3.1 DENSITY DEPENDENCE IN SINGLE-SPECIES POPULATIONS[1]

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:

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

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

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

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

$$N_{t+1} = \underset{\substack{\uparrow\\ \text{fraction that survives to generation } t+1}}{\left(\frac{1}{\alpha} N_t^{-b}\right)} \underset{\substack{\uparrow\\ \text{no. of progeny at generation } t}}{(\lambda N_t)}. \tag{3}$$

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

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

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

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

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_t from this steady state must satisfy

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

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

$$\delta_{t+1} \simeq \left.\frac{df}{dN}\right|_{\bar{N}} \delta_t .$$

But

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

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

$$0 < b < 2. \tag{7}$$

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

$$N_{t+1} = N_t \exp r(1 - N_t/K), \tag{8}$$

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

$$N_t = N_{t+1} = K$$

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

$$f(N) = N \exp r(1 - N/K) \tag{9}$$

we have

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

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

$$f'(K) = 1 - K(r/K) = 1 - r. \tag{11}$$

Thus stability is obtained when

$$|1 - r| < 1, \qquad \text{or} \qquad 0 < r < 2. \tag{12}$$

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

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

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

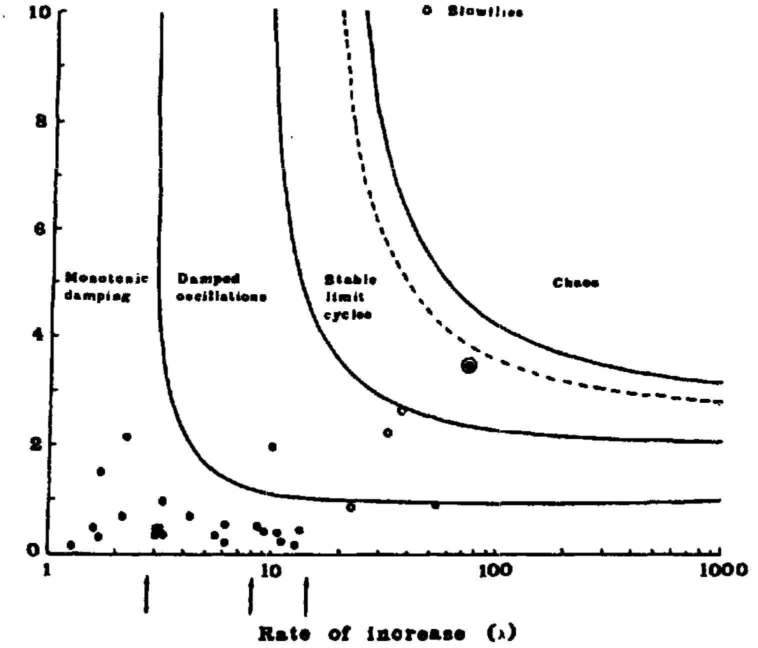

Figure 3.1 Stability boundaries for the density-dependent parameter b and the population growth rate λ from equation (13). The solid lines separate the regions of monotonic, oscillatory damping, stable limit cycles, and chaos. The broken line indicates where two-point limit cycles give rise to higher-order 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, Hassel 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} = number of hosts in previous generation × fraction not parasitized × reproductive rate (λ),

