

3 Applications

of Nonlinear Difference Equations to Population Biology

*Great fleas have little fleas upon their backs to bite 'em.
And little fleas have lesser fleas, and so ad infinitum.
The great fleas themselves in turn have greater fleas to go on,
While these again have greater still, and greater still, and so on.*

Anonymous (1981). *The brand x anthology of poetry*, Burnt Norton edition,
William Zaranka, ed. Apple-wood Books, Cambridge, Mass.

*They hop in tens and in hundreds they fly
Thousands lie still while millions go by
That makes billions of bugs who jump and who crawl
So try as you will, you can't count them all.*

Haris Petie (1975). *Billions of bugs*, Prentice-Hall,
Englewood Cliffs, N.J.

Methods developed in Chapter 2 prove useful in addressing the population dynamics of organisms that have distinct breeding periods and life-cycle stages, notably insects and other *arthropods* (the phylum consisting of segmented-leg organisms). Since insects often compete with humans for crops or natural resources, efforts at pest management have been of fundamental economic interest.

Recognizing that chemical sprays and toxins are as unhealthy in the long run for people as for pests, recent efforts have been directed at biological control of pest

species using other potential competitors, predators, or parasites. Folk tradition has held that this would lead to eradication of the undesirable pest. In fact, however, the outcomes of biological intervention are not always as clear-cut as we might naively expect. We discover time and again that interactions of a species with the environment, with other members of its own species, or with another population can be potentially complex and bizarre.

To understand some of the outcomes of population interactions, an examination of fairly elementary mathematical models proves quite illuminating. Here again, we make no claim to describe the full intricacies of a given situation. Rather, the approach is to examine the consequences of several simplifying assumptions. Often these assumptions lead us to predictions that are biologically unrealistic (see the Nicholson-Bailey model, for example, as described in Section 3.3). It is then instructive to consider how modifying the underlying assumptions tends to change the predictions.

To introduce discrete models into population dynamics we first consider single-species populations in Section 3.1. As indicated in Chapter 2, nonlinear difference equations arise rather naturally in models for populations that have nonoverlapping generations. Many of these models are based on the observation that the net growth rate of the population depends in some way on its density. These effects may stem from competition of individuals for limited resources or from numerous other environmental considerations including predation, disease, and so forth. Single-species models are often based on empirical formulae rather than on detailed interactions in the population. We examine several of these in Section 3.1.

In many ecological settings one finds that two or more species are intimately related in their influence on each other. A classic example, that of the host-parasitoid system, is outlined in Sections 3.2 through 3.4. Here one species (the parasitoid) can reproduce only in the presence and at the expense of the other (its host). We observe that under the simplest reasonable assumptions, a model for such systems (the Nicholson-Bailey model) predicts growing population oscillations in the two species. Section 3.4 summarizes a number of potentially stabilizing influences.

Models described in Sections 3.1 through 3.4 proceed largely from detailed choices for functions that represent growth rates, fraction of hosts parasitized, or survivorships. In a model for plant-herbivore interactions (Section 3.5) we depart somewhat from this traditional approach. We observe that certain logical deductions about population behavior can be made even when only broad features of the system are known. For would-be modelers this approach is an instructive one and reappears in later material. Sections 3.5 and 3.3 as well as 3.1 contain several explicit examples of how to apply the stability criteria derived in Chapter 2. As such, these examples may enhance your appreciation of the techniques previously developed.

The concluding section of this chapter contains some introductory material on population genetics. This topic provides an excellent example of yet another realm in which discrete difference equations are important.

Note to the instructor: For rapid coverage of this chapter, include only Sections 3.1 through 3.3 and 3.6, leaving Sections 3.4 and 3.5 for further independent study by more advanced students.

3.1 DENSITY DEPENDENCE IN SINGLE-SPECIES POPULATIONS¹

An assumption that growth rate, reproductive rate, or survivorship depends on the density of the population leads us to consider models of the following form:

$$N_{t+1} = f(N_t) \quad (1)$$

where $f(N_t)$ is some (nonlinear) function of the population density.

Quite often single-species populations (of insects, for example) are described by such equations, where f is a function that is fit to data obtained by following successive generations of the population. Here we consider several models of this type and demonstrate their properties.

1. A model by Varley, Gradwell, and Hassell (1973) consists of the single equation

$$N_{t+1} = \frac{\lambda}{\alpha} N_t^{1-b}. \quad (2)$$

Here λ is the reproductive rate, assumed to be greater than 1, and $1/\alpha N_t^{-b}$ is the fraction of the population that survives from infancy to reproductive adulthood. The equation is thus best understood in the form

$$N_{t+1} = \left(\frac{1}{\alpha} N_t^{-b} \right) (\lambda N_t). \quad (3)$$

$\uparrow$ no. of progeny at generation t
 $\uparrow$ fraction that survives to generation $t + 1$

where $\alpha, b, \lambda > 0$. Since the fraction of survivors can at most equal but not exceed 1, we find that the population must exceed a certain size, $N_t > N_c$ for this model to be biologically reasonable (see problem 1).

Populations satisfying equation (3) can be maintained at steady density levels. To observe this we look for the steady-state solutions to (3) by setting

$$\bar{N} = N_{t+1} = N_t.$$

Substituting into (3) we find that

$$\bar{N} = \frac{\lambda}{\alpha} \bar{N}^{1-b}. \quad (4)$$

Cancelling the common factor $\bar{N}$ and rearranging terms gives us

$$\bar{N} = \left(\frac{\lambda}{\alpha} \right)^{1/b} \quad (5)$$

Next, we let

$$f(N) = \frac{\lambda}{\alpha} N^{1-b}$$

1. This section contains material compiled by Laurie Roba.

and proceed to test for the stability of $\bar{N}$. We find that perturbations δ_i from this steady state must satisfy

$$\begin{aligned}\bar{N} + \delta_{i+1} &= f(\bar{N} + \delta_i) \\ &\approx f(\bar{N}) + \left. \frac{df}{dN} \right|_{\bar{N}} \delta_i + \dots\end{aligned}$$

Since $\bar{N} = f(\bar{N})$, recall that this simplifies to

$$\delta_{i+1} \approx \left. \frac{df}{dN} \right|_{\bar{N}} \delta_i.$$

But

$$\left. \frac{df}{dN} \right|_{\bar{N}} = \frac{\lambda}{\alpha} (1 - b) N^{-b} \Big|_{\bar{N}} = 1 - b. \quad (6)$$

Thus stability of $\bar{N}$ hinges on whether the quantity $1 - b$ is of magnitude smaller than 1; that is, $\bar{N}$ will be stable provided that

$$-1 < 1 - b < 1,$$

or

$$0 < b < 2. \quad (7)$$

It is clear that $b = 0$ is a situation in which survivorship is not density-dependent; that is, the population grows at the rate λ/α . Thus the lower bound for the stabilizing values of b makes sense. It is at first less clear from an intuitive point of view why values of b greater than 2 are not consistent with stability; it appears that density dependence that is *too* strong is destabilizing due to the potential for boom-and-bust cycles.

2. A second model cited in the literature (for example, May, 1975) consists of the equation

$$N_{i+1} = N_i \exp r(1 - N_i/K), \quad (8)$$

where r, K are positive constants. The quantity $\lambda = \exp r(1 - N_i/K)$ could be considered the density-dependent reproductive rate of the population. Again, by carrying out stability analysis we observe that

$$N_i = N_{i+1} = K$$

is the nontrivial steady state. To analyze its stability properties we remark that for

$$f(N) = N \exp r(1 - N/K) \quad (9)$$

we have

$$f'(N) = [\exp r(1 - N/K)](1 - Nr/K). \quad (10)$$

Evaluated at $\bar{N} = K$, (10) leads to

$$f'(K) = 1 - K(r/K) = 1 - r. \quad (11)$$

Thus stability is obtained when

$$|1 - r| < 1, \quad \text{or} \quad 0 < r < 2. \quad (12)$$

We observe that when $N < K$ the reproductive rate $\lambda > 1$, whereas when $N > K$, $\lambda < 1$ (see problem 3). This property is shared with equation (11) of Chapter 2 where $K = 1$. K is said to be the *carrying capacity* of the environment for the population. In the next chapter we shall see examples of similar density-dependent relationships within the framework of continuous populations.

3. Yet a third model, proposed by Hassell (1975), is given by the equation

$$N_{t+1} = \lambda N_t (1 + aN_t)^{-b}, \quad (13)$$

for λ , a , b positive constants. Analysis of this equation is left as a problem for the reader.

One generally observes with models such as 1, 2, and 3 (and with other discrete equations such as the prototype given in Chapter 2) that the dynamical behavior depends in a sensitive way on parameter settings. Typically such equations have stable cycles of arbitrary periods as well as chaotic behavior. Each model thus describes a highly complex range of dynamic behavior if parameter values are pushed to high values. For example, equation (13) has the behavioral regimes mapped out on the λb parameter plane shown in Figure 3.1. The values $\lambda = 100$ and $b = 6$ fall

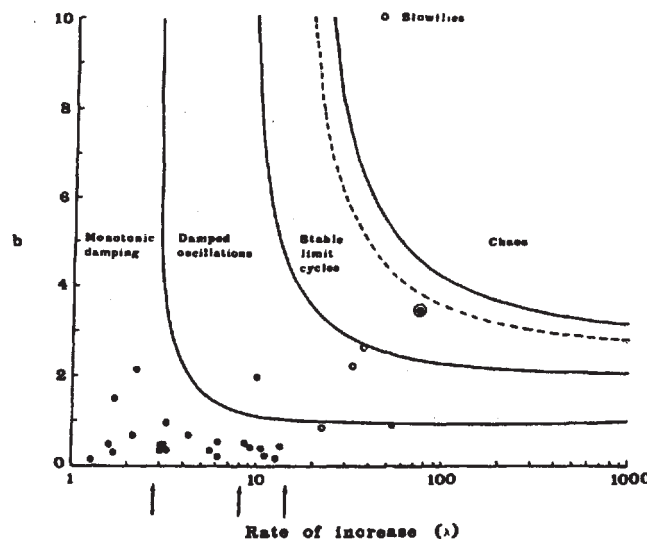


Figure 3.1 Stability boundaries for the density-dependent parameter b and the population growth rate λ from equation (13). The solid lines separate the regions of monotonic, oscillatory damping, stable limit cycles, and chaos. The broken line indicates where two-point limit cycles give rise to higher-order cycles. The solid circles come from analyses of life table data; the hollow circles from

analyses of laboratory experiments. [Reproduced from Michael P. Hassell, *The Dynamics of Anthropod Predator-Prey Systems. Monographs in Population Biology 13*. Copyright © 1978 by Princeton University Press. Fig. 2.5 (after Hassell, Lawton, May 1976) reprinted by permission of Princeton University Press.]

in the chaotic domain, so that populations fluctuate wildly. The values $\lambda = 100$ and $b = 0.5$, correspond to a stable steady state, so that a perturbed population undergoes monotonic damping back to its steady-state level.

For a given single-species population, density fluctuations may or may not be described well by a model such as equation (13). If so, parameters such as b and λ can be estimated by following the observed levels of the population over successive generations. Such observations are called *life table data*. Studies of this sort have been carried out under a variety of conditions, both in the field and in laboratory settings (see Hassell et al., 1976). Typical species observed in the field have included insects such as the moth *Zeiraphera diniana* and the parasitoid fly *Cyzenis albicans*. Laboratory data on beetles and on the blowfly *Lucilia cuprina* (Nicholson, 1954) have also been collected.

Pooling results of many observations in the literature and in their own experiments, Hassell et al. (1976) plotted the parameter values b and λ of some two dozen species on the $b\lambda$ parameter plane. In all but two of these cases, the values of b and λ obtained were well within the region of stability; that is, they reflected either monotonic or oscillatory return to the steady states.

