmental variation. Animals, especially, devote a considerable portion of their metabolic and structural effort to the processing of environmental signals. This would be very inefficient if variation was random - in fact, one would expect organisms to ignore the random component of variation and respond only to trends in environmental change.[85]

ALPHA : But despite this, isn't the association of the term 'unstable' with the occurrence of large fluctuations a useful descriptive step.

BETA : Only if the system under scrutiny can legitimately be described under the assumptions of the stability approach, and this still remains unproven for biological systems generally. If the system behaviour is uniform then, of course, a propensity for large oscillations revealed by an equilibrium analysis would indeed suggest overall instability in a sense all biologists would agree to. But such responsive constancy is not, from available evidence, a general feature of biological systems.[86] Therefore, to suggest that equilibrium analysis can determine stability by measuring the potential population oscillation is a nonsense, an absurdity. The equilibrium analysis is irrelevant in such matters until it can be demonstrated that the required local/global equivalence of behavioural response is a verifiable fact.

The same sort of argument applies to the concept of structural stability used by May. System inflexibility is an absolute requirement for this particular definition to have any relevance to a dynamic system. Considering biological systems, is it reasonable to assume that parameter change will not be accompanied (and compensated for ?) by more basic changes of response equation structure ? In addition, is continuity of response a valid criterion for any comment on the stability of a biological system ? Considerable difficulties arise here surrounding the definition of system components.

Consider a community in which some species are active only in years in which conditions favour their development, and which pass unfavourable years in the form of spores or resistant seeds or the such-like. Can we say that the community in a year when the species are active is qualitatively different from that in a year when the species are dormant ?

And again, considering a single population , if an environmental change provokes a mass change in behaviour, this is certainly a structural instability. Yet this type of change is typical of many species.[87] Once more it can be seen that a stability definition is only useful for homogeneous systems, and has doubtful use in describing the biological world.

The usefulness of the many theoretical corollaries to such concepts is also brought into doubt.[88]

* * * * *

BETA : What, then, is the next subject for discussion ?

GAMMA : Analyses based on the community matrix.

ALPHA : Surely 'a quantity of direct biological significance' (p.25), summarizing as it does all the inter-relationships within a community.

BETA : Of significance ? Which meaning of significance do you call upon here ? Meaning 'of importance' perhaps ? Or simply 'meaningful' ? On both these counts I would say that it fails. Such a naively compounded summation has very little biological significance.

ALPHA : Have you good reasons for this dismissal, or is this another intuitive leap to knowledge ?

BETA : No, the reasons are straightforward. On the one hand there is the inordinately difficult task of characterizing and delimiting a community. And on the other the questionable wisdom of representing complex, spatio-temporally varying relationships by single, immutable, orthogonal figures.

ALPHA : But on an abstract level, a community must comprise a number of species and, in any interval, these species have some net effect, one on another.

BETA : An undeniable set of facts, truisms indeed. A community _is_ a set of interacting species by current definition. But, in reality, the patterns of interaction are rather more open-ended than is suggested by this restricted definition. The community may be no more than a geographically-mediated conceptual convenience, a testimony to the limitations of the human mind. As it stands, the definition does no more than identify some of the more obvious specific correlations and accretions of a seemingly continuous organic manifold. As a means of describing the dynamic properties of that manifold it is cripplingly limited.[89]

ALPHA : But there are well-defined communities. On islands for example.

BETA : If you intend to set up your argument by reference to the special case of island communities, then you must use induction to plead the global case. As necessary as this is in all theorizing, and as undeniable as its validity may be given an ultimate conception of a mechanistic universe, its use as a logical means of rebuttal has no force here.

The fact remains that the word community, as an ecological concept, has no single satisfactory definition. The community matrix idea is based on a community of fixed membership with reasonably constant interactions. This is not a generally acceptable definition. Investigating the properties of such a rigid system is more a mathematical game than a scientific pursuit.

It's interesting to note, in relation to this question of reasonable model complexity - a problem really of satisfactory minimum dimensional descriptions, that the point is made, in demarcating the usefulness of a geometrical technique, that 'the topology of two-dimensional surfaces can be different in qualitative ways from that of higher dimensions'(p.26).

Between what other dimensional boundaries are there such qualitative discontinuities, similarly constraining various analytic techniques ?

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GAMMA : Would you suggest then, Beta, that we abandon all the insights which have arisen from the stability analysis approach ? For example, the potentially destabilizing effect of time lags.

ALPHA : It would seem to me that this example vindicates the approach. The effect is quite obvious.

BETA : Exactly so. It is obvious. But it is not dependent on the rationale of stability analysis. The observation that time lags may destabilize a system is not one that depends on any single mathematical approach.

There is a set of systems in which time delays tend to destabilize, and a set in which they tend to stabilize, further sets in which there are no connections, or no time delays, and so on and so on.

The stability approach that can be implemented, the one that is tractable, is one in which time delays do tend to destabilize. Even if it is shown that in biological systems generally this same time-lag/stability relationship holds (and this is where scientific endeavour is involved - in determining the properties of real biological systems) very little confidence can be added to the conclusions of stability analysis, without the evidence of additional modes of parallel behaviour. In respect of this potential equivalence of theoretical and empirical systems, the time lag property remains logically autonomous.

* * * * *

GAMMA : Does this imply that there is a set of mathematical approaches which should be abandoned ?

BETA : If by this you mean that we should extend our rejection of hypotheses to cover all systems containing the assumptions for which I reject the stability approach, then yes. Amongst these assumptions, one of the first is well illustrated by the statement 'thus so long as all relevant populations in the food web are reasonably large, the deterministic approach .... should suffice' (p.33).

To thus deny the possibility that communities may contain small populations obligatory to the integrity of the community, when so little work has been done on community structure, seems unwise to the point of foolishness in the business of ecological theorizing.[90]

ALPHA : Ridiculous!. You yourself stated the case for imaginative science, the exploring to exhaustion of unlikely hypotheses. While we do not <u>know</u> the structure of communities, we must explore, mathematically, those possible structures which are amenable to such analysis. In the absence of ratified knowledge this remains the only area of enquiry.

GAMMA : What do you say to that then, Beta ? The theorist has always had such free rein. Do you want now to curtail this freedom – to confine ecology with empiric shackles ?

BETA : Yes. Partly to prevent it causing damage in the real world, but mainly to make clear the fact that our basic systems of definition are so imprecise that we can no longer reject statements from any reasonably sophisticated theoretical models by conventional scientific philosophical principles. We have lost the yardstick with which to measure our ecological progress in a jungle of unkempt jargon. This being the case our only recourse is a return to empiricism until we can find a more secure conceptual base.

* * * * *

GAMMA : We must now return to the stability-complexity argument proper. I think this may fairly be summarized as follows : simple observation suggests that populations in complex communities are numerically more stable than those in simple communities; this type of relationship is not displayed in theoretical investigations of the stability of community networks, by small-scale experimental manipulations of communities, or in examples of the epidemicity of pest species. Current opinion is that the posited stability-complexity relationship is a misinterpretation of an intricate situation. Various people have suggested that generalization is inappropriate in this matter.[91]

ALPHA : Part of the confusion is that between stability and vulnerability. The examples of continental invasion by pest species and of community collapse after removal of one constituent species, show the limitations of the stability-complexity generalization.

BETA : On the contrary. I would say that these examples expose the limitations of the stability concept introduced by the physics-weaned theoreticians. This simple 'number-of-components' complexity leads to such ridiculous notions of increased complexity as the addition of 'a spanner to the works'.

But I do recognize the confusion between stability and vulnerability. The former is concerned with community response when isolated from qualitative structural change; the latter, with the effect of qualitative structural change itself.

However, the resolution of such problems is not going to be helped by an approach described thus : 'The relation between the present mathematical models and the complications of the natural world should be emphasized .... we restrict attention to the simplest models .... however unrealistic they may or may not be .... In this way we may hope to get a feeling for the effects of diversity (in the sense of a large number of species) per se'(p.40).

It is difficult to imagine how the study of such population and community models, simplified beyond recognition as real populations and communities by any competent biologist, can possibly lead to any basic understanding of the natural world. The few characteristics given to these assemblages are not at all typical, let alone universal facets, of natural groups; and the criteria by which they are judged far removed from those of natural evolution.[92]

ALPHA : Such criticism may ultimately be correct, but our path to understanding must gradually be trodden. The value of this analytic approach lies mainly in the doors it closes, for example, the refutation of Elton's arguments for complexity implying stability.

BETA : But I see this 'closing-of-doors' as the greatest danger of the approach - areas of enquiry are undermined and then dismissed by specious reasoning. The refutation you specify is as flawed as the general stability analysis case, and for the same reason - too limited a definition.

May's counter to Elton's argument[93]: that it 'is only germane if the analogous mathematical models of many predator- many prey systems are correspondingly more stable'(p.40), is not true except under May's restricted definition of complexity in a simple numerical sense. With complexity of interaction assumed, a much more sophisticated counter is required.

Elton's argument in fact proceeds as follows : the simple (mathematical) interaction is unstable; any more stable interaction must, in some sense, be more complex : therefore complexity implies stability. The error is in confusing the properties of the sub-set, complex-stable, with that of the super-set, complex.

The unrealistic assumptions continue in the discussion of anti-symmetric models. It seems strange that Professor May should be 'skeptical of any interpretation of the fluctuations observed in natural populations which is based on the pathological neutral stability character of a set of specially anti-symmetric Lotka-Volterra equations'(p.53), and yet be untroubled by the even more unlikely character of the framework in which such studies, as well as some of which he approves, are carried out - namely communities consisting entirely of predators and prey, or entirely of competing species. Would it be fanciful to suggest that all models composed in such frameworks are irrelevant to natural science ?

ALPHA : But predation and competition are both components of community structure.

BETA : But they are not isolated according to type such that the behaviour of mass predator-prey systems can be invoked as a guide to the behaviour of real communities.[94]

GAMMA : As a step towards greater realism then, let us consider the study of communities structured into trophic levels, and in particular the relationship of the response of any one trophic level to that of the whole network.

BETA : Would you first clarify what you mean by the response of a trophic level - are you talking about the ups and downs of the individual species in a level, or about the gross biomass of the level ? These of course lead to entirely different conceptions of trophic response, be it stability or whatever else you may care to measure.

ALPHA : We are talking about individual populations, and the theoretical standpoint is that the response of individual trophic level and of total community network tend to be similar, but that dissimilar responses are quite possible.

BETA : So we have another marvellous hypothetical construct in which no possibilities are disbarred, and which therefore can never be disproved by experiment. What use, therefore, are these mathematical ramblings, remembering of course that they are based on unrealistic, generalizing assumptions, thereby disallowing a defence on the grounds that they are plausible extrapolations of accepted theory or fact ?

Don't answer! There is no need to bother if we, yet again, consider the framework in which these questions were asked. Is the trophic concept useful in the interpretation of population and community change ? Is it really useful at all except as an ordering crutch for vague and woolly-minded enquiry ?[95]

ALPHA : Are you denying that organisms can be classified as producers or herbivores, carnivores or detrivores ?

BETA : No. But I would question the idea of visualizing these as levels, internally egalitarian. Do you really believe that, as far as the dynamic functioning of a community is concerned, those primary producers, the algae and the trees can be regarded as equivalent ?

Once again the physical aspects of community structure assume importance, spatial and temporal scaling re-iterate their role.

ALPHA : But if these components are included in community models, the models become unwieldy and not at all amenable to analytic methods.

BETA : A very sound and pragmatic reason for abandoning these analytic methods. If they cannot cope with essential features of the systems under study, then they ought to be discarded. It is ridiculous to carry out simplifying or sub-dividing transformations on processes, merely to allow the use of particular analytic methods, without first examining the validity of the transformations themselves.

ALPHA : How do you propose to measure the validity of a particular transformation ? By the probability of correct mimicking of the real system by the transformation model ?

BETA : Yes. Something of that sort. In making the transformation, various input parameters and system variables are designated as critical and representative of the total assemblage. These, no doubt, can be identified with objects and processes in real systems. It only remains to compare the performance of the the transformation model with that of a number of systems of which it is supposed to be representative. It need only be shown that some significant aspect of change in a real system is the result of a feature debarred by the transformation to decide the reliability of that transformation.[96]

ALPHA : Suppose then that we apply this line of reasoning to random web models.[97] Here we have a community represented by a matrix whose elements describe the interactions of pairs of the constituent populations near equilibrium. In summary, we can see, as May states 'that too rich a web connectance (too large a C) or too large an average interaction strength (too large an s) leads to instability' and that 'roughly speaking, this suggests that, within a web, species which interact with many others (large C) should do so weakly (small s), and conversely those which interact strongly should do so with but a few species' .[98]

BETA : Yet another example of the semantic confusion which abounds in theoretical ecology. In this case, the confusion has probably resulted from the absence of spatial and temporal limitations to species interaction in the theoretical framework. If, however, the problem of defining feeble and strong interactions in relation to numbers of interactants, is set in a more realistic framework where time and space are restrictive, it can be seen that these quantities, interaction strength and connectance, have partially correlated definitions. The 'conclusions' presented as to their relationship from the random web argument are not gleaned from the transformations of this mathematical treatment, but are implicit in the concepts of 'web' and 'interaction'. These correlations remain unaltered by the formal re-arrangements, and arise from observation of the real world.

The case is presented in such a way as to suggest that the matching of the relationship between interaction strength and connectance in theoretical and real world observations in some way ratifies the operation of the theoretical model as representative of real systems. It does nothing of the sort. It is as faulty an argument as to suggest that, if a clockwork duck were manufactured of perfectly mimicking colouration, the movement of the model duck must be representative of that of the real duck - even if it could only hop on one leg in ever-decreasing circles.

ALPHA : And what of the further corollary, that of the stabilizing effect of block structuring. That cannot be dismissed in so facile a manner.

BETA : Can it not, indeed ? Not in the same way perhaps, but quite easily by presenting an alternative reason for block structuring.

In the sense used by May, block structuring is such that if a species A interacts with a species B and also with a species C, then an interaction between B and C is implied,

i.e. $A \leftrightarrow B,\ A \leftrightarrow C \implies B \leftrightarrow C$

inasmuch as these three, by virtue of the propositional statements, are located in the same block or sub-system. In natural systems interactions occur in relation to any niche dimension. All that is required for the term block-structuring to be applied properly to a system is that discontinuities occur along these dimensions. Such things as habitat preference and absolute size differences would account for certain interactions or non-interactions. These can be explained easily, and in fact are most commonly explained, using a niche separation argument based on single interactions and not on whole web properties, and may be a necessary result of specialization and speciation.[99]

GAMMA : A number of other models are presented relating to the complexity argument. These generally support the complexity implies instability theorem.

ALPHA : And as they display different methods of analysis in examining the problem, their collective agreement must have some scientific weight.

BETA : No more weight of evidence collectively than each individually. They suffer from a common fault of definition, in treating complexity as an absolute number property. By this definition, Ashby's 'loosely-coupled sub-systems' are less complex than mass systems of higher connectance or stronger linkage, despite their interactive hierarchy. What a nicely perverse counter to the complexity implies stability argument these models are.[100]

As yet another example of the dubious quality of such modelling work, what better than that of Smith 'on simple 3- or 4- species straight chain ecosystems' who found, according to May, that 'If the initial system is stable, additional complication and diversity can usually be grafted on without destroying the stability. On the other hand, if the basic simple system is unstable, the addition of complications and diversity generally makes things even worse'(p.70). The emptiness of such statements, revealed when one considers the vistas of possibility opened up by the addition of an unstable basic simple system to a stable basic simple system, is ignored, as platitudinous slogans, devoid of information, are coined. The true value of the results, in drawing attention to the shortcomings of the methods of analysis - which demonstrably cannot distinguish the criteria for stability or instability, is ignored. Such oversights of self-criticism are increasingly common in theoretical ecology.[101]

GAMMA : Understandable considering the complexity of the subject. One must not be harsh on errors which may only be the result of restricted vision.

ALPHA : And you, Beta, may be a little mellower in your criticisms of qualitative stability which next features in Professor May's book. Have you any immediate criticism of the concept of examining a system according to the types of its constituent interactions.

BETA : I have. The approach involves the assumption that all links between system components can be assigned constant values of some sort or other. If there are links which are of variable sign, then the approach may not be accurate. If there are critical links of variable sign i.e. essential fluxing interactions, then the approach is invalid. This condition of use is not stressed in reports of qualitative stability analysis, in fact it is rarely stated at all.

As to details, the conditions for stability of a system include non-logarithmic growth for all populations, and the absence of closed loops of three or more members. May can state, despite obvious real-world violations of these conditions for stability, that 'the general tendencies revealed by qualitative stability theory are useful'(p.73).[102]

By what criterion can this statement be made ? Can useful conclusions be drawn from the study of synthetic systems whose properties, in major respects, do not correspond to those of real systems? Can we take seriously, studies in which an ecosystem is defined in context as an open straight chain with one population per level ?

A more distressing symptom of the engulfing power of the analytical approach is the rehabilitation of definitions to allow some sort of conformity between real-world occurrence and theoretical hypothesis. In the cause of qualitative stability analysis, mutualism is abandoned, 'its importance in populations in general is small'(p.73). Conventional examples of this phenomenon are explained away as commensalism or amensalism, both of which fit more neatly into the qualitative stability framework.[103]

Again we see a tendency to pervert definitions, and to exclude awkward cases, as in this case symbiotic gut floras, in pursuance of a single philosophical approach. Having decided, by a simple analysis, that mutualism is destabilizing, attempts are made to remove counter examples by redefining them. A common, if not very helpful, practice.

ALPHA : But your counter examples are not so clear cut as to prove the case either way. In the case of the gut flora especially, the difficulties of establishing mutual effects between organisms whose spatial and temporal characteristics are vastly different makes confident labelling as either mutualistic or commensal a daunting proposition.

BETA : Which is exactly the conclusion to be drawn from such cases. The double sign classification of interactions is only properly applicable to interactants of comparable size and life span. In the case of dissimilar organisms how does one define beneficial or harmful effects - can they be defined in relation to the individual on the one hand and to a population on the other. It is obvious that the limitations of the classification system impose corresponding constraints on the analysis developed from them. As a result, interactions between organisms of different temporal and spatial scales are excluded. Yet such interactions, such as those between individuals and populations or communities of very much smaller individuals, are features of almost all ecosystems. The method of analysis presented here is therefore debarred from useful comment on these natural systems.

Yet even in the final token gesture to reality, an addendum concerning closed ecosystem models - neatly placed away from the main argument, May at once recognizes decomposer populations as components of ecosystems, and yet glosses over their necessary invalidation of the qualitative stability class definition.

GAMMA : So where has this discussion of the stability/complexity debate taken us ? Can we, in turn, draw any general conclusions ?

We have seen that, from studies of ecological models, complexity does not produce stability; and yet there is the conventional (empirically-based) wisdom that complexity does produce stability. Are we now sufficiently wise to judge the relative merits of these views ?

ALPHA : The mathematics remains correct. The purpose of the analyses was only to make general statements. These, in context, are correct.

BETA : Of course I agree with this. It is the assignment of context with which I disagree. These analytical studies belong to the realm of ecological mathematics, that is mathematics inspired by ecology, rather than to mathematical ecology, that is formalized ecological theory. They are formed around mixtures of definitions incorrectly and illogically concatenated. These definitions were formed for different reasons and in different situations, by biologists and others of widely different interests. It is a folly to think that they can simply be combined to provide a more complete description of ecological systems. In many cases the individual definitions are incomplete, being only partial descriptions of complex events. Others are ambiguous terms whose definition could never be made more precise without significant loss of meaning.[104]

ALPHA : But unless ecological terms are made precise they cannot be analysed.

BETA : You mean, of course, that they cannot be analysed by conventional methods. The common mistake in this situation is to analyse some simplified definition, all the while imagining that it is the original, more broadly-based, definition being examined. The errors in the analytic approach are of this sort. The original definitions and relationships expressed by earlier naturalist ecologists were not presented in the sort of precise style required and used by modern theoretical ecology. These latter methods are entirely inappropriate to the resolution of the validity of general ecological statements.

If, indeed, there ever was a desire to establish a 'complexity implies stability' general theorem, the mathematical analyses have added no weight of evidence to either proof or disproof. There is no fallacy in the intuitive arguments presented 'that the greater the number of links and alternative pathways in the web, the greater the chance of absorbing environmental shocks, thus damping down incipient oscillations'(p.75). The fallacy lies in the mathematical counter-argument where simplified and usually homogeneous general systems are assumed to be representative of real ecological systems.

The so-called paradox between real world observation and theoretical analysis is therefore revealed to be a disjunct comparison.

As to the complexity implies stability theorem itself, the empirical evidence is indecisive as far as any causal promotion of stability by complexity, but that evidence does suggest a correlation, possibly a mutual causation in circumstances of high energy throughput.

ALPHA : Your criticisms of these models become repetitious. The same basic comment is re-vamped as a counter to all of the models.

BETA : Because all of the models have the same basic and important fault - simplification to the point of absurd parody. The appeal of these models over simple logical, that is verbal, analyses is their precision. But is there any value in this increased precision ? Is there a concomitant increase in clarity ?[105]

GAMMA : Perhaps, in order to clear the point, we should turn to some more realistic models of more limited scope, those with only a few species.[106]

ALPHA : And to predator-prey models with some moderately realistic features such as birth-rate density dependence, for which there is adequate empirical evidence.

BETA : Though such evidence may be tautological, in that there is necessarily a limit to growth, and the longer the study of a population continues the more likely becomes observation of a decline in increase, especially when, experimentally, populations are commonly viewed as discrete units. Given a more flexible view of populations, and with recognition of emigration as a common feature of these, mass density-dependent descriptions are less obviously correct.

ALPHA : Though that phenomenon remains a locally definable feature. Other characteristics, such as functional response, are more broadly based and so less susceptible to such criticism.

BETA : But the arguments supporting some of these models of total predator dynamics are based on the assumption of stability as a goal. If the real dynamics are boundary-oriented rather than equilibrium centred, the arguments and therefore the supports, fail.[107]

GAMMA : Let's move on to the analysis proper - a nonlinear stability analysis of one-predator/one-prey community models. The dynamics of these need not be stable and constant, but can also be stable limit cycles, the characteristics of which are set by birth rates, predation rates and so on.

BETA : As a first cautionary comment, let me ask whether these quantities are conserved during population change, or do they vary along with other genetic/behavioural/physiological properties of the population ?

GAMMA : To carry on, Kolmogorov used such a system to determine the conditions which necessarily lead to either a stable point or a stable limit cycle for the system. These nine conditions are easily translated into biological terms for the one-predator/one-prey system.[108]

BETA : Kolmogorov's theorem seems a reasonable description of closely-coupled two-species interactions both in its conclusions and in its interactions - but its apparent robustness must be placed within the constraints of its basic mathematical form (normalization of parameters, etcetera.). As to a multi-dimensional analysis, this is of more doubtful value - close coupling of more than two components is a less probable circumstance to envisage.[109]

ALPHA : The next sections deal with time delays, on which you have already made substantial attacks, Beta. I think we may therefore pass over these.

BETA : After I have pointed out a few interesting comments. Professor May says, in reference to the revisions of the Wangersky - Cunningham model that 'as the basic prémise seems ill-chosen this is somewhat beside the point' [110] Considering the character of some of the premises of the stability analysis approach, I would say that this comment itself seems rather ill-chosen. In any case, a person of as dubious a background in biology as Professor May is not a good choice as a judge of ecological assumptions.[111]

On a less personal level, there are the examples of complexity enhancing stability : in one case by the addition of a trophic level to a time-lag unstable system, and in the other where a combination of factors, neither one of which is conducive to stability, may produce a stable state.[112]

ALPHA : If you can resist the temptation to attack the man rather than the ideas, Beta, perhaps we can continue to discuss a further addition to models, which permits greater realism - that of randomly fluctuating environments. Here the points and levels of the deterministic model are replaced by probability distribution functions. I would guess that your major criticisms of the analytic method apply here also, Beta, so perhaps if you can deal only with additional points or perhaps those of particular interest, we can speed the proceedings along.

BETA : Very well then. The appeal of the stochastic approach is that it neatly sidesteps the question as to whether population interactions are tight enough to validate the use of deterministic models. But similar questions must arise concerning the nature of the probability functions, and in particular the simple cloud equilibria of the stochastic models. The nature of the distributions is as critical a point here as it was as a rebuttal of deterministic models. Normality of characteristics is not established for the types of characteristic used in these models, yet it is assumed as a procedural convenience.[113]

ALPHA : But these models must give some impression of possible events.

BETA : Ah yes - the impressionistic pictures of things favoured by these analysts. But impressionistic in what sense : as to 'giving a general impression' this is debatable as a correct use of the adjective (and in my opinion an incorrect use), but it is certainly not, as the alternative definition would have it, in line with Impressionistic philosophy. This was greatly concerned with the recording of direct sense impressions and not at all with theoretical idealizations.

In any case, the stochastic approach again dwells on a definitional equivalence of stability with small perturbations, which is simply too naive a view to be given any regard.

These models represent hardly any advance over the deterministic models. All they possess, in the attempt to mimic reality, are slightly defocussed levels of operation and effect. The principles behind the models are the same in both cases. The difference is only a little superficial cosmetic surgery, not a re-analysis of fundamental issues.[114]

ALPHA : May argues that the benefit of the stochastic model approach is that, together with deterministic models, these methods allow one 'to bracket reality between these extremes'(p.117).

BETA : This is a fallacious argument. It implies that the behaviour of systems other than the deterministic or white noise systems is bounded by the behaviour of these; that in some sense they can be constructed as some direct combination of the two. The fact is that the ecological systems under study are characterized by partitioned spectra with long term correlations.[115] The behaviour of such systems is not bounded by the behaviour of the two 'extreme types' presented. The topics of non-white spectra and of internal resonance are raised by May only to be immediately and perfunctorily dismissed, thereby avoiding a discussion of the properties of real systems which would severely damage his thesis.[116]

GAMMA : Let us move on then, to consider another area to which the methods of stability analysis have been applied, that of niche overlap and limiting similarity. Here the questions to be asked, for Professor May at least, are : 'how similar can competing species be if they are to remain in an equilibrium community; how identical is "identical" ; how closely can species be packed in a natural environment ?'.[117]

ALPHA : Questions to which the stability analysis approach provides unequivocal answers which do not, I think, suffer from the limiting assumptions our friend Beta has been at pains to point out for the other areas of application.

As Professor May says, the 'general result is a robust one, being rather insensitive to the details of the mathematical model ' (p.141).

BETA : Putting aside for the moment any comment on the nature of the general result, let me first ask what is meant by 'insensitive to the details of the mathematical model'. Can I take this to mean that <u>any</u> mathematical model would produce the same result ? Or do 'details' include only for example, parameter changes ?

Of course many forms of model must be proscribed for any particular result to hold true. Other results can be imagined and, for these, chains of development set down leading from whatever initial premise may be chosen. This is the power of mathematics - that all conceivable situations can be formalized. Its weakness lies in the fact that each conceivable situation can be formalized in innumerable ways - for the decision by which a particular form is chosen to represent a particular state of existence is not one to be made haphazardly.[118]

Professor May's comment on the robustness of the results he presents is a misleading and subjective statement. Such comments should not have a place in scientific texts. However, they are all too common where there is a need to conceal flawed arguments and spurious correlations.

As to the details of method and results, do the following quotations from Professor May's book need further comment ?:

'the discussion pertains to situations dominated by competition within one trophic level, which tends to restrict the circumstances in which theory confronts reality'(p.142)

'if the multi-dimensional niche approximates the interdependent simplex, it is difficult to assign meaning to δ and ω.... Comparison with experiment is not to be looked for here'(p.165)

(Are perfect orthogonality and perfect interdependence, in May's sense, truly the limits to ecological possibility)

' the theory is restricted to communities whose constituent species' niches are sorted out by competition within a single trophic level'(p.165)

By what tortuous logical process can we legitimately extend the results of such assumptions to give a description of the complexities of the real world ?

Professor May gives warning of the prejudices which might arise through experimental exposure to particular types of community structuring - he might do well to recognize the true import of these prejudices as testimony to the complexity of complexity, as it were, to the variety of types of structure and of organization which interlock to allow whatever cohesive aspect there is to communities.[119]

Professor May makes a case for continuing this kind of theoretical work on the grounds that further realism may be attained by future additions of trophic levels, predation etcetera. Of course each of these additions, unless they are perfectly orthogonal additions, will probably make irrelevant the results from the previous simpler systems, and so of course the complete range of analysis will have to be re-applied. As a means of maintaining job security, and no doubt as a means of job creation, this is all very well, but is it contributing significantly to our knowledge of ecological systems ?

The method is based on the study of systems whose characteristics are simplified versions of gross definitions, only partially correlated with empirical knowledge. Even at a fairly limited level of interaction the models used approach the limits of tractability for these mathematical forms.

The correspondence with reality which is frequently used to advertise the success of the models is, more often than not, a product of the initial premises rather than of the mathematical approach involved. As such, the correspondence with reality is hardly surprising, as it is based on empirical observation which has, in the selection of basic mathematical forms for the models (Lotka-Volterra types which lead to competitive exclusion and the like), become, inadvertantly one hopes, embedded in the structure of the model.

As to Professor May's final 'Speculations', I am interested to note that the conventional ecological wisdom of former chapters that 'complexity implies stability' has changed to 'complexity begets stability'. This substitution of causation for correlation is conveniently placed for a final denunciation of the intuitive and empirical ecology of the past. However, as a rider to his own work, Professor May has to admit that 'Natural ecosystems, whether structurally complex or simple, are the product of a long history of co-evolution of their constituent plants and animals. It is at least plausible that such intricate evolutionary processes have, in effect, sought out those relatively tiny and atypical regions of parameter space which endow the system with long term stability' (p.173)

Indeed this is a truism given sufficient time for the system to settle (stability in this case being functionally equivalent to persistence); and of course if conditions do not allow settling of the system, the case for stability-oriented life-strategies must anyway be abandoned.

The conclusion to be drawn, which can be done without reference to mathematical models, is that the important characteristics of ecological systems are to do with structure, not mass number properties, and that different components of a system are differently necessary to that system.

Ideas such as species number constancy tend to support the thesis of common and obligatory structures for communities, that is conservation of structure despite constituent changes. The complex specifications of any one structural unit may necessarily require some redundancy and laxity of definition, thereby allowing alternatives within any type of community.

The type of detailed analysis required to define such structural composition is in marked contrast to the present theoretically based quasi-experiment involving such concepts as total niche volume and effective niche volume per species, which can only be defined tautologically, in relation to the very characteristics they are supposed to explain - in this case number of species present. These concepts are statistical shorthand descriptions of the species number characteristic and not independently existing reasons for that characteristic.

Given that Professor May, one of the leading lights of the theoretical ecology movement, recognizes that :

'There will be no simple answers to these questions'(of stability and complexity, p.174) and,

'we would do well to preserve large chunks of pristine ecosystems. They are unique laboratories '(p.174),

one wonders at the general readiness of theorists to flaunt their models as guidelines to the solution of real world problems, and their enthusiastic involvement in ecological management schemes.[120]

The greatest danger though is that acceptance of this type of approach blinkers future research on the dynamics of biological systems. The approach shields possibly faulty definitions from critical view and, in stressing characteristics which can be well defined and measured, tends to promote the abandonment of less precise ideas by implying their irrelevance.

6.1.3 Critical summary

The stability theory approach deals with systems of dynamic units in equilibrium and the response of these systems to changes (in numbers of the units) imposed by external forces. These changes are categorized as either small(local) or large(global). The approach only properly succeeds in the local case (unless the global response is a simple extension of the local response), and the response is, as the initial perturbation, a change in number of system units.

Discussion of these models in relation to real systems often centres around comparison of gross patterns of population change in model and reality. The theme of the preceding criticism is that such comparisons provide no sort of valid test of the models, and that any testing of the models must deal with initial premises or assumptions. Those assumptions are shown, in several cases, to be contradictory to established experimental and observational evidence. Further, as no measure is available of the effect of relaxing those assumptions on the conclusions to be drawn from the models, a caution is given regarding the use of such models in predicting the activity of real systems, or in the formulation of general biological system concepts.

6.2 Towards A New Synthesis

There is no synthesis of the empirical results presented, with the theoretical tradition discussed and criticized. The synthesis of the section title is of attitudes to research, of modes of enquiry. I believe that the theoretical approach described has restricted our approach to the study of dynamic processes in populations and communities, and threatens to increasingly restrict such studies, and this with a most tenuous foundation in fact. This proceeds because definitive terms of dynamic activity are coined by theoreticians and these used to form the framework of experimental studies.

It is allowed to proceed because specialization in science has reduced much of the element of competition between conflicting ideas, and has restricted the flow of information between disciplines; which flow, in any case, approaches the bounds of individual assimilation. This would not be important if the various areas of study were not competing for the resources necessary to continue those studies. But they are, and the criteria by which the competition is decided have no basis in any standard of scientific merit, for no such standard exists.

As a step towards the synthesis of such a standard I will review, by quotation, various attitudes and statements of belief. The sub-section headings are fairly loosely interpreted.

6.2.1 On analytical methods in ecology

E.G.Leigh(1968) : 'The bond between theory and application was that prediction rquired simple yet meaningful description. Computers disrupt this bond: one no longer needs simple theory for prediction. Indeed, for accurate prediction we quickly resort to models too complex too understand. This proliferating complexity may have strange consequences. After all, one can predict planetary motion quite accurately by introducing enough Ptolemaic epicycles. Yet, even though it makes no difference to the relativity theorist whether we center our world on earth or sun, we cannot 'understand' the dynamics of planetary motion unless we do away with the epicycles by sending the earth round the sun. Many scientific revolutions, many advances of understanding, were brought about by the demands of simplicity. Since applications do contribute to such advances, the computer's dissociation of prediction and understanding may greatly affect the development of science. It is distressingly easy to see how such a dissociation could lead to a proliferation of abstract theory, no longer needed for, and therefore undisciplined by, application; and an applied technique more dependent than ever on elaborate machinery, and thus more a slave of circumstance.'

H.Skolimowski(1974) : 'Biology is nowadays a special science, for it has become a philosophical battlefield on which a new paradigm for all human knowledge is being established. The reign of physics as the universal paradigm is now over. Biology is aspiring to provide a new paradigm. Though its aspirations are perhaps justified, the passage to this new paradigm proves to be exceedingly rough and thorny.

'... the particular difficulties in which we now find ourselves in the realm of biology, and also in relation to the whole heritage of our scientific knowledge, stem from the restrictive harness of a rationality which is no longer adequate for the recent extensions of our knowledge and for the cognitive needs of contemporary man. The rationality developed under the auspices of physical science is a harness, for it ties us down to a certain conceptual framework and obliges us to observe criteria of validity that are specific for this framework.

'... the new paradigm for all human knowledge which biology attempts to provide cannot be successfully established unless we simultaneously reconstitute the notion of rationality and the criteria of the validity of accepted knowledge.

'...In the post-Renaissance civilization, physical science has been the major influence in determining the scope and the nature of our rationality. And so much so the 'rational' has come to be used interchangeably with the 'scientific', and conversely.

In the universe of modern western man, the rational is that which is valid within a given scope of knowledge; on the other hand, the valid is that which is rational within a given scope of knowledge. Thus the validity of knowledge is interlocked with rationality. One is defined through the other. Rationality is a framework on which knowledge is based but which itself is abstracted from this knowledge. This circularity is unavoidable as long as we remain in the purely cognitive realm. If there is a non-circular justification of rationality, then this justification must be sought outside the realm of pure cognition.

'...Positivism dies hard. One of the reasons is that it is such a well-defined doctrine, with clear-cut boundaries, clear-cut criteria of validity and well-formulated language. The language of positivism has almost become the official language of science. In contrast, the phenomenon of life in its development might be characterised by its inherent fuzziness. How can we grasp adequately the fluidity and fuzziness of life having at our disposal only razor sharp concepts ?

'...The favourite strategy which molecularists and positivist-oriented scientists assume .... is to argue that <u>there is no evidence</u> to support the claims of antireductionists. The strategy 'there is no evidence' deserves special attention for it not only signifies a semantic manoeuvre but it also signifies an important aspect of the positivist epistemology. When Bronowski and others use this phrase, or any of its variants, they mean to imply that there is no evidence in terms of physical science. Of course there <u>cannot</u> be. The essential point is that when the evolutionist exhibits the limitations of physics and wants to transcend the scope of physics, he cannot give physical evidence. To produce this kind of evidence is to support the cause of positivism (physicalism). If the evolutionist provided this kind of evidence, he would simply undermine his claim that there is more to the behaviour and function of the organism than physics can explain. Therefore, whoever argues that there is no (physical) evidence for the non-physical manifestations or functions of organisms is either very naive or is intellectually dishonest by surreptitiously trying to force the opponent into the mould from which he seeks to liberate himself.

'...By a complex system we have come to recognise a large number of parts that interact in a non-simple way, that is, in such a way that 'the whole is more than the sum of the parts, not in an ultimate, metaphysical sense, but in the important pragmatic sense that given the properties of the parts and the laws of their interaction,it is not a trivial matter to infer the properties of the whole'(Simon,1962; 1969, 86). Most important among those complex systems are hierarchic systems.

'...John Platt(1970) has argued that a hierarchical structure, particularly of an organism,acquires new characteristics as the result of 'hierarchical jumps'.

'...It is hard to deny Platt's contention, which he shares with Michael Polanyi and Arthur Koestler, that acts of hierarchical growth are never rationally deducible from the smaller system structures that precede them.

Another inescapable conclusion is that hierarchy and complexity in living organisms are equivalent to nonreducibility. When we comprehend the function of these organisms in terms of complexity and hierarchy, we invariably go beyond the physicochemical rudiments of these organisms.

In a similar antireductivist spirit, A.Katchalsky emphasises that function in the biological organism is not the product of structure but is another expression of living texture; a point which Dobzhansky will carry much further.

'...The evolution of our understanding has been frozen at the level of the static model of traditional physics. We have physical concepts, chemical concepts, electromagnetic concepts which we recognise. In science we do not possess concepts that attempt to grasp and depict the higher levels of the complexity of matter: matter endowed with self-consciousness and with spirituality. There is thus a great discrepancy between the dynamic units of actual biological evolution and the static and petrified units of conceptual evolution. A truly evolutionary epistemology requires matching the states of conceptual evolution with the appropriate stages of biological evolution. Ernst Mayr (1961, 1969) and others have eloquently argued that the physical interpretation of certain rudimentary biological concepts makes a caricature of these concepts.'

L.Van Valen and F.A.Pitelka : 'When a new approach becomes respectable, it often happens that its adherents try to suppress other views. This is now occurring to some extent in ecology.

'...Mathematical ecologists used to have difficulty publishing their papers, as happens to any unorthodox outlook and is true now for newer ones.