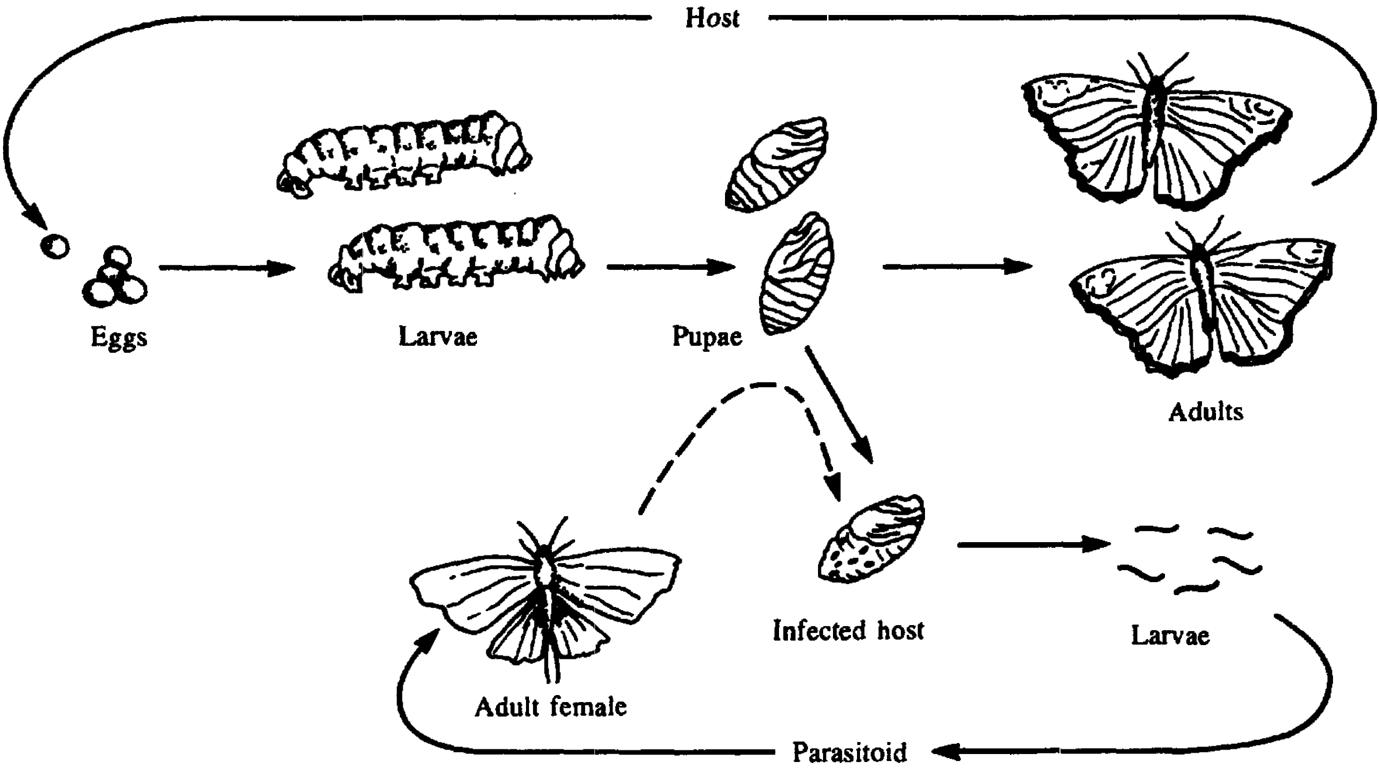

***Figure 3.2** Schematic representation of a host-parasitoid system. The adult female parasitoid deposits eggs on or in either larvae or pupae of the host. Infected hosts die, giving rise to parasitoid progeny. Uninfected hosts may develop into adults and give rise to the next generation of hosts.*

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

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

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

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

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.

$$N_e = aN_tP_t, \tag{15}$$

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

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

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

$$\mu = \frac{N_e}{N_t}. \tag{17}$$

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

$$\mu = aP_t. \tag{18}$$

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

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

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

$$f(N_t, P_t) = p(0) = \frac{e^{-aP_t}}{0!}(aP_t)^0 = e^{-aP_t}. \tag{19}$$

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,

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

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:

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

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

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

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

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

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

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

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

These imply that

$$\bar{P} = \frac{\ln \lambda}{a}, \tag{24a}$$

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

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

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

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

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

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

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

(*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

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

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

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

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

$$\bar P = \frac{\ln \lambda}{a}, \tag{27b}$$

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.