Hassell et al. (1976) found two examples of unstable populations. The only one occurring in a natural system was that of the colorado potato beetle (shown as a circled dot in Figure 3.1), which is known to fluctuate periodically in certain situations. A single laboratory population, that of the blowfly (Nicholson, 1954), was found to have (λ, b) values corresponding to the chaotic regime in Figure 3.1. Some controversy surrounds the acceptance of this single example as a true case of chaotic population dynamics.

From their particular set of examples, Hassell et al. (1976) concluded that complex behavioral regimes typical of discrete difference equations are not frequently observed in reality. Of course, to place this deduction in its proper context, we should remember that only a relatively small sample of species has been sufficiently well studied to be represented, and that Figure 3.1 describes the fit to one particular model, chosen somewhat arbitrarily from many equally plausible ones.

One of the contributions of mathematical modeling and analysis to the study of population behavior has been in bringing forward questions that might otherwise have been of lesser interest. Comparison between observations and model predictions indicate that many dynamical behavior patterns, which are theoretically possible, are not observed in nature. We are thereby led to inquire which effects in natural systems have stabilizing influences on populations that might otherwise behave chaotically.

Hassell et al. (1976) comment on some of the key elements of studies based on data collected in the field versus those collected under controlled laboratory conditions. In the former, the survival of a population may depend on multiple factors including predation, parasitism, competition, and environmental conditions (see Sections 3.2–3.4). Thus a description of the population by a single-species model is, at best, a crude approximation.

Laboratory experiments on the other hand, can provide conditions in which a population is truly isolated from other species. In this sense, such data is more suitable for interpretation by single-species models. However, the influence of a somewhat artificial setting may result in effects (such as competition in close

confinement) that are not significant in the natural setting. Thus, data for laboratory studies such as those of Nicholson's blowflies, in which erratic chaotic behavior is observed, may reflect not a realistic trend but rather an artifact observed only in the laboratory.

3.2 TWO-SPECIES INTERACTIONS: HOST-PARASITOID SYSTEMS

Discrete difference-equation models apply most readily to groups such as insect populations where there is a rather natural division of time into discrete generations. In this section we examine a particular two-species model that has received considerable attention from experimental and theoretical population biologists, that of the *host-parasitoid system*.

Found almost entirely in the world of insects, such two-species systems have several distinguishing features. Typical of insect species, both species have a number of life-cycle stages that include *eggs*, *larvae*, *pupae* and *adults*. One of the species, called the *parasitoid*, exploits the second in the following way: An adult female parasitoid searches for a *host* on which to *oviposit* (deposit its eggs). In some cases eggs are attached to the outer surface of the host during its larval or pupal stage. In other cases the eggs are injected into the host's flesh. The larval parasitoids develop and grow at the expense of their host, consuming it and eventually killing it before they pupate. The life cycles of the two species, shown in Figure 3.2, are thus closely intertwined.

A simple model for this system has the following common set of assumptions:

1. Hosts that have been parasitized will give rise to the next generation of parasitoids.
2. Hosts that have not been parasitized will give rise to their own progeny.
3. The fraction of hosts that are parasitized depends on the rate of *encounter* of the two species; in general, this fraction may depend on the densities of one or both species.

While other effects causing mortality abound in any natural system, it is instructive to consider only this minimal set of interactions first and examine their consequences. We therefore define the following:

N_t = density of host species in generation t ,

P_t = density of parasitoid in generation t ,

$f = f(N_t, P_t)$ = fraction of hosts not parasitized,

λ = host reproductive rate,

c = average number of viable eggs laid by a parasitoid on a single host.

Then our three assumptions lead to:

$$N_{t+1} = \text{number of hosts in previous generation} \times \text{fraction not parasitized} \\ \times \text{reproductive rate } (\lambda),$$

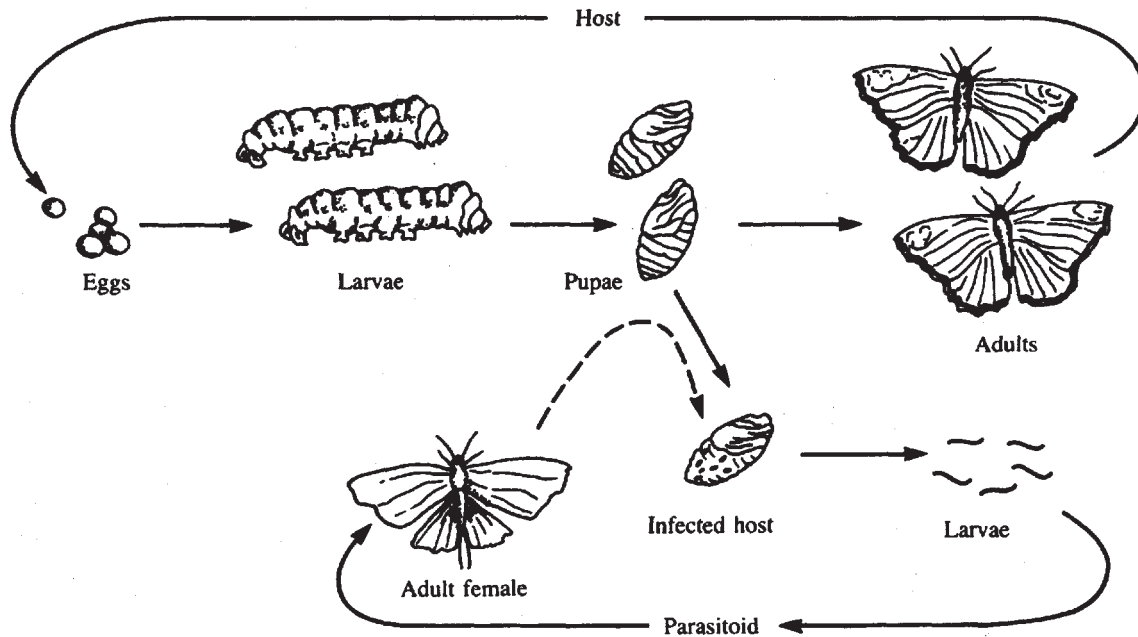


Figure 3.2 Schematic representation of a host-parasitoid system. The adult female parasitoid deposits eggs on or in either larvae or pupae of the

host. Infected hosts die, giving rise to parasitoid progeny. Uninfected hosts may develop into adults and give rise to the next generation of hosts.

P_{t+1} = number of hosts parasitized in previous generation $\times$ fecundity of parasitoids (c).

Noting that $1 - f$ is the fraction of hosts that are parasitized, we obtain

$$N_{t+1} = \lambda N_t f(N_t, P_t), \quad (14a)$$

$$P_{t+1} = c N_t [1 - f(N_t, P_t)]. \quad (14b)$$

These equations outline a general framework for host-parasitoid models. To proceed further it is necessary to specify the term $f(N_t, P_t)$ and how it depends on the two populations. In the next section we examine one particular form suggested by Nicholson and Bailey (1935).

3.3 THE NICHOLSON-BAILEY MODEL

A. J. Nicholson was one of the first biologists to suggest that host-parasitoid systems could be understood using a theoretical model, although only with the help of the physicist V. A. Bailey were his arguments given mathematical rigor. (See Kingsland, 1985 for a historical account.)

Nicholson and Bailey made two assumptions about the number of encounters and the rate of parasitism of a host:

4. Encounters occur randomly. The number of encounters N_e of hosts by parasitoids is therefore proportional to the product of their densities.

$$N_e = aN_iP_i, \quad (15)$$

where a is a constant, which represents the searching efficiency of the parasitoid. (This kind of assumption presupposes random encounters and is known as the *law of mass action*. It is a common approximation which will reappear in many mathematical models; see Chapters 4, 6, and 7.)

5. Only the first encounter between a host and a parasitoid is significant. (Once a host has been parasitized it gives rise to exactly c parasitoid progeny; a second encounter with an egg-laying parasitoid will not increase or decrease this number.)

The Poisson Distribution and Escape from Parasitism

The *Poisson distribution* is a probability distribution that describes the occurrence of discrete, random events (such as encounters between a predator and its prey). The probability that a certain number of events will occur in some time interval (such as the lifetime of the host) is given by successive terms in this distribution. For example, the probability of r events is

$$p(r) = \frac{e^{-\mu} \mu^r}{r!} \quad (16)$$

where μ is the average number of events in the given time interval. (For more details on the Poisson distribution consult any elementary text in statistics, for example, Hogg and Craig, 1978.) In the case of host-parasitoid encounters, the *average* number of encounters per host per unit time is

$$\mu = \frac{N_e}{N_i}. \quad (17)$$

Note that by equation (15) this is the same as

$$\mu = aP_i. \quad (18)$$

Thus, for example, the probability of exactly two encounters would be given by

$$p(2) = \frac{e^{-aP_i}}{2!} (aP_i)^2.$$

The likelihood of escaping parasitism is the same as the probability of zero encounters during the host lifetime, or $p(0)$. Thus

$$f(N_i, P_i) = p(0) = \frac{e^{-aP_i}}{0!} (aP_i)^0 = e^{-aP_i}. \quad (19)$$

Based on the latter assumption it proves necessary to distinguish only between those hosts that have had no encounters and those that have had n encounters, where $n \geq 1$.

Because the encounters are assumed to be random, one can represent the probability of r encounters by some distribution based on the average number of encounters that take place per unit time. It transpires that an appropriate probability distribution for describing this situation is that of Poisson, highlighted briefly in the box on page 80.

Combining assumptions 4 and 5 with the comments about the Poisson distribution leads us to the expression for the fraction that *escapes* parasitism,

$$f(N_t, P_t) = p(0) = e^{-aP_t}, \quad (20)$$

given by the zero term of the Poisson distribution.

Thus the assumption that parasitoids search independently and randomly and that their searching efficiently is constant (depicted by the parameter a) leads to the Nicholson-Bailey equations:

$$N_{t+1} = \lambda N_t e^{-aP_t}, \quad (21a)$$

$$P_{t+1} = cN_t(1 - e^{-aP_t}). \quad (21b)$$

We now analyze this model using the methods developed in Chapter 2. The steps include:

1. Solving for steady states.
2. Finding the coefficients of the Jacobian matrix (for the system linearized about the steady state).
3. Checking the stability condition derived in Section 2.8.

Nicholson-Bailey Model: Equilibrium and Stability

Let

$$F(N, P) = \lambda N e^{-aP}, \quad (22a)$$

$$G(N, P) = cN(1 - e^{-aP}). \quad (22b)$$

Solving for steady states, we obtain the trivial solution $\bar{N} = 0$, or

$$\bar{N} = F(\bar{N}, \bar{P}) = \lambda \bar{N} e^{-a\bar{P}}, \quad (23a)$$

$$\bar{P} = G(\bar{N}, \bar{P}) = c\bar{N}(1 - e^{-a\bar{P}}). \quad (23b)$$

These imply that

$$\bar{P} = \frac{\ln \lambda}{a}, \quad (24a)$$

$$e^{-a\bar{P}} = 1/\lambda, \quad (24b)$$

$$\bar{N} = \frac{\lambda \ln \lambda}{(\lambda - 1)ac}. \quad (24c)$$

From these equations we observe that $\lambda > 1$ is required, since otherwise $\bar{N}$ would be a negative quantity. Computing the coefficients a_{ij} of the Jacobian, we obtain

$$a_{11} = F_N(\bar{N}, \bar{P}) = \lambda e^{-a\bar{P}} = 1, \quad (25a)$$

$$a_{12} = F_P(\bar{N}, \bar{P}) = -a\lambda\bar{N}e^{-a\bar{P}} = -a\bar{N}, \quad (25b)$$

$$a_{21} = G_N(\bar{N}, \bar{P}) = c(1 - e^{-a\bar{P}}) = c(1 - 1/\lambda), \quad (25c)$$

$$a_{22} = G_P(\bar{N}, \bar{P}) = ca\bar{N}e^{-a\bar{P}} = ca\bar{N}/\lambda. \quad (25d)$$

(Comment: The notation $F_N(\bar{N}, \bar{P})$ is shorthand for $\partial F / \partial N|_{(\bar{N}, \bar{P})}$.) To check the stability of $(\bar{N}, \bar{P})$ the quantities we need to examine are thus

$$\beta = a_{11} + a_{22} = 1 + ca\bar{N}/\lambda = 1 + \frac{\ln \lambda}{\lambda - 1}, \quad (26a)$$

$$\gamma = a_{11}a_{22} - a_{12}a_{21} = ca\bar{N}/\lambda + ca\bar{N}(1 - 1/\lambda) = ca\bar{N} = \frac{\lambda \ln \lambda}{\lambda - 1}. \quad (26b)$$

We now show that $\gamma > 1$. To do so we need to verify that $\lambda(\ln \lambda)/(\lambda - 1) > 1$ or $S(\lambda) \equiv \lambda - 1 - \lambda \ln \lambda < 0$. Observe that $S(1) = 0$, $S'(\lambda) = 1 - \ln \lambda - \lambda(1/\lambda) = -\ln \lambda$. So $S'(\lambda) < 0$ for $\lambda \geq 1$. Thus $S(\lambda)$ is a decreasing function of λ and consequently $S(\lambda) < 0$ for $\lambda \geq 1$.