'...But mathematical ecology has now entered the Establishment and appears to be pursuing a policy of competitive exclusion.

'...Unlike population genetics, ecology has no known underlying regularities in its basic processes, the growth and regulation of populations. Models based on very restrictive assumptions, often implicit, are commonly used to make 'discoveries' whose range of application is not considered worthy of mention. The possibility of explaining a known phenomenon is often taken as proof of a theory without full documentation or without consideration of the likelihood of alternatives. Applications of some mathematical criteria for concepts such as niche width have no necessary relation to their verbal counterparts, and occasionally are even opposite to them in direction. Sometimes conclusions are made for which the formal theory is superfluous, saying the same thing more impressively (but less generally and at greater length) to fewer people. Restriction within a known mathematical framework has inhibited discoveries that generalize, or at least lie outside, this framework.'

B.Blazek, J.Petz and J.Stoklasa (1974) : 'The approaches of individual branches of science within anthropo-ecology are based on semantical and historical genesis peculiar to each branch. Therefore, the results searched for are unobtainable through mere interdisciplinary co-operation, even if based on extended search of a common language. To arrive at a common denominator it is necessary, primarily, to analyze the partial points of departure of the individual scientific branches, and through unveiling the implicit assumptions to elucidate the methodological adequacy of the partial approaches.

'...The entire process escapes understanding if perceived only from without i.e. if based on the classical methodological apparatus; such approach must alternate with a deliberate approach from within the system. Next to rational factors, those intrinsic value factors must equally be taken into consideration which mostly have been unconscious, assuming the status of implicit assumptions.

'...To increase the objectivity of the decision-making process it is not sufficient only to search for novel and different forms of quantification of factors resisting quantification so far. It is necessary, first of all, to bring to light the maximum possible number of implicit assumptions underlying partial approaches and to put them on a common basis, methodically. Only then is it possible to introduce an apparatus of mathematical formalization already invested with highly refined methodology, permitting application to all branches of science whose points of departure have been clearly formulated.'

E.Laszlo (1972) : 'Since the time of Galileo and Newton, modern science has been dominated by the ideal of explanation by reduction to the smallest isolable component's behaviour in causal terms. Phenomena, however complex, were sought to yield isolated causal relations , and the sum of these were believed to constitute an explanation of the phenomena themselves. Thus two-variable linear causal interaction emerged as the principal mode of scientific explanation, applying to the primitive components of a given complex of events. Explanation in these terms presupposed atomism and mechanism as a general world view. But when contemporary science progressed to the rigorous observation, experimental testing and interpretation of what Warren Weaver called 'phenomena of organized complexity', such explanations no longer functioned.'

R.Rosen (1972) : '... both the experimental tools with which we observe biological systems, and the conceptual constructs by means of which we attempt to describe them, are drawn from a nonbiological science, not concerned specifically with the complexity and the highly interactive character typical of biological organisms. Therefore, in order to orient ourselves properly with regard to understanding how the modeling of biological systems is to be effectively accomplished, we must understand more specifically the nature of the biases which our physical tools, both experimental and theoretical, impose on us.

'...It is one of the goals of science to be able to match up the two kinds of system description .... The external description is a functional one; it tells us what the system does, but not in general how it does it. The internal description,on the other hand, is a structural one; it tells us how the system does what it does, but in itself contains no functional content. We would like to be able to pass effectively back and forth between the two kinds of system description;'

'...Many biological activities are in fact defined and observed only functionally, in terms of an input-output formalism. On the other hand, we can, as noted previously, employ many observational techniques (borrowed from physics) to obtain a wide variety of structural information. But there is no reason to expect bthat the structural information we find easy to measure should be related in a simple way to the external functional descriptions in terms of which so many biological phenomena are defined. Stated another way, the internal state variables which we find easily accessible bear no simple relation to the functional activities carried out by a biological system; and conversely, the external descriptions appropriate to the functional behaviour of biological systems bear no simple relation to the structural observables which our physical techniques can measure.'

W.G.Wellington (1977) : 'Economic entomologists are not the only applied biologists who have suffered from the delusion that a treatment which cures one ailment should automatically cure many others. But allowing that delusion to persist in pest management is likely to have more serious consequences than in other professions, as long as our resources continue to dwindle while our own population grows.

'..."Trial-and- error" approaches to pest control may not totally deny the central role that the attributes of individual organisms play in creating problems for applied biologists, but they certainly discount it more than the recent history of insect resistance to pesticides suggests thst they should.

Some theorists in population and evolutionary biology might dismiss these ad hoc habits as the uncouth sort likely to be found wherever the scientific method is not well understood. But some of their analytical styles include similar elements, and so are not beyond reproach. Beneath the highly polished surfaces of our major population theories lies a shadow of the same disregard for the properties of organisms that is expressed more frankly in the "try-it-and-see" approach to pest control. In both instances, the organism at times seems to be viewed as though it were a distraction from, instead of the source of, the problem.

'...For decades, a "population" has been viewed as a passive, monolithic lump of protoplasm, out of which chunks are carved by all the lethal agents assailing it. The comparative evolutionary or practical values of any agent have been judged primarily by the size of the chunk it removes. Neither in theory nor in practics has there been much interest in the qualities of the residual lump; the common preoccupation has been with the forces that reduce numbers in a generation. And since the numbers dying have received more attention than the numbers surviving, whether chance or superior quality contributes more to the survival of the few individuals who finally become parents is a question that has seldom been seriously considered.

'...we should be asking more relevant questions e.g., "How do successful species, including pests, continue to survive and multiply, despite the hostile forces in their environment ? What adaptations allow them to evade extinction ? Are there weaknesses in their life style which we could exploit ?"

Most of our conventional population theories have ignored those questions. Certainly none has answered them, even inadvertantly.

'...Attempting to discover the rules for survival leads to a very different view of insect ecology. Detailed mortality records become less central to one's endeavor. Details of activities that may promote the survival of individuals becomes more interesting. The population no longer seems an inert structure composed of interchangeable building blocks; it dissolves into groups of individuals differing markedly in their ability to survive. Comparative studies of behaviour thus become important in field work.

'...The procedure is deceptively simple. It consists mainly in trying in as many ways as possible to scan the environment from the organism's point of view. That is, to try to adopt more of a zoocentric than an anthropocentric attitude.

'...The idea that the causes of numerical fluctuations can be discovered by studying numbers has a remarkably tenaceous grip on the vitals of population management. It might be more easily exorcised if we compared some practices there with those we expect other applied biologists to follow.'

W.M.Wheeler (1927) : ' ... the unique qualitative character of organic wholes is due to the peculiar non-additive relations or interactions among their parts. In other words, the whole is not merely a sum, or resultant, but also an emergent novelty, or creative synthesis. This conception was long ago advanced by J.S.Mill, G.H.Lewis and Wundt, and since the various sciences are concerned with the investigation of wholes of different degrees of complexity, it is, perhaps implicit in Comte's hierarchy of the sciences, to which we still adhere, and in our various chemical and biological classifications. According to Spaulding certain specific relations, recognized, named and technically formulated in special sciences, organize parts into wholes, and there are states of affairs resulting (we should now say emerging) that are identical with new properties, and that are different and distinct from the individual parts and their properties. Therefore the reduction of these new properties to those of the parts in the sense of identification, and the finding of a causal determination also in this same sense, is impossible.'

S.Rose (1979) : '...I want to turn to some issues of theory - not unlaced with semantics and occasional political point scoring - which have muddied the waters of biologico-philosophical controversy around such themes as sociobiology and genetics/intelligence in the past few years.

'...there are some mechanically-minded reductionists who would qualify for the term hereditarian. Apart from outright ideologists I would include among this category a tradition of mathematical games players .... which begins by assuming genetic models for the phenomena it wishes to study and then attempts to fit algebra round them; .... some of the new grand synthesizers around Hamiltonian and Wilsonian sociobiology - and of course the desperately intellectually impoverished me too trait-measurers of psychometry.

'...Both hereditarian and environmentalist positions are phrasing the relevant questions in quite the wrong terms, implying a dichotomy which modern biological thinking is at pains to transcend

'...Evolution has resulted .... in a genetic programming for plasticity and adaptability in response to environmental modification...

'...genes and environment do not interact as fixed quantities in some linear algebraic question....

'...It is for these reasons that one has to understand the gene/envirnment interaction as dialectical, not mechanically reductionist ... a true biological explanation of the gene/ environment dialectic transcends crude algebraic additions or attempts to partition out components of individual differences between arbitrarily defined hypothetical components.'

C.S.Holling (1973) : 'Our traditions of analysis in theoretical and empirical ecology have been largely inherited from developments in classical physics and its applied variants. Inevitably, there has been a tendency to emphasize the quantitative rather than the qualitative, for it is important in this tradition to know not just that a quantity is larger then another quantity, but precisely how much larger. It is similarly important, if a quantity fluctuates, to know its amplitude and period of fluctuation. But this orientation may simply reflect an analytic approach developed in one area because it was useful and then transferred to another where it may not be.

Our traditional view of natural systems, therefore, might well be less a meaningful reality than a perceptual convenience. There can in some years be more owls and fewer mice and in others, the reverse. Fish populations wax and wane as a natural condition, and insect populations can range over extremes that only logarithmic transformations can easily illustrate. Moreover, over distinct areas,during long or short periods of time, species can completely disappear and then reappear. Different and useful insight might be obtained, therefore, by viewing the behaviour of ecological systems in terms of the probability of extinction of their elements, and by shifting emphasis from the equilibrium states to the conditions for persistence.

An equilibrium centered view is essentially static and provides little insight into the transient behaviour of systems that are not near the equilibrium.'

G.R.Conway (1970) : 'But perhaps the major difficulty has been the sheer complexity of ecological systems. This has meant that to keep the modeling manageable only a small set of the possible contributing factors could be considered and .... considerable manipulation and labor was required to produce any results. One effect of this has been a tendency to mold the biological data to fit mathematical models chosen for their tractability. Many models of considerable elegance have thus been built which are, nevertheless, based on quite untenable assumptions. Over the years this has given mathematical modeling a bad name, particularly among applied ecologists who are more closely aware of the realities of the situations being modeled.'

D.E.Reichle, R.V.O'Neill, S.V.Kaye, P.Sollins and R.S.Booth (1973) : 'Environmental systems analysis, or systems ecology, deals with the mathematical modeling of environmental systems as sets of coupled compartments with time dependent changes in amounts of elements, compounds and energy described by mathematical equations. A basic premise is that environmental systems may be simulated with mathematical equations utilising the same assumptions about underlying properties that permit the use of similar equations in engineering.'

W.T.Schoener (1979) : '..this modeling strategy necessitates the treatment of major effects one at a time ..... However, the approach assumes the non-existence of qualitatively new outcomes resulting from interactions between major effects. Hassell recognizes the problems and claims that such interactions are unimportant...'

J.R.Beddington, C.A.Free and J.H.Lawton (1976) : '..the populations of most species in many ecosystems appear to fluctuate around characteristic mean levels of abundance .... a reasonable inference is that the persistent, quasi-stable populations which we observe in real ecological communities demand parameter values in their model counterparts whci lead to locally stable equilibria or to limit cycle behaviour .... For a population interaction to persist, the parameters of the appropriate population model should be such that the model implies either a locally stable equilibrium or a limit cycle.'

R.E.Ricklefs (1973) : 'In the long run, measurements of population size are likely to reveal relatively little about the biological factors that cause regular fluctuations in populations. As Kendall(1948) has pointed out, "Experience seems to indicate that few things are more likely to mislead in the theory of oscillatory series than attempts to determine the nature of the oscillatory movement by mere contemplation of the series itself".'

Commenting on normal distribution theory, H.Poincare (1912, p.171, quoted by Bradley, 1968) : 'Everyone believes in it (the law of errors) however, said Monsieur Lippmann to me one day, for the experimenters fancy it is a theorem in mathematics and the mathematicians that it is an experimental fact.'

6.2.2 From other disciplines

S.Sutherland (1978) : 'The attempt to demonstrate on a priori grounds that natural science can never fully explain human behaviour has been a fashionable parlour game amongst philosophers for some time.

'...We can no more explain human activity in terms of goings-on in individual nerve cells than we can explain how a computer program works in terms of transistors. To understand how any organized system of matter works, we must develop concepts appropriate to that kind of system. We can understand and predict the hunting behaviour of a system incorporating negative feedback only in terms of control theory not in terms of previously existing physical concepts. Similarly, the scientific explanation of behaviour requires the development of concepts appropriate to understanding the organisation of the brain in relation to the external world : such concepts may not be physioal or even physiological, but in as far as they are both precise and render human actions intelligible in a rigorous way, they are nonetheless scientific.'

G.F.Chew (1970) : 'Physicists usually perceive their discipline's goal as the reduction of nature to fundamentals, and the high energy arena has correspondingly been dominated by the search for "basic building blocks"......There exists, nonetheless, a 180-degree inverted point of view, which envisions the absence of fundamentals as the ultimate triumph; this is the bootstrap attitude.

The bootstrapper seeks to understand nature not in terms of fundamentals but through self-consistency, believing that all of physics flows uniquely from the requirement that components be consistent with one another and with themselves. No component should be arbitrary. Now by definition a "fundamental" component is one that is arbitrarily assignable; thus, to a bootstrapper, the identification of a seemingly fundamental quark would constitute frustration.'

G.F.Chew (1968) : ' Although the term bootstrap has different significance for different scientists, in a uniformly accepted implication self-consistency is accorded a central role. In the broadest sense, bootstrap philosophy asserts that "nature is as it is because this is the only possible nature consistent with itself". In such vague terms the bootstrap idea is much older than particle physics...'

'...Conventional science requires the a priori acceptance of certain concepts, so that "questions" can be formulated and experiments performed to give answers. The role of theory is to provide a set of rules for predicting the results of experiment, but rules necessarily are formulated in a language of commonly accepted ideas

'...science, as we know it, requires a language based on some unquestioned framework. Semantically, therefore, an attempt to explain all concepts can hardly be called "scientific".

Additional insight into the peculiarities of bootstrap philosophy is acheived by remembering that physical theories have always been approximate and "partial". A key discovery of Western culture has been the discovery that different aspects of nature can be individually "understood" in an approximate sense without everything's being understood at once. All phenomena ultimately are interconnected, so an attempt to understand only a part necessarily leads to some error, but the error is often sufficiently small for the partial approach to be meaningful. Save for this remarkable and far from obvious property of nature, scientific progress would be impossible.

'...Historically there has been a continuing systematic improvement in the accuracy of experiments and a progressive unification of different areas covered by theory, which have allowed the theories to become more and more accurate. But can this progress of science continue indefinitely ? Some scholars, such as Eugene Wigner, argue that at a certain point the question of consciousness must enter the picture, that we cannot indefinitely ignore the observer's role in the nature he tries to understand. To me this conclusion seems inescapable, but such a development lies outside the conventional framework of natural science, which accepts as unambiguous the concept of observation.

Carried to its logical extreme, the bootstrap conjecture implies that the existence of consciousness, along with all other aspects of nature, is necessary for self-consistency of the whole. Such a notion, though not obviously nonsensical, is patently unscientific'

R.Harris (1978) : 'Libraries of books have been written to proclaim the pretensions of economists as planners, forecasters and controllers of our economic (and political) destiny. Models have been refined,statistics multiplied, theoretical jargon conjured up, the slogans coined to coax us into "headlong charges down frustrating cul-de-sacs"(Jewkes, 1978).

Under the same spell, generations of students were conditioned to believe that a complex economic system could be "fine-tuned" by manipulating macro-magnitudes like investment, public-spending, consumption and taxation.'

C.Welch (1978) : 'These professors inhabit a plane of abstraction so lofty that ordinary mortals find breathing difficult. Abstraction is indeed appropriate to rigorous reasoning. It has other advantages. It .... renders nigh invisible to the naked eye all sorts of quite common-place prejudices and assumptions, logical errors and faulty or incomplete arguments which are supposed to find no place in the onion (sic) of the abstract thinker. It elicits respect for what is not respectable; it clothes naked emperors in a decorous and impenetrable fog; it repels the incurious, irreverent and unqualified.

'...What does this matter, you may ask, if few read these professors and fewer still understand them ? It matters because the fish, as the French say, rots from the head first. It matters because bad ideas do, like damp, seep through. Suitably vulgarized they filter finally into demagogic speeches and envious journalese, into political thought and action, into practical affairs, into parliaments and pubs.

6.2.3 Matters of scientific philosophy

P.B.Sears (1960) : 'Scientists distinguish their methodical approach from crude trial and error by calling the latter empirical. Philosophers, taking advantage of their irritating freedom on the sidelines, recognize correctly enough that science itself is a matter of trial and error, however refined. To them, scientific knowledge is also empirical - a wholesome thing for us to keep in mind.

This means that the scientist has both right and duty to tackle phenomena at any level that interests him, whether it is millions of light years away or under his feet.

'...it is our knowledge of the organism as a whole that gives point and meaning to more detailed and precise analysis. Any tendency to construct a hierarchy of scientific values in inverse proportion to a scale of possible precision should be scotched, not as a matter of personal privilege, but on the score of plain intellectual honesty.

The physicists are now working with brilliant results on the ultimate components of matter. But they would be the last to assert that they are near the end of the rōad, or that the study of higher levels of organization is demode, unprofitable or essentially of less scientific importance than the tasks that engage them. Their camp-followers, as is so often the case, are perhaps less perceptive.

Granting fully the need to analyze the components of any system, the system itself, and systems of systems are no less important to understand.

'...Analysis is the instrument of perspective, and sound perspective the end toward which science serves the human mind. Perspective becomes manifest to us in form, organization and process. Only as these are understood do the results of analysis become significant. Only as analysis proceeds does it provide knowledge and techniques for the study of large and complex phenomena. One of the most disturbing trends in modern biology is the tendency to undervalue the classical aspects of that subject. Doctoral candidates have been known to report learnedly on minute characteristics of organisms of whose taxonomy - to say nothing of their relationships in the living state - they knew little or nothing. While this may be explained by the exacting demands of critical modern techniques, it cannot be excused so readily.'

F.N.Egerton (1973) : 'When one studies evolution and genetics it is important to recognize both the forces of stability and of change and to formulate scientific hypotheses, theories, and laws accordingly. The same is true in ecology. The forces of stability and change must be carefully studied and then applied to the subject of the balance of nature. Then critical scientific generalizations can be formulated which do not have their foundation in hidden traditions that extend all the way back to Greek mythology.'

R.Levins (1966) : 'A mathematical model is neither an hypothesis nor a theory. Unlike the scientific hypothesis, a model is not verifiable directly by experiment. For all models are both true and false. Almost any plausible proposed relation among aspects of nature is likely to be true in the sense that it occurs (although rarely and slightly).Yet all modells leave out a lot and are in that sense false, incomplete, inadequate. The validation of a model is not that it is "true" but that it generates good testable hypotheses relevant to important problems. A model may be discarded in favor of a more powerful one, but it usually is simply outgrown when the live issues are not any longer those for which it was designed.

'...The multiplicity of models is imposed by the contradictory demands of a complex, heterogeneous nature and a mind that can only cope with few variables at a time; by the contradictory desiderata of generality, realism and precision; by the need to understand and also to control; even by the opposing esthetic standards which emphasize the stark simplicity and power of a general theorem as against the richness and diversity of living nature. These conflicts are irrecincilable. Therefore, the alternative approaches even of contending schools are part of a larger mixed strategy. But the conflict is about method, not nature, for the individual models while they are essential for understanding reality, should not be confused with that reality itself.

R.H.Peters (1976) : 'A popular tautology is that presented by Volterra's model of competition .....It assumes that two populations grow in a limited system such that, eventually, increase in one population produces a decline in the other. These conditions are presented as constants in the Lotka-Volterra equations, from which a strictly mathematical logic shows that two results may be obtained : one population or the other disappears. Because the argument is logically derived from the assumptions, it is tautological. Nevertheless, the argument has received considerable attention, possibly because the conclusions, which are evident in a verbal statement, are more difficult for us to see in the mathematical form.

This tautology might form the deductive portion of a combined theory, but this would require that the axioms be phrased as testable theories. Andrewartha and Birch (1954) maintain that this is impossible : one can determine the necessary constants only by fitting the results of the competition experiment to the general form of the equations. Thus the results must be predicted from the results themselves. A more acceptable phrasing is that the results are classified in terms of the model. The verification offered by Gause (1935) represents a post facto correspondency with the model, not its proof.

R.Miller (1976) : 'An adequate description of a scientific theory is that, given a set of initial conditions which permit an array of possible empirical results, the scientific theory makes predictions about which results will occur. The theory would be falsified if results other than those predicted occurred with a greater frequency than predicted. A tautology, on the other hand, is merely a logical argument which consists of premises or axioms whose consequences follow by logical necessity. As such, tautologies are self-contained or abstact deductive arguments whose conclusions are implicit in the axioms, and which cannot be falsified and are not predictive.

'...Tautologies have considerable heuristic value in ecology, but should be recognized for what they are, and not become dogmas substituted for scientific theory.

'...Nevertheless, they are liable to be accepted somewhat uncritically at times, and may in fact become so solidly entrenched in textbooks and the literature that they lead us away from profitable lines of scientific investigation.'

W.G.Wellington (1965b) : 'Although population theorists often disagree, such conflict would be welcome if it included suggestions for experiments designed to disprove hypotheses. More often than not, however, it involves only comparisons of all-embracing theories. At least this is how it seems to field ecologists, who also find a disturbing gap between what the major theories say should happen in the field, and what actually happens there. Many investigators therefore have been dissatisfied with population theory for a long time.

'...My own experience made me notice an operational weakness in most studies of population dynamics. In many of these studies there was a tendency to concentrate on the developmental and reproductive processes of the animals, and on measurement of their mortality or survival, to the virtual exclusion of their behaviour and activity. But this approach overlooked the stubborn fact that an animal that does not behave properly, or that does not maintain a certain level of activity at critical periods in its life, simply does not survive, let alone develop and reproduce.

The more I thought along these lines, the more I felt that the right kind of observation would show that widespread neglect of the influence of individual behaviour on survival was actually obstructing the development of population theory. And this feeling was not just a product of the scientific chauvinism that might be expected from my studies of behavior; it arose from the observation that some of the major theories could not really be falsified in their existing form.

'...At the border of the unknown, one must consciously strive to escape from the mesh of former frames of reference, and to remain outside the generally accepted range of opinion concerning one's problem, for a very good reason : the problem is rarely what accepted opinion says it is! But the difficulty is that one tries so hard to keep one's thinking free on larger issues that one overlooks the danger of continuing to think about apparently smaller issues in terms of older concepts. This lapse is always dangerous, and sometimes disastrous, because there is no small issue at a frontier. And how can one observe what does not yet exist as a conceptual possibility ?'

R.C.Lewontin (1977) : 'Powerful theories that offer to explain large parts of the world of appearances carry, immanent within them, their own caricatures. Indeed, their liability to absurd reduction is precisely in proportion to their originality and power. There are inevitably those who, dazzled by the great insights of others but understanding them only superficially, push these theories far beyond their valid domain of explanation.

'...Evolutionary theory was rescued fromits excesses by Huxley's ideas of allometric growth which enabled us to understand that many morphological features of organisms are simply epiphenomenal consequences of relative changes in different growth fields or in different dimensions, and by Sewall Wright's demonstration that precisely the same selective forces can lead different populations to quite different phenotypic compositions because of random processes operating in a field of multiple stable equilibria.

'...For more than forty years evolutionary theory has remained free of a naive selectionism, but in recent times there has been a return to the extreme form of the adaptationist program, as evolutionists have rediscovered behaviour.'

J.Weizenbaum (1976) : '... ideas which seem at first glance to be obvious and simple, and which ought therefore to be universally credible once articulated, are sometimes buoys marking out channels in deep intellectual seas. That science is creative, that the creative act in science is equivalent to the creative act in art, that creation springs only from autonomous individuals, is such a simple and, one might think, obvious idea. Yet Polanyi has, as have many others, spent nearly a lifetime exploring the ground in which it is anchored and the turbulent sea of implications which surrounds it.

'... in large organized systems the characteristics of the individual units are subordinate to the pattern of organization in determining the characteristics of the total system.(p.10)

'...No term of a theory can ever be fully and finally understood. Indeed, to once more paraphrase Kaplan (1964), it may not be possible to fix the content of a single concept or term in a sufficiently rich theory (about, say, human cognition) without assess- the truth of the whole theory.(p.141).

'... a theory expressed in computer language, and then run with suitable values becomes "a model to which the theory applies". (p.145)

'... there are people who believe it possible to build a computer model of the human brain on the neurological level. Such a model would, of course, be in principle describable in strictly mathematical terms. This might lead some people to believe that the language our nervous system uses must be the language of our mathematics. Such a belief would be an error .... John von Neumann, the great computer pioneer, touched briefly on this point himself :

"When we talk mathematics, we may be discussing a secondary language, built on the primary language truly used by the central nervous system. Thus the outward forms of our mathematics are not absolutely relevant from the point of view of evaluating what the mathematical or logical language truly used by the central nervous system is." ' (p.150)

'...(quoting psychologist George A.Miller) "that the only reason something cannot be done by a universal Turing machine is that we don't understand it. Given this interpretation of what 'understanding' consists of, any attempt to suggest counterexamples becomes merely a confession of ignorance or, if one persists in claiming that he can understand something he cannot describe explicitly, one becomes a prototypical member of that class of people known as mystics" ' (p.158)

'... Like sociology too, psychology mistook the most superficial property of physics, its apparent pre-occupation with numbers and mathematical formulas, for the core that makes it a science. Large sections of psychology therefore tried to become as mathematical as possible, to count, to quantify, to identify its numbers with variables (preferably having subscripted Greek letters), and to manipulate its new found variables in systems of equations (preferably differential equations) and in matrices just as the physicists do . The very profusion of energy expended on this program was bound to guarantee that some useful results would be achieved.

'... the computer, used as "number-cruncher"...., has often .... put muscles on analytic techniques that are more powerful than the ideas those techniques enable one to explore. (p.159)

'... A person's belief structure is a product of his entire life experience. All people have some common formative experiences e.g. they were all born of mothers. There is consequently some basis of understanding between any two humans simply because they are human. But even humans living in the same culture will have difficulty in understanding one another where there respective lives differed radically. Since, in the last analysis, each of our lives is unique, there is a limit to what we can bring another person to understand. There is an ultimate privacy about each of us that absolutely precludes full communication of any of our ideas to the universe outside ourselves and which thus isolates each one of us from very other noetic object in the world.

There can be no total understanding and no absolutely reliable test of understanding.

To know with certainty that a person understood what has been said to him is to perceive his entire belief structure and that is equivalent to showing his entire life experience. It is precisely barriers of this kind that artists, especially poets, struggle against.

This issue must be confronted if there is to be any agreement as to what machine "understanding" might mean.(p.192)

'... A theory is of course itself a conceptual framework. And so it determines what is and what is not to count as fact. The theories - or, perhaps better said, the root metaphors - that have hypnotized the artificial intelligentsia, and large segments of the general public as well, have long ago determined that life is what is computable and only that. As Prof. John McCarthy, head of Stanford University's Artificial Intelligence Lab. said, "The only reason we have not yet succeeded in simulating every aspect of the real world is that we have been lacking a sufficiently powerful logical calculus. I am currently working on that problem."(BBC Broadcast Radio 2, August 30 1973 - Lighthill Debate)

Sometimes when my children were still little, my wife and I would stand over them as they lay sleeping in their beds. We spoke to each other in silence, rehearsing a scene as old as mankind itself. It is as Ionesco told his journal : "Not everything is unsayable in words, only the living truth." ' (p.200)

'... Not all computer scientists are still so naive as to believe, as they were once charged with believing, that knowledge consists of merely some organization of "facts". The various language-understanding and vision prorams, for example, store some of their knowledge in the form of assertions, i.e. axioms and theorems and other of it in the form of processes. Indeed in the course of planning and executing some of their complex procedures, these programs compose sub-programs, that is, generate new processes that were not explicitly supplied by human programmers. Some existing computer systems, particularly the so-called hand-eye machines, gain knowledge by directly sensing their environments. Such machines thus come to know things not only by being told them explicitly, but also by discovering them while interacting with the world. Finally, it is possible to instruct computers in certain skills, for example, how to balance a broomstick on one of its ends by showing them how to do these things even when the instructor is himself quite incapable of verbalizing how he does the trick. The fact then, and it is a fact, that humans know things which they cannot communicate in the forms of spoken or written language is not by itself sufficient to establish that there is some knowledge computers cannot acquire at all. (p.207)

'...(quoting Poincare : reprinted in 'The World of Mathematics' Vol.IV pp. 2041-2050, 1956; Simon and Schuster, New York) The conscious self is narrowly limited, and as for the subliminal self we know not its limitations .... calculation .... must be made in the .... period of conscious work, that which follows the inspiration, that in which one verifies the results of this inspiration and deduces their consequences. The rules of these calculations are strict and complicated. They require discipline, attention, will and therefore consciousness. In the subliminal self on the contrary, reigns what I should call liberty, if we might give this name to the simple absence of discipline .... the priveleged unconscious phenomena, those susceptible of becoming conscious, are those which directly or indirectly. affect most profoundly our emotional sensibility. The role of this unconscious work on mathematical invention appears to me incontestable, and traces of it would be found in other cases where it is less evident.' (p.216)

'...(quoting Jerome Brunner :'On knowing',1973; Athaneum, New York) One thing has become increasingly clear in pursuing the nature of knowing. It is that the conventional apparatus of the psychologist - both his instruments of investigation and the conceptual tools he uses in the interpretation of his data - leaves one approach unexplored. It is an approach whose medium of exchange seems to be the metaphor paid out by the left hand. It is a way that grows happy hunches and lucky guesses, that is stirred into connective activity by the poet and the necromancer looking sideways rather than directly. Their hunches and intuitions generate a grammar of their own - searching out connections, suggesting simimlarities, weaving ideas loosely in a trial web ..

(The psychologist) too searches widely and metaphorically for his hunches. He reads novels, looks at and even paints pictures, is struck by the power of myth, observes his fellow men intuitively and with wonder. In doing so, he acts only part-time like a proper psychologist, racking up cases against the criteria derived from hypotheses. Like his fellows, he observes the human scene with such sensibility as he can muster in the hope that his insight will be deepened. If he is lucky or if he has subtle psychological intuition. he will from time to time come up with hunches, combinatorial products of his metaphoric activity. If he is not fearful of these products of his own subjectivity, he will go so far as to tame the metaphors that have produced the hunches, tame them in the sense of shifting them from the left hand to the right hand by rendering them into notions that can be tested. It is my impression from observing my colleagues and myself that the forging of metaphoric hunch into testable hypothesis goes on all the time.(p.218)

'... the altogether plausible conjecture that the forms of information manipulated in the right hemisphere of the brain, as well as the corresponding information processes, are simply differerent from those of the left hemisphere. And may it not be that we can in principle come to know those strange information forms and processes only in terms that are fundamentally irrelevant to the kind of understanding we seek ? When, in the distant future, we come to know in detail how the brain functions on the neurophysiological level, we will, of course be able to give an ultimately reductionist account of the functioning of the right hemisphere. But that would not be understanding in the sense we mean here, anymore than detailed knowledge of the electrical behaviour of a running computer is, or even leads to, an understanding of the program the computer is running. On the other hand, a higher level account of the functioning of the right hemisphere may always miss its most essential features, namely, those that differentiate it from the functioning of the left hemisphere. For we are constrained by our left hemisphere thought modalities to always interpret messages coming from the right in left-hemisphere terms.(p.219)

'... It is much too easy, especially for computer scientists, to be hypnotized by the 'fact' that linguistic utterances are representable as linear strings of symbols. From this 'fact' it is easy to deduce that linguistic communication is entirely a left hemisphere affair. But human speech also has melody, and its song communicates as well as its libretto. Music is the province of the right hemisphere, as in the appreciation of gestures. As for written communication, the function is surely, at least in large part, to stimulate and excite especially the auditory imaginations of both the writer and the reader.

We may never know whether the conjecture that a part of us thinks in terms of symbolic structures that can only be sensed but not usefully explicated is true or false. Scientists of course abhor hypotheses that appear not to be falsifiable. Yet it may be that, under some profound conception of truth, the hypothesis is true. Perhaps it helps to explain why we remain lifelong strangers to ourselves and to each other, why every word in our lexicon is enveloped in at least some residual mystery, and why every attempt to solve life's problems by entirely rational means always fails.

But the inference that I here wish to draw from my conjecture is that, since we cannot know that it is false any more than it is true, we are not entitled to the hubris so bombastically exhibited by the artificial intellegentsia. Even calculating reason compels the belief that we must stand in awe of the mysterious spectacle that is the whole man - I would even add, that is the whole ant. (p.220)

'... (quoting D.C.Denett , 'The abilities of Men and Machines' - paper delivered to the American Philosophical Association, Dec 29 1970) .. while the constraints and limitations of logic do not exert their force on the things of the world, they do constrain and limit what are to count as defensible descriptions and interpretations of things.

Were they (psychology and A.I.) to recognize that, they could then take the next liberating step of also recognizing that truth is not equivalent to formal probability.(p.222)

'... I have argued that there is an aspect to the human mind, the unconscious, that cannot be explained by the information-processing primitives, the elementary information processes, which we associate with formal thinking, calculation and systematic rationality.

Yet we are constrained to use them for scientific explanation, description and interpretation. It behooves us, therefore, to remain aware of the poverty of our explanations and of their strictly limited scope. It is wrong to assert that any scientific account of the whole man is possible. There are some things beyond the power of science to fully comprehend.(p.223)

'...The mechanization of reason and of language has consequences far beyond any envisaged by the problem-solvers we have cited. Horkeimer ... long before computers became a fetish and gave concrete form to the eclipse of reason, gave us the needed perspective :

"Justice, equality, happiness, tolerance, all the concepts that .... were in preceeding centuries supposed to be inherent in or sanctioned by reason, have lost their intellectual roots. They are still aims and ends, but there is no rational agency authorized to appraise and link them to objective reality. Endorsed by venerable historical documents, they may still enjoy a certain prestige and some are contained in the supreme law of the greatest countries. Nevertheless, they lack any confirmation by reason in the modern sense. Who can say that any one of these ideals is more closely related to truth than its opposite ? According to the philosophy of the average modern intellectual, there is only one authority, namely, science, conceived as the classification of facts and the calculation of probabilities. The statement that justice and freedom are better in themselves than injustice and oppression is scientifically unverifiable and useless. It has come to sound as meaningless in itself as would the statement that red is more beautiful than blue, or that an egg is better than milk.'(p.252)

Nature (1979) : '... the same cognitive computer programme can be run successfully on different computers with quite different basic components and architecture. In other words, the specifically mental part of the system is in an important sense quite independent of the physical part .... Consider also the implications for the doctrine of reductionism in the philosophy of science. If biological processes are computational processes running on a physicochemical system, then it is not necessarily the case that the nature of the physical world determines them.

Another important notion for the psychology and philosophy of mind is that of systems and mechanisms which have the property of mutual recursion, that is, the relationships between any parts of the system are not confined to being disjoint or part-whole or overlapping, but A can be a part of B which is at the same time a part of A, infinite regresses being avoided by stopping conditions.'

D.P.Barash (1973) : 'I hope to demonstrate that remarkable parallels exist between ecology and Zen Buddhism .... a fundamental of Zen practice (is) the interdependence and thus, unity of all things and the consequent artificiality of "dualistic" thought patterns. Dichotomous thinking is basic to Western thought .... Such thinking was always anathema to Zen, as it now is to ecology .... The man-nature dichotomy of Western thought has had disastrous consequences, as a fundamentally antagonistic attitude has encouraged us to "conquer" outer space, mountains and forests and to exploit nature as something external to ourselves .... Thus ecologists more and more find themselves as a resistance movement, counseling Zen-like inaction as the best "action".

Western dualism is also manifested in linguistic conventions;

thus, the subject-predicate dichotomy underlies the Western world view .... By contrast the ideogram of most Eastern languages provides for a unified "picture" with emancipation from restrictive linear thinking .... Significantly, modern ecologists have recently moved beyond simple "cause-effect" analysis. This derives in part from the conception of natural systems as multidependent, interacting complexes .... Thus a linear cause-effect relationship cannot be superimposed on the elaborate interconnecting networks ecologists now recognize .... The complexity of natural systems involves the interaction of so many factors that no one can be singled out as the cause - and indeed, the impact of these factors is so multifaceted that no single "effect" can be recognized as well. Systems exist as a whole, not as isolated causal sequences.'

I.Lakatos (1976) : 'There is a longstanding tradition of inductivist style in science. An ideal paper written in this style starts with painstaking description of the layout of the experiment followed by the description of the experiment and its result. A "generalisation" may conclude the paper. The problem-situation, the conjecture which the experiment had to test, is hidden away. The author boasts of an empty, virgin mind. The paper will be understood only by the few who actually know the problem-situation - Inductivist style reflects the pretence that the scientist starts his investigation with an empty mind whereas in fact he starts with a mind full of ideas. This game can only be played - not always with success - by and for a selected guild of experts. Inductivist style, just like its deductivist twin (not counterpart!), while claiming objectivity, in fact fosters a private guild-language, atomises science, suffocates criticism, makes science authoritarian.

Counter-examples can never occur in such presentation : one starts with observations (not a theory), and obviously unless one has a prior theory one cannot observe counter-examples.'

6.2.4 General philosophical points

P.Winch (1978) : ' "But how will you look for something when you don't in the least know what it is ? How on earth are you going to set up something you don't know as the object of your search ? To put it another way, even if you come up against it, how will you know that what you have found is the thing you didn't know ?

Plato's Meno is one of the earliest extant texts in the philosophy of education. Its greatness is connected with its obedience to Socrates's injunction to follow the argument wherever it may lead.

'... we have the benefit of sophisticated laboratory, observational and statistical techniques; we have the money, donated by governments and successful industrialists, to apply those techniques on a large scale. It would be silly to deny the real potentialities of such techniques ...

'... But it is no less important to reflect on the limits to waht can be achieved by their means and to heed Wittgenstein's warning : "the existence of experimental methods makes us think we have the means of solving the problems which trouble us; though problem and methods pass one another by".

'... the learner's passage to knowledge and understanding from their absence takes place within a context of other things already known and understood.

'... In the absence of such knowledge nothing I read (and I must know how to do that too) or observe would have any significance for me; it would not inform me of anything.

It looks then as though the aquisition of knowledge and understanding presupposes previously existing knowledge and understanding.

'... But then how can any learning process ever get started ? It must depend on previously existing knowledge which, if it was learnt, must depend on previously existing knowledge which .... It looks as though we can only make sense of the notion of learning at all if we admit the existence of knowledge which is a priori absolutely and not merely relatively.

