# 5

# Modelling Population Dynamics

**CHAPTER OUTLINE**

## 5.1. Introduction

This chapter covers population dynamic models where state variables are the number or biomass of individuals or species. The growth of one population is used — see Sections 5.2 and 5.3 — to present the basic concepts. Afterward, the interactions between two or more populations are presented. The famous Lotka-Volterra model and several more realistic predator-prey and parasitism models, are shown. Age distribution is introduced and computations with matrix models are illustrated, including the relations to biological growth. Finally, the last three sections illustrate the use of fishery/harvest models, metapopulation dynamics, and infection models.

## 5.2. Basic Concepts

This chapter deals with biodemographic models, which are population models characterized by numbers of individuals or kilograms of biomass of individuals or species as typical units for state variables. As early as the

1920s, Lotka and Volterra developed the first population model, which is still widely used (Lotka, 1956; Volterra, 1926). So many population models have been developed, tested, and analyzed since that it would not be possible to give a comprehensive review of these models here. This chapter mainly focuses on models of age distribution, growth, and species interactions. Only deterministic models will be mentioned. Those interested in stochastic models can refer to Pielou (1966, 1977), which gives a very comprehensive treatment of this type of population dynamic model.

A *population* is defined as a collective group of organisms of the same species. Each population has several characteristic properties, such as population density (population size relative to available space), natality (birth rate), mortality (death rate), age distribution, dispersion, growth forms, and so forth.

A population changes over time, and we are interested in its size and dynamics as it grows or shrinks. If N represents the number of organisms and t the time, then $dN/dt$ = the rate of change in the number of organisms per unit time at a particular instant (t), and $dN/(Ndt)$ = the rate of change in the number of organisms per unit time per individual at a particular instant (t). If the population is plotted against time, then a straight line tangential to the curve at any point represents the growth rate.

*Natality* is the number of new individuals appearing per unit of time and per unit of population.

We have to distinguish between absolute natality and relative natality, denoted B and $B_r$, respectively:

$$B = \Delta N/\Delta t \tag{5.1}$$

$$B_r = B/N \tag{5.2}$$

where $\triangle N$ = production of new individuals in the population.

*Mortality* refers to the death of individuals in the population. The absolute mortality rate, M, is defined as:

$$M = \Delta M/\Delta t \tag{5.3}$$

where $\triangle M$ = number of organisms in the population that died during the time interval, $\triangle t$, and the relative mortality rate, $M_s$, is defined as:

$$M_s = M/N \tag{5.4}$$

## 5.3. Growth Models in Population Dynamics

The simplest growth models consider only one population. Its interactions with other populations are taken into consideration by the specific growth rate and the mortality, which might be dependent on the magnitude of the considered population but independent of other populations. In other words, we consider only one population as a state variable. The simplest growth model assumes unlimited resources and exponential population growth. A simple differential equation can be applied:

$$dN/dt = B_s N - M_s N = rN \tag{5.5}$$

where $B_s$ is the instantaneous birth rate per individual, $M_s$ is the instantaneous death rate, $r = B_s - M_s$, N is population density, and t is time. Equation (5.5) represents first-order kinetics (see exponential growth in Chapter 2, Section 2.3, equation 2.2a). If r is constant, then we get after integration:

$$N_t = N_0 e^{rt}, \tag{5.6}$$

where $N_t$ is the population density at time t and $N_0$ is the population density at time 0. A logarithmic presentation of Eq. (5.6) is given in Figure 5.1.

The net reproductive rate, $R_0$, is defined as the average number of age class zero offspring produced by an average newborn organism during its entire lifetime. Survivorship, $l_x$, is the fraction surviving at age x. It is the probability that an average newborn will survive to that age, designated x. The number of offspring produced by an average
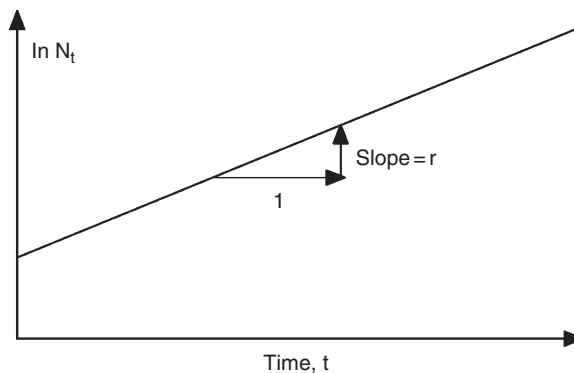


**FIGURE 5.1** In $N_t$ is plotted versus time, t.

organism of age x during the age period is designated $m_x$. This is termed *fecundity,* while the product of $l_x$ and $m_x$ is called the *realized fecundity.* According to its definition, $R_0$ can be found as:

$$R_0 = \int_0^\infty l_x m_x dx \qquad (5.7)$$

A curve that shows $l_x$ as function of age is called a survivorship curve. Such curves differ significantly for various species, as illustrated in Figure 5.2.

The so-called *intrinsic rate of natural increase*, **r,** is like $l_x$ and $m_x$, dependent on the age distribution, and it is only constant when the age distribution is stable. When $R_o$ is as high as possible, that is, under optimal conditions and with a stable age distribution, the maximal rate of natural increase is realized and designated $r_{max}$. Among various animals it ranges over several orders of magnitude (Table 5.1).

Exponential growth is a simplification, which is only valid over a certain time interval. Sooner or later every population must encounter the limitation of food, water, air, or space, as the world is finite. To account for this we introduce the concept of *density dependence*; that is, vital rates, like r, depend on population size, N (while we now ignore
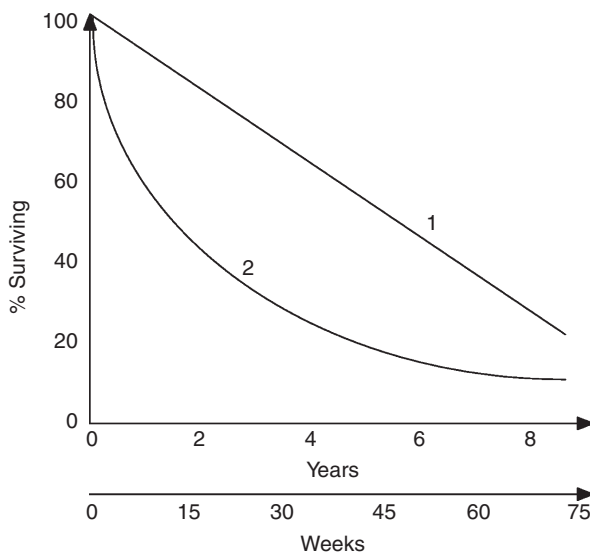


**FIGURE 5.2** Survivorships of (1) the lizard Uta (the lower x axis) and (2) the lizard Xantusia (the upper x axis). *(After Tinkle, 1967).*