We have verified that $\gamma > 1$ and so the stability condition given in Chapter 2, equation (32), is violated. We conclude that the equilibrium $(\bar{N}, \bar{P})$ can never be stable.

From the analysis we observe that the Nicholson-Bailey model has a single equilibrium

$$\bar{N} = \frac{\lambda \ln \lambda}{(\lambda - 1)ac}, \quad (27a)$$

$$\bar{P} = \frac{\ln \lambda}{a}, \quad (27b)$$

and that the equilibrium is never stable; small deviations of either species from the steady-state level leads to diverging oscillations. Curiously enough, a host-parasitoid system consisting of a greenhouse whitefly and its parasitoid was found to have such dynamics when grown under particular, albeit somewhat contrived, laboratory conditions (see Hassell, 1978, for details). Figure 3.3 demonstrates the fluctuations observed in this laboratory system and a comparison with the predictions of the Nicholson-Bailey model.

Most natural host-parasitoid systems are certainly more stable than the Nicholson-Bailey model seems to indicate. It would therefore seem that the model is not a satisfactory representation of real host-parasitoid interactions. However, before dismissing it as an ineffective model we shall exploit this theoretical tool to experiment with a number of conjectures on the effects (in natural systems) that might act as stabilizing influences. In the following section we therefore focus on more realistic assumptions about the searching behavior of the parasitoids and the host survival rate.

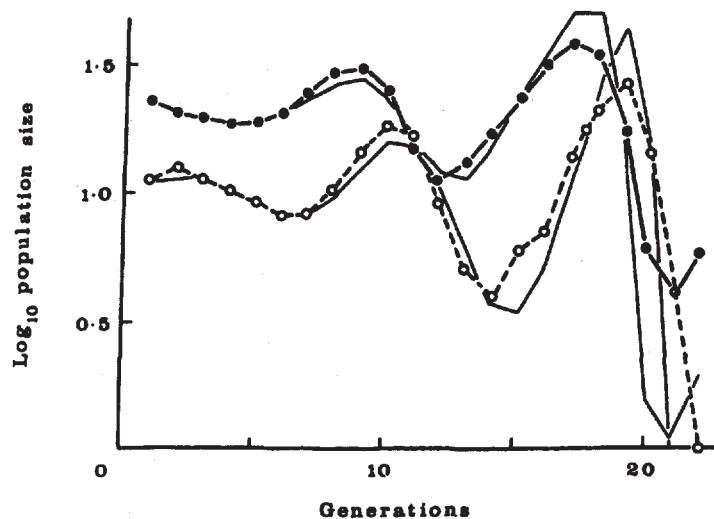


Figure 3.3 The Nicholson-Bailey model, given by equations (21a,b), predicts unstable oscillations in the dynamics of a host-parasitoid system. The fluctuations of a greenhouse whitefly *Trialeurodes vaporariorum* (●) and its chalcid parasitoid *Encarsia formosa* (○) give evidence for such behavior. The solid lines are predictions of

equations (21) where $a = 0.068$, $c = 1$, and $\lambda = 2$. [From Michael P. Hassell, *The Dynamics of Arthropod Predator-Prey Systems. Monographs in Population Biology 13*. Copyright © 1978 by Princeton University Press. Fig. 2.3 (after Burnett, 1958) reprinted by permission of Princeton University Press.]

3.4 MODIFICATIONS OF THE NICHOLSON-BAILEY MODEL²

Density Dependence in the Host Population

Since the Nicholson-Bailey model is unstable for *all* parameter values, we consider first a modification of the assumptions underlying the host population dynamics and investigate whether these are potentially stabilizing factors. Thus, consider the following assumption:

6. In the absence of parasitoids, the host population grows to some limited density (determined by the carrying capacity K of its environment).

Thus the equations would be amended as follows:

$$\begin{aligned} N_{t+1} &= N_t \lambda(N_t) e^{-aP_t}, \\ P_{t+1} &= N_t (1 - e^{-aP_t}). \end{aligned}$$

For the growth rate $\lambda(N_t)$ we might adopt

$$\lambda(N_t) = \exp r(1 - N_t/K),$$

2. This section is based on a review by David F. Dabbs.

as in equation (8). Thus if $P = 0$, the host population grows up to density $N_t = K$ and declines if $N_t > K$. The revised model is

$$N_{t+1} = N_t \exp [r(1 - N_t/K) - aP_t], \quad (28a)$$

$$P_{t+1} = N_t(1 - e^{-aP_t}). \quad (28b)$$

This model was studied in some detail by Beddington et al. (1975). They found it convenient to discuss its behavior in terms of the quantity q where

$q = \bar{N}/K$ = the ratio of steady-state host density with and without parasitoids present.

The value of q indicates to what extent the steady-state population is depressed by the presence of parasitoids.

Equations (28a,b) are sufficiently complicated that it is impossible to derive explicit expressions for the states $\bar{N}$ and $\bar{P}$. However, these can be expressed in terms of q and $\bar{P}$ as follows:

$$\bar{P} = \frac{r}{a}(1 - \bar{N}/K) = \frac{r}{a}(1 - q), \quad (29a)$$

$$\bar{N} = \bar{P}/(1 - e^{-a\bar{P}}). \quad (29b)$$

It transpires that the resulting model is stable for a fairly wide range of realistic parameter values, as desired. Even so, the return to equilibrium in these ranges is typically rather complex. As parameters are changed, the equilibrium does lose its stability property, so that cycles and other more complicated dynamics ensue. Beddington et al. (1975) demonstrate that stability depends on r and the quantity $q = \bar{N}/K$ with the system stable within the shaded range in Figure 3.4. We see that for each value of r , there exists a range of q values for which the model is stable; the larger the value of r , the narrower the range.

When the equations of a model are difficult to analyze explicitly, computer simulations can prove particularly revealing. In Figures 3.5 through 3.8 the behavior

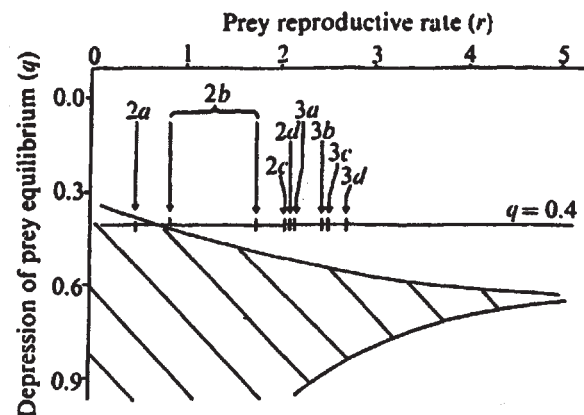


Figure 3.4 The density-dependent Nicholson-Bailey model (equations 28) is stable within the hatched area. Note how the area of stability narrows for

high values of r . [Reprinted by permission from Nature, 255, 58–60. Copyright © 1975 Macmillan Journals Limited.]

of solutions to equations (28a,b) obtained with a simple computer simulation are displayed for a variety of parameter choices. A TURBO - PASCAL program, written by David F. Dabbs and run on a personal computer, was used to generate successive values of N_i and P_i and to plot these simultaneously. What is somewhat novel about these plots is that in this two-variable system, time is suppressed and (N_i, P_i) values are plotted in the plane sometimes referred to as the NP phase plane. (In a later chapter a similar technique will be applied to systems of two differential equations in two variables.)

To interpret these figures, note that a central cross indicates the position of the steady state of the equations. The initial values (N_0, P_0) are specified at the top right-hand corner of the graph. In Figure 3.5 successive values proceed in a counterclockwise manner, visiting each of the arms of the "spiral galaxy" in succession. In Figures 3.6 through 8, $q = 0.40$ is kept fixed, while r is given the values 0.50, 2.00, 2.20, and 2.65.

For small values of r , the equilibrium point $(\bar{N}, \bar{P})$ is stable; any initial value spirals in toward it (Figure 3.5) and will eventually reach it. As r grows past a certain value, the equilibrium becomes unstable and new patterns emerge.

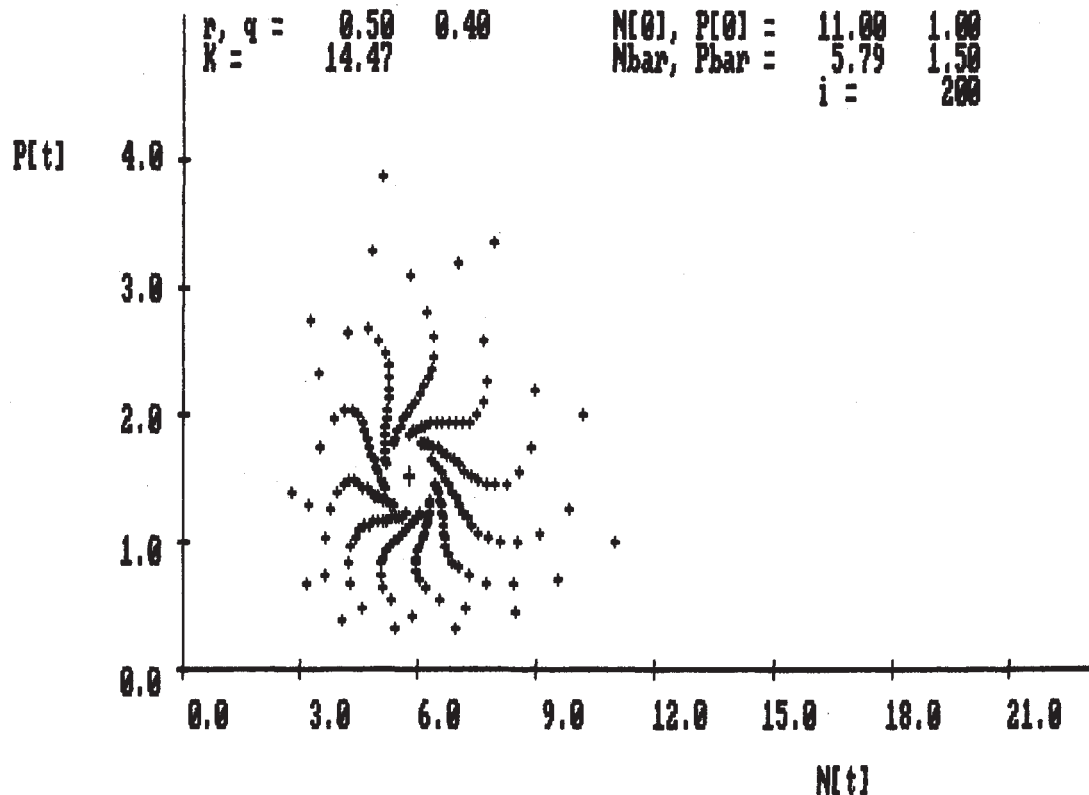


Figure 3.5 A single approach to equilibrium from an arbitrarily chosen outlying point. Note that the direction of flow is counterclockwise about the

steady-state point, not inward along the spiral arms. [Computer-generated plot made by David F. Dabbs.]

