

3.3 Predator-prey models, stochasticity

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3.3.1 Introduction

Population growth in time and space can be simulated using the techniques presented in Chapter 2, and is illustrated for polycyclic epidemics in Section 3.1. Applying these methods to predator-prey or host-parasite systems would result in population models for either predator and prey, or host and parasite. In such models, the interaction between predator and prey, or host and parasite, determines the decrease in prey numbers due to predation, and the growth in the number of predators as a result of feeding.

Predator-prey or host-parasite relations are probably the most frequently modelled phenomena in population biology. Predator-prey models, at all levels of detail and complexity, can be found in the literature. These models vary from differential equations expressing predator-prey relations in terms of a single variable, to very detailed predator-prey models at individual and population levels; incorporating much ethological and physiological information. Stochastic elements are often included. In this Section, a simple model of the population dynamics of prey and predators is presented. The behavioural and physiological factors influencing predation rate are then considered at the level of the individual. Finally, methods are introduced which can be used to calculate population changes using models of predation rates for individuals.

3.3.2 Lotka-Volterra equations for predator-prey interactions

The logistic growth equation (Section 3.1, Equation 37) can be applied in predator-prey systems to both prey and predator. The predation process is then introduced as a reduction in the growth rate of the prey population, and the increase in predator numbers is made dependent on the availability of prey. Lotka (1925) and Volterra (1931) proposed the following equations for changes in prey and predator numbers:

$$\text{for the prey, } \frac{dx}{dt} = (a - b \cdot x) \cdot x - c \cdot x \cdot y; \quad \text{Equation 58}$$

$$\text{for the predator, } \frac{dy}{dt} = -e \cdot y + d \cdot x \cdot y. \quad \text{Equation 59}$$

In these equations, the following implicit assumptions are made:

1. Densities of prey and predators can be expressed as single variables;

2. Interaction between prey and predator responds instantaneously to changes in density;
3. In the absence of predation (i.e. with $c \cdot x \cdot y = 0$), the prey population grows according to a logistic growth equation;
4. In the absence of prey, the predator population declines exponentially;
5. The rate of consumption of prey is proportional to the product of prey and predator densities;
6. The effects of predator satiation are negligible.

None of these assumptions is valid in real predator-prey systems. Nevertheless, these equations may help to provide some insight into the operation of predator-prey systems. It is possible, for example, to use them to study the behaviour of such systems at equilibrium. Here, the rates of change are zero, so conditions at equilibrium can be defined as:

for the prey: $\frac{dx}{dt} = 0$, so $a - b \cdot x - c \cdot y = 0$;

for the predator: $\frac{dy}{dt} = 0$, so $-e + d \cdot x = 0$.

Figure 35 shows the trajectory of the system when $b/c > 0$. When the densities of prey or predator, x and y respectively, are below their equilibrium, the rates of change are positive and their numbers increase (Equations 58 and 59). When prey or predator densities are above their equilibrium, the rates are negative and the numbers of x and y decrease. As a result, the numbers of x and y approach an equilibrium value at the junction of both equilibrium lines. The system moves in an anti-clockwise spiral towards stable equilibrium. If $b/c < 0$, however, the system spirals away from equilibrium, until either the predator population or both prey and predators become extinct. Apparently, the ratio between the parameter which expresses intraspecific effects of the prey population (b) and the parameter which expresses predation activity (c), determines whether stable equilibrium, or extinction of prey or predator populations, will be reached. This ratio determines the position of both equilibrium lines; the graphical representation helps to explain the consequences of the change in b/c .

Exercise 43

Plot the changes in the populations of prey, x , and predators, y , as functions of time, for $b/c < 0$, $b/c = 0$ and $b/c > 0$. Try to explain these phenomena.

To evaluate the consequences of changing various parameter values for population fluctuations of prey and predator, a simple simulation model may help.