**Table 5.1**   Estimated Maximal Instantaneous Rate of Increase ($r_{max}$, per Capita per Day) and Mean Generation Times (in Days) for a Variety of Organisms

| Taxon | Species | $r_{max}$ | Generation Time |
|---|---|---|---|
| Bacterium | *Escherichia coli* | ca. 60.0 | 0.014 |
| Algae | *Scenedesmus* | 1.5 | 0.3 |
| Protozoa | *Paramecium aurelia* | 1.24 | 0.33–0.50 |
| Protozoa | *Paramecium caudatum* | 0.94 | 0.10–0.50 |
| Zooplankton | *Daphnia pulex* | 0.25 | 0.8– 2.5 |
| Insect | *Tribolium confusum* | 0.120 | ca. 80 |
| Insect | *Calandra oryzae* | 0.110(0.09–.011) | 58 |
| Insect | *Rhizopertha Dominica* | 0.085(0.07–0.10) | ca. 100 |
| Insect | *Ptinus tectus* | 0.057 | 102 |
| Insect | *Gibbium psylloides* | 0.034 | 129 |
| Insect | *Trigonogenius globules* | 0.032 | 119 |
| Insect | *Stethomezium squamosum* | 0.025 | 147 |
| Insect | *Mezium affine* | 0.022 | 183 |
| Insect | *Ptinus fur* | 0.014 | 179 |
| Insect | *Eurostus hilleri* | 0.010 | 110 |
| Insect | *Ptinus sexpunctatus* | 0.006 | 215 |
| Insect | *Niptus hololeucus* | 0.006 | 154 |
| Octopus | — | 0.01 | 150 |
| Mammal | *Rattus norwegicus* | 0.015 | 150 |
| Mammal | *Microtus aggrestis* | 0.013 | 171 |
| Mammal | *Canis domesticus* | 0.009 | ca. 1000 |
| Insect | *Magicicada septendecim* | 0.001 | 6050 |
| Mammal | *Homosapiens* | 0.0003 | ca. 7000 |

differences caused by age). Let the *carrying capacity,* K, be defined as the density of organisms at which r is zero. At zero density, $R_o$ is maximal and r becomes $r_{max}$. The logistic growth equation has already been mentioned in Section 2.3, equation 2.4. The application of the logistic growth equation requires three assumptions:

**1.** All individuals are equivalent.
**2.** K and r are immutable constants independent of time, age distribution, and so forth.
**3.** There is no time lag in the response of the actual rate of increase per individual to changes in N.

All three assumptions are unrealistic and can be strongly criticized. Nevertheless, several population phenomena can be nicely illustrated by using the logistic growth equation.

## Illustration 5.1

An algal culture shows a carrying capacity due to a self-shading effect. In spite of "unlimited" nutrients, the maximum concentration of algae in a chemostat experiment was measured to be 120 $g/m^3$. At time 0, 0.1 $g/m^3$ of algae was introduced and 2 days after a concentration of 1 $g/m^3$ was observed. Set up a logistic growth equation for these observations.

### Solution

During the first 5 days, we are far from the carrying capacity and we have with good approximations:

$$\ln 10 = r_{max} 2$$

$$r_{max} = 1.2 \text{day}^{-1}$$

and since the carrying capacity is 120 $g/m^3$ (C = algae concentration), we have:

$$dC/dt = 1.2C(120 - C/120)$$

Integration and use of the initial condition C(0) = 0.1 yield

$$C = 120/(1 + e^{(a-1.2t)})$$

where

$$a = \ln((120 - 0.1)/0.1) = 7.09.$$

This simple situation in which there is a linear increase in the environmental resistance with density, that is, logistic growth is valid, seems to hold well only for organisms that have a very simple life history.

In populations of higher plants and animals that have more complicated life histories, there is likely to be a delayed response. Wangersky and Cunningham (1956, 1957) have suggested a modification of the logistic equation to include two kinds of time lag: (1) the time needed for an organism to start increasing, when conditions are favorable, and (2) the time required for organisms to react to unfavorable crowding by altering birth and death rates. If these time lags are $t - t_1$ and $t - t_2$, respectively, then we get:

$$dN/dt = rN_{t-t_1}(K - N_{t-t_2})/K \qquad (5.8)$$

Population density tends to fluctuate as a result of seasonal changes in environmental factors or due to factors within the populations themselves (so-called intrinsic factors). We will not go into details here, but will just mention that the growth coefficient is often temperature dependent and since temperature shows seasonal fluctuations, it is possible to explain some seasonal population fluctuations in density in that way.

## 5.4. Interaction Between Populations

The growth models presented in Section 5.3 might have a constant influence from other populations reflected in the selection of parameters. It is, however, unrealistic to assume that interactions between populations are constant. A more realistic model must therefore contain the interacting populations (species) as state variables. For example, in the case of two competing populations, we can modify the logistic model and use the following equations, often termed the Lotka-Volterra equation:

$$dN_1/dt = r_1 N_1 (K_1 - N_1 - \alpha_{12} N_2)/K_1 \qquad (5.9)$$

$$dN_2/dt = r_2 N_2 (K_2 - N_2 - \alpha_{21} N_1)/K_2 \qquad (5.10)$$

where $\alpha_{12}$ and $\alpha_{21}$ are competition coefficients. $K_1$ and $K_2$ are carrying capacities for species 1 and 2. $N_1$ and $N_2$ are numbers of species 1 and 2, while $r_1$ and $r_2$ are the corresponding maximum intrinsic rate of natural increase.

The steady-state situation is found by setting Eqs. (5.9) and (5.10) equal to zero. We get:

$$N_1 = K_1 - \alpha_{12}.N_2$$
$$N_2 = K_2 - \alpha_{21}.N_1, \tag{5.11}$$

These two linear equations are plotted in Figure 5.3 giving dN/dt isoclines for each species. Below the isoclines, populations will increase, above them, they decrease. So, four cases result, as illustrated in Figure 5.3 and summarized in Table 5.2.

Lotka-Volterra also wrote a simple pair of *predation equations*:

$$\frac{dN_1}{dt} = r_1.N_1 - p_1 N_1.N_2 \tag{5.12}$$

$$\frac{dN_2}{dt} = p_2.N_1.N_2 - d_2.N_2 \tag{5.13}$$
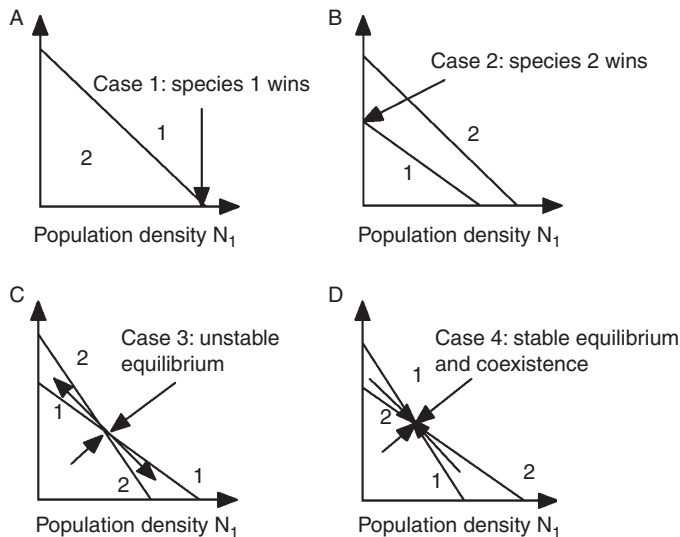


FIGURE 5.3 The four cases of Lotka-Volterra competition equations; see Table 5.2.