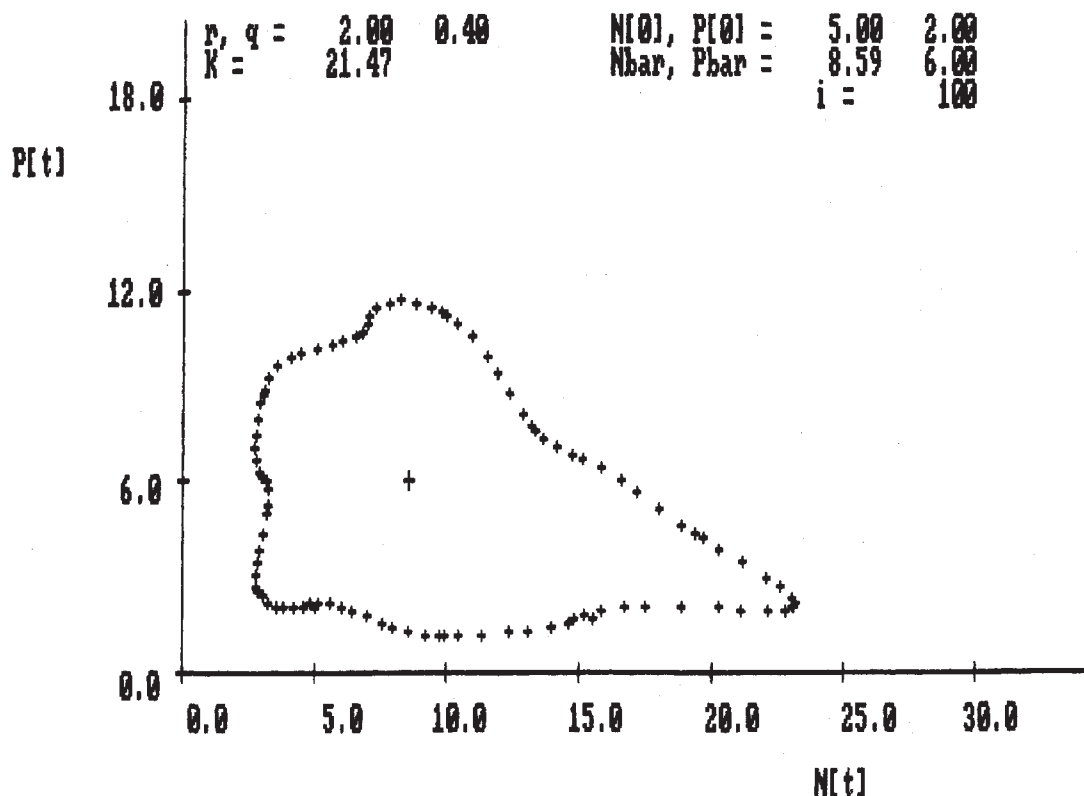


Figure 3.6 This stable "limit" cycle is jagged about the edges. Similar cycles for smaller values of r have smooth edges. [Computer-generated plot made by David F. Dabbs.]

Away from the single equilibrium point, the model will settle into a stable limit cycle around the equilibrium point, as shown in Figure 3.6. Larger values of r result in larger and larger cycles. Beyond a certain point there appear cycles whose periods are multiples of 5 (Figure 3.7). Still larger values of r yield either chaos or cycles of extremely high integral period. For large enough values of r , this chaotic behavior will seem to fill in a sharply bounded area (Figure 3.8).

As Figure 3.4 indicates, q and r are both involved in determining the dynamic population behavior. This figure can be interpreted to mean that the greater the depressing influence of parasitoids on their hosts, the lower the growth rate r that suffices to induce chaotic dynamics.

Other Stabilizing Factors

As we have just shown, the Nicholson-Bailey model is rendered more stable, and hence more realistic for most natural host-parasitoid systems, by taking into account the limitations of the environment and the fact that populations are not capable of infinite growth. Several other effects have been studied (notably by Beddington et

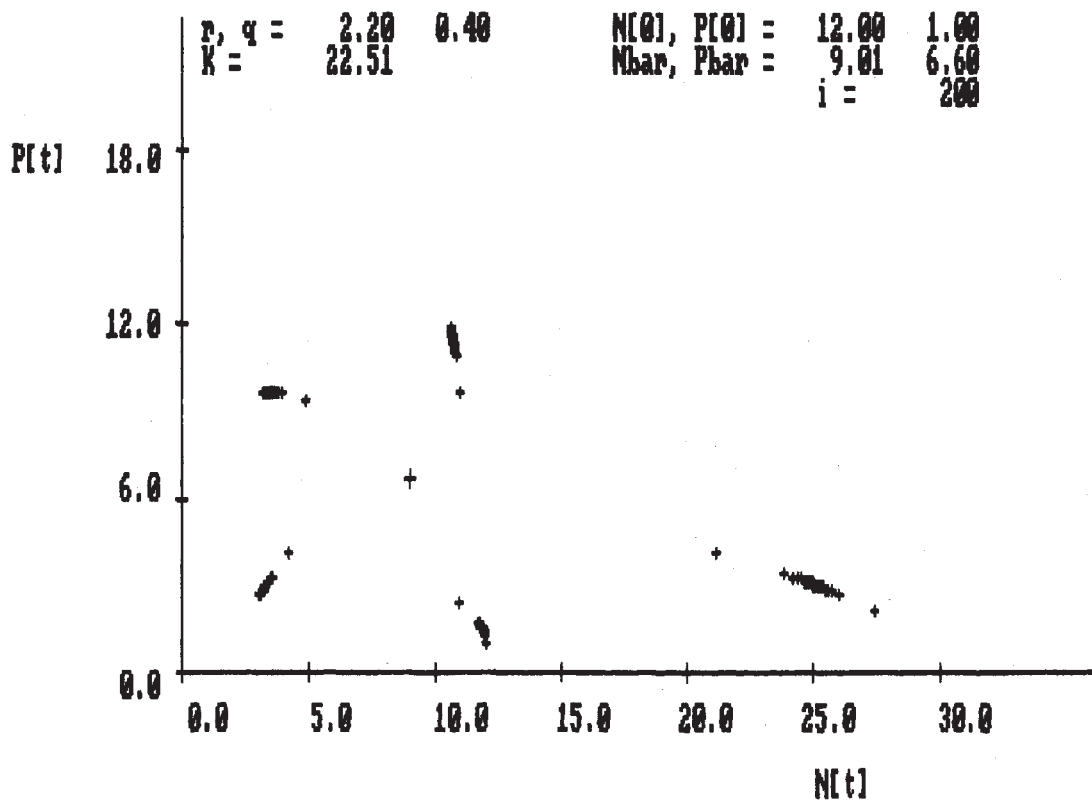


Figure 3.7 This cycle shows a cycle whose period is 5. Further increasing r slowly would produce cycles of periods 10, 20, 40, and so on.

[Computer-generated plot made by David F. Dabbs.]

al., 1978) in further exploring the interactions that stabilize the host-parasitoid populations. Two of these are as follows.

1. Efficiency of the parasitoids

The density of the attacking parasitoids may have some effect on their efficiency in searching for hosts. It is observed that efficiency generally decreases somewhat when the parasitoid population is too large. This effect is modeled by changing the assumed form of $f(N_i, P_i)$. One version studied by Beddington et al. (1978) is

$$f(N_i, P_i) = \exp -(aP_i)^{1-m}, \quad (30)$$

where $m < 1$. (See Beddington et al., 1978, for a discussion of this assumption and predictions of the model.)

2. Heterogeneity of the environment (refuges)

A second factor that has been brought into closer scrutiny in recent years is the supposed homogeneity of the environment. Researchers recognize that the physical set-

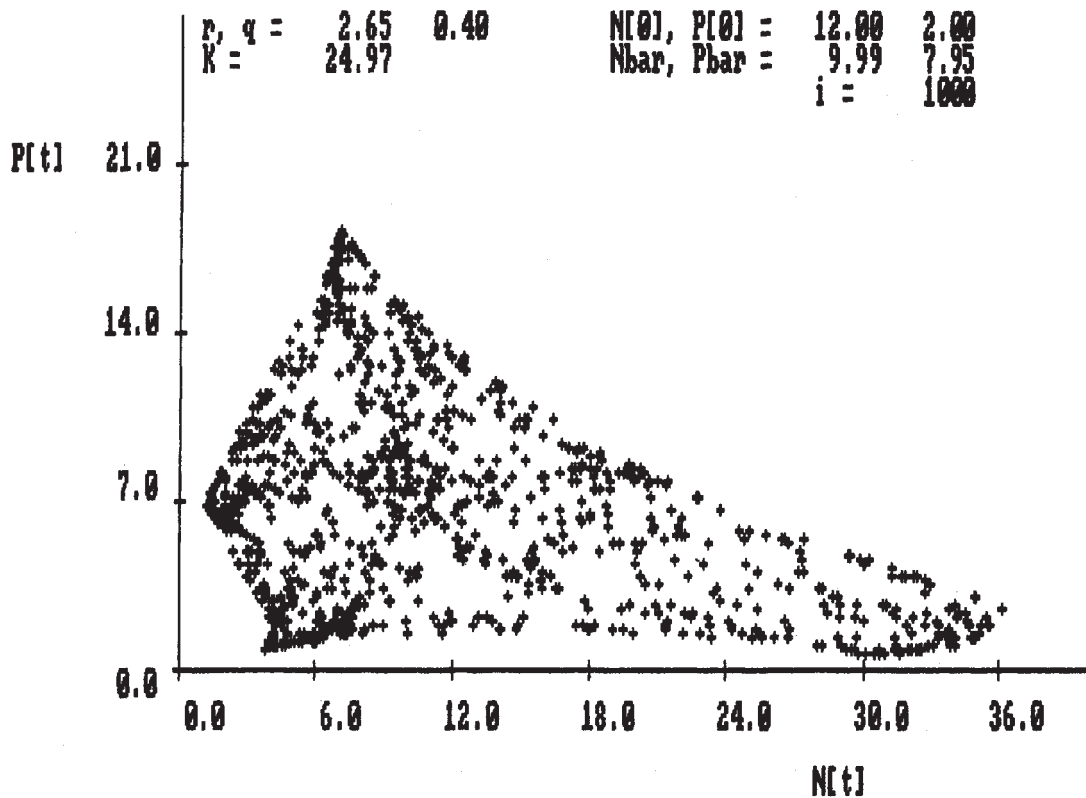


Figure 3.8 This sharply bounded figure shows definable areas without any points. For slightly lower r values these areas are better defined; for

higher r values they tend to fill in. [Computer-generated plot made by David F. Dabbs.]

ting is never perfectly uniform, so part of the host population may be less exposed and thus less vulnerable to attack. It has become popular to refer to *patchy* environments, which are spatially as well as temporally heterogeneous.

While a full treatment of spatial variation would lead us to models that involve several independent variables (for example, time as well as physical position), it is possible to consider a simple example that gives some broad indication of the effects. This is generally done by assuming that there exists a small refuge, representing some physical location to which some fraction of the attacked population can retreat for safety from the attackers. For example, let us assume that E is the fraction of the carrying capacity population K that can be accommodated in safe refuges. Then at any given time

EK/N_i = the fraction of the population that can retreat to a refuge,

$1 - EK/N_i$ = the fraction vulnerable to attack.

The equations would then be modified accordingly (see problem 11 and the original articles cited by the sources listed in the References). It has been a recurrent

theme of articles by Hassell, May, and others that the patchiness of ecosystems leads to stabilization. Part of the argument is that refuges serve as sites for maintaining vulnerable species that might otherwise become extinct. Such sites also indirectly benefit the exploiting species since a constant spillover of victims into the unprotected areas guarantees a constant food source. You are encouraged to pursue these topics by reading the excellent summaries and reviews and through further independent research.