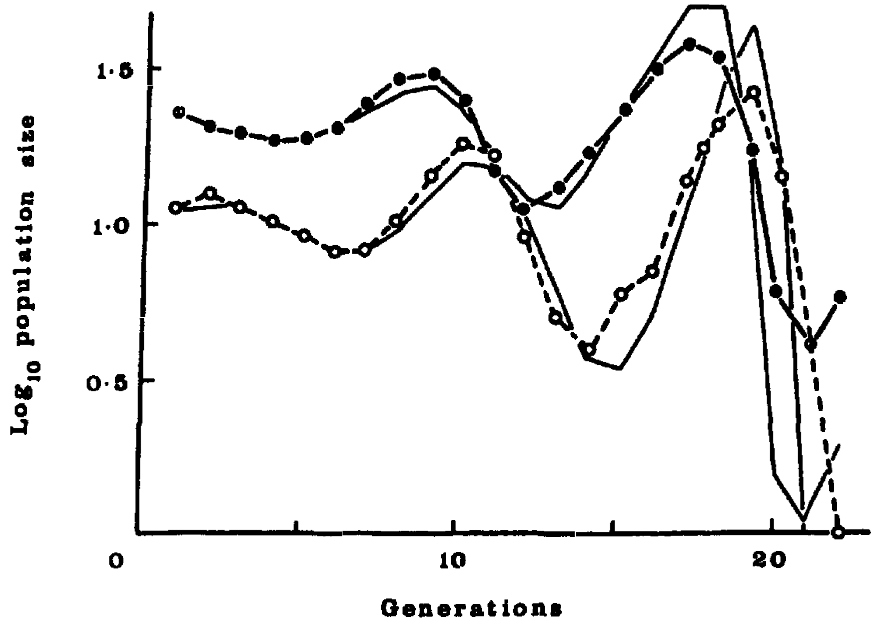

Figure 3.3 The Nicholson-Bailey model, given by equations (21a,b), predicts unstable oscillations in the dynamics of a host-parasitoid system. The fluctuations of a greenhouse whitefly Trialeurodes vaporariorum *(●) and its chalcid parasitoid* Encarsia formosa *(○) give evidence for such behavior. The solid lines are predictions of equations (21) where* a = 0.068, c = 1, *and* λ = 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 MODEL[2]

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:

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

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

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

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

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:

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

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

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

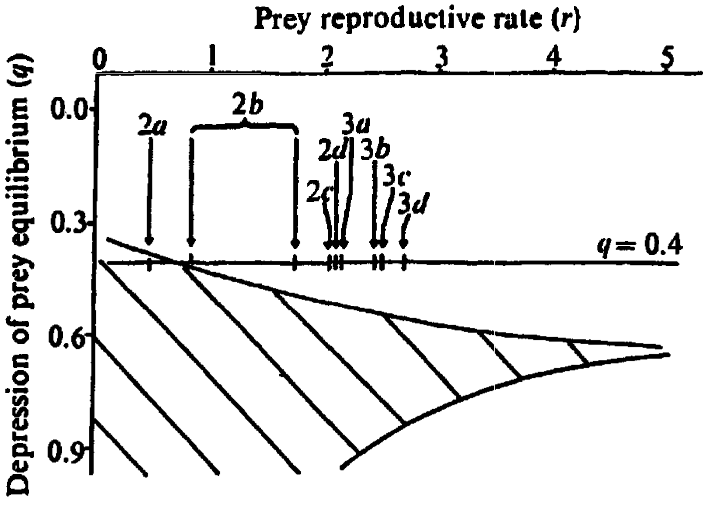

Figure 3.4 The density-dependent Nicholson-Bailey model (equations 28) is stable within the hatched area. Note how the area of stability narrows for high values of r. *[Reprinted by permission from* Nature, *255, 58–60. Copyright © 1975 Macmillan Journals Limited.]*

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_t and P_t and to plot these simultaneously. What is somewhat novel about these plots is that in this two-variable system, time is suppressed and (N_t, P_t) 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.