**Table 5.2** Summary of the Four Possible Cases of Lotka-Volterra Competition Equations

| | Species 1 Can Contain Species 2 ($K_2/\alpha_{21} < K_I$) | Species 2 Cannot Contain Species 2 ($K_2/\alpha_{21} < K_I$) |
|---|---|---|
| ($K_1/\alpha_{12} < K_2$) | Either species may win (Case 3) | Species 2 always wins (Case 2) |
| ($K_1/\alpha_{12} > K_2$) | Species 1 always wins (Case 1) | Stable coexistence (Case 4) |

where $N_1$ is prey population density, $N_2$ is predator population density, $r_1$ is the intrinsic (maximal) rate of increase of the prey population (per head), $d_2$ is the mortality of the predator (per head), and $p_1$ and $p_2$ are predation coefficients. Each population is limited by the other and in absence of the predator, the prey population increases exponentially. By setting the two right-hand sides equal to zero, we find, respectively,

$$N_2 = \frac{r_1}{p_1} \tag{5.14}$$

$$N_1 = \frac{d_2}{p_2} \tag{5.15}$$

Thus each isocline of the two species corresponds to a particular density of the other species. Below the threshold prey density, the predator population will always decrease, whereas above that threshold, it will increase. Similarly, the prey population will increase below a particular predator density but decrease above it (Figure 5.4). A joint equilibrium exists where the two isoclines cross, but prey and predator densities do not generally converge to this point; instead any given pair of initial densities results in oscillations of a certain magnitude. The amplitude of fluctuations depends on the initial conditions. These equations are unrealistic since most populations encounter either self-regulations, density-dependent feedbacks, or both. The addition of a simple self-damping term to the prey equation results either in a rapid approach to equilibrium or in damped oscillations. Perhaps a more realistic pair of simple equations for modelling the *prey-predator relationship* is
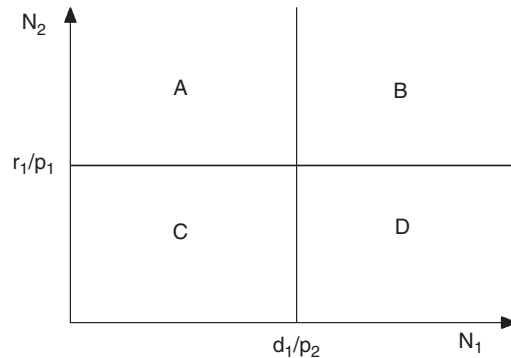


**FIGURE 5.4** Prey-predator isoclines for Lotka-Volterra prey-predator equation. (A) both species decrease; (B) predators increase, prey decrease; (C) prey increase, predators decrease; (D) both species increase.

$$\frac{dN_1}{dt} = r_1.N_1 - z_1.N_1^2 - \beta_{12}.N_1.N_2 \tag{5.16}$$

$$\frac{dN_2}{dt} = \gamma_{21}.N_1.N_2 - \beta_2.\frac{N_2^2}{N_1} \tag{5.17}$$

where $r_1$, $z_1$ and so on are coefficients.

The prey equation is a logistic expression combined with the effect of the predator, while the predator expression considers a carrying capacity dependent on the prey concentration.

The literature of ecological modelling contains many papers focusing on modified Lotka-Volterra equations, but the equations can also be criticized for not following the conservation principle. The increase in the biomass of the predator is less than the decrease in the biomass of the prey. Kooijman (2000) developed many population dynamic models based on the energy conservation principles; they give new and emerging properties of the energy flow in ecosystems. His approach is recommended when energy is in focus or if a more complex food web is considered.

However, Eqs. (5.16) and (5.17) can also easily be criticized. The growth term for the predator is a linear function of the prey concentration of density. Other possible relations are shown in Figure 5.5. The first relation (a) corresponds to a Michaelis-Menten expression (see Section 2.3, equation 2.5), while the second relation (b) only approximates a Michaelis-Menten expression by using a first-order expression in one interval and a zero order expression in another. The third relation (c) shown in Figure 5.5 corresponds to a logistic expression: With increasing prey density the predator density first grows exponentially and afterward a damping takes place. This relation is observed in nature and might be explained as follows: The energy and time used by the predator to capture a prey is decreasing with increasing density of the prey. This implies that the predator can capture more prey due to increasing density, and less of the energy consumed is used to capture the next prey.

Thus, the density of the predator increases more than proportionally to the prey density in this phase. Yet, there is a limit to the food (energy) that the predator can consume and at a certain density of the prey, a further decrease in the energy used to capture the prey cannot be obtained. So the increase in predator density slows down as it reaches a saturation point at a certain prey density.

A

B

C

D
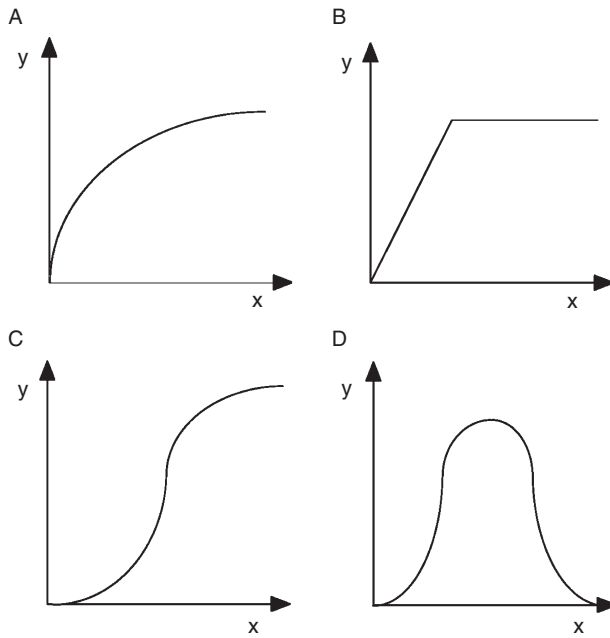
FIGURE 5.5 Four functional responses (Holling, 1959) where y is number of prey taken per predator per day and x is the prey density.

The fourth relationship (d) is similar to the relation between growth and pH or temperature. It is characteristic here that the predator density decreases above a certain prey density. This response might be explained by the effect of the waste produced by the prey on the predator. At a certain prey density the concentration of waste is sufficiently high to have a pronounced negative effect on predator growth.

Holling (1959, 1966) developed more elaborate models of prey-predator relationships. He incorporated time lags and hunger levels to attempt to describe the situation in nature. These models are more realistic, but they are also more complex and require knowledge of more parameters. Besides these complications, we have coevolution of predators and prey. The prey will develop better and better techniques to escape the predator and the predator will develop better and better techniques to capture the prey. To account for the convolution, it is necessary to have a current change of the parameters according to the selection taking place. The effect of *parasitism* is similar to that of predation, but is different because members of the host species affected are seldom killed, but may live for some time after becoming parasitized.

This is accounted for by relating the growth and the mortality of the prey, $N_1$, to the density of the parasites, $N_2$. Furthermore, the carrying capacity for the parasites is dependent on the prey density.

The following equations account for these relations and include a carrying capacity of the prey:

$$\frac{dN_1}{dt} = \frac{r_1}{N_2} N_1 \left( \frac{K_1 - N_1}{K_1} \right) \tag{5.18}$$

$$\frac{dN_2}{dt} = r_2 . N_2 \left( \frac{K_2 . N_1 - N_2}{K_2 . N_1} \right) \tag{5.19}$$

*Symbiotic relationships* are modelled with expressions similar to the Lotka-Volterra competition equations simply by changing the signs for the interaction terms:

$$\frac{dN_1}{dt} = r_1 . N_1 \left( \frac{K_1 - N_1 + \alpha_{12} N_2}{K_1} \right) \tag{5.20}$$

$$\frac{dN_2}{dt} = r_2 . N_2 \left( \frac{K_2 - N_2 + \alpha_{21} N_1}{K_2} \right) \tag{5.21}$$

Another criticism of the Lotka-Volterra prey-predator model is that it isolates two entities out of their larger contextual web of interactions. In reality, a complex food web both provides and constrains the behavior of species comprising it. The control is much more distributed and decentralized than is evident from the Lotka-Volterra model, which packs all causation into lumped parameters of natality, mortality, and interference.