3.5 A MODEL FOR PLANT-HERBIVORE INTERACTIONS

Outlining the Problem

In Sections 3.1 to 3.4 we saw numerous models that describe particular responses of a population to its environment, to another species, or to intraspecific competition. A notable feature of many such models is that they contain functions that are chosen to fit empirical data and that may or may not reveal any basic insight into underlying population behavior. What does one do when a plethora of empirical data is unavailable and one knows only vague, general properties of the processes? Is it always necessary to restrict attention to well-defined functional relationships when proceeding with a model?

As the model in this section will demonstrate, often even when data are available, it may be an advantage to study the problem in a rather general framework before fitting exact functional forms to the empirical observations. In this section we introduce a problem stemming from plant-herbivore systems and then use this general approach to study its properties. The problem to be considered here is hypothetical but sufficiently general to apply to a variety of cases. We use it to illustrate a technique and later comment on its applicability.

Consider herbivores that feed on a vegetation and consume part of its biomass.³ Unlike predation it need not be true that the damage or consumption inflicted by the herbivore, commonly called *herbivory*, necessarily leads to death of the victim, which in this case is the host plant. Rather, herbivores might reduce the biomass of vegetation they consume, possibly also causing other qualitative changes in the plant. In this first attempt at modeling plant-herbivore interactions we will focus only on quantitative changes, i.e., changes in the biomass of the populations. Some comments about plant quality will be made at the end of this section.

To give structure to the problem, we make the following broad assumptions:

1. Herbivores have discrete generations that correspond to the seasonality of the vegetation.

(*Comment:* We can thus treat the problem using a set of difference equations; the generation span will be identical for the two participants. This assumption is fairly realistic. Many herbivores have *coevolved* with their host

3. The term *biomass* is often used as a measure of population size in units of mass rather than, say, density or numbers of individuals.

plant species and have life cycles that are closely linked to seasonality or to stages of growth of the vegetation.)

2. The availability of vegetation and the current population density of herbivores are the main factors that determine fecundity and survivorship of the herbivores.

(*Comment:* While this statement seems plausible, we are surreptitiously assuming that other factors *do not* play major roles. This is an arguable point, to which we shall return.)

3. The abundance of the vegetation depends on the extent of herbivory to which the plant was subjected in the previous season as well as on the previous biomass of the vegetation.

(*Comment:* This too seems to be a reasonable basic hypothesis. To take one example, leaf biomass in deciduous trees contributes to production and storage of substances that will eventually be used to produce the next season's crop of leaves. Thus the plant biomass contributes in a positive sense to its future abundance. On the other hand, defoliation or herbivory might reduce the potential of a plant to grow and so would contribute negatively to the abundance of the vegetation in the next season.)

The model will be written in terms of the following two variables:

v_n = vegetation biomass in generation n ,

h_n = number of herbivores in generation n .

From our three assumptions we infer that the most general framework for a model of this plant-herbivore system would consist of the two equations

$$v_{n+1} = F(v_n, h_n), \quad (31a)$$

$$h_{n+1} = G(v_n, h_n). \quad (31b)$$

The functions F and G , which govern the population levels of the vegetation and herbivores respectively, will not be assigned particular mathematical expressions. Rather, we will use certain qualitative features of these functions to reason further. Our purpose below is to shed light on the following question: *Under what assumptions will it be true that the herbivores and plant populations are mutually regulating?* (The question is deliberately phrased in a vague way and bears more careful discussion. Before proceeding, you are encouraged to attempt to decipher this question independently.)

For a "mutually" regulated situation it must be true, first of all, that the model consisting of equations (31a,b) admits a nonzero steady-state solution $(\bar{v}, \bar{h})$. That is, the populations can coexist at some constant levels at which neither increase nor decrease occurs. We recall that these values must, by definition, satisfy the relations

$$\bar{v} = F(\bar{v}, \bar{h}), \quad (32)$$

$$\bar{h} = G(\bar{v}, \bar{h}).$$

In dealing with even the simplest model, it often proves enormously useful to scale the equations in terms of quantities that are inherent to the process. In this way we will reduce the number of parameters to consider. For those of you who do not wish to scrutinize the details of this rescaling procedure (in the following subsection), the idea is equivalent to assuming that the values $\bar{v}$ and $\bar{h}$ are both equal to 1.

Rescaling the Equations

We define new variables that are ratios of the old variables and their steady-state values as follows:

$$v_n^* = v_n / \bar{v}, \quad (33a)$$

$$h_n^* = h_n / \bar{h}. \quad (33b)$$

The equations rewritten in terms of the new, scaled variables will have steady-state values $\bar{v}_n^* = \bar{h}_n^* = 1$.

Example

The equations

$$x_{n+1} = \alpha x_n y_n^\beta, \quad (34a)$$

$$y_{n+1} = \gamma \frac{y_n}{\delta + x_n}, \quad (34b)$$

have the corresponding steady states

$$\bar{y} = \alpha^{-1/\beta}, \quad (35)$$

$$\bar{x} = \gamma - \delta, \quad \gamma > \delta.$$

Defining

$$x_n^* = x_n / (\gamma - \delta), \quad (36)$$

$$y_n^* = \alpha^{1/\beta} y_n,$$

we obtain the rescaled form

$$x_{n+1}^* = x_n^* y_n^{*\beta}, \quad (37)$$

$$y_{n+1}^* = \frac{y_n^*}{\epsilon + x_n^*(1 - \epsilon)},$$

where $\epsilon = \delta/\gamma$. It can be verified (see problem 14) that the steady-state solutions to (37) are

$$\bar{x}_n^* = \bar{x}_{n+1}^* = 1,$$

$$\bar{y}_n^* = \bar{y}_{n+1}^* = 1.$$

Notice that two parameters rather than the previous four appear in equations (37).

With the justification given in this example we may at this point assume that equations (31a,b) have been rescaled and are written in terms of new variables, as follows:

$$\begin{aligned} v_{n+1}^* &= F^*(v_n^*, h_n^*), \\ h_{n+1}^* &= G^*(v_n^*, h_n^*), \end{aligned} \quad (38)$$

with steady-state solutions

$$\bar{v}_{n+1}^* = \bar{h}_{n+1}^* = 1. \quad (39)$$

For convenience of notation, we shall drop the asterisks, return to the form shown in (31), and simply assume that both steady-state levels are unity. The reasons for making this simplification will emerge.

Further Assumptions and Stability Calculations

Assuming that equations (31a,b) have steady states $\bar{v} = 1$ and $\bar{h} = 1$ will simplify analysis of the model. To continue defining the problem we use several assumptions to deduce features of the functions F and G . From the comment on assumption 3 we may infer that the following two statements are true.

- 3a. The greater the herbivory, the lower will be the abundance of vegetation in the next season.
- 3b. The greater the current vegetation biomass, the greater will be next season's vegetation biomass.

Since the vegetation level is governed by equation (31a), these statements lead us to deduce that F is a decreasing function of h and an increasing function of v . Mathematically this means that

$$\begin{aligned} \frac{\partial F}{\partial h} &< 0 && \text{(from 3a),} \\ \frac{\partial F}{\partial v} &> 0 && \text{(from 3b).} \end{aligned}$$

In other words, assumptions (3a) and (3b) determine the signs of the partial derivatives of the function F (see Figure 3.9).

We shall treat the second function in a slightly different way, first noting that it represents herbivore recruitment. Assuming the herbivore population changes by reproduction or mortality (and not by migration), we shall rewrite G as a product of the number of herbivores and the net recruitment per individual; that is, assume G has the form

$$G(v_n, h_n) = h_n R(v_n, h_n). \quad (40)$$

The function R is the net number of adult herbivores that are progeny of a single individual herbivore when both fecundity and survivorship are taken into account. It

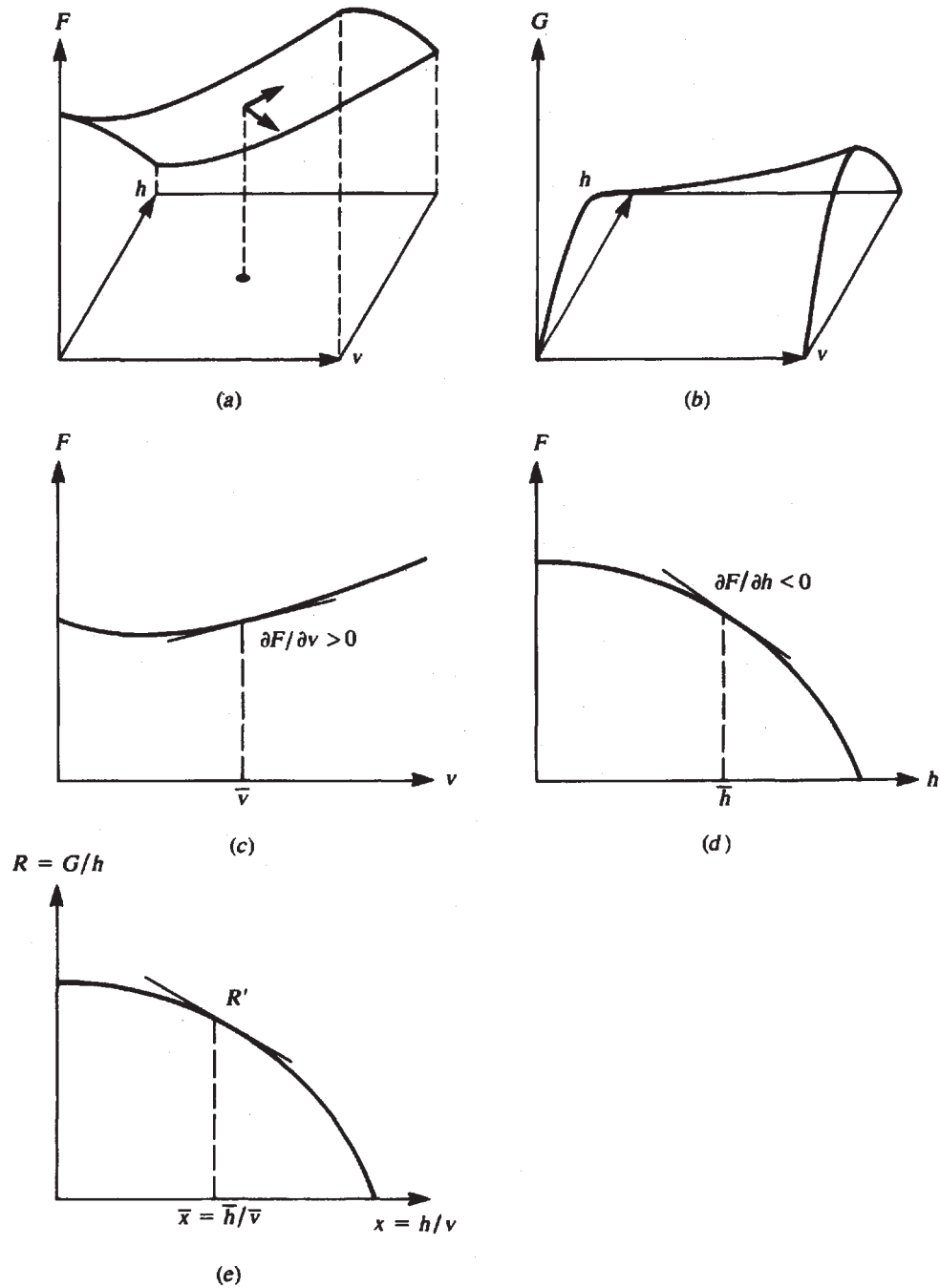


Figure 3.9 The functions F and G , which depict plant and herbivore responses, may depend on v and h in some complicated way as shown in (a) and (b). (c–e) In analyzing the plant-herbivore model

we have only used information about the slopes (partial derivatives) of F and $R = G/h$ at the steady-state point $(\bar{v}, \bar{h})$.

follows from equation (40) that

$$\frac{\partial G}{\partial v} = h \frac{\partial R}{\partial v}, \quad (41a)$$

$$\frac{\partial G}{\partial h} = h \frac{\partial R}{\partial h} + R. \quad (41b)$$

We now complete the formulation of this model by making assumptions about the function R .