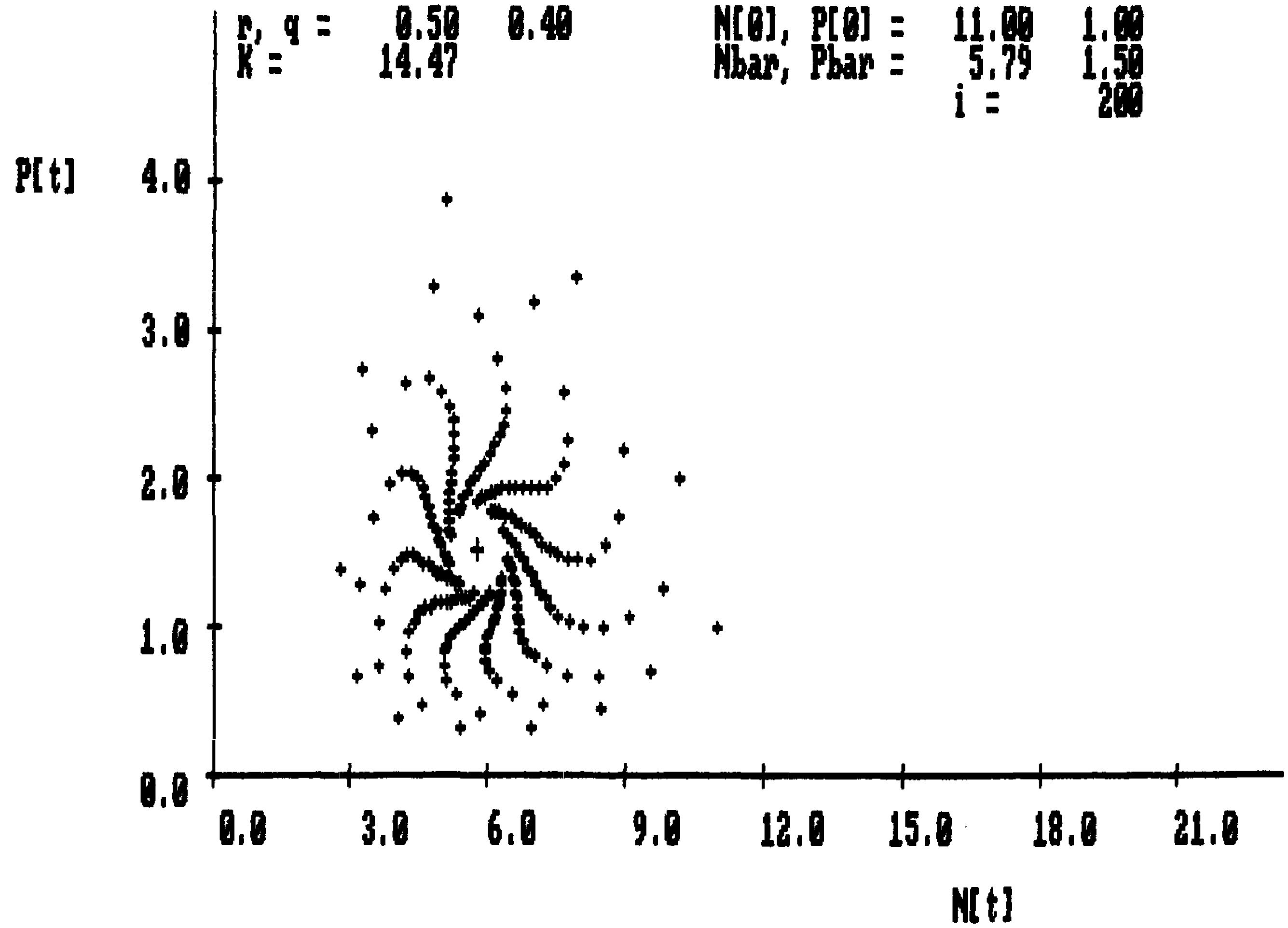

Figure 3.5 A single approach to equilibrium from an arbitrarily chosen outlying point. Note that the direction of flow is counterclockwise about the steady-state point, not inward along the spiral arms. [Computer-generated plot made by David F. Dabbs.]