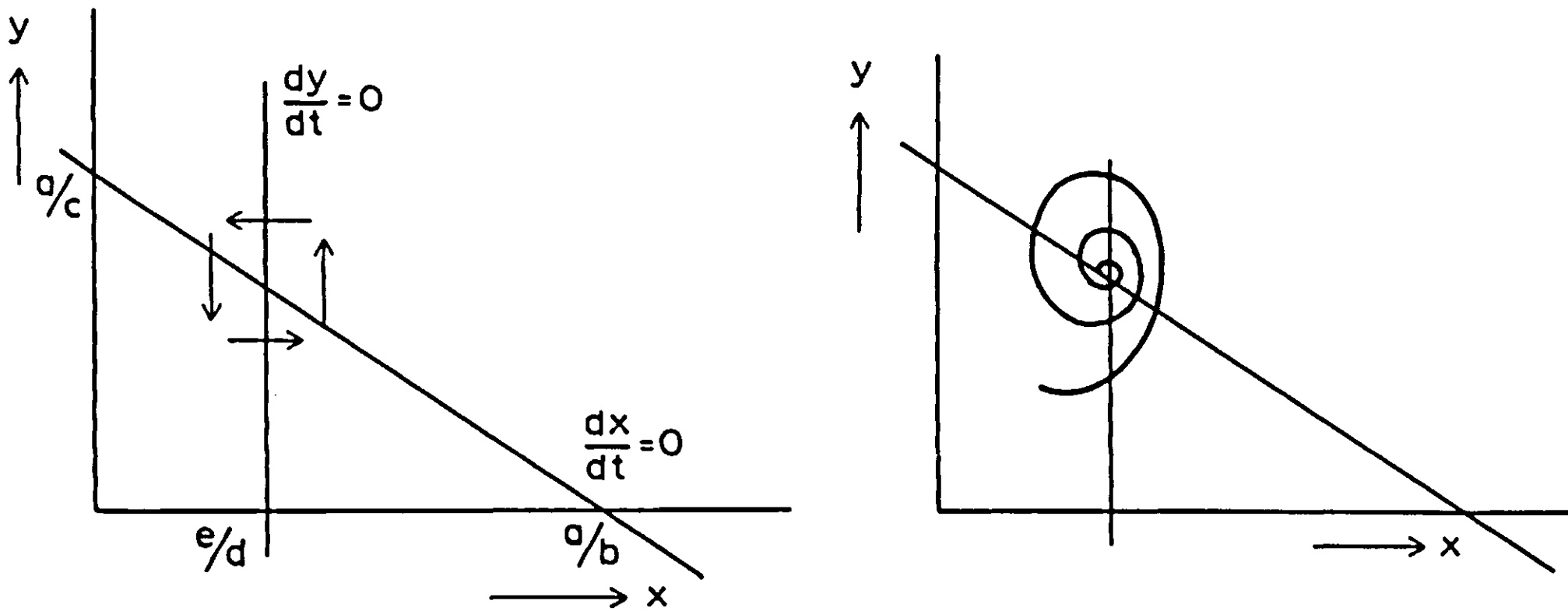


Figure 35. Equilibrium conditions for prey and predator populations; when $b/c > 0$ there will be a stable equilibrium.

This is formulated in the simulation language CSMP (see Appendix 5). Such a program reads as follows:

TITLE PREDATOR-PREY

INITIAL

INCON PREYI = 10., PREDI = 2.

PARAM A = 0.1732, B = 0.0577, C = 0.0867, D = 0.1540, E = 0.2310

DYNAMIC

PREY = INTGRL(PREYI, RPREY)

PRED = INTGRL(PREDI, RPRED)

RPREY = (A - B * PREY) * PREY - C * PREY * PRED

RPRED = -E * PRED + D * PREY * PRED

TIMER FINTIM = 50., DELT = 0.4, OUTDEL = 5.

OUTPUT PREY,PRED

METHOD RECT

END

STOP

ENDJOB

Exercise 44

Give the time coefficients of this simple system. What are the dimensions of A, B, C, D and E? Test the sensitivity of the output to changes in the values of these parameters. Explain the outcomes of the model. Run the model with various combinations of parameter values.

This simple predator-prey model may offer some insight into the functioning of predator-prey systems. It is a conceptual model, which can be used at the very beginning of the scientific approach to the problem. The addition of further detail may improve the model's realism and, ultimately, yield a comprehensive simulation model. This 'top-down' approach is different from the 'bottom-up' approach used in Section 3.1 for the epidemiological models. Here, we can proceed by modifying the model's assumptions. This increases its realism but does not imply that it is now a comprehensive explanatory model. It is still conceptual and various other ways of improvement, discussed below, are possible. For example, assumption 2, that both prey and predator react instantaneously to changes in density, is unrealistic as there is generally a considerable time delay in the numerical response of predator density to changing prey density. To take this delay into account, a separate state variable is introduced which accumulates the numbers of recently consumed prey. The state variable PREYP is emptied, and its content multiplied by the inverse of a time coefficient of, for example, 3 days, so that an exponentially weighted average of prey consumption rate is found:

$$\text{PREYP} = \text{INTGRL}(0., C * \text{PREY} * \text{PRED} - \text{PREYP}/3.)$$

This state variable, expressing predation activity, is used as the independent variable of the table from which D is read:

$$D = \text{AFGEN}(\text{DT}, \text{PREYP})$$

Thus, as far as numerical response is concerned, the model has become more realistic. Even so, the changes are arbitrary and lack experimental quantitative support.