In nature, interactions among populations often become intricate. The expressions (5.20) and (5.21) might be of great help in understanding population reactions in nature, but when it comes to the problem of modelling entire ecosystems, they are in most cases insufficient. Investigations of stability criteria for Lotka-Volterra equations are an interesting mathematical exercise, but can hardly be used to understand the stability properties of real ecosystems or even of populations in nature.

The experience from investigations of population stability in nature shows that it is necessary to account for many interactions with the environment to explain observations in real systems (e.g., Jørgensen & Fath, 2007).

The stability concept was widely discussed during the 1970s, but today almost all ecologists agree that the stability of an ecosystem is a very complex problem that cannot be solved by simple methods and

at least not by examinations of the stability of two coupled differential equations. It is also acknowledged that there is no simple relationship between stability and diversity (May, 1974, 1975, 1977). Stability must be considered a multidimensional concept because the stability is dependent on the particular changes we are concerned with. Some changes the ecosystem might easily adsorb, some other changes can cause drastic reorganization in the ecosystem by minor changes in the forcing function. The buffer capacity introduced in Section 2.6 (see Figure 2.12) may be a relevant concept to use, because it is multidimensional. There is a buffer capacity for each combination of state variable and forcing function.

## Illustration 5.2

This illustration concerns an anaerobic cultivation of two species of yeast first described by Gause (1934). The two species are *Saccharomyces cerevisiae* (Sc) and *Schizosaccharomyces pombe* (Kephir; K). Gause cultivated both species in mono-cultures and in mixture, and the results suggest that the two species have a mutual effect upon each other. His hypothesis was that a production of harmful waste products (alcohols) was the only cause of interactions.

A conceptual diagram for this model is shown Figure 5.6. The model has three state variables: the two yeast species and the waste products. The amount of waste products depends on the growth of yeast. The growth of the yeast species depends on the amount of yeast and the growth rate of the yeast, which is again dependent on the species and a reduction factor. This accounts for the influence of the waste products on the growth. The observed and computed values for growth of the two yeast species are shown in Table 5.3. The fit between observed and
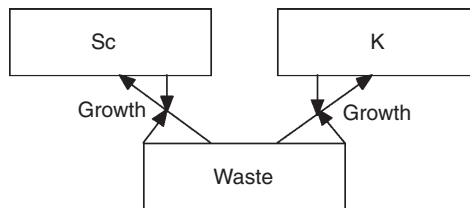


**FIGURE 5.6** Conceptual diagram of the model presented in Illustration 5.2. Waste is alcohol that affects the growth of two yeast species Sc and K.

**Table 5.3**   Observed and Calculated Values for the Growth of Two Species of Yeasts in Mono-Cultures and Mixtures

**Schizosaccharomyces "Kephir"**

| | Volume of Yeast (arbitrary units) | | | |
| --- | --- | --- | --- | --- |
| | *Mono-culture* | | *Mixed* | |
| Hours | Observed | Calculated | Observed | Calculated |
| 0 | 0.45 | 0.45 | 0.45 | 0.45 |
| 6 | — | 0.60 | 0.291 | 0.59 |
| 16 | 1.00 | 0.95 | 0.98 | 0.81 |
| 24 | — | 1.34 | 1.47 | 0.88 |
| 29 | 170 | 1.64 | 1.46 | 0.89 |
| 48 | 2.73 | 3.04 | 1.71 | 0.89 |
| 53 | — | 3.44 | 1.84 | 0.89 |
| 72 | 4.87 | 4.72 | — | — |
| 93 | 5.67 | 5.51 | — | — |
| 117 | 5.80 | 5.86 | — | — |
| 141 | 5.83 | 5.96 | — | — |
| **Saccharomyces cerevisiae** | | | | |
| Hours | Observed | Calculated | Observed | Calculated |
| 0 | 0.45 | 0.45 | 0.45 | 0.45 |
| 6 | 0.37 | 1.72 | 0.375 | 1.70 |
| 16 | 8.87 | 8.18 | 3.99 | 7.56 |
| 24 | 10.66 | 11.83 | 4.69 | 10.86 |
| 29 | 12.50 | 12.46 | 6.15 | 11.47 |
| 40 | 13.27 | 12.73 | — | 11.75 |
| 48 | 12.87 | 12.74 | 7.27 | 11.77 |
| 53 | 12.70 | 12.74 | 8.30 | 11.77 |

calculated values is acceptable for the mono-culture experiments, but it is completely unacceptable for the mixed culture experiments. It can be concluded that the two species do not interfere solely through the production of alcohol. Additional biological knowledge about the interference between the two species must be introduced to the model to explain the observations.

## Illustration 5.3

This illustration is a summary of an example presented by Starfield and Bleloch (1986) in their book on population dynamics titled *Building*

*Models for Conservation and Wildlife Management.* The example illustrates a very common and generally applicable approach to use population dynamic models in wildlife management. This illustration also demonstrates how an analysis of the focal problem can be used to construct a model. The equations are all based on semiquantitative to quantitative known relationships between determining factors on the one side and the influence on the state variables on the other. It is a clear illustration of how "down to earth" considerations might be used to construct models. As many interacting species are involved, the model is rather complex by including many different relationships between the different state variables of the model. The illustration is concerned with a spectrum of herbivores, while no significant predators are present. The principal grazers are warthog, wildebeest, zebra, and the white rhinoceros. The principal browsers are giraffe, kudu, and the black rhinoceros. Impala and nyala are the two most important mixed feeders.
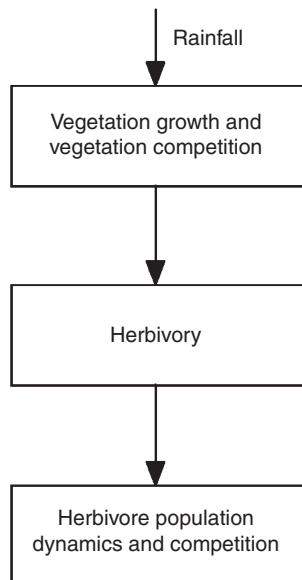


**FIGURE 5.7** Conceptualization of the problem in Illustration 5.3. The influence of rainfall on the vegetation, the competition among the different forms of vegetation, the food availability for the herbivorous state variables, and the competition among the herbivores should all be considered in the model.

The problem is illustrated in Figure 5.7. It implies that the model should consider the interactions between rainfall and vegetation, between vegetation and herbivores, and the competition among the herbivores for food.

The first question to consider is How many classes of species do we need? Clearly the giraffe should be a class of its own, as only this animal can browse on tall trees. The black rhinoceros and the kudu browse on shrubs and short trees. Both the white rhinoceros and zebra are grazers that can use relatively tall, coarse grass, while wildebeest and warthog are grazers that require short grass. Finally, impala and nyala are mixed feeders, utilizing short grass, shrubs, and short trees. By this short analysis we have suggested how to reduce the number of state variables of herbivores from nine to five. Converting one variable to another is made by using the concept of equivalent animal units (EAU), defined as the daily food intake of a domestic cow. The black rhinoceros is about 2 EAU, while a kudu is only about 0.4. When we lump the two animals in one group, each black rhinoceros is equivalent to 5 kudu. The same considerations are made for the other species.