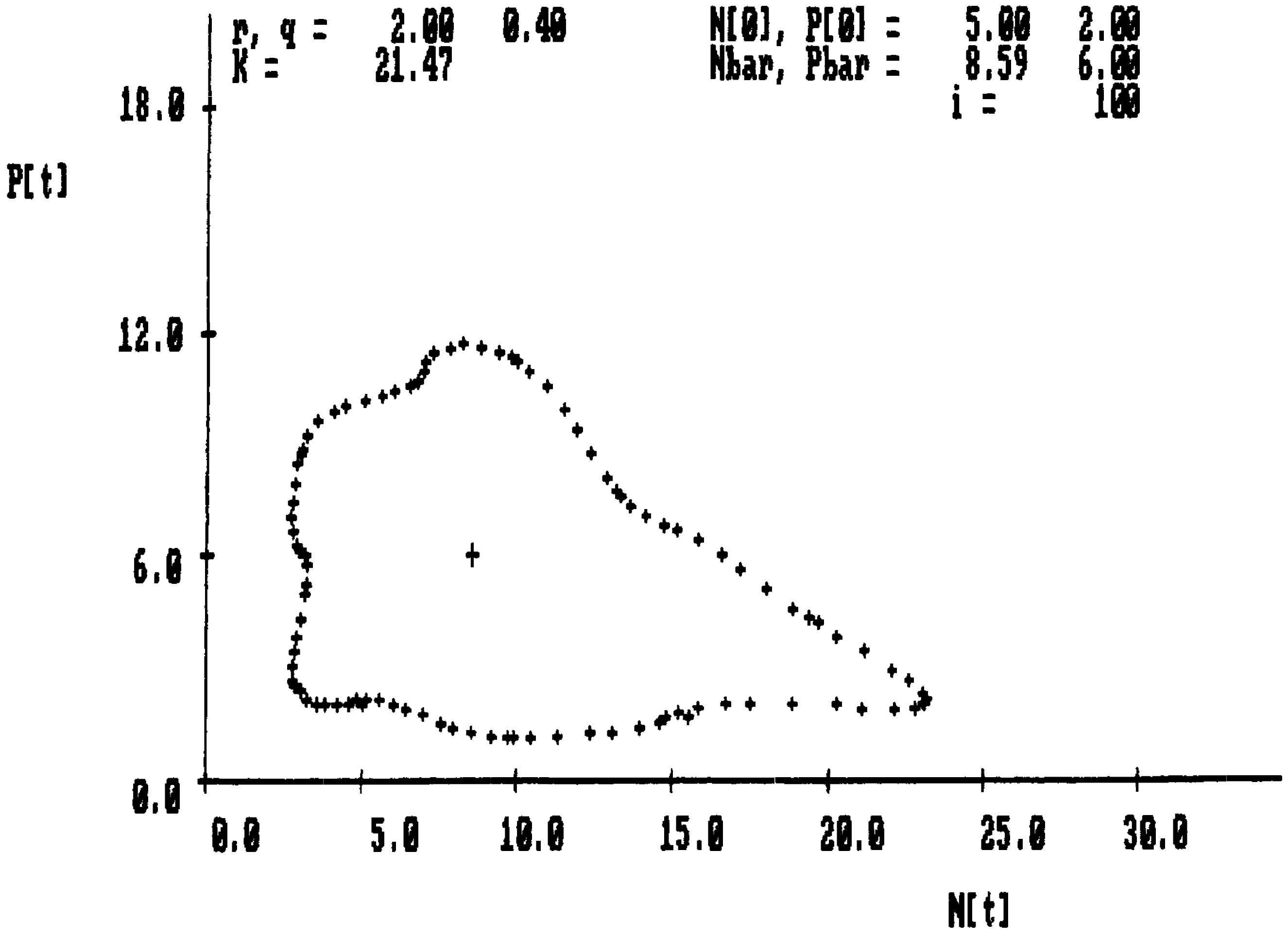

Figure 3.6 This stable "limit" cycle is jagged about the edges. Similar cycles for smaller values of r *have smooth edges. [Computer-generated plot made by David F. Dabbs.]*