2a. Recruitment of herbivores depends on the extent of competition for the vegetation, i.e., on the average number of herbivores that must share a unit of available vegetation.

2b. The greater the competition in generation n , the lower the recruitment for the next generation.

(Comment: This will be true of some but not all plant-herbivore systems. A number of leading biologists maintain that competition for resources plays a minimal role, if any, in herbivory. See, for example, Strong et al., 1984. The question is a controversial one.)

By assumption (2a), R is a function of the ratio $x = h_n/v_n$ of the two variables; by assumption (2b), it is a decreasing function of its argument. To summarize:

$$R = R(x), \quad \text{where } x = \frac{h_n}{v_n} \quad (\text{from 2a})$$

$$\frac{dR}{dx} < 0. \quad (\text{from 2b})$$

Using the *chain rule* of elementary calculus we notice that

$$\frac{\partial R}{\partial h} = \frac{dR}{dx} \frac{\partial x}{\partial h} = \frac{R'}{v}, \quad (42a)$$

$$\frac{\partial R}{\partial v} = \frac{dR}{dx} \frac{\partial x}{\partial v} = \frac{-R'h}{v^2}. \quad (42b)$$

where $R' = dR/dx$.

Collecting all equations and assumptions of the model so far, we have the following two equations:

$$V_{n+1} = F(V_n, h_n), \quad (43)$$

$$h_{n+1} = G(V_n, h_n) = h_n R(x_n), \quad (44)$$

where $x_n = h_n/V_n$, $R'(x) < 0$, and the partial derivatives of F satisfy $F_h < 0$, $F_v > 0$.

We now explore the outcome and predictions of the model. We return to a question posed earlier in this section to determine when the plant-herbivore system is

self-regulating in the sense that the nonzero steady state is stable. To determine when this holds, we resort to the stability criteria outlined previously. To formulate these in a convenient way, we use the following symbols to represent quantities that enter into a stability calculation:

Let

$$\nu = \left. \frac{\partial F}{\partial v} \right|_{ss}, \quad (45a)$$

$$-\mu = \left. \frac{\partial F}{\partial h} \right|_{ss}, \quad (45b)$$

$$-\epsilon = \left. \frac{dR}{dx} \right|_{ss}, \quad x = h/v, \quad (45c)$$

where ss means the steady-state value, $\bar{v} = \bar{h} = 1$. The constants ν , μ , and ϵ are positive, and signs preceding them depict our conclusions about the derivatives of the functions F and R . Note that partial derivatives are all evaluated at the steady state $\bar{v} = \bar{h} = 1$. Using the last definition one can show that

$$\begin{aligned} \left. \frac{\partial G}{\partial h} \right|_{ss} &= 1 - \epsilon, \\ \left. \frac{\partial G}{\partial v} \right|_{ss} &= \epsilon. \end{aligned} \quad (46)$$

[See problem 12(b).] Thus the Jacobian of (43) and (44) at the steady state $\bar{v} = \bar{h} = 1$ is

$$J = \begin{pmatrix} \left. \frac{\partial F}{\partial v} \right|_{ss} & \left. \frac{\partial F}{\partial h} \right|_{ss} \\ \left. \frac{\partial G}{\partial v} \right|_{ss} & \left. \frac{\partial G}{\partial h} \right|_{ss} \end{pmatrix} = \begin{pmatrix} \nu & -\mu \\ \epsilon & 1 - \epsilon \end{pmatrix}. \quad (47)$$

Comment: The fact that equations were scaled in terms of the steady-state values and that herbivore recruitment depends only on the ratio $\bar{h}/\bar{v}$ results in a total of three independent parameters in equation (47).

The characteristic equation for (47) is

$$\lambda^2 - \beta\lambda + \gamma = 0, \quad \text{where} \quad \begin{aligned} \beta &= \nu + (1 - \epsilon), \\ \gamma &= \nu(1 - \epsilon) + \mu\epsilon. \end{aligned} \quad (48)$$

For stability of the steady state, both roots of the characteristic equation must satisfy $|\lambda| < 1$. Using the stability criteria (see Chapter 2, equations 32), we conclude that for this to be true

$$|\beta| < 1 + \gamma < 2,$$

that is,

$$|\nu + (1 - \epsilon)| < 1 + \nu + \epsilon(\mu - \nu) < 2. \quad (49)$$

Deciphering the Conditions for Stability

Although the mathematical steps leading to a stability condition are now complete, there is still work to be done; we must now extract some meaningful information from the murky inequality in (49). To do so it is necessary to “unravel” the tangle of parameters to reach a clearer statement and then to interpret the results in their biological context by using the original definitions. The process of manipulating the appropriate inequalities is illustrated in the following:

	$ \beta < 1 + \gamma < 2:$	
1.	$ \beta < 2$ means that $-2 < \nu + 1 - \epsilon < 2$, so $-3 < \nu - \epsilon < 1.$	(50a)
2.	$\beta < 1 + \gamma$ means that $\nu + 1 - \epsilon < 1 + \nu + \epsilon(\mu - \nu).$ Therefore, $-\epsilon < \epsilon(\mu - \nu),$ $-1 < \mu - \nu,$ $\nu - \mu < 1.$	(50b)
3.	Subtracting (50b) from (50a) produces $\mu - \epsilon < 0$, or $\mu < \epsilon.$	(50c)
4.	$1 + \gamma < 2$ means that $\nu - \mu < 1.$	(50d)
(See problem 13.) <i>Note:</i> This is covered by the results of (50b), so no new information is obtained.		
5.	$ \beta < 1 + \gamma$ means that $-1 - \gamma < \beta < 1 + \gamma$	
so by problem 13,		
	$\epsilon < \frac{2(1 + \nu)}{1 - \mu + \nu}.$	(50e)

The above procedure yields a set of three relationships (50a–c) linking pairs of parameters and one inequality of a more complicated form (50e). To interpret these conditions for stability we now summarize what the parameters represent.

$$\nu = F_v|_{ss} \approx \frac{\Delta v_{n+1}}{\Delta v_n} \quad \text{at } (\bar{v}, \bar{h}) = \text{the change in next year's vegetation biomass caused by a change in the current vegetation biomass.}$$

$$-\mu = F_h|_{ss} \approx \frac{\Delta v_{n+1}}{\Delta h_n} \quad \text{at } (\bar{v}, \bar{h}) = \text{change in next year's vegetation biomass due to an increment in current herbivore level.}$$

$$\epsilon = G_v|_{ss} \approx \frac{\Delta h_{n+1}}{\Delta v_n} \quad \text{at } (\bar{v}, \bar{h}) = \text{change in next year's herbivore population } h_{n+1} \text{ due to increment in current plant biomass.}$$

$$1 - \epsilon = G_h|_{ss} \approx \frac{\Delta h_{n+1}}{\Delta h_n} \quad \text{at } (\bar{v}, \bar{h}) = \text{change in } h_{n+1} \text{ due to increment in current herbivore population.}$$

Note: all these quantities are computed when the populations are close to their steady-state levels.

We see that from equations (50a–e) we can reach the following conclusions:

1. $\mu < \epsilon$ (50c) means that, close to the steady state,

$$-\frac{\partial F}{\partial h} < \frac{\partial G}{\partial v}. \quad (51a)$$

When paraphrased, equation (51a) implies that

$$\left. \begin{array}{l} \text{the decline in vegetation} \\ \text{biomass due to an} \\ \text{increment in herbivory} \end{array} \right\} \text{ is less than } \left\{ \begin{array}{l} \text{the increase in the herbi-} \\ \text{vore population due to an} \\ \text{increase in vegetation mass} \end{array} \right.$$

2. $\nu - \mu < 1$ (50b) means that, close to the steady state,

$$\frac{\partial F}{\partial v} + \frac{\partial F}{\partial h} < 1. \quad (51b)$$

To interpret, this would mean that the combined changes in plant biomass due to slight increases in both v and h are not too drastic. It is interesting to note that if F is independent of h , the condition reduces to the stability condition for the plant in isolation (i.e., $\partial F / \partial v|_{ss} < 1$).

3. $-3 < v - \epsilon < 1$ (50a) means that, close to the steady state,

$$-3 < \frac{\partial F}{\partial v} - \frac{\partial G}{\partial v} < 1. \quad (51c)$$

Thus changes in v and h caused by an increment in the vegetation biomass should be roughly balanced within the indicated bounds.

Other conclusions are left as an exercise in the problems.

To understand why some of these conditions are a prerequisite for stability, consider a hypothetical situation in which v_n and h_n are close to (but not at) the steady state; for example, $v_n = 1 + \Delta v$, $h_n = 1$.

If condition (51a) is not satisfied, the following chain of events might occur: the biomass increment causes herbivores to proliferate ($h_{n+1} > 1$). This causes a *large* decline in plant biomass ($v_{n+2} < 1$), which leads to a drop in herbivores ($h_{n+3} < 1$). The plant biomass increases again ($v_{n+4} > 1$), and the cycle repeats. By this means a periodic behavior could be established with both populations cycling about their steady-state values. By considering several other scenarios, the student should be able to give similar justification for these stability conditions.

Comments and Extensions

Perhaps the most important conclusion to be drawn from the example discussed above in the previous subsection is that it often makes good sense to treat a problem in an "impressionistic" way. Rather than adopting particular functional forms for describing the population growth, fecundity, and interactions, one might consider first trying rather broad assumptions about their dependence on population levels.

What makes this approach attractive is that it can ease the burden of manipulating complicated mathematical expressions. After the appropriate inequalities are derived, it is generally straightforward to determine when particular functions are likely to satisfy these conditions and so lead to stability in the population. Moreover, given a whole *class* of growth functions or fecundity functions, one can identify the particular *feature* that contributes to stabilizing the population. [For example, inequality (51b) tells us that F cannot be a very steeply varying function of its arguments: small changes in the population levels should not engender large changes in the predicted vegetation biomass.]

Yet a third positive feature of this general analysis is that it leads to much greater ease of experimentation with the model, as suggested by several problems at the end of the chapter. For example, we might like to determine how changing one assumption alters the conclusions. This is rather easy to do in the abstract and usually does not require a repetition of all the calculations.

As a conclusion to this model, it may be wise to shed a somewhat broader perspective on the topic of plant-herbivore interactions. Recent biological research on this problem has revealed that interactions between herbivores and their vegetation may be extremely diverse, subtle, and full of surprises. This is especially true of insect herbivores, whose evolution may be closely linked to those of their plants. In

many cases it has been discovered that plants have active defense strategies (using many forms of chemical weapons) or are able to undergo qualitative changes that may adversely affect their attackers.

Models that treat only the quantitative aspects of herbivory such as reduction in plant biomass are relatively naive and rarely accurate in portraying the situation. For this reason, we would want to develop a different type of model that treats more fully the changes in character of the plant and its host. (For a hint on how this might be done, see problem 17.)

Several recent books and articles provide excellent summaries of current thoughts on plant-herbivore interactions. Among these, Crawley (1983) and Rhoades (1983) are strongly recommended sources for further reading and research.

3.6 FOR FURTHER STUDY: POPULATION GENETICS

The genetics of populations with discrete generations is yet another topic well suited for difference equation techniques. Many excellent books and articles on this subject can be recommended for independent research. (A partial list is given in the References.) This section is an elementary introduction to Hardy-Weinberg genetics, which is explored further in the problems following the chapter.