So Socrates argued in response to Meno. And so, somewhat later Chomsky argued against Skinner. As Hamlyn puts it, the inadequacies of accounts of learning in terms of "genesis without structure" lead to an account in terms of "structure without genesis".

'... Knowledge and understanding involve objectivity, an interpersonally established conception of truth as something to be arrived at by recognized procedures. There is no way of arriving at such conceptions if the potential knowing subject is thought of as an isolated individual faced with an environment of which he is to make sense all by himself.'

G.Steiner (1979) : '(Feyarabend) ... has two principal and related aims : to demystify the alleged rationality and methodological integrity of the"exact" sciences and to remove these sciences from the prestigious, politically and socially determinant role which they play in current Western society. To borrow Nietzsche's tag, Profeesor Feyerabend is arguing for a 'revaluation of all values'.

'...Feyerabend's position might be defined as that of a "therapeutic anarchist"

'... But the fundamental enemy - and here Feyerabend's polemic is precisely on target - is "the rise of intellectualism in Ancient Greece", and the unfoldings of this intellectualism in the methodologies of Descartes and Kant and in the scientific world-image of Newton and his modern inheritors. It is this "intellectualism", this belief ("illusory, naive, finally ludicrous, says Feyerabend) in "objective truths" and in the disinterested passions of abstract, mathematically-grounded theorising, which have brought the west to its current state of confused inhumanity. Trapped in our naive, wasteful "scientism", we no longer even have access to the pluralistic possibilities inherent in the "animism", in the "mysticism", in the intuitive, mythologically articulate mentalities and wealth of humane insight in cultures, in modes of apprehension which we ostracised as "primitive" or "irrational" (as if the actual proceedings which led to the Copernican revolution or to Einsteinian relativity were not, in their own way, "primitive" and "irrational")

'... Profeesor Feyerabend's plea for a new catholicity of understanding is often poignant and persuasive ..... the issues raised are of the first importance.

Nature (1978) : 'Science and numeracy are undoubtedly important parts of rationality, but they are by no means the whole of it; and scientists do a disservice to both by pretending that they are. In part they fail to distinguish the process of science from the product. Science in the making - like a projected risk - is always conjectural and hypothetical; it is confirmed by repeatability (part of the philosophy of a democracy of risk) and acceptance within the scientific community (a social event). It is never a matter of "experts"; that is mere scholasticism.

'... It is objective and rational to take account of imponderable factors. It is subjective, irrational, and dangerous not to take account of them. As that champion of rationality, the philosopher Bertrand Russell, would have argued, rationality involves the whole and balanced use of human faculty, not a rejection of that fraction of it that cannot be made numerical. By all means let us have numbers, where they can be agreed upon; but let us not be mesmerised by them.'

<u>K.R.Popper</u> (1972) : 'For we can interpret traditionalism as the belief that in the absence of an objective and discernible truth, we are faced with the choice between accepting the authority of tradition, and chaos; while rationalism has, of course, always claimed the right of reason and of empirical science to criticize, and to reject, any tradition, and any authority, as being based on sheer unreason or prejudice or accident.'

<u>S.C.Pepper</u> (1972) : 'The world forces irrational decisions upon us, and irrationally we believe in what we decide. But if we are artional and study things to the bottom we must "doubt all things". At bottom the evidence is evenly balanced for all things.

It is barely possible that such may be the nature of things. But note that this a theory about the nature of things. This is no simple, naive, easy, or secure attitude. It is forced, sophisticated and very insecure.(p.6)

'... we shall define a dogmatist as one whose belief exceeds his cognitive grounds for belief. By this definition, dogmatism is a cognitive error, that is, a fallacy. (p.11)

'... A dogmatist often begins as a reasonable man; but, having such an attitude, he resists the search for new grounds, and even when these are presented he refuses to change his attitude accordingly.(p.13)

'... A man who acts with conviction is not necessarily a dogmatist. It may be that dogmatists as a rule act with more conviction than reasonable men. But that only shows that they are socially more dangerous than might have been supposed. And it may be that reasonable men do not always act with as much conviction as they should. But that only shows that reasonable men should be still more reasonable and realize the necessity of conviction where action demands it.(p.14)

'... Authority is a legitimate and socially indispensable secondary criterion of cognitive belief. But we legitimately credit an authority, not because whatever he utters is true, but because he utters, we trust, only what he believes to be true. We legitimately credit an authority, not because he is an ultimate source of knowledge, but because he is not. We believe he is a reliable indicator mediator and transmitter of knowledge the ultimate validity of which lies elsewhere.

Similarly with the feeling of certainty. This feeling is an excellent sign of factuality and even of the probability of empirical principles. What we feel certain about is generally very trustworthy. But the feeling is not what constitutes its trustworthiness .... So far as we are well adjusted to our environment the things we feel certain of are very likely to be true .... Authority and the feeling of certainty properly understood are legitimate cognitive criteria, but never infallible authority nor utter certainty. (p.36)

'... There appear to be two broad types of evidence : uncriticized, and criticized, or refined, evidence .... Uncriticized evidence has been called .... common sense.... The first trait of a common sense fact, then, is that it is not definitely cognized and generally not definitely cognizable .... A second trait of common-sense material is its security .... Common sense is not stable. But it is secure - that is never lacking. (p.42) .... No cognition can sink lower than common sense, for when we completely give up trying to know anything, then is precisely when we know things in the common-sense way. In that lies the security of common-sense.

But, thirdly, common sense is cognivitely irritable. Secure as common sense is, and grateful as we may be to it for its limitless stores of material for cognition, still as cognizers the more we know it the less we like it.(p.43).... This tension between common sense and expert knowledge, betweem cognitive security without responsibility and cognitive responsibility without full security, is the interior dynamics of the knowledge situation. The indefiniteness of much detail in common sense, its contradictions,its lack of established grounds, drive thought to seek definiteness, consistency and reasons.(p.44) .... Common sense continually demands the responsible criticism of refined knowledge, and refined knowledge sooner or later requires the security of common-sense support (p.45) .... We therefore acknowledge the importance and legitimacy of common-sense facts as evidence even in the face of the most polished critical evidence. We regret the instability and irresponsibility of common sense and shall therefore weigh it judiciously, but we shall not ignore it. Because of its need of criticism, we shall find it convenient to call a common-sense fact a dubitandum, an item of evidence that ought to be doubted. (p.47)

H.A.Meynell (1976) : 'questions can be divided into two types: those for reflection and those for intelligence. Those for intelligence are those which we ask when we are looking for some explanation of a set of data, some theory to account for it. Those for reflaction are those in which we ask whether the theory we have arrived at is so or is not so, whether the kind of thing that we have postulated exists or does not exist, whether the state of affairs which we have conjectured is so or is not so. Questions for reflection are unlike those for intelligence in that they may all be answered Yes or No.

Given provisional answers to intelligence questions, it is appropriate to ask further whether these provisional answers are correct; and such further questions can appropriately be answered Yes or No. These examples illustrate another fact about cognition which is of some importance : that every question for reflection presupposes the answer to a question for intelligence. (p.7)

'... while direct insight gets the point or sees a solution, an inverse insight is to the effect that there is no point, the solution is that there is no solution. An inverse insight is not the same as a correction of insights previously reached, it finds fault not with answers but with questions. Its essence is the denial of an expected intelligibility.

In a demonstrative science it is to prove that a question of a certain type cannot be answered. In an empirical science it is to put forward a successful hypothesis or theory that assumes that certain questions mistakenly are supposed to require an answer.(p. 14)

'...The significance of inverse insight may be brought out by the introduction of the notion of an empirical residue. This empirical residue consists in positive empirical data, is to be denied any immanent intelligibility of its own, and yet is connected with some compensating higher intelligibility. Particular places and times pertain to the empirical residue, each differs from every other, as a matter of fact. As differences in time and place have no immanent intelligibility, they do not modify that of anything else. Mere difference in place or time as such does not involve difference in observations or experimental results. If it did so, each place and time would have to have a physics, chemistry and biology of its own; and since a science cannot be worked out instantaneously in a single place, science would be impossible. On the contrary, of course, it is actually the case that scientists can collaberate and pool results gained from many places and times. Still more important for science than collaberation is generalisation. Each chemical element and compound differs from every other, and these differences have to be explained. But there is also a sense in which single atoms of hydrogen differ from each other, and these differences, fortunately, do not have to be explained. Here is another aspect of the empirical residue - that it is so simply as a matter of fact, without explanation.(p.15)

'... In brief, individuals differ, but the ultimate difference in our universe (between individual instances of exactly the same kind) is a matter of fact to which ther corresponds nothing to be grasped by direct insight.

Abstraction is properly speaking a matter of grasping the essential and avoiding the inessential (the colour of the cartwheel, and the material out of which it is made, were not matters relevant to the determination of why it was round). For any insight or cluster of insights the essential or important consists of those aspects of the data necessary for the insight to occur and the set of concepts necessary to express the insight. In the study of insight itself, the particular examples of insight chosen to provide insight into insight are, of course, irrelevant;.... In any subject, "one comes to master the essentials by varying the incidentals" - and so it is with the study of insight.(p.15)

'... The simple curve with which one joins the points could represent the actual law; but there is an infinite number of other curves each of which could pass through all the known points, and hence represent the law .... In every empirical enquiry there are knowns and unknowns - the knowns being typically the data of sense, which are apprehended whether or not one understands. The unknowns are what one will grasp by insight, and formulate in conceptions and suppositions. (p.18)

'... Similarities are of two kinds "There are the similarities of things in their relations to us. Thus, they may be similar in colour or shape, similar in the sounds they emit, similar in taste or odour, similar in the tactile qualities of hot and cold, wet and dry, heavy and light, rough and smooth, hard and soft. There are also the similarities of things in their relations to one another. Thus they may be found together or apart. They may increase or decrease concommitantly. They may have similar antecedents or consequents. They may be similar in their proportions to one another, and such proportions may form series of relationships such as exist between the elements in the periodic table of chemistry or between the successive forms of life in the theory of evolution. (p.19)

'... Someone might ask which was the rational choice, science or common sense. But the question is wrongly posed, since it is rational not to choose between them, but to follow the exigencies of both, science to master the universal, common sense to deal with the particular. (p.20)

'... Scientists achieve understanding only at the end of an enquiry; and yet the enquiry is methodical. Now this evidently involves something of a paradox. Method implies the adjustment of means to ends; and the question arises of how means can be adjusted to the end of a knowledge which is not yet acquired ... The answer to this puzzle is the heuristic structure. .... the scientific anticipation is of some unspecified correlation to be specified .... and now the task of specifying .... is carried out .... by reaching insight into the tabulated measurements, and by expressing that insight through some general correlation or function that, if verified, will define a limit on which converge the relations between all subsequent appropriate measurements ....this type of heuristic structure, which anticipates the kind of intelligibility that may be grasped by direct insight, may be called classical.(p.21)

'... In unsystematic, as opposed to systematic, process there is no single insight or set of insights from which the whole process and all its events may be mastered. .... Now whether the world process as a whole is systematic or non-systematic does not seem to be a matter which can be settled _a priori_ .... if world process as a whole turns out to be non-systematic, it will follow that some forms of science at least will be irreducibly statistical, and hence that a science which is content with the assigning of probabilities is not a mere cloak for ignorance.(p.22)

'... Classical investigations are concerned with what would be so if other things were the case .... Statistical investigations, on the other hand, are concerned directly with aggregates of events .... The theoretical considerations which may affect individual instances are set aside by the statistical investigator. (p.23)

'... Classical investigation acts on the principle that no difference is to be neglected; statistical, that to seek intelligibility in random differences is merely silly .... Statistical enquiry finds intelligibility in what classical enquiry neglects; a defect in intelligibility of one kind is replaced by intelligibility of another kind. (p.24)

'... The discoveries made by both methods are universal and abstract; but the type of abstraction involved is different in the two cases. Classical laws .... abstract from co-incidental aggregates inasmuch as they demand the qualification "all other things being equal". On the other hand, statistical states express an intelligibility immanent in co-incidental aggregates and, to reach this intelligibility, they abstract from the relative differences in relative actual frequencies.

Roughly, classical laws state what would happen if conditions were fulfilled; statistical laws, how often one can expect them to be fulfilled. Thus the kind and manner of prediction involved differ from one another. Classical predictions can be exact within assignable limits; but statistical prediction cannot be so, just because relative actual frequencies differ at random from probabilities .... A range of observations may be amenable either to classical or to statistical understanding; which is appropriate cannot be settled a priori, but only by trial and error.(p.25)

'... One of the most important consequences of acknowledging the existence of the non-systematic is that it leads to the affirmation of the existence of successive levels of enquiry, and of different types of entity investigated by each of these levels. "If the non-systematic exists on the level of physics, then on that level there are co-incidental manifolds that can be systematized by a higher chemical level without violating any physical law" And the same will apply to the biological level in relation to the chemical, the psychical level (of animal sensations and emotion) in relation to the biological, and of the specifically human level of insight and reflection, deliberation and choice in relation to the psychical.

'... At each level of reality(the subatomic, the chemical, the biological and so on) the intelligible laws constitutive of that level render systematic patterns of events which are only co-incidental from the point of view of the laws governing the level below. Thus, things at each higher level cannot properly be claimed to be "nothing-but" aggregates of things at the next level below since they are characterized by properties constitutive of that level but not of lower ones. Thus the argument underlying physicalism .... can be refuted. (p.149)'

6.2.5 Comment

Ecologists engaged in the study of populations and communities find themselves using words which are ambiguous or at best very loosely defined. The ambiguity of the words reflects the ambiguity of the underlying concepts, an ambiguity integral to the systems they study, and totally interrelated with all the properties of the system - behaviour, dynamics and so on.

Scientific theories are amalgamations of empirical data and formal description - the mapping of formal disciplines (mathematics, logic etc.) onto empirical sets(sensory data - direct or indirect). The role of philosophy in science is to question the possibility, feasibility and potential modes of such mappings.

Much of the so-called theory of ecology is no more than mathematical games-playing. The lure of games-playing affects all theoreticians. As academic exercise there is no doubt of its value. However, in the development of simple observations to extended abstractions, the point at which reality is left behind is often hard to define. The theoretical systems so produced are characterized by the difficulty of locating the point at which they may be empirically and objectively tested i.e. without dependence on parallel and analogous theoretical systems.

The saddest aspect of this development of theoretical ecology is the obsession with total objectivity it reflects, taken to the point at which preference is given to any account of an explicitly logical process over an account in which objectivity cannot be so easily demonstrated, regardless of the other merits and demerits of the accounts.

I have started from the belief that population and community ecology is to do with the behaviour of populations and communities, and that these entities must be studied in their own right. In attempting to justify this holistic theme my main target is the reductionist approach which develops ideas of population and community behaviour from the activities of individuals. This is neither to deny the ultimate practicability of such a method (a truism given a causal mechanistic universe) nor to promote any mystical super-organism conception of these groups of organisms. It is, rather, to stress the importance both of emergent characteristics in group behaviour, and of inter- and intra- organismic flexibility. Together, these properties preclude the use of many object and process definitions common in theoretical ecology, except under very stringent conditions, and they also raise important questions of epistem ology.

It seems to me likely that we are, in examining ecological systems, dealing with objects and processes of a qualitatively different sort from those objects and processes which are the base materials of the study of the lower levels of organization. Our methods, indeed our basic scientific philosophy, were developed during the heyday of physics and chemistry and were necessarily constrained by the properties of that scientific subject matter. So far it has been assumed that all biological investigations are amenable to the same type of enquiry, but while this may be true at the biochemical level, it does not follow that other sectors of biology are to be so explored.

The ecological truths of complex co-ordinated evolutionary systems must impose their form on the philosophical sub-structure of science, and reduce previous physical conceptual frameworks to the status of special cases under simplified conditions. To do otherwise is to use pure induction - a method difficult to defend in the matter of acquisition of knowledge - in an area of critical importance to Man's continued existence.

This is not merely a caution affirming the possibility of different world views - that trivial point can be made at any stage of logical development of any empirical subject at any time - but is a reminder of the substantiated evidence already at odds with the conventional viewpoint. That the current theoretical formalism remains, is probably due more to the divisive results of academic specialization than to any reasoned debate of the matter. If there are to be ecologically valid analytic methods then a new symbolism is required whose operands and operators are of a type different to those currently in use, and homeomorphic with the subjects of study.

6.3 Future Points Revisited

Many points have been raised which suggest enquiries to be made in relation both to the specific biological enquiry (into Acarus siro) and to more general ecological questions. These are outlined here, appearing in order of their point of origin in the preceding text, categorized to section or sub-section level as appropriate :

Section 4.1

1) Experimental measurement of the fluctuations in temperature, carbon dioxide concentration and humidity in the experimental chambers : miniature electronic devices for temperature measurement and for gas analysis are easily available, and are sufficiently precise to detect any changes which might reasonably be expected to induce metabolic changes in the mites. The filter paper base of the cells would facilitate insertion of the devices, which could then be sealed into place with shellac (as are the bases to the cells).

2) Verification of the amounts of delivered suspension, beyond the precision of the method of observing variance changes, is more difficult.

Micro-calorimetry is a possibility, as are various chemical micro-assay methods to be used for specific components of the food mixture. These would provide both a measure of total delivered food and of the variation in composition of the delivered food (arising from the different particle sizes in the suspension)

3) The question of the actual size distribution of the mites of any one age class taken for experiment is only important inasmuch as these sizes affect the type of experiment done. The effect can be measured by repeating the experiments with more stringent size selection of the mites.

An initial experiment might be to select one particular situation which has shown extreme variation in result, for example D30-300 - thirty deutonymph mites with 300µg of food, and repeat the mortality experiments with a greater number of replicates, and in three sets : using mites from the lower, middle and upper ranges of the size distribution for deutonymphs (length ranges of 275-300µm, 300-325µm and 325-350µm). The value of such an experiment presupposes a more precise estimate of food delivery.

4) The significance of the position of the mites within the extraction dish could similarly be examined, by repeating mortality experiments with both stringent size selection and deliberate and explicit segregation of mites from different areas within the dish.

In relation to this let me mention an experimental design which arose from observations (by me) of differential distribution of mite life stages and sexes in mass culture. The design is based on a technique developed by Haarløv and Weis-Fogh(1962). The basic idea is for the mites to be cultured in narrow tubing made of some permeable or semi-permeable material e.g. Visking cellulose, filled with the usual 3:1 yeast/wheatgerm mixture. The tubing can be filled with measured quantities of food and, because of its plastic nature, be sealed at either end with some simple and removable pressure device e.g. bulldog clips. The permeability properties of the material and the intended narrow diameter of tubing to be used (14 mm) mean that temperature and, more importantly, humidity can be controlled and maintained throughout the food medium.

On completion of the required growth period, the tubes will be suspended above 40% formalin solution in order to kill and fix the organisms present. The clips will then be removed, with the tubes in a horizontal position to minimise disturbance of the medium, and the tubes then immersed in a hot (70°C) 2% solution of agar-agar until the solution has completely saturated the food and mite mixture. The tubes will then be removed and allowed to cool, when the agar gel can be hardened in 96% alcohol in preparation for sectioning. It seems likely that sections of as little as $\frac{3}{4}$mm thickness will be possible, and these permanently mounted in a glycerol/gelatine mixture.

This design allows a number of possible experiments, including the basic determination of the distibution of age classes in a column of food medium; the effects of particle size and structure on distribution; partitioning of classes in mixed-media systems; and analysis of the progress of a mite population in a tall column of food medium.

Section 4.2

5) As a first step towards determining the possibly beneficial effects of the death of one mite on the survival of others, I would suggest experiments in which mortality in groups of mites without any food was compared with mortality in groups of similar status (of number as well as the characteristics mentioned above) confined with the body of a freshly killed mite.

It would be preferable to use an adult mite in order to maximize any effect related to the amount of mite tissue present. Such an experiment would not be resticted to the four day period of the experiments already done, and the progress of the groups should be followed more closely through the course of experiment.

(Is the life of the post-reproductive female a mechanism for making available extra food when the normal supply runs out.? The adult female contains a large food mass - if she dies after her egg-laying cycle is finished, this food is presumably quickly lost to other mites through dessication. If she survives in order to be cannibalized, the possible benefit might compensate for the food presumably lost in maintaining her.)

6) Given that some effect was shown in the previous experiment it would be necessary to show that mite tissue was ingested by surviving mites. This could be done by radio-labelling the dead mite presented, and could be combined with the previous experiment.

7) Regarding the mechanisms of possible injury, there seems to be no obvious alternative to prolonged and detailed observation of groups of mites within a cell, with conscientious regard to the progress of individuals, especially those in a supine position. Thus it might be possible to verify the hypothesis that mites are aided in moving from a supine position by the presence of other mites, or to demonstrate that those mites which do become stuck in a supine position are more likely to die than those which do not. A photographic record of the course of experiments would be useful, especially of the interactions of individual mites. An epidiascopic projection of the experimental cell would be an aid to observation in removing the need for prolonged observation by microscope (fluorescent lighting would be needed to alleviate heating effects)

8) The effect of nutritional status on the recovery of mites from injury might be studied by artificially injuring mites with the use of micro-dissection equipment (simple puncture of the cuticle by a micro-needle, for example), nutritional status being varied by different periods of starvation. It might be interesting to examine the susceptibility to injury of mites recently emerged after ecdysis.

9) The nature of feeding, whether food-limited or ingestion-rate limited could be studied by subjecting the mites to various levels of food availability for different times and then determining times to starvation death on removal from the food.

Section 4.4

10) The function of the chemoreceptor organs on the legs of Acarus siro would, if established, most likely give significant insight to the components of its environment important in controlling its behaviour. I am not conversant with the neuro-physiological techniques probably needed to determine such function, and therefore can only suggest that such experiments be attempted, without specifying any details of approach.

Section 5.1

5.1.1

11) The hypopus of A.siro (and those of other members of the Acarus siro complex) needs to be located more accurately. This would involve a lengthy observational study of likely insect (and mammalian ?) vectors at the time at which hypopal dispersal is most likely (probably early summer). Many phoretic mites are non-specific in association, being located according to similar structures on the insects they use as transport, for example under the

elytra of beetles (Lindquist, 1975). Mere observation of the hypopi would be insufficient as their taxonomy is difficult; it would be necessary to get them to apolyse and then rear them to maturity for proper identification.

12) In addition a more thorough search for members of the A.siro complex in natural habitats is required, with bird and mammal nests the prime target, and post-harvest cereal fields a second likely location. The influence of certain farming practices e.g. stubble-burning, must not be ignored in its effect on the distribution of the various species concerned.

13) Given that the species are found in animal nests or in post-harvest fields, the nature of these environments must be considered in designing experiments to do with control of hypopus formation. Seasonal (or successional ?) effects here could be most important.

14) Some light might be thrown on the question of whether the mites are principally granivorous or fungivorous by examining their feeding behaviour, their catabolic structure and their growth rates on the various types and species of these foodstuffs.

15) Given identification of the likely vectors of A.siro, study of these would be necessary to identify the routes by which the mite could pass from one suitable environment to another. If the production of hypopi was seasonal, this study would have to be seasonal as well.

5.1.2

16) The degree of genetic separation of the various species of the Acarus siro complex may be better approached with a mass mixed-culture system than with single pair matings (of F_1 and F_2 gener-

ations). If the species were co-located in nature then there would be no formal restrictions as to which species or hybrids chose to mate. It might be interesting to mix two, three or more of these sibling species in mass culture, and let this mixture develop for several generations before examining the outcome, as a preliminary to more specific genetic interchange studies.

5.1.3

17) A primary requirement for a major switching system is multiplication of genetic sequences and retention of the copies. Complete genetic systems would have to be co-ordinately blocked or expressed in order to allow only compatible sub-systems to occur together. (Of course there might be more or less random assortment, accounting for some aspects of hybrid sterility in Acarus, for example). As candidates for the time of switching the egg must come first, and then the hypopus, both involving structural organization the former, presumably, to the greater degree.

Experiments would first be needed to determine the cues for apolysis of hypopi for all A.siro complex species. Then, if biochemical analysis suggested a basic genetic synonymity of any of these species, experiments could be directed to find the cues for change of expression.

Might it be fanciful to suggest that, if the hypopus is involved in this switch, that a parallel exists with the development of holometabolous insects. In the insect case, one morphological form, the larva, is followed by a transition form, the pupa, from which develops a different morphological form, the adult. Perhaps in the Acarus case we have one morphological line producing a transition form, the hypopus, from which can develop one of a number of morphological lines, according to circumstance.

In all experiments attempting to determine the mechanisms of change of behaviour and/or physiology, it is important to remember that conditions in nature change gradually and that the mechanisms looked-for have evolved under these conditions. It may be unwise, therefore, to use sudden changes of condition in the attempt to induce changes. This may very well account for the failure of many Acarus strains to produce hypopi under laboratory experimental conditions.

The factors that should be examined first as possible causes of change are : food density (independently of its role as a supporting medium - usually the mites are grown solely in food - an alternative might be a mixture of powdered food and some relatively inert filler such as wood sawdust or vermiculite); gas concentrations; humidity; temperature; signal chemicals (as possibly, the 'minty' oil of Acarus siro); toxic waste products; trigger effects of local flora (hypopus production as a response to a particular yeast, fungal or bacterial growth).

It would be desirable to alter these conditions at rates similar to those estimated to occur in nature. For one must remember the point made by Boyer (1976), ' .. if past events alter later physiological or behavioural states of any animal, there arises the theoretical question of the extent to which measurement over a short interval in present time can compensate for ignorance of past history of the population'

Section 6.1

The value of modelling approaches which make assumptions of the "linear k-value/log-density relationship" sort could initially be examined by comparing simulation models of populations with the same gross characteristics, but with such gross effects obtained in different ways : at one extreme the homogeneous populations required by analytical modelling, at the other extreme internally-structured populations of the same 'mean' response. By gradually relaxing the homogeneous assumptions of the former one might be able to determine the points at which the behaviour of such an altered significantly differed from the purely homogeneous system. By differently relaxing the assumptions of the analytic model and comparing simulations of behaviour, one would then be able to define the limits to usefulness of that model.

On an empirical level, it is only necessary to show that significant effects occur in populations and communities which could only be explained by properties not allowed in the framework of a particular model, to disbar that model as a general description.

NOTES

1) The defensive, if not servile, posture adopted by many experimental ecologists when faced with theoretical ecologists augurs ill for productive debate in ecology. The reasons for this deference, I think, are two. Firstly, the experimentalist, who is by necessity confined to the study of the particular, generally feels his research subordinate to any research of a more extensive and cohesive kind. Secondly, and most probably as a result of the essentially amathematical history of ecology, the experimental ecologist is in awe of mathematical techniques because of his usual incompetence in these. The experimental ecologist does not recognize that the precision and internal consistency of theoretical forms are largely results of expediency, and not infrequently dictated in form by fashion; as a result he becomes directed by these rather than, by making critical comment, actively directing them.

The lack of critical self-confidence shown by experimental ecologists has probably arisen because of the opacity of mathematical symbolism. This will only be remedied by a rigorous interpretation of theoretical arguments in more conventional verbal terms.

2) The distinction between r-selection and K-selection was developed originally by MacArthur and Wilson (1967)

Pianka (1970, and also 1974) characterized r-selected pests as follows :

Climate : Variable and/or unpredictable; uncertain
Mortality : Often catastrophic
Non-directed. Density-independent
Survivorship : Type III
Population size : Variable in time, non-equilibrium
Usually well below carrying capacity
Unsaturated community or portion thereof
Ecological vacuum
Recolonization each year
Intra- and inter-specific competition. : Variable often lax
Selection favours: 1. Rapid development
2. High maximal rate of increase, r_{max}
3. Early reproduction
4. Small body size
5. Single reproduction

Length of life : Short, usually < 1 year
Leads to : Productivity

As variation there is the description by Southwood _et al_ (1974):

Habitat : Temporary and/or unpredictable
τ/H : approaches 1 i.e. animals generation time, τ, approaches length of time habitat remains favourable (H).
Niche hypervolume: frequently empty
Population levels: all levels
Size : Small and have small scale of trivial movements
Mortality : Increases with time after invasion
Finite rate of increase, λ : maximal where $\ln\lambda$ = gains − losses $= \ln(R_n - R_k)/T_c$
Generation time τ: low
Maximum natality (R_n) : high
Fecundity : high } { to produce
Ratio ♀/♂ at birth: may be high } { high R_n
Migration : important feature of loss component
Mate-finding tactics: efficient at all densities
Extinction point : very low

Generally we can say :

	r	K
Organism	smaller	larger
	higher metabolic activity	lower metabolic activity
	omnivorous	specialist
	highly mobile in relation to size	
Food source	energy rich	energy poor
	easily assimilable	not easily assimilable
	spatially or temporally patchy	continuous

In the case of animals, r-selection is a response to a patchily distributed or ephemeral, high-energy, easily assimilable food source. The optimum strategy here is to consume the food as rapidly as possible and to produce sufficient offspring to optimize the probability of discovering a new food patch. The food source is patchy in this case, so as to ensure its survival – the strategy being to become less apparent rather than to become less appealing (less easily assimilable)

K-strategists are those whose strategy has been to concentrate on the less appealing food plants which because of their lesser appeal (assimilability) can adopt a continuous distribution.

As to the association between variability and the position of a species in the r-K spectrum there are reasons to expect the more r-selected species to exhibit greater variability than K-selected species.

On the one hand the r-selected species may be expected to show evidence of the 'founder' effect (Mayr,1942) in that their populations, by definition, show great changes in number and are exploitive colonizers. These populations will therefore arise from small numbers of founder animals, and the subsequent genetic composition of the population will roughly bounded by that of the founders. As the population develops, the absence of competitive pressures removes the effect of selective disadvantage in confining variation within the population, and hence a broader base of variable genotypes may be allowed. The variability can therefore be seen to exist : firstly between founder populations, and secondly, and increasingly, as the population develops.

In contrast, the K-selected species are, by definition, of steady-state populations, where the founder effect is absent and where competition restricts variation in a situation where the population is entirely confined to one niche.

The distinction between r- and K- species becomes confused in species exhibiting mixed strategies either temporally (planktonic immatures becoming sessile adults) or spatially (wide-ranging organisms adopting whichever strategy suits their local environment)

3)Continuous and discontinuous variation are, in the simplest case of Mendelian inheritance, only quantitatively different in that the characteristics are determined by different numbers of genes - the greater the number of genes the greater the apparent continuity. This interpretation is due to East (1910, cited by Ricklefs, 1973).

Additional effects promoting contiuous variation include quantitative environmental effects (nutritional variation, etcetera).

4) This type of population structure was noted by Carl (1971) for ground squirrels (Spermophilus undulatus) and by Waage (1972, 1973) for the damsel fly Calopteryx imaculata, amongst others.

5) According to the maxim 'Complete competitors cannot co-

exist' – the principle of competitive exclusion (Hardin, 1960) mentioned in Section 1.2.1, also stated as 'Two or more species living in the same habitat and competing for the same limiting resources cannot stably co-exist unless their relative fitnesses are inversely related to their frequencies' by Ayala and Campbell (1974).

In whatever form it is stated, it is dependent on the restrictive characteristics of the Lotka-Volterra dynamics within which it was developed, and is a tautological statement of doubtful practical value.

6) We are here discussing not whether there is no variation within a population, but whether the variation is significantly different from some unimodal system which could be simply characterized.

Some obvious examples of heterogeneous populations are those of social insects (though of course the situation here is one in which the definition is unresolved : however, that it is a difficult case, is not a reason for excluding it from discussion); cases of maintained discontinuous variation (as of balanced polymorphisms – see Note 31) within unified breeding groups. It matters not whether the variation is maintained by post-natal conditioning (as of some classes of social insect), conflicting genetic pressures (balanced polymorphism), or by partial (temporal or spatial) segregation of different forms : all of these lead to a population which cannot be described by averaged attributes.

7) For example, in a genotype of orthogonal, equally-polygenic characteristics (unrealistic as that may be), the contribution to fitness of each genotype being linearly proportional to the proportion of the more fit allele for each characteristic, it is easy to see that a range of combinations have equal fitness. Consider three characteristics (A,B, and C) each of four levels (1-4), then :

$$A_1.B_3.C_2 = A_2.B_2.C_2 = A_2.B_1.C_3 = \text{etcetera.}$$

Of course linearity and orthogonality are unlikely but, imagining the more realistic case where extremes of allelic type are less fit, the median types may also form a compensatory spectrum of the same sort.

8) The correct terminology is lethal genes. The usual case is of lethal recessives :

$$\underbrace{\underline{A}A \quad Aa \quad a\underline{A}}_{\text{viable}} \qquad \underset{\text{lethal}}{aa}$$

The discontinuous characteristics need not themselves be subject to such a regime, nor need the destructive interaction be of similar recessive alleles. The observed characteristic may be linked to the destructive, and the destructive combination be of interacting genes rather than interacting genes rather than interacting alleles.

9) Procrustes was the giant Polypemon, encountered by Theseus on his journey to the palace of his father Aegeus in Athens. Procrustes would force 'his victims to lie on a bed too short for them and then cut off whatever overlapped. Alternatively he would stretch them if the bed proved too long. Theseus made him undergo the same treatment' (New Larousse Encyclopaedia of Mythology, 1968, p.176)

10) The historical development of normal distribution theory in relation to the question of distribution-free statistical tests is concisely given in the introduction of Bradley's (1968) book. The misuse of normal statistics has been succinctly described by Peters (1943, quoted by Bradley) :

'Once making the assumptions, the mathematics is simple and exact and fascinatingly beautiful; and mathematicians will frankly say that it is our concern as researchers, not theirs, whether the assumptions are legitimate in the particular research situations with which we work. It happens that in most of the research in our field the assumptions are so far-fetched as to abort the results for careful work.'

11) Suggestions as to the possible experiments are included in Section 6.3 . The important thing here is to stress that critical experiments are to be designed, experiments which will differentiate alternative hypotheses. This type of experiment remains the only means of advancing scientific knowledge, as opposed to mere observational knowledge which is informal and subject to many kinds of implicit assumption. The scientific experiment must include a well-defined and explicitly-recognized environment.

12) A sort excellent discussion of normal and distribution-free statistics occurs in Chapter Two of Bradley's (1968) volume on statistics. This volume, and Siegel's (1956) volume provide a good introduction to the methods of distribution-free (or non-parametric)statistics.

13) The disparity between our own abilities and our ability to formally explain these abilities is nowhere demonstrated better than in research into artificial intelligence. Even at so basic a

level as character recognition our failure to generate automatic means of processing the varieties of human script, is a reminder of the unparalleled processing power of our own minds. See Sebastyen (1963).

14) Epistemology is the philosophical examination of the logical processes by which we make statements of fact about the universe. It has been formally defined as :

'The theory or science of the method or grounds of knowledge' (S.O.E.D)

'The branch of metaphysics which deals with the nature and validity of knowledge' (The Penguin English Dictionary)

15) This opinion, cited with no material evidence whatsoever, is an intuitional corollary to the observation of Note 13 i.e. that the power of the human mind exceeds our state of formal processing. This is based on a hypothetical homology between patterns of organization in the external world and the patterns of processing in the brain. It appeals, almost unscientifically, to an evolutionarily influenced idea that the working of the human brain is, in order to efficiently process environmental signals, organized in a complex parallel-processing manner reflecting the environment. Hence human language structure, limited as it is in its capacity to precisely display our thought processes, has more of the texture of environmental functioning than does the abstracted language of mathematics. Of course the correlation, if it exists, may be spurious, but there is no a priori means of comparing the merits of verbal and mathematical arguments.

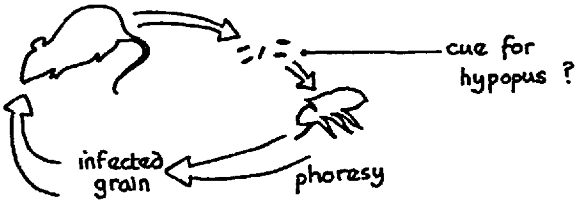
16) 'Given a species which is reduced sharply in numbers at more or less regular intervals by unfavourable conditions, what is the optimal genotypic structure of the population which will both guarantee its survival in low numbers during unfavourable periods, and also give it a high rate of increase in favourable times, and allow it to maintain very large populations at peak periods ?' (R.C.Lewontin, 1970)

17) The need here is to carry out a more rigorous search for the hypopus of Acarus siro and for populations which might exist outside the stored-food environment as a result of phoretic dispersal. If, as is possible, the mite is to be found in populations of a more dispersed sort than those usually examined, it will be difficult to prove these statistically significant in any distribution or composition simply because they are adapted for persistence at

low densities. Such a difficulty of course accompanies all studies of organisms which are dispersed, at the extreme solitary, in nature. The larger, more dense, populations are more prominent and so have received most attention. It is probable that our conception of population dynamics has been biased by this.

18) See Sinha (1964,1966,1968), and other papers by Sinha and his colleagues on mite-fungi inter-relationships referenced by Hughes (1976).

19) Other cues for the production of the hypopus might include passage of mites through the digestive tracts of rodents :



Chmielewski (1970) demonstrated the survival through such a passage, for the mites Carpoglyphus lactis and Tyrophagus entomophagus, especially the eggs and immature stages. Griffiths (1966) demonstrated, for A.immobilis, that nutrient imbalance and scarcity, and also the hormone precursor ergosterol, may be necessary for hypopus production. He also showed that the fate of the protonymph was fixed during the first thirty hours of the protonymphal instar, when co-incidently certain neuro-secretory cells are developed (Hughes, 1964) nutrient dependently. Seasonal effects may also exist (Robinson, 1953, quoted by Hughes, 1976 p.25)

I am at present uncertain as to the role the source of stored food (e.g. cereal crops for stored grain) plays in forming a suitable habitat for the growth of Acarus. It would seem that it could only be important at the beginning of autumn, when seeds have fallen and atmospheric humidity has risen sufficiently for Acarus to roam freely.

Experimental observation shows that hypopus production is induced by a decrease in quality of the food supply (providing there is an adequate vit.B supply). Logical reasoning suggests that this would be a suitable cue for production of the phoretic hypopus (physical conditions having remained approximately constant)

As far as I am aware, no experiments have been done to determine the response of A.siro populations to other types of environmental change. It would be interesting to observe their response to such things as decreasing oxygen, increasing carbon dioxide, decreasing humidity, increasing temperature. As these changes are possibly reversible in a given situation, in contrast to the irreversible nature of food deterioration, there might be a qualitative difference in response.

The known tolerance of A.siro to rapid changes of environment for significant lengths of time (for example, 3 days in carbon dioxide) and its observed physiological resilience (recovery from CN poisoning) and are also factors to be taken into consideration in determining its plan for survival.