Assumptions 5 and 6 are equally unrealistic, since a predator cannot continue to eat indefinitely. Long before its appetite is satisfied, the predator becomes more selective and tends to accept only the most attractive prey, which may then be only partially consumed. This selective behaviour, which depends on satiation, can be introduced into the Lotka-Volterra equations by inserting a state variable representing, for example, the gut content. The predation rate is then dependent on this gut content.

3.3.3 Prey preference and predator satiation

Several animal ecologists have tried to quantify the physiological conditions determining predator behaviour. Holling (1966), Fransz (1974) and many other workers quantified the influence of physiological conditions on predation activity. They determined the effect of this state variable on predator behaviour, and its consequences for the interactions between prey and predator populations.

Detailed observations have shown the presence of a functional response; as the number of prey per unit area increases, predation activity also increases until a certain plateau is reached. Holling (1966) distinguishes three basic functional responses (Figure 36). Type 1 includes a linear increase in predation rate per predator, as prey density increases, until a maximum predation rate is reached. This type of response is found only in a few filter-feeding crustaceae. As prey density increases, predation rate also increases until the filters are completely full; at that level, increases in prey density do not result in a further increase in predation rate.

Type 2 is often found in arthropod predators. Predation increases at a decreasing rate with increasing prey density, until a plateau is reached. The flattening is due either to satiation, which decreases predation activity, or to the time needed for the various components of the predation process to accumulate. Prey handling, prey consumption, and prey searching; all require time, which becomes a limiting factor at higher prey densities. Thus, time limitation and satiation together limit the predation rate. The predator gradually reaches satiation and, as a result, the predation rate steadily approaches its maximum value. The type 2 functional response can be described with a hyperbolic function, or may be tabulated with an Arbitrary Function GENERator (in CSMP: AFGEN).

Exercise 45

Introduce the type 2 functional response into the Lotka-Volterra equations. Adapt the simulation program and run it with various self-chosen values for the parameters.

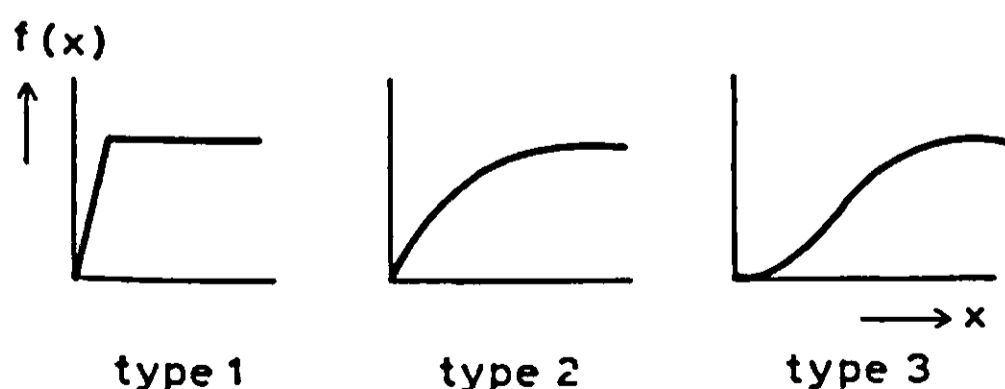


Figure 36. Three functional responses of predation rate with regard to prey density. (Source: Holling, 1966).

The type 3 functional response is often found in vertebrate predators. It differs from the type 2 response in that the predation rate at low prey densities, shows a more than proportional increase with prey density. This could be due to several reasons. First, if the prey occurs in clusters or patches, the predator may leave low-density patches, but remain for a longer time in dense prey clusters (e.g. the parasitoid, *Aphelinus thomsoni* (Collins et al., 1981)). Second, predators may 'switch' from one habitat type to another, depending on the densities of prey available (e.g., the predatory groundbeetle, *Pterostychus coerulescens* (Mols, 1989)). Finally, some predators may develop a 'search image' for a particular prey species if this species is abundant (e.g. the great tit, *Parus major* searching for caterpillars or aphids (van Balen, 1973)).