The next problem concerns the food preferences. Here Starfield and Bleloch (1986) have suggested setting up the preferences in table form (see Table 5.4). This implies that we have to increase the number of herbivore types from five to six, as shown in the table. For example, Impala will first choose palatable grass, then palatable shrubs, and as last resort, less palatable grass. Kudu, on the other hand, have only two preferences: fist palatable shrubs, then unpalatable shrubs. The effect of switching to a

**Table 5.4** Food Preferences of the Herbivores

| Species | Preference 1 | Preference 2 | Preference 3 |
|---|---|---|---|
| Giraffe | Palatable tall trees | Palatable shrubs | Unpalatable trees |
| Impala | Grass, palatability > 0.8 | Palatable shrubs | Less palatable grass |
| Kudu | Palatable shrubs | Unpalatable shrubs | |
| Warthog | Grass, palatability > 0.8 | Less palatable grass | |
| Wildebeest | Grass, palatability > 0.8 | Less palatable grass | |
| Zebra | Grass, palatability > 0.6 | Less palatable grass | |

second or third preference is accounted for by a condition index with an arbitrarily chosen scale from 1 to 6. A value of 1 corresponds to the peak condition, while a 6 means extremely poor condition. It is important whether an animal class has an inadequate diet for just one month or for a number of consecutive months. The scale is therefore used to consider the cumulative effect and it is used stepwise. The condition index influences the mortality, particularly the juvenile mortality, which will increase sharply as the condition index approaches 6.

For each of the five classes, we consider two subclasses: adults and juveniles. We estimate, for example, that an adult kudu requires B kg and a juvenile b kg of food per month, which is selected as the time step of the model. If there are K adult kudu and k juveniles, then the kudu population in that park will potentially eat KB + kb kg of leaves in the next month. The model calculates a demand for food, first assuming that every species eats only its first preference. If there is sufficient for all, then the food is shared accordingly, but if there is a shortage, the model allocates a share of each animal's second preference, which determines a possible change of the condition index.

Except for zebra, all births take place during the first months of the summer. It is assumed that zebra produce their young throughout the year. The annual birthrate varies from 0.2 for giraffe to 0.95 for warthog.

Six types of vegetation are considered in the model: A grass, B shrubs + small trees, and C tall trees; each with a palatable and unpalatable subclass. The growth in leaf biomass for the two subclasses of B and C are modelled by using the following equation:

$$dl/dt = r * f * S * [1 - L/(q * S)] - b \tag{5.22}$$

where L denotes the leaf biomass, r a growth parameter, f is a rainfall correction factor, S the woody component, q the maximum leaf mass that one unit of wood mass normally can support, and b is calculated from the herbivore module as the food requirement. Equation (5.22) is based on the following assumptions:

1. New leaf growth depends on how many bushes/trees, S, there are.
2. Rainfall will influence production.
3. Herbivores will consume some biomass each month.
4. There is an inhibitory effect of existing leaf biomass, which is considered in the expression [1 − L/(q*S)].

The application of Eq. (5.22) implies that we have to model the wood mass, S. This is made by using:

$$dS/dt = r_s * f_s * S * [1 - (\Sigma S)/T_{max} * C] \tag{5.23}$$

where $r_s$ is the growth parameter for woody biomass, $f_s$ is the rainfall correction factor for the woody biomass of shrubs and trees, S is the present total wood mass, $T_{max}$ is the saturation level for woody biomass, and C is the competition from grass. C is found from:

$$C = \exp(-[p * c * A * h + \Sigma I])/U \tag{5.24}$$

where p is a competition factor (must be calibrated), c is converting grass volume to biomass, A is the grass area, h the height of the grass, $\Sigma I$ is the total leaf biomass, and U is the saturation level for green production.

A and h are state variables, too. Equations for the grass area ($m^2$), A, and for the grass height (m), h, are included in the model:

$$dA/dt = r_a * f_g * A * C \tag{5.25}$$

$$dh/dt = r_h * f_g * h[1 - h/h_{max]} - G/(c * A) \tag{5.26}$$

where $r_a$ and $r_h$ are the growth parameters for A and h, $f_g$ is the rainfall correction factor for grass area and grass height, $h_{max}$ is the saturation height for grass, and G is the grass biomass consumed by herbivores (kg/month). All of these variables are obtained from the herbivore module. Empirical tables are available for f. For instance, $f_g$ is dependent on the rainfall, whether it is low, medium, and high, and it is dependent on the season.

Figures 5.8 and 5.9 show some of the simulations carried out by the model. The number of kudu versus the number of years is plotted in Figure 5.8, while Figure 5.9 gives the palatable browse on shrubs in the same period. The condition index will roughly be opposite this curve. When the palatable browse is high, the condition index is low and vice versa.

Rain is — not surprisingly — of very great importance for the herbivorous populations, as is seen in Figure 5.7, where the indirect effect from rain on herbivores is obvious. This effect is seen by the violent fluctuations in palatable browse on shrubs, which can be explained by fluctuations in rainfall.
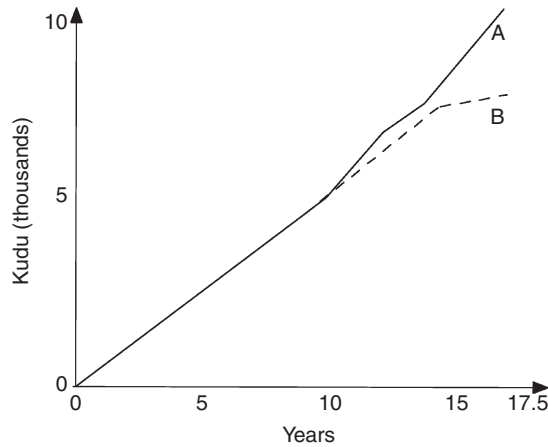
**FIGURE 5.8** The kudu population is plotted versus the number of years. A corresponds to cropping of the impala, whenever their population exceeds 6000. B corresponds to no cropping of impala under otherwise similar conditions.
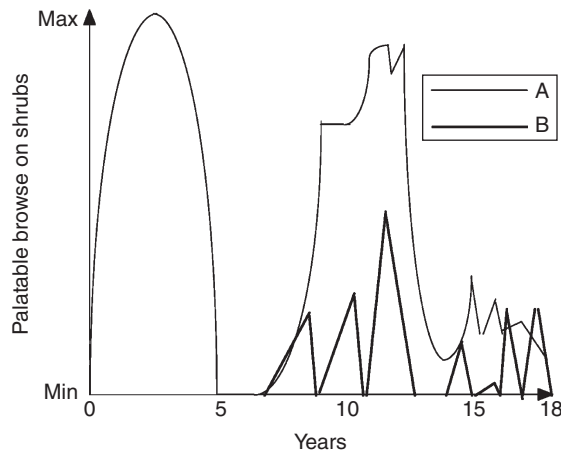


**FIGURE 5.9** The amount of palatable browse on shrubs and short trees is plotted versus the time. A corresponds to cropping of the impala, whenever their population exceeds 6000. B corresponds to no cropping of impala under otherwise similar conditions.

## 5.5. Matrix Models

Another important aspect of modelling population dynamics is the influence of the age distribution, which shows the proportion of the population belonging to each age class. If a population has unchanged

$l_x$ and $m_x$ schedules, then it will eventually reach a stable age distribution. This means that the percentage of organisms in each age class remains the same. Recruitment into every age class is exactly balanced by its loss due to mortality and aging.

The growth equations (5.6) and (5.8) assume that the population has a stable age distribution. The intrinsic rate of increase, r, the generation time, T, and the reproductive value, vx, is conceptually independent of the age distribution, but might be different for populations of the same species with different age distributions. Therefore, the models presented in Sections 5.2 and 5.3 did not need to consider age distribution, although the parameters in actual cases reflect the actual age distribution.