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

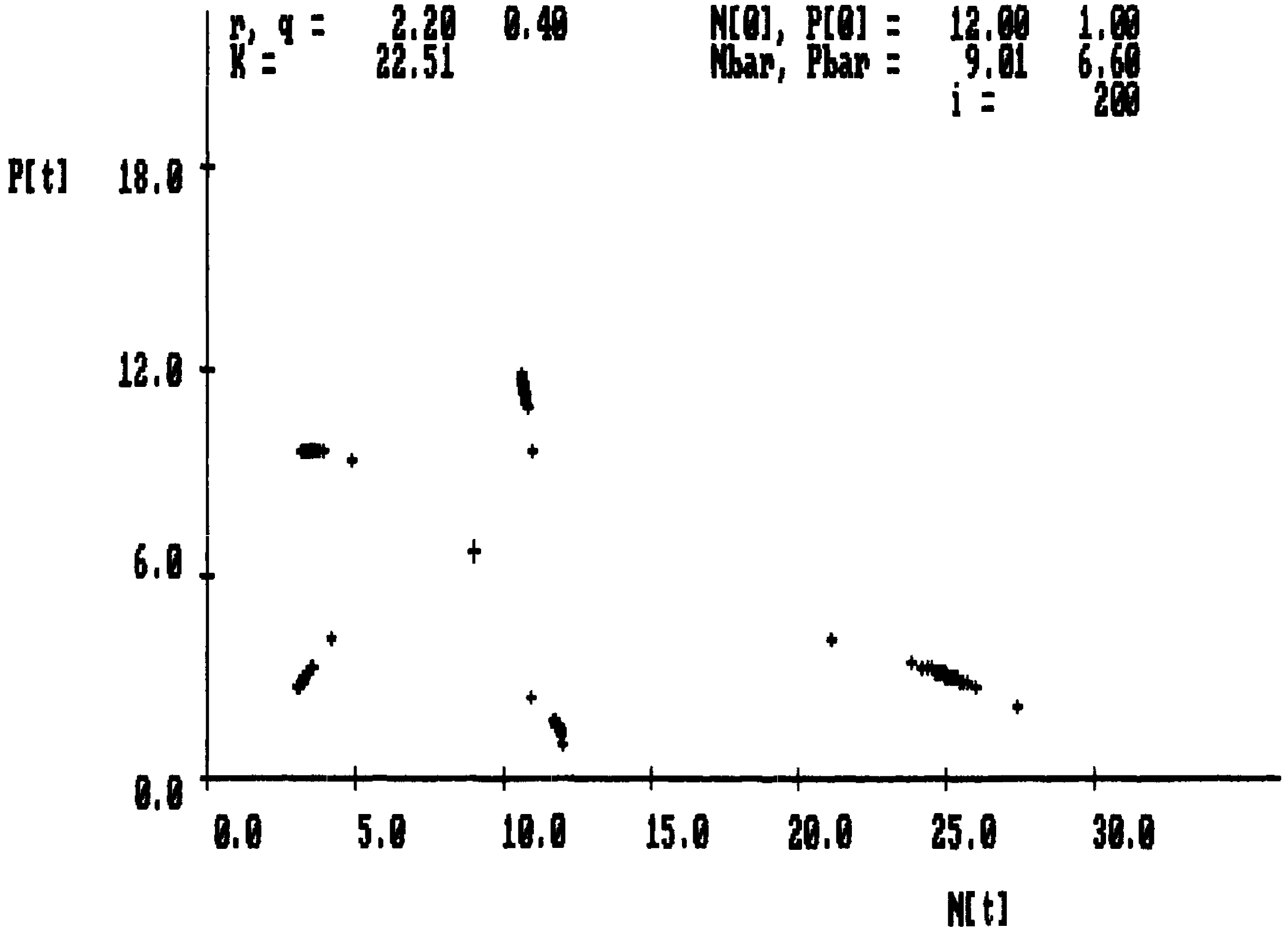

Figure 3.7 This cycle shows a cycle whose period is 5. Further increasing r *slowly would produce cycles of periods 10, 20, 40, and so on.* *[Computer-generated plot made by David F. Dabbs.]*