Returning to the known mechanisms for hypopus production, there is a need to determine the strategies favouring maximum survival of hypopi, and also maximizing the probability of a hypopus founding a new population. Among the areas which might be examined are:

a) More precise definition of the cues triggering hypopus formation.

b) Mechanisms which satisfy the nutritional requirements for hypopus production e.g. cannibalism, fungus feeding.

c) Mechanisms increasing the probability of hypopi initiating new populations e.g. altered sex ratios among hypopi, or in the post-hypopal generation; pre-phoretic fertilisation (suggested by the observation that adult males are often seen apparently copulating with nymphal females)

20) A key to the species of the Acarus genus is given by Griffiths (1970), the basis for which is given in Griffiths (1962, 1964a and 1964b).

Referring to the hypopi of A.siro and A.farris, Schulze (1924a and 1924b) originally stated that both types were produced by a single species (and further that both could result from a single pair mating), but this was contested by Oudemans (1924). However Oudemans later retracted this statement in print in the 1940's (D.A.Griffiths, personal communication) and supported the view that both types of hypopus could be produced by _Tyroglyphus farinae_ (Acarus siro).

Hughes (1976, p.21) says, 'The distinction between the two types (of hypopi - active and inert) is not a rigid one and structurally they tend to grade into one another. Although hypopi only resemble the adults in certain details, those of related species are usually of the same type.'

Zachvatkin (1941) regarded the various strains of the then single species Acarus siro as not being of specific importance because of the number of intermediate forms to be found - this tends to support the idea of major gene paths through a multi-characteristic field.

21) 'Hybrid intermediacy is a well known phenomenon in many branches of zoology. It is considered that the intermediate nature of the morphological characters depend upon the combined quantitative effect of multiple genes, usually referred to as multi-factor or polygenic inheritance. It can be recognized in laboratory crosses between two inbred parent forms if the variation in the F_2 generation is much greater than the variation in each of the parental and F_1 generations, in which generations the variation should be about the same.' (Griffiths, 1964b) In this paper, such intermediacy in crosses between A.farris and A.immobilis was demonstrated by Griffiths.

22) In the cases of both Tyrophagus putrescentiae (Schrank, 1781) and T.palmarum (Oudemans, 1924), field populations will not breed with stored product populations. In the case of T.putrescentiae, there are slight morphological differences which might allow definition of a new species, but in the case of T.palmarum there are no discernible differences. (D.A.Griffiths, pers.comm.)

23) Not necessarily absolute incompatability - there may be all levels of incompatability leading to reduced viability, sterility etcetera, none of which will interfere with an individual's impact on the environment. A sterile hybrid will still compete for resources, similarly a fertile but less efficient form. Blank spots may occur in the realized field because of lethal gene interactions of the type mentioned in Note 8.

24) Differences between individuals reduce effective competition by separating the individuals along environmental gradients. Aggregation of like individuals will occur by necessity, because of their morphological, behavioural and physiological similarities. The basis of speciation will therefore be present and competition within the sub-groups so formed will result in pressure for greatest efficiency for the characteristic properties of the sub-group. The tendency is therefore towards a population of homogeneous sub-groups of different, and differently efficient, characteristics, which although sympatric in some senses, are isolated in the competitive sense and therefore reproductively separate. Stable combinations in a multi-species field therefore proliferate at points favouring particular combinations of characteristics creating

homogeneous seemingly distinct populations.

An almost linear example of this occurs in the bird world in the ring species connecting the herring gull and lesser black-backed gull, and in the amphibians, in the example of salamanders of the genus Ensatina (Stebbins 1949, cited by Ricklefs, 1973)

25) It is doubtful whether the costs of these two approaches can be compared, for certainly neither can be said to have intrinsic advantages of predictive truth over the other. However the pragmatic approach, based on aphoristic practices evolved over centuries as part of the trade lore of farmers and grain merchants, has the weight of historical evidence behind it. The modelling approach, notwithstanding the obvious shortcomings of past trial and error, relies on faith in precise formulation.

The main practical danger of the modelling approach, however, is the scope it gives to centralized economic decision-making, based on abstraction and standardization of resource. The risks associated with such an homogenization of approach to complex situations have not been examined.

26) It is true that the current taxonomic position of the genus Acarus is a reflection of real differences in structure. What is in question is the usefulness of current taxonomic criteria of categorization of organisms in the study of dynamic ecological processes. The concept of species has changed during this century with the increase of our genetic knowledge. Many organisms have, as a result been re-classified. Even so, in many cases, the taxonomic species are not homogeneous in terms of gene flow, and fail even to satisfy the genetic requirements of a species definition. The ecological requirements of a species definition are themselves undefined and we can therefore have no measure of the inadequacy of taxonomic divisions in this respect.

Our continued and unquestioning retention of taxonomic categories in ecology is mere traditionalism; scientific rationalism insists that we must repeatedly and critically examine our system of ecological classification. The first step in the development of a metaphysic is the recognition of objects and the second classification of these objects according to demonstrable properties. Interactions of objects can then be examined with a view to deduction of a logical system which will explain the displayed pattern of objects. It may be that the object properties defining interactions do not completely define the logical system required, and further that these object properties may not be members of the set of classification properties. If, however, the interaction properties are linked in some degree to the classification properties, then there will be some potential for deducing the interaction system.

For some discussion of the conflicts of ecology and taxonomy see Snaydon (1973) and Heywood (1973).

27) Introducing a politico-economic note, the evaluation of the risks associated with centralized and standardized decision-making as contrasted with those associated with regional and sub-regional decision-making is largely unexplored territory. Distancy and abstracting effects (in reducing the role of local conditions in decision-making) will increase the potential for disparity between prediction and actuality. The greater precision of modelling methods may lure those unused to distinguishing precision and accuracy.

There is an interesting parallel here with economics, in the contrast between centralized and free-market economics. See Jewkes (197)

28) It is important to remember that these cautionary notes are intended to restrict not the construction of certain models or types of model, but the application of these. The criticisms are less immediately important to pure research except when they cast doubt on the testability of the theoretical frameworks involved. It would be well for the modellers to remember that the decisions regarding choice of pest control strategies are often made by people incapable of judging their true scientific or rational merit, and who may be impressed more by precision and advanced technology than by logical accuracy.

29) Absolute genetic differences may arise within populations for a number of reasons : they may be the result of genetic feedback reflecting variations in selective pressure (see Pimentel, 1961) in order to maintain flexibility of response to environmental change (Slobodkin, 1964) and often resulting in genetic gradients within species (McMillan, 1960) spatially, or temporally (Mertz, 1971); accidental (non-selective) aquisition of genetic material, for example plasmid transference in bacteria (for example, see Saunders, 1977); possible non-selective maintenance of co-adapted sets of alleles in satellite DNA (see Dover, 1978) or the internal re-arrangement of genetic material (Nevers and Saedler, 1977); or, of course, as a result of random mutation or random mixing of

(in species with alternating life cycles of dispersed and infestive forms).

30) Though, of course, structuring of the population is not a necessary condition for variability of individuals.

But the main point here is that if structured populations exist, then the elements of structure must have different properties. The overall statistical treatment is in that case invalid. The development of ecological ideas on such a base is as ridiculous as would be the development of a team strategy in rugby football based on the mean properties of individuals. Such a team would be out-jumped in the line-outs, out-shoved in the scrums and out-manoeuvred in the backs, and would rapidly be driven to 'extinction'.

31) A balanced polymorphism is a state of equilibrium between two alelles, whereby both alleles are maintained in the population because the heterozygote (having both alleles) has superior fitness to either homozygote (having a pair of one allele only). The subject is extensively dealt with by Ford (1971).

32) Mertz (1971) discusses the advantage of individual flexibility over absolute genetic change.

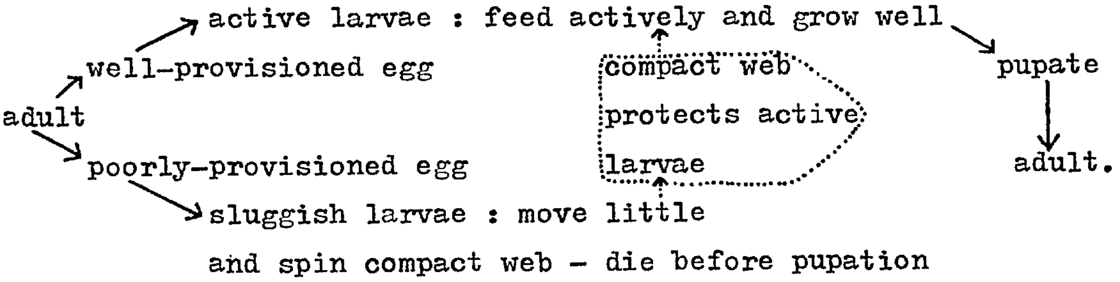
As to the concept of qualitatively indispensable sub-groups of the population, consider the following : individuals of similar behaviour tend to aggregate, if only because they respond to the same environmental cues; if a population is structured in behaviour, the sub-groups will be subject to different risks because of their aggregation and separation; a population in which the structure is the result of differential expression of the same genetic material will be able to survive and recover more quickly from the loss of any one sub-group, than a population structured on an absolute genetic basis, which may not be able to survive at all. One would expect, therefore, that a population in which the sub-groups were exposed to greatly different risks would be structured in an expressional way.

33) For discussion of social insects in all aspects of their behaviour, see the works of Wilson (1971, 1975) which are admirable in this respect, even if controversial in other matters.

34) The desert locust, Schistocerca migratoria, is determined in its morphological and behavioural forms (though these may be disjunct) during the early juvenile stages. For a detailed account see Uvarov (1966, 1977), or for a sketched account, Baron (1972). Much of the information is usefully summarized by the Anti-Locust

Research Centre (1966).

35) The work on the Western tent caterpillar (Malacosoma pluviale, Dyar) was carried out by Wellington (1957, 1960, 1964, 1965a; Sullivan and Wellington, 1953). In summary, populations of the caterpillar were found to consist of active and sluggish forms. The active forms showed directed movement and travelled further, in both adult and larval stages, than the sluggish forms, and were therefore primarily responsible for the inception of new colonies remote from the parent colony. In successive generations of the new colonies, the proportion of sluggish forms increased until the population met its demise through starvation or disease. The situation was summarized by Ricklefs (1973) as follows :



Wellington described the development of the experiments within the framework of his own dissatisfaction with theoretical population studies (1965b).

A similar, but more stable, division into active and sluggish forms may exist in the case of the Monarch butterfly (Danaeus plexippus, Linnaeus, 1758) in America (see Urquhart and Urquhart, 1979, and the references contained therein).

A free population contains sub-populations which will move away and therefore reduce the pressures on the parent population. When confined, these animals must compete but, as they are not adapted for competition, but for founding new populations, they will be more likely to die. They are likely therefore not to be observed in laboratory conditions.

36) The determination of form of a multi-morph genome by conditions in previous generations is easy to explain in the case of the parent generation effect, and only slightly more difficult in the case of a grandparent effect.

The parent effect is most commonly a maternal effect (see Levine, 1971, p.114) in which the genotype of the offspring is overridden by the effects of maternal metabolites in the egg cytoplasm. Transitory or permanent changes may occur (for example, the moth Ephestia and the snail Limnaea, respectively). In this respect it is worth noting that the eggs of A.siro are large-yolked (Hughes, 1976). A paternal effect may also be possible in those species in which the male looks after the young and influences their environment (for example, sea horses and similar fish)

The grandparent effect may be to determine some property of the parent germ cells which in turn determines the structure of the offspring. This is then a two-stage irreversible switch. If it were the case that the final offspring change required a switch set in both parent and grandparent, this would be a convenient mechanism for avoiding response to transient conditions in cases where the individual life-span was greater than the generation time.

37) It is important to recognize confusion as a mechanism limiting the exploitation of resources by an organism. Stress may be viewed as a measure of confusion, which in the limit case can be described as 'threshing'(computer systems jargon) - where more time is spent making decisions as to which activity to follow than is spent in carrying out all these activities. As a consequence of this it is important to examine the reasons for absence of an expected activity, as well as the reasons for the presence of an activity. Confusion displays some of the conflicting selective pressures on different attributes of an organism, which attributes nevertheless have to form part of a common genetic system.

Stress demands interaction with the environment, a capacity for monitoring and responding to environmental states and events, and is the period of re-orientation of metabolism towards a different environmental state. In a constantly changing environment an organism is in a perpetual state of stress, for stress is a characteristic of a situation in which an organism is physiologically attuned to an environment other than that in which it is located.

Hence the importance of switching as a means of reducing the time spent on decision-making.

Among the ways stress may affect a population, consider the following : assume stress tolerance is normally distibuted in a population, and that low tolerance takes the form of a maximum number of stress days which can be born before a translocation to a low stress area must be effected.

Then a long term resource supporting a high density population (in which change is of interactions with other individuals) becomes to a stress-intolerant animal, a transient resource to be used for limited periods of time. At other times some other resource must be used, and the animal is forced away from the rich area to poorer areas where different strategies must be utilized in order to survive.

Thus stress effects the maintenance of a variety of life strategies. Stress in a dense population tends to force individuals out from areas of otherwise optimal conditions into sub-optimal areas where different pressures operate. The drive outwards from the central population area is likely to result in the formation of population sub-groups whose genetic make-up is significantly different from that of the central group. The effect is, therefore, to diversify the genetic pool of the total population thereby maintaining its fitness (resilience) in the face of counter-pressure operating in the optimal area, where selection is for maximal efficiency in a specific environment.

38) Isogenic : having the same genetic constitution. A useful term for recognizing the expressional variants of the same genotype.

39) In a multi-resource environment where ranking according to resource is non-orthogonal, the population can be divided into survivor populations which are set for different conditions, and there will be unequal survival functions for the various sub-populations.

If the variability in this sense is not genetically discontinuous but only expressionally discontinuous, then the overall fitness of the population is greater.

This is midway between the adaptability of a genetically variable population and that of a behaviourally variable population - the latter involving decision-making and therefore time delays and inefficiency. Similarly a multi-gene system with variable expression would be more adaptive, even if the expressional change took more than one generation to occur.

The suggestion is of a system in which, for example, major structures are independently associated across a field of recognizable species, between which there is some gene flow. Only those genotypes in which complete replacement of alternative structures has occurred are independently viable in an evolutionary sense - the intermediates are less fit. Further, in each stable genotype, the morphological form of an individual is determined between a number of alternatives by switch mechanisms reacting to environmental cues.

The species complex therefore obtains great advantages for, whilst displaying wide-ranging structural heterogeneity and flexibility, any specific combination of characters can be reformed by the interaction of other dissimilar specific forms. This structure has some similarities with the 'Rassenkreise' of Rensch (1959).

40) The r-K concept is well developed by Southwood et al (1974)

The attitude of the theorists in searching out a general ecological theory via abstracted characteristics is well represented by Hassell (1975) :

'What factors affect the stability of interacting populations ? How are the stability, persistence and complexity of communities related ? These are now central questions for ecology and when answered will pave the way for something approaching a 'General Theory of Ecology'.

41) Mayr (1963, p.136) defined a deme as 'a group of individuals so situated that any two of them have an equal probability of mating with each other and producing offspring'. D.S.Wilson (1975, 1977) has examined the structure of demes in relation to individual interactions other than mating. He terms these ecological/behavioural analogues of demes 'trait groups' in order to separate the genetic interaction, which is often concentrated around a dispersal stage, from the other activities of life, feeding etcetera, which commonly occur over a much smaller area than that defined by the deme. This distinction might be important in resolving the difficulties surrounding the taxonomy of the Acarus genus.

Over and through this structural division of the population there are many sorts of genetic gradients and fluxes which further complicate patterns of dynamical activity. These gradients may allow continuity of type over a range of habitats (McMillan, 1960), or local adaptations can be swamped or disrupted by the migration of forms adapted to more favourable environments, forced to move from those by the higher densities there (Mayr, 1970), mentioned by Emlen (1978) in relation to the land birds of the Florida peninsula. Apparently disadvantageous characteristics can be maintained by high transmission rates of the relevant alleles, drifting through a population yet within any small group being lost as the group stabilizes, as in the example of lethal genes in mice transmitted by heterozygous males to over 90% of their progeny (Dunn, 1961).

The importance of spatial movement as a counter-balance to competitive selective forces, has been examined by Taylor and Taylor (1977), who stress the dangers of ignoring such spatial considerations, and the presence of populations which regularly flux in their distribution patterns (examples given are of the moths, Agrochola lychnidis and Xanthorhoe fluctuata). Their case for a more explicit recognition of the fluid nature (in distribution terms) of animal populations, at least, is very strong. The general subject of animal dispersion was extensively discussed by Wynne-Edwards (1962) especially in relation to social structure and communication. His criticism of the static nature of the Lotka-Volterra lineage of theoretical models was based on this study of dispersal and communication.

42) Hierarchical is used here to mean a division of types of organism into levels, each level able to exist only as a result of the activities of subordinate levels. Such is the case for ecological pyramids where the species are arranged according to their source of energy. In the present context, however, the hierarchy is of levels of organization of components - the members of one level are not separate from those of lower levels, but are composed of the lower level members in some organized way.

43) Strict and necessary arrangement is meant here to imply that, for example, all populations are organized into communities, all communities into ecosystems - in short, that no members of a level exist independently where there is a superior level, and that this is an unavoidable consequence of the characteristics of the lowest levels of organization.

44) We are comparing here the behaviour of a whole and complete system with the behaviour of its components. A simplifying interaction of components is one in which the system formed by the organization of the components has a simpler behaviour than that of the individual components. A complexifying interaction is one in which the behaviour of the complete system is more complex than that of its components. By behaviour we mean the expressed behaviour characteristic of the object we are considering, whether it be system or component.

System and components must be viewed in turn as black boxes. So for example, the behaviour of a computer or the human brain may be regarded as the result of complexifying interactions, whereas that of a timed power control box, whose total behaviour is limited to on or off, is the result of a simplifying interaction.

45) For more general discussion of control system theory see Ashby (1956), or for more mathematically-centred texts, Willems (1970) or Rosenbrock and Storey (1970).

46) Animals are limited in their perception of their environment. Sense organs are bounded in their information capacity, their range of perception and their reliability.

Where reception of a stimulus is critical, there is selective pressure to overcome these limitations. For the sake of argument, it must be assumed that the structural evolution of the sense organ has proceeded to the state of maximum sensitivity and reliability commensurate with other considerations and limitations. For example, there must be some trade-off between sensitivity and robustness. The bounding effect of an evolutionary path will also be in evidence - organisms with two eyes are highly unlikely to evolve into organisms with three eyes.

So we turn to organizational evolution to satisfy the continuing evolutionary pressure and in particular to the organization of information.

Consider a group of animals which must respond to some environmental stimulus, S, in order to survive. If the probability of each individual correctly interpreting the stimulus is P, then in the absence of any communication between individuals the proportion of the group surviving a single stimulus is P.

If, however, individuals can signal to communicate the fact that they have received a stimulus e.g. rabbits 'thumping', deer 'tail-flashing', we can say that they are 'alert' to the stimulus. This must not be confused with the <u>response</u> to the stimulus which, in the case of alarm calls as in the examples given, is flight from the cause of the stimulus.

Now if animals can properly respond to a stimulus either through direct perception or by being aware of the state of alertness of the animals surrounding it, then the proportion of the group surviving a single stimulus becomes greater than P - the fitness of the group is increased.

If $\underline{a}$ is the total number of animals in the group, $\underline{n}$ the number of other animals perceived by one individual, and $\underline{X}$ the minimum proportion of $\underline{n}$ to which an individual will respond, then the increase in survival (given as a proportion of the total number) is :

$$\frac{(1 - P)\ \underline{n}!\ (\underline{a} - \underline{n})!}{\underline{a}!} \sum_{\underline{y} \geqslant X\underline{n}}^{\underline{y} = \underline{n}} \left(\frac{(P\underline{a})!}{\underline{y}!\ (P\underline{a} - \underline{y})!}\right)\left(\frac{((1-P)\underline{a})!}{\underline{n} - \underline{y}!((1-P)\underline{a} - (\underline{n}-\underline{y}))!}\right)$$

(the variables $\underline{a}$, $\underline{y}$ and $\underline{n}$ are integer quantities, while P and X are real numbers on the interval 0 - 1)

The variable X must have a lower bound greater than E, where E is the probability that an individual will become alert in the absence of the stimulus, S. This is to prevent unecessary responsive action as a result of an indirect, or secondary, stimulus.

To take the process further, let us consider the case where an individual not only responds to an indirect stimulus but is also alerted. It can easily be shown that in this case, assuming that awareness of the $\underline{n}$ local individuals is perfect, the response of the group rapidly becomes total.

The following cases can therefore be recognized :

1) Animal *responds* only to direct stimulus.
2) Animal *responds* to direct stimulus or surrounding alertness , but is *alerted* only by direct stimulus.
3) Animal *responds* and is *alerted* by direct stimulus or surrounding alertness.
4) Animal *alerted* by direct stimulus or surrounding alertness, but *responds* only to surrounding alertness.
5) As 4, but animals *de-alerted* by lack of alertness in surrounding animals. This case may be complex and have analogies with the Life Game of John Horton Conway.

47) For a discussion of the problems of analysing computer circuits see J.W.R.May (1972), and Szygenda, Rouse and Thompson (1970). An interesting corollary in the testing of microprocessors is put forward by Kewney (1978).

48) Examples of abstracted energy analyses occur in the Silver Springs study (H.T.Odum, 1957a) and in the text of E.P.Odum (1971). Specific energy analyses are represented by studies of a laboratory aquatic system (Whittaker, 1961) and of a small trout stream in Michigan (Ball and Hooper, 1963). In the case of spatial analyses, there has now been an attempt at synthesis of the abstract and specific in the work of Taylor and Taylor (1971). Keever's (1950) study of plant succession in fields in North Carolina is a specific temporal analysis, while examples of abstract temporal analyses are to be found in the works of Monk (1966) and Odum (1969, 1971).

49) Anyone in doubt as to the importance of macrobe/microbe

interactions in determining the dynamics of animal and plant populations should consult Buchner (1965).

50) For details of computer structure and design principles, see Hollingdale and Toothill (1965), Walker (1967) and Sobell (1970)

51) I would recommend the section on community ecology in Ricklef's (1973) text as a very comprehensive account of the community idea.

52) Static ordering means here the containment of populations or species by physical barriers e.g. mountains, seas etcetera, which by their nature provide an invariant control, in contrast to the dynamic control of population feedback mechanisms. These physical barriers are discussed by Elton (1958).

53) The term 'co-scalar interactions' refers to interactions of organisms of similar size and generation time, which are therefore not separated in their dynamic properties by scale effects. The greater the difference in scale, the more likely it is that apparently competing organisms will be limited by factors external to their own direct interaction.

54) Co-evolution depends on stabilization of communication in the sense that the interactions of organisms depend on the passage of information between those organisms - the predator must recognize his prey, the herbivore its plant food. No general rule can be given as to the nature and extent of the signals so communicated - the cues for action in the natural world; but where there is pressure for an interaction to change (for a prey to avoid its predator for example) the option exists for change in communication rather than only for changes in basic structure (the prey evolving different colouration, for example, rather than altering its structure in order to run faster).

The stabilization of communication then involves for the individual organisms, a balancing of conflicting pressures, and for the interactions, a balance of flexibility wherein both interactants retain the ability to respond to the changes in the other's signals. Thus variation continues, but all interactants retain the ability to cope with this variation.

55) The subsistence of micro-organisms without destructive activity refers to the presence of microbes utilizing resources lost to the energy cycles of larger organisms - the leftovers of the macro world. These activities are essential to the re-cycling of nutrients in the biological world.

56) Some relevant comments on the structure of communities are those of :

Paine (1966) on predators as stabilizers of communities by preventing single species monopolizng resources.

Hairston, Smith and Slobodkin (1960) who presented a verbal argument that producers, carnivores and decomposers were resource limited and that therefore interspecific competition occurred within these trophic levels, but that herbivores were limited by predators and were not likely to compete for common resources. The latter statement follows from the observation that the world is green, that is, that 'plants are abundant and largely intact'. This argument was criticized by Murdoch (1966), on several grounds of premise and logic, who made some perceptive comments on the state of ecological epistemology which remain pertinent to this day. The argument was also criticized by Ehrlich and Birch (1967), and both criticisms answered by Slobodkin, Smith and Hairston (1967).

Frank's (1968) discussion of age effects and of the place of long-lived species in stable communities.

Sutherland's (1974) experimental demonstration of the equivalence of significant historical events with multiple stable states, and his conclusion from this that different approaches to community studies were needed according to knowledge of the number of potentially stable states of the system.

Pianka's review of hypotheses to explain the correlation with latitude of variation in community structure (as diversity) and functioning (as stability). The particular hypothesis which relates this gradient to faster evolution in warmer regions, whereby the tropical systems are more mature than temperate and polar systems is also discussed by Dunbar (1960) and by Stehli, Douglas and Newell (1969).

The role of decomposers, of the detritus element in ecosystems, is often underestimated or even ignored (especially in mathematical models). Yet the functioning of the community, of every individual organism, is dependent on the recycling of nutrients. This ommission may seriously distort our view of ecosystem and community functioning. An analysis of the importance of detritus in lake ecosystems is presented by Rich and Wetzel (1978).

57) The disquiet has mostly been expressed as a questioning of theoretical generalizations by experimental ecologists, for example, Wellington (1965b), and a questioning of the logic of theor-

etical ecology by more philosophically-minded ecologists, as by Peters (1976). The conflicts of opinion suggested by these reactions are more fully stated in Section 6.2 .

58) The mechanistic views of the traditional physicist were overtaken by a new philosophy and rationale, well described by Capra (1976), borne this century of the great advances in particle physics made by unconventional thinkers. One need only consider the reflections of Bohr (1934) :

"The great extension of our experience in recent years has brought to light the insufficiency of our simple mechanical conceptions and, as a consequence, has shaken the foundation on which the customary interpretation of observation was based.",

and Heisenberg (1963) :

"The violent reaction on the recent development of modern physics can only be understood when one realizes that here the foundations of physics have started moving; and that this motion has caused the feeling that the ground would be cut from science."

59) 'log-linear response of a process of change to change itself' means that the response to change is proportionally greater the greater the initial change, that is for a response of n units to a change of 1 unit, the response to 2 units of change will be greater than 2n units. Thus in a strict log-linear response, the response to a change of n units will be a power function involving n as an index.

60) The models used in theoretical ecology in stability analyses contain parameters describing the characteristics of the system under study. The use of these parameters involves the acceptance of assumptions which are seldom questioned, remaining implicit because of the plausibility of abstraction within a philosophical framework which abhors inconstancy.

61) Most notably among philosophers, Wittgenstein (1961), as a result of whose work a reappraisal of our apprehension of the world was instigated in several movements, popularly summarized by Kohl (1965) and Passmore (1966), and presented from the biologist's standpoint by Arber (1964). Other scientific reactions have been noted elsewhere, as in Note 56 and in Section 6.2 .

62) 'externals' meaning the objects of our, or other organism, sense perceptions, the classification of objects and processes around which can be developed ideas of pattern and dynamic activity.

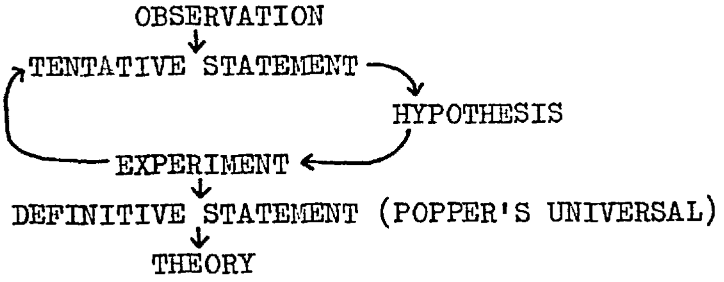
63) In all spheres of human enquiry concerning complex phenomena there is continuing debate of the means of aquisition of knowledge. The approaches and methodologies are many and various. Often the analytic is challenged by the verbally rational (as in economics, where the latter, as a free-market philosophy, has regained prominence) and sometimes by the mystical (as in particle physics with its much vaunted parallels with eastern philosophy). The latter has been suggested in ecology, not quite seriously I think, by Barash (1973), in its extreme form of direct apprehension as the only source of true knowledge (particularly stressing Zen Buddhist philosophy).

64) Theory represents the premises or axioms of a tautological system. Experiments are usually attempts to disprove the secondary statements of those systems i.e. statements derived from those axioms by inference and logical necessity, in order to falsify the theory.

It is assumed that the process of logical expansion of axioms is objective. However the logical relations themselves are defined in relation to specific classifications of objects, and may only properly be used to connect objects of the relevant class, that is objects which satisfy the definition of properties of objects used in that classification system.

Theory is a self- consistent structure of universal statements. Universal statements are tested by experiment, in which they are regarded as the hypotheses. The combinatorial aspects of theory are upheld only in the domain of logic and the theory is therefore largely determined by the vocabulary of the science in question.

Our general approach to knowledge may be thought of as : observe, measure, interpret. The scientific approach can be described as :



Theory is then a set of connected definitive statements. A model is a formalization of either a hypothesis or of a theory - in the former case it may most aptly be called a developmental model, in the latter case a predictive model.

65) 'Implication-in-context' may be defined as the tactical positioning of a factual example, which ambiguously conforms to the principle being presented, in such a way that it may be read as direct evidence for that principle. This is a common practice among politicians, but one would have hoped to find it absent in scientific arguments.

66) The example as given by May et al(1974) is :

'The two curves in Fig.4 show population changes of the water flea, Daphnia magna Strauss, cultured at 18°C and 25°C. Clearly the effect of the temperature change has been to alter the term 'β T' from a little greater than 0.37 (= e^{-1}, see Table 1b) to approximately 1.6 (=$\pi/2$). Presumably, increased temperature has led to increased competition.'

(May et al's Figure 4 is given here as Figure 6.1.2 and their Table 1b is given in Chapter 1 as Table 1.2.2)

This statement is reasonable under the assumptions of the theoretical form, but even then counter examples can be framed e.g. increased temperature leads to increased lassitude which then leads to decreased competition. The supposed empirical link here is an induction from theoretical preconceptions of dynamic mechanism and does not lend weight to the argument.

67) The error lies not with the true principle of Occam's Razor, which is that entities should not be multiplied unecessarily, but in that distorted interpretation held dear by theoreticians which has it that simple forms of explanation are intrinsically better than complex forms. This reasoning, compounded by an irrational (though not unproductive) desire for elegance in mathematical description, is, however, entirely at odds with the spirit of William of Occam's philosophy. This philosophy was a modified Nominalism, maintaining the distinction between concrete realities and the abstraction of universals, in which it was claimed that purely intellectual abstractions are not valid knowledge and that reason must be based on experimental proof.

The concatenation of demonstrable biological categories to provide some theoretically-meaningful construct, such as characteristic time, a process common to analytic studies, is therefore doubly at odds with Occam. Firstly in constructing additional system characteristics of doubtful necessity, and secondly in advancing a realist interpretation of the world.

Further, the appeal to the distortion of Occam's Razor represents a tautological appeal to presupposition of the sort from which develops analytical theory, namely that simple interactions are the general rule in this universe.

68) The example as given by May et al (1974) is :

'A second example comes from the work of McNeill(1973 and unpublished) on the dynamics and energetics of the grassland mirid, Leptoterna dolobrata (L.). Figure 5 summarizes some of his results from a simulation model of the system. They indicate that increasing temperatures again cause a change from monotonic damping to oscillations. This, too, is mediated through increased competition at higher temperatures.'

(May et al's Figure 5 is given as Figure 6.1.3)

69) The experiments involved competition for fixed quantities of food in laboratory systems. Known numbers of newly-hatched larvae were put with 1g of meat to serve as food. The results, plotted as k-value changes against initial populations, are shown in Figure 6.1.4.

70) The distinction between populations and population models must be maintained if we are to avoid unjustified application of model conclusions. The paper under discussion has been used in subsequent papers (by other authors) in support of practical schemes of wildlife management. While the assumptions of the model remain largely implicit in its formulation, no tests are likely to be made of its suitability in any given situation. A model of this sort must be presented with explicit guidelines as to the conditions for its proper use.

71) The paper in question is by Albrecht, Gatzke and Wax (1973) and was a disproof of earlier work by May(1972) on predator-prey models. Albrecht et al "...remark, finally, that our system 2 " (which exhibits neutrally stable behaviour) "need not be of any biological significance." May, in his reply to this (1973c), says "such neutrally stable periodic solutions are unlikely to be of biological significance. Albrecht et al themselves make this point"

Note the contrast between 'need not be' and 'are unlikely to be'. That this distortion of statement was allowed in a reputable journal (Science) is even more surprising when one considers that the two quotes above came, not only from the same page, but from the same column.

72) As an example of a synchronized change in behaviour (to kill two birds with one stone) consider the aggregation behaviour

of the cellular slime moulds e.g. Dictyostelium discoideum . The aggregation occurs when a food supply is exhausted and is co-ordinated by a chemical signal (in some cases acrasin - cyclic AMP). For further details see Bonner (1967), Allen and Kamiya (1964) and Martin and Alexopoulos (1969).

The capacity for behavioural changes and synchronization of behaviour is, no doubt, much greater in higher organisms.

73) As an example of entrenchment in the framework of a model, consider the following (Beddington, Free and Lawton, 1976) :

'the populations of most species in many ecosystems appear to fluctuate around characteristic mean levels of abundance' .... 'A reasonable inference is that the persistent, quasi-stable populations which we observe in real ecological communities demand parameter values in their model counterparts which lead to locally stable equilibria or to limit cycle behaviour.'.... 'For a population interaction to persist, the parameters of the appropriate population model should be such that the model implies either a locally stable equilibrium or a limit cycle.'

A more reasonable approach to the general problem of modelling communities is offered by Barclay and Van den Dreissche (1975). They use a model of four trophic levels with ten species in a web and although they use time-lagged Volterra equations as the basis for the model, their solutions are numerical and avoid major linearizing assumptions. Included is an explicit caution : 'many assumptions are inherent in the model, and predictions must be restricted to situations where these are valid.', but sadly no list of these assumptions is presented in order to easily identify the true area of applicability.

Mazanov (1976) presenting a compartmental model for analyzing the effects of time lags, and using Ashby's (1956) equation of 'stability' and 'bounded', makes a case for using such models because their structure, stable independent of connectance, complexity or duration of time lags, reflect the stability of natural systems. Though welcome as a reaction against linearized models, the evidence presented in support of his approach is as flimsy as that supporting those linearized models. While no consensus is present as to the general properties of ecological systems, the sweeping generalizations of both approaches have little merit as scientific statements.

74) For example, in May's (1974) book, the statements :

'This work seeks to gain general ecological insights with the help of general mathematical models.' (p.v)

'... general models, even though they do not correspond in detail to any single real community, aim to provide a conceptual framework for the discussion of broad classes of phenomena.' (p.11)

'..we restrict attention to the simplest models for individual interactions between species ... to get a feeling for the effect of diversity (in the sense of a large number of species) per se.' (p.40)

75) It is a basic axiom of the reductionist approach that the components of a system can be analysed separately, and the relations thus disclosed amalgamated simply to generate the behaviour of the complete system. It is this putting together of the simple analyses that is meant by 'additive alteration'. That this approach to ecological systems is likely to prove successful is <u>not</u> supported by current biological knowledge.

Professor May himself makes this point (1975b) : 'So many of the successes of physics and engineering derive from <u>linear</u> problems, where a complicated process may be disarticulated into a sequence of relatively simple steps, and the whole then validly synthesized as the linear sum of its parts. Most ecological systems are intrinsically <u>nonlinear</u>, and do not admit of such simplification.'

As to actual examples of non-additive responses consider Camin (1963) on ticks : 'In addition, these acarines frequently have responses to combinations of extrinsic factors which differ markedly from the reactions they exhibit when subjected to the same stimuli one at a time. For example, Lees (1948) demonstrated that the sheep tick, <u>Ixodes ricinus</u>, is strongly attracted to sheep wool and other animal hair at 37°C, but the same individual tick is repelled by a temperature of 37°C in the absence of wool and is completely insensitive to the wool at room temperature.'

Other examples include : changes in light response of the two-spotted spider mite according to food(plant leaf) status (Suski and Naegele, 1963); the interactive effect of olfactory stimuli and phototaxic reaction in silkworm larvae (Shimizu and Kato, 1978), where it is suggested that the olfactory information (about mulberry leaves) which suppresses phototaxis is stored, gradually diminishing in the absence of further olfactory stimulus; the response of Acarus siro (see Figures 1.3.5 - 1.3.7) to temperature and humidity.

76) It is not sufficient merely to list the various shortcomings of the models. There is an implication from this, albeit slight, that these shortcomings are relatively unimportant and that attention has been focussed on the main points of system organization. This is not an attitude supported by experimental evidence, and therefore some attempt should have been made to estimate the possible effects of these omissions. For it may be that the effects not taken into account are of sufficient importance to invalidate the conclusions arrived at from the simpler analysis.

77) Efficient prediction and manipulation of course demands a correct overview of the working of natural systems (the alternative is a blind trial and error process).

One interesting case of system manipulation where theoretical argument was immediately countered by experimental evidence and further theoretical counter-argument, is that of the potential destabilizing effect of the enrichment of ecosystems. The relevant papers are Rosenzweig (1971), McAllister, LeBrasseur and Parsons (1972) and Gilpin (1972).

Much has been made of the ability of simple models to produce apparently chaotic results (May 1975a, 1976; May and Oster; and Oster, Ipaktchi and Rocklin, 1976). The intended implication is that natural complexity may be explained by simple deterministic mechanisms, and that environmental effects do not need to be invoked as a driving force.

This may be seen as a continuation of the debate characterized by the Cold Spring Harbor Symposium (1957) mentioned in Section 1.1.2 . The counter argument of density independent regulation has been put recently by Enright (1976).

A historical perspective of the balance of nature debate is provided by Egerton (1973).

78) This is, I think, most clearly illustrated by the literature on succession in communities, a general view of which may be gained from Ricklefs (1973, pp. 751-775).

79) Individual organisms may have the ability to adopt many types of behaviour, of resource use, and to express these at different levels. For example, according to the relative availability of different sorts of food, omnivorous animals may act predominantly either as predators or herbivores. The community of which

they form a part may therefore exhibit a change of functional structure without there being any change in individual membership.

80) The model presented has, of course, many drawbacks - perhaps as many as the model it is trying to replace. Its great advantage, however, is that it stresses the potential for change in the biological part of the system. If this is further complicated by the idea of linked units moving over the response surface e.g.

in a dynamic balance

then, I believe, an even more realistic picture of ecosystem behaviour is gained.

81) It seems to be the case that the simple systems which support the analytic approach to ecology are almost exclusively laboratory systems, where the environment is very much more simplified than that of the natural world. The relevance of such systems in constructing general ecological models must, therefore, be in grave doubt.