At high prey densities, satiation or handling time again limit the predation rate. Type 3 is thus sigmoid (Figure 36). Other factors, which can be important in determining the predation rate, include mutual interference between searching predators (Hassell & May, 1973) and the spatial distribution of prey and predators (see Subsection 3.2.4).

In addition to the effects of predation on prey mortality rate, the second main component of the predator-prey interaction (at the population level) is the effect of predation on the predators' rate of increase. In many insect parasitoids, each act of 'predation' (i.e. oviposition in a host) results in the production of a new 'predator' (parasitoid). In true predators, however, this relation is less direct; for example, a predator's feeding rate may determine either its rate of reproduction or its probability of surviving to maturity (Dixon, 1959).

Although the likely effects of these relations have been widely studied using general analytical models (Hassell, 1978), the complexity of real systems often means that numerical models must be used to study particular examples.

There is another reason for developing simulation models. During the predation process, some stochastic phenomena play a role; e.g. a certain probability for predator-prey encounters (which are discrete events) occurring within a limited time period. The effects of these stochastic elements on the predation process, and their consequences for the predation rate, can be evaluated using a numerical simulation model.

3.3.4 Stochastic and deterministic models

Many phenomena in ecology are stochastic: the appearance of a spore from a pustule, its arrival at a particular place at a particular time, the sampling of a population, or the killing of a prey by a predator. All these events occur with a certain probability. However, it is not the event as such that is important (except for the individual concerned), but its consequences for the overall rates. Thus sporulation rate, landing rate, predation rate etc., must be examined. Simulation models of the predation process are used to compute the expected number of prey killed, over time. The expected values are the means of many simulation experiments with individual predators. As the interval between the

captures is a state variable with a certain probability distribution, each experiment is a stochastic process with a variable number of captures in a well-defined time interval. The expected number of captures is estimated by dividing the total number of catches in a collection of experiments by the number of experiments. There may be important differences between the results of deterministic and stochastic models. In deterministic models, computations are based on the expected values of the parameters. However, this may introduce errors, since the mean of the values computed, using unprocessed values of the components, does not necessarily equal the value calculated using the expected values of the components: $\varepsilon(f(x)) \neq f(\varepsilon(x))$. In addition, stochastic models compute both the mean and the variance. Thus, generally, there are two reasons for using stochastic models:

1. Curvilinear relations between stochastic characteristics and rate variables mean that the use of mean values introduces a significant bias into the results;
2. Stochastic models can provide estimates of the variation in the system's behaviour. Sampling errors, for example, may have important consequences in interpreting the results.

To illustrate the consequences of deterministic and stochastic simulation of the predation process, simple deterministic and stochastic models of the predation process will be described and their results compared.

A computer model Assume that P is the number of prey killed by a predator in a certain time. The predation rate, dP/dt , depends on the predator's velocity, V , which has a uniform probability distribution between 0 and 1, so $0 \leq V \leq 1$.

If the rate of predation, dP/dt , is proportional to V , then $dP/dt = cV$, where c is a parameter whose value expresses predation efficiency; here $c = 10$.

A deterministic simulation of predation during the course of a day can be written in CSMP as:

TITLE DETERMINISTIC PREDATION

INITIAL

INCON PI = 0.0

PARAM V = 0.5, C = 10.0

DYNAMIC

P = INTGRL(PI, C * V)

TIMER FINTIM = 24., DELT = 1., OUTDEL = 1.

METHOD RECT

OUTPUT P

END

STOP

ENDJOB

Alternatively, this process can be modelled stochastically (with the velocity changing at random every hour) using the following program:

```
TITLE STOCHASTIC PREDATION
```

```
INITIAL
```

```
FIXED M
```

```
M = 315
```

```
INCON PI = 0.
```

```
PARAM C = 10.0
```

```
DYNAMIC
```

```
P = INTGRL(PI, C * V)
```

```
V = RNDGEN(M)
```

```
NOSORT
```

```
M = M + 2
```

```
TIMER FINTIM = 24.0, DELT = 1.0, OUTDEL = 1.
```

```
METHOD RECT
```

```
OUTPUT P
```