The genetic material in *eukaryotes*⁴ is made up of units called *chromosomes*. Organisms (such as humans) that are *diploid* have two sets of chromosomes, one obtained from each parent. A *locus* (a given location on a chromosome) may contain the blueprint instructions for some physical trait (such as eye color), which is determined by the combination of genes derived from each of the parents. A given gene may have one of several forms, called *alleles*. [It is not always known how many alleles of a given gene are present in the *genetic pool* (i.e., total genetic material) of a population.]

Suppose that there are two alleles, denoted by a and A , and that these are passed down in the population from one generation to the next. A given individual could then have one of three combinations: AA , aa , or aA . (The first two combinations are called *homozygous*, the last one *heterozygous*.) It is of interest to follow the distribution of genes in a population over the course of many generations.

A question we might explore is whether the relative frequencies of genes will change, and, if so, whether some new stable distribution will emerge. Until 1914 it was believed that any rare allele would gradually disappear from a population. After a more rigorous treatment of the problem it was shown that if *mating is random* and all *genotypes* (combinations of alleles, which in this case are aa , AA , and aA) are *equally fit* (have an equal likelihood of surviving to produce offspring), then gene frequencies do not change. This fact is now known as the *Hardy-Weinberg law*.

In the problems we investigate how the Hardy-Weinberg law can be demonstrated, and then explore other areas in which the theory can be extended. For further independent reading, Li (1976), Roughgarden (1979), Ewens (1979), and Crow

4. *Eukaryotes* are organisms whose cells have well-defined nuclei in which all the genetic material is contained.

and Kimura (1970) are recommended. A mathematical treatment of the case of unequal genotype fitness is given by Maynard Smith (1968) and in a more expanded form by Segel (1984).

To outline the problem, several definitions and assumptions are needed. By convention we shall define the frequencies of the alleles A and a in the n th generation as follows:

$$p = \text{frequency of allele } A = \frac{\text{total number of } A \text{ alleles}}{2N},$$

$$q = \text{frequency of allele } a = \frac{\text{total number of } a \text{ alleles}}{2N},$$

where $p + q = 1$, and N = the population size.

We now incorporate the following assumptions:

1. Mating is random.
2. There is no variation in the number of progeny from parents of different genotypes.
3. Progeny have equal fitness (that is, are equally likely to survive).
4. There are no mutations at any step.

We define the genotype frequencies of AA , aA , and aa in a given population to be:

u = frequency of AA genotype,

v = frequency of aA genotype,

w = frequency of aa genotype.

Then $u + v + w = 1$. Since aA is equivalent to Aa , it is clear that

$$p = u + \frac{1}{2}v, \quad (52a)$$

$$q = \frac{1}{2}v + w. \quad (52b)$$

The next step is to calculate the probability that parents of particular genotypes will mate. If mating is random, the mating likelihood depends only on the likelihood of encounter. This in turn depends on the product of the frequencies of the two parents. The *mating table* (Table 3.1) summarizes these probabilities. (Six missing entries are left as an exercise for the reader.)

Table 3.1 *Mating Table*

Genotype			Fathers		
			AA	Aa	aa
			u	v	w
Frequency %			u	v	w
Mothers	AA	u	u ²	uv	uw
	Aa	v	—	v ²	—
	aa	w	—	—	—

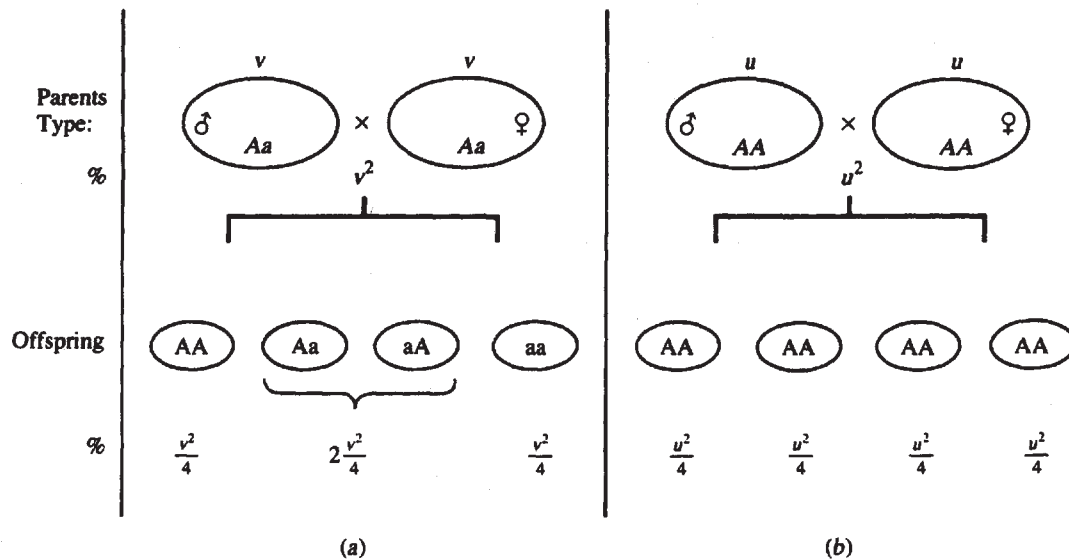


Figure 3.10 Offspring of (a) the cross $Aa \times Aa$ and (b) the cross $AA \times AA$ are shown with the relative frequencies with which they occur.

Based on the likelihood of mating, one can determine the probability of a given match resulting in offspring of a given genotype. To do this, it is necessary to take into account the four possible combinations of alleles derived from a given pair of parents. Figure 3.10 demonstrates what happens in the case of two heterozygous or two homozygous parents. Other cases are left for the reader. The *offspring table* (Table 3.2) is a convenient way to summarize the information. (Some entries have been left blank for you to fill in—see problem 18.)

Table 3.2 Offspring Table

Type of Parents	Frequency	Offspring Genotype Frequencies		
		AA	aA	aa
$AA \times AA$	u^2	u^2	—	—
$AA \times Aa$	$2uv$	uv	uv	—
$AA \times aa$	—	0	—	—
$Aa \times Aa$	v^2	$v^2/4$	$v^2/2$	$v^2/4$
$Aa \times aa$	—	0	—	—
$aa \times aa$	—	0	—	—
Total		$(u^2 + uv + v^2/4)$	—	—

Note: All genotypes are assumed to have equal likelihood of surviving to reproduce. If *fitness* depended on genotype, these entries would be weighted by the probability that a given parent survived to mate.

By counting up the total frequency of offspring of each type, we get values for u , v , and w for the next generation, which we shall call u_{n+1} , v_{n+1} , and w_{n+1} . It can be shown (see problem 18e) that these are related to the n th-generation frequencies by the equations

$$u_{n+1} = u_n^2 + u_n v_n + \frac{1}{4} v_n^2, \quad (53a)$$

$$v_{n+1} = u_n v_n + 2u_n w_n + \frac{1}{2} v_n^2 + v_n w_n, \quad (53b)$$

$$w_{n+1} = \frac{1}{4} v_n^2 + v_n w_n + w_n^2. \quad (53c)$$

As an example, consider equation (53a) and note that the cumulative number of offspring of genotype AA (in the vertical column of Table 3.2) leads to the given relationship.

In the problems, you are asked to show that these equations lead to the conclusion that gene frequencies p and q , as well as genotype frequencies u , v , and w , do not change under random mating with equal fitness. In addition, Hardy-Weinberg equilibrium is attained after a single generation. This conclusion depends on an assumption that the genes are not located on the chromosomes that determine the sex of an individual.

PROBLEMS*

1. The model for density-dependent growth due to Varley, Gradwell, and Hassell (1973) given by equation (3), has the undesirable feature that, for low population levels, the fraction of survivors $f = N_s/N_i = \frac{1}{\alpha}(N_i)^{-b}$ is greater than 1.
 - (a) Explain why this is faulty.
 - (b) Find the critical population level, N_c , below which this happens. (N_c should be expressed in terms of α and b .)
 - (c) Suggest how the model might be modified to alleviate this problem.
2. Sketch the fraction of survivors as a function of population size for the following models:
 - (a) Equation (3).
 - (b) Equation (13).
3.
 - (a) In the model for single-species populations given by equation (8), show that $N = 0$ is one steady state and $N = K$ is another (the only *nontrivial* steady state).
 - (b) Verify equation (10).
 - (c) Show that the population increases if $N < K$ and decreases if $N > K$ by considering the magnitude of the reproductive rate

$$\lambda = \exp r(1 - N_i/K).$$
4. In this problem we investigate the model for density dependence due to Hassell (1975) given by equation (13).

Problems preceded by an asterisk () are especially challenging.

- (a) What are the effects of the three parameters, λ , a , and b ? Do increased values of these parameters strengthen or weaken the growth of the population?
- (b) For certain parameter ranges, this equation has a biologically meaningful nonzero steady state. Show that this steady state is given by

$$\bar{N} = \frac{\lambda^{1/b}}{a},$$

and discuss the appropriate parameter constraints. (*Hint*: Recall that $\bar{N}$ has to be positive.)

- (c) Determine conditions for stability of the above steady state.
5. Hassell et al. (1976) give the following estimates for the parameters λ and b of equation (13) for several insect populations.

	b	λ
Moth: <i>Zeiraphera diniana</i>	0.1	1.3
Bug: <i>Leptoterna dolabrata</i>	2.1	2.2
Mosquito: <i>Aedes aegypti</i>	1.9	10.6
Potato Beetle: <i>Leptinotarsa decemlineata</i>	3.4	75.0
Parasitoid wasp: <i>Bracon hebetor</i>	0.9	54.0

- (a) Plot these values on a λb -parameter plane. (Recommendation: use a log scale for the λ axis.)
- (b) Use your results from problem 4 to determine which of these species will have a stable steady-state population level.
6. (a) Give two examples of physical processes that can be described by a Poisson distribution. (You may wish to consult a text on probability and statistics.)
- (b) Sketch $p(r)$ as a function of r .
- (c) Support the claim that in a host-parasitoid system the average number of encounters per host per unit time is

$$\mu = \frac{N_e}{N_i} = aP_i.$$

- (d) Suppose we relax the assumption 5 of Section 3.3 and instead assume that if a host is encountered *once*, it gives rise to c parasitoid progeny; if a host is encountered *twice* or more, it gives rise to $2c$ parasitoid progeny. How would the Nicholson-Bailey model change?
7. (a) From the stability calculations for the Nicholson-Bailey model we observe that the predictions are independent of the parameters a and c and depend only on λ . Explain the following observation: Consider a somewhat different formulation of the model. Define

$$n_i = acN_i,$$

$$p_i = aP_i,$$

where a , c are the constants defined in Section 3.3. Substitute the new variables into equations (21a, b) to obtain equations in terms of n_t and p_t . How many (new) parameters do these equations contain?

- (b) Interpret n_t and p_t .
- *(c) Determine whether the instability of the Nicholson-Bailey model is accompanied by oscillations by determining whether $\beta^2 - 4\gamma < 0$ for β , γ given by equations (26).

8. *Project:* One problem that leads to the oscillations in the Nicholson-Bailey model (equations 21a, b) is the fact that at low parasitoid densities the host population behaves approximately as follows:

$$N_{t+1} = \lambda N_t;$$

that is, it grows at an unchecked rate. Notice that this eventually causes the parasitoids to increase in number until their hosts are overwhelmed by the attack. This is what sets up the increasing oscillations in the system.

Consider the effect of introducing other types of density dependence into the host population. Two examples include

$$N_{t+1} = \lambda N_t \frac{(K - N_t)}{K} e^{-aP_t}, \quad (54)$$

and,

$$N_{t+1} = \lambda N_t^{1-b} e^{-aP_t}, \quad (55)$$

(see Varley and Gradwell (1963) and Hassell (1978)). Use the literature, computer simulations, and your own analysis to compare the predictions of these models and to comment on their applicability and/or special features. (*Note:* Stability analysis may be algebraically messy in such models.)