82) For example, the references to the work of Zwolfer (1963) on Lepidoptera, Hairston _et al_ (1968) on microbe interactions, and Paine (1966) on intertidal communities, in relation to the question of stability and complexity . (May, 1973, pp.38-39)

83) From May (1973, p.16). The method was originally presented by Liapunov (1893); more recent works on the method include those of Hahn (1963), LaSalle and Lefschetz (1961), and the general dynamic-system text of Willems (1970).

84) The type of enquiry referred to here will be quite comprehensively defined by study of the works of Levins (1963, 1968, 1969), Lewontin and Cohen (1969), Smith (1972), May (1973b) and Feldman and Roughgarden (1975).

85) This sensory effort is well illustrated by the trend in animal evolution towards a greater capacity for information processing, sometimes together with a proliferation of sensory apparatus.

86) In fact I would be interested to know of a single natural biological system in which no species exhibited gross changes of behaviour. With so many examples of such changes in individual species, it _must_ lie with the proponents of homogeneous system theories to establish that these departures from uniform behaviour are

insignificant in the behaviour of real systems.

87) For example, the behaviour of the cellular slime moulds, described in Note 72; the common patterns of bird migration with change of season; the phase changing of the desert locust (see Note 34).

88) For example, Smale's (1966) proof 'that structurally stable systems are, in a precise sense, rare in more than three dimensions', mentioned by May (1973a, p.18)

89) Imagine, if you will, applying the community matrix approach to a small town which has both causal and accidental correlations and associations, lines of information and material flow, relative spatial cohesion : properties all of which are displayed by non-human communities. Would you then apply a constant figure to all the relationships between groups in that town and expect the resulting matrix behaviour to parallel the behaviour of the real town ?

90) Some members of communities are necessarily small - larger carnivores because greater numbers could not be supported. In other cases it is common to dismiss rarer members of the community as being on the path to extinction, caught in evolutionary cul-de-sacs and hence in decline. This is not a substantiated view, and in any case does not deny these populations an important place in community dynamics. Their dismissal may be the result of the intrinsic difficulty of examining the dynamics of small, rare or dispersed populations, rather than the result of rational enquiry and reflection.

91) In relation to the complexity-stability debate the question of the effect of latitude is mentioned in Note 56, and the particular value of random web models to the resolution of this matter discussed in Note 97.

As to the cautions against generalization mentioned, May specifically refers to that of Southwood and Way (1970) stressing the importance of community structure. Other cautions appear, not explicitly directed at the generalization in question, in Hutchinson's (1959) discussion of the abundance of animal species and in Smith's (1972) discussion of spatial heterogeneity.

The stability-diversity question in agricultural systems is discussed by Van Emden and Williams (1974) who stress an evolved correlation between stability and diversity.

Re-emphasizing that the question originally concerned community stability and not the stability of component species, McNaughton (1977) presents experimental evidence in support of the stability-complexity correlation, and questions the usefulness of 'rigorous' mathematical models. In summary he says : 'The diversity-stability hypothesis developed over the past 25 years appears widely misunderstood by ecologists, although it simply states that species diversity mediates community functional stability through compensating interactions to environmental fluctuations among co-occurring species .... As components of natural science, models are true only insofar as they are verified as accurate descriptions of the systems they purportedly characterize. The data on diversity-stability relationships in plant communities indicate that the traditional verbal model is considerably more robust than the recent 'more rigorous' mathematical models.

92) Professor May explicitly states many of the characteristics of real biological systems which he omits in his quest for 'a feeling for the effects of diversity per se'. These include predator switching, spatial heterogeneity and boundary effects.

How can he thereafter justify his approach as a rational means of ecological enquiry or is he, by explicitly stating these ommissions, removing his work from the realm of science, thereby avoiding empirical scientific criticism ?

93) The argument under discussion is the first of six on the stability-complexity question by Elton (1958) and is stated by May (1973a, p.40) as : 'simple mathematical models of one-predator / one prey systems do not possess a stable equilibrium, but exhibit oscillatory behaviour.'.

94) This is as absurd as predicting the behaviour of human populations from models relating the activities of police and criminals.

95) The usefulness of the trophic concept is another unresolved question of ecological terminology. I would suggest that its usefulness lies in forming part of a larger functional classificat- of organisms in which scale effects especially are included. As a single classification of organisms in dynamic enquiries its use would seem to preclude useful results.

96) It would be important in such testing that the models provided accurate information about the mass properties of the system (energy throughput and standing biomass, for example) as well as about the internal structure (varying composition). This of course

means that the model must recognize the essential structural features of the system and there is, at present, no suitable means of classification. Empirical research into community structure must attempt to find parallels with species function, preceding attempts to model structure. Dynamic processes cannot be explained unless we identify the critical units of structure. The present approach, of formalizing and manipulating previously coined partial definitions of system structure and function, seems a remarkably haphazard course in scientific enquiry.

97) The use of the random web approach to the study of the behaviour of large systems may be said to start with the work of Gardner and Ashby (1970), though it arose from Ashby's earlier (1950) work on nerve networks, who showed that for large systems there was a sharp transition from stability to instability accord-to the degree of connectance of the system. May (1972) developed this work for species webs, but his general conclusion that larger webs were rarely stable was criticized by Roberts (1974) on the grounds that the majority of the webs analyzed included negative species values, and showed that if these were excluded, so as to allow only biologically feasible webs, then the probability of stability increased with increasing web size. Robert's work was in turn criticized by Gilpin (1975) on the grounds of his assumptions about the component species : Gilpin showed that neither predation nor competition could occur in the model, and presented another model which was consistent with May's conclusions while recognizing feasible systems.

De Angelis (1975) presented a model which allowed increasing stability with increasing connectance for three cases : (1) where the biomass assimilated by the consumer species is a small fraction of the biomass removed from the prey species in the feeding process (2) the higher trophic level experiences a strong self-damping population regulation (3) where there is a bias towards donor-dependence.

A means of stability analysis for for real systems was presented by Smith (1975). This analysis did not depend on differential equations but used power-law approximations. It was noted that the stability of an ecosystem could be enhanced by increasing the number of non-linear interactions that exist between the ecosystem components.

From the foregoing statements it can be seen that the conclusions from the various random web models are contradictory. The approach has not been productive and appears unlikely to be so. It might be salutory to introduce a comment by Lawlor (1978) : 'With less than one chance in a googol of constructing an ecosystem with a random-number generator, any analysis of the complexity-stability question in ecological systems clearly must begin by examining systems known a priori to be biologically acceptable. The question is not whether randomly constructed systems become more (or less) stable as their complexity is increased, but rather what the specific structural patterns distinguishing real ecosystems from randomly constructed systems are and how these observed structural properties of real ecosystems contribute to their stability (or instability). Clearly the relationship between complexity and stability in large scale model ecosystems remains an open question'.

98) From May (1973, pp.66-67) : Connectance (C) is a characteristic of the total web and measures the probability that any pair of species will interact.

Interaction strength (s) is a measure of the magnitude of the interaction. An average interaction strength is usually specified in order to define a symmetrical distribution of strengths with mean value zero and mean square value s^2.

99) Associations between species may arise because of similar ecological requirements, for example species specialized for feeding on different parts of a particular plant.

The separation of species along any dimension of limiting resource is well documented. There is always pressure for species competing for a resource to evolve different requirements. There is therefore an ever present selective pressure for organisms to become associated with different resources.

100) The idea of 'loosely-coupled sub-systems' was presented by Ashby (1952). The use of a simple number concept of complexity makes irrelevant any organization of a system - hence a system of n components is deemed more complex than a system of n-1 components regardless of their relative degrees of organization.

101) And these are not compensated for by any appreciable element of criticism in the scientific literature. Rigorous criticisms of published work are rare, probably because the quantity of published material is so great that specialist journals have arisen within which a common philosophy holds sway, while criticism from other fields of study is made difficult because there is insuffic-

ient time for one person to consider any but the literature of one field in any depth. This glut of data and theories means that cross-fertilization of ideas between fields is virtually absent. The lack of recognition of many new developments in population and individual genetics by those engaged in research into the dynamics of populations is an adequate demonstration of this.

102) The phrase 'closed loops' is used by May in the sense that the effects of i on r, r on q,......, k on j, and finally j back on i, are all non-zero. Any inclusion of decomposers and feeders on decomposers violates this condition.

Of other approaches to qualitative stability, that of catastrophe theory (Thom 1969, Jones 1975), much criticized by Professor May as merely descriptive, is worth mention. As stated by Thom, 'the problem is to explain the stability and the reproduction of the global spatio-temporal structure in terms of the organization of the structure itself'. The approach is particularly concerned with sudden changes in system behaviour, called catastrophes.

According to Jones (loc.cit.) 'there are four basic system properties of elementary catastrophe structures. Whenever observations reveal one or more of these properties, it would be fruitful to look for others and for an underlying catastrophe topology. If such a structure can be found or hypothesized, the whole body of Thom's theory can be brought to bear'. The four properties are :

Bimodality : clustering of properties around two or more statistical measures.

Discontiuity : large changes in behaviour associated with small changes in input variables.

Hysteresis : delayed responses to changing stimuli which result in a different response to the same stimulus according to the direction in which the stimulus is changing.

Divergence : when nearby starting conditions evolve to widely separated final states.

The theory is an attempt to provide a coherent theoretical approach to such systems for which, because of the above properties, the use of classical quantitative models is prohibited.

103) In addition to referring to the work of Buchner (1965), already mentioned in Note 49, it is worth mentioning the mutual adaptations of certain insects and the mites which they carry, for

example some tropical carpenter bees have an abdominal pouch on the female that clearly functions as an acarinarium for large Dinogamasus mites (Lindquist, 1975). A similar situation is noted for wasps and may be true for many kinds of beetles, bugs and orthopterans.

Note also the case of mixed groups of small animals (such as the wandering parties of small birds - titmice, goldcrests and warblers noted by Wynne-Edwards, 1962) which may be a mutualistic behaviour evolved to take advantage of the protective effects of moving in large groups.

104) Into this category fall such terms as : population, species, community, habitat and stability.

105) Clarity in the sense of removing unwanted noise without impairing the accuracy of the view obtained. Precision in itself is not a desirable attribute; it must be linked to accuracy.

106) These models arise mostly from, or because of, the work of Lotka and Volterra (see Section 1.2.1). The bulk of Volterra's work is seldom referred to directly, but an account by Scudo (1971) gives details of most of his contributions to ecology.

A fairly recent overview of predation, in both experimental and theoretical systems, is the very extensive work of Murdoch and Oaten (1974). Of the other work on predator-prey systems, I should mention Rosenzweig and MacArthur's development of graphical representation (1963); Solomon's (1969) experiments on the interactions of the mites <u>Acarus siro</u> (prey) and <u>Cheyletus eruditus</u> (predator); Levin's (1970) extension of the competitive exclusion principle; Maynard Smith and Slatkin's (1973) work, which included recognition of differential hunting abilities in the predator population; Rapport and Turner's (1975) work suggesting multiple equilibria of predator-prey systems; Roughgarden and Feldman's analysis of the effect of predation on prey species packing (1975); and Armstrong's (1976) development of a graphical method (different to that of Rosenzweig and MacArthur) to analyse predator-prey interactions.

107) This is a re-phrasing of the environmental regulation case in that that argument relied on the control of populations by extremes of external condition i.e. the limits to growth of particular species with regard to any habitat variable.

108) Described by May (1973, pp.86-90), referencing Kolmogorov's original (1936) work, as well as reviews by Scudo (1971) and Rescigno and Richardson (1967).

109) However, even if the two dimensional confines of the Poincare-Bendixson theorem are breached, we must carefully examine the relevance of closely-coupled systems to real biological systems. As I understand it, 'closely-coupled' means correlated (though not necessarily in a linear sense) to a highly significant degree. The generally open-system nature of the biological world suggests that a close-coupling of more than a few species would be difficult simply because of the spatio-temporal problems involved. Close-coupling demands a high degree of information passage between species : increasing numbers of interacting species must decrease the passage of information between each, and also increase the distance between these species, thereby exposing these to potentially different circumstances. In combination these effects must produce a diminution of coupling within that species system.

110) The text quotation is from May (1973a,p.104). May's criticism is that, in the original work by Wangersky and Cunningham (1957) and in the later work by Goel, Maitra and Montroll (1971), the predator-prey systems are invariably less stable than those with prey alone. This is a reasonable criticism in the light of real world experience, but it remains true that this type of empirically-based criticism is one which May rarely applies to his own work (or to that of his disciples).

111) To question Professor May's aptitude for ecological pronouncements is not mere vitriol, it is a recognition that a man's upbringing and cultural background are important factors in the development of his world view and his personal and scientific philosophy. Science and scientific research are not isolated from man's other activities, and the more complex the subject of study, the greater the possibility that influences external to science - political, social, personal, whatever - will colour the interpretation of events. Professor May trained as a physicist, and in his own words (1973a, p.vi) : 'My background is in theoretical physics and I am at least aware of the danger that my interests are liable to be animated too much by elegance and too little by common sense'.

112) The examples of a vegetation-herbivore-carnivore system given by May (1973a, pp.106-107) in which the addition of carnivores to an unstable vegetation-herbivore system produces a stable overall system, a result which remains even if the predator - herbivore system is intrinsically unstable.

113) Normality of characteristics can only be assumed within a group of organisms if we can assume a relatively constant set of selective pressures acting on that group. Given the variety of situations, especially in exploiter populations, where groups of animals are, at various stages of population history, aggregated and then dispersed, at times subject to founder effects and non-competitive growth, at other times exposed to stringent selective pressures, normality seems an unlikely state of affairs. The experimental evidence is not available to directly prove or disprove normality as a general rule, but what evidence is available suggests that it should not be a primary assumption of theoretical models.

114) The main effect of these stochastic models is to give more latitude to the fitting of models to experimental data. This would be a reasonable aim if the underlying patterns of distribution and potential noise were deduced from a detailed analysis of the physiological mechanisms of the object of study, rather than loosely estimated from the gross behaviour of these objects in interaction.

115) The phrase 'partitioned spectra with definite long-term correlations' refers firstly to the extent of correlation between the variables making up the random element of the environment (negative correlation between rainfall and illumination, for example) and secondly to the very obvious presence of cycles and trends in climatic changes, changes which are of neither too short nor too long a period to be regarded as insignificant in population studies. These would be of lesser importance if organisms were largely independent of these changes or merely accidentally affected by them, but there is a very large body of evidence detailing specific mechanisms by which such changes are used as physiological and behavioural cues.

116) In that the methods he uses include, as implicit premises, assumptions as to the form of environmental variation; and that there are no estimates as to the effect of relaxing these assumptions. The conclusions he draws are, therefore, practically irrelevant to any system which does not abide by these assumptions, and will remain so until it can be shown that any such departures are insignificant to the process of drawing those conclusions.

The reference to non-white spectra and internal resonance concerns the situation where the quality of the random noise affecting the system is correlated with some cyclical activity of the system. This sort of effect is well illustrated by most climatic variables - rainfall per hour, illumination per hour, for example - where although, in the short term, variation appears random, the pattern of distribution changes seasonally, as do many aspects of population dynamics (quite often triggered by the changes in climatic distribution).

117) The text quotation is from May (1973a, p.139).

These questions are certainly interesting, but not for immediate translation to more precisely defined mathematical analogues, because they then lose too many of their possible meanings.

The scientific examination must be preceded by a verbal discussion of the meaning of these questions and of the words in which they are phrased.

Questions of similarity and identicality can be approached either structurally (on an absolute genetic basis) or functionally (according to real resources shared). The first approach once again brings into question the whole concept of species in the context of dynamic enquiries. The latter approach brings in the anti-competitive aspects of scale in time and space. Further, additional to both, there remains the unanswered question of the extent of variability in genetically intermixing groups of organisms. These are inextricably linked to the niche question, which cannot be answered until they have been (at least partially) resolved.

118) I have noticed a complete lack of understanding of this point (that experimental results, for example, can be described formally, to the same level of statistical significance, in innumerable ways) amongst biologists who have adopted a theoretical stance similar to that of Professor May. They, unlike Professor May, do not have the mathematical competence to discuss the significance of such a possible variety of interpretation. They seem content to impose linear forms on the data (or on simple, for example logarithmic, transformations of these), and when questioned as to their reasons for such interpretation, invoke Occam with the same fervour as the religious fanatic invoking divine authority.

119) Professor May (1973a, p.166) warns that : '... for such communities'(of higher vertebrates)'near the top of the trophic ladder, competition is liable to be the predominating influence in species packing. It is among such communities that we look to test the theory. On the other hand many insect communities, and many

plant communities, have complex multidimensional niche structure involving, inter alia, a variety of chemical dimensions. In addition, predation and other interactions beyond simple competition are pervasive in these invertabrate and plant communities. Such situations are best avoided for the time being.

(These remarks prompt the observation that people whose field work involves creatures such as birds - where censuses can show remarkable uniformity from year to year - are apt to look more kindly on simplistic theoretical forays of the sort in this chapter than are people whose field work involves, say, rose thrips. In turning to the underlying questions, one should try to dissociate oneself from the prejudices induced by either extreme experience in the field)'

Perhaps the only way to compensate for the bias introduced by such prejudicial experience is to ensure that all theoretical forays are accompanied by an explicit account of the scientific background of the author.

As to the above quotation, it surprises me that Professor May, recognizing the biases of others, does not give more time to introspection.

120) The influence of the theorists in practical ecological management is only partly demonstrable in terms of their obvious effect in the literature of applied ecology. Perhaps more far-reaching in effect is their presence on editorial boards, government advisory committees, and their involvement in environmental consultancies. In all cases the untutored layman, impressed by their numeracy and seeming professionalism, can easily be swayed to accept their pronouncements. Where their consulters are commercial or political interests, the decisiveness of theoreticians is an overwhelmingly attractive alternative to the incoherence of the multiply-conditioned view provided by experimentalists. The homology between the philosophies of successful businessman, successful politician and successful theoretician ensures the acceptance of the views of the latter by the former two.

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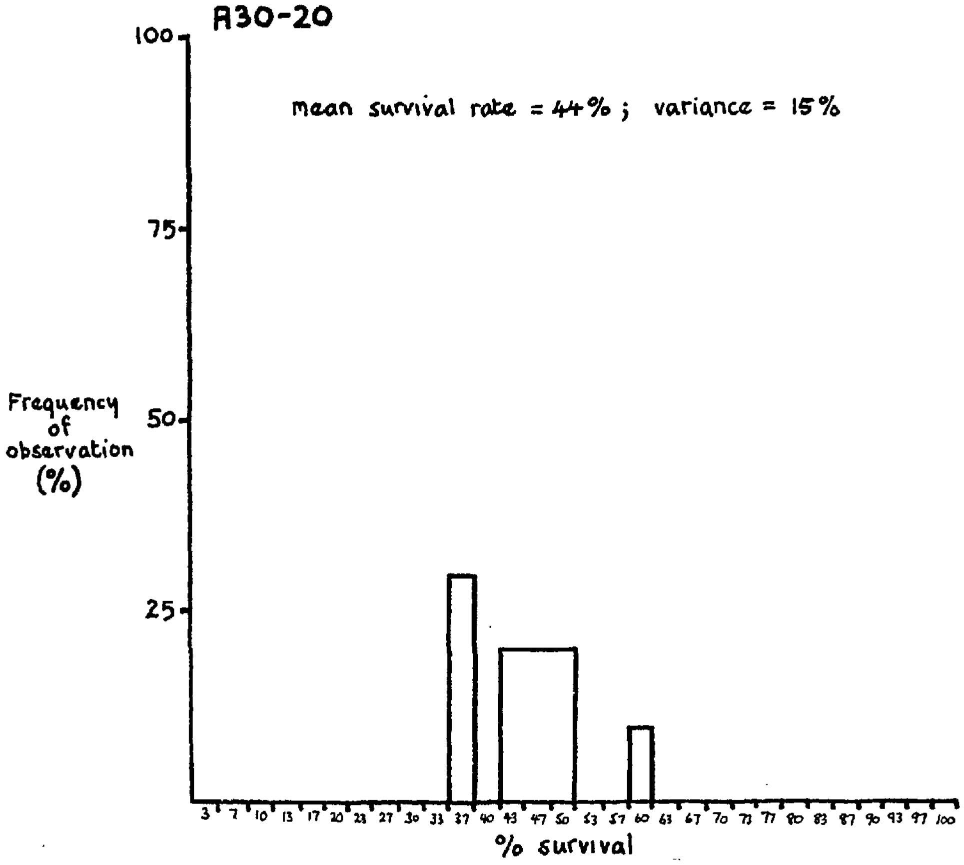
APPENDIX A : Results of preliminary experiments

The basic survivorship data are displayed in the form of histograms for each experimental condition (denoted in the same way as in Section 2.3.5) relating frequency of observation to observed survival rate (categorized according to possible observed rates). In these histograms the vertical scales (of frequency of observation) have been adjusted so as to give an area proportional representation of the distribution of mite survivorship through the set of graphs, it being felt that this gives a more accurate visual impression than a linear proportional representation in compensating for the effect of different sample sizes.

A30-20

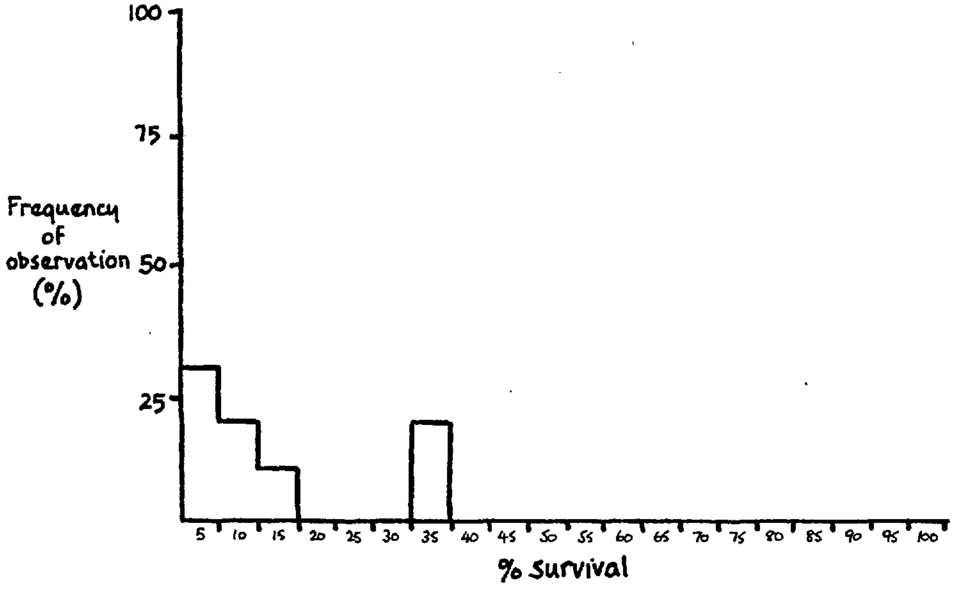


mean survival rate = 44% ; variance = 15%

A20-20

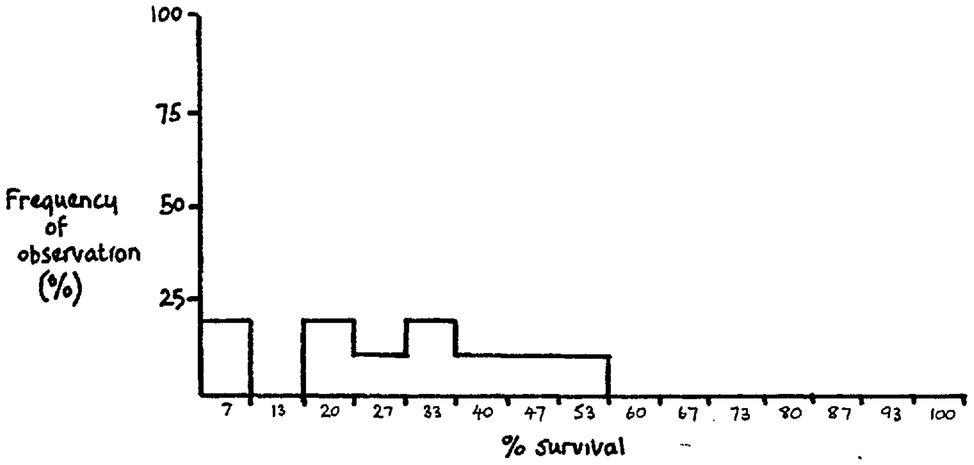
zero survival was recorded for replicates involving 20% of the mites observed

mean survival rate = 12% ; variance = 30%



A15-20

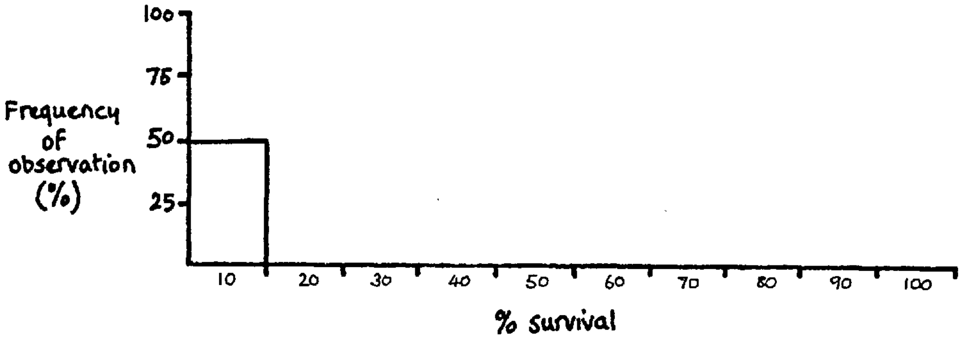
mean survival rate = 29% ; variance = 33%



A10-20

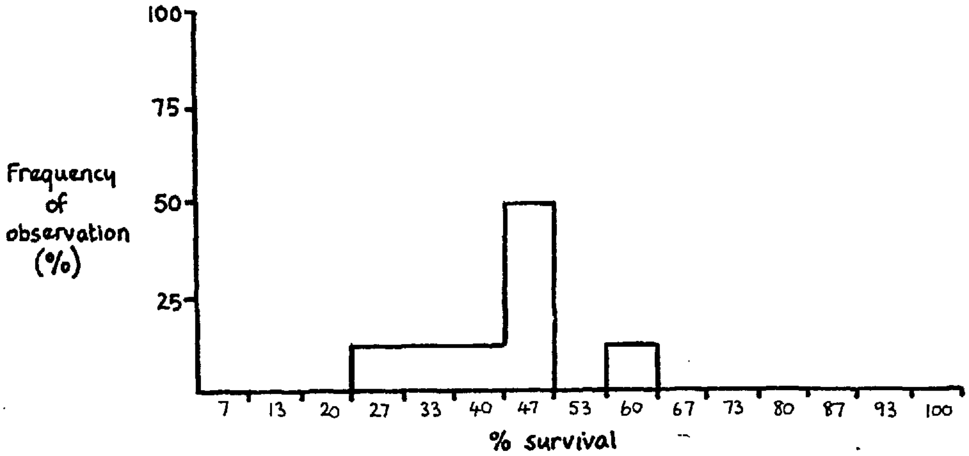
zero survival was recorded for replicates involving 50% of the mites observed

mean survival rate = 5% ; variance = 3%



A15-40

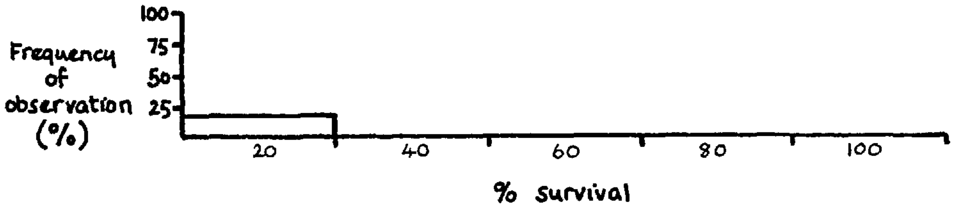
mean survival rate = 43% ; variance = 13%



A5-20

zero survival was recorded for replicates involving 80% of the mites observed

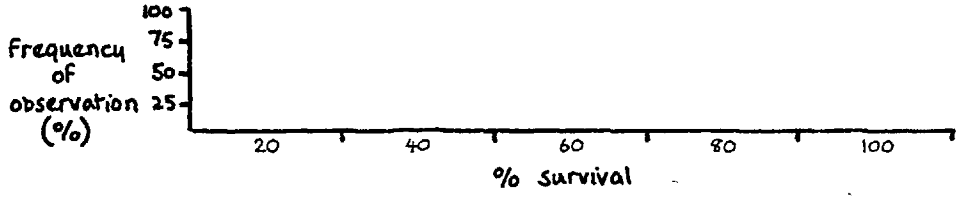
mean survival rate = 4% ; variance = 3%



A5-40

zero survival was recorded for replicates involving 100% of the mites observed

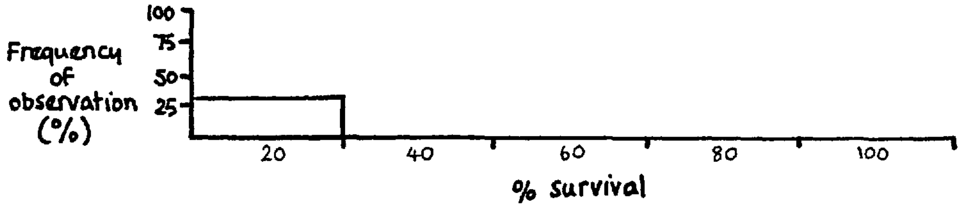
mean survival rate = 0% ; variance = 0%



A5-100

zero survival was recorded for replicates involving 70% of the mites observed

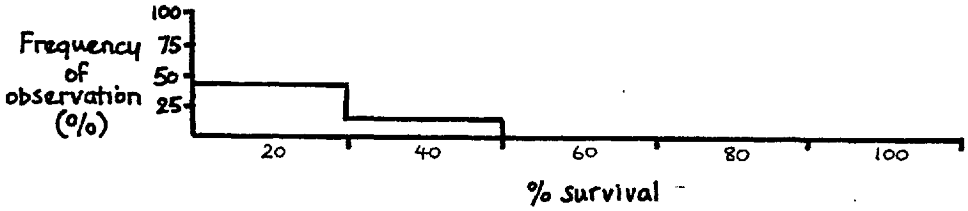
mean survival rate = 6% ; variance = 4%



A5-200

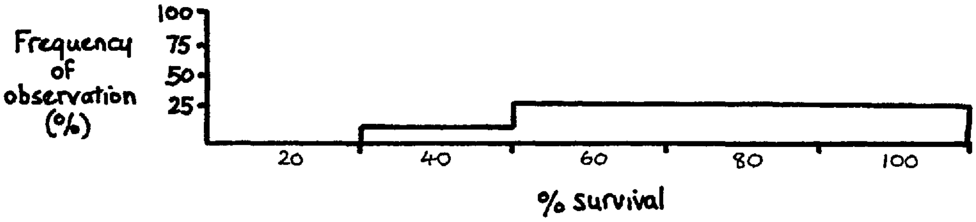
zero survival was recorded for replicates involving 50% of the mites observed

mean survival rate = 12% ; variance = 9%



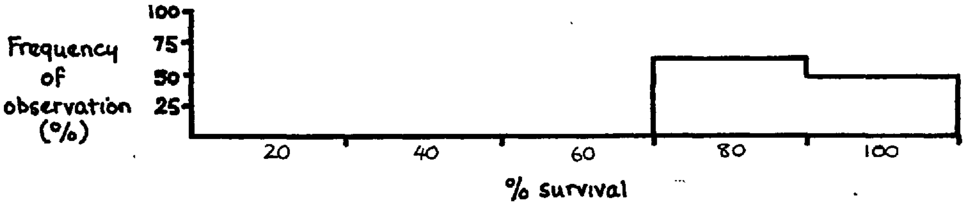
A5-300

mean survival rate = 76% ; variance = 19%



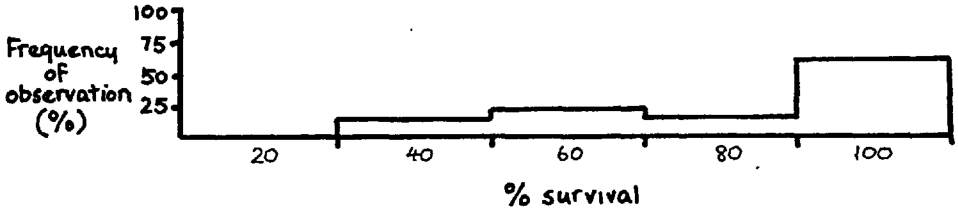
A5-400

mean survival rate = 88% ; variance = 5%



A5-500

mean survival rate = 84% ; variance = 23%



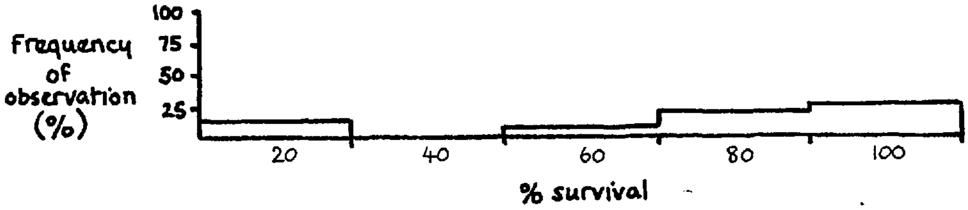
APPENDIX B : Results of the primary experiments

The results are displayed in the same way as those in Appendix A.