The statement $V = \text{RNDGEN}(M)$ is a CSMP function, which draws (each time interval of integration, DELT) a number at random from a standard uniform probability distribution between 0 and 1. M is an arbitrary odd integer chosen to initialize the random number generator. PI is the initial value of P , and C is a constant. The program uses time steps of 1 hour and continues the calculations for one day (24 hours). The expected value of P (ϵP) is the mean result of many replicates of the experiment (in this case 1000). The commands to repeat the performance 1000 times and to calculate the expectation value are given below in FORTRAN.

```
TERMINAL
```

```
PARAM NREP = 1000.
```

```
INCON SUMP = 0., COUNT = 0.
```

```
    SUMP = SUMP + P
```

```
    COUNT = COUNT + 1.
```

```
    IF (COUNT.GE.NREP) GOTO 1
```

```
    CALL RERUN
```

```
    GO TO 2
```

```
1 EP = SUMP/COUNT
```

```
    WRITE (6,100) EP
```

```
100 FORMAT (H1, F10.4)
```

```
    2 CONTINUE
```

```
END
```

```
STOP
```

```
ENDJOB
```


This TERMINAL section is performed once per run, when TIME reaches the value FINTIM.

With a uniform probability distribution, an analytical solution of $\varepsilon(P)$ is possible because P is the sum of a number of stochastic variables:

$$\varepsilon(P) = PI + 24 \cdot \varepsilon(cV)$$

$$\varepsilon(cV) = \int_0^1 cV dV = \frac{1}{2} \cdot cV^2 \Big|_0^1 = 5$$

$$\varepsilon(P) = 0 + 24 \cdot 5 = 120$$

The deterministic computation of this model is found by accumulating the expected values during the observation period.

$$P = PI + 24 \cdot c \cdot \varepsilon(V)$$

$$\varepsilon(V) = 0.5$$

$$P = 0 + 24 \cdot 10 \cdot 0.5 = 120$$

Thus, with dP/dt proportional to V , the deterministic model (using \bar{V}) yields the same result as the stochastic version, since $\varepsilon(f(x)) = f(\varepsilon(x))$. If the relation between dP/dt and V is non-linear, however, the deterministic model introduces important errors.

Consider the following simple example. We wish to determine the mean rate of predation by a predator whose velocity varies at random as assumed above. The individual predation rate is

$$dP/dt = c \cdot V^{\frac{1}{2}}$$

and V has a uniform distribution between 0 and 1. A deterministic model, using the population's mean V gives

$$P = PI + 24 \cdot c \cdot (\varepsilon(V))^{\frac{1}{2}}$$

where $\varepsilon(V) = 0.5$, so

$$P = 0 + 240 \cdot (0.5)^{\frac{1}{2}} = 169.7$$

A stochastic model, however, which allows for variation in V , yields:

$$P = PI + 24 \cdot c \cdot \varepsilon(V^{\frac{1}{2}})$$

$$\varepsilon(V^{\frac{1}{2}}) = \int_0^1 V^{\frac{1}{2}} dV = \frac{2}{3} V^{3/2} \Big|_0^1 = 0.67,$$

so $P = 0 + 240 \cdot 0.67 = 160.8$

The use of $\varepsilon(V)$ in the deterministic model, thus results in an overestimation of the total predation. This is because the curvilinear relation, between the predation rate and the velocity of the individual predators, means that

$$d(\varepsilon(P))/dt \neq c \cdot (\varepsilon(V))^{\frac{1}{2}}$$

Exercise 46

Use a deterministic model and a stochastic model to calculate the number of prey killed per day when the relationship between the number of prey killed per hour and the predator's velocity is described by $dP/dt = cV^{3/2}$; c equals 8 and V has a standard uniform probability distribution. Make these calculations both numerically and analytically.

The case of the stochastic simulation is described above. When the parameters are dependent upon environmental factors or a relation, such as the dependency of predation rate on velocity, more complicated simulation models are needed. However, the basic structure remains the same.

Basically, the process of sampling from a population, needed in many population studies, is the same. This is explained by de Wit & Goudriaan (1978) for a population model of protozoa growing on a bacterial culture.

3.3.5 *Modelling at the population level*

The model STOCHASTIC PREDATION simulates prey mortality caused by a predator moving with a velocity that changes unpredictably during the 24 hour foraging period. When the relation between V and dP/dt is non-linear, models that fail to account for the variation in V yield erroneous results.

Similar problems are encountered in modelling changes at the population level. For example, the effects of a population of predators cannot be accurately modelled by using the population mean of the search parameters (velocity, handling time, etc.), unless these parameters are the same for all individual predators; in which case, stochastic models can be used to simulate the consequences of individual variation.