A model predicting the future age distribution was developed by Lewis (1942), Leslie (1945), and Levine (1980). The population is divided into n + 1 equal age groups — group 0, 1, 2, 3, . . ., n. The model is then presented by the following matrix equation:

$$
\begin{matrix}
f_0 & f_1 & f_2 & \ldots & f_{n-1} & f_n & n_{t,0} & n_{t+1,0} \\
p_0 & 0 & 0 & \ldots & 0 & 0 & n_{t,1} & n_{t+1,1} \\
0 & p_1 & \ldots & \ldots & 0 & 0 & n_{t,2} & n_{t+1,2} \\
\ldots & \ldots & \ldots & \ldots & \ldots & \ldots & . & . \\
\ldots & \ldots & \ldots & \ldots & \ldots & \ldots & . & . \\
0 & 0 & 0 & \ldots & p_{n-1} & 0 & n_{t,n} & n_{t+1,n}
\end{matrix}
\tag{5.27}
$$

The number of organisms in the various age classes at time t + 1 is obtained by multiplying the numbers of animals in these age classes at time t by a matrix, which expresses the fecundity and survival rates for each age class. $t_{,0}$, $f_1$, $f_2$ . . . $f_n$ give the reproduction in the $i^{th}$ age group and $P_0$, $P_1$, $P_2$, $P_3$, $P_4$ . . . $P_n$ represent the probability that an organism in the $i^{th}$ age group will still be alive after promotion to the $(i + 1)^{th}$ group.

The model can be written in the following form:

$$
A * a_t = a_{t+1}
\tag{5.28}
$$

where A is the matrix, $a_t$ is the column vector representing the population age structure at time t, and $a_{t+1}$ is a column vector representing the age structure at time t + 1. This equation can be extended to predict the age distribution after k periods of time:

$$
a_{t+k} = A^k * a_t
\tag{5.29}
$$

Matrix A has n possible eigenvalues and eigenvectors. Both the largest eigenvalues, $\lambda$, and the corresponding eigenvectors are ecologically meaningful. $\lambda$ gives the rate at which the population size is increased:

$$A * v = \lambda * v \qquad (5.30)$$

where v is the stable age structure. In $\lambda$ is the intrinsic rate of natural increase. The corresponding eigenvector indicates the stable structure of the population.

# Illustration 5.4

Usher (1972) gave a very illustrative example on the use of matrix models. This model is based upon data for the blue whale before its sharp changes in survival rates.

The eigenvalue can be used to find the number of individuals that can be removed from a population to maintain the same number in each age class. It can be shown that the following equation is valid:

$$H = 100(\lambda - 1)/\lambda$$

where H is the percentage of the population that can be removed.

The blue whales reach maturity at between four and seven years of age. They have a gestation period of about one year. A single calf is born and is nursed for about seven months. On average, not more than one calf is born to a female every two years. The male-to-female sex ratio is approximately equal. Survival rates are about 0.7 each 2 years for the first 10 years and 0.78 for whales above 12 years. We divide the population into 7 groups with a 2-year period for the first 6 groups and the age of 12 years and above as the seventh group. The fecundity for the first two groups is according to the information about zero. The third group has a fecundity of 0.19, and the fourth group, 0.44. The maximum fecundity of 0.50 is reached between ages of 8 and 11 years. The fecundity of the last group is 0.45.

Find the intrinsic rate of natural increase, the stable structure of the whale population, and the harvest, which can be taken to maintain a stable population size.

## Solution

The eigenvalue can be found either by an iterative method or by plotting the number of whales (totally or for each age class separately) versus the period of time. The slope of this plot will, after a stabilization period, correspond to r, the intrinsic rate of increase, or ins. We find that r = 0.0036 1/year or $\lambda$ or l = antilog 0.0036 = 1.0036 (for one year) or

1.00362 = 1.0072 for two years. Using Eq. (5.30), the corresponding eigenvector is found to be a = [1000, 764, 584, 447, 341, 261, 885] as the Leslie matrix is

$$
\begin{matrix}
0 & 0 & 0.19 & 0.44 & 0.50 & 0.50 & 0.45 \\
0.77 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0.77 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.77 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.77 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0.77 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0.77 & 0.78
\end{matrix}
$$

The harvest that can be taken from the population is estimated to be

$$H = 100(\lambda - 1)/\lambda = 0.71\%$$

every two years or about 0.355% every year.

If the harvest exceeds this value, then the population will decline. Population models of r-strategies generally cause some difficulties when developing models of K-strategies due to the high sensitivity of the fecundity. The number of offspring might be well known, but the number of survivors to be included in the first age class and the number of recruits is difficult to predict. This is the central problem of fish population dynamics, since it represents nature's regulation of population size (Beyer, 1981).

## 5.6. Fishery Models

Figure 5.10 shows the growth rate dN/dt versus the biomass or the number for the logistic growth equation. It is a parabolic shape in accordance with the s-shape of the logistic growth equation. The slope has maximum at an intermediate value of N, but is zero for N = 0 and for N = K.

It is also possible to include harvest, H, which is of interest in fishery and forest models. The following expression is used:

$$dN/dt = rN(1 - N/K) - H$$

The harvest H is proportional to N and to the fish effort E:

$$dN/dt = rN(1 - N/K) - fEN \tag{5.31}$$
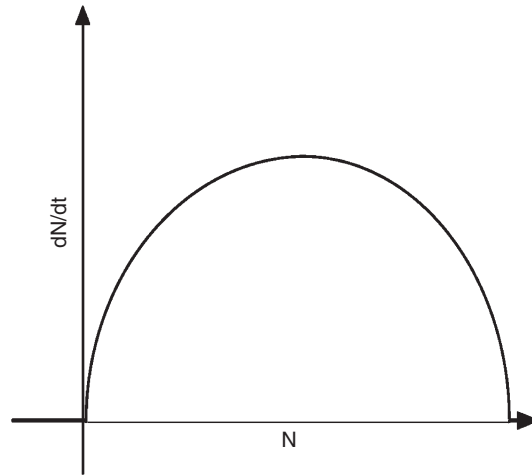
where f is a proportional constant.

**FIGURE 5.10** dN/dt is plotted versus N for the logistic growth equation.

This expression has two equilibriums corresponding to $dN/dt = 0$ $N_1 = 0$ and $N_2 = K(1 - fE/r)$.

$N_2$ can be found graphically as shown in Figure 5.11.

If the specific fishing mortality fE is $>r$, then there is no equilibrium value $N_2$, only the equilibrium value $N_1 = 0$. For a sustainable harvest
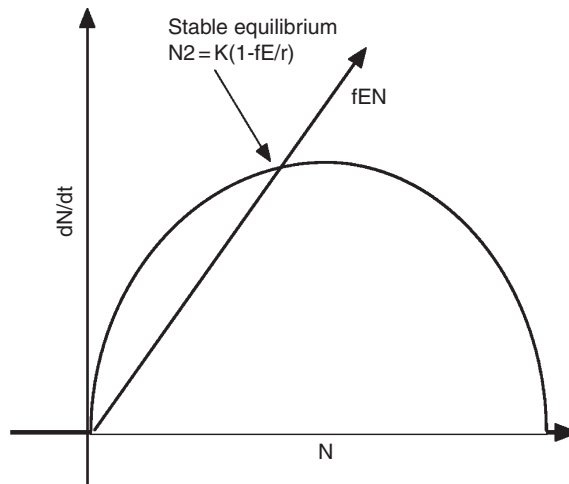


**FIGURE 5.11** The growth rate of the logistic growth as function of N and the fishing mortality as function of N are both plotted. A stable equilibrium is obtained where the two functions are equal. A sustainable fishery will therefore require that the fishing mortality is equal or less than the increase of N due to the logistic growth.