A5-20

zero survival was recorded for replicates involving 40 % of the mites observed

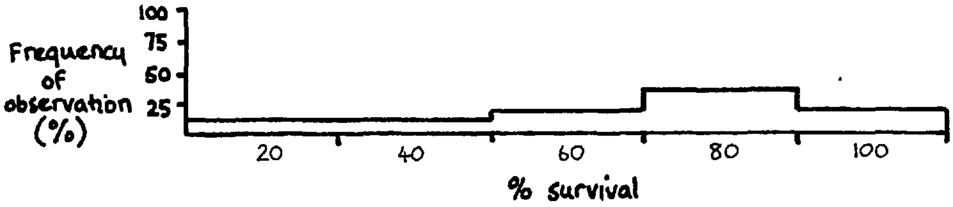
mean survival rate = 46% ; variance = 94%



A5-150

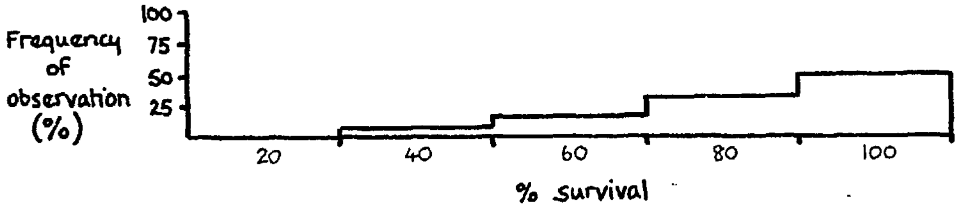
zero survival was recorded for replicates involving 5% of the mites observed

mean survival rate = 66% ; variance = 40%



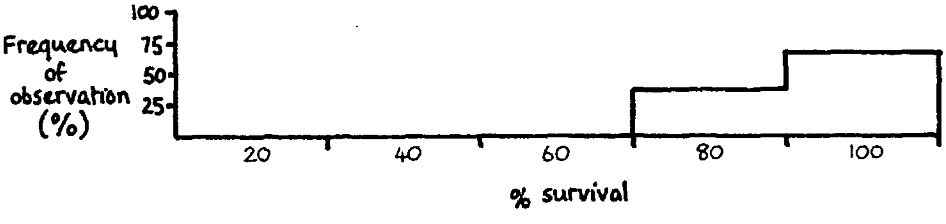
A5-300

mean survival rate = 85% ; variance = 16%



A5-450

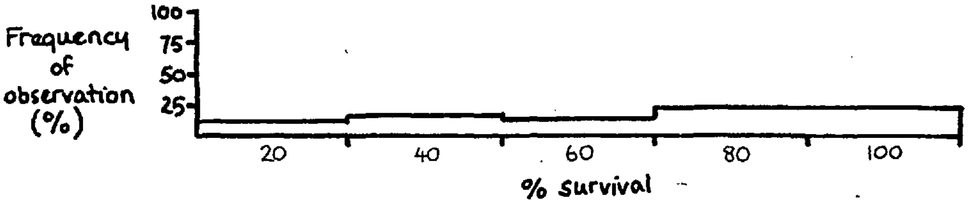
mean survival rate = 93% ; variance = 5%



D5-20

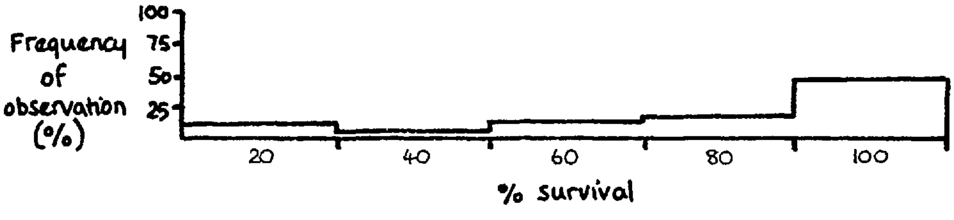
zero survival was recorded for replicates involving 5% of the mites observed

mean survival rate = 64% ; variance = 45%



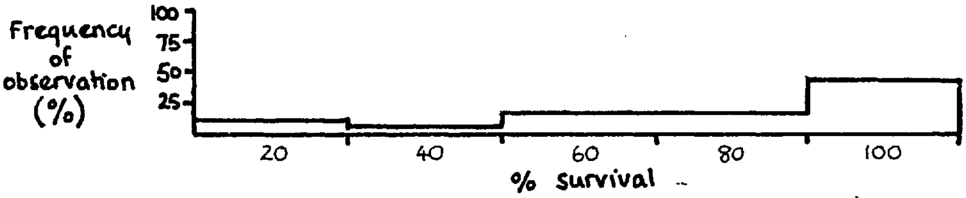
D5-150

mean survival rate = 79% ; variance = 35%



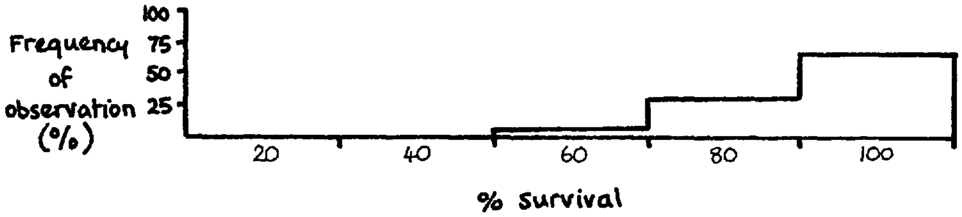
D5-300

mean survival rate = 77% ; variance = 35%



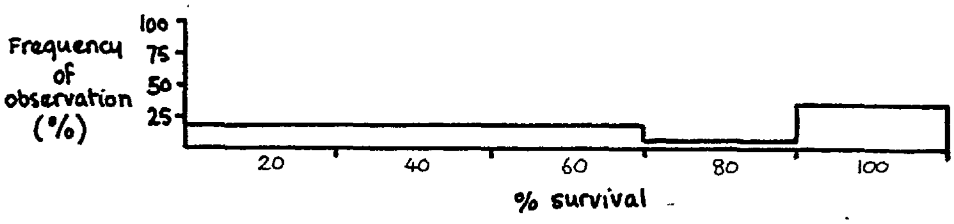
D5-450

mean survival rate = 92% ; variance = 7%



P5-20

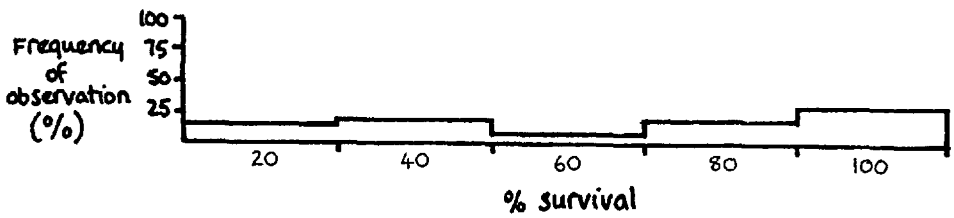
mean survival rate = 61 % ; variance = 49%



P5-150

zero survival was recorded for replicates involving 10 % of the mites observed

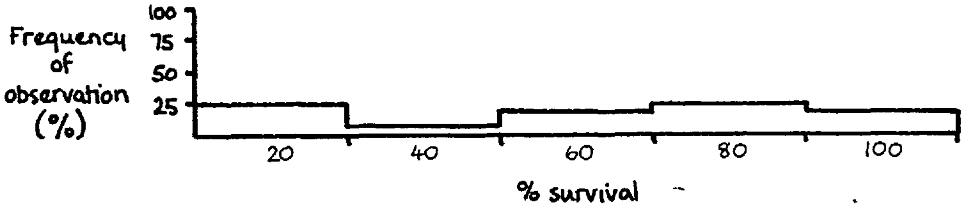
mean survival rate = 60 % ; variance = 62%



P5-300

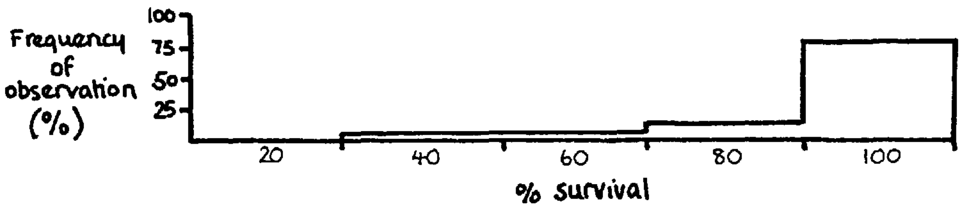
zero survival was recorded for replicates
involving 5% of the mites observed

mean survival rate = 59% ; variance = 51%



P5-450

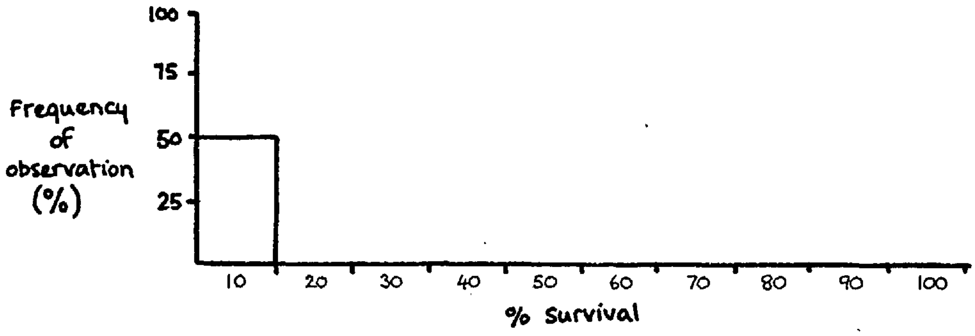
mean survival rate = 93% ; variance = 13%



A10-20

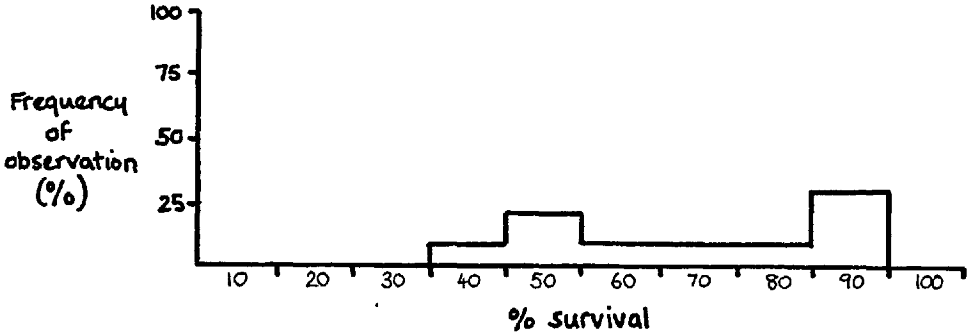
zero survival was recorded for replicates involving 50% of the mites observed

mean survival rate = 5% ; variance = 3%



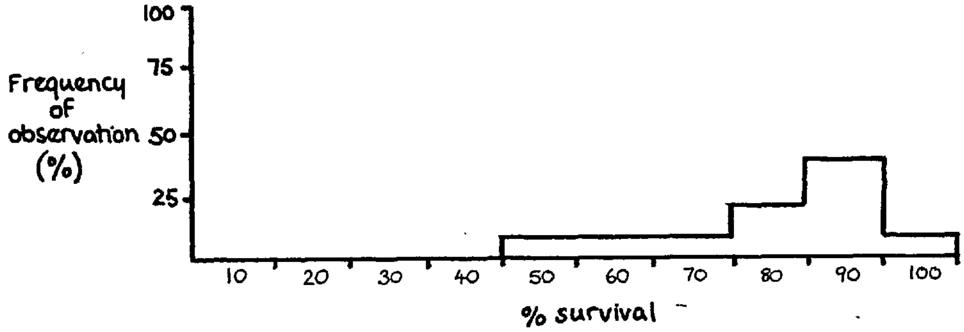
A10-150

mean survival rate = 70% ; variance = 32%



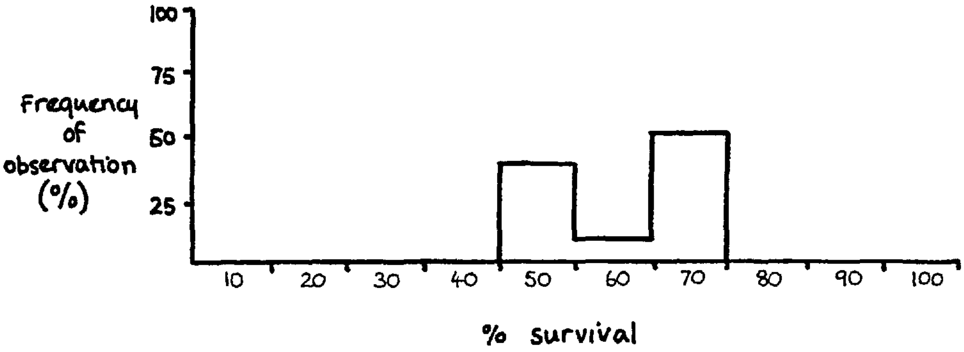
A10-300

mean survival rate = 80% ; variance = 22%



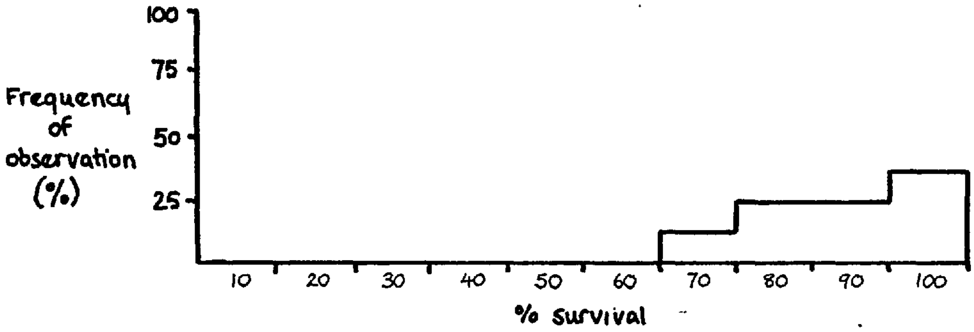
A10-450

mean survival rate = 61% ; variance = 9%



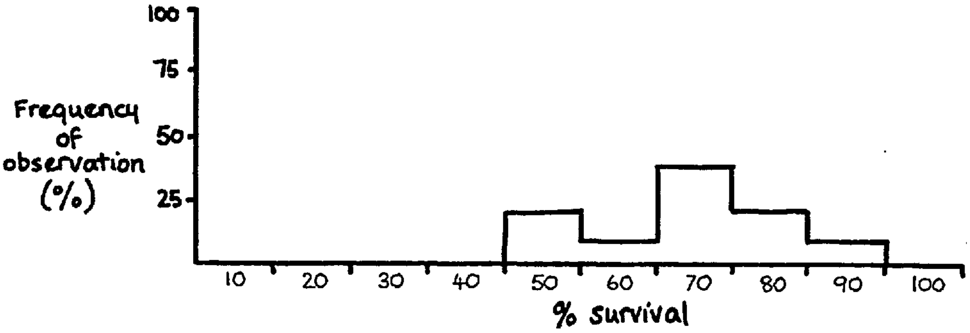
D10-20

mean survival rate = 89% ; variance = 11%



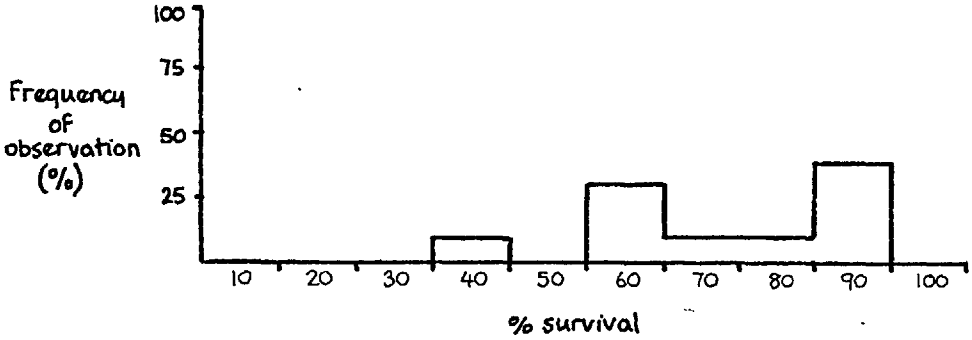
D10-150

mean survival rate = 69% ; variance = 15%



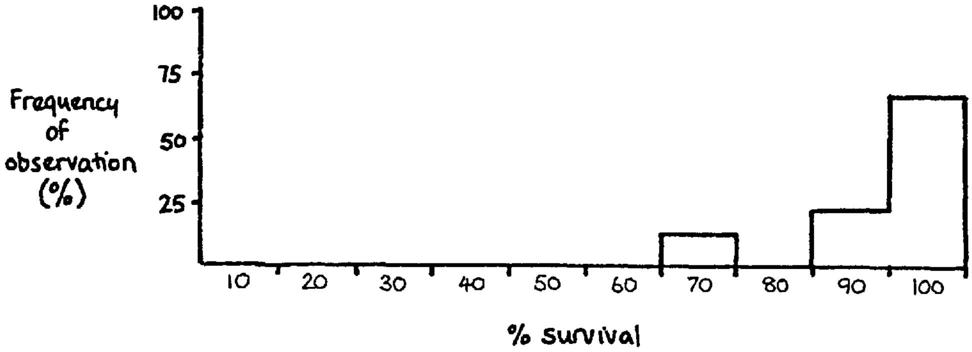
D10-300

mean survival rate = 72% ; variance = 36%



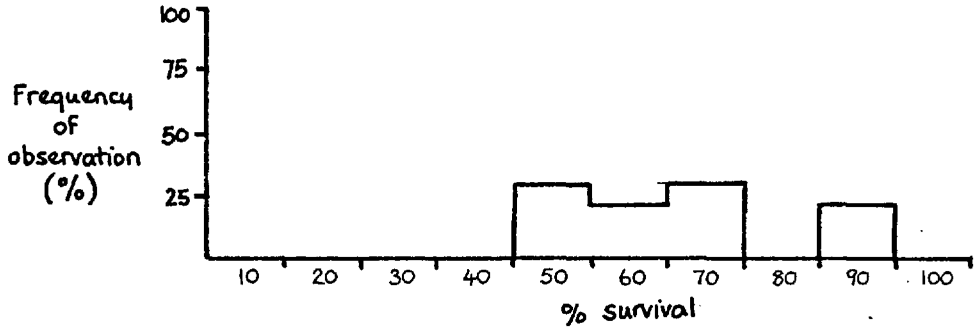
D10-450

mean survival rate = 94% ; variance = 9%



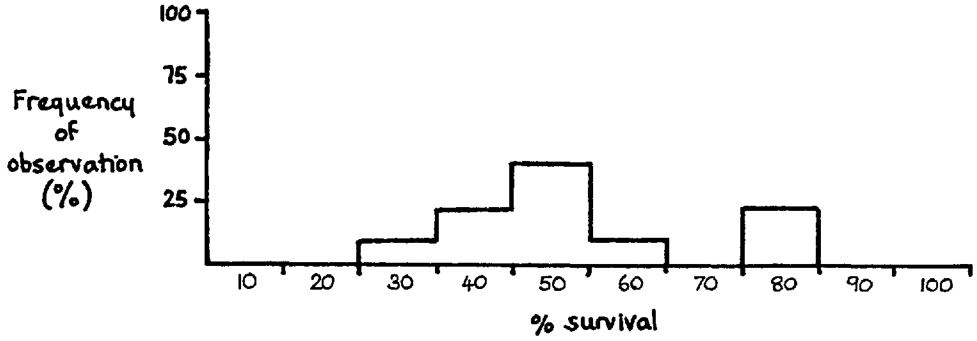
P10-20

mean survival rate = 66% ; variance = 20%



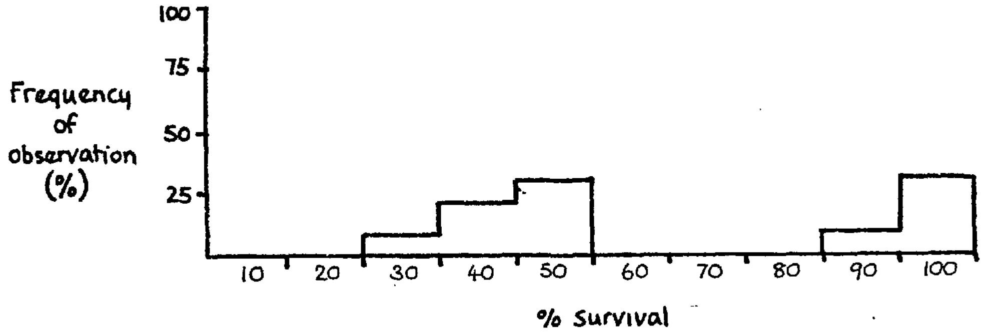
P10-150

mean survival rate = 53% ; variance = 24%



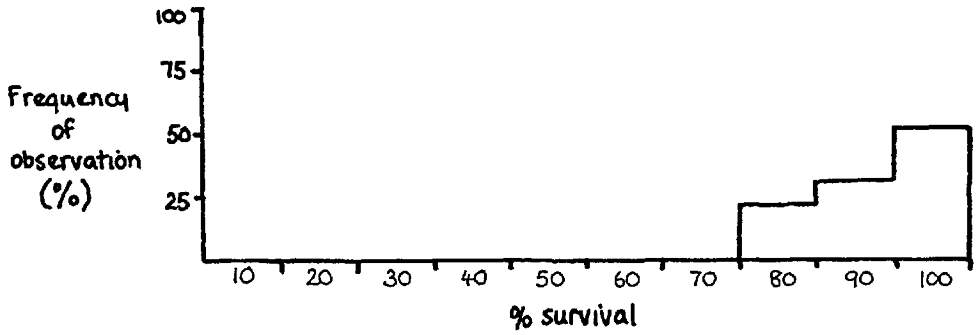
P10-300

mean survival rate = 65 % ; variance = 75%



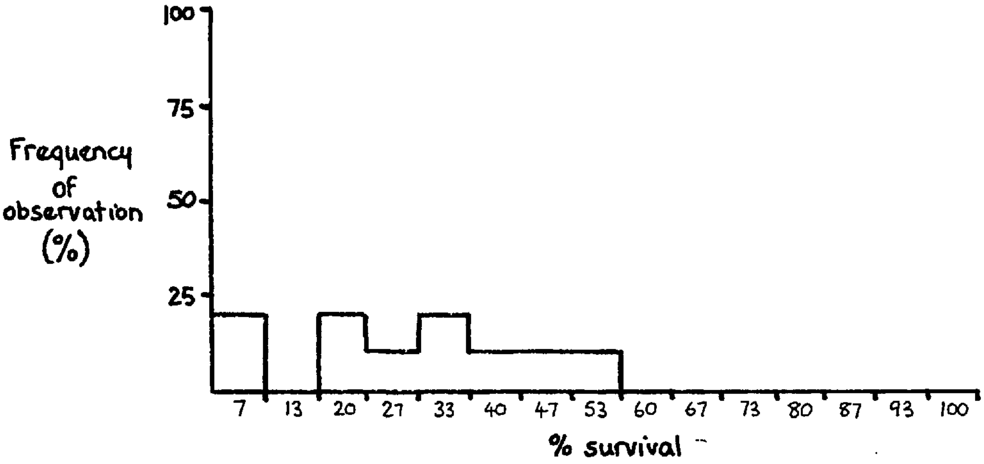
P10-450

mean survival rate = 93 % ; variance = 6%



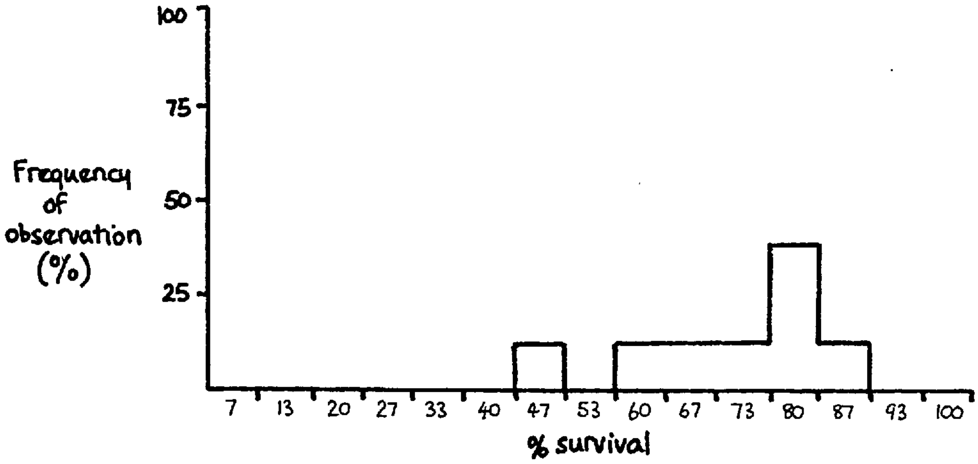
A15-20

mean survival rate = 29%; variance = 33%



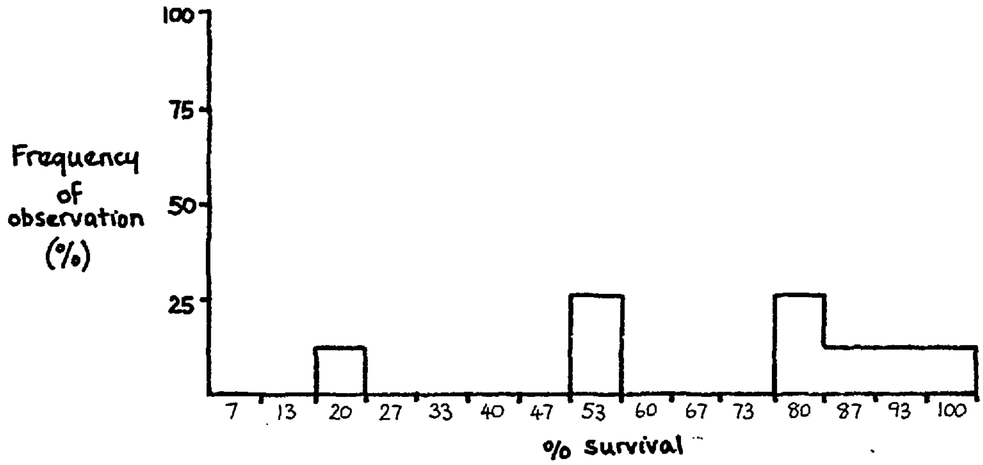
A15-150

mean survival rate = 72%; variance = 23%



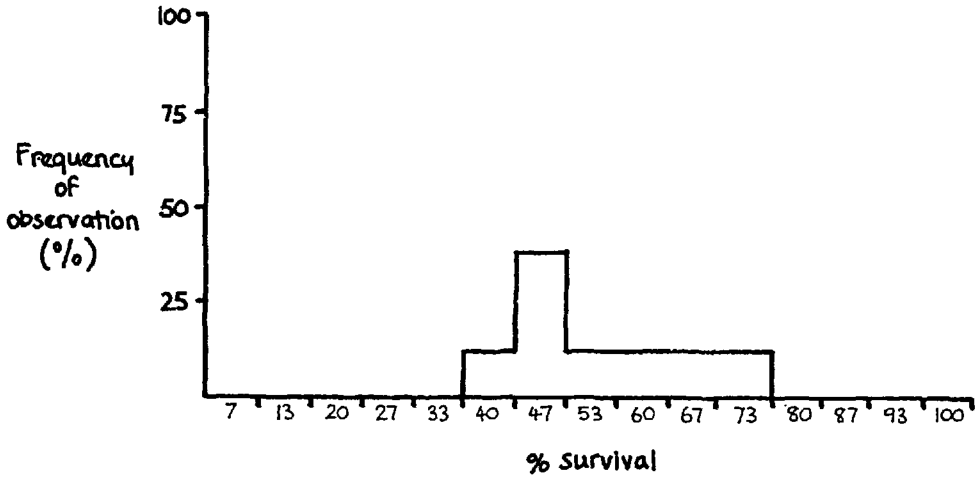
A15-300

mean survival rate = 71%; variance = 93%



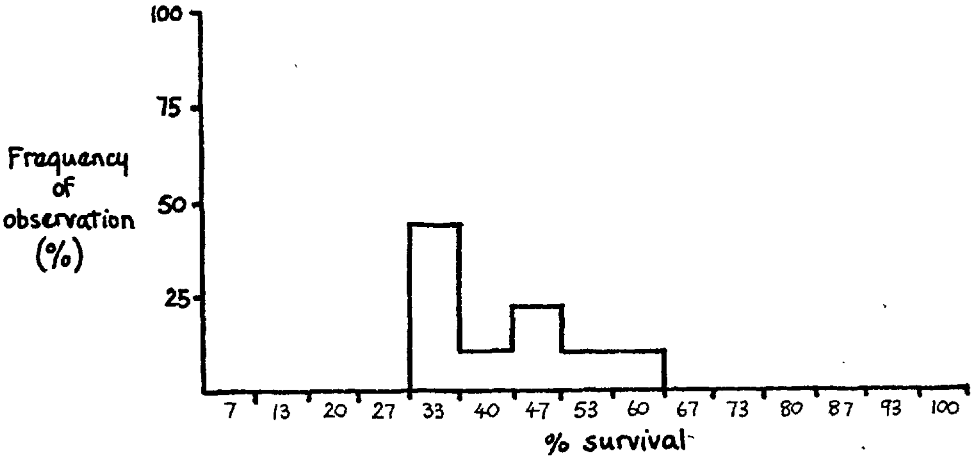
A15-450

mean survival rate = 54% ; variance = 17%



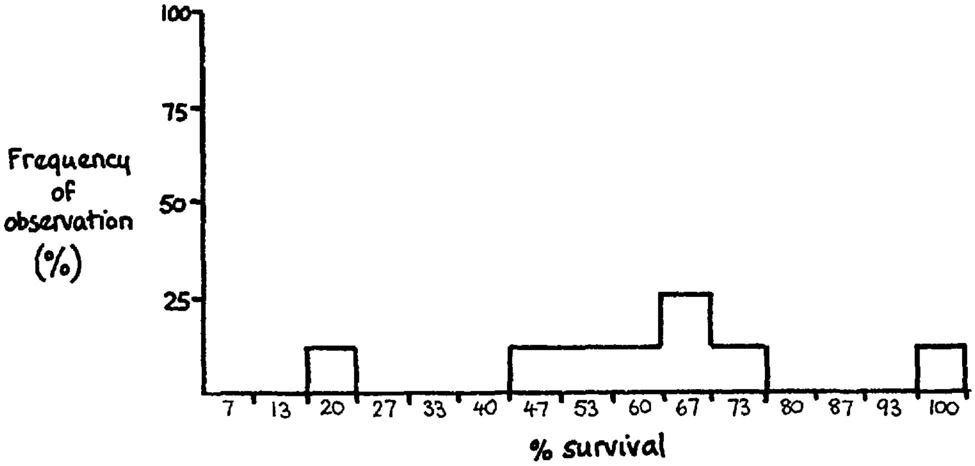
D15-20

mean survival rate = 42% ; variance = 13%



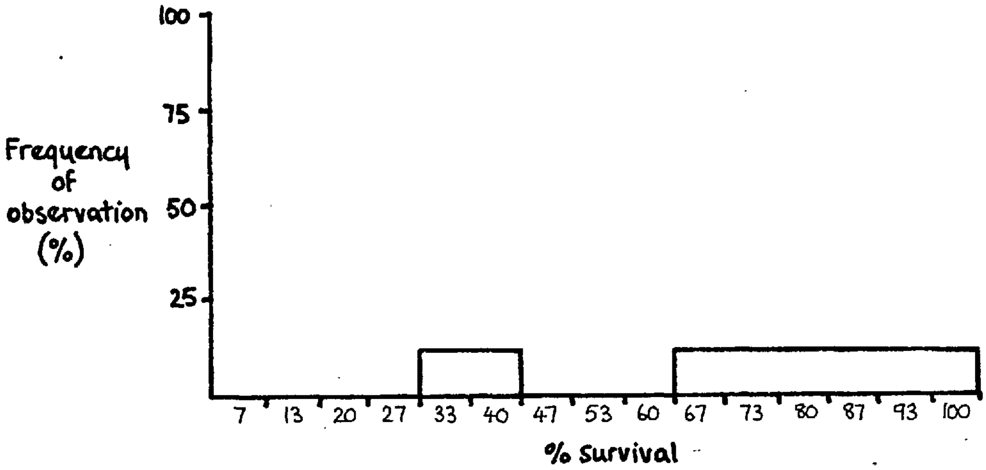
D15-150

mean survival rate = 61% ; variance = 69%



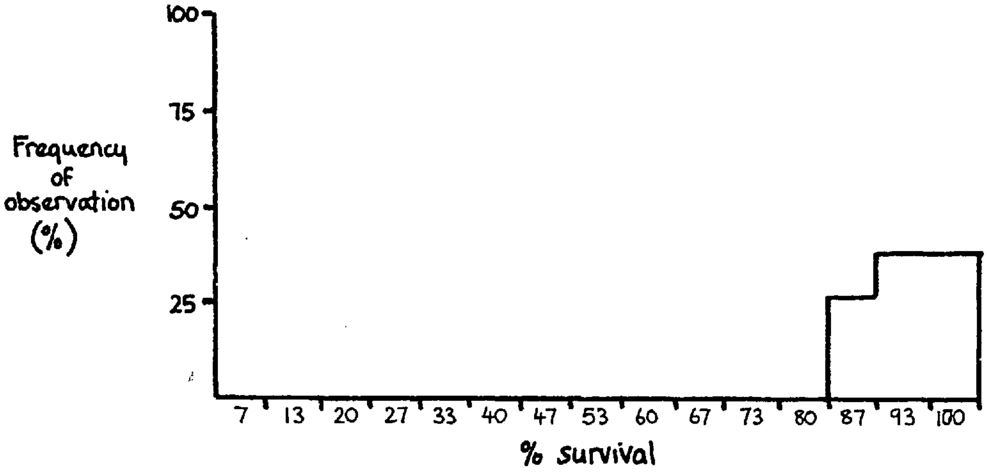
D15-300

mean survival rate = 68% ; variance = 60%



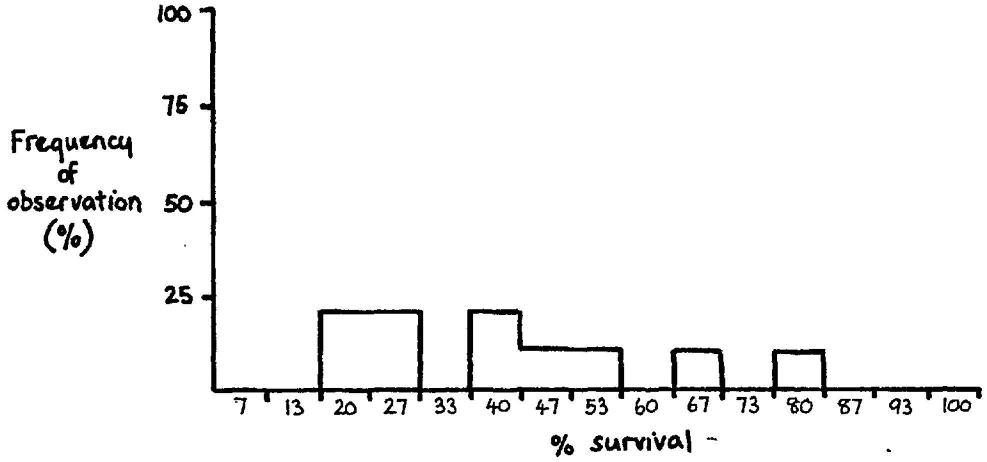
D15-450

mean survival rate = 94% ; variance = 4%



P15-20

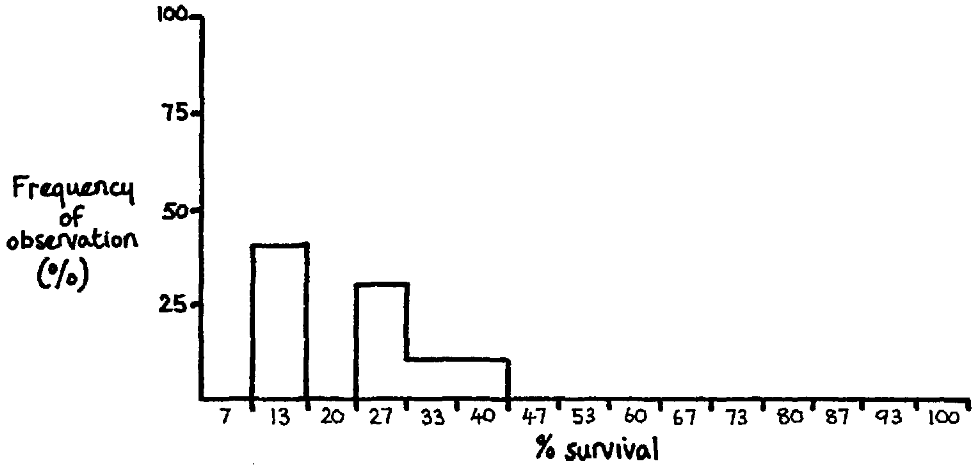
mean survival rate = 42% ; variance = 55%



P15-150

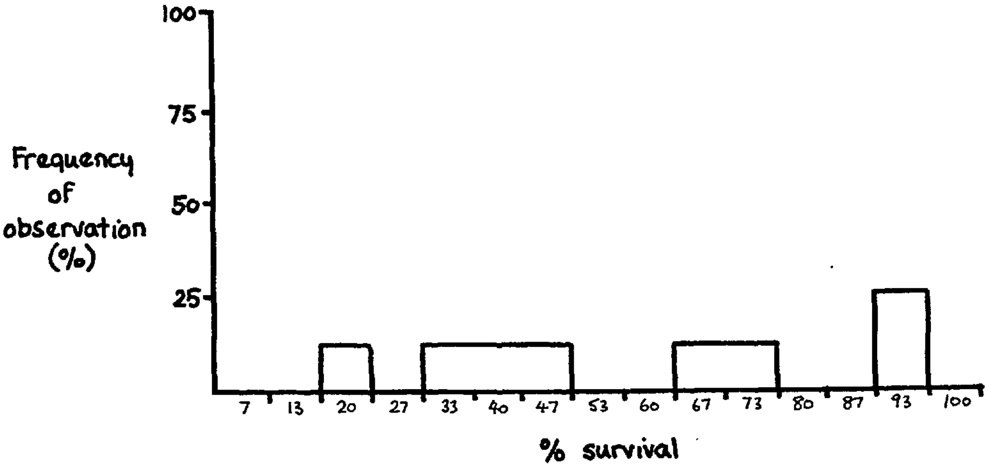
zero survival was recorded for replicates
involving 10% of the mites observed

mean survival rate = 21% ; variance = 19%



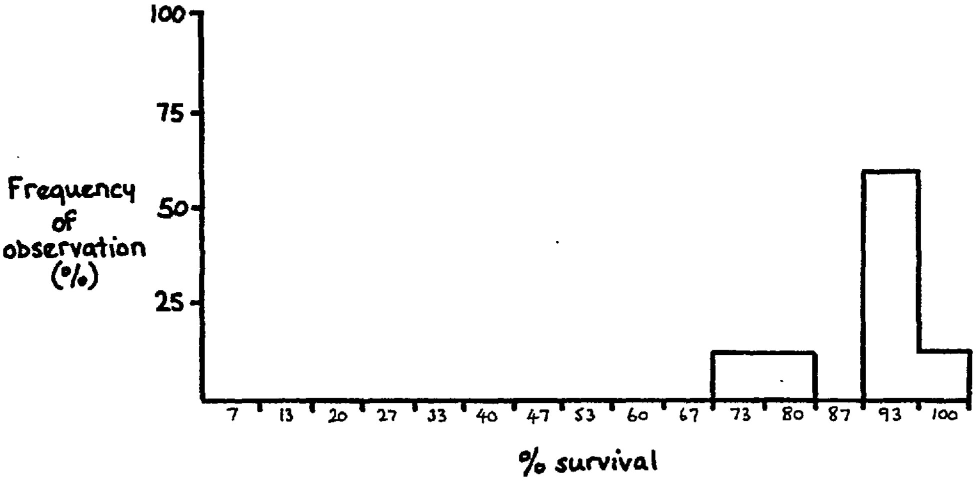
P15-300

mean survival rate = 68% ; variance = 99%



P15-450

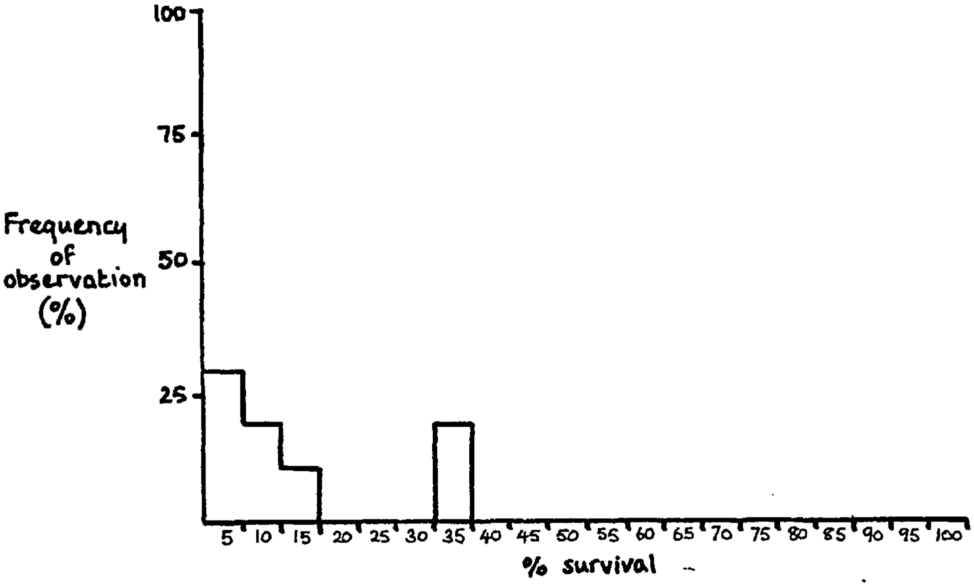
mean survival rate = 90% ; variance = 10%