Areas where true stochasticity is important at the population level include, for example, mortality in small populations and the effects of sampling. For examples and discussion of these areas see Pielou (1974) and de Wit & Goudriaan (1978). An example based on the predation process above: in the stochastic model for a population of individuals the assumption is made that velocity has a well-defined probability distribution. The average velocity is:

$$V = \sum_{i=1}^n V_i/n_i$$

where V_i is the velocity of individuals in one predation experiment. When V_i is constant, then a deterministic model could be used. However, this is virtually never true; therefore, calculations using various individual velocities should be done. The mean and variance may be computed because the rates in a single predation experiment have a uniform probability distribution. Therefore, the mean velocity is computed as: $\varepsilon(V_i) = 0.5$, and its variance computed as:

$$\text{var}(V_i) = \int_0^1 V_i^2 dV_i - \left(\int_0^1 V_i dV_i \right)^2 = 1/3 V_i^3 \Big|_0^1 - (1/2 \cdot V_i^2 \Big|_0^1)^2 = 1/3 - 1/4 = 1/12$$

In a population of n individuals the mean velocity is thus:

$$\varepsilon(V) = n/n \cdot 0.5 = 0.5$$

and its variance is computed as

$$\text{var}(V) = n/n^2 \cdot 1/12 = 1/(12n)$$

As with the 'individual' model, the results of this 'population' model differ from the deterministic model of an individual predation process because of the curvilinear relationship between stochastic variables and the state or rate variables. Also, the variance of the model is different.

The results in this section serve to emphasize an important problem in the use of experimental data on individuals to construct models to simulate the dynamics of populations. Unless features of population dynamics depend linearly on components of individuals' behaviour (e.g. velocity), the use of the mean behaviour may introduce significant errors into simulations at the population level. Therefore, where rate variables depend non-linearly on variable or stochastic state (or rate) variables, deterministic models are often inadequate.

3.3.6 *Other methods*

The model STOCHASTIC PREDATION illustrates the use of Monte Carlo analysis to obtain results at the population level using information about individual predators. Effectively, it 'samples' 1000 predators at random, and uses each predator in a simulated experiment. In principle, therefore, it solves the problem of stochasticity in the same way as the model of dispersal, described in Subsection 3.2.3 (Sabelis, 1981).

Repeated use of stochastic models, however, is time-consuming and expensive, so other methods, such as the queuing approach of Curry & De Michele (1977) and the compound simulation of Fransz (1974), have been developed to mimic stochasticity. The queuing technique requires only a limited amount of computer time. Basically, this method may be compared with calculating the waiting time of a patient in the dentist's waiting room. The patient may enter the waiting room (be encountered by a predator) with a certain expectance of service (being eaten).

Compound simulation is an intermediate approach between the stochastic model, which gives correct results but requires a lot of computing time, and the deterministic model, which requires less computer time but gives erroneous results. In this intermediate approach, deterministic simulation is applied to classes of the stochastic variables. The classes in this method of compound simulation, are chosen in such a way that within the classes the relation between velocity and predation rate is approximately linear. The number of classes depends on the balance required between accuracy and computer time. The calculation, for each class of individuals, is made at each time step of integration, after which the contents of the classes are updated and another computation starts with the redistributed classes of individuals. In this way, only one simulation needs to be carried out for each set of conditions, instead of 1000 runs, as required for the Monte Carlo method. Replication of all computations is omitted, and replaced by a complicated, but not time-consuming, system of book-keeping of predators, distributed each time interval among classes of individuals.

Sabelis (1981) described the application of Fransz's compound simulation, Monte Carlo techniques and queuing techniques to the predation process of mites. He showed that all three methods produced results that were within the confidence intervals of the measurements. The queuing techniques required the least computing time, whereas the deterministic model gave erroneous results. Although these mimicking procedures have contributed a great deal to the accurate simulation of predation rates, they are still too complicated to be applied to population models of prey and predators.

3.3.7 *Equilibria*

Simulation of individual predators shows that if prey density is kept roughly constant, the predator population reaches equilibrium. In that situation, the physiological condition of the predator oscillates, with low amplitudes, around a constant level. Changes in this equilibrium level are slow in comparison with changes in population composition. The time coefficient of this change is thus large in comparison with those for other changes in the system, such as development and growth. This equilibrium level is determined by prey and predator densities, and by temperature. At equilibrium, velocity and other variables determining predation rate also vary slightly, relative to the system as a whole. This characteristic of many predator-prey systems permits the computation of the predation rate at each level of the motivation state or physiological condition of the predator, using the expected values of the component variables. Use of this approach in population models for predator-prey systems will be illustrated for an acarine system in Section 3.4.