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 $f(N_t, P_t)$. One version studied by Beddington et al. (1978) is

$$f(N_t, P_t) = \exp -(aP_t)^{1-m}, \qquad (30)$$

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-

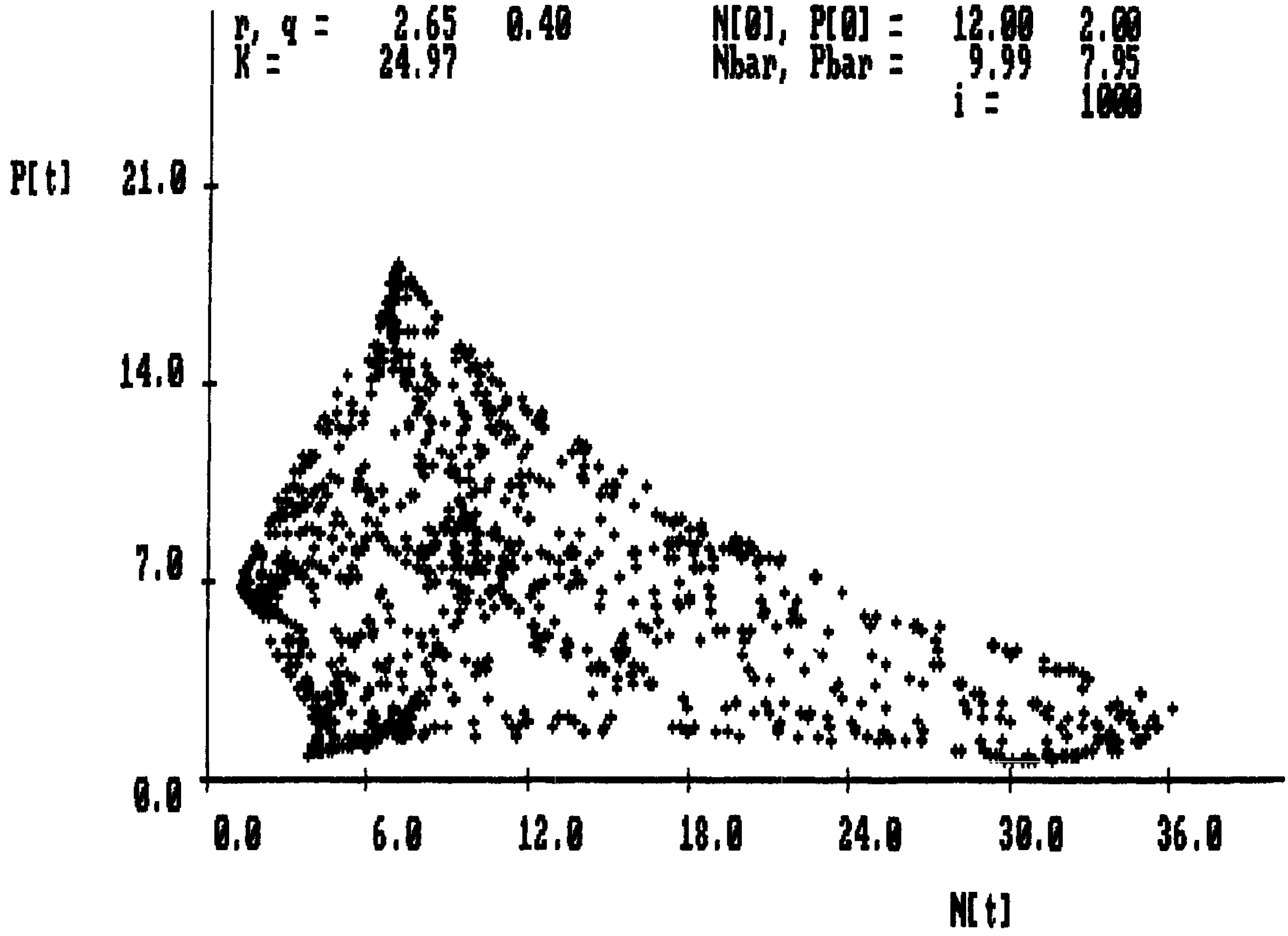

Figure 3.8 This sharply bounded figure shows definable areas without any points. For slightly lower r values these areas are better defined; for higher r values they tend to fill in. [Computer-generated plot made by David F. Dabbs.]

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

$$EK/N_t = \text{the fraction of the population that can retreat to a refuge,}$$
$$1 - EK/N_t = \text{the fraction vulnerable to attack.}$$

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

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[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.