A20-20

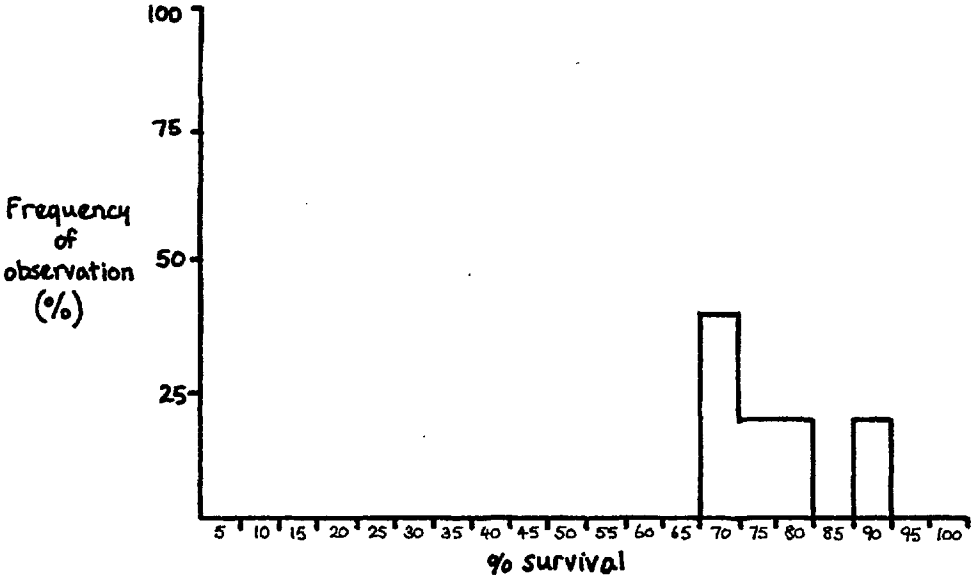
zero survival was recorded for replicates involving 20% of the mites observed