- 9. (a) Show that equations (28a, b) have the steady state given by (29), where q is defined as $q = \bar{N}/K$.
 - (b) Find the Jacobian matrix that corresponds to the linearized version of (28).
 - *(c) Find the stability conditions in terms of the parameter q and other parameters appearing in equations (28a, b).
 - *(d) Reason that Figure 3.4 is the expected stability domain in the qr parameter plane.
10. In this problem we consider the effect of parasitoid searching efficiency in the Nicholson-Bailey model.
- (a) Explain the restriction $m < 1$ in equation (30).
 - (b) Write a set of host-parasitoid equations that incorporate equation (30).
 - (c) Investigate the effect of the new assumption about $f(N_t, P_t)$. Determine whether steady states are elevated or depressed and whether stability is affected.
 - (d) Suggest other forms of $f(N_t, P_t)$ that might be reasonable in view of the biological assumption that parasitoids interfere with each other less and are hence more efficient at low densities.

11. In this problem we consider a host population that has refuges from parasitoid attack.

- (a) Explain the assertion that EK/N_t is the fraction of the population that can retreat to a refuge.
 (b) Explain why the fraction of hosts *not* parasitized is

$$f(N_t, P_t) = \frac{EK}{N_t} + \left(1 - \frac{EK}{N_t}\right)e^{-aP_t}.$$

- (c) Write an equation for N_{t+1} .
 (d) Explain why at time $t + 1$ the parasitoid density is given by

$$P_{t+1} = (N_t - EK)(1 - e^{-aP_t}).$$

- *(e) *Longer Project:* Consult the literature and use computer simulations and/or other analysis to explore the results and predictions of this model.

Questions 12 through 17 are based on the model for plant-herbivore interactions described in Section 3.5.

12. (a) Show that the function R takes on the value

$$R(\bar{h}/\bar{v}) = 1$$

for $\bar{h} = 1$ and $\bar{v} = 1$, the steady state of equations (31a, b).

- (b) Use part (a) and the results of Section 3.5 (subsection "Further Assumptions and Stability Calculations") to show that for $x = h/v$ and

$$-\epsilon = \left. \frac{dR}{dx} \right|_{ss}$$

it follows that

$$\left. \frac{\partial G}{\partial h} \right|_{ss} = 1 - \epsilon,$$

$$\left. \frac{\partial G}{\partial v} \right|_{ss} = \epsilon.$$

13. (a) Demonstrate that the inequalities (50d) and (50e) are correct.
 (b) Interpret the biological meaning of (50e).
 (c) Discuss why conditions (50d) and (50e) might be necessary to avoid instability of the plant-herbivore system.
14. Verify that steady-state solutions of equations (37) have the values $\bar{x} = 1$ and $\bar{y} = 1$.
15. Consider the following model for leaf-eating herbivores whose population size (number of individuals) is h_n on a tree whose leaf mass is v_n :

$$\begin{aligned} v_{n+1} &= f v_n (e^{-a h_n}), \\ h_{n+1} &= r h_n \left(\delta - \frac{h_n}{v_n} \right), \quad \text{where } v_n \neq 0 \end{aligned}$$

and where f, a, r, δ are positive constants.

- (a) Find the steady state(s) $\bar{v}$ and $\bar{h}$ of this system. What happens if $f = 1$? What restrictions on the parameters should be met for a biologically reasonable steady state?
- *(b) Show that by rescaling the equations, it is possible to reduce the number of parameters. To do this, define

$$V_n = v_n/\bar{v}, \quad H_n = h_n/\bar{h}.$$

Show that the system of equations can then be converted to the following form:

$$\begin{aligned} V_{n+1} &= V_n \exp k(1 - H_n), \\ H_{n+1} &= bH_n \left(1 + \frac{1}{b} - \frac{H_n}{V_n} \right). \end{aligned}$$

What is the connection between b , k , and the previous four parameters f , a , r , and δ ?

- (c) Show that the equations in part (b) now have steady-state solutions
- $$\bar{Q} = \bar{H} = 1.$$
- (d) Determine whether the functions in the equations of the model fall into the general category described in Section 3.5.
- (e) Determine when the steady state will be stable.
16. In this question we explore several variants of the model outlined in Section 3.5.
- (a) Suppose that for low levels of herbivory the function F , which represents the vegetation response, does not depend on the herbivore population and that $\partial F/\partial h < 0$ only beyond some value $h = \hat{H}$. How would this affect the conclusions of the model?
- (b) In some plants it is observed that moderate to low herbivory actually promotes enhanced growth. How would this be incorporated into the model and what would be the results?
- (c) Suggest other ways of incorporating the availability of the vegetation into the response of the herbivore population and explore the outcomes of these assumptions.
- (d) Suppose that migration into the patch of vegetation takes place at some rate that is enhanced by greater plant abundance. How would this be modeled, and how would it change the problem?
17. (Note to the instructor: Problem 17 gives the student good practice at formulating a model and gradually increasing its complexity. Do not expect the later stages of this problem to be as amenable to further direct analysis as the more elementary model. More advanced students may wish to implement their models in computer simulations.) As indicated near the end of Section 3.5, an important influence on herbivores is the quality of the host vegetation, not just its abundance. If the plants have induced chemical defenses or other protective responses, the population of attackers may suffer from increased mortality, decreased fecundity, and lower growth rates.

- (a) Define a new variable $\hat{q}_n$ as the *average quality* of the vegetation in generation n . Suggest what general equations might then be used to model the $v_n, \hat{q}_n, h_n$ system.
- (b) Instead of treating the vegetation as a uniform collection of identical plants, consider making a distinction between plants that are nutritious (or chemically undefended) and those that are not. For example, with h_n as before, let

u_n = number of undefended plants,

v_n = number of defended plants.

Now suppose that plants make the transition from u to v after attack by herbivores and back from v to u at some constant rate that represents the loss of chemical defenses. Formulate a model for v_n, u_n , and h_n .

- (c) As a final step, consider vegetation in which plants can range in quality q from 0 (very hostile to herbivores) to 1 (very nutritious to herbivores). Assume that the change in quality of a given plant takes place in very small steps every $\Delta\tau$ days at a rate that depends on herbivory in time interval n and on previous vegetation quality. That is,

$$q_{n+1} = q_n + F(q_n, h_n)\Delta\tau,$$

where F can be positive or negative. Let $v_n(q)$ be the percentage of the vegetation whose quality is q at the n th step of the process, and assume that the total biomass

$$V_n = \int_0^1 v_n(q) dq,$$

does not change over the time scale of the problem. Can you formulate an equation that describes how the distribution of vegetation quality $v_n(q)$ changes as each plant undergoes the above defense response?

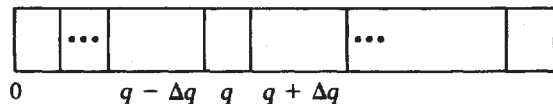


Figure for problem 17(c).

Hint: Consider subdividing the interval $(0, 1)$ into n quality classes, each of range Δq . How many plants leave or enter a given quality class during time $\Delta\tau$?

Questions 18 through 20 deal with the topic of population genetics suggested in Section 3.6.

18. (a) From the definitions of u , v , and w it is clear that

$$u + v + w = 1.$$

Show that $p + q = 1$.

- (b) Fill in the remaining six entries in Table 3.1.

- (c) Draw a diagram similar to that of Figure 3.10 for the mating of parents of type $AA \times aa$ and $Aa \times AA$.
- (d) Fill in the remaining entries in Table 3.2.
- (e) Verify that the cumulative frequencies of genotypes AA , Aa , and aa in the offspring are governed by equations (53a, b).
- (f) Show that

$$u_{n+1} + v_{n+1} + w_{n+1} = 1,$$

i.e., that u , v , and w will always sum up to 1.

- (g) Suppose that $(\bar{u}, \bar{v}, \bar{w})$ is a steady state of equations (53a, b). Use the information in part (f) to show that

$$\bar{u} = \bar{v}^2 / 4\bar{w}.$$

- (h) Since w_{n+1} is related to u_{n+1} and v_{n+1} (similarly for w_n , u_n , and v_n) by the identity in part (f), we can eliminate one variable from equations (53a, b). Rewrite these equations in terms of u and v .
- (i) Using part (h) show that

$$u_{n+1} = (u_n + \frac{1}{2}v_n)^2,$$

$$v_{n+1} = (u_n + \frac{1}{2}v_n)[2 - 2(u_n + \frac{1}{2}v_n)].$$

- (j) Now show that

$$(u_{n+1} + \frac{1}{2}v_{n+1}) = (u_n + \frac{1}{2}v_n).$$

- * (k) Show that this implies that the frequencies p and q do not change from one generation to the next; i.e., that

$$q_{n+1} = q_n, \quad p_{n+1} = p_n.$$

Hint: you must use the fact that $p^2 + 2pq + q^2 = 1$. When you succeed at this problem, you have proved the Hardy-Weinberg law.

19. Now consider the following modification of the random mating assumption: Suppose that individuals mate only with those of like genotype (e.g., Aa with Aa , AA with AA , and so forth). This is called *positive assortative mating*. How would you set up this problem, and what conclusions do you reach?
20. In *negative assortative matings*, like individuals do not mate with each other. Different types of models may be obtained, depending on assumptions made about the permissible matings. In the questions that follow it is assumed that homozygous females mate only with homozygous males of opposite type and that heterozygous females (Aa) mate with AA and aa males depending on their relative prevalence. The permitted matings are then as follows:

Females		Males
AA	$\times$	aa
aa	$\times$	AA
Aa	$\times$	AA
Aa	$\times$	aa

Assuming that a single male can fertilize any number of females results in a mating table that depends largely on the female frequencies, as shown in the mating table.

		Males		
		AA u	Aa v	aa w
Females	Genotype	Frequency		
	AA	u		
	Aa	v		
	aa	w		
		0	0	u
		$\frac{vu}{u+w}$	0	$\frac{vw}{u+w}$
		w	0	0

It is assumed that $u + v + w = 1$.

- Explain the entries in the table.
- Derive an offspring table by accounting for all possible products of the matings shown in the above mating table.
- Show that the fractions of AA, Aa, and aa offspring denoted by u_{n+1} , v_{n+1} , and w_{n+1} satisfy the equations

$$u_{n+1} = \frac{1}{2} v_n \frac{u_n}{u_n + w_n},$$

$$v_{n+1} = u_n + w_n + \frac{1}{2} v_n,$$

$$w_{n+1} = \frac{1}{2} v_n \frac{w_n}{u_n + w_n}.$$

- Show that $u + v + w = 1$ in the $(n + 1)$ st generation. Use this fact to eliminate w from the equations.
- Show that the equations you obtain have a steady state with $\bar{v} = \frac{2}{3}$. Is there a unique value of $(\bar{u}, \bar{w})$ for this steady state? Is this steady state stable?
- Show that the ratio u/w does not change from one generation to the next.

PROJECTS

- Write a short computer program to simulate the Nicholson-Bailey model and display the oscillatory behavior of its solutions.

2. Journal Article Report Difference Equations

The references contain a list of journal articles, grouped into several general topics. Select one topic and write a short, concise review of the material presented in these articles. The objective of this project is to get you to read and think about some of the original work in the field. Thus your summary should deal critically with the ideas, methods, and presentation in these articles, rather than merely restating the contents. Following are some questions you may wish to address:

1. What is the main focus of the article(s); is a particular question being addressed?
2. Do the mathematical models help in illuminating the topic; if so, in what ways?
3. Are there alternative methods or approaches that might have been suitable for answering the questions the authors addressed?

In certain cases you may need to fill in background details by consulting the sources cited by the authors of these articles.

Note: The reference list at the end of this chapter is by no means a complete survey. You may wish to propose your own topic and search through the literature for relevant papers. Possible sources include the *Journal of Theoretical Biology*, *American Naturalist*, the *Journal of Animal Ecology*, *Ecology*, *Theoretical Population Biology*, and the *Journal of Mathematical Biology*.

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