$fE/r < 1.0$. The sustainable yield $= fEN_2$ can be found as function of the fishing effort by using the previously shown expression for $N_2$:

$$\text{Yield} = fEN_2 = fEK(1 - fE/r) \tag{5.32}$$

This graph yield 0 f(E) is shown in Figure 5.12. The optimal effort is found by:

$$d\text{Yield}/dE = fK - 2f^2EK/r = 0, \tag{5.33}$$

which leads to:

$$E = r/(2f) \text{ and the maximum yield} = rK/4. \tag{5.34}$$

In populations of higher plants and animals with more complicated life histories, there is likely to be a delayed response. Wangersky and Cunningham (1957) suggested a modification of the logistic equation to include two kinds of time lag: (1) the time needed for an organism to start increasing under favorable conditions, and (2) the time required for organisms to react to unfavorable crowding by altering birth and death rates. If these time lags are $t - t_1$ and $t - t_2$ respectively, then we get:

$$\frac{dN}{dt} = rN_{t-t_1}\left(1 - \frac{N_{t-t_2}}{K}\right) \tag{5.35}$$
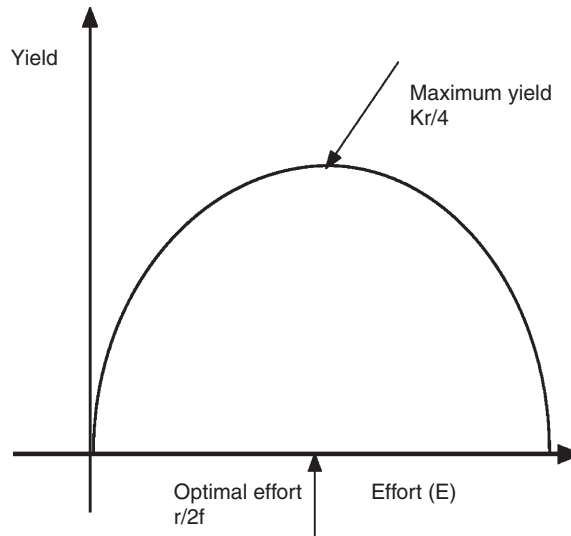


**FIGURE 5.12** Yield is plotted versus fishing effort E. The optimum yield $=$ Kr/4 is obtained by E $=$ r/2f. A sustainable fishery will therefore require that E $<$ r/2f.

Population density tends to fluctuate as a result of seasonal changes in environmental factors or due to factors within the actual populations (so-called intrinsic factors). We will not go into details here, but will just mention that the growth coefficient is often temperature dependent and since temperature shows seasonal fluctuations, it is possible to explain at least some seasonal population fluctuations in density as temperature changes.

The simple fishery model presented earlier focuses on one species only, and it is insufficient for setting up an optimal fishery strategy. It is necessary to include several species, because all species interact and influence each other. A fishery policy based on one species will inevitably fail. Consequently, the European fishery policy for the North Sea is based on a multi-species fishery model used to assess the optimal fishery strategy. The fishery is, however, not optimal because the politicians are not following the recommendations given by the model.

## 5.7. Metapopulation Models

A regional set of local populations that occupy isolated habitat patches but are interconnected by dispersal movements are denoted metapopulations (see an example in Figure 5.13). All of the local populations have a finite possibility of becoming extinct. Even if the local population is fairly large, extinction may still occur through catastrophic events.
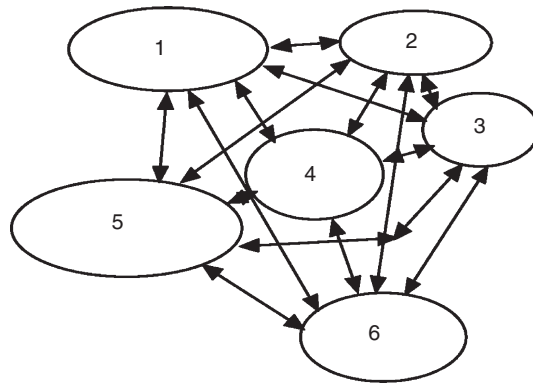


**FIGURE 5.13** Conceptual model of metapopulation interactions. The populations occupy isolated patch habitats (1-6) that are connected by dispersal corridors.

The dispersal movements are essential to reestablish populations that have faded or crashed. Species that are widely distributed in many local populations have reduced likelihood to be extinct regionally.

Landscape fragmentation has increased due to human expansion. Populations that were formerly continuously distributed have become broken into separate localized groupings. Dispersal may even be inhibited by hazards in traversing the human-transformed areas separating suitable habitats. Metapopulation models assess the risks of species extinctions as a consequence of such fragmentations and identify how actions such as providing dispersal corridors can reduce the risks.

The metapopulation concept was formulated by Levins (1969) and further modified by Hanski (1994, 1999). P is the proportion of sites occupied by populations, E is the extinction rate of these populations, and C is the colonization rate of vacant sites by migrants from occupied patches. The change over time in the proportion of patches, dP/dt, occupied is a matter of balance between colonization and extinction:
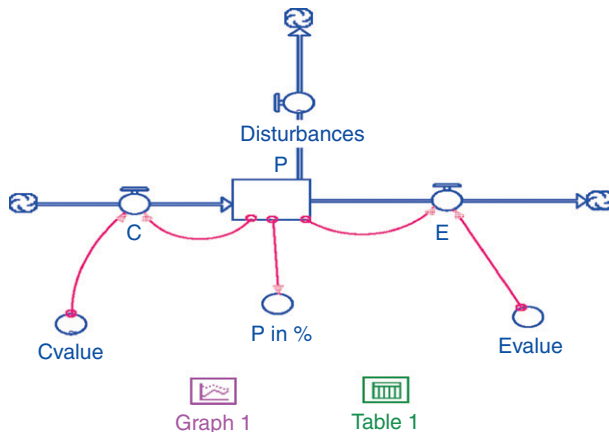
$$dN/dt = CP(1 - P) - EP \tag{5.36}$$

The equilibrium proportion $P_{eq}$ is given by

$$P_{eq} = 1 - E/C \tag{5.37}$$

As seen from Eq. (5.36) the patch occupancy will become zero if the extinction rate exceeds the colonization rate.

Figure 5.14 shows a STELLA diagram for a metapopulation model based on Eq. (5.36) plus the introduction of temporal disturbances.



FIGURE 5.14 A STELLA diagram of a metapopulation model with disturbances (removal of patches).

The model can be applied to give the consequences of disturbances such as road construction that interrupts connections among population sites. The populations in the threatened population sites may become extinct due to unbalanced natality and mortality that require immigration to be in balance. A simple simulation of the threatened populations will be able to assess the E-value as a consequence of the disturbances.

## 5.8. Infection Models

Population models of disease dynamics have the proportion of the host population that is infected as the focal state variable. A simple infection model is shown in Figure 5.15. Susceptible hosts, S, become infected at rate b. After a period of time, the infected hosts either recover, maybe with long-lasting immunity, or die. The number of infected hosts is reduced at a rate corresponding to m + r, where m is the mortality rate and r is the recovery rate. The disease spreads as a result of contact between infected and susceptible hosts. The following equation can be used to express the number of infected hosts, I:

$$dI/dt = bSI - vI \tag{5.38}$$
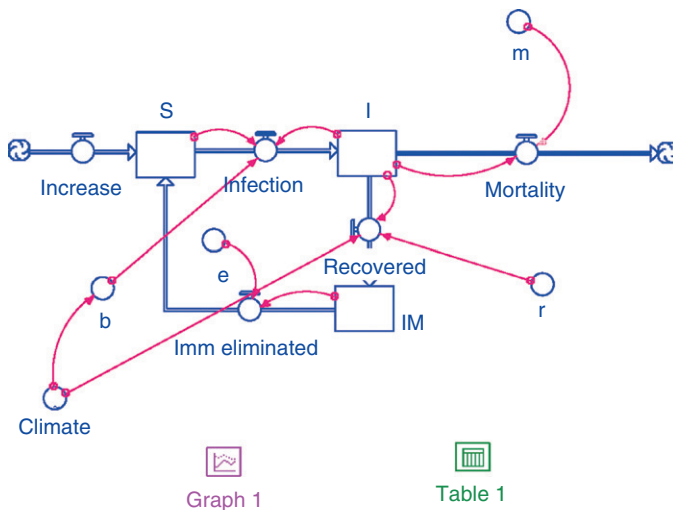


**FIGURE 5.15** A conceptual STELLA diagram for an infection model is shown. The model has three state variables: the number of susceptible hosts, the number of infected hosts, and the number of immune hosts. The infection rate is b, the mortality rate is m, the recovery rate is r, and the rate of immunity elimination is e. IM is …., and Imm is ….

The duration of recovery, D, is the inverse of the rate of recovery from the infection:

$$D = bN/v \tag{5.39}$$

where N is the susceptible hosts, which initially may be equal to the total population, denoted N.

Notice that Eq. (5.38) implies that the infection will spread very fast because it is at a rate that is $S \times I$. Figure 5.15 shows a conceptual diagram of an infection model with three state variables: susceptible hosts, infected hosts, and immune hosts. The spreading of the infection follows Eq. (5.38). The infected hosts either die at a rate m or recover at a rate r. The immunity is eliminated at a rate e, which implies that immune hosts are transferred to the susceptible hosts at a rate e. The state variables are S, I, and IM. It is sometimes necessary to distinguish between recovered hosts that still can transmit the infection and completely immune hosts. In this case, a fourth state variable is introduced to represent the recovered hosts that can still transmit the infection.

The influence of the climate is included in the model. The auxiliary variable "climate" (see Figure 5.15) follows a sine-like curve with higher values during the winter time (maximum in February with an approximate value of 2.0) and lower during the summer time, with an approximate value of 0.3. Both b and the recovery rate are influenced by the climate. B is dependent on a number of factors. Vaccination or isolation of infected individuals will decrease b. For some diseases, the transmission is dependent on the proportion of susceptible individuals within the population rather than on their absolute number. This is the case for sexually transmitted diseases, where spread is frequency dependent.

The equations of the model are shown in Table 5.5. The result of a simulation with the duration of 1000 days is shown in Figure 5.16. As expected, the number of infected hosts increased very rapidly, although b is only 0.000001. The number of susceptible hosts is 1,000,000 at time = 0, and the number of infected hosts has as an initial value 1.0. These numbers could be realistic for an influenza epidemic. Notice that the number of infected hosts after the peak has been reached is decreasing, but with fluctuations according to the auxiliary variable climate. The fluctuations of the number of immune hosts and infected hosts are opposite with maximum for infected hosts when the number of immune hosts are in minimum.

**Table 5.5**   Equations Using STELLA for the Model Shown in Figure 5.15

```
I(t) = I(t - dt) + (infection - mortality - recovered) * dt
INIT I = 1
INFLOWS:
infection = b*S*I
OUTFLOWS:
mortality = m*I
recovered = I*r*climate
IM(t) = IM(t - dt) + (recovered - imm_eliminated) * dt
INIT IM = 0
INFLOWS:
recovered = I*r*climate
OUTFLOWS:
imm_eliminated = IM*e
S(t) = S(t - dt) + (imm_eliminated + increase - infection) * dt
INIT S = 1000000
INFLOWS:
imm_eliminated = IM*e
increase = 200
OUTFLOWS:
infection = b*S*I
b = 0.000001*climate
e = 0.025
m = 0.002
r = 0.05
climate = GRAPH(TIME)
(0.00, 1.40), (20.4, 1.91), (40.8, 2.00), (61.2, 1.80),
(81.6, 1.35), (102, 0.85), (122, 0.61), (143, 0.4), (163,
0.32), (184, 0.29), (204, 0.36), (224, 0.43), (245, 0.81),
(265, 1.08), (286, 1.26), (306, 1.46), (327, 1.60), (347,
1.75), (367, 1.86), (388, 1.96), (408, 2.00), (429, 1.87),
(449, 1.53), (469, 0.86), (490, 0.62), (510, 0.44), (531,
0.35), (551, 0.3), (571, 0.34), (592, 0.5), (612, 0.73),
(633, 0.97), (653, 1.39), (673, 1.75), (694, 1.94), (714,
2.00), (735, 1.97), (755, 1.86), (776, 1.68), (796, 1.43),
(816, 1.18), (837, 0.9), (857, 0.6), (878, 0.42), (898,
0.3), (918, 0.35), (939, 0.55), (959, 1.01), (980, 1.28),
(1000, 1.45)
```

## Problems

1. Set up a STELLA model representing Lotka-Volterra equations. How is it possible to consider the conservation principles, which is a prerequisite for the application of STELLA?
2. Express the model in Illustration 5.1 by STELLA.
3. Make a conceptual diagram of a four species model based on Eq. (5.10).
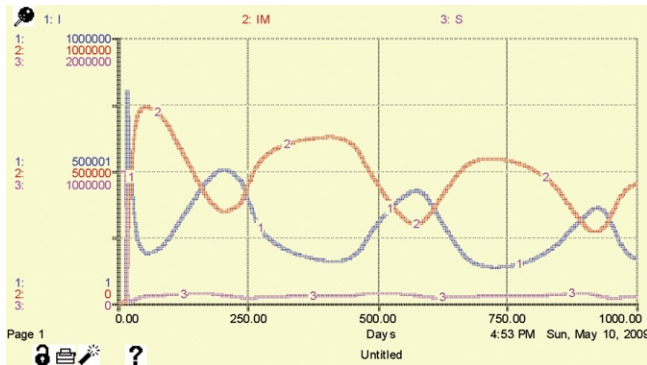
**FIGURE 5.16** The simulation results of the model shown in Figure 5.15. The equation is applied in Table 5.5. Notice the rapid increase due to the equation $dI/dt = bIS$. The peak of infection is after ten days. The fluctuations of all three state variables, particularly for I and IM, are due to the auxiliary variable "climate."

4. Mention at least 3 reasons for the unrealistic nature of the Lotka-Volterra model.

5. A fish culture has a carrying capacity of 50 g/L. Set up a logistic growth equation for the fish culture when the initial concentration at day 0 is 1 g/L and after 10 days the concentration 2 g/L is obtained. How long does it take to increase the concentration from 24 g/L to 48 g/L? Find an equation that expresses the doubling time as a function of the time.

6. Explain under which conditions the four functional responses may occur.

7. Set up a matrix model for a bird population that has the following characteristics:
   a. Life span 7 years
   b. 4 eggs from the second year per pair, increasing to 5 eggs the third year, and 6 eggs the following years
   c. The mortality is 30% the first year, 20% the following years, except the last year where it is 100%. What is the steady-state age distribution?

8. Give an overview of factors that may be able to limit the carrying capacity of a population.

9. Make a conceptual diagram of a four-species model based on population interactions representing prey-predator-top predators and two competing top predators.

10. The following equation is valid for a fish population: $dN/dt = 0.025*$ number of fish$* (1 - \text{fish}/1.5*10^7)$. The fishing effort, E, is 0.22 and $f = 0.66$. By using $dN/dt$ find the stable equilibrium. What is the maximum yield? What is the optimal effort?