mean survival rate = 12%; variance = 30%



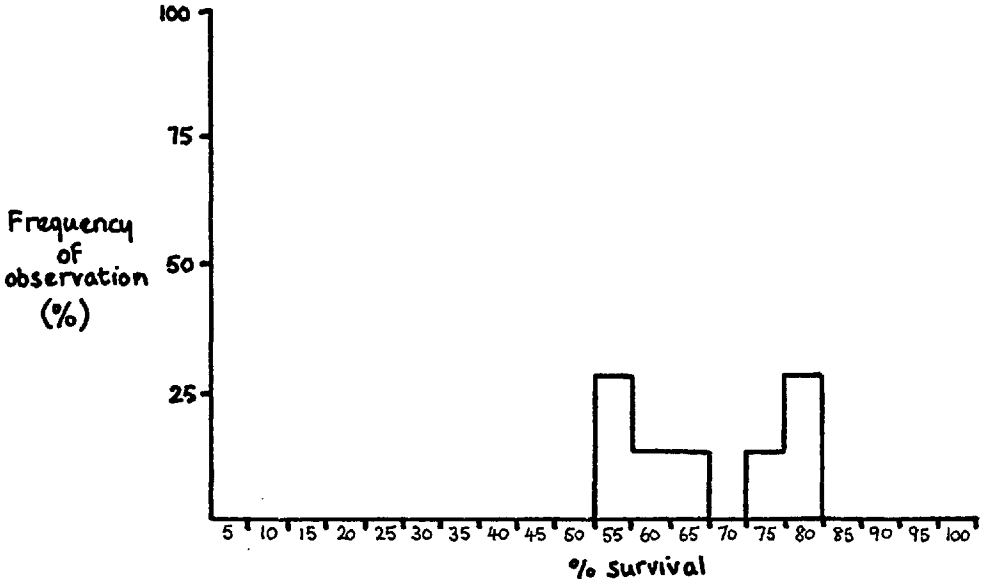
A20-150

mean survival rate = 77%; variance = 11%



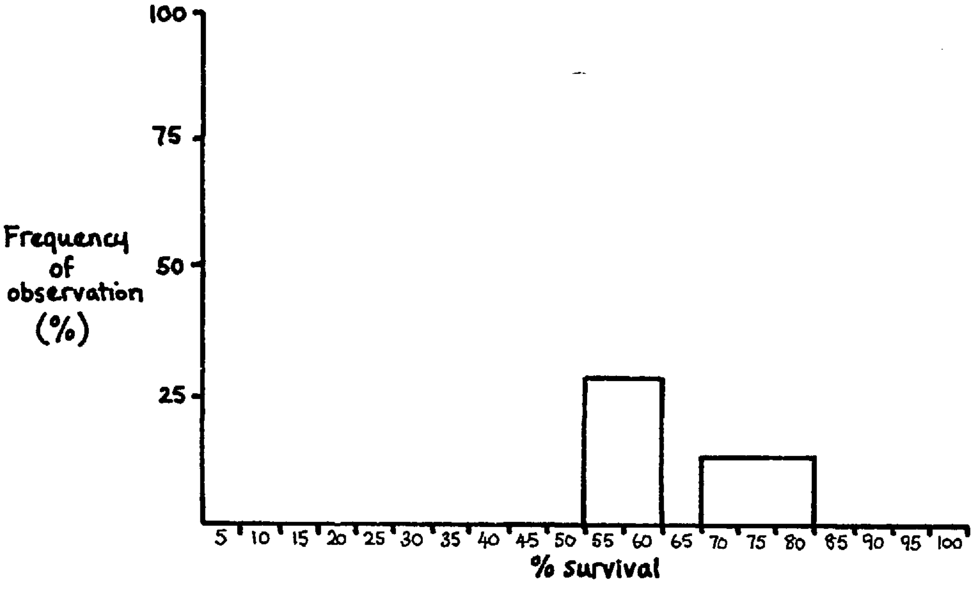
A20-300

mean survival rate = 67% ; variance = 21%



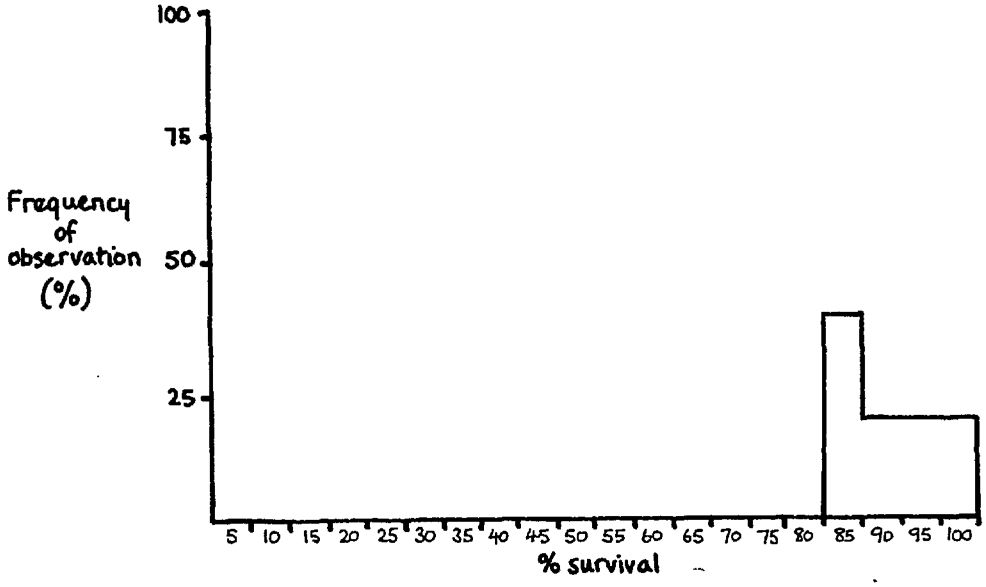
A20-450

mean survival rate = 65% ; variance = 17%



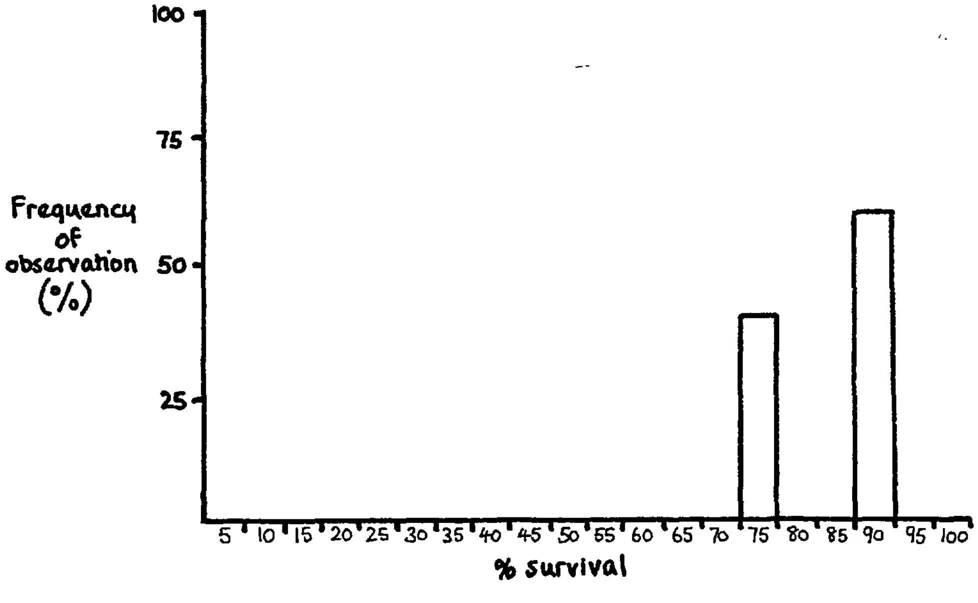
D20-20

mean survival rate = 91 %; variance = 7%



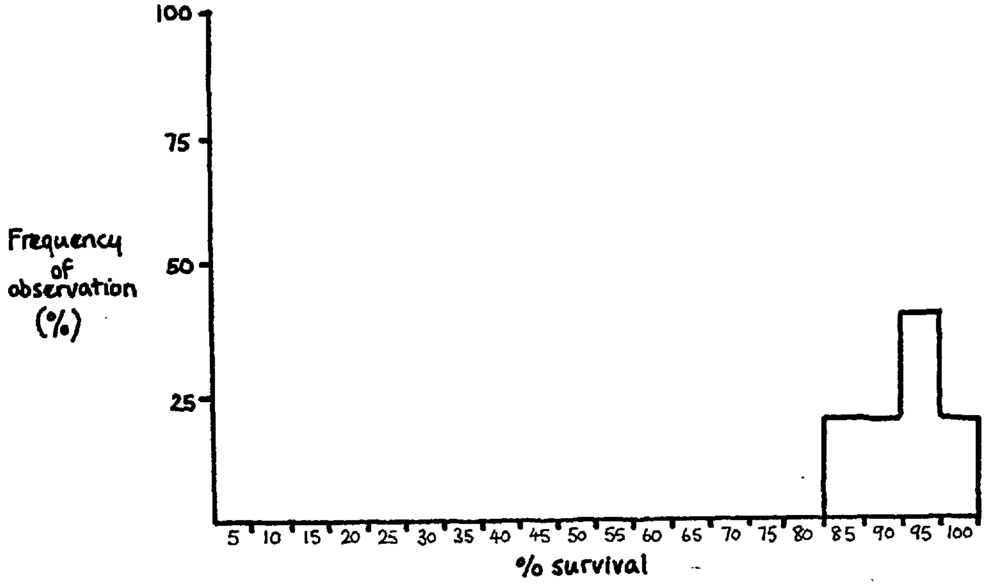
D20-150

mean survival rate = 84%; variance = 11%



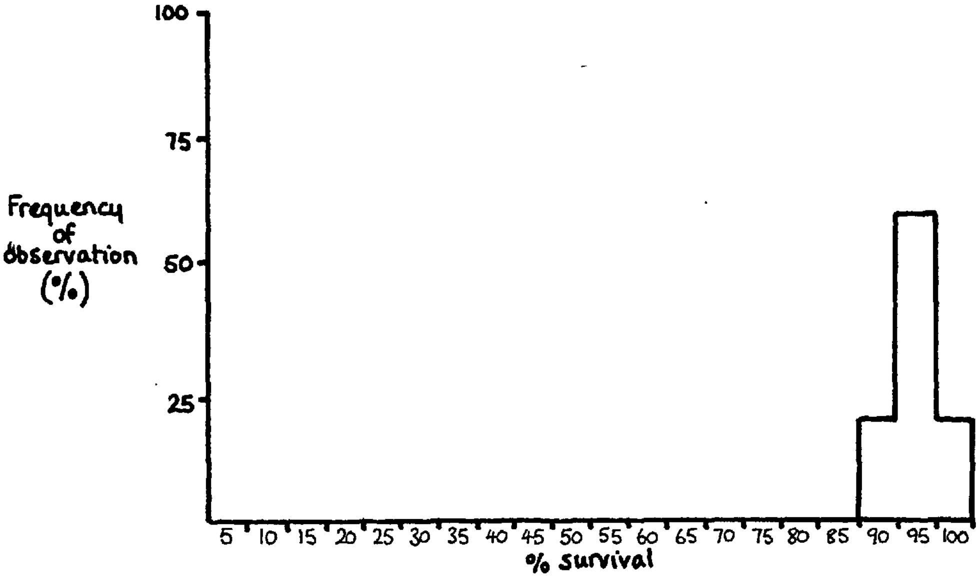
D20-300

mean survival rate = 93% ; variance = 5%



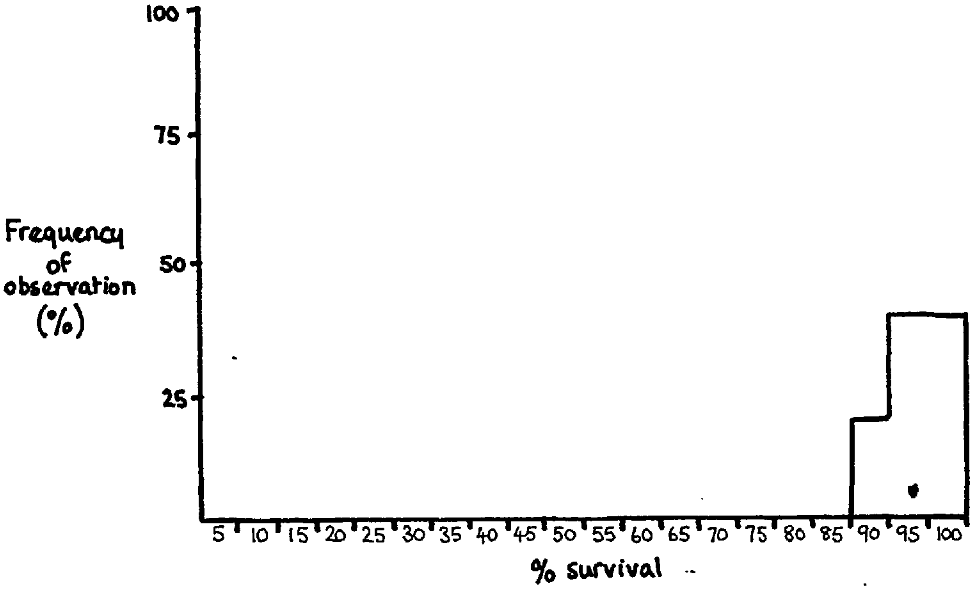
D20-450

mean survival rate = 95% ; variance = 2%



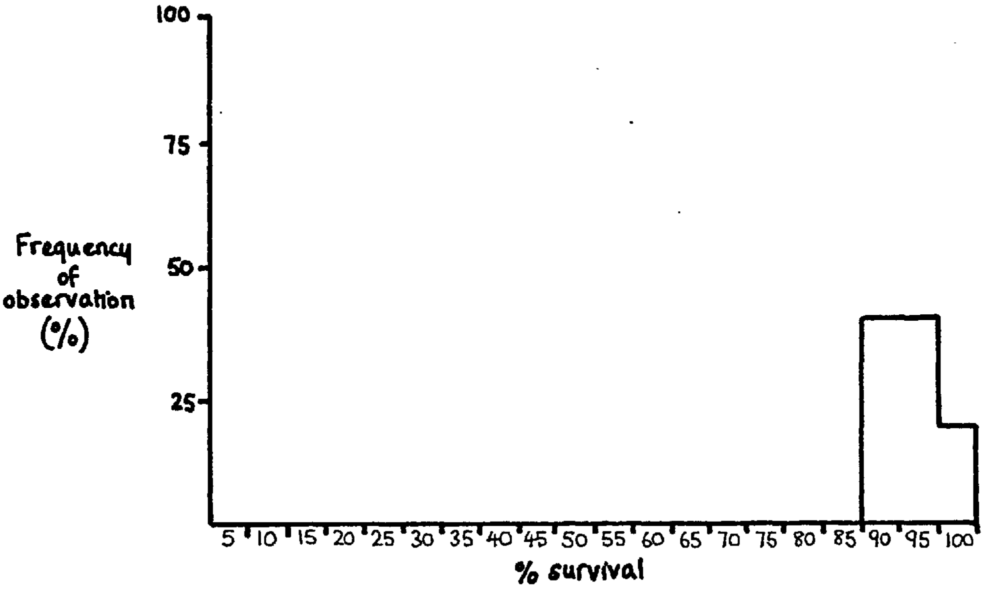
P20-20

mean survival rate = 96%; variance = 3%



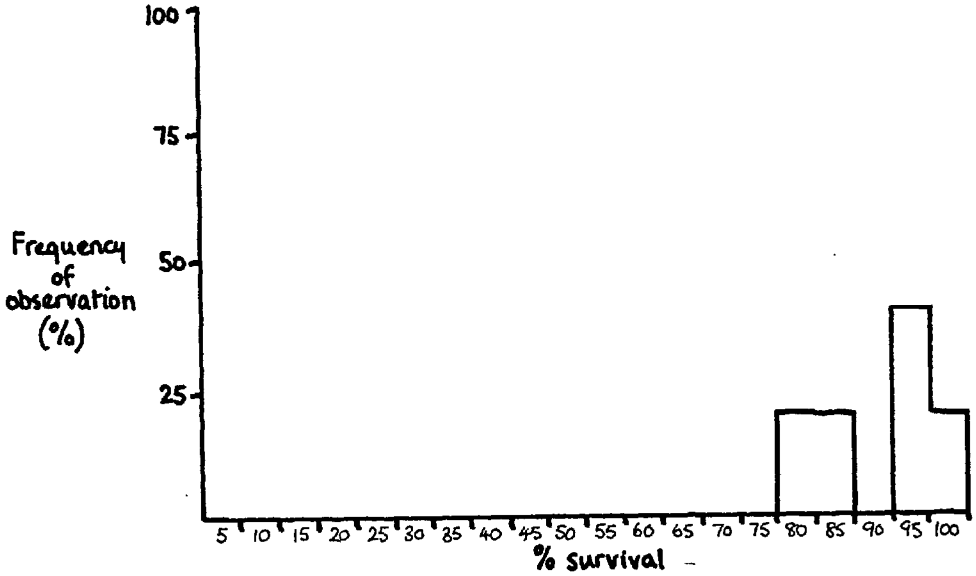
P20-150

mean survival rate = 94%; variance = 3%



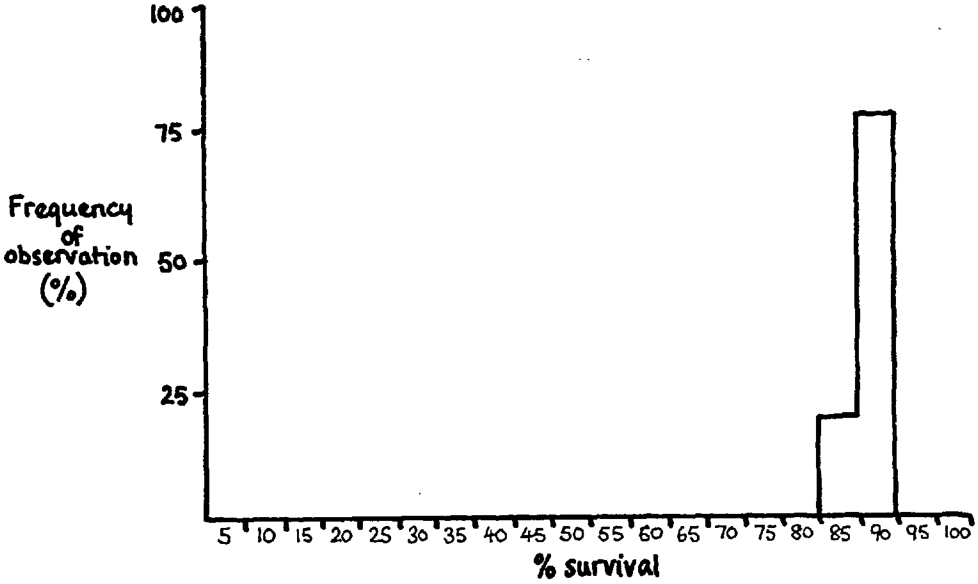
P20-300

mean survival rate = 91%; variance = 11%



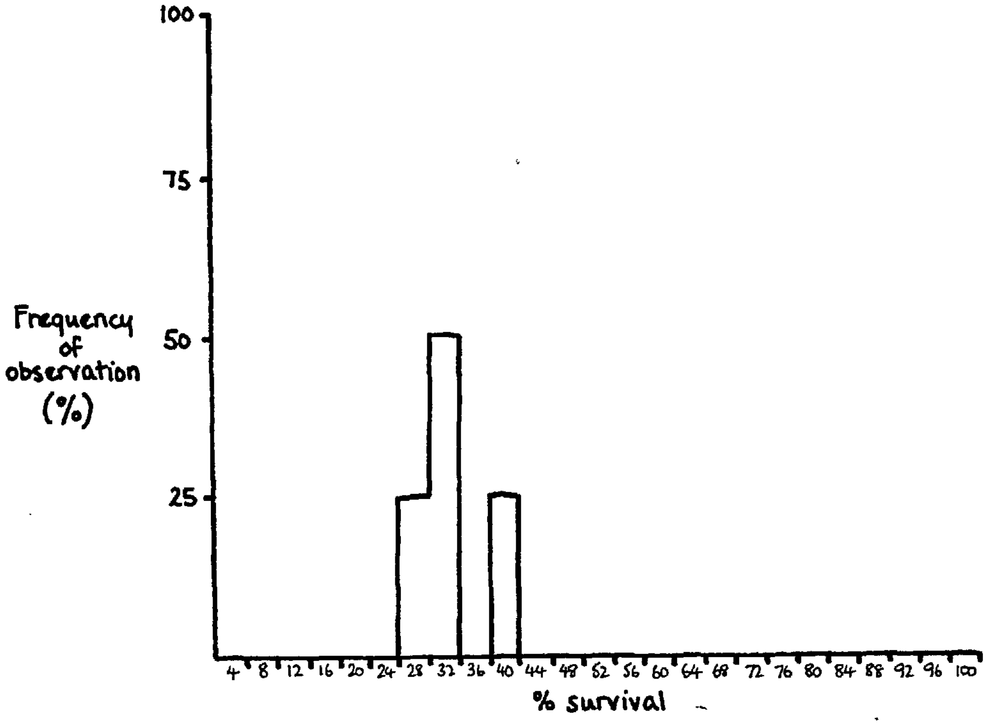
P20-450

mean survival rate = 89%; variance = 1%



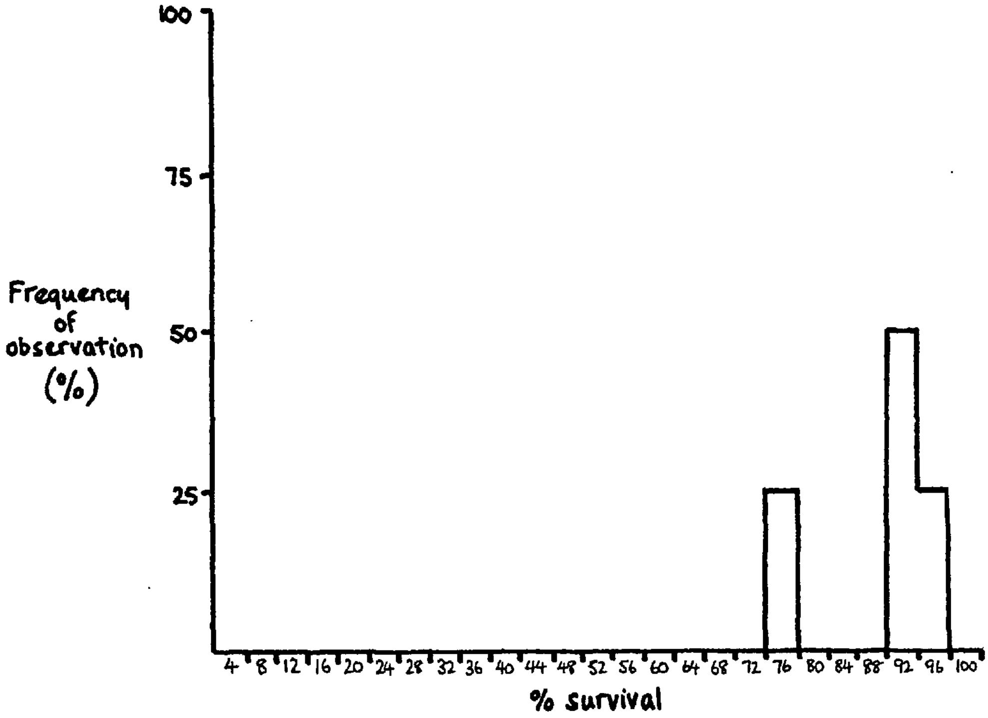
A25-20

mean survival rate = 33% ; variance = 5%



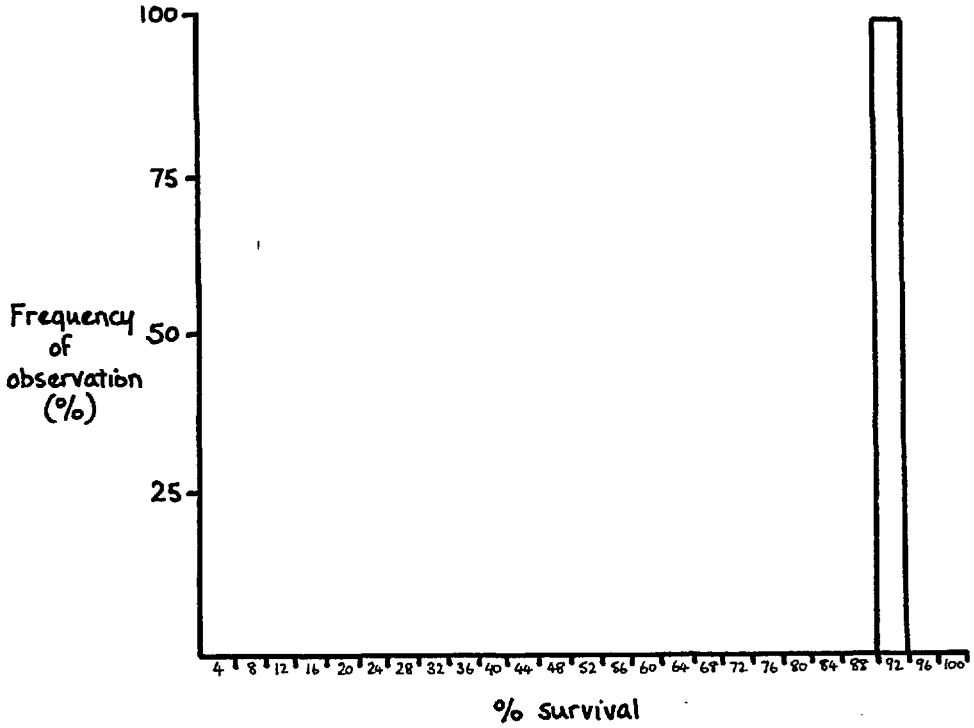
A25-150

mean survival rate = 89% ; variance = 15%



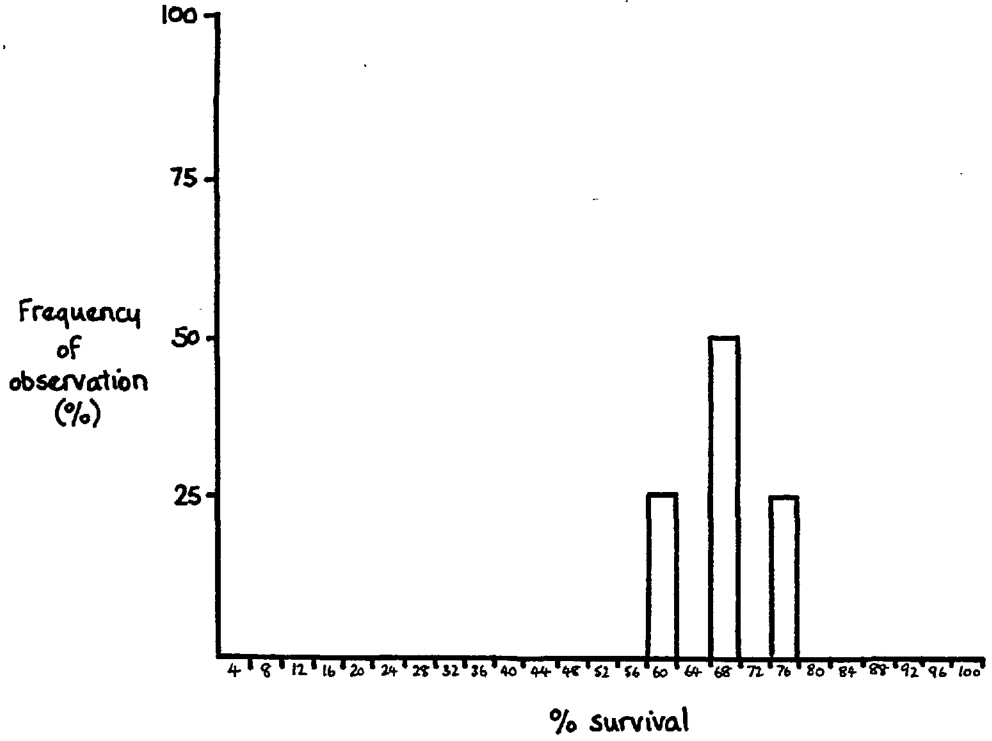
A25-300

mean survival rate = 92 % ; variance = 0%



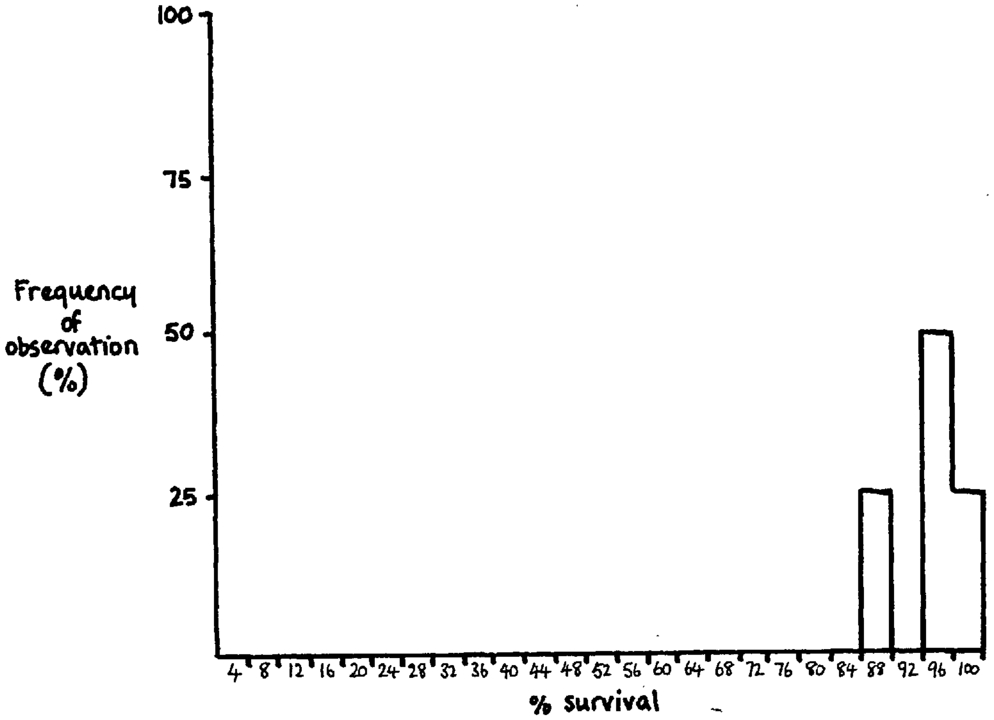
A25-450

mean survival rate = 68 % ; variance = 7%



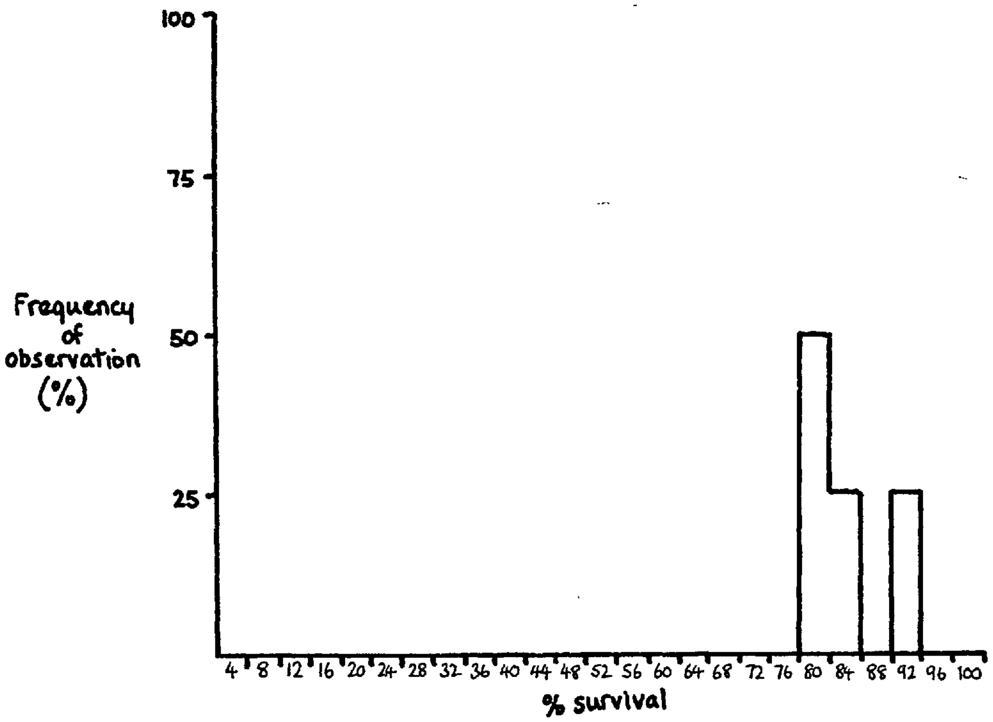
D25-20

mean survival rate = 95%; variance = 5%



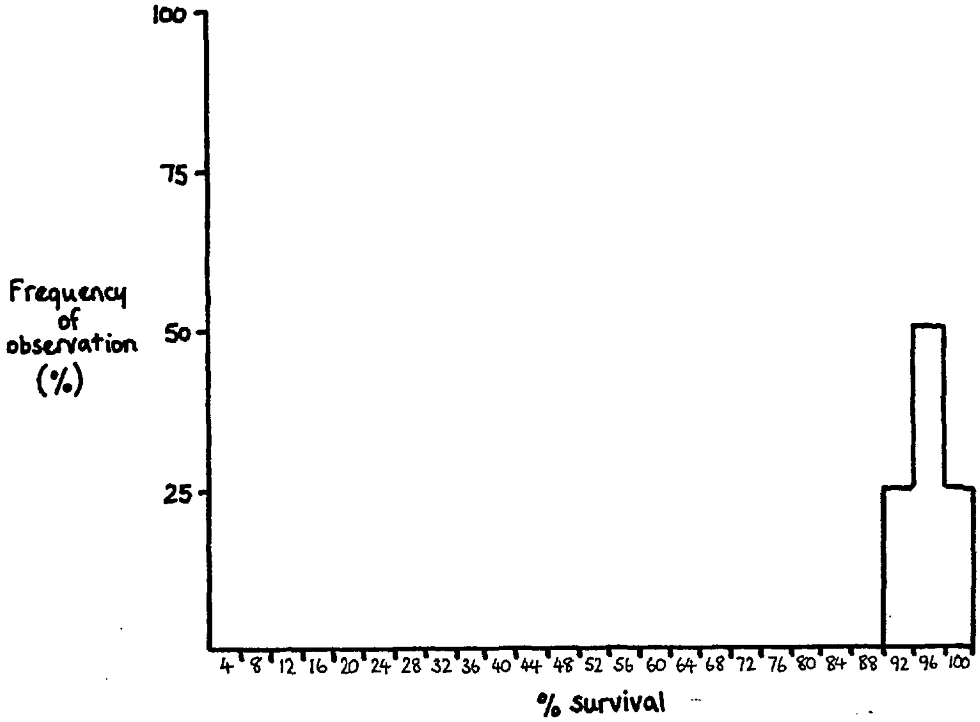
D25-150

mean survival rate = 84%; variance = 6%



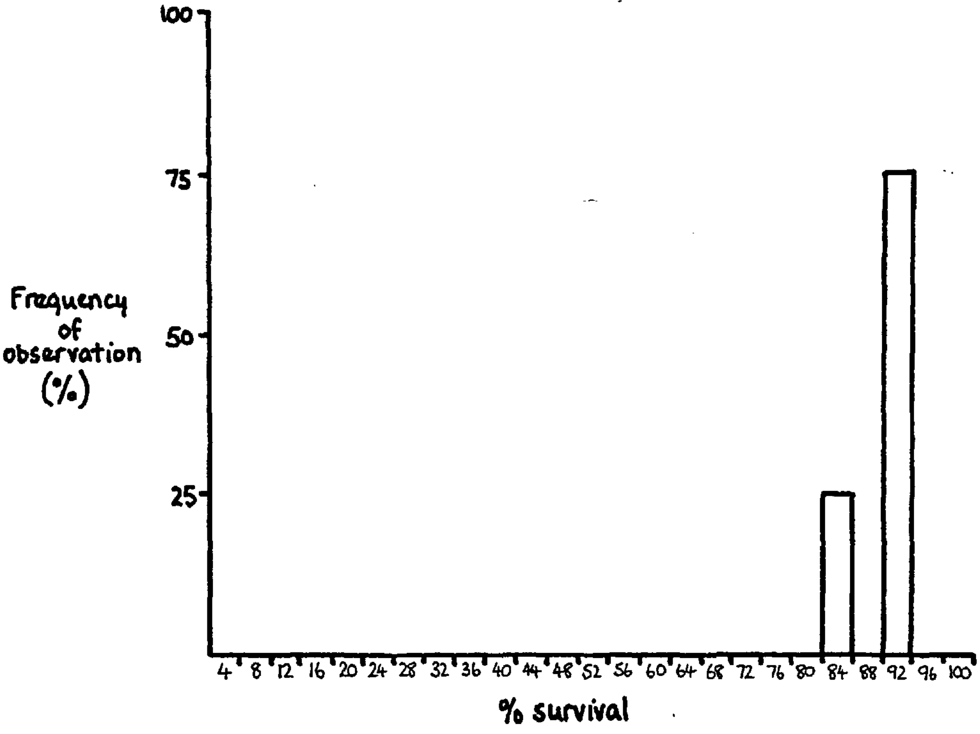
D25-300

mean survival rate = 96 % ; variance = 2%



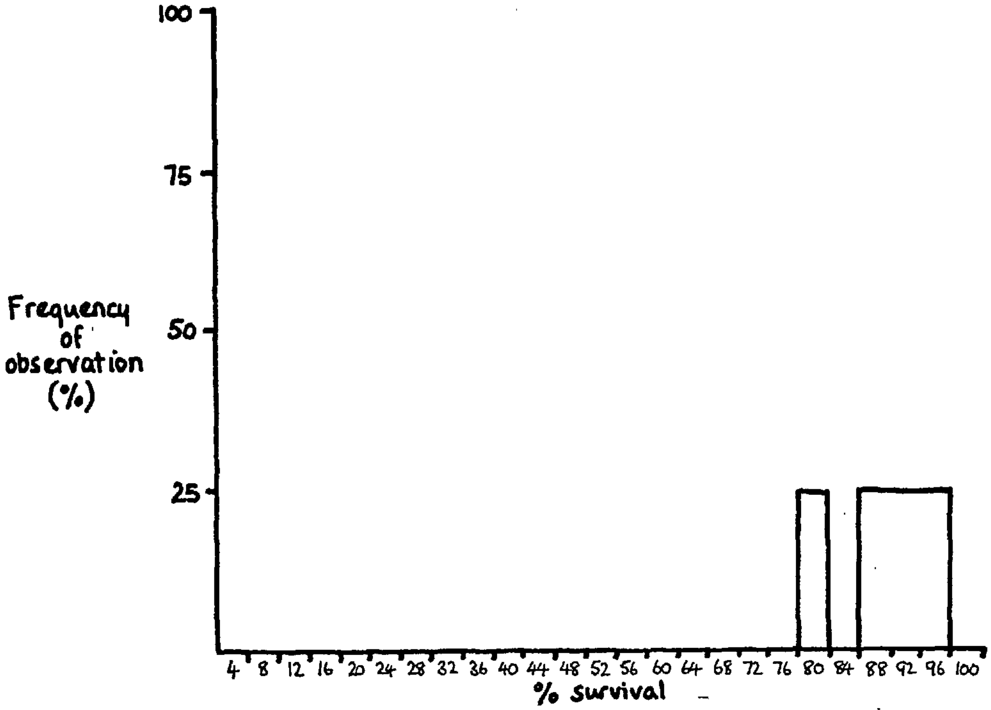
D25-450

mean survival rate = 90 % ; variance = 3%



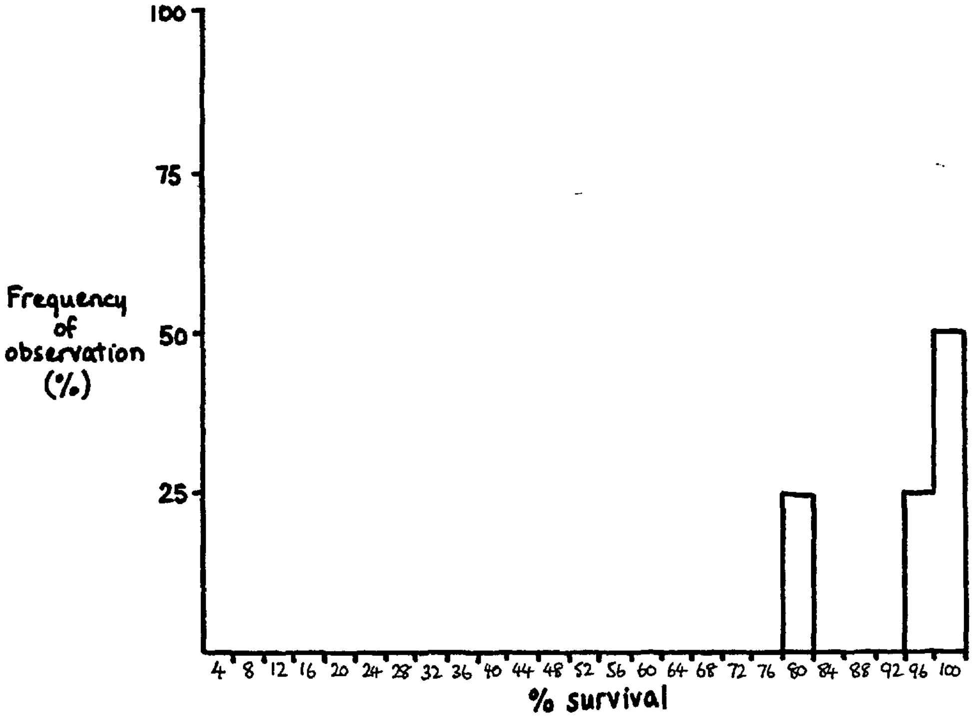
P25-20

mean survival rate = 89 % ; variance = 9%



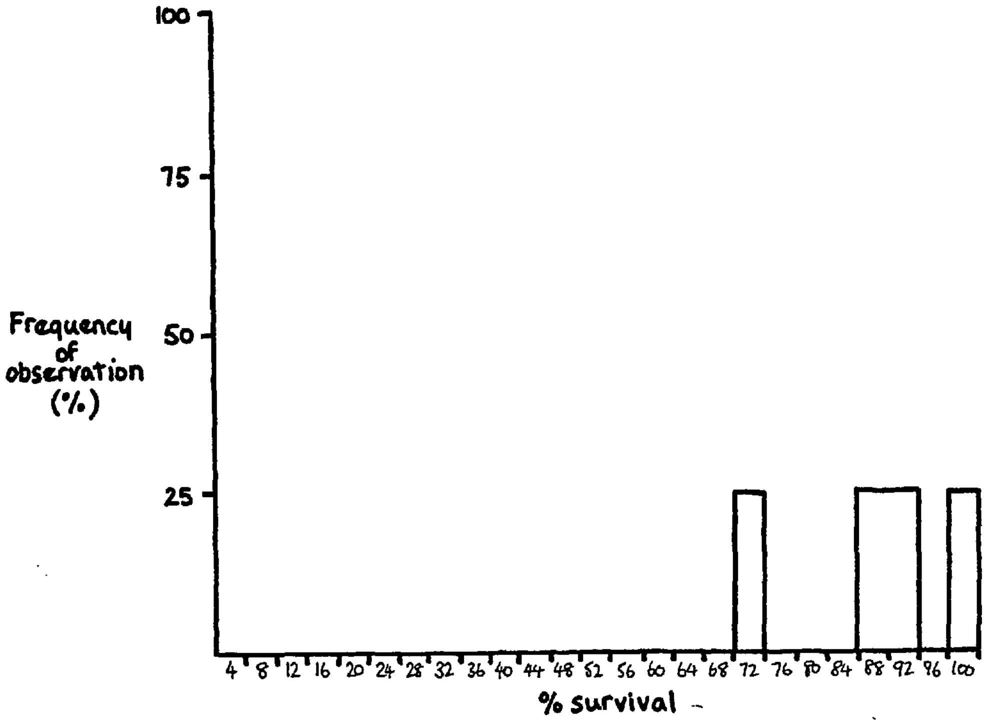
P25-150

mean survival rate = 94 % ; variance = 17%



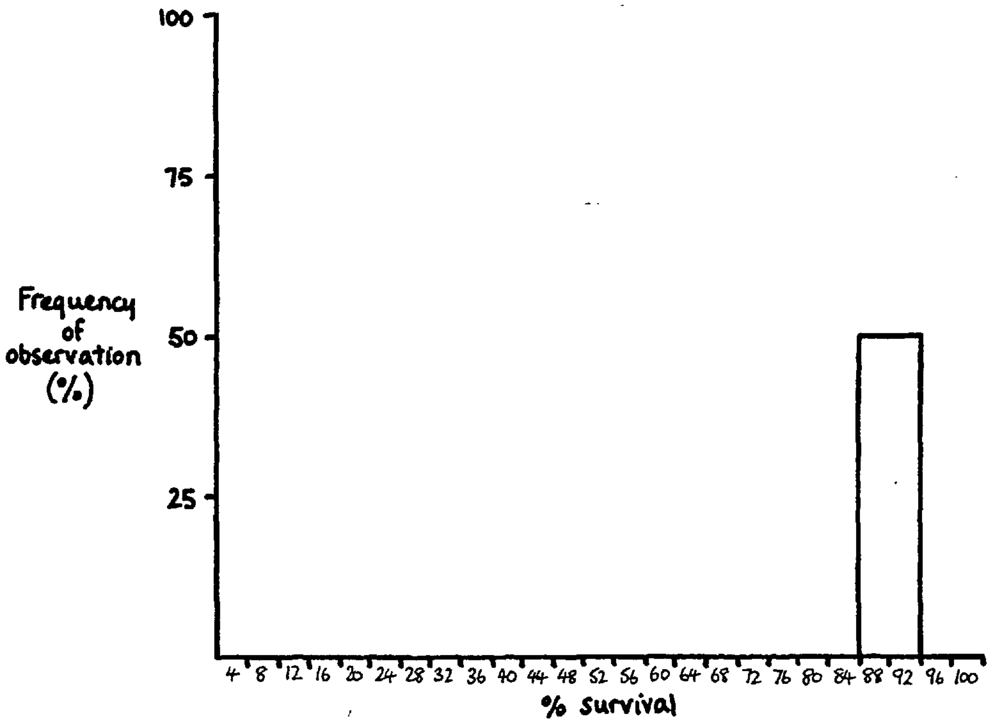
P25-300

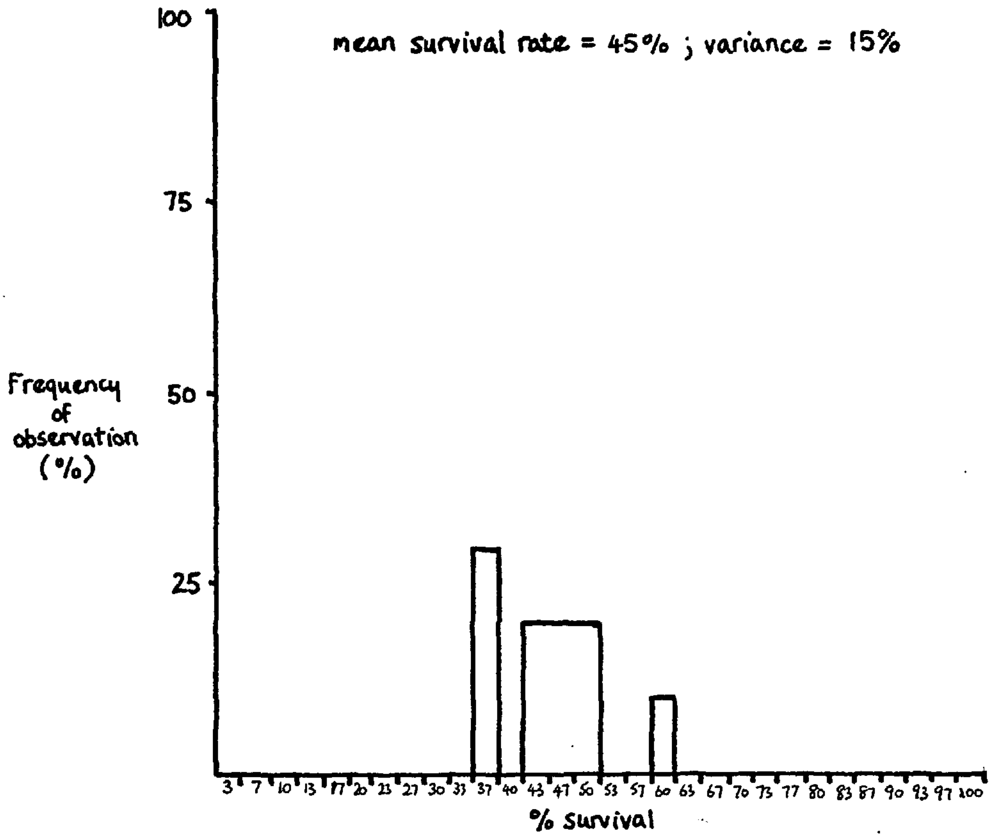
mean survival rate = 88%; variance = 26%



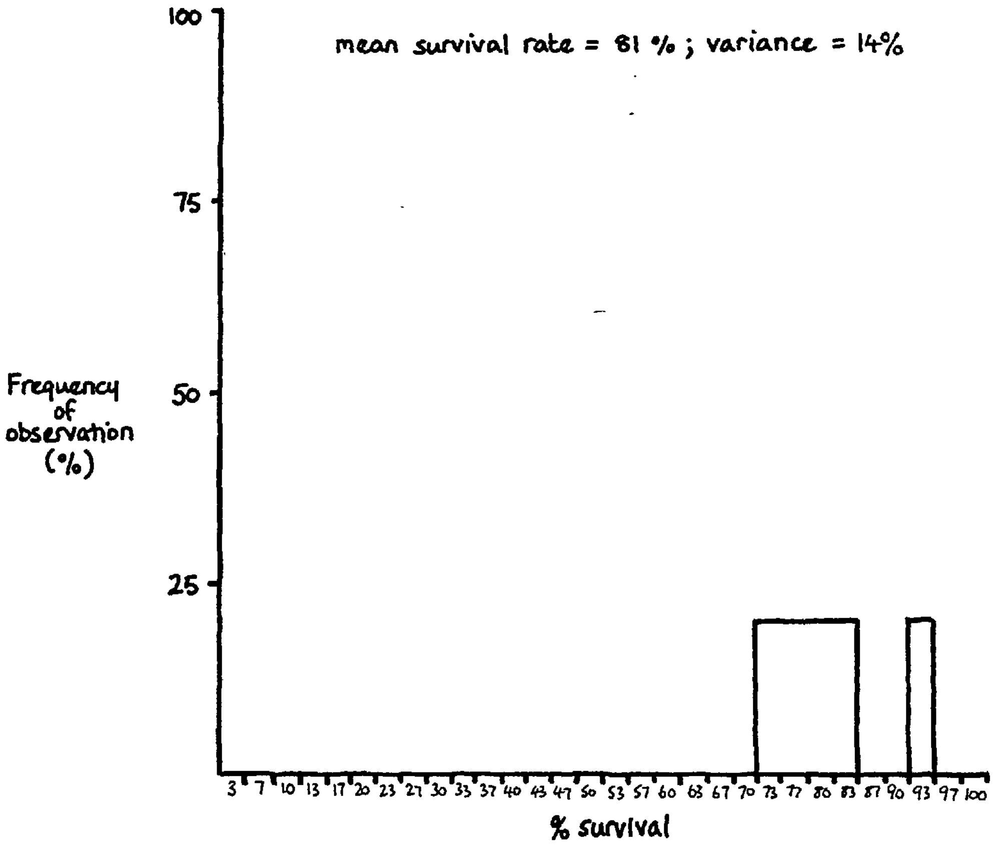
P25-450

mean survival rate = 90%; variance = 1%

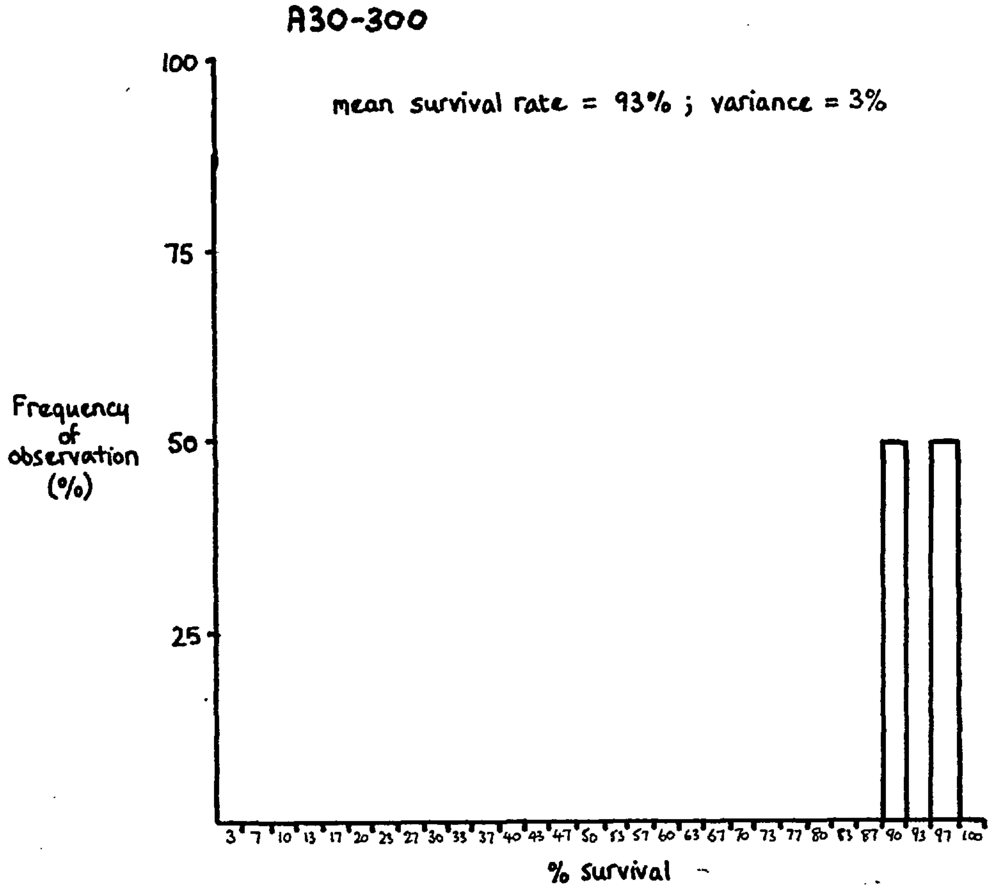


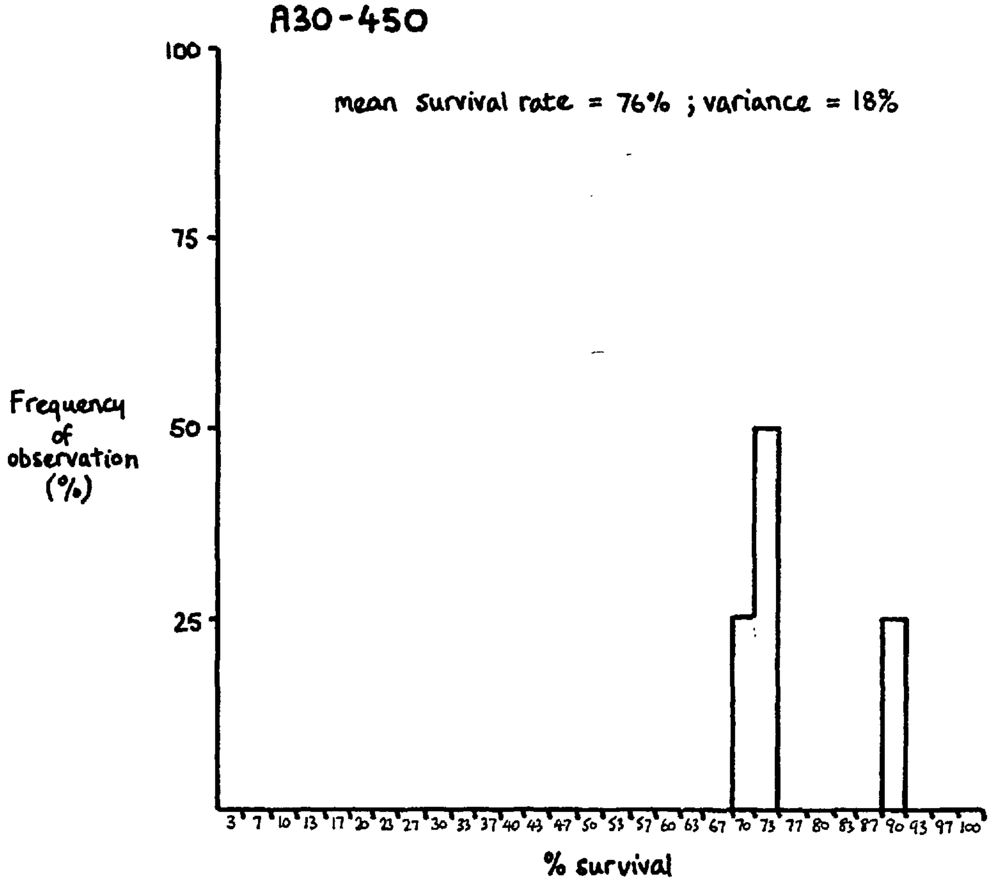


A30-20

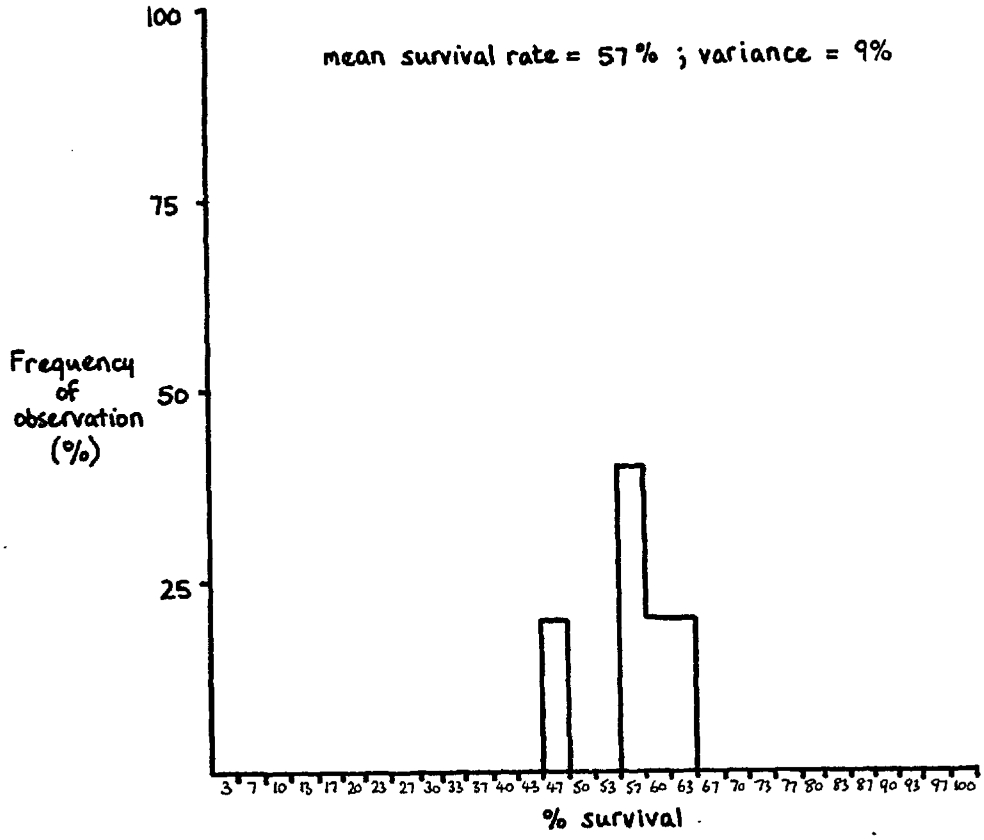


A30-150

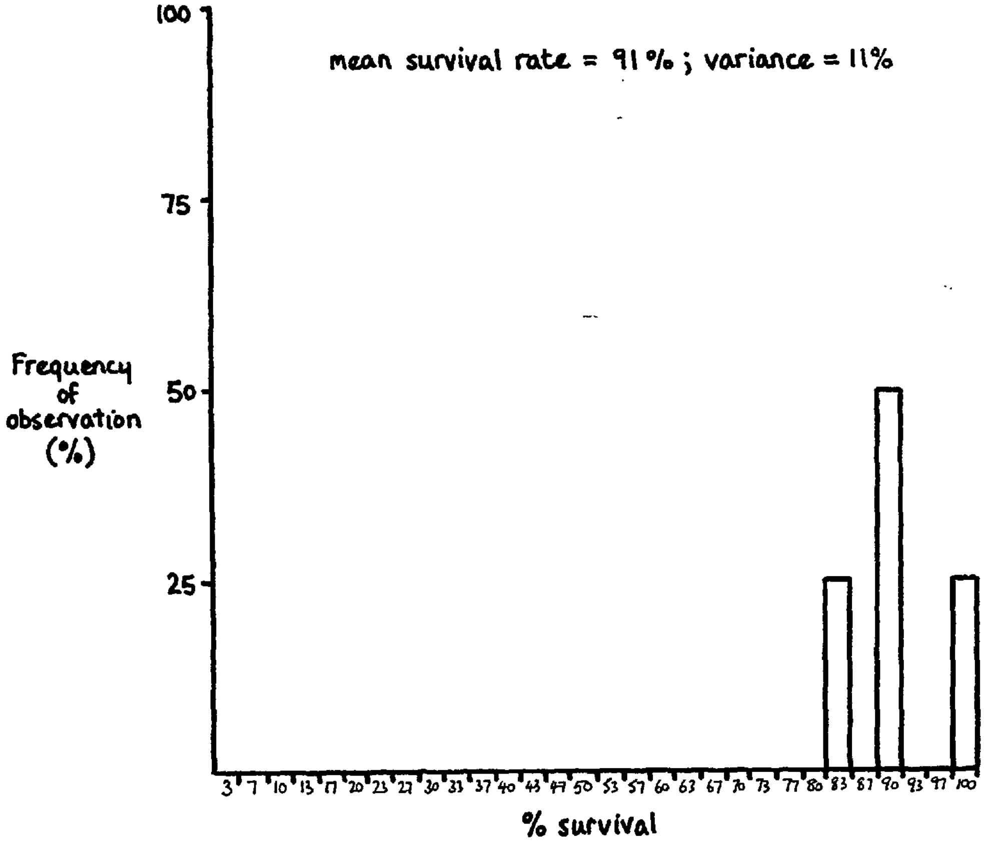

A30-300
mean survival rate = 93% ; variance = 3%
Frequency of observation (%)
100
75
50
25
3
7
10
13
17
20
23
27
30
33
37
40
43
47
50
53
57
60
63
67
70
73
77
80
83
87
90
93
97
100
% survival


A30-450
mean survival rate = 76% ; variance = 18%
Frequency of observation (%)
100
75
50
25
3
7
10
13
17
20
23
27
30
33
37
40
43
47
50
53
57
60
63
67
70
73
77
80
83
87
90
93
97
100
% survival

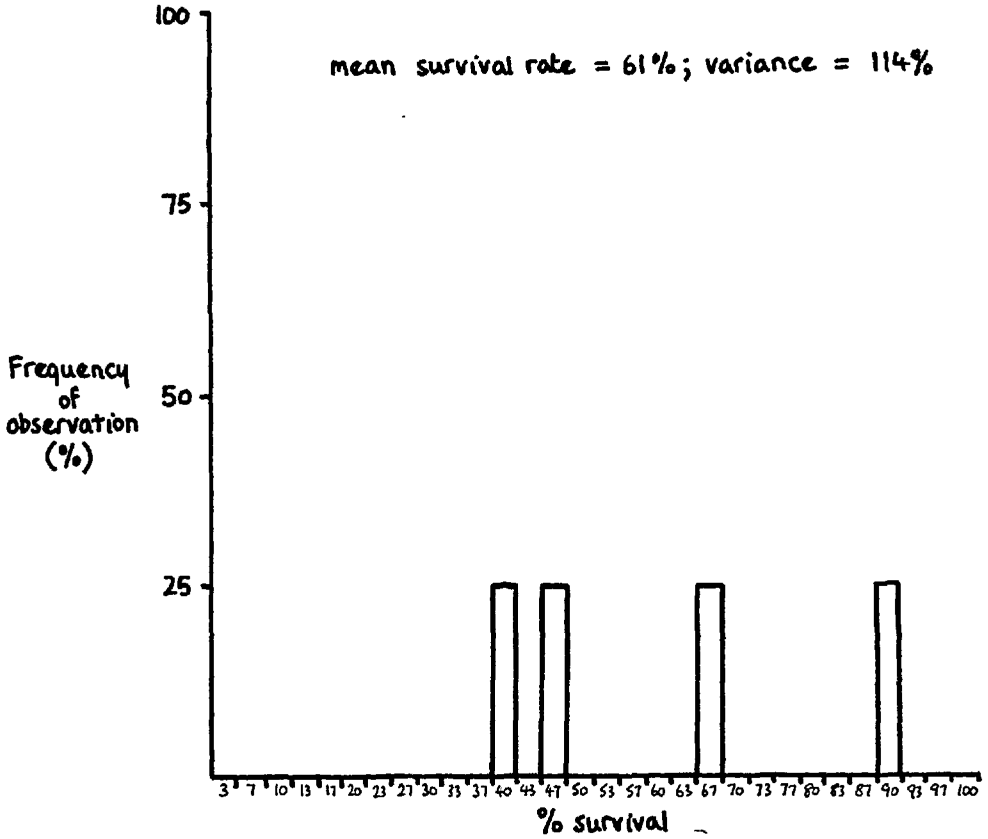
D30-20



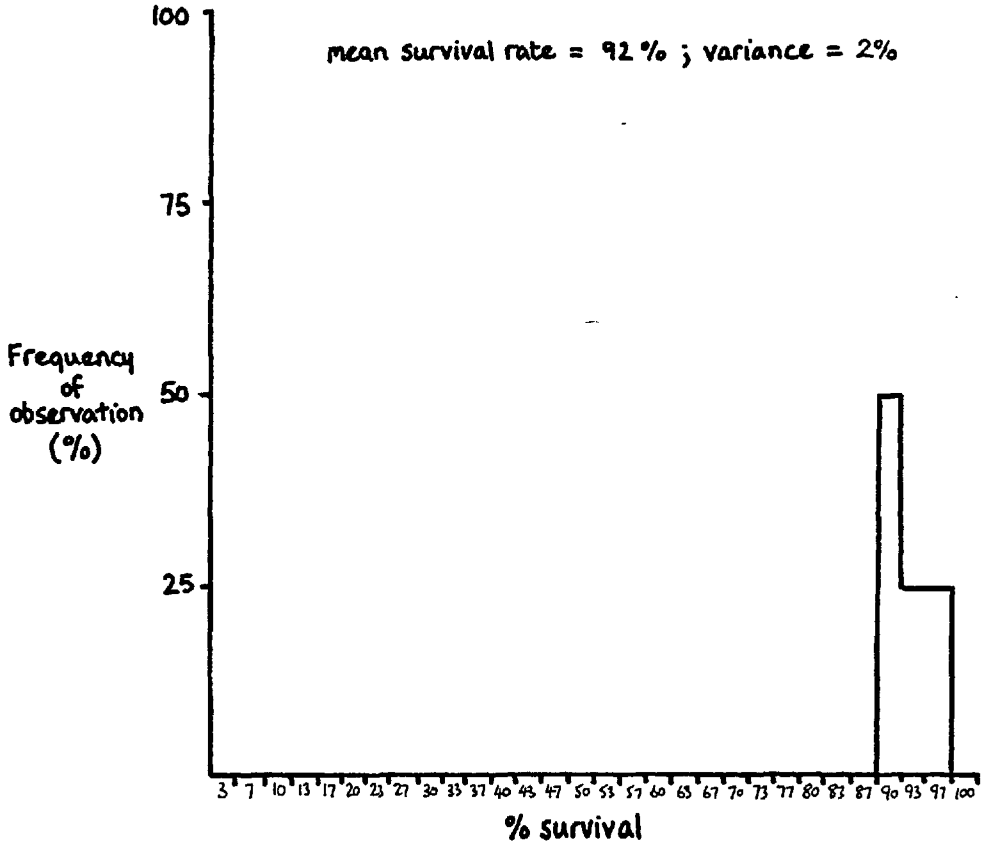
D30-150



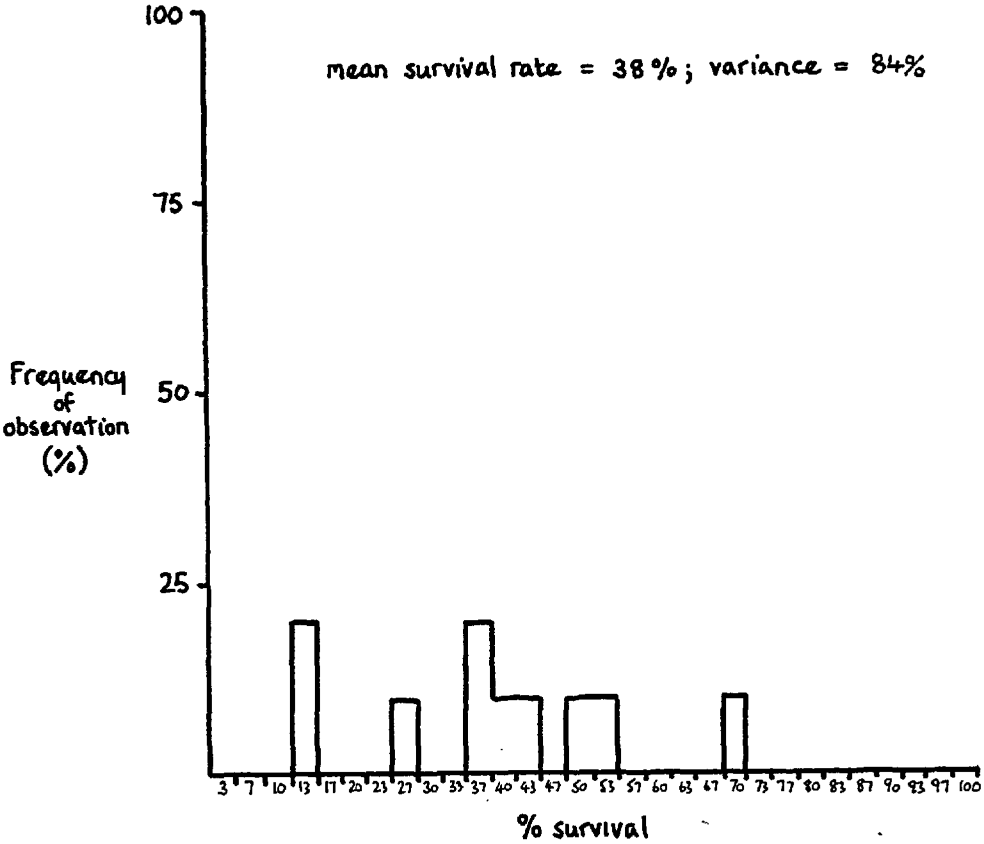
D30-300



D30-450

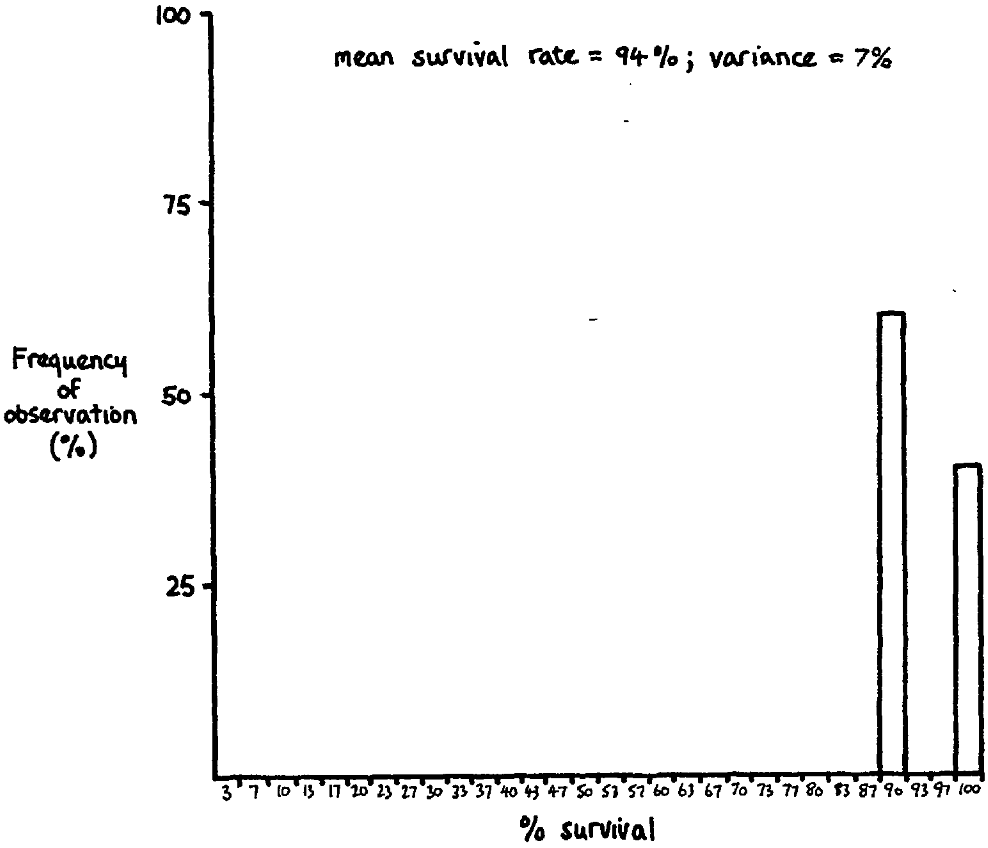


P30-20



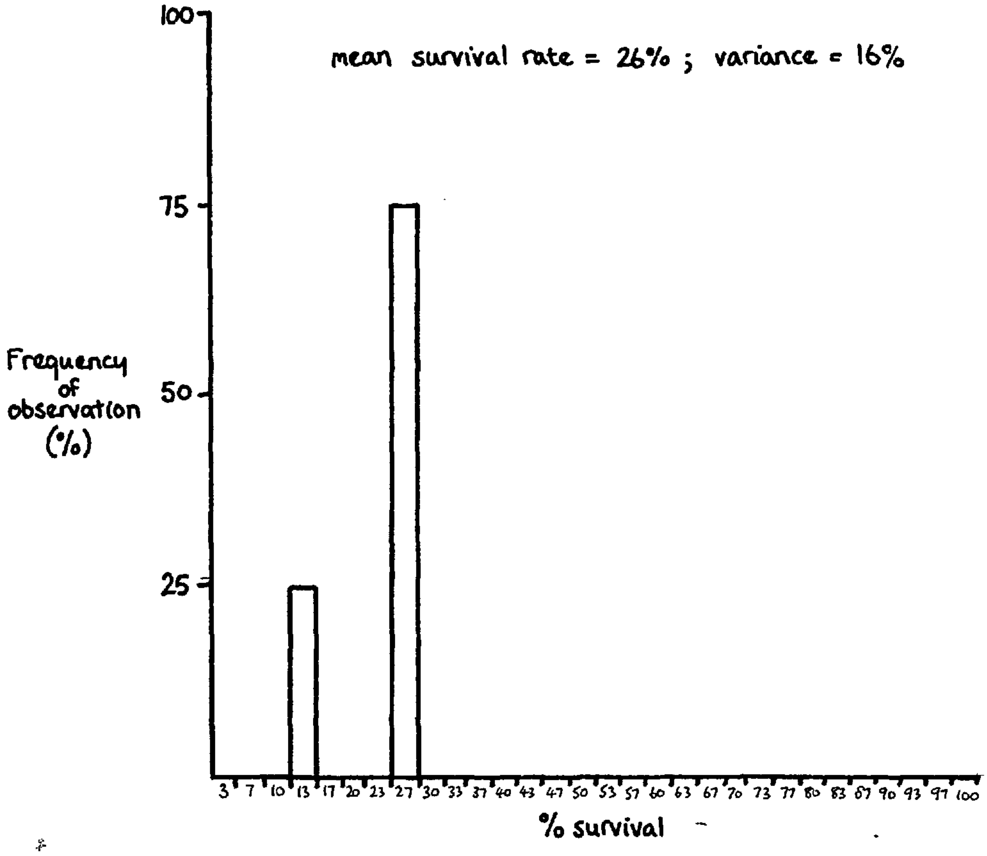
mean survival rate = 38 %; variance = 84%

P30-150



mean survival rate = 94 %; variance = 7%

P30-300



